POPULATIONS OF CARABID BEETLES AND INDIVIDUAL BEHAVIOUR. GENERAL ASPECTS

P. J. DEN BOER

Biological Station of the Agricultural University (Wageningen),
Kampsweg 27, 9418 PD Wijster, The Netherlands

ABSTRACT

It is tried to outline the background of the investigations taking place at the Biological Station, Wijster: Because field populations are composed of individuals, population processes can only be understood by studying the differences in relevant properties between individuals living together in 'interaction groups'. The consequences of this view are illustrated by discussing the chances of survival of two carabid species at Kralo Heath.

The different contributions of our research group to this volume (DEN BOER, VAN DIJK, VAN HUIZEN, MOLS) are introduced within this general frame-work.

The main results of .BAARS' work in this connection are also mentioned (have recently been published in Oecologia).

When we are occupied with population dynamics, population genetics, population ecology or population biology, sooner or later we will ask: 'What **is** a population?' This question appears to be difficult to answer: on the one hand, in theoretical studies 'the population' is generally treated as a uniform entity*; on the other hand, in the field we are mainly confronted with individuals, and therefore with the problem how to delimit 'our population', i.e. a group of individuals.

This delimitation will be greatly influenced by the problem one wants to study, but because of the widely diverging interests among ecologists field populations may thus be as different, as the population of larvae of some staphylinid species in a single mushroom is, from the stork population of Western Europe. Although such 'populations' are in no way comparable, both students may consider their 'population' as an entity, and wonder how it is 'regulated'. For, a holistic view of 'population' is widespread and as old as field biology, since it is based upon an assumption that carries us back to Darwin, namely the presupposition that the members of a population are somehow continuously competing and will thus keep abundance between certain limits.

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* This means: in theoretical studies population processes are generally described by differential equations, which tacitly assume that all members are equal and form a closed group in a homogeneous and generally constant environment.

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Especially to test critically this competition hypothesis, one must be able to delimit comparable and natural population units, viz. groups in which the individuals can at least meet, and thereby possibly – but not necessarily – influence each other: interaction groups. If one does not take up a position in this competition/regulation question it seems nevertheless useful to work with 'interaction groups' as a kind of standardized units of population. This was already realized by BAKKER (1964, 1971), but met with the difficulty that ecologists did not see an easy way to generally delimit 'interaction groups' in the field. In the case of carabid beetles, however, working with interaction groups appeared to be not only feasible, but even inevitable.

Carabid beetles are generally sampled with the help of pitfalls, and therefore, the individuals caught in the same pitfall were potentially able to meet, i.e. form a sample from the same interaction group (see further: DEN BOER, 1977). The usefulness of this method was underlined by BAARS (1979b): at several sites on Kralo Heath and in several years, just before the start of reproduction, he fenced part of a locality and then trapped all individuals of two abundant species living there. The mean densities thus obtained were compared with the catches during that season in a nearby (20–120 m distant) standard set of pitfalls. In this way he could show that the catches in a pitfall, totalled over the whole season (or year), give a surprisingly accurate – but of course relative – measure of mean density, and at the same time a relative measure of the numerical size of the pertinent interaction group (note: within the same area different interaction groups of a certain species are apparently living on equally sized surfaces).

When we turn now to the whole area of the Heath of Kralo and Dwingeloo (1200 ha), which is more or less continually inhabited by *Pterostichus coerulescens* L. (= *versicolor* Sturm), one may wonder as to how far the numbers of individuals of this species, caught yearly in different sets of pitfalls, are samples from the same or from different interaction groups (subpopulations). Since the fluctuations of these numbers used to be quite different at the different sample sites (see: DEN BOER, 1971), we got the impression that especially in the more distant localities, i.e. more than 200–300 m apart, different interaction groups were sampled.

By marking individuals of *Pt. coerulescens* and of *Calathus melanocephalus* L. radioactively and localizing these individuals each day BAARS (1979a) was able to characterize and quantify the walking pattern of these species. This pattern was simulated in a computer model, after which he could not only test the reliability of this simulated pattern with the results of several independent field experiments, but also calculate what distances could be covered by average individuals during their lifetime. It then appeared that even very old individuals of *Pt. coerulescens* (3–4 years old) will not cover on an average more than 250–300 m (during the first breeding season about 150 m is covered). In the case of *C. melanocephalus* these numbers are much smaller: during the first breeding season an average of only 50 m, whereas old individuals (2–3 years old) will hardly cover 100 m. This means, that by the numbers of *Pt. coerulescens* caught, pitfall series that are more than 300 m apart will register population processes, that are highly independent of each other. In the case of *C. melanocephalus* this will

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already occur with pitfall series that are more than 100 m apart.

A pitfall estimates the fluctuations in composition and of numbers of the interaction group of which it automatically forms the centre; therefore pitfalls in different localities of the same more or less continually inhabited area, together give a reliable picture of the effects of the heterogeneity in the relevant conditions.

It thus appears, that for *Pt. coerulescens* the Heath of Kralo and Dwingeloo is very heterogeneous, i.e. the risks of large fluctuations are spread over a number of very different localities by which, in the area as a whole, the numbers are rather stable (see further: DEN BOER, 1968, 1971, 1973). For *C. melanocephalus*, on the other hand, the same area is much less heterogeneous; in different localities the fluctuations of numbers are more or less parallel, i.e. the risks are only poorly spread by which, seen over the whole area, the numbers fluctuate as heavily as in an arbitrary subpopulation (Fig. 1). Hence, under overall stationary conditions *C. melanocephalus* will run a much greater risk of dying out than *Pt. coerulescens*.

Now we have seen, that the numerical stability of a species over a large area can only be understood as being the result of the fluctuations of numbers of different interaction groups (subpopulations), the question of the causes of numerical fluctuations as such shifts, and the priority becomes: what are the processes that run within single but different interaction groups?, i.e. what are the processes that result from summing up the courses of life of the individuals? (see also DEN BOER, 1973).
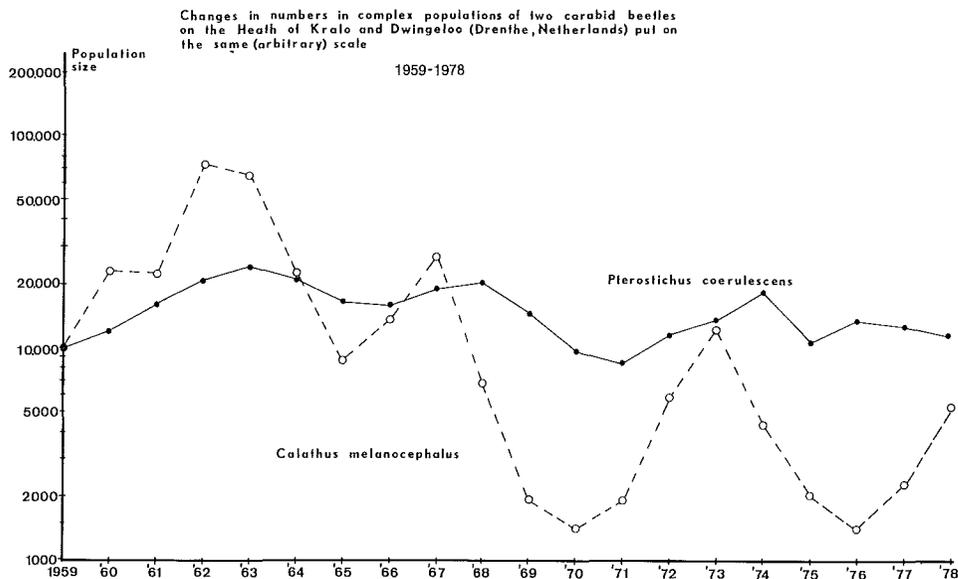

Fig. 1. Fluctuations of numbers in two carabid species on Kralo Heath to show the difference in magnitude, assuming that the subpopulations studied, together give a reliable estimate of the changes in numbers in the 'population as a whole'. To facilitate comparison it is assumed that in 1959 the two species were equally abundant.

Because abundance results from natality, mortality and migration, we are firstly interested in the conditions that determine or alter the chance of survival and/or the chance of reproduction of different individuals, at present especially of individuals of different ages. VAN DIJK, who took on this aspect, will deal with this subject in this volume. Next – in connection with migration – it will be important to know under what kind of conditions an individual will leave the area of the interaction group, either to contact other groups and possibly to contribute to a levelling of local differences in abundance (like in *Pt. coerulescens*, see above; see also: BAARS & DEN BOER, in prep.), or to disperse out of the habitat and possibly to contribute to the foundation of new groups (see further: DEN BOER, 1977, 1979). In the latter case in many carabid species the normal kind of locomotion, walking, will change into flying. Elsewhere in this volume VAN HUIZEN will report on both the morphological and the environmental conditions that determine frequency and level of flight behaviour in carabid beetles.

The numerical result of individual reactions (like feeding, copulating, egg-laying, sheltering, dying, walking or flying away) to different conditions – which can be partly studied in the laboratory – in the field will depend highly on the frequency by which each of these conditions is encountered. In the case of carabid beetles – like in many other animals – this frequency of encountering will directly be determined by the walking pattern. BAARS (1979a) showed that this walking pattern – by analysing the distances covered per day – is composed of two, randomly .alternating elements: random walk, and directed movement. Most probably the random walk should be considered the generalized result of different kinds of searching behaviour, whereas the directed movement in some (unknown) way seems to be connected with dispersal (individuals that, while moving around, get out of their preferred habitat change over to an extreme kind of directed movement).

To further analyse the frequency of encountering some condition it was necessary to study the walking pattern more closely, viz. also within a day. Important questions are then: at what time-scale is random walk still random, and: at what distance do the beetles react to certain local conditions? Concerning encounters with prey this is now being studied by MOLS (see his contribution to this volume). We hope to study other aspects of individual behaviour along the same lines, e.g. egg-laying behaviour.

Again to get to grips with the processes behind the numerical changes of the interaction group we generally follow the strategy:
1. studying the relevant aspects of individual behaviour in such a way that each element can be quantified.
2. simulating this behaviour, and checking the model in independent experiments with real animals (the results of these experiments could be predicted): an example of this is discussed in this volume by MOLS (see also: BAARS, 1979a);
3. integrating the different, sufficiently tested submodels into a master-model with which eventually the numerical fluctuations of the interaction group – as they are found in the field – can be simulated and thus predicted.

4. Simplifying the master-model in such a way that the quantitative effects of the submodels are saved without the necessity of simulating all aspects of individual behaviour; this simplification will be repeated at different levels;

5. With such a simplified master-model we can also try to simulate the effects of integrating a number of different interaction groups (subpopulations), i.e. we can try to return to our observations from Kralo Heath, which were our starting point.

Meanwhile we will also have learned whether or not a 'population' should be considered a kind of entity to be able to understand the patterns of numerical fluctuations as they are observed in the field.

With similar arguments also KAISER (1979) advocates an individuals approach of population dynamics.

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