

Facts, hypotheses and models on the part played by food in the dynamics of carabid populations*

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ABSTRACT

A survey is given of the foraging behaviour of carabid beetles as far as it is known at the moment. It is tried to understand the different kinds of walking behaviour in relation to feeding, especially in prey clusters. This is connected with the degree of availability of different kinds of prey, with the "motivational state" of the predator and with the degree of sensitivity of the predator to prey stimuli. It is discussed how far such foraging behaviour can be called "optimal". In fact we only know that it is more or less "effective", which would imply that in general there is sufficient food to survive and reproduce, so that only a small part of the resources would be utilized. It is tried to explain why this need not conflict with the current neo-darwinistic opinions. Because of the rather simple central nervous system of carabid beetles foraging must necessarily be a broad compromise between the amount of energy that can be invested in walking and the amount that overall can be expected to be saved from the food. Preferences within the group of prey that can be overpowered can hardly be expected to play an important part in the field, in spite of the fact that there appear to be great differences in quality for egg production between different prey.

The sudden collapse of the population of the most important prey, *Enicocyla pusilla* of the carabid *Pterostichus oblongopunctatus* did not influence the numbers of the latter. Immediately after an outburst of the heather beetle the numbers of the carabid *Calathus melanocephalus* decreased sharply, among others possibly because of a low egg production per female. In the course of 20 years this happened four times. Are larvae of the heather beetle a low quality food for egg production? In both cases the carabid beetles did not influence the numbers of their prey significantly. This is different in the case of the predation of polyphagous beetles on the pupae of the winter moth in Wytham Woods: a severe negatively density dependent predation caused by a high concentration of larvae and adults in clusters of pupae under certain trees. There are more indications that polyphagous beetles can be important controlling agents of some noxious insects, but it is generally difficult to quantify this conclusively. It is suggested that polyphagous predators by taking away the peaks of abundance of potential prey can significantly contribute to the "stability of nature".

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INTRODUCTION

An organism can be considered a kind of negative-entropy machine which has to take up energy from its surroundings to build up its tissues, to stay alive, and to propagate its genes. This principle often is held to be the essence of life. Processes and structures which enable organisms to take up energy, or which determine the transport, transformation, and storing of energy, therefore rightly take a central place in many branches of biology, and not in the least in ecology. Animal organisms take their energy from other organisms either directly or from their products or remains. Together these most basic processes can be designated as "feeding" or "foraging". The "success" of an animal species (evolutionary spoken) will thus depend on the degree to which its individuals on the average are capable to get sufficient energy to keep up the stream of individuals through time, and it is therefore not surprising that animals spend the greater part of their lives looking for suitable food and feeding (see also: Elton 1927). Carabid beetles are no exceptions in this respect.

THE FORAGING BEHAVIOUR OF CARABID BEETLES

Carabids are primarily carnivorous (Thiele 1977), and in most cases this will mean they are polyphagous predators, i.e. they feed on different kinds of living animals (e.g. Hengeveld 1980). However, like most predators (e.g. among vertebrates) many carabids do not despise dead bodies, so that it can be wondered whether the animal remains in their guts originate from dead or from living animals, but this does not imply that they would be more carrion feeders than predators, as is sometimes supposed. On the other hand, many incidental observations indicate that most carabids prefer wounded or otherwise mutilated prey to undamaged ones, again like most predators: they are possibly attracted by the smell of the haemolymph of a wounded prey. It may even be hypothesized that polyphagous carabids often will only unambiguously recognize a prey as potential food, if (by chance?) they have put their mandibles in it, i.e. have tasted the haemolymph. After such an experience they are apparently inclined to also more directly attack other prey of the same kind (if available), probably because in this way they have been sensitized for adequate touch and/or visual stimuli too. It may be doubted, however, whether in polyphagous carabids such a "searching image" (Tinbergen 1960) will persist very long, if it is not reactivated rather frequently by experiences of the same kind.

This doubt derives from observations of Mols (1979, and this volume): when a prey is consumed the behaviour of the beetle changes, it now shows a highly tortuous walking pattern (area restricted search: Mols, 1979; his Fig. 9), with the antennae bent downwards, around the place where the prey was found. The beetle is evidently in search for more prey of that kind, and if one is found it will be readily attacked. If no other prey is encountered within a relatively short time, however, this behaviour gradually turns into the normal (random) walking pattern (Mols, 1979; his Fig. 10) with the anten-

nae stretched forward. When showing the latter kind of behaviour the beetle is apparently less sensitive to stimuli which might emanate from adequate prey, and then it may graze or even run over a lot of potential prey before attacking one of them. We have the impression that if the beetle does not feed during some days this sensitivity to prey-stimuli may fall even more, whereas the walking pattern further changes towards the "directed walk" described by Baars (1979: his Fig. 1). How this insensitive disposition can be broken through again is not known at the moment; it may be hypothesized (and this is supported by incidental observations) that the density of some potential prey, i.e. the frequency of encounters, will play an important part in it. Hence, the form of the walking pattern (more or less tortuous, or even directed) apparently somehow reflects the sensitivity of the predator to stimuli emanating from a certain kind of prey.

As many of the potential prey of carabids will occur in the field in smaller or larger patches or clusters the above picture of the foraging behaviour of polyphagous carabid beetles may be expected often to boil down to a sequence of shorter or longer runs of monophagous feeding behaviour separated by periods during which less — or even nothing — is eaten but larger distances are covered by walking (Baars, 1979: his Fig. 1). This pattern of alternating foraging bouts and walking bouts fits the walking pattern of radio-actively marked carabid beetles as it is described by Baars (1979) fairly well. He found periods of small distances covered per day in random directions, alternating with periods of directed movement with large distances covered per day. Whether in different foraging runs the same or different kinds of prey are eaten will mainly depend on the spatial distributions of the different potential prey. The range of numbers of a certain prey species that will be eaten in different foraging runs, however, will not only depend on the degree of patchiness of its spatial distribution, but also on the degree of availability of that kind of prey. Features like size, mobility, period of activity, preferred places, concealing properties, defensive behaviour, palatability, etc. will highly influence both the availability of the different kinds of prey to predation and the success ratio of the predator with respect to these different kinds of prey. To avoid misunderstanding: I consider the availability of a certain kind of prey to the predation by a certain kind of predator to be the relationship between the biological properties of the prey and the foraging behaviour of the predator, i.e. it will be the expectation value of the predation risk of the prey, which in itself will vary in space and time under the influence of factors such as weather conditions, structure of vegetation and soil, changing sensitivity of the predator (see above), and the changing "motivational state" of the predator.

This "motivational state" is the output of part of a computer model, which in its entirety continuously simulates changes in the level of locomotory activity as well as in the walking pattern of a carabid beetle, and which is constructed by Mols (1979) to quantify the observed relationship between feeding and behaviour. The driving force of the activities of a carabid beetle is considered to be the "hunger level", which is defined as the relative gut content, i.e. the degree to which the gut is filled with food. The capacity of the gut is not a constant, however. It is highly influenced by other

products stored in the body, such as eggs or fat. A female beetle filled with ripe eggs, for instance, can only eat small quantities of food at a time, because its gut capacity is low, and this highly influences its activities (see also: Mols, in press, and in this volume). I will not go into these highly interesting findings here: these will be treated extensively by Mols and by Van Dijk.

However, I will take this opportunity to speculate somewhat about the possible relationship between the "motivation" of a carabid beetle to become active, and its sensitivity to prey-stimuli. This sensitivity is highest in a hungry beetle that just has consumed a small but adequate prey. While showing the characteristic area restricted search (see above) it will thus easily find other prey of that kind if these are close by, i.e. if the prey is clustered. We saw already that if other prey is less easily found the beetle will become less attentive and at the same time it will gradually abandon the area restricted search. The more time has elapsed since its last meal, i.e. the more hungry the beetle, the more it will be inclined both to become active and to show a walking pattern that deviates from the area restricted search, i.e. a pattern by which generally greater distances will be covered (with the "directed" walk as its extreme). But exactly in this situation the beetle does not appear to be very sensitive to prey-stimuli (see above). This seems not to be very "adaptive" at first sight, except when potential prey would indeed usually occur in distinct patches. In the latter case the beetle may thus avoid to spend a considerable amount of time and energy in the search for isolated prey or small clusters. Now it will mainly be stopped by distinct and long-lasting (i.e. frequently emanated) prey-stimuli; in other words it will only abandon its random or directed walk when arrived in a dense and not very small cluster of prey, i.e. in a place of high "profitability" (Royama 1971) where it can feed for a reasonable time without spending much energy in walking.

OPTIMAL FORAGING

The above picture comes close to ideas developed in "optimal foraging theories" (for a recent survey see: Kamil and Sargent 1981). However, it must be noted in this connection that a kind of foraging behaviour that appears to be sensible or even "adaptive", needs not to be "optimal", not only in our case of polyphagous carabid beetles, but more in general in cases where "optimal foraging" is assumed. The only thing we know, is that the feeding behaviour apparently is sufficiently sensible to allow the pertinent populations to survive and reproduce. We don't know how much improvement might still be possible by a sophisticated manipulation of the gene pool (that might e.g. be realized by skilled artificial selection), let alone that we should know that none of the theoretically possible improvements is within the reach of natural selection. But only in the latter case we would be justified to call the behaviour "optimal" within the restrictions given by the gene pool. An actually "optimal" behaviour would also mean, that in fact evolution would have come to an end, and would have been reduced now to a marginal adjusting of an otherwise already fixed pattern, that can only be changed any-

more (but also improved?) by major mutations. My thoughts about evolution are quite different: as long as populations are present evolution will go on as it has always done, but because of its opportunistic nature this does not necessarily mean that the survival time of the populations concerned will be improved by it; many populations are little by little "manipulated" by natural selection into dead ends, but in others a new life tactic (Stearns 1976) may gradually be rigged up.

But let us return to the foraging behaviour of carabid beetles, which can thus better be called "effective foraging" instead of "optimal foraging". The partly still hypothetical picture we arrived at seems to indicate, that carabid beetles usually move from one rather dense cluster of potential prey to another, and that the distances between are generally covered by directed movement in an arbitrary direction, during which they are not very sensitive to prey-stimuli. This behaviour can only be a profitable one, of course, if the majority of available prey indeed occurs in rather dense clusters. But even if potential prey is more often clustered than not (and we are convinced that this is a rather common situation), this will not occur in all habitats and always to a sufficient extent, and moreover, it will probably not apply to all prey species in an always significant degree. In other words, the foraging behaviour of carabid beetles appears to suggest, that they can usually "allow" themselves to neglect many — not densely clustered — prey. Does this mean that there is plenty of food for polyphagous carabid beetles? I don't know, and I think that we can only say that apparently there is no absolute shortage of food (Andrewartha and Birch 1954), because they are unable — as a consequence of their foraging behaviour — to use all the potential food. On the other hand, egg production in the field is much lower than under comparable experimental conditions with plenty of food, as Van Dijk will show you. But in spite of the fact that this does not point into the direction of "optimal foraging", this is not an exceptional situation: according to White (1978) the abundance of many — if not most — animals (both herbivore and carnivore) seems to be limited by a relative shortage of food, because not all the food is equally suitable, equally available, or otherwise not "optimally" used. As a result of this the abundance of many animal species seems closely to follow the fluctuations of the food resources, in spite of the fact that in many of such cases only a small part of the resource is utilized; Dempster and Pollard (1981) give some very clear examples of this phenomenon. In these cases the food shortage is not only relative, but also extrinsic, i.e. it is imposed upon the predator population from outside as a change in availability.

A convinced neo-darwinist will not be charmed by the above picture. He will object: "if indeed only a small part of the resource is utilized, each carabid beetle that succeeds in using somewhat more of it will be favoured by selection by an increase of its egg production; hence, such a situation cannot persist very long and can therefore hardly be expected to be encountered." There are several reasons why such an objection need not be valid.

The most important reason is that this attitude of the average neo-darwinist is highly deterministic, and that matters change appreciably if we try to take into account the enormous variability in space and time of all the elements that operate in the process

feeding-reproduction in the field. First of all: even under constant conditions the egg production of individual females of the same age and from the same population appears to be very different (Van Dijk 1979a and b) with the standard deviation of egg production between females being of the same magnitude as the mean, i.e. this variation is even greater than according to a Poisson distribution, and will thus most probably already throw into the shadow most kinds of environmentally induced variation in egg production. Next, the generally high level of variation in space and time of abiotic factors (e.g. weather), structural properties of the habitat and distributions of potential prey will include a high chance that an individual's advantage at one place and/or at one time will turn into a disadvantage at another place and/or at another time. As there is some circumstantial evidence that significant individual differences in egg production may go with corresponding differences in metabolic rate it may even be hypothesized that in this way the risk not to get enough food to keep up reproduction over the whole season may be spread over females with different metabolic needs (cf. Den Boer 1968a, 1971), in that the lower the metabolic rate the more time it will take before the female becomes hungry, and possibly also before it becomes "spent" prematurely because of food shortage; but the price for this small advantage (generally only few females become already "spent" during the reproductive season) will be an overall lower egg production. Therefore, at the moment this is only speculation at my own responsibility.

Preying highly effectively (or even "optimally") in a heterogeneous and ever changing environment on very different arthropods in fact would ask for nearly unlimited learning capabilities, i.e. for a highly developed central nervous system which will go far beyond the modest possibilities of carabid beetles. Therefore, insects generally answer environmental challenges (evolutionary spoken) with a rigid but none the less often surprisingly effective behaviour. It could therefore already be expected that carabid beetles would show a rather simple kind of foraging behaviour which will appear to be effective on the average, a kind of rigid behaviour in which only one thing will be about optimized (or even maximized), viz. the chance that under feeding conditions which highly vary both in space and in time sufficient energy can be saved to survive and to reproduce. In other words: better a just sufficient reproduction in many years and at many places than a very successful reproduction in only a few years and at few places but no success in most years and at most places. Such an averaged behaviour will have to be a compromise between the amount of energy and time that can be invested in walking and searching and the thus resulting reduction of the unpredictability of the amount of energy that might be saved from the food. It may be expected that very different distributions of available prey will result in different levels at which this compromise is realized. As Mols and Stouthamer try to construct a model which predicts the walking pattern from the prey distribution via our knowledge of the foraging behaviour, it seems possible once to say something sensible about prey distributions if the walking pattern is known, or vice versa. It is therefore a pity that at the moment we cannot even guess how much energy is used in walking and searching, and thus which part of the potential egg production will be lost by it under certain field conditions, the more so since egg production is already provisionally incorporated in the above model and thus only "awaits"

its net energetic evaluation. In connection with the latter point: we will also have to estimate the differences in quality between different kinds of potential prey. Van Dijk will show you that the carabids studied by him produce much more eggs on maggots as a food than on mealworms. This also brings into the picture the relationship between possible preferences of the beetles and the quality of the food. In spite of "optimal foraging theory" this need not necessarily be a simple relationship, such as: prey of a higher quality will be preferred more. How will possible preferences work out in the field? Will a hungry beetle actually neglect a dense cluster of a less preferred prey with the risk that it will not or not easily find a suitable cluster of a more preferred prey, or will it only feed shorter in a cluster of a less preferred prey than in a cluster of a more preferred one? All questions that will have to be answered if we want to understand the foraging behaviour of carabid beetles in terms of the dynamics of populations. And most difficult of all: we will have to study the actual distributions of both potential and available prey in the field to a sufficient extent to be able to construct artificial distributions (both in experiments and in the computer) that do not deviate inadmissibly from common field situations, so that we can estimate the numerical consequences of different kinds of distribution.

FOOD AND THE DYNAMICS OF CARABID POPULATIONS

A reader who has followed me so far may ask: "Why trying to study the foraging behaviour and dynamics of polyphagous predators if this appears to give so many difficulties? Why not concentrate on monophagous predators and thus avoiding problems such as different qualities of different prey, different and probably even changing preferences, different spatial distributions of different prey?" The answer is that polyphagous predators are more common in nature than monophagous ones, and, that exactly the mentioned difficulties may have to do something with the appealing but recalcitrant problems around the "stability of nature" (which by many ecologists is thought to be a "balance of nature"; but see: Ehrlich and Birch 1967; Den Boer 1968). Moreover, as soon as we try to bring experiments on and modeling of more simple predator-prey relations closer to reality we get into comparable difficulties (see e.g. Murdoch 1979), and we therefore prefer to tackle these problems more directly and thus most generally. However, this does not alter the fact, that we are still rather far from an actually quantitative understanding of the part played by foraging in the dynamics of polyphagous carabid populations.

Sometimes the most fundamental features of a complicated situation come distinctly to the front under extreme conditions. In our case we may wonder what will be the population dynamical effect to a carabid species of the sudden disappearance of the most abundant one among the prey available, or the other way round, what will be the effect of such an increase in abundance of one of the kinds of prey that it outnumbers all other available prey? It may be expected that such extreme situations will teach us something about the influence of major changes in the size of the food supply, supposing of course,

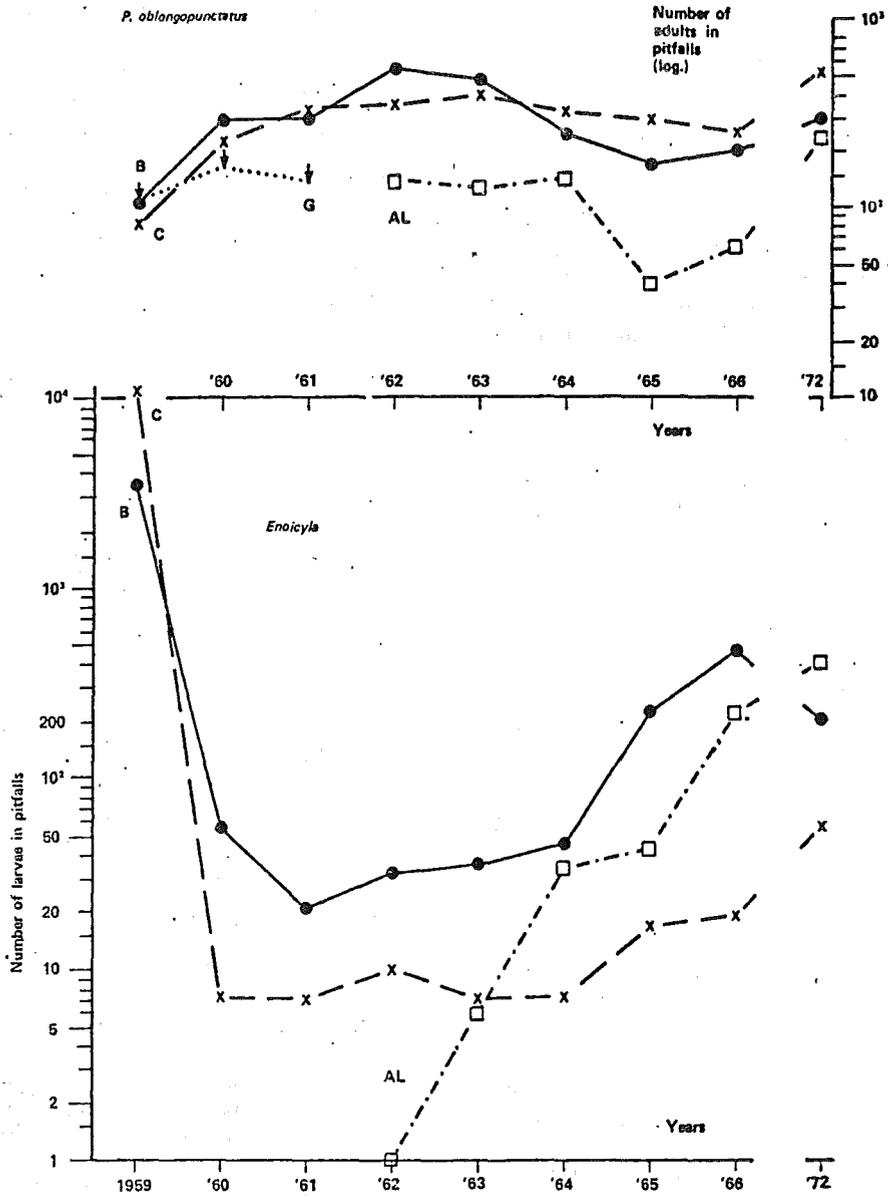
that even polyphagous predators will show some degree of dependence on extreme changes in the abundance of some kind of prey.

The first situation, the sudden collapse of the population of a very abundant potential prey, occurred at the very start of my investigations in Wijster. In the spring of 1959 very high abundances of the larvae of the caddish fly *Enoicyla pusilla* (Trichoptera, Limnophilidae) were established in the litter of two moist forests (B, C) where carabid beetles were sampled with standard sets of pitfalls (Fig. 1, below). Though the exact densities were not estimated there could be little doubt that these larvae greatly outnumbered most — if not all — other arthropods in the litter (which otherwise seems not to be a very exceptional situation: Rathjen 1939; Van der Drift 1963): in our pitfalls were caught 10,959 ind. (C) and 3387 ind. (B) respectively of these only slowly moving animals, against only 490–500 collemboles and still less mites, isopods, diplopods, etc. As was nicely demonstrated to us by Szyszko in 1978 *Enoicyla*-larvae are readily attacked and consumed by the adults of *Pterostichus oblongopunctatus*, which is not only by far the most abundant carabid species in our moist deciduous forests (see e.g. Den Boer 1968b), but which also reproduces when the fullgrown larvae of *Enoicyla* can easily be encountered in the litter. As a consequence of the dry summer and autumn of 1959 recruitment of *Enoicyla* nearly completely failed (see also: Van der Drift 1963), and in the spring of 1960 only very few larvae were captured in our pitfalls (7 in C, 55 in B Fig. 1, below). It was expected that the disappearance of such an abundant food supply would be reflected in the dynamics of *Pterostichus oblongopunctatus*. Nothing of this kind was observed, however: in 1961 and 1962 the numbers were not lower than in 1960, while the increase in catch-numbers of *Enoicyla*-larvae in AL was not paralleled in the numbers of *P. oblongopunctatus* (Fig. 1).

This independence of the numbers of *P. oblongopunctatus* from the abundance of *Enoicyla*-larvae seems to indicate that in the absence of *Enoicyla*-larvae the adults of *P. oblongopunctatus* will feed on other arthropods to about the "normal" extent, i.e. the food resources are apparently not limiting the numbers of *P. oblongopunctatus*. As we did not measure egg production in the critical years (1959–1961) it can also be supposed, however, that egg production is independent of recruitment (e.g. because of great and highly unpredictable larval mortalities) so that a possibly much higher egg production in 1959 than in following years would not necessarily have influenced the numbers of *P. oblongopunctatus*. It may even be supposed that the mortality among the

Figure 1. Successive year-catches in the same pitfalls of *Pterostichus oblongopunctatus* and its potential prey — *Enoicyla pusilla*

Number (log) in pitfalls of adults of the carabid beetle *Pterostichus oblongopunctatus* (above) and of larvae of the caddish fly *Enoicyla pusilla* (below), a potential prey of *P. oblongopunctatus*, in three remnants of old, moist, deciduous forest in Drenthe (The Netherlands): B, C and AL. To support the independence of the numbers of *P. oblongopunctatus* from those of *Enoicyla* still more also the three succeeding year-catches of *P. oblongopunctatus* in a dryer, deciduous forest G, in which *Enoicyla* does not occur, are added (above).



larvae of *P. oblongopunctatus* is negatively density-dependent (e.g. by cannibalism), so that a supposedly much higher egg production in 1959 merely resulted in a higher larval mortality as compared with following years. But let us leave this world of speculation, and save ourselves by restricting ourselves to establishing that the dynamics of *P. oblongopunctatus* are not influenced by the disappearance of an apparently available and highly abundant food resource.

A probably comparable case is found in the relationship between the dynamics of *Calathus melanocephalus* and the abundance of the larvae of the heather beetle, *Lochmaea suturalis* (Coleoptera, Chrysomelidae). The heather beetle, which feeds on the small leaves of *Calluna vulgaris*, shows a spectacular abundance cycle: each 5 or 6 years (at least at Kralo Heath) the abundance of *Lochmaea*-larvae is so high that in most places large patches of heather are severely damaged and the remaining leaves have discolored into brownish: (Fig. 2, above). The larvae of *Lochmaea* are then forced to leave the overcrowded plants and to look for still undamaged ones. Because of this during July and August of a pest year high numbers of these larvae are moving over the soil surface

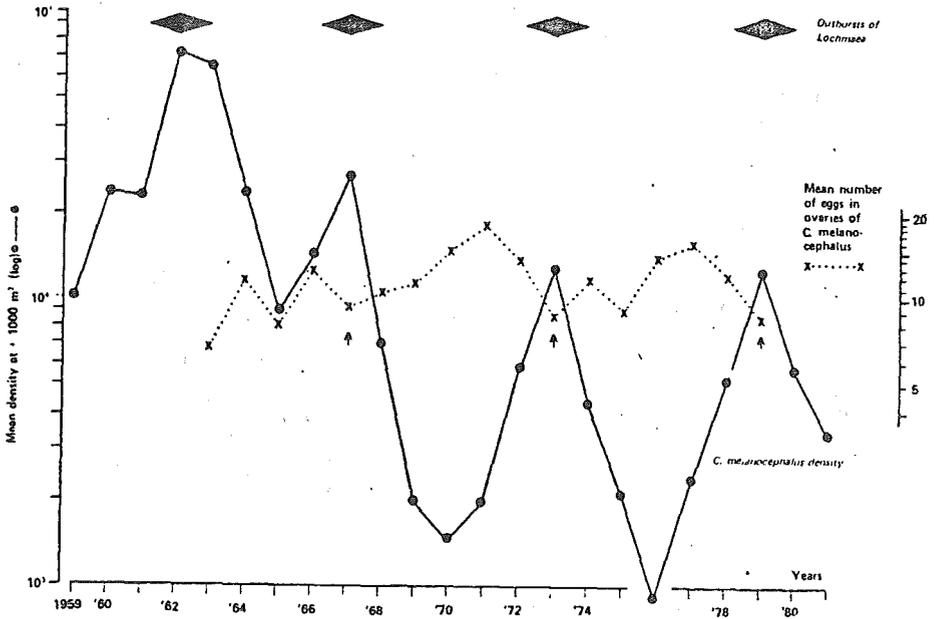


Figure 2. Relationship between the occurrence of potential food — prey and density and reproduction of predator — *Calathus melanocephalus*

The occurrence of abundant potential food, viz. the larvae of the chrysomelid beetle *Lochmaea suturalis* during an outburst (at the top of Figure), and the density (year-catches in pitfalls) resp. amount of reproduction (eggs in ovaries) of the carabid beetle *Calathus melanocephalus* at Kralo Heath, Drenthe (The Netherlands); correlation mean density/m² — mean number of eggs/female. $\rho_s = -0.6667$ ($P=0.0076$, two-sided), Model II-regression (Bartlett): eggs/female = $13.2117 - 0.16297 \cdot \text{density/m}^2$.

and are conspicuously present in our pitfalls. They are an easy prey then for the adults of *Calathus melanocephalus*, by far the most abundant carabid species on Kralo Heath which reproduces there at that time of the year. Indeed, the adults of *C. melanocephalus* do not despise *Lochmaea*-larvae, what is also mentioned by Van der Dries and Helmer-Kraaijenbrink (undated report), though we doubt whether it is a highly preferred prey. After an outburst during many years *Lochmaea* is remarkably sparse at Kralo Heath, whereas a new outburst is built up very rapidly, usually in only a single year (see e.g.: Appendix 8 in the report of Van der Dries and Helmer-Kraaijenbrink where our pit-fall catches of larvae and adults from 1959 up to and including 1966 are given). This pattern of overall low densities which are broken through periodically within a very short time by outbursts that disappear again suddenly, is also found in Germany in a number of *Lepidoptera* which feed on pines (see e.g.: Schwerdtfeger 1968: 305–313), and which is called "gradation" (both English and German).

It seems reasonable to suppose that during an outburst of *Lochmaea* the population of *C. melanocephalus* will experience a significant increase of its food resources, and will thus be able to realize a higher egg production than in other years. But to our surprise exactly in outburst years of *Lochmaea* the egg production of *C. melanocephalus* is distinctly lower than in the years immediately preceding or following an outburst (N. B.: in *C. melanocephalus* the number of eggs in the ovaries gives a reasonable relative estimate of egg production: Van Dijk 1979b: Fig. 2). As these outburst years – remarkably enough – are also the years with highest densities of *C. melanocephalus* (Fig. 2) these low egg productions per female result in a significant negative correlation between density and mean egg production, which again led Baars and Van Dijk (1984b) to suppose that egg production might be density dependent, e.g. because at high densities a significant competition for food would occur. Though such an hypothesis can neither be rejected nor corroborated, of course, without a rather detailed knowledge on the overall changes of the availability of food in the course of the years, the present data seem not at all to support such an hypothesis*. But how to explain this curious decrease of egg production in *C. melanocephalus* in outburst years of *Lochmaea*? Van Dijk (pers. comm.) suggests that *Lochmaea*-larvae could represent a low quality kind of food for egg production (e.g. because of toxins in the haemolymph of the larvae), a kind of food, on the other hand, that can hardly be avoided during outburst years, even if it is not a preferred food. Hence, as in an outburst year *Lochmaea*-larvae apparently highly outnumber other prey the beetles are forced, so to say, by their rather simple foraging behaviour (the majority of prey clusters will contain *Lochmaea*-larvae) to feed frequently on these larvae. This interesting hypothesis, which significantly withdraws from ideas about "optimal foraging", again underlines the importance to study the different qualities of different kinds of food for the reproduction of polyphagous predators.

* Note, however, that the lowest egg production measured (in 1963) coincides with the highest density of *C. melanocephalus*, and that in that year the heather beetle was very sparse (see Appendix 8 of Van der Dries and Helmer-Kraaijenbrink).

These two cases of the possible relations between the numbers of some carabid species and the sometimes extreme abundance of some potential prey species also seem to suggest that carabid beetles apparently cannot effectively reduce the density of an abundant prey: the dramatic crash of *Enoicyla pusilla* in 1960 was undoubtedly caused by abiotic factors (see above) but not by the foraging of *P. oblongopunctatus*, and the periodic collapses of *Lochmaea suturalis* can safely be attributed to severe overcrowding of the *Calluna*-plants over large surfaces, whereas the rapid build up seems to occur under the influence of certain abiotic factors (Van der Dries and Helmer-Kraaijenbrink), but neither will have been significantly affected by the foraging behaviour of *C. melanocephalus**. But as so often in ecology also these examples cannot be generalized, and be considered representative for many or even most kinds of potential prey of carabid beetles.

To show this I will now discuss a counterexample that is burrowed from the work of Varley and Gradwell on the population dynamics of the winter moth (*Operophtera brumata*) in Wytham Woods: Varley, Gradwell and Hassell (1973, 123–125). When studying the different winter moth mortalities with the help of key-factor analysis they found that the heavy pupal mortality was strongly density dependent: the higher the initial pupal density the greater the proportional mortality (Varley et al. 1973: their Fig. 7.4). By performing some experiments in the field they discovered that this mortality was due to predation by polyphagous predators: shrews and the predatory beetles *Pterostichus madidus*, *Abax parallelepipedus* and *Philonthus decorus*. More than half of this mortality could be ascribed to the predatory beetles, 38% to the carabids, and 30% to the spring breeding staphilinid *Philonthus decorus* (East 1974), the larger larvae of which successfully attack winter moth pupae (Kowalski 1976). Varley, Gradwell and Hassell (1973) did not observe, however, the expected delayed density dependent reaction of the *Philonthus* density, though Kowalski (1976) is inclined to attach some value to the indications of a "numerical response" in the autumn densities of *Philonthus*. He supposes that the latter is caused by a better larval survival with higher densities of winter moth pupae, but this effect is nullified again by the "over winter loss" of young adults which is negatively correlated with density.

Be that as it may, also in this case the overall dynamics of the polyphagous predator seem hardly to depend on the numerical changes of its most important prey. In fact, the predator population is more stable than could be expected from its contribution to the numerical stabilization of this prey. According to East (1974) this stability is only indirectly due to the "over winter loss" in *P. decorus* (Kowalski 1976), and more directly to the movements of the adults. Both during the latter half of the breeding season and throughout autumn adults of *Philonthus* tend to aggregate under trees where the density of winter moth pupae is high. Because of this more eggs will be laid in dense clusters of pupae than in less dense ones, with a higher predation by larvae in denser clusters as a result. In autumn also more young adults will thus emerge in dense clusters of pupae,

* The remarkable pseudo-cyclic fluctuation pattern of *C. melanocephalus* itself (Fig. 2), which will closely resemble the "gradation" of *Lochmaea suturalis*, is also closely connected with periodic changes in abiotic factors (Baars and Van Dijk, 1984a).

and it may be supposed from the data of East (1974) that even a further concentration of young adults might occur in such clusters. This will again accentuate the "overpredation" of dense clusters, and at the same time it will result in high numbers of young adults overwintering in dense clusters of winter moth pupae. During winter shrews will not only prey upon winter moth pupae in such clusters, but also on the overwintering adults of *Philonthus* (East 1974). Since the beetles had already highly concentrated in dense clusters of pupae a similar kind of behaviour by the shrews could easily result in "overpredation", and thus in the "over winter loss" as mentioned by Kowalski (1976).

THE BIOLOGICAL SIGNIFICANCE OF POLYPHAGOUS PREDATORS

The work on the winter moth showed already that polyphagous predators like carabids and e.g. *Philonthus* may be the cause of heavy mortality in an insect that sometimes is noxious in forests. Also Basedow (1973) found that carabid beetles can take a heavy toll of some insects that are injurious in cereal fields. Still more important is, that at least in the case of the winter moth polyphagous predators seemed to be the only mortality factors that possibly "controlled"* high densities of the studied population to some extent. Apparently there are good reasons to pay more attention to polyphagous predators when planning programs for biological control. This could already be a sufficient argument to study the foraging behaviour and the population dynamics of polyphagous carabid beetles. But there is more.

Why should polyphagous predatory beetles better "control" the density of the winter moth than a number of more specialized parasitoids (Varley, Gradwell and Hassell 1973)? As the density of many specialized predators (parasitoids included) highly depends on the density of the prey (host) with a delay of one generation (numerical response), in many cases they either "overdo" the job by eradicating first the prey and next itself, or "let escape" the prey when its density is growing rapidly. This is already known for a long time, and resulted in many failures of biological control; it was called the "risk from density-dependent factors" by Den Boer (1968a). This risk will be reduced (spread) if the predator also can utilize some kind of alternative prey, i.e. if it is less monophagous. It is then better capable to also keep its numbers at a reasonable level during periods of scarcity (or even absence) of its preferred prey, so that it is "ready" to resume predation as soon as its chief prey increases in numbers again. In other words, the density of the predator has become less dependent on that of its chief prey. From the viewpoint of "control" the best thing would even be if the density of the predator would be independent of that of its preferred prey, so that it could always switch over to its chief prey whenever this is "profitable". In fact we have thus "constructed" a polyphagous predator with a distinct preference for some noxious prey species. I guess that *Philonthus decorus*

* If only high densities are reduced in a more or less density-dependent manner I prefer to use "control" instead of "regulation", since the latter is closely connected with ideas about a return to "equilibrium densities".

(and probably also *Abax parallelepipedus*; East 1974) in Wytham Woods will reasonably answer this picture, whereas it will be reserved to further investigations to decide whether *Agonum dorsale* and *Pterostichus melanarius (vulgaris)* in the cereal fields of Basedow (1973) will be following candidats. Other possible candidats may also be *Bembidion lampros* and *Trechus quadristriatus* as effective predators of the eggs of the cabbage root-fly (*Erioischia brassicae*) (Mitchell 1963; see also: Thiele 1977). Hence, among polyphagous predators we may expect a number of effective "controlling" agents.

This does not mean, of course, that we will always succeed in finding some carabid species (or other polyphagous predator) that will do the job, i.e. "control" a certain noxious insect. Many herbivorous insects dispose of effective mechanisms of defense, (e.g. toxins), and whereas many monophagous predators appear to be able to "answer" (evolutionary spoken) this by the development of new methods of attack, especially polyphagous predators will be much more hampered in such a situation. As far as possible polyphagous predators will learn to avoid such prey, as it is known to occur in many birds. For polyphagous carabids, however, the possibilities will be much more restricted in this respect: like a "searching image" also an "avoiding image" cannot be expected to last very long, and will have to be reactivated frequently. I told already, that we suppose that the adults of *Calathus melanocephalus* are severely hindered in this way by the presence of very high numbers of the larvae of the heather beetle.

However, if we are not only interested in the "control" of injurious insects, but more generally in the "stability of nature" most carabid species can be expected to play a significant part. Because of their foraging behaviour, that apparently can be characterized as feeding in a number of rather dense clusters of potential prey alternated by walking, it can be expected that some prey that has increased more than others often will be preyed upon proportionally more; not only since there will be more dense clusters of such a prey, but also because more carabid individuals will be "caught", so to say, in such clusters to feed there for some time. The nice story of the predation of winter moth pupae in Wytham Woods can be considered a clear example of this principle. Therefore, I like to pose the hypothesis, that carabid beetles, like most other polyphagous predators, will usually "eat away", so to say, the peaks of abundance of their potential and available prey, by which they will significantly contribute to the keeping down of the numbers of many arthropods of the surface layers of the soil. But if other conditions are unusually favourable for some kind of prey (e.g. weather conditions) density may increase so rapidly that also polyphagous predators cannot "control" it, and density will rather suddenly be pushed up and sometimes reach or even overshoot carrying capacity. I guess that many of the "gradations" in herbivorous insects originate in this way; whether or not this also applies to the "gradation" of the heather beetle remains to be investigated.

If more predator species (in the broad sense, i.e. also parasites, parasitoids etc., included) prey upon the same animal population this will not only contribute to a comparatively low level of abundance but — paradoxically — may also favour the survival time of the prey population. The latter results from the fact that a greater number of "factors" influencing density will increase the chance (spreading of risk: Den Boer 1968a) of a significant reduction of the range of density fluctuations (Reddingius and

Den Boer 1970), and this reduction of the range of fluctuations often appears to be more important than the simultaneously lowered density level. This principle is nicely illustrated by two laboratory populations of the azuki bean weevil (*Callosobruchus chinensis*) which were bred during 68 generations by Utida (1957), the one with only a single species of parasitoid, the other with two species. Den Boer (1971: his Fig. 8) showed that in the case with two species of parasitoid not only the abundance level was lowered with more than 50% as compared with the culture with a single species of parasitoid, but also the range of density fluctuations was reduced with about 30% and the violence of density fluctuations was even reduced with more than 50%. Together these effects result in a more than two times higher expectation of the survival time in the case with two parasitoid species, as could be shown by simulating and comparing the patterns of density fluctuation of these two populations with the help of the computer.

As in all kinds of natural habitat and in all times of the year a number of polyphagous predators (together with a number of more monophagous ones) will be foraging, most animal species can be expected to be influenced in the above ways; abundance levels will be kept relatively low and densities will fluctuate within rather narrow limits. Therefore, I hypothesize that "the stability of nature" mainly results from predation in the broad sense, and that such stable natural situations will thus be characterized by surprisingly high numbers of species that occur in only low numbers (see also: Connell 1971). The latter phenomenon was already well known to Darwin: "Rarity is the attribute of a vast number of species of all classes, in all countries" (1859; 319). That is why we suppose that studying the foraging behaviour and the population dynamics of carabid beetles is studying some of the processes that significantly contribute to the "stability of nature".

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