

Carabids as Objects of Study

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Among students of beetles carabids always have been beloved objects, possibly because there are very appealing creatures among them (Carabus), possibly because the identification of beetles naturally starts with the carabids. After the necessary morphological, taxonomic and historical studies, which have still to be continued (e. g. Nagel, 1979; Hammond, 1979; Koch, this volume; Matthews jr., 1979) especially outside Europe (see Erwin et al., 1979), rather early already (as compared with other groups of insects) a comparison of life cycles was undertaken (Larsson, 1939), which opened a highly fruitful field of ecological investigations (Thiele, 1977; Ferenz, this volume; Erbeling and Paarmann, this volume), and is still the base of the current discrimination between spring and autumn breeders (e. g. Hurka, this volume). By extending these studies to carabid life cycles outside the temperate plains of Europe not only interesting new relationships with the environment were discovered (e. g. Brandmayr, this volume; Paarmann, this volume), but we also got some insight into the evolution of carabids and of carabid life cycles (Erwin, 1979; Paarmann, 1979). In general, carabids more and more appear to be favourable subjects for comparative ecological studies, because they show a sufficient range not only of reproductive cycles (den Boer, 1985), but also of habitat choice, of sizes of individuals, and of physiological and behavioural reactions within an otherwise rather homogeneous group that is surprisingly rich in species (Thiele, 1977).

Another area of research in which carabid beetles had an early start - in fact as early as Charles Darwin - is the occurrence, biogeographical significance and possible genetics of wing dimorphism (Darlington, 1943). It was especially Carl Lindroth (1949), who clearly saw the great research possibilities of wing dimorphism in carabids. By visiting the first meeting of European carabidologists in 1969 at Wijster (den Boer, 1971), and keenly discussing the meaning of dispersal, he

highly stimulated continuing these studies with a more ecological outlook (den Boer, 1977; van Huizen, 1979; den Boer et al., 1981; Brandmayr, 1983; Aukema this volume; Desender et al., this volume). The interest in the fascinating predatory behaviour of carabid beetles, on the other hand, was excited relatively late (Faasch, 1968), but then developed favourably (e. g. Bauer, 1974, 1979, 1982; Ernsting and Joosse, 1974; Gilbert, this volume; Paarmann et al, this volume). Stimulated by the convenient body sizes and manageability of many carabid beetles at the same time other aspects of carabid behaviour roused interest too, such as walking patterns (Baars, 1979a; Mols, 1979), locomotion (Evans, 1977, and this volume; Mossakowski and Stier, 1983), parental care (Brandmayr and Brandmayr, 1979).

The night/day rhythms of locomotory activities naturally led to the study of circadian rhythms (Lamprecht and Weber, 1971, 1979; Weber, 1983), and their dependence on different conditions such as geographic latitude (Thiele, 1979; Leyk et al, this volume). Because of this development carabid beetles became interesting physiological objects too. Fleissner and Fleissner (this volume) and Dube and Fleissner (this volume) succeeded in localizing the circadian pacemaker in the carabid Pachymorpha sexguttata. But also the study of the photoperiodic and hormonal control of development and reproduction in carabids emerged from the ecophysiological work of Thiele (1977); Ferenz (1973 and e. g. this volume). This mutual stimulation of behavioural, physiological and ecophysiological research in carabid beetles possibly is one of the more outstanding developments in this field during the last decade, a development that was undoubtedly stimulated by the meetings of European carabidologists, in this case especially the third one in Grietherbusch in 1978 (den Boer et al., 1979), and the fourth meeting in Haus Rothenberge (Westphalia) in 1981 (Brandmayr et al., 1983).

After the second world war the collecting of carabid beetles got a more quantitative aspect by the general use of pitfalls. By combining this technique with mark-recapture van der Drift (1951) most probably was the first who tried critically to test the quantitative value of pitfall sampling. It is a pity that this scrutiny got lost again in the following decades when the use of pitfalls became a widespread and even popular technique for the collecting and sampling of ground beetles. The evident simplicity of this technique apparently trapped many central-european carabidologists into an unrealistic interpretation of the numbers of carabid individuals caught in the pitfalls. Following Renkonen (1938) and Tischler (1949, 1955) the catch-number of some species was - and still is, as was experienced by the editors of this volume - considered a kind of quantitative estimate of the "ecological role" of that species in the "community", which was therefore expressed as the percentage (= dominance) of the total number of carabid beetles of all species captured, i. e. without taking into account differences in behaviour, life cycle, activity level, capture efficiency (Luff, 1975, and this volume), size of individuals, etc. between the species. Until the present day this dominance concept still governs research activities which till about the sixties were known as "biocoenology", i. e. a kind of quantitative

faunistics (see further e. g. Balogh, 1958; Thiele, 1977, Ch. 2), and at present are absorbed in "community ecology". As a consequence of these uncritical interpretations of pitfall catches the editors of this volume were also confronted with a lot of confusion about the use of some common (and necessary) ecological terms. Therefore we propose to apply these terms as far as possible in the sense as these were already used by Charles Elton in 1927, and only to deviate - if necessary - in the same practical spirit. We hope that the following proposals will remove much of this confusion:

Population: a group of individuals of the same species that more or less continually (in space) inhabit the same locality, which is usually recognized by us (but not necessarily) physiognomically. Such a local population can be part of a natural population, i. e. a more or less coherent group of local populations on a geographic scale (Andrewartha and Birch, 1954, 1984), which can also be considered the natural unit of evolution. If sampling methods are adequate (e. g. mark-recapture in carabids) within a local population one or more (multipartite population: Andrewartha and Birch, 1984) interaction groups (den Boer, 1977) = neighbourhoods (Wright, 1969), or subpopulations, can be distinguished, i. e. groups of individuals that will potentially interact significantly (at least to copulate). A deme (Wright, 1969) is a local population that consists of a single interaction group only.

Habitat: the locality of a local population, described in ecologically (not geographically) relevant terms (Elton, 1927). It is common usage - and practical - to describe habitats in simple physiognomical (structural) terms, but other (relevant) characterizations are also possible, of course, as long as these are not refined to such an extent that habitat will approach "ecology of the species".

Niche: the functional place (trade) of an organism (such as: surface-predator of collemboles, cutter of litter, etc.) (Elton, 1927). Attempts to put more into "niche" gradually reduce it to "the life history (or ecology)" of the species. "Fundamental niche" = "ecology of the species".

Guild: group of coexisting species at the same functional place (in the same "Eltonian niche"), e. g. the surface dwelling, polyphagous, and spring breeding carabid beetles of about the same size.

Fauna: group of species (usually belonging to a specified taxonomic group, e. g. carabid beetles), found in a certain habitat, or in a spatial group of habitats (local fauna), or in a certain area (regional fauna). The fauna can be described qualitatively (list of species) or quantitatively. Interrelations are not considered.

Community (biocoenosis): that group of species out of the local flora and fauna, which show evident ecological interdependences (e. g. as prey-predator, host-parasite, plant-phytophage, hence, not e. g. the "community of carabid species", but the "community of carabid beetles

(as predators) and their preys"): Elton (1927, 1966). Together these species form the web of biotic functions (food chains, food webs). Although - strictly speaking - most coexisting species will show some relations, it is strongly dissuaded only for this theoretical consideration to call each group of coexisting species (= fauna) a "community" (parable: though in most towns some trade will occur, not each town will be a "trade-centre", there are even "satellite towns" and "dormitory towns"). A correct use of "community" makes it possible to distinguish different communities (biocoenoses) as functional groups in the same locality, e. g. the community of leaf-consuming arthropods on some tree, including their enemies (predators, parasitoids, etc.), but also the community of litter-cutting arthropods (with enemies) underneath.

Biotope: the habitat of a biocoenosis, described in ecological terms. It is advisable to use "biotope" especially in cases where the conditions under which the community could develop and be maintained are sufficiently understood, so that "biotope" is not synonymous with "kind of locality".

Ecosystem: the system in which different materials are transformed and/or recycled by the operation of biotic processes (e. g. cycling of C and/or N are functional parts of some "ecosystem"). In the ecosystem concept one or more biocoenoses are considered as transformers of energy and material, and are thus reduced to some rough kind of chemical and/or energy factories. In such a "factory" different functional (trophic) levels are distinguished (primary producers, secondary producers or first-order consumers, first order predators and parasites, etc.). It is advised to use "ecosystem" only in studies on material and/or energy transformations, and not as a synonym for "community" or even "fauna" (let alone as a synonym for "environment", or even for "flora + fauna + environment"!).

Because of the erroneous interpretations of pitfall catches it is not surprising that the pitfall sampling technique met with a lot of criticism (see e. g. Southwood, 1966). These critics were not only concerned with the indiscriminated adding of the numbers of individuals of different species (dominance percentages), but also - and even in the first place - with the use of the catch-numbers of a single species as relative estimates of mean density. As long as the summed catches of the whole year (year-catch) - or at least of the entire breeding season - are considered as a single relative estimate of mean density around the pitfalls, this critique is not sound (den Boer, this volume). Baars (1979b) could even show that the data of the critics themselves are reasonable relative estimates of density if treated as year-catches.

Possibly this confusion about the use and misuse of pitfall catches, which in fact was already removed by van der Drift (1951), for some time hampered a healthy development of the population ecology of carabids. We hope that this volume will help definitively to take away this impediment. Carabidologists should realize that the method of pitfall sampling (if applied critically, of course) places them in a favourable position to contribute to the development of a comparative popula-

tion ecology, at least as far as adult carabids are concerned. Careful comparisons between coexisting species, between populations of the same species at different sites, between features of the same population in different years, etc., will enable us to find out which phenomena are exceptional and which more general, so that the narrowly based generalizations which are rather common in population and community ecology can be tested (e. g. den Boer, 1977). In this volume such comparisons are made: between species (den Boer, Grün), between succeeding faunas (Szyszko), between life history phenomena (Adis et al., Loreau), between subpopulations at different altitudes (Sota), and between succeeding years (Hemmer et al.). When it is necessary to make direct quantitative comparisons between the populations of different species we can best follow Szyszko (this volume) by using biomass instead of numbers of individuals, because this will better approach "the ecological role in the community" (e. g. as generalized predators) of the biocoenologists. The faunal comparisons of Mader (this volume) and of Plachter (this volume) might have been still more interesting then, I suppose.

Recently carabid beetles also entered the lists for the "unifying concepts" of ecology, such as regulation of numbers (Baars and Van Dijk, 1984; Den Boer, this volume), and interspecific competition (den Boer, 1980; Lenski, 1984; Loreau, this volume; den Boer, 1985). Taking part in these fundamental discussions will bring to light also some weaknesses of working with carabid beetles: How can egg production in the field be estimated? (Van Dijk, 1983; Hemmer et al., this volume), and how will we feasibly estimate density and spatial distribution of the larvae in the field? What quantities (and qualities) of food are actually available in the field (van Dijk, this volume)? The latter problem is especially critical when asking whether carabids do indeed compete for food (Lenski, 1984), or are passively manipulated by the overall changes of the food resources as is suggested by the data of Szyszko (this volume); compare also Dempster and Pollard (1981). In practice this will reduce to asking whether carabid beetles are able to use the greater part of potential food or only a small fraction of it. These problems made the theme of the fifth meeting of European carabidologists in 1982 at Stara Brda Pilska (Poland) (den Boer et al., 1986).

At first sight, the hypothesis that in general carabid beetles only use a small part of potential food, seems to contradict the observations of carabids taking away a substantial fraction of some developmental stage(s) of a pest insect (see e. g.: Thiele, 1977, Ch. 4). This contradiction is removed, however, if we realize that most ground beetles are polyphagous predators that, just as do most predators (or parasitoids) in a prey (or host) cluster, show an area-restricted search; see further: Mols (1979, 1986). Because of this, locally and temporarily a high percentage of some prey species can indeed be taken, but at the same time other prey species are spared. Hence, as a result of the walking patterns (Baars, 1979a; Mols, 1979) carabid beetles will switch to that prey species that has become most abundant, but will take other prey when this species has significantly decreased in numbers. It can thus be expected that carabid numbers will hardly be influenced by

even a dramatic change in abundance of one of the prey species, as long as the overall food resources stay sufficiently available. Den Boer (1986) supposes that the fact, that the numbers of the carabid Pterostichus oblongopunctatus in two small forests did not react to the dramatic and lasting reduction (with a factor of 60 and 1500 respectively) of its formerly probably most abundant (and eagerly taken) prey, the larvae of the caddis fly Enoicyla pusilla, must be understood in these terms: apparently, the availability of alternative prey was such, that for carabids the overall food situation stayed about "normal". Note, that "normal" need not be "optimal", because in the field the accessibility of food for ground beetles is also affected by different degrees of clustering of potential prey species (in relation to walking patterns), by structure of feeding sites (which influences both detectability and success of defence reactions of prey), by weather conditions, and possibly even by behaviour to escape from predators (see also: White, 1978; van Dijk, this volume). This view fits in well with the significantly density-dependent predation of the pupae of the winter moth in Wytham Wood near Oxford by polyphagous predators: these predators (including carabids) are continuously present in sufficient numbers and will only assemble in clusters of winter moth pupae when these have increased in abundance more than other potential prey species (see further: den Boer, 1986). Only, if in the course of a number of years, the whole spectrum of prey species accessible for carabids changes directionally, as seems to occur in aging pine stands in Poland (Szyszko, this volume) can the numbers of many carabid species be expected to show a distinct trend, and finally the whole carabid fauna may change.

Now the taxonomy of carabid larvae is reasonably well known (e. g. Brandmayr et al., 1980; Hürka, 1980, this volume; Kúrka, 1971; Luff, 1972, 1980; Thompson, 1979) we can agree with Brunsting et al. (this volume), that we should pay more attention to the ecology of carabid larvae, especially to the availability of food and to mortality risks. Larval mortality generally will appear to be the key-factor for the fluctuations of numbers, i. e. the factor with the greatest variance, which variation at the same time is of the order of magnitude of that of population numbers: e. g. in both Calathus melanocephalus and Pterostichus versicolor $\text{Var}(\ln \text{recruitment rate})$ is much greater than both $\text{Var}(\ln \text{survival rate/adults})$ and $\text{Var}(\ln \text{eggs/female})$, whereas it is of the magnitude of $\text{Var}(\ln \text{adult numbers})$ (den Boer, this volume). But since in both species this key-factor is neither correlated with the parent population numbers, nor with the estimated (from eggs in ovaries) numbers of eggs produced by the parent females, there are no indications so far that the mortality rate (= 1-recruitment rate) of the larvae would "regulate" the numbers of these carabid populations. Just as in other insects (see e. g. Uvarov, 1931) also in carabids (Thiele, 1977), and probably in most poikilothermic land animals, the mortality risks of (early) developmental stages are so deeply affected by abiotic factors, that the latter will greatly determine the magnitude of the fluctuations in the amount of progeny. See further: Andrewartha and Birch (1954, 1984).

Even powerful density-dependent mortality factors will not be the most probable "regulating" agents, at least not in carabid beetles, because the main problem of (carabid) population dynamics seems not to be: "Which processes limit high densities?", but "Which processes lower the chance of extinction?" (den Boer, this volume). Although processes that limit high densities may operate, of course, these will not keep density within sufficiently narrow bounds, if not also comparably efficient processes prevent the occurrence of fatally low densities. As at low densities individuals can hardly be expected to influence each other, unless very indirectly - and then negatively: underpopulation effects (Andrewartha and Birch, 1954, Ch. 9) - the chance of extinction can only be lowered then by spreading of risk (den Boer, 1968, 1981). This also means that studying the conditions determining the amount of reproduction (van Dijk, 1979; Baars and van Dijk, 1984) should have priority over the study of mortality factors. All this underlines the need of both long-term and comparative population studies: under what conditions of place and time do what species fail to maintain themselves, and why? As it is equally necessary for that, however, to study single populations in sufficient details (e. g. Hemmer et al., this volume) population ecologists continuously work in a conflict situation: if only a single population is studied closely, how to evaluate the results in terms of general phenomena, but if more populations are studied at the same time, how to analyse sufficiently deeply to understand actually what happens? The apparently high chance of extinction of local populations (den Boer, this volume) again emphasizes the general significance of dispersal phenomena in relation to the possibilities of colonization, which brings us back to the theme of the first meeting of European carabidologists (den Boer, 1971).

So far ground beetles have hardly entered population genetics. Turanchik and Kane (1979) and Kane (1982) studied the genetic variability within and between populations of the cave dwelling carabid Neaphaenops tellkampfi, using polyacrylamide gel electrophoresis. They attained the surprising result that, whereas genetic variation within local populations is high, different local populations showed a high degree of genetic similarity. Supported by the same technique Liebherr (this volume) tried to reconstruct the speciation processes within the species group of Agonum extensicolle. Also Mossakowski et al (this volume) are mainly interested in speciation processes. Between individuals of sympatric populations of the carabid species Carabus lineatus and C. splendens a high degree of hybridization appears to occur. In laboratory experiments Roschen and Mossakowski (this volume) tried to compare the preferences for temperature, humidity, and time of activity of the hybrids with those of the parental species, and concluded that, because of overlapping preferences, in the field hybridization cannot be prevented.

Population genetics of carabids has probably stayed underdeveloped so far because ground beetles are impractical subjects for cross-breeding and for selection experiments over a number of generations. Generation time is long, and breeding is time- and space-consuming, whereas one may happen upon specific difficulties connected with the

control of annual rhythms (see: Thiele, 1977, Ch. 6B). Nevertheless, cross-breeding and selection experiments with carabids might importantly increase our insights into the processes of adaptation and speciation in general. For instance, it could hardly be expected that two very closely related species, such as *Calathus melanocephalus* and *C. erythroderus*, would show different genetic systems concerning wing dimorphism, though considered afterwards the adaptive value of this difference is evident (Aukema, this volume). No less surprising was the discovery of the sibling species *Pterostichus nigrita* and *P. rhaeticus*, which appear not only to differ in ecophysiological properties but also in karyotype (Koch, this volume; Nettmann, this volume). Especially the latter illustrates that the variability within and between carabid species can show unexpected patterns (Serrano, this volume; Nettmann, this volume). It is not yet clear, however, how the karyotype patterns found by Serrano and Nettmann should be understood in terms of relationships.

Turanchik and Kane (1979) explain the high genetic variability within versus the high genetic similarity between local populations of *Neaephaenops tellkampfi* (above), which is in sharp contrast with the patterns in other cave dwelling species, as resulting from a high level of exchange of individuals between the - generally numerous - local populations, each of which occupies an environment that is supposed to be experienced by the beetles as very heterogeneous. Kane and Ryan (1983) explain the latter as follows: the cave environment is rather predictable - though still variable - by which natural selection will become more and more subtle, i. e. the individuals will develop a high sensitivity to small differences and changes in the environment. Hence, a high genetic variability will be maintained, but will concern other features. For the moment this hypothesis will not get much support, because it is neither clear how much exchange of individuals is necessary to keep up a high level of genetic similarity, nor known how much exchange can be expected to occur between different cave populations. Therefore, it seems useful to study non-cave-dwelling carabid species in the same way. It can be expected, that most carabid habitats will be at least as heterogeneous as the cave environment (Kane and Ryan, 1983), so that in cases with a supposed high level of exchange between local populations the same kind of results as those of Turanchik and Kane (1979) should be found. One may even think of long-term field experiments in which the level of exchange of individuals between local populations is manipulated, and the effect upon genetic variability within versus genetic similarity between local populations is followed in time. In this way the population ecology of carabid beetles might develop into population biology.

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