

MOTIVATION AND WALKING BEHAVIOUR OF
THE CARABID BEETLE *PTEROSTICHUS*
COERULESCENS L. AT DIFFERENT
DENSITIES AND DISTRIBUTIONS OF THE PREY.
A PRELIMINARY REPORT

P. J. M. MOLS

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

Communication no. 203 of the Biological Station, Wijster

ABSTRACT

In this study it is tried to analyse and partly to quantify the most important factors which govern the predatory and walking behaviour of the polyphagous carabid beetle *Pterostichus coerulescens* L. in relation to the distribution of the prey. Hunger, defined as the gut capacity minus the actual gut content is assumed to be the most important factor influencing the behaviour of the beetle. Hunger is determined by ingestion and digestion but its effect is also influenced by the quantity of the fatbody and by the ovarial activity. To integrate the most important factors affecting the hunger of the beetle a computer model is constructed according to the state variable approach (DE WIT & GOUDRIAAN). With help of this model the 'motivational state of the predator' can be computed continuously. An outline of the components of predatory and walking behaviour is given. The walking patterns can be divided roughly into two types: a random walking pattern, and a walking pattern with a high frequency of turning movements following feeding, the latter of which is similar to the pattern described in literature for many insect predator and parasitoid species.

1.1. INTRODUCTION

Prey populations may occur aggregated in different places depending on their preferences (SOUTHWOOD, 1966). There are strong indications that predators can react to this by concentrating in the most profitable sites (ROYAMA, 1970, 1971; COOK and HUBBARD, 1977; HASSELL et al., 1976). The predation risk of a clumped prey would thus be higher than is expected with a homogeneous prey distribution.

Three processes have been proposed to explain this phenomenon. The first process is, that a sensory detection threshold is most likely to be exceeded when preys are encountered in locally high densities (KREBS, 1973). The second explanation is, that many predators decrease their moving speed after feeding, simultaneously with an increase of the rate of turning (FLESHNER, 1950; BANKS, 1957; DIXON, 1958; MITCHELL, 1963; MURDIE and HASSELL, 1973; EVANS, 1976; HASSELL and MAY, 1974). This

behaviour should be an obvious adaptation to hunting aggregated prey, by which encounters with prey are expected to increase. The third process that is often proposed, is the development of learned searching patterns, such as specific search images, which appears to proceed more rapidly when preys are clumped (TINBERGEN, et al, 1967; CROZE, 1970). The latter occurs especially in vertebrates because of their high learning ability.

A higher predation of clumped prey will thus result only, of course, when the prey has not developed an effective group defence or warning behaviour.

1.2. THE AIM OF THE INVESTIGATION

Our studies are concentrated on the following questions: Does a polyphagous predatory beetle like *P. coerulescens* change its walking behaviour depending on the prey distribution pattern, and does this result in a change of the predation rate?

2.1. PREDATOR

Pterostichus coerulescens (L.) is chosen for this investigations as it is a polyphagous predator whose autecology has already been studied several times (KREHAN, 1970; VAN DIJK, 1979). The beetle is easy to manipulate and is abundant around the Biological Station at Wijster where our experiments are carried out. It lays its eggs in the spring; these hatch without dormancy after which the larvae grow up in summer, pupate in late summer and moult into adults in autumn. Hibernation occurs in the adult stage. The beetle is usually active during the day (GREENSLADE, 1963; LAUTERBACH, 1964). The species is abundant in moist-dry heathlike vegetations but also lives in more weedy vegetations. It is macropterous but the wings are generally small and are usually unsuitable for flying. Thus walking is the normal way of movement.

2.2. PREY

The studies are restricted to preys which do not show any kind of group defence.

3.1. APPROACH OF THE PROBLEM

To gain insight into relations between the predator and its preys answers to the following questions have to be found:

- a. Which are the dominant components of behaviour of the predator in the predation process?
- b. What is the 'motivation' of the predator?

- c. Which relationships exist between the motivation and the relevant components of behaviour of the predator?

As soon as we have the information on the motivation, on the relevant components of behaviour and on their interactions, we can integrate this knowledge into a model. Such a model describes the sequence of events at the level of the input information, but can also have a predictive value at a higher level. With the help of this model we can try to simulate the behaviour of the predator with several densities and distributions of the prey from its behaviour with respect to a single prey individual. Comparing the model output with experimental results will increase our insight into the processes involved, and thus we hope to understand the interactions between predators and prey in the field.

3.2.1. The state variable approach

The models are constructed according to the state variable approach (DE WIT & GOUDRIAAN, 1978). This implies that the state of the system at any particular time can be expressed quantitatively and that the changes in the system can be described in mathematical terms. In state determined models, state variables, driving or forcing variables, rate variables, auxiliary variables and output variables can be distinguished.

State variables characterize and quantify all properties that describe the current state of the system. Examples of state variables are amount of biomass, number of animals, amount of food, water content, temperature of the soil, and so on. The values of all state variables have to be known at the onset of simulation. In mathematical terms they are quantified by the contents of integrals.

Driving or forcing variables are those that are not affected by processes within the system but characterize an influence from outside. These may be macrometeorological variables, the amount of food added in the course of time, and so on. It should be realized that depending on the boundaries of the system to be simulated, the same variables may be classified either as state or as driving variables.

Rate variables quantify the rate of change of the state variables. Their values are determined by the state variables and the driving variables according to rules formulated from the knowledge of the underlying ecological, physiological and physical processes. These processes may be so complicated that the calculation process becomes much more lucid when use is made of properly chosen intermediate or auxiliary variables.

Output variables are the quantities which the simulation produces for the user. Sometimes they are state variables, sometimes rates and sometimes auxiliary variables that may be calculated especially for this purpose.

3.3. SENSITIVITY ANALYSIS

To determine the relative importance of the rates, the parameters and the initial

values, and to evaluate structural changes in a model, a sensitivity analysis is executed. Concerning rates, parameters and initial values such a sensitivity analysis consists of varying the values within a certain range and comparing the relative changes of the values with the relative changes in the output of the model. A sensitivity analysis on structural changes consists of eliminating parts of the program and evaluate the influence on the output.

This is done to validate the model concept we have in mind. If the influence of a certain parameter input or structural change is comparatively small a further analysis in that direction may be delayed, but if the influence is great, the features of these parameters or input should be analysed thoroughly. The result of such an analysis should be a guide-line for further experiments and programming.

Finally the output of the model has to be compared with the results of realistic field experiments in order to estimate the explanatory value of both the input data and the structure of the model.

4.1. MOTIVATION OF THE PREDATOR

In HOLLING's (1966) model of the mantid *Hierodula crassa* the motivation for feeding behaviour is hunger defined as the degree of emptiness of the gut. Hunger increases through the combined action of assimilation and defecation, and declines during feeding approaching a minimal value when the gut is filled completely. Feeding behaviour is governed by the hunger level in which thresholds for different components of behaviour may be distinguished, such as the search, pursuit, capture and consumption of the prey. FRANSZ (1974) considered the satiation level, which is opposite to hunger, of the predatory mite *Typhlodromus occidentalis* to be the driving force for its behaviour. In other investigations it has also been shown that the satiation level of predators is a factor which significantly influences both the predation activity and the preference for different prey species (RABBINGE, 1974; JOHNSON et al., 1975).

From these studies it was concluded that insight into the predation activity and the prey preference of the groundbeetle *P. coerulescens* could be obtained only when the predation process is studied in relation to the hunger level of the predator.

The hunger level may also be influenced by other physiological factors, for example the fatcontent of the body and the ovarial activity, and these on their turn may be regulated by hormonal and neural processes. Thus we have to integrate the most important factors that will govern the hunger level in what may be called 'the state of the predator'.

4.2. STATE OF THE PREDATOR

In fig. 1 a simple relational diagram of the feeding, digestion and reproduction of the

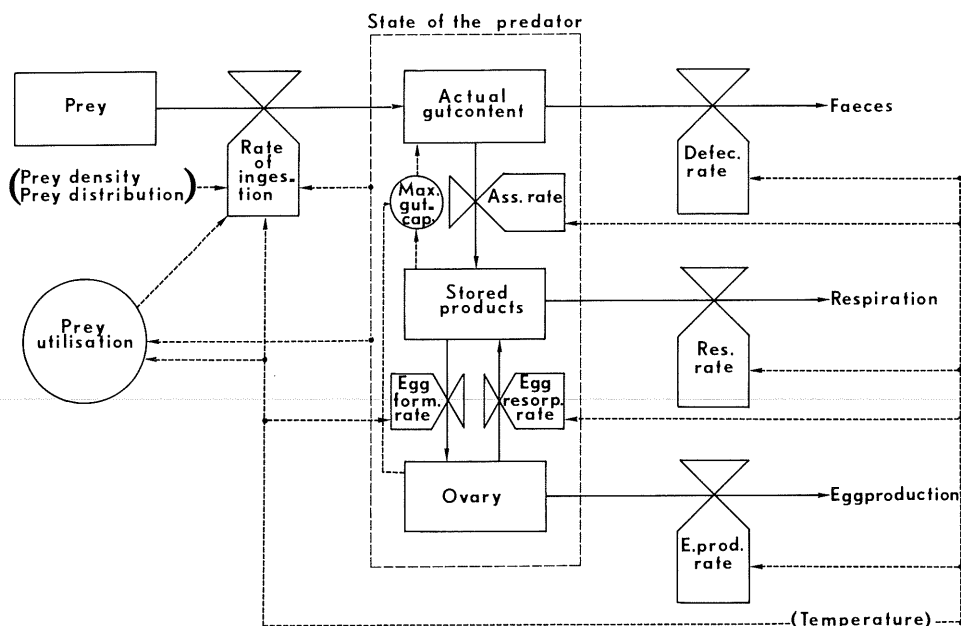


Fig. 1. Relational diagram of the state of the predator, according to the conventions of FORRESTER (1961).
 □ state variables, ⚗ rates of change, ○ auxiliary variables → flow of material, ----→ flow of information.

beetle is given. The predator consumes a captured prey at a certain rate: the ingestion rate. The food enters the gut until the beetle is completely satiated: the gut capacity. The indigestible parts leave the body by defecation and the remainder is assimilated. This assimilated fraction is partly respired or can be stored in the fatbody or be used for egg production. Hunger, for practical reasons it is defined as the gut capacity minus the actual gut content, is used as the motivation for the components of feeding behaviour. In this paper we will treat superficially the different factors that influence the hunger level of the predator. Other aspects will be published separately.

4.2.1. The ingestion rate

The ingestion rate of a captured prey depends on temperature, the hunger level of the predator and the prey species. Prey with thick and hard integuments require a longer handling time and thus the ingestion rate is decreased. The handling time becomes more important as a greater proportion of the predation time is spent on this activity.

4.2.2. The gut capacity

In the laboratory the gut capacity is measured, at 20°C, by weighing initially starved beetles before and after periodic feeding till satiation. Experiments in which young hungry beetles were fed sequentially (fig. 2) showed that the gut capacity is not a

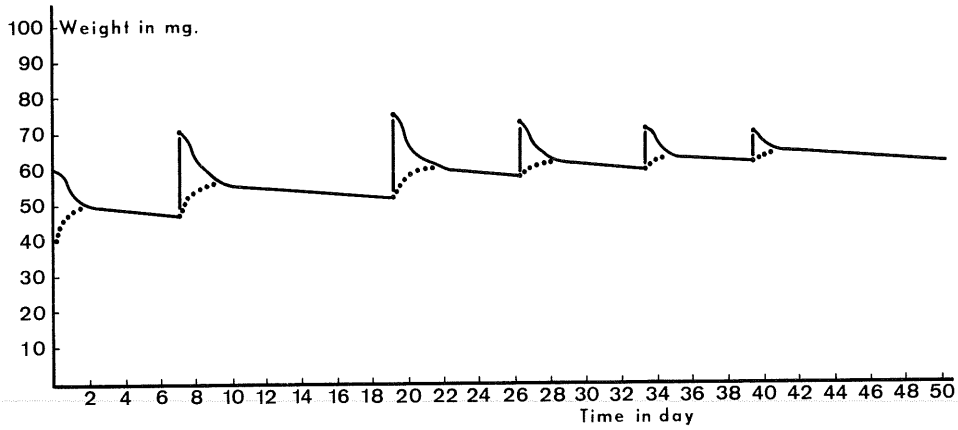


Fig. 2. Mean weight of 10 young female beetles fed periodically at 20°C.

constant but is greatly affected by the volume of the fatbody (fig. 3a + b).

The same relation is found to exist between gut capacity and the volume of the reproductive organs, especially the number of the eggs (fig. 4). In the breeding season the fatbody is reduced so that the abdomen of the females is nearly completely filled with eggs.

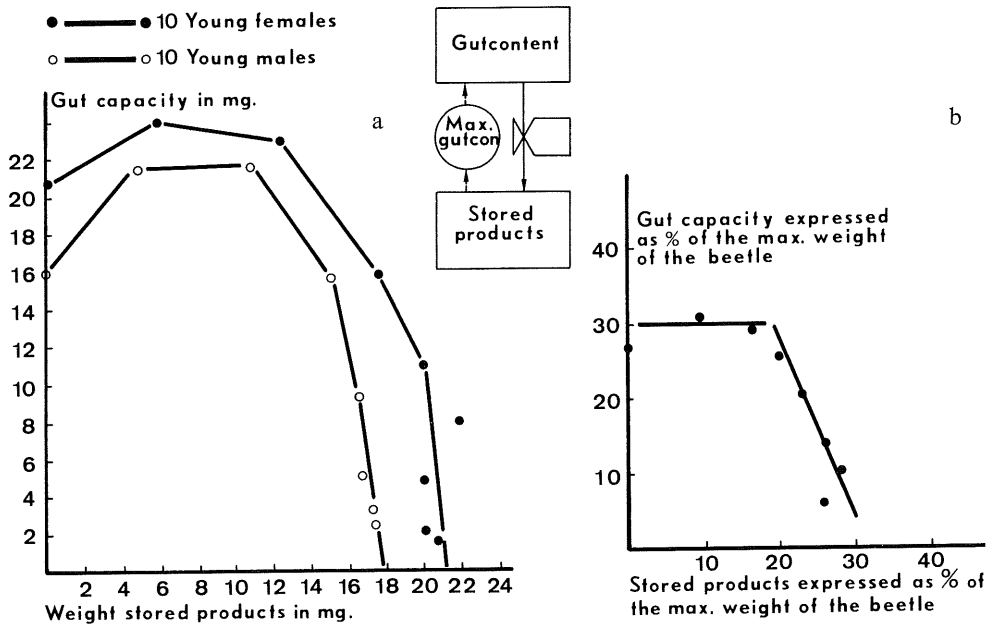


Fig. 3a, b. The relation between the gut capacity and the weight of stored products in young beetles expressed in (a) mg fresh weight and (b) as a proportion of the maximum weight of the beetle.

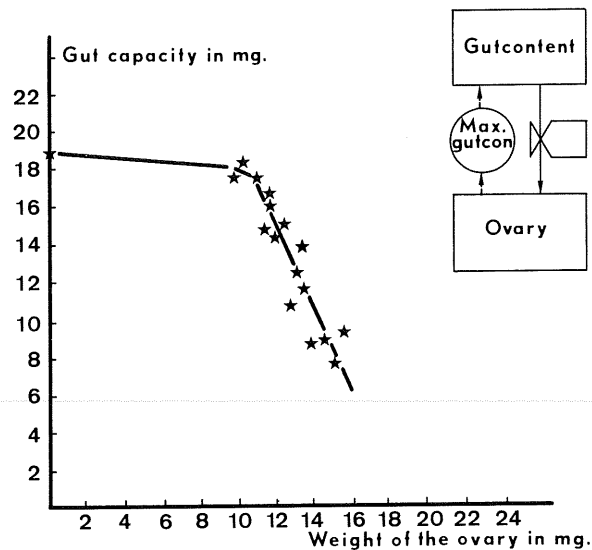


Fig. 4. The relation between the gut capacity and the weight of the ovaries during the reproduction period.

We assume that at the start of adult life the actual size of the crop will be the factor restricting the amount of food ingested, but when the fatbody or the ovarioles grow the available space in the abdomen is reduced and the crop cannot expand to its maximum size.

4.2.3. The digestion rate

The relative digestion rate is defined as the reciprocal of the mean residence time of the food in the gut. To measure this residence time hungry beetles are fed until they are satiated. After a few hours, depending on the temperature, the production of faeces starts. The period needed for the production of 50% of the total amount of faeces is used as the average residence time of the food in the digestive tract, assuming that the digestion rate is proportional to the actual gut content. An illustration of this process is given in fig.'s 5a + b which show the decrease in weight caused by defecation and respiration. The corresponding accumulation of faeces pellets is given in the same figure. The presented rates are highly dependent on temperature, therefore the experiment is done at a constant temperature of 20°C.

4.2.4. The assimilation rate

Calculation of the assimilation rate is only possible when the food utilisation by the beetle is known. The food utilisation is defined as: the increase in weight of the beetle after having completely digested the ingested food, corrected for by the weightloss caused by respiration during digestion, and divided by the total amount of food ingested. In our experiments with larvae of a blowfly (*Calliphora* sp.) as prey the food

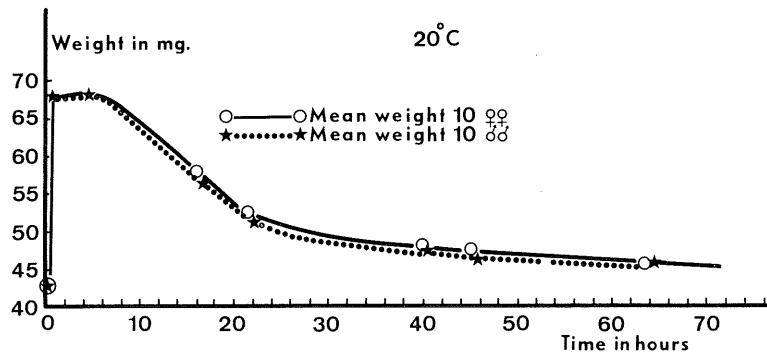


Fig. 5a. The loss in weight of the beetle by digestion and respiration.

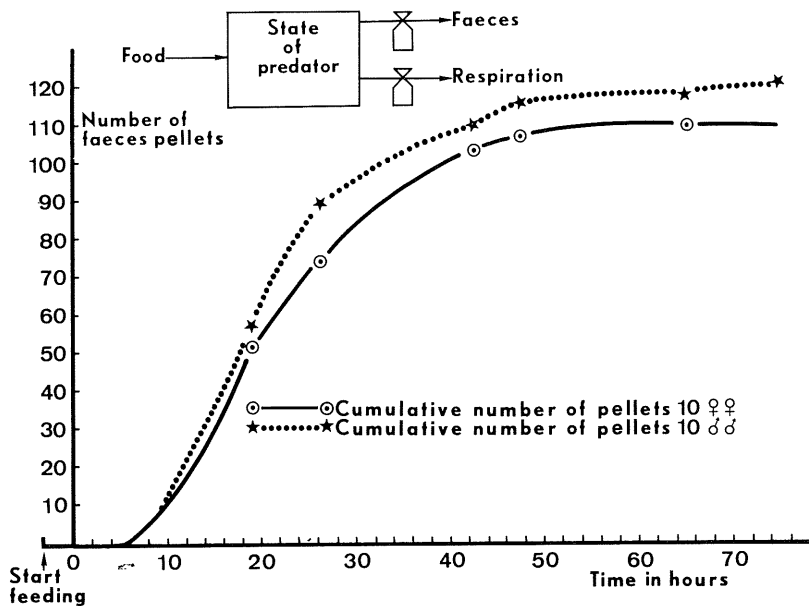


Fig. 5b. The production of faeces pellets after satiation and without further feeding.

utilisation is about 30%, but other more chitinous prey species may give very different results. The assimilation rate is thus assumed to be 30% of the digestion rate using blowfly larvae as prey.

4.2.5. The respiration rate

The respiration rate is affected by temperature and by the physiological stage of the beetle. Therefore, measurements were done both with young beetles, with beetles in hibernation and during aestivation, and with preovipositing females at several temperatures. Preovipositing beetles and young active beetles before hibernation have about the same respiration rate. The results of those measurements are shown in fig. 6.

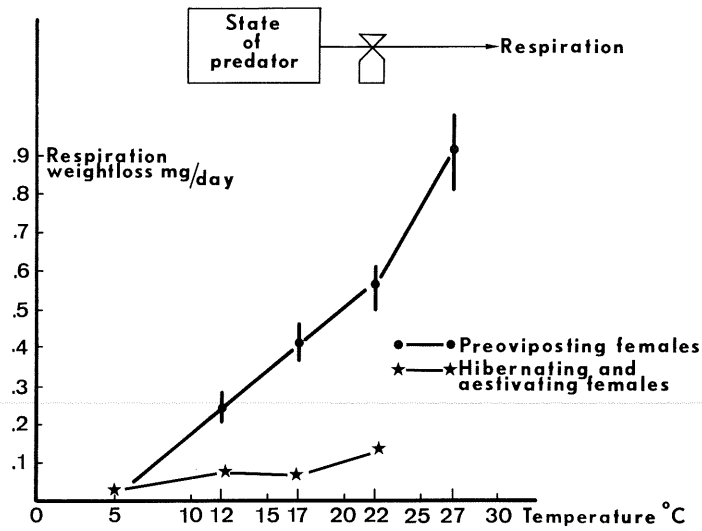


Fig. 6. Weightloss by respiration in relation to temperature.

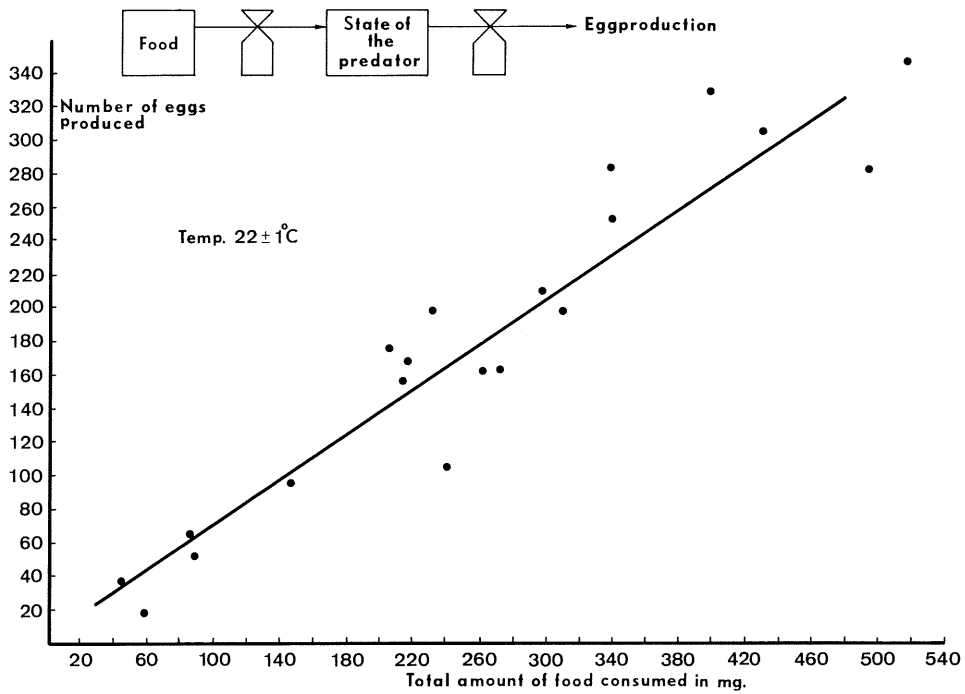


Fig. 7. Relationship between the total amount of food consumed during the reproduction period and the number of eggs produced.

Hibernating and aestivating beetles have a much lower respiration rate than active ones, due to a low level of activity and probably of other metabolic processes.

4.2.6. The reproduction rate

The reproduction rate depends on food consumption, but food consumption is greatly affected by the size of the ovaries in the abdomen of the beetle. Voluminous ovaries diminish the gut capacity and thus the food consumption, so that at each temperature the actual reproduction rate is greatly influenced by a negative feed back-loop dependent on food availability. For each quantity of available food and for each temperature a different equilibrium value for reproduction and food consumption occurs. The relation between egg production and food consumption at 22°C is given in fig. 7. The weight of one egg is about 0.5 mg.

The food conversion into eggs, using this egg weight, thus has an efficiency of about 30%. This is equal to the efficiency of the conversion of food into fat.

5.1. COMPONENTS OF THE BEHAVIOUR OF THE PREDATOR

Closely looking at a beetle when it walks in the field or in an artificial arena gives us a first impression of the most eye-striking components of its behaviour. An active beetle viviously walks around with a certain velocity. The velocity of this walking depends

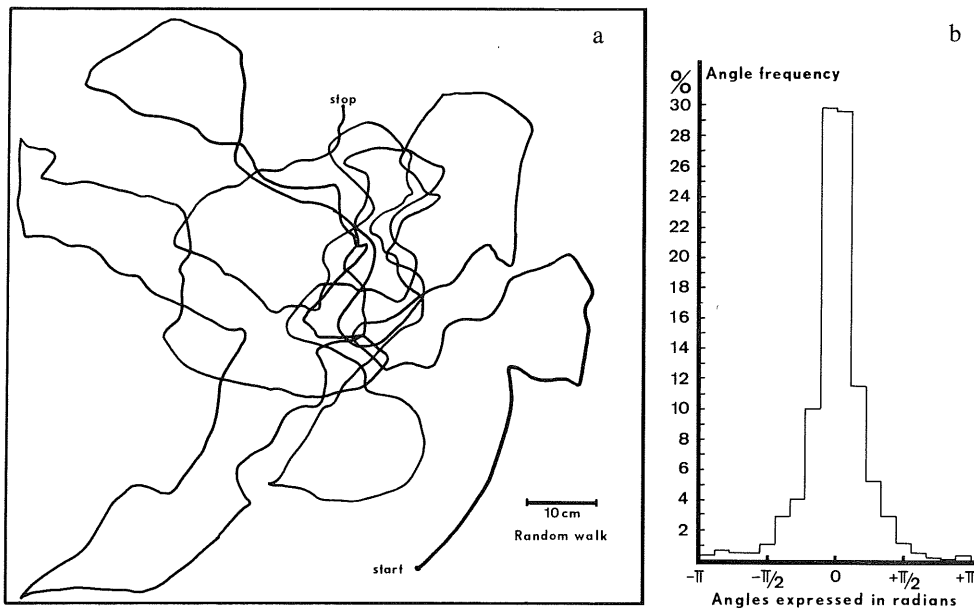


Fig. 8. (a) An example of a random walk pattern with (b) the angle frequency distribution, analysed with 1 cm steps. Total $N = 946$ steps $\sigma/\sqrt{N} = .012$.

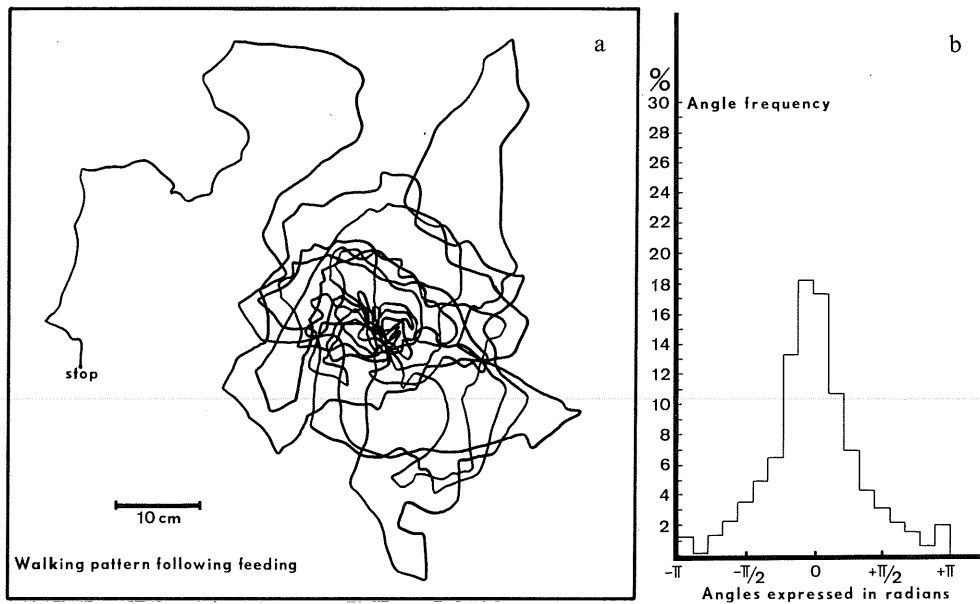


Fig. 9. (a) An example of a walking pattern following feeding with (b) the angle frequency distribution, analysed with 1 cm steps. Total of $N = 945$ steps, $\sigma/\sqrt{N} = .020$.

on external factors such as the surface structure, the vegetation, temperature, and also on the motivational state of the beetle.

Another aspect of walking is that it occurs in an almost continuously changing direction. The degree of change of these directions depends probably also on the above mentioned external factors, and on the motivational state of the predator. Both changing speed and direction result in walking patterns in which we can roughly distinguish two types. The first is a more or less random walking pattern as pictured in fig. 8a, b, whereas the second is characterized by a high frequency of turning movements following feeding (fig. 9a, b). If no prey is encountered during the latter way of walking it will gradually turn into the first type of walking. The duration of the second pattern has appeared to depend on the hunger level of the beetle.

Periods of walking alternate with periods of cleaning, resting, mating or ovipositing, usually at sheltered places under vegetation cover or in litter. The proportion of time spent walking is called the predator activity. A randomly walking beetle keeps its antennae stretched forward, whereas a searching beetle frequently bends the antennae downward and moves them over the surface. A potential prey may be perceived either by direct contact with the antennae or by visual perception. The latter implies a distance of perception which may vary with the hunger level of the predator (HOLLING, 1966), with the size of the prey, with the mobility of the prey, and with light intensity (BAUER, 1977; ERNSTING, 1978). The number of encounters with prey per time unit is called the encountering rate. An encounter is successful when it results in

killing of the prey. The number of successful encounters divided by the total number of encounters is thus named the success ratio. The success ratio is greatly affected by the hunger level of the predator (FRANZ, 1974; RABBINGE, 1976). Capturing a prey is followed by a period of handling the prey, which includes a period of feeding. The predation rate can be formulated as follows:

Predation rate = activity predator \times encountering rate \times success ratio \times coincidence in space.

The last factor accounts for the phenomenon that in vegetation predator and prey may walk on different horizontal levels and thus pass over or under each other.

Summarizing we can state that also in carabid beetles the most relevant components of predatory behaviour are influenced by the motivational state of the beetle, i.e. hunger.

6.1. FURTHER ASPECTS OF THE INVESTIGATION

The purpose of our study is to quantify the relevant components of predatory and walking behaviour in relation to the motivational state of the beetle. The walking behaviour is recorded with the help of a video-outfit (SABELIS, in prep.) and the walking patterns are analysed concerning the distributions of velocities and of angle-frequencies at different hunger levels. The success ratio, distance of perception, period of handling the prey are quantified in experiments with different prey species and at different hunger levels.

The results of these experiments are incorporated into a computer model which aims to simulate the walking and predatory behaviour. The simulated walking behaviour is based on the assumption that the direction of each step deviates from the direction of the previous step. The angle of this deviation is taken from an experimentally established frequency distribution. Autocorrelation is taken into account by way of a correction factor that is based on a detailed analysis of the autocorrelations (RUARDY, in prep.). With the help of this model we hope to predict the rate of successful encounters at different distributions of preys and thus to gain more insight into the effect of clustering of preys on their predation risk.

ACKNOWLEDGEMENTS

Thanks are due to Dr. P. J. den Boer and Dr. R. Rabbinge for the critical comments and stimulating discussions on the manuscript, and to several colleagues for reading early drafts of this paper, to Mr. A. Spee for drawing the figures and to Mrs. G. H. Weijenberg-Boer for typing the manuscript.

REFERENCES

- BANKS, C. J.: The behaviour of individual coccinellid larvae on plants. *J. Anim. Behav.* **5**: 12–24 (1957).
- BAUER, T.: The relevance of the brightness to visual acuity, predation, and activity of visually hunting ground-beetles (Coleoptera, Carabidae). *Oecologia (Berlin)* **30**: 63–73 (1977).
- COOK, R. M. and S. F. HUBBARD: Adaptive searching strategies in insect parasites. *J. Anim. Ecol.* **46**: 115–125 (1977).
- CROZE, H.: Searching image in carrion crows. *Z. Tierpsychol.* **5**: (suppl.), 1–86 (1970).
- DIJK, TH. S. VAN: On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus* L. and *Pterostichus coeruleus* L. (Coleoptera, Carabidae). *Oecologia (Berlin)* **40**: 63–80 (1979).
- DIXON, A. F. G.: A study of the searching behaviour of certain insects feeding on aphids. D. Phil. thesis, Oxford, 1958.
- ERNSTING, G.: Predation of springtails. Drukkerij Ernsting, Wageningen, 88 p., 1978.
- EVANS, H. F.: The searching behaviour of *Anthocorus confusus* (Reuter) in relation to prey density and plant surface topography. *Ecological Entomology* **1**: 163–169 (1976).
- FLESCNER, C. A.: Studies on the searching capacity of the larvae of three predators of the Citrus red mite. *Hilgardia* **20**: 233–264 (1950).
- FORRESTER, J. W.: *Industrial Dynamics*. MIT-press, Boston, 1961.
- FRANSZ, H. G.: The functional response to prey density in an acarine system. Pudoc, Wageningen, 149 p., 1974.
- GREENSLADE, P. J. M.: Daily rhythms of locomotory activity in some carabidae (Coleoptera). *Ent. Exp. Appl.* **6**: 171–180 (1963).
- HASSELL, M. P., LAWTON, J. H. & BEDDINGTON, J. R.: The components of arthropod predation I. The prey death rate. *J. Anim. Ecol.* **45**: 135–164 (1976).
- HASSELL, M. P. and R. M. MAY: Aggregation in predators and insect parasites and its effect on stability. *J. Anim. Ecol.* **43**: 693–726 (1974).
- HOLLING, C. S.: The functional response of invertebrate predators to prey density. *Memoires Entomol. Soc. Canada*, no **48**: 86 p. (1966).
- JOHNSON, D. M., AKRE, B. G. and P. H. CROWLEY: Modelling arthropod predation: Wasteful killing by damselfly Naiads. *Ecology* **56**: 1082–1093 (1975).
- KREBS, J. R.: Behavioural aspects of predation. In *Perspective in ethology* (P. P. G. Bateson, P. H. Klopfer eds.) New York: Plenum Press, 73 p. 1973.
- KREHAN, I.: Die Steuerung von Jahresrhythmik und Diapause bei Larval- und Imagoüberwinterung der Gattung *Pterostichus* (Col. Carab.). *Oecologia (Berlin)* **6**: 58–105 (1970).
- LAUTERBACH, A. W.: Verbreitungs- und aktivitätsbestimmende Faktoren bei Carabiden in sauerländischen Wäldern. *Abhandl. Landesmus. Naturkunde Münster* **26**: 1–100 (1964).
- MITCHELL, B.: Ecology of two carabid beetles *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schränk). 1. Lifecycles and feeding behaviour. *J. Anim. Ecol.* **32**: 289–299 (1963).
- MURDIE, G. and HASSELL, M. P.: Food distribution, searching succes and predator prey models. *The Mathematical Theory of the Dynamics of Biological Populations*. Academic Press London, 87–101, 1973.
- RABBINGE, R.: Biological control of the fruit-tree red spider mite. Pudoc, Wageningen, 228 p., 1976.
- ROYAMA, T.: Factors governing the hunting behaviour and food selection of the great tit (*Parus major*). *J. Anim. Ecol.* **39**: 619–688 (1970).
- ROYAMA, T.: Evolutionary significance of predators response to local differences in prey density: a theoretical study. In P. J. den Boer and G. R. Gradwell (ed.) *Proc. Adv. Study Inst. Dynamics Numbers Popul.* Oosterbeek, 344–357, 1971.

- RUARDY, P.: Intern rapport from Theoretical production ecology. Agricultural University, Wageningen.
- SABELIS, M. W.: Evaluation of predatory mites for the control of spider mites. (In prep.)
- SOUTHWOOD, T. R. E.: Ecological methods. Methuen, London, 391 p., 1966.
- TINBERGEN, N., M. IMPEKOVEN and D. FRANCK: An experiment on spacing out as a defence against predation. *Behaviour* **28**: 307–321 (1967).
- WIT, C. T. DE and J. GOUDRIAAN: Simulation of ecological processes. Pudoc, Wageningen, 175 p., 1978.