RESEARCH PROGRAM ON SURFACE ARTHROPODS AT THE BIOLOGICAL STATION, WIJSTER (PROVINCE OF DRENTHE, THE NETHERLANDS)

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1. THE AIM OF THE INVESTIGATION

What are the most important factors responsible for the fitting of animal species to certain habitats? That such a fitting exists is shown by the fact that experienced collectors will successfully spot, in an unknown locality, the most suitable sites to find the species they are interested in. This means that one or more of the physiognomical features in which certain types of habitat differ from each other, must be correlated more or less distinctly to the factors which are responsible for the presence of certain animal species there. It seemed possible to find indications as to what the most important factors characterizing the habitat of certain animal species are by taking samples as objectively as possible in various types of habitat (DEN BOER, 1967).

As practically no species is confined to a single type of habitat the numerical distribution of the catches of one species over several habitats may give indications as to what factors govern the fitting.

During the investigation which was started in 1959, it soon became apparent that the numerical distribution over the various habitats changed from year to year due e.g. to variation of the weather. Therefore the method of research had to be quantitative and strictly comparative; viz. a comparison of different habitats extending over several years, which, if possible, would have to comprise several species.

2. THE SUBJECT OF THE INVESTIGATION

We have chosen ground-beetles (Carabidae, Coleoptera) for our investigation because:

a. they can be collected objectively by using pitfalls and/or funnels (we place three traps in each locality at equal distances from each other); moreover this can be done continuously and numerically with a reasonable accuracy, for they having no 'home range' move rather haphazardly over the surface of the soil and can be caught, unlike many other animals, without the - interfering - use of a lure such as bait, light decoys, etc. (cf.4);

b. they are one of the best known groups of Arthropods systematically and in addition one with which the author had some experience before.
Moreover it is an interesting group on systematic and evolutionary grounds because of the occurrence of 'rare species', geographical races, 'sibling species', polymorphism, etc. In many species wing di- or polymorphism occurs, which makes it an ideal group for the study of the means of dispersal (DEN BOER, 1962a; PALMEN, 1944) and of other zoogeographical problems (DARLINGTON, 1936; LINDROTH,1949);

c. the number of species which can be expected to live in different localities is sufficient for a comparative study; it includes congeneric species living sometimes in a limited number and sometimes in a wide range of habitats; the number of species occurring in a locality in Drenthe is in addition not overwhelmingly large either, viz. 8-40 species per series of 3 pitfalls;

d. due to the suitability of the carabids for ecological studies (see a) many investigations have recently been, and still are being carried out with them in Europe (England, Sweden, Denmark, Finland, Germany, Eastern Europe especially Czechoslovakia).
Results from many investigations, more or less similar to our own, but carried out in other geographical areas are therefore available for comparison; exchange of information and large series of specimens have become possible (cf. e.g. DEN BOER, 1965b).

3. THE SITES OF INVESTIGATION

The sites chosen for our studies at first, are as 'natural' (uninfluenced by man) as possible. This is important as:

a. the natural sites must be considered to be the primary ones from which all others, viz. fields, plantations, gardens, waysides, etc. have been derived;

b. they are gradually disappearing in the Netherlands; their total area is relatively small already, so that it seems desirable to investigate them before it is too late;

c. I consider that nature preserves should, in the first place, be available for research, and that, on the other hand, the results of such research will be of great value to the fulfilment of the task of Nature Preservation management;

d. the structural changes taking place in natural sites are often more gradual than those in cultivated grounds. This makes it possible to study certain natural areas for several years in a nearly unchanged condition.

More or less natural areas in Drenthe are remnants of deciduous woods, heath, Sphagnum bogs and blowing sands. For comparison some samples were taken from plantations of deciduous trees as well as of coniferous ones. In the near future we hope to extend our research to fields and pastures, because:

a. they cover the greater part of the province of Drenthe and greatly influence the natural areas, e.g. by introducing migrants into the natural sites;

b. many foreign ecologists, especially in Eastern Europe pay special attention to agricultural areas, and comparison of their results with results obtained in similar sites in Drenthe, therefore, would be very interesting (e.g. for the study of the influence of differences in climate);

c. of the relative uniformity of fields and pastures, which creates certain interesting situations for the analysis of special problems;

d. carabids (and spiders) as polyphagous predators, apparently have a much greater influence on many of the culture pests, than was originally assumed on theoretical grounds (cf. 7e).

4. METHODS OF RESEARCH

The quantitative distribution of carabid beetles over different localities was established by means of continuous (weekly) sampling over a number of years with the aid of pitfalls. This method enables us to find approximately that measure of population (activity density) which is required for our research, i.e. a relative measure of 'suitability' of the various habitats for the survival and/or the reproduction of a certain species. As the differences in the degree of this 'suitability' for various species is influenced by specified characters of the species (behaviour, rate of moving, activity-area, food, size, life-cycle, etc.) it is necessary to consider the species individually first. This problem - which is an actual one for many of the sampling techniques in common use - is responsible for the precariousness of those ecological interpretations of combinations of species, which are not based on an autecological study of the individual species. Therefore I think that comparisons of combinations of species (faunae) must be seen as rough estimates only, and that, in order to be of real value, they must be based on great differences in the numbers of the same species caught in different localities during the same period (cf. DEN BOER, 1965a (1960) and Comm B.S., nr. 115, 1963).

The carabids caught were identified, 'sexed', counted, mounted, catalogued, etc. (from 1959 to the end of 1967 more than 175 000 specimens were treated in this way). From 1963 on the specimens of the most numerous species are preserved in formalin, which enables us to study the development of the ovaries and the content of the crop. For wing-dimorphic species the ratio between macropterous and brachypterous specimens is determined. As a number of the winged beetles may be expected to fly away and the wingless ones will be more bound to the

population it is possible to obtain an idea of the relative age of populations by determining the ratio of the two morphs in different localities.
For some species it is possible to determine in this way which specimens caught, in for the species unusual sites, have arrived there by migration of winged specimens. The winged morph may be considered the 'dispersal phase' or 'diaspore'. In this way we hope to gain some insight in the quantitative significance of dispersal for the maintenance of the species in specified areas (cf. 7c).

Papers on this subject on Pterostichus strenuus PANZ. and Carabus problematicus HBST. are being prepared.

Of a few species the shifting proportion of special morphs in the catches during several consecutive years was related to the variation in the meteorological conditions during the same period (DEN BOER, Comm. B.S., nr. 103a, 1962b). In field trials and by breeding in walled-in sites the causal background of such relationships is being tested further with Pterostichus oblongopunctatus F.

As many specimens as possible from rather isolated populations of Pterostichus oblongopunctatus F., Agonum assimile PAYK., and Calathus piceus MARSH. are caught, individually marked and released. Recaptures should give information on 'hibernation-success', size of progeny, longevity, individual differences in activity, and the influence of these factors on the number caught.

The spatial structure of the sampled localities was recorded by photographs, some of which were taken perpendicularly from above, and by several measurements. The development of suitable techniques for the measurement of the vegetation structure is rather slow owing to understaffing. Techniques for automatic registration of microcomponents of the weather with computers working out the data are planned by a group of 'soil zoologists' (in which the Zool. Lab. at Leiden, Utrecht, Nijmegen and at Free University, Amsterdam, the State Museum of Nat. Hist. at Leiden, the Institute for Applied Biological Research in Nature (I.T.B.O.N.), the Ecological Institute at Arnhem and the Biological

Station at Wijster are taking part). Leiden (Zool. Lab.) has already developed a workable apparatus and at Groningen a comparable one is being prepared independently. We hope that technical coordination between the Zool. Lab. at Leiden, the Zool. Lab. at Groningen, the Zool. Lab. of the Free University, Amsterdam and the Physical-Technical Department at Wageningen (for the Biological Station, Wijster) may soon lead to the development of a many-sided apparatus useful for our research program. In the meantime we use randomly placed max- and min-thermometers, which are moved frequently (nine of these are placed in each of two sites under comparison).

5. SOME RESULTS

a. The striking differences from year to year in the numbers of different carabids caught in different localities suggest that the humidity of the substrate is one of the most important factors influencing carabids in their choice of habitat. This humidity is influenced by the structure of the soil (e.g. sand, loam, peat) and by that of the surface layer (e.g. litter), by the groundwater level and amount of precipitation (DEN BOER, Comm. B.S., nr. 115, 1963).

This hypothesis will be tested for several species of carabids separately.

b. The spatial structure of the vegetation of a locality is apparently another important factor influencing the occurrence of special carabids i.e. by hampering their movements, by affording them cover and, indirectly, by determining the micro-weather.

Mosaic vegetations are particularly interesting in this respect. Techniques for measuring the vegetation structure are being developed. In time the causal relation between vegetation structure, micro- and macro-weather will be measured, recorded and worked out automatically; we are not only planning to study natural, but also artificial structures. Dense vegetation as e.g. grass and some kinds of mosses probably forms an obstacle to the movements of several ground-beetles.

c. Qualitative differences in the composition of the vegetation do not seem to have much influence on habitat fitting of carabids.

There may, however, be a relation between some, probably phytophagous, species and special host plants (DEN BOER, Comm. B.S., nr.115, 1963).

d. The development of the ovaries was studied in large series of females of some species; in all species studied females reproducing in the first and in the second year were found side by side (see also VLIJM and VAN DIJK, 1967), indicating a complex reproductive cycle within the population, and in Calathus erratus SAHLB. and melanocephalus L. moreover, females reproducing once or twice in two more or less overlapping periods of the same year may be present.

e. Pterostichus strenuus PANZ., a wing-dimorphic species, entirely depends on the winged individuals for its dispersal. In Drenthe it mainly lives in sparse populations in isolated remnants of deciduous woods surrounded by fields with many ditches which form an impassable barrier to the wingless individuals. Winged individuals obviously fly off and are often caught in places deviating from the one they normally inhabit.

The always wingless Carabus problematicus HBST. entirely depends on its walking capacity for its dispersal. It is therefore seriously hampered in its movements by dense grass. Living normally in woods, the progeny of migrants in heath can apparently reach the third larval stage normally; whether some of the pupae will survive in heath or not probably depends on the weather; only if June is exceedingly wet, a few will reach the adult stage.

f. Pterostichus oblongopunctatus was bred in walled-in sites. It occurs in two groups of morphs: one group with few (4-5) pits on the elytra, the other with many (6-10(-12)). The development of the larvae of the 'high-pitters' is obviously favoured by a highly humid substrate, while the larvae of the 'low-pitters' are relatively favoured by a lower degree of humidity (DEN BOER, Comm. B.S., nr. 103a, 1962b). Experiments to prove this to be due, at least in part, to genetic differences are running (preliminary results from 1964 and 1966 seem to confirm our hypothesis).

g. Comparison of our results with those obtained by other investigators in the Netherlands and elsewhere suggest that geographical variation in ecology occurs at least in a number of species. There may be differences in the reproductive cycle - its type and seasonal rhythm, e.g. in Calathus melanocephalus - and (or) in the choice of habitat (DEN BOER, 1965a (1960)).

6. REVISED FORMULATION OF THE PROBLEM

Although there appeared to be a correlation between the occurrence of some species of carabids and certain types of habitat (cf. 5a and 5b) especially with regard to the structure of vegetation, type of soil and humidity, the original formulation of our problem has proved to be too simple (cf. 1).

It became more apparent every year, that it is impossible to get neat answers to such a question (1) without subjectively neglecting part of the field results, e.g. by judgement of some assumed 'representativeness' of data.

The intensity of the habitat-determining factors varies from place to place within each habitat, and changes also in time, fluctuating widely (especially due to meteorological factors). Moreover the beetles themselves react individually to differences in and changes of environmental conditions, and are also influenced differently in successive stages of development. Therefore our problem is not a deterministic or typological one (the 'fitting' of a species' to specified 'factors'), but a probabilistic one, i.e. a problem concerning the developmental and phenotypic variation in space and time within a population, the pattern of which is more or less distinctly correlated to the variation in space and time of important ecological factors in the habitat of the population. This correlation is continually preserved by natural selection shifting from one phenotype to another.

As was shown by some examples mentioned in 1965 (DEN BOER, Comm. B.S., nr. 131, 1965c), variation should not be considered a drawback of field data which makes it difficult to detect the 'typical' or 'representative' case (and makes us feel the need of 'intuition'), nor should we try to circumvent it by withdrawal into laboratory tests with genetically homogeneous material and constant conditions (although I am convinced that this analytical method often yields indispensable additional results), but variation should be recognised as a fundamental feature of a natural situation!

The method employed (2, 3, 4) was not changed by this revision, as it were the results obtained thereby (5) which led to our changed attitude towards the problem. However, more attention is paid now to heterogeneous and varying situations.

The importance of variation within a population, which enables it to cope with varying and heterogeneous situations by means of variation in tolerance between individuals and so to survive in time and space, is especially studied now.

This leads to the concept of 'spreading of risk'.

7. SPREADING OF RISK

In times of rapid economical changes an industry producing only one kind of article runs a greater risk of failing than one manufacturing several, because in the latter case there is a spreading and thereby a diminishing of the risk and so a greater chance to overcome. On this relation between spreading of risk and chance to survive the insurance business is based.

Similarly, the greater the variation between individuals within a population, the greater the population's chance of survival will be under drastically changing conditions (the greater the spreading of the risk). This has nothing to do with the 'group-selection' of WYNNE - EDWARDS (1962). In our case only the statistical effect of a continually varying selection of individuals is meant.

a. Spreading of risk by genetic and phenotypic variation

In the forest species Pterostichus oblongopunctatus F. the developmental stages (probably the larvae) of different morphs show an at least partly genetically determined differing sensitivity towards the humidity of the substrate (5f). Therefore the risk run during changes in the weather is spread over a number of morphs, increasing in this way the range of tolerance of the population as a whole to changes in humidity.

This finds its expression by changes in the ratio between the frequencies of these morphs in consecutive generations and its relation to the amount of rainfall during their development.

By this spreading of the risk populations of Pterostichus oblongopuntatus are able to cope with the apparently strong selective influence of changes in the humidity of the substrate: 'losses' of some morphs are compensated more or less by smaller 'losses' or 'gains' of others, which are genetically different.

The fluctuations of animal numbers of the population as a whole are more or less stabilized in this way. Good examples of this from the literature are e.g.: Adalia bipunctata, TIMOFEEFF-RESSOVSKY (1940) and Purpura lapillus, STAIGER (1954, 1957); MAYR (1963, p.165) too draws the attention to the survival value of a great genetic variation.
As no natural population is genetically homogeneous - no two individuals from a bisexual population will ever be genetically the same (except for identical twins) - it is to be expected that spreading of the risk by genetic variation will play a part in the survival of practically every natural population.

b. Spreading of risk in space

The 'Kralose Heide' is a macro-mosaic composed of elements of different structures such as Molinia vegetation, Erica heath, Calluna heath, vegetation of Festuca and Nardus and such as micro-mosaics in the heath and on blowing sands, which all show greater or smaller differences in groundwater level. A number of these sites have been sampled with the aid of pitfalls during several years. Of Calathus melanocephalus L. the ovaries of large numbers of females were studied. There proved to be fluctuations in the number of reproducing individuals within each locality from year to year; if however, the results from the various localities were added, these fluctuations were less pronounced (DEN BOER, Comm. B.S., nr. 131, 1965c).
In other words: extreme changes in one place are compensated more or less by less extreme ones in others, so that the number of individuals of the whole population is relatively more stable than the numbers of individuals of parts composing such a population: spreading of the risk in space. In general: when the habitat of a population is not homogeneous, the chances of survival and reproduction will differ for individuals living in different parts of the habitat. The risk of showing extreme fluctuations in numbers is thus spread over the different parts of the population. As greater as well as smaller differences in the structure of localities will influence the individuals inhabiting them, and no natural habitat is absolutely homogeneous, it is to be expected that spreading of the risk in space will play some part in nearly every natural population.

c. Spreading of the risk of extinction and rarity

The most extreme form of change in animal numbers is the case in which (part of) a population dies out completely. When a population consists of a large number of groups, of which regularly some die out while others are able to replace them within a reasonable time by producing migrants, it may be that, due to the effect of spreading of the

risk in space, the population as a whole is comparatively stable. A good example of such a situation was described by NICHOLSON (1957) for Cactoblastis cactorum (although he interprets it in quite a different way). A number of good examples are also given by ANDREWARTHA and BIRCH (1954); their 'general theory' is implicitly based to a large extent on this form of spreading of the risk in space. To obtain a reasonable spreading of the risk of extinction a population must be composed of a large number of parts which in general means that it will inhabit a rather large and more or less continuous area.
As the size of the inhabited area will be 'critical' especially for sparse populations (rare species!), a large area will generally harbour more rare species per unit of surface than a small one. This is in accordance with the experience of many nature preservers and collectors. The reason that the heath of Kraloo and Dwingeloo is relatively rich in rare species of carabids (compared with other natural localities in Drenthe) is, among other things, probably due to its size; more than 1200 hectares (3000 acres) uninterrupted 'natural' area. Sparse species must have a relatively high dispersal capacity.

On a larger geographical scale a similar relation between the size of a more or less continuously inhabited area and the spreading of the risk of extinction between populations may be expected. If this is true, then a large isolated area will harbour more species per unit of surface, especially rare ones, than a small one. DARLINGTON found this to be true for carabids (1943) and for several other groups of animals and plants (1957) (cf. PRESTON, 1962). See also MAYR (1942, p, 224).

A paper on the relation between rarity and the spreading of the risk of extinction is in preparation.

d. Spreading of risk in time

In the Netherlands Calathus erratus and melanocephalus hibernate either as a larva or as an imago (cf. VLIJM and VAN DIJK, 1967). Neither differences in habitat nor the yearly ones in the weather conditions seem to affect the hibernating imagos much (cf. 7b), the larvae on the other hand are apparently much more sensitive to changes during the hibernation period (DEN BOER, Comm. B.S., nr.131, 1965c). In this way the hibernation risk is spread over different stages with unequal sensitivity, and this usually results in the formation of groups within the population, each with a different time of reproduction. In this way the population achieves a spreading of the risk in time, as the chance of survival and reproduction will vary during the year.

In the populations of Calathus erratus and melanocephalus studied there are probably four groups, each with a different amount of reproduction, and partly too with a different season of reproduction. Studies by VLIJM and VAN DIJK (Zool. Lab., Free University, Amsterdam) on the island of Schiermonnikoog indicate that the reproductive cycle of Calathus melanocephalus there deviates (2 or 3 reproducing groups were found there) from that at Kraloo (cf. VLIJM and VAN DIJK, 1967). These findings have led to an extensive exchange of data.

The six species of carabids of which the ovaries were studied up to now all showed some form of spreading of the risk in time (cf. 5d).

It seems that this kind of spreading of the risk, which is due to the heterogeneous age composition of the population is very common. It is to be expected that the quantitative importance of the several reproducing groups will be influenced by climate, as by definition natural selection will preserve those groups which are best adapted to the prevailing conditions. In regions with a capricious climate, as the Netherlands, different reproductive groups will survive together because of spreading of the risk in time; now one group, then another being selectively favoured. The same applies, of course, more or less to the effect of spreading of the risk by phenotypic or genetic variation (cf. 7a)

e. Spreading of risk in the relation to other species

The number of individuals of a monophagous (specific) predator will depend on the amount of available prey, and consequently will follow

the fluctuations in the numbers of the latter, contributing to them in time by its own numerical fluctuations. When very homogeneous conditions prevail, this will lead - as a result of a time-lag - to oscillations with an ever increasing amplitude, ultimately with the risk of self-destruction of the predator-prey system (NICHOLSON and BAILEY, 1935; HUTCHINSON, 1954).
This risk of self-destruction is decreased when the habitat is sufficiently heterogeneous in structure so as to guarantee a spreading of the risk in space (cf. 7b and 7c): SCHNEIDER (1939), VARLEY and GRADWELL (1958), NICHOLSON (1957), BAILEY, NICHOLSON and WILLIAMS (1962).

I believe the risk will also be decreased if the population(s) of the predator and, or, prey are sufficiently heterogeneous to involve a spreading of the risk by phenotypic or genetic variation (7a) and, or, spreading of the risk in time (7d). This risk is ultimately reduced if the predator is not monophagous, and can supplement one kind of prey with another: spreading of risk in food (NICHOLSON, 1933; SCHNEIDER, 1939; VOÛTE, 1946). This argumentation, of course, applies to specific and non specific parasites as well, and something similar is likely to take place with all species that are mutually dependent e.g. as symbionts, commensals, or even as competitors. The prey (host) population too will profit if the risk of being consumed, or killed in some other way, is spread over a number of predator or parasite species. In all these cases a spreading of risk in the relations to other species has a stabilizing effect on the number of individuals of each of them, resulting in an increase of their population's chance of survival.

f. The balance of nature

The preceding paragraph (7e) shows that: the greater the number of species living together in the same place, the greater the chance will be that spreading of risk in the relations to other species will play an important part in stabilizing animal numbers in the populations. In my opinion the 'balance of nature' is the result of an intricate system of spreading of risk in the relations between species. Therefore I consider non-specific relations more important than subtle specific ones, if any (while these are often believed exclusively to cause the balance of nature), for only non-specific spread relations will yield the necessary variations in the chances to survive and reproduce.

A similar idea is expressed by MACARTHUR (1955), who shows that the number of ways in which the energy can pass through the food web (spreading of risk in food, 7e), is a measure of the stability of the community.

HUTCHINSON (1959) even declares that a species taking over part of the 'niche' of another, usually a closely related one (a rival), compensates the possible reduction in numbers of the species originally present by increasing stability of numbers, which is of benefit to both. This agrees with the calculations by WILLIAMS (1947, 1951, 1964), viz. that on the avarage more congeneric species occur in the same habitat than can be explained merely by a chance distribution. The same phenomenon is demonstrated by the carabid catches made near Wijster (full details will be published).

It is probable that the stability of a biocoenosis, which is rich in species, is not only due to a many-sided spreading of the risk between these species, but also to a heterogeneous biotope (spreading of the risk in space), as such a biotope can harbour more species than a less heterogeneous one. In their turn the many species living there will increase the heterogeneity of the biotope by their many-sided activities.

The large-scale activities of man will inevitably upset the 'balance of nature', firstly by extermination, directly or indirectly, of a number of species, which decreases the spreading of risk in the relations between species, and secondly by making the habitat more homogeneous. This decreases spreading of the risk in space and increases the fluctuations in animal numbers of the local populations. The extreme form of this is the monoculture, with a minimum of spreading of the risk in space resulting ultimately in catastrophic fluctuations in the numbers of some of the few remaining species

(SCHNEIDER, 1939; VOÛTE, 1946). Therefore fluctuations in animal numbers will be small in a biocoenosis which is rich in species e.g. in some tropical regions and relatively large in one poor in species e.g. in arctic regions (THOMPSON, 1929; SOLOMON, 1949; MACARTHUR, 1955; and others).

8. REGULATION VERSUS STABILIZATION OF ANIMAL NUMBERS

For about half a century the problem of the survival of populations - in spite of, often large, fluctuations in animal numbers - has dominated the ecological literature. According to one group of authors the animal numbers of natural populations are 'regulated' by density-dependent factors e.g.: specific predators or parasites, intraspecific competition (a.o. NICHOLSON, 1933, 1934, 1957; NICHOLSON and BAILEY, 1935) viz. by some form of negative feedback (PIMENTEL, 1961; WILBERT, 1962).

This regulation should prevent extinction, or, increase to catastrophically high densities of populations fluctuating under the influence of density-independent factors (especially weather), according to these authors.

Another group propounds that the density of a population is determined solely by chance, i.e. by density-independent factors (a.o. BODENHEIMER, 1928, 1930; ANDREWARTHA and BIRCH, 1954); the fluctuations in density will usually vary between certain limits but in extreme cases exceed them; decrease to extinction (often followed by recolonisation of the locality) and increase to very high densities are not excluded, especially in populations of Arthropods.

MILNE (1957, 1962) has tried to unite certain aspects of these two standpoints. He assumes that density-dependent factors come into play only when the density becomes very high, viz. in the form of intraspecific competition.

As no ecologist will maintain that no population is ever exterminated nor that no population ever may increase to catastrophic density, neither that, in the case of an extreme food-shortage, there will never be a more or less density-dependent mortality due to this factor, in my opinion the controversy can be formulated thus:

1. How many generations can the density of a population fluctuate exclusively under the influence of density-independent factors (chance) before it becomes extinct or before it has increased to such densities that it has exceeded the capacity of the habitat?

2. If enough data are available to give an adequate answer to the preceding question is it then possible to understand the fluctuations in the animal numbers of natural populations or is it then still necessary to assume the existence of some 'regulating mechanism'?

a. In 7 (a-f) I have expounded that there are many ways to spread the risk of extinction and that they all have a stabilizing effect on animal numbers.

Consequently, in answer to the above question I would propose the following hypothesis: 'Stabilization of animal numbers is due to spreading of risk', a hypothesis which is opposed to the existing one, according to which the regulation of animal numbers is due to density-dependent factors. According to me all the different ways of spreading of the risk together, stabilize the density of a population, so that the greater the number of factors affecting the density, the greater the chance that too strong an influence of one factor will be inhibited by the influence of other ones.

A paper on: 'Spreading of risk and stabilization of animal numbers' will be published shortly (DEN BOER, 1968).

That the number of factors influencing density must have a stabilizing effect on the fluctuations of animal numbers has been postulated by several authors, e.g. by THOMPSON (1929, 1939, 1956), GLEN (1954), MILNE(1957, 1962), REYNOLDSON (1957) and most clearly by RICHARDS (1961), while SCHWERDTFEGER (1958) has even developed a (too) simple model to support this hypothesis.

In Communication B.S., nr. 127(DEN BOER, 1966) with a mathematical model (adapted as much as possible to the natural situation) I tried to demonstrate that the number of weather factors affecting density (net rate of reproduction:R), may have a favourable effect on the relative stabilization of animal numbers.

We made use of weather conditions in our model because, firstly, they are available over many consecutive years in tabels published by The Royal Netherlands Meteorological Institute and, secondly, because they are an important point under discussion in the literature: KLOMP (1962) and WILBERT (1962) propound that the number of weather factors does not have a levelling effect.*

Hence, the weather conditions used were not chosen because they might represent the most important factors responsible for the relative stabilization of animal numbers.

Organisms always undergo the influence of the weather modified by the heterogeneity of their habitat as micro-weather. The micro-weather will affect the differing individuals of a population in diverse measure (spreading of the risk in time and spreading of the risk by phenotypic variation) according to their individual tolerances and preferences. It will also effect the different species of a biocoenosis to a different degree according to their specific behaviour and sensitivity.

If we imagine a population composed of two sexes, of different phenotypes (or genotypes), of a number of developmental stages (or age classes), divided in a number of groups living in different micro-environments with migration between them with different micro-weather varying in time, consuming different kinds of food, influenced by a

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* Discussion by letter of this point with Klomp (Zool. Lab., Wageningen) in 1961 had a stimulating effect on the working out of our model and has brought about a decided reconciliation of our ideas.

number of different predators, parasites and other animals, we get some idea of the immense number of interacting factors (amount of heterogeneity and variation) influencing density. In general the various ways of spreading of the risk discussed in 7 can be assumed to furnish the most important stabilizing factors (cf. SCHNEIDER, 1939).

It is easier to demonstrate adequately, the stabilizing influence of a number of weather components by means of a model, than that of spatial or genetic heterogeneity, although the latter would not have given a fundamentally different model.

Together with REDDINGIUS (Zool. Lab., Groningen) and with the aid of the Mathematical Centre of the State University of Groningen the mathematical model (cf. Comm. B.S., nr. 127, 1966) was converted into a better one suitable for operation by a computer, which enabled us to work it out more extensively; at the same time it is possible to test models with different premisses.

A joint paper dealing with our results will be published shortly.

b. It has already been pointed out (7e) that a strong density-dependence between the numerical fluctuations of a monophagous predator and that of its prey is a great hazard (cf. NICHOLSON & BAILEY, 1935; HUTCHINSON, 1954). Also the explanations by different authors of how the populations manage to survive have been discussed. These explanations are all based on heterogeneity in the habitat (spreading of the risk in space) which also brings about a certain degree of levelling out of dependence and minimizes the chance to prove the existence of density-dependence within the population. In the example given by NICHOLSON (1957) viz.: that of Opuntia and Cactoblastis, density-dependence will probably not play a part of any importance to the population as a whole.

This problem is of course not confined to the relation between a monophagous predator and its prey, but in general, density-dependence will mainly exist under homogeneous or only slightly varying circumstances for as soon as heterogeneity or variation (spreading of the

9. POSSIBILITIES OF FURTHER RESEARCH

During nine years a great number of data was collected in the vicinity of Wijster by which factors determining the fifting of about 100 species of ground-beetles to their natural habitat (1) are indicated.

The ways in which this was done are described in 2-4 and some of our conclusions are given in 5 a-c.

The obvious procedure would now seem to be to experiment on tolerance and preference in the classical way to find out the reaction of the carabids to the degree of humidity of the substrate, the structure of the vegetation and such like factors, and then trying to explain the distribution over natural habitats with the aid of the data so obtained. Although such experiments often give valuable confirmation of the field-data, according to me they leave the crux of the problem unsolved. They are based on a deterministic or typological premise, with regard to the fitting to the habitat: viz. the fitting of a certain species (as a fixed type) to the special circumstances prevailing in the experiments - in other words on the assumption of a fixed situation. However, according to me the crux of the problem is the degree to which a population, with its developmental and phenotypic variation is adjusted to the changes which its habitat undergoes in space and time (6). This adjustment is achieved by means of spreading of the risk (7) and finds its expression in fluctuations in the numbers of individuals (8) and in changes in morph-(gene-)frequencies. Therefore it was decided to postpone laboratory experiments on tolerance and preference and try to obtain previously some insight into the heterogeneity of populations and habitats, in order to determine the best way in which such experiments can be carried out.

We will now discuss the possibilities of further research.

a. Continuation of sampling as described in 4, in a limited number of habitats. In the first place we need more specimens of some abundant species for the study of the reproductive cycle and the contents of the crop.

b. From the carabids caught near Wijster, in the last nine years, we have learned something about the choice of habitat and the changes therein from year to year. It is now possible to prospect with some certainty what changes will take place in the carabid fauna if one habitat is changed into another. For such experiments some area is necessary; near Wijster such an area will be available in the future. On the land owned by the late BEIJERINCK, which has lately been acquired, a number of such experiments is in preparation i.e. the conversion of pine wood into birch wood or Calluna heath, and the removal of Molinia tussocks.

In the future such experiments, together with the sampling on cultivated grounds, will replace the one described under 9a.

c. To obtain the basic data on the suitability of carabids to live in certain localities, 73 different sites were sampled during one year or longer. It is not, at the present time, advisable to increase this number how desirable this would be, although an exception will be made for some special tests which will be carried out on the grounds of the Biological Station (9b), and in the near future on cultivated grounds.

Of great importance to our insight is the 'Regional Experiment' (9h), the investigations running at Meijendel and at Schiermonnikoog, the catches by VAN DER DRIFT (ITBON) and many investigations made on carabids abroad. It would be well if many nature reserves in the Netherlands could be investigated in the same way (cf. 3 and DEN BOER, 1967).

d. Besides carabids, many other animals, mainly Arthropods are caught in our pitfalls. During eight years these have been conserved too, all except Collembola, mites, worms, caterpillars and ants, which were counted only. These catches are of importance as the fauna of Drenthe has hardly been studied up to the present, and only incidental collections made by BEIJERINCK were available from this area. Drenthe is proving relatively rich in northern species, what is interesting in connection with their fitting to particular habitats. We are trying to persuade various specialists to identify the extensive material at our disposal. The State Museum of Natural History and the Zoological Laboratory at Leiden are interested in connection with their research at Meijendel, and several private specialists too are collaborating with us.

Several groups of Arthropods have already been worked out partly and this has led to faunistic surprises everytime, just as we ourselves have encountered in the carabids (DEN BOER, 1967).

It is especially important to test the data obtained in the investigation of carabids with those to obtain from other groups: the Lycosidae and the Staphylinidae are especially suitable for such comparisons.

e. The larvae caught must be identified as far as possible, after which they can be sorted out into the different stages, and these can be correlated to the periods in which imagos are present. However, the larvae of many carabid species are still undescribed (or described incompletely) or hardly distinguishable; the literature on them is widely spread and difficult to obtain, moreover much of it is published in Slavonic languages. Our large collection of larvae may be useful for the study of the systematics of carabid larvae.

Up to now only Carabus-larvae were identified as well as part of the Calathus-larvae in combination with the Zool. Lab. at Leiden. This has led to some interesting new findings, e.g. with regard to Carabus problematicus (cf. 5e); it is our intention to continue our collaboration with the Zool. Lab. at Leiden on this point.

f. Apart from the development of the ovaries (9g) already the presence of young animals, the ratio of juveniles and adults of both sexes, the periods in which larvae are caught (as far as available by identification: 9e) and the period in which the males are caught with protuding genitals, will give a first indication of the reproduction period(s). For such a general comparative investigation we possess more than 175 000 specimens (apart from the larvae) belonging to more than 150 species and taken from 73 localities during nine years. Although these data are not sufficiently detailed for the investigation of spreading of the risk in time and space, they show the presence of a remarkable heterogeneity within certain species.

g. Study of the development of the ovaries in large series of females obtained from structurally different sites and during a number of consecutive years. The technique of the study of the ovaries has been developed in cooperation with VLIJM (Zool. Lab., Free University, Amsterdam) and has been greatly improved since we started in 1963. It is now possible to determine the range of variation in the reproductive cycle of a population with a reasonable degree of accuracy and to measure the differences in this variation in structurally different habitats and in consecutive years (influence of weather conditions): spreading of the risk in time and in space (resp. 7d and 7b).

Further refinements of the technique will improve the reliability even more. Up to now a few species only were studied and these but preliminary, Calathus erratus and melanocephalus being the only ones which were investigated somewhat more fully; the results are promising already (5d and 7d: DEN BOER, Comm. B.S., nr. 131, 1965c, especially in comparison with those obtained by VLIJM and VAN DIJK on the Island of Schiermonnikoog.
We have specimens of 15-20 abundant species, preserved in formalin, which were collected from 1964 onwards; these are very suitable for this investigation.

h. Another way to determine the influence of weather conditions on the reproductive cycle of certain species is to sample specimens in a number of localities within an (almost) identical vegetation and soil structure but in climatologically different situations. Preferably the collections, made by the aid of pitfalls, should be taken at set times (9i) and as many factors as possible taken into account (9k). The 'Group of Soil Zoologists' is planning a number of simultaneous observations in this way in different parts of the Netherlands and will later perhaps do the same in other parts of Europe as well.

A simple preliminary experiment ('Regional Experiment') was set up in 1964 in seven (oak-)birch woods in the Netherlands (Nijmegen, Arnhem, Meijendel, Flevoland, Wijster, and Terschelling).
In each locality ten funnels were placed, which were emptied weekly. The catches were sorted out at Leiden (State Museum of Natural History: WIEBES). At Wijster we received the carabids for further study. Understaffing has prevented us from finishing the identifications up to now, but some preliminary results are very promising.

i. The micro-weather firstly determines the degree of activity including perhaps the developmental activity of the ovaries; to investigate this in greater detail we need data from shorter periods than the weekly ones we now investigate (9a).
To obtain such data it is necessary to catch the beetles continuously, collecting them every 2, 4, 6, 8, 12, or 24 hours. This is only possible if the collecting jar is automatically changed at a set time. To this end batteries of jars, e.g. 12 to a set, are in use at Meijendel (Zool. Lab. at Leiden) and in a different design at the Island of Schiermonnikoog (Zool. Lab., Free University, Amsterdam). Shortly the apparatus will be standardized by the 'Group of Soil Zoologists' and then we will use it at Wijster too.

j. For the interpretation of the data on spreading of the risk obtained from the study of ovaries (9g) augmented by the study of larvae, etc. (9e and 9f) we must further take into account the quantitative differences in the structure of the habitat, especially of its vegetation. Owing to understaffing this important aspect is still in the initial phase; several ways of taking photographs have been tried out, to record the vegetation structure. For recording the soil structure, several of the existing techniques could be adapted to our purpose, but we have been too short-handed to do so as yet.

k. Knowledge of the micro-weather of the habitat and its variation in time and space is of the utmost importance in respect to the data obtained by the investigation of the ovaries (9g). Because of the tremendous number of data which are required to obtain a more or less reliable result (8a) the only way to obtain them in adequate series will be to take the measurements by means of self-registrating instruments and to have them worked out by means of a computer. This technique is being developed at Leiden ('Group of Soil Zoologists': 4); if possible the changes in the humidity of the substrate will also be recorded automatically.

l. For many students of soil zoology, of vegetation (9j) and microclimate (9k) an exact knowledge of quantitative relations between soil structure, vegetation and microclimate would be highly interesting and even more so if it could be combined with data on the concerning macroclimate. With such data it would be possible to analyse the influence of vegetation structure on the relations between macro- and microclimate. It is mainly the structure of the vegetation (with the condition of the soil), of course, which turns the macro- into micro-weather. To find out which model would serve best, it will probably be useful to work with simplified structures on identical substrates(e.g. a turf besides a tussocky structure, homogeneous heath besides a heath with mosaic structure, etc.) or even with artificial structures.

m. The great amount of specimens of carabids at our disposal, gives us the opportunity to critically revise the systematical status of some populations. Especially the genus Amara offers some interesting problems in this respect. Also it enables us to study the morphological variation within some populations and the changes in this from year to year. These changes in morph frequency link up with the possibility of spreading of the risk by phenotypic (genetic) variation within the population. Interesting results in this respect were obtained with Pterostichus oblongopunctatus (5f and 7a). Such investigations should afford information which may give us a better insight into the processes of speciation (a.o. FORD, 1964).

n. In order to solve special problems of systematics (9e) and to investigate the genetic background of some morphs (9m), as well as to test their selective significance it will sometimes be necessary to breed and cross the different morphs in the field as well as in the laboratory. Up to the present only a few of such experiments have been done in the field with Pterostichus oblongopunctatus (5f and 7a); these investigations are comparable to those carried out by WOLDA (Zool. Lab., Groningen).

o. Wing di-(poly-)morphism is the most important form of morphological variation occurring in carabid populations. Not only is it possibly correlated to spreading of the risk by phenotypic (genetic) variation (cf. 9m) but it also plays an important part in decreasing the risk of extinction of a group of populations, by means of the difference in the dispersal powers of the two morphs (cf. 5e and 7c). It is our intention to inspect the development of the wings in all specimens caught in due time, of which only a part have been studied as yet. The data obtained by the 'Regional Experiment' in 1964 of the 'Group of Soil Zoologists' (9h), illustrates convincingly that the macropterous morph is the dispersal phase (diaspore) of the population, i.e. because in the species under consideration there was an unusually high percentage of winged specimens in the recently reclamed polder Flevoland. The possibly different selective significance of macropterous and brachypterous specimens will have to be determined experimentally (cf. 9m)

p. The frequency distribution of the relative abundance of different species of animals in random samples give us a measure of 'rarity' (WILLIAMS, 1964). Rarity appears to be very common, and it is therefore desirable to investigate its ecological consequences especially whether it may have some selective value. The dispersal possibilities and the degree of spreading of the risk in space (7b) seem to be important in this respect.

q. In general there are more congeneric species (which are potential competitors) present in the same habitat, than can be accounted for merely by chance (cf. WILLIAMS, 1947, 1951, 1964); we also found this to be true for our carabids (cf. 7f).
The 'exclusion principle of Gause' and the effects of interspecific competition have to be discussed again in the light of these facts. It is necessary to investigate the advantages and disadvantages of the living together in the same habitat of closely related species (cf. HUTCHINSON, 1959).

r. In general carabids are polyphagous predators, which makes them a suitable subject for the study of 'spreading of risk in food' (cf. 7e). The undigested chitinous fragments of the prey can be identified from the crop contents (kept in Fauré) (cf. SMIT, 1957). In the formalin collecting funnels both the carabids and some of their potential preys are caught. We have made many hundreds of slides of crop contents of 5 species, and more are being made, mostly from females of which the ovaries are studied. The data so obtained, together with those of critical preference experiments may give an impression of the degree in which different species are polyphagous. The next step would be to investigate if there is a relation between the degree of polyphagy and the degree of numerical fluctuations; stabilization of animal numbers could be due to spreading of the risk brought about by feeding habits. Also an impression may be obtained what part 'food specialization' of some carabids plays in their choice of habitat (in continuation of 9b) and in the fluctuations in habitat fitting from year to year (cf. 9q).

s. Individual differences in longevity, size of the progeny, degree of activity, dispersal activity and the real fluctuations in animal numbers, which are due to these factors, can be studied more accurately when working with individually marked specimens. In 1966 we started such a study by marking as many individuals as possible of certain populations and by analyzing the recaptures. We shall continue this several years. In this connection we also intend to develop a technique with which to measure the amount of dispersal of these populations and this if possible, separately for brachypterous and macropterous individuals.

t. Comparative investigations on the distribution of animals over several habitats can not be done without incalculating the fluctuations of animal numbers (ANDREWARTHA and BIRCH, 1954). In this way our research contacted the fundamental theoretical problems of ecology, viz. those concerned with the background of the fluctuations in animal numbers (cf.8) and because our data differed from those mostly used in population dynamics, a new approach seemed obvious (cf. also ANDREWARTHA and BIRCH, 1954). This has led to the introduction of the concept of 'spreading of risk' (cf. 7).

u. Since 1961 the theoretical consequences of this principle have been traced and expounded provisionally. Intensive exchange of views with the staff of the Zool. Lab. at Groningen (Ecological discussion group and particularly with REDDINGIUS and WOLDA), KLOMP (Zool. Lab., Wageningen), BAKKER (Zool. Lab., Leiden) and the 'Population dynamics Club'(Wageningen, Arnhem) have given me the opportunity to test this principle with other people's ideas and data. Our investigations are based more and more on these concepts and problems have to be formulated in new ways (cf. 6). See also DEN BOER (1968).

As the principle of 'spreading of risk' influences not only our views on the fluctuations of animal numbers, but also on competition, natural selection, adaptation, rarity, polymorphism, speciation and therefore on the process of evolution in general, a reorientation in the literature on these topics has become necessary.

10. THE POSSIBILITIES OF THE BIOLOGICAL STATION AT WIJSTER

The investigations are stimulated by the situation of the Biological Station in the midst of a number of more or less natural areas. Only the daily contact with nature can convince the investigator of the importance of variation and heterogeneity in natural situations and prevent him from thinking statically. This daily contact will impress him with the need for a statistical approach and with the importance of spreading of risk.

For investigations as discussed in the foregoing, it is not sufficient to be permanently in the field, but one must also have a modern institute at hand to keep the collections, documentation, library and where calculations can be made and simple experiments can be carried out (9n and 9r). One should also have an area for field experiments, with some structural variation (cf. also 9b, 9i and 9l), and last but not least enough 'man power' to keep up more or less with the temporal variations in nature in a much energy requiring race.

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* Some communications of the Biological Station at Wijster are not generally available. However, reprints of most of them can still be sent on request. Please, apply to the librarian of the Biological Station, Kampsweg 27, Wijster (Province of Drenthe), The Netherlands.

SUMMARY

In this paper a survey is given of the development and the possibilities of the zoological investigations at the Biological Station, Wijster.
The investigation was started from the observation (1959) that experienced collectors will often successfully spot, in an unknown locality, the most suitable sites to find the species they are interested in. This means that one or more of the physiognomical features in which certain types of habitat differ from each other, must be correlated more or less to the habitat-determining factors. It appeared to be possible to find indications as to what the most important factors characterizing the habitat of certain animal species are by sampling as objectively as possible in various types of habitat. Up till now the investigation is confined to carabid beetles, which are sampled with pitfalls and/or funnels. It soon became apparent that the numerical distribution of certain species over various habitats changed from year to year and that practically no species is confined to a single type of habitat. These changes in numerical distribution of the catches over different sites suggests that the most important factors influencing carabids in their choice of habitat, are: the humidity of the substrate and the spatial structure of the habitat, especially of vegetation. The qualitative composition of the vegetation does not appear to be important.
After some years already the results (some examples are given) clearly indicated that our problem was posed too simple: the intensity of habitat-determining factors varies from place to place and also in time; the animals react individually to differences in and changes of environmental conditions and are differently influenced

in successive instars. Hence, our problem is not a typological but a statistical one. In the course of time attention shifted from homogeneous and constant situations to heterogeneous and varying ones, which has led to the concept: "spreading of risk". The greater the variation between the individuals of a population, the greater the population's chance of survival will be under varying environmental conditions, i.e. the greater the spreading of the risk of extinction. Different ways of spreading of the risk are discussed and examples from the present investigation are given:

a. Spreading of risk by genetic and phenotypic variation.
b. Spreading of risk in space: the effect of extreme conditions in one site will be levelled out more or less by less extreme conditions in others.
c. Spreading of the risk of extinction and rarity: the greater the area inhabited by a population or species the greater spatial heterogeneity and the smaller the risk of extinction will be. Hence, a large habitable area will generally harbour more sparse populations (rare species) per unit of surface than a small one.
d. Spreading of risk in time: variation between individuals in time and rate of development and/or reproduction will level out the effects of extreme weather conditions of short duration. Temporary heterogeneity in the reproductive cycle appears to be very common among carabid species.
e. Spreading of risk in the relations to other species: polyphagy will result in a spreading of the risk of starvation; a comparable argumentation applies to more than one predator (parasite) species to a prey, hyperpredation, hyperparasitism as well, and something similar is likely to take place with all species that are mutually dependent e.g. as symbionts, commensals, or even as competitors.
f. Balance of nature: the greater the number of interrelations between species, i.e. the richer in species the "biocoenosis", the greater the chance that spreading of risk plays an important

part. Since only non-specific (spread) relations will yield the necessary variations in the chances to survive and to reproduce, the number of species in a biocoenosis may be more important to its stability than its composition.

The different ways of spreading of the risk all have one and the same effect: a relative reduction of the amplitude of fluctuations of animal numbers. As opposed to the hypothesis according to which the "regulation" of animal numbers is due to density-dependent factors, is proposed the hypothesis: stabilization of animal numbers is due to spreading of risk. Density-dependence will mainly exist under homogeneous conditions for as soon as heterogeneity or variation occurs, the degree of interdepence will be diminished (levelled out) by spreading. Apart of this, density will be limited when the capacity allowed by the habitat is approached.

A survey is given of the possibilities of further research.