

FORAGING BEHAVIOUR OF THE
CARABID BEETLE
PTEROSTICHUS COERULESCENS L.
(= *Poecilus versicolor* Sturm)
AT DIFFERENT DENSITIES AND
DISTRIBUTIONS OF THE PREY.

(PART II)

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ABSTRACT

By means of systems analysis and simulation, predation and egg production of the carabid beetle *Pterostichus coeruleus* L (= *Poecilus versicolor* Sturm) is studied in relationship to prey density and prey distribution. Foraging behaviour is divided into its most dominant components: searching, acceptance of prey and feeding which are in turn related to the most important internal and external factors. Hunger or its opposite, the relative satiation level (RSATL), is the internal factor that determines the 'motivation' for a large part of the behaviour and it results from the physiological state of the beetle. RSATL is estimated by means of a simulation model (Mols, 1988) and correlated to the behavioural components that play a role in searching and predation. The hunger level has a strong influence on the locomotory activity, walking speed, duration of area-restricted search and prey acceptance. Three types of searching behaviour were distinguished: 1. Straight high-speed walking when RSATL is below 5%, 2. Intermediate walking when RSATL exceeds 5% and 3. Intensive tortuous walking behaviour (area-restricted search) after consumption of a prey.

The searching model developed shows the advantage of the tortuous walk (TW) when prey is aggregated and its disadvantage in random prey distributions. When the searching model is coupled to the motivation model the advantage of TW is restricted to aggregated prey at overall low prey densities (< 1 prey/m² generally). Walking speed, time spent walking and success ratio (prey captured/prey discovered), which in turn all depend on the relative satiation level, in combination with prey density and prey aggregation determine the predation rate and the egg production.

1.0 INTRODUCTION

Obtaining food is a basic requirement for every organism. Animals that actively search for food, for themselves or for their offspring make different choices concerning the locality to search for, the period during which to search, the kind of food to search for and ultimately the quantity of food to ingest. In that searching behaviour a number of factors play an important role which can be divided in: a) species specific properties, like the way of locomotion, the perception of habitat and prey and the internal motivation to come into action and b) environmental properties which determine the availability and attainability of the prey like vegetational composition and habitat structure, and the prevailing microclimatological conditions that affect the rates at which several vital processes of both prey and predator take place.

The ultimate aim of this study is to gain insight into the impact of spatial distribution and density of prey on predatory behaviour and on the resulting egg production of the carabid beetle *Pterostichus coerulescens*. This may lead to better insight and understanding of the survival strategy of this carabid beetle, reflected in its ability to cope with specific prey distributions varying from random to aggregated.

The carabid beetle, *Pterostichus coerulescens* L. (= *Poecilus versicolor* Sturm), is a predator of small arthropods such as aphids, spiders, caterpillars and maggots (Hengeveld, 1980), and lives in heathland and grassland poor in nutrients. In most cases prey distribution is aggregated, which is a general phenomenon (Southwood, 1966). Flight has only rarely been observed in *P. coerulescens*. Therefore, all vital behavioural functions such as searching for food, finding a mate, escaping from predation by birds, toads and rodents (Larochelle, 1974 a,b) occur by walking. The pattern of movement in relation to the density and distribution of the prey affects the rate of feeding and as a consequence the rate of reproduction and thus the spatial and temporal dynamics of the population in the field.

To understand the dynamics of the processes governing searching and predatory behaviour, information is required on the motivational drives for predatory behaviour. In many species behaviour is governed by some internal 'motivational drive'. For several predators this motivational drive is found to be equivalent to the satiation level of the gut (Holling, 1966; Nakamura, 1972; Fransz, 1974; Rabbinge, 1976; Sabelis, 1981; Kareiva et al., 1987). For *P. coerulescens* the apparent gut capacity (which is the weight of a meal to satiate a beetle that starts eating with an empty gut), is used as a measure for the 'motivation' of the beetle (Mols, 1988). The apparent gut capacity cannot exceed a physical maximum

(the maximal gut size) and it depends on the size of other organs and tissues needed for egg formation and storage of reserves as well. The actual gut content changes by ingestion, excretion and resorption. The rates of changes are predominantly affected by ambient temperature and daylength, the latter determining the onset of vitellogenesis. Thus the physiological drive for behaviour, i.e. the satiation level or its complement hunger, results from a complex of internally related states which in their turn are affected by the rate of prey ingestion under various climatic conditions.

The internal factors which determine the 'motivational state' of the beetle (here used as an equivalent for the term relative satiation level: RSATL) were integrated in a simulation model (Mols, 1988). The output of that model was compared with the results of experiments and showed that it was possible to estimate continuously the 'motivational state' of the beetle. This 'motivational state' of the beetle is used as the most important state variable that dictates walking and predatory behaviour.

1.1 COMPONENTS OF BEHAVIOUR

In general the predation rate is determined both by the encounter rate (E_r) with prey, and by the fraction of encountered prey killed by the predator :the succes ratio (S_r) (Fransz, 1974; Sabelis, 1981).

The encounter rate is a function of the following variables:

- (A) Locomotory activity: The fraction of the time that both predators and prey are locomotory active. If the prey is mainly sessile and the predatory beetle hides away in the soil or litter when resting, only the locomotory activity of the predator has to be considered.
- (V) Velocity: The walking speed of the beetle (cm/sec) of both predator and prey. In *P. coerulescens* the majority of prey items are small caterpillars, aphids and maggots (Hengeveld, 1980), which show a very low walking speed in comparison to the beetle. In those cases the speed and the turning rate of the prey can be neglected. If mobile spiders and ants are important prey items, then walking speed has to be included in the resulting velocity, but if only immobile or slowly walking specimens are important prey items their velocity may be neglected also.
- (E_r) Effectiveness of searching per unit of walking distance depends on the windingness of the walking pattern. The latter can be expressed by the turning rate (expressed as degrees/time unit) or by the turning angle per unit of distance. When the pattern is very windy the effectiveness of searching per unit of walking distance decreases because recrossing of previous visited spots will occur more often.
- (R) Reaction distance: The distance at which a predator reacts to a prey. It determines the searching path width of the predator and therefore it plays an important role in the area of discovery of the beetle.
- (D) Density of the prey. In case of prey aggregation its density will differ from

place to place. To avoid confusion in terminology the following terms will be used:

1. 'Overall density' is the total number of prey items (prey total in an area) divided by the surface of the total area.
2. 'Within cluster density' is the number of prey items in a cluster divided by the surface of a prey cluster.

From this follows that the area of discovery will be dependent both on the walking speed, the effectiveness of searching (determined by the windingness of the walking track) and on the reaction distance. For clumped prey distributions increased winding may result in a longer stay of the predator in the prey cluster and in a more intensive search over the area, which ultimately may result in a higher encounter rate with prey.

If it is assumed that the predator searches at random and that the walking directions of both predator and prey are mutually independent, the predation rate can be calculated from the encounter rate multiplied with the success ratio (Sabelis, 1981; Mols 1986)

$$P = E_r \cdot S_r \quad (1)$$

$$E_r = 2 \cdot R \cdot V \cdot D \cdot A \cdot E_{\pi} \quad (2)$$

However, searching is not at random when a predator is able to orient itself towards prey individuals or to prey cues, or when both the walking speed and direction of walking are changed after contact with prey. In such cases these formulae cannot be used, or have to be restricted to those parts of time in which searching is still at random. Then it is necessary to quantify the walking behaviour itself and to relate its features (speed and turning rate) to the internal and external stimuli. In that case the distribution of the prey becomes very important, because it will interact with the degree of windingness of the searching behaviour and thus with the efficiency of searching. The searching efficiency then depends on the type of walking behaviour (speed and turning rate) and has to be included as a separate function in the predation function.

In the predation process not every encounter with a prey is followed by an attack and not every attack is successful. Among others this depends on the motivational state of the predator (Fransz, 1974; Rabbinge, 1976; Sabelis, 1981, Mols, 1987). A hungry predator will be more eager to attack a prey and will continue an attack longer resulting in a higher success ratio. Prey exhibiting a defensive reaction, for example some caterpillars, may have a greater chance to escape. This implicates that the success ratio depends on the relative satiation level of the beetle. Thus the predation rate is a function of:

$$P = f(R, V, E_{\pi}, D, A, S_r) \quad (3)$$

The behavioural components mentioned above may be both determined by the relative satiation level of the beetle and by external stimuli such as tempera-

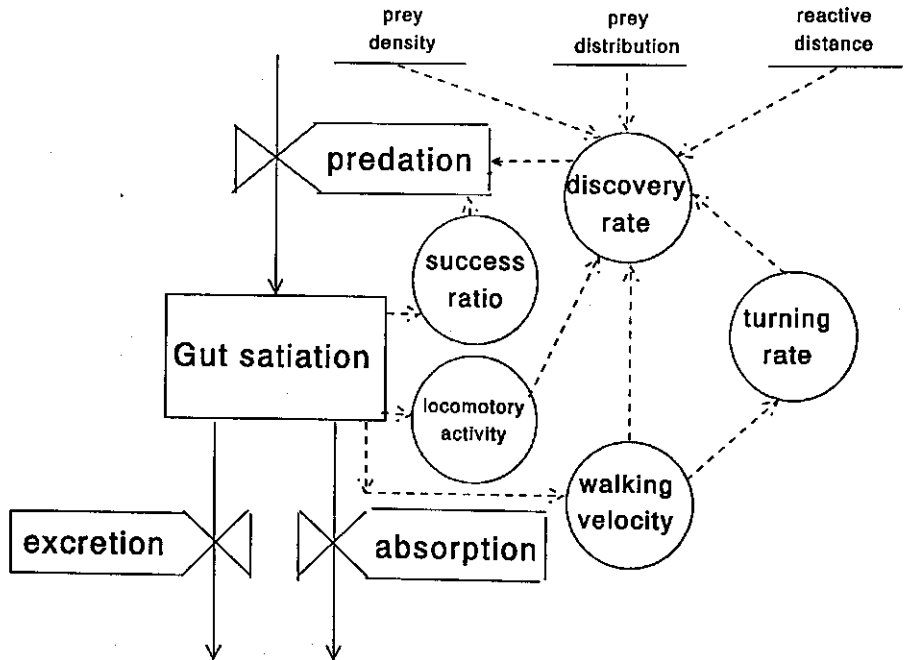


FIG. 1.1 Relational diagram of the relationship between behavioural components involved in searching and predation. (Rectangles are state variables, valves are rate variables, circles are auxiliary variables, underlined statements are parameters. Solid lines represent streams of matter, broken lines represent streams of information).

ture and diurnal rhythmicity (fig. 1.1). These factors change both throughout the day, and after consumption of prey as has been observed in many predators (e.g. Coccinellids, Dixon 1958; Anthocorids, Evans, 1976).

1.2 APPROACH

Therefore, the relationships between the relative satiation level and locomotory activity, walking behaviour and success ratio had to be quantified experimentally and integrated into a model that simulates predation and that is coupled to the motivational model (Mols, 1988). With this model it is possible to simulate walking behaviour and egg production under different sets of environmental conditions, prey densities and prey distributions.

The value of specific behavioural components in the total predation process can be estimated for these different conditions thus giving insight when specific behaviour shows full advantage for the predator. The results obtained may offer basic background information for the interpretation of the functional and numerical response of the beetle to different prey densities which are important features of the population dynamics of this species in time and space.

2.0 QUANTIFICATION OF THE COMPONENTS OF BEHAVIOUR IN RELATION TO HUNGER

The set up of the experiments in general is such that they are done in relatively simple environments (Petri-dishes, arena's with light vegetation etc.) under relatively constant conditions of temperature, humidity, light intensity and prey type to quantify the relationships between the components of searching behaviour and the motivational state. The field situation may be much more complex, but the basic processes are assumed to be the same and therefore this approach may lead to the unraveling of this complex system.

2.1 LOCOMOTORY ACTIVITY

2.1.1. *Methods*

Measurements of locomotory activity in relation to the satiation level were restricted to the reproductive period, because the beetles are most active then. Before the experiments the beetles were weighed and their apparent gut capacity was estimated. Ten pairs of male and female beetles were each placed in large Petri-dishes (20 cm diam.). The substrate on the bottom of the dish consisted of loamy sand and some peat-mull. On the substrate small pieces of bark were placed under which the beetle could hide. The females were marked by a small dot of yellow paint on one of the elytra so that during observation they could be easily distinguished from the males. The observations were carried out at $20 \pm 1^\circ\text{C}$ and at $12 \pm 1^\circ\text{C}$ during a period of 16 hours (from 5 am to 9 pm, this was also the duration of the photoperiod). Two days before the start of the observations the beetles were placed in the dishes without food, to standardize them and to accustom them to the situation. The first day of the observation for two hours from 6-8 am the beetles were given abundant food to satiate them. The food consisted of dead blowfly maggots. After this feeding period the prey remains were removed. Next the beetles were starved for four days. This sequence of feeding and starvation was repeated three times. The last starvation period took five days. The fifth day of the last starvation period the beetles were offered food at 11 am.. That day the activity was followed until 4 pm.

Every hour the beetles were observed for a period of 15 min (the observation period) and their activity was recorded. The satiation level was estimated with the help of the motivational model (Mols, 1988).

After the period of hourly observations the beetles were held in the same Petri dishes and fed abundant maggots every third day. Each day at 9 am and at 2 pm the activity was recorded for a quarter of an hour. The egg production was measured by washing the substrate each week following the method of Mols

Locomotory activity
Pterostichus coeruleus L.

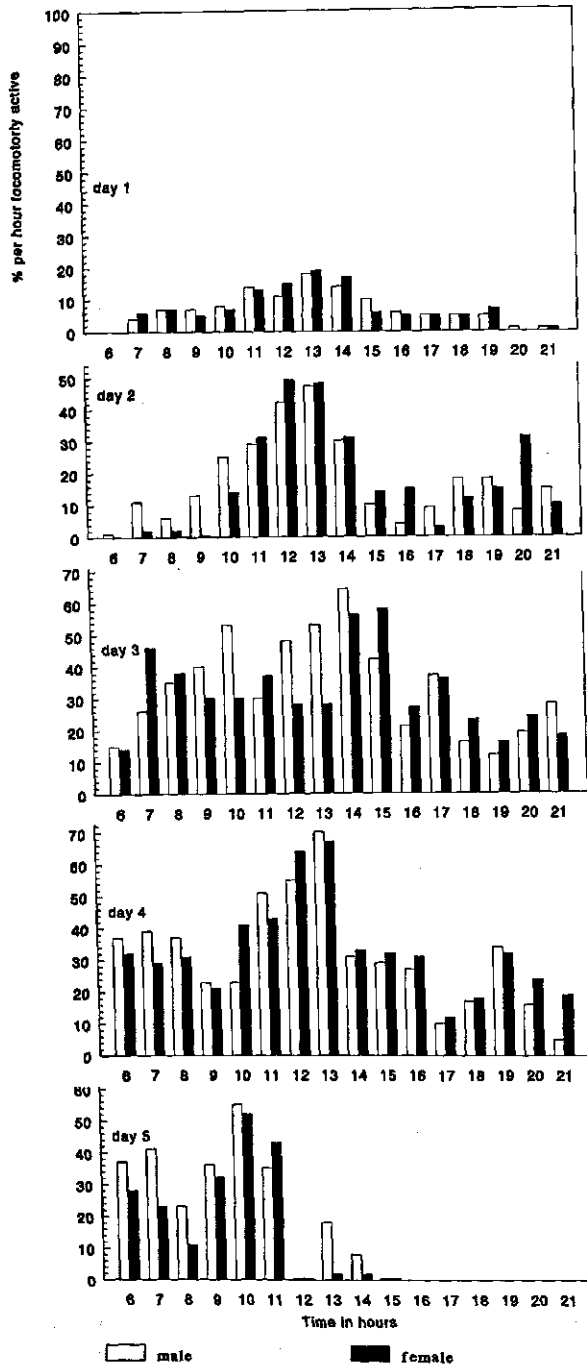


FIG. 2.1 Hourly distribution of locomotory activity of *P. coeruleus* at 20°C for starved beetles on 5 successive days. The 5th day food was offered at 12.00. Light period from 5.00 to 21.00.

et al. (1981). The observations were finished at the end of the reproduction period of each beetle. From these observations a relationship between locomotory activity and egg production could be established and information on the persistence of the individual locomotory activity in the course of time both during the intensive and the extensive observation period could be collected.

2.1.2 Results

Frequency distribution of the locomotory activity during daytime.

The distribution of the percentages of hourly locomotory activities over the day for each of the five days in sequence is shown in fig 2.1. In general locomotory activity increases until noon, next it decreases. The level of activity increases up to the third day. At the fourth and fifth day activity is already high at the start of the photoperiod. At the end of the day also a weak increase in locomotory activity can be observed. When food is offered at the noon of the fifth day the activity drops drastically especially in the females. This clearly shows the influence of satiation on the level of locomotory activity. The effect of the satiation level on the daily distribution pattern of locomotory activity is eliminated by dividing the duration of activity calculated for each hour by the corresponding daily duration of activity. This gives an average pattern of locomotory activity over the day that is independent of the relative satiation level. Thus a distinct diurnal rhythm of locomotory activity was found (fig. 2.2), with a maximum at noon and a minimum during the night.

In the experiment carried out at 12°C the beetles showed hardly any activity during the observational period. Only very short moments of activity could be recorded. The activity at this temperature was about 10% of the activity at 20°C.

Duration of daily locomotory activity.

It is assumed that during a quarter of an hour sufficient information is obtained to be able to estimate the hourly locomotory activity of the beetles. Therefore, the duration of locomotory activity per hour was estimated by multiplying by four the duration of locomotory activity measured during a quarter of an hour. By summing up the hourly estimates over the whole daily observation period the duration of daily locomotory activity was estimated. The daily sum of locomotory activities during the successive days following feeding is shown in fig 2.3. The duration of locomotory activity increases from the day of satiation until a level (MAXACT) of 5.3 hours/day is reached at the third day. This level remains approximately constant at least until the fifth day. No significant difference in the duration of daily locomotory activity could be observed between the sexes.

The locomotory activity in relation to the relative satiation level.

At 20°C it takes two days to empty the gut (Mols, 1988) while in the experiments it took 2 days to reach the maximum level of locomotory activity. To express the relationship between locomotory activity and the relative satiation

circadian rhythmicity
Pterostichus coerulescens L.

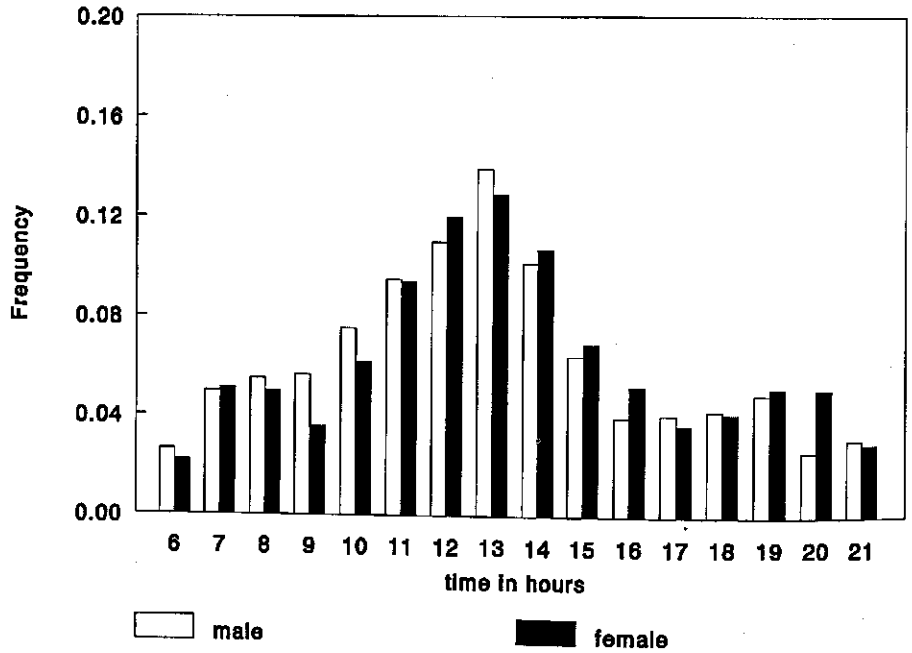


FIG. 2.2 Average frequency distribution of locomotory activity during the lightperiod at 20°C.

Sum of the mean daily
 activity in hours

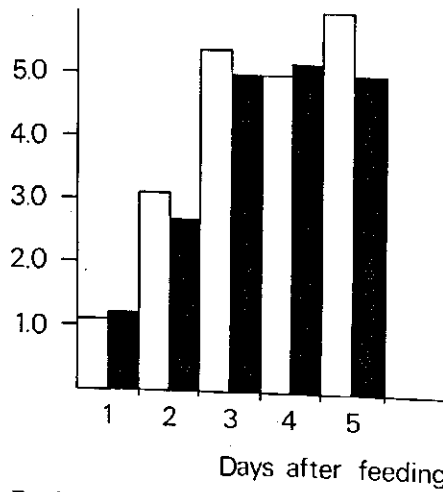


FIG. 2.3 Increase of total daily locomotory activity after complete satiation on the first day.

level, the effect of the time of the day on locomotory activity (diurnal rhythmicity of locomotory activity) has to be corrected for. Therefore, the locomotory activities during the hourly observation periods on the first and second day were calculated as a fraction of the average maximum activity found for the corresponding hour of the third, fourth and fifth day. The relative satiation level of the beetle in each observation period was computed by the motivation model (Mols, 1988). In this way it was possible to obtain an estimate for the relative locomotory activity at a range of satiation levels. The relation is shown in fig.2.4. The relative locomotory activity, here called the relative activity coefficient (AC), has a correlation with the relative satiation level (RSATL). This relationship can be fitted by the hyperbolic equation :

$$AC = 1/(5.7*RSATL+1) \quad r^2 = 0.80$$

The locomotory activities of the males and the females were combined in this figure, because between the sexes no significant difference in locomotory activity could be observed

Locomotory activity and reproduction.

The average locomotory activity measured at 9 am and 2 pm during daytime

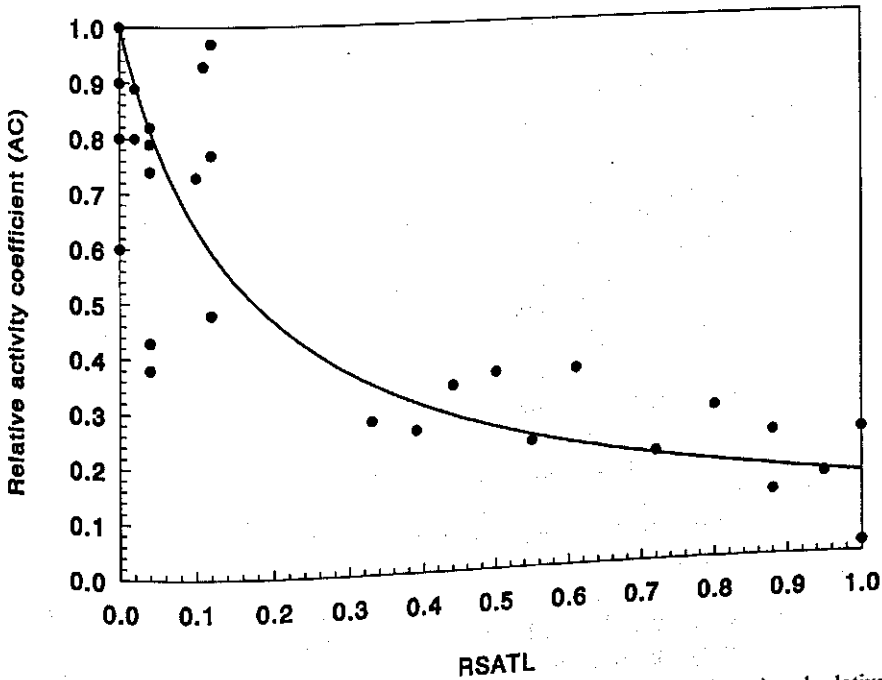


Fig. 2.4 Relationship between the relative locomotory activity coefficient (see text) and relative satiation level.

was used as an index for the overall locomotory activity of each beetle. These data are given in table 2.1 together with the individual total reproduction and the average of the locomotory activity at the same hours during the intensive observation periods.

To compare activity levels of the beetles in the pre-reproductive period and in the reproductive period the activities are expressed as a percentage of the total activity of all beetles in the experiment.

TABLE 2.1 The relationship between the locomotory activity (LA) in the pre-oviposition and in the oviposition period and the egg production of a beetle. (Spearman's $r_{ab} = 0.87, P = 0.009$; $b_c r = 0.81, P = 0.015$; $a_c r = 0.56, P = 0.093$)

beetle no	1	2	3	4	5	6	7	8	9	10
egg production	376	73	320	32	113	134	141	211	198	465
a) eggs% of total	21.0	4.8	17.9	1.8	6.3	7.5	7.9	11.8	11.1	26.0
b) LA in repro%	25.4	4.7	9.8	1.4	5.4	2.6	11.1	7.4	24.4	32.9
c) LA.in pre-repro%	27.1	9.0	11.8	10.5	16.7	10.1	23.1	7.9	23.9	42.2

The table shows that if the activity and the egg production are ranked in increasing order beetles with a high level of activity have also a high egg production. The ranks of locomotory activities in the pre-reproductive period and in the reproductive period resemble each other quite well, though not yet significantly so. The table also shows the great differences in the general level of activity between the beetles, for instance beetles 2 and 4 are 'low activity' beetles and 1 and 10 are 'high activity' beetles.

2.1.3 Discussion

Under the highly simplified experimental conditions the course of locomotory activity through the day at constant temperature apparently follows a rhythmic periodicity with a peak at daytime and a dip at night, although the latter was not measured in the experiments. This rhythmicity is similar to observations in other carabids (Greenslade, 1963; Luff, 1978). For example the nocturnal groundbeetle *Pterostichus oblongopunctatus* L. at constant temperatures shows a clear peak during the night and non or a low activity during daytime (Brunsting, 1983). But in this species the activity increases with increasing temperature and extends partly to the daytime. In *P. coeruleus* at field temperatures nocturnal activity amounts to approximately 10% of total activity (Greenslade, 1963) and the level of this nocturnal activity probably depends on night temperature. Although it was not measured in the experiments the high activity, at the start of the photoperiod after two days of starvation, may be an indication that nocturnal activity was raised also. In the field the difference between diurnal and nocturnal activity will be more extreme, because of the difference between daytime temperatures and those occurring during the night.

Satiation level influences the level of daily locomotory activity. The increase

from a low activity level after satiation till the maximum level after two days corresponds closely to the time needed for a beetle to digest the food at 20°C (Mols, 1988). The effect of satiation, or the inverse, hunger on the level of locomotory activity of insects was first found by Edney (1937) who provided quantitative data that starvation for a few hours caused a marked increase in the 'spontaneous activity' of the locust *Locusta migratoria migratorioides*. Further evidence is given in later papers by Ellis (1951) and Chapman (1954). Barton-Browne and Evans (1960) studied the effect of feeding and starvation on locomotory activity in the fly *Phormia regina* (Meigen). It was found that flies fed glucose, fructose or mannose were much less active than were flies that had been starved for 24 hours. Immediately after feeding flies were less active than any other time, but activity increased progressively thereafter. Evidence was given that locomotory activity is some function of crop volume and, hence of the rate of crop emptying. This last hypothesis corresponds closely with the observations in *P. coerulescens*. Also Sirota (1978) found that the larvae of *Culex pipiens molestus* moved more intensively at low food levels than at higher ones. Williams (1959) was able to increase the activity during day of the nocturnal carabid *Pterostichus madidus* by feeding the beetles during daytime only. Grüm (1966, 1971) found that starving beetles showed a higher overall locomotory activity and more activity by daytime.

The locomotory activity at 12°C (10% of that at 20°C) was extremely low. One may wonder whether this is caused solely by the slow decrease of the relative satiation level after satiation or by a combination of temperature and relative satiation level. The relative satiation level can be estimated with relative gut emptying rate at 12°C (Mols, 1988). The food was offered every third day thus, after 54-68 hours RSATL did decrease to about 20%. The relative activity coefficient at 20°C for this hunger level is about 0.45 (see fig. 2.4). If is assumed that maximum daily activity (= 5.3 hours) is the same for each temperature, the total daily activity at the third day should be approximately 2½ hours. Thus in the observation period of a quarter of an hour at noon (according frequency distribution of total activity in fig 2.2) the beetles should be $0.13 \cdot 150/4 = 4.9$ minutes active (or 32.5% of the observation period), but only 10% activity was observed. This is an indication that total daily activity is also directly temperature-dependent and not only governed via the satiation level and that it decreases with decreasing temperature. This is also known from field observations (Luff, 1978, Kegel, 1990) The latter states that in diurnal species daytime activity is positively correlated with soil temperature.

It may be hypothesized that for insects starvation is a direct stimulus for locomotion but that its level also depends directly on temperature. The metabolic rate of poikilothermic animals increases with increasing temperature. This was also found in *P.coerulescens* (Mols, 1988). This increases the need for food. Therefore the duration of locomotory activity and/or the speed of walking have to be extended with increasing temperature to be able to cover a larger area in search for food. In *P.coerulescens* we know now that both speed (Mossakowsky, 1985) and locomotory activity are increased.

In the experiments the individual difference in locomotory activity was very high. This individual variation in locomotory activity was strongly correlated with egg production. As the latter results from a high intake of food and a rapid and efficient food conversion it may be hypothesized that the relative rate of gut emptying (RRGE) and the efficiency of food conversion (EFF) (See Mols, 1988) are the most important variables at this level.

Luff(1978), Desender et al.(1984) and Kegel (1990) did not found differences in daily activity patterns of males and females, which is confirmed by the present study.

2.2 ANALYSIS OF WALKING PATTERNS

2.2.1 Method

Set up for observations in the laboratory.

The beetles were studied in an artificial arena of 85-100 cm. The substrate consisted of loamy sand with some litter and a few heather plants. Video-equipment was used to registrate the walking pattern of the beetle (fig. 2.5).

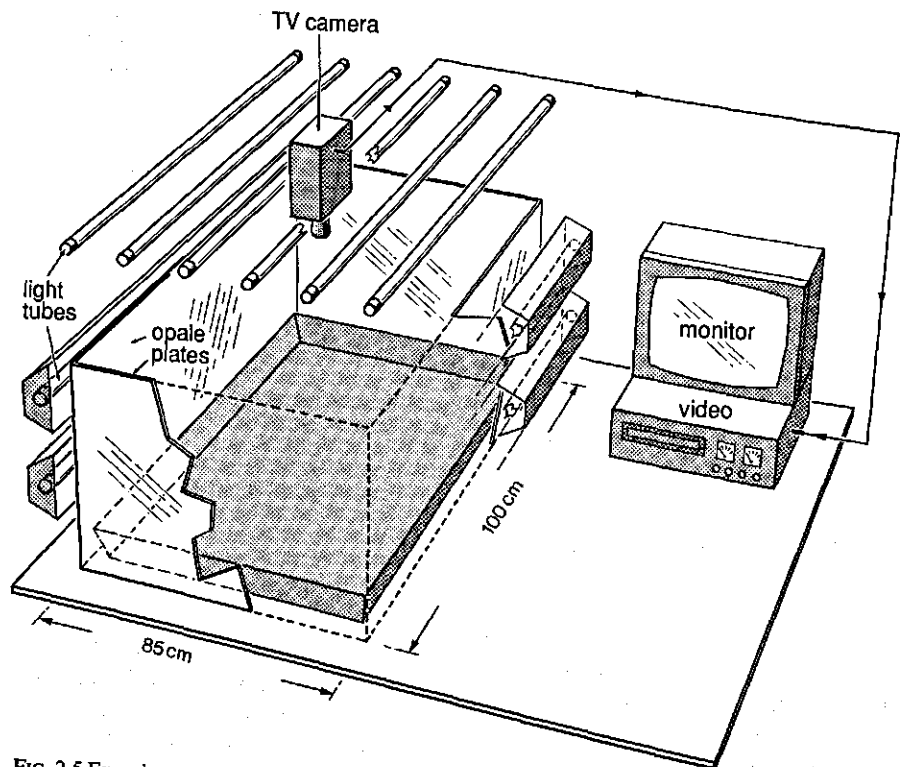


FIG. 2.5 Experimental set-up for observing of walking patterns in the laboratory.

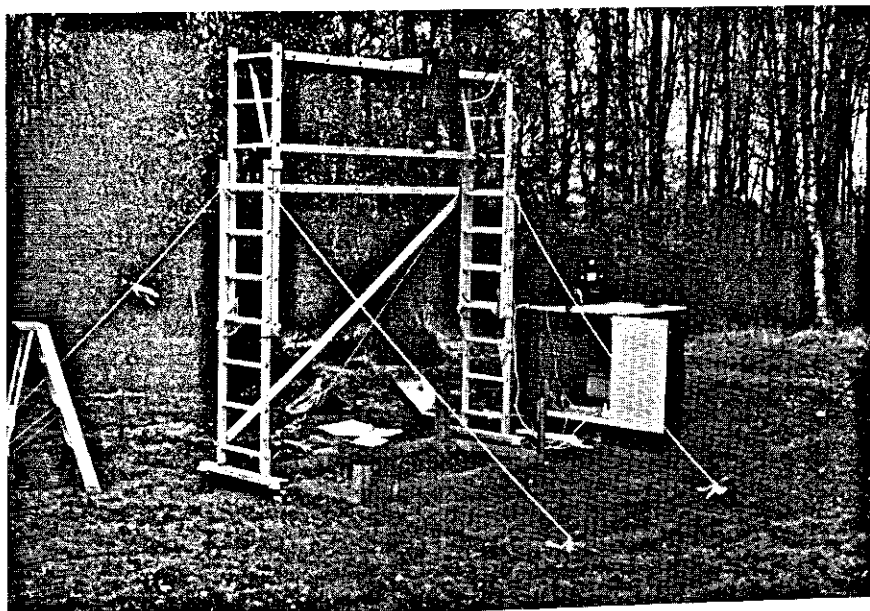


FIG. 2.6 Experimental set-up for observing of walking patterns in the field.

To prevent possible orientation of the beetle to an unequal light distribution or to a horizon silhouette, the experimental arena was enclosed by four opal Perspex plates, which spread the light of the light tubes behind them. A row of 6 fluorescent light-tubes hung above the arena. The light intensity was about 1800 lux. The temperature during the observations was 20 ± 1 °C.

Set up for field observations.

To registrate the walking patterns in the field an arena was constructed of 100*200 cm. The temperature in the arena was registrated by thermo-couples. Here also video-equipment was used to registrate the walking behaviour (fig 2.6). The intention here was to see how far the walking behaviour was comparable with that found in the laboratory. The observation equipment only allowed observations during dry weather. The vegetation in the arena was more dense than in the laboratory set up.

Beetles were marked individually with small dots of yellow paint on the elytra.

Experiments.

The walking patterns of beetles with different motivational states were observed. The beetles used in the observations were weighed before and had a known quantity of food in their gut. The hunger levels ranged from: starved for three days at 20°C (RSATL = 0) to completely satiated (RSATL = 1). The different relative satiation levels were obtained by feeding beetles up to satiation and then starve them for different time periods before recording the walking

behaviour. Before the observations the beetles were brought into the arena where they were allowed to adapt to the situation for approximately half an hour.

The observations made were:

- a) the walking pattern of the beetle without extra feeding. This pattern represents the behaviour belonging to a specific relative satiation level. As time passed on during these observations the appropriate RSATL was calculated for each walking pattern recorded.
- b) the walking pattern after consumption of a small prey. A weighed maggot of 1-2 mg was carefully offered at the point of a long pincet just before the mandibles of the beetle. In most cases the beetle accepted the maggot and started feeding immediately. The appropriate RSATL of the beetle was calculated.
- c) The walking pattern in an arena with prey clusters. Small prey clusters consisted of 7 maggots of 2 mg. at 10 cm from each other: One in the centre and the others at the corners of a hexagon at a distance of 10 cm from the central one.

Analysis.

The recorded walking patterns were traced on a plastic sheet taped on a monitor. The walking pattern was recorded in units of two-second steps. The positions of the two-second points was read into a computer by means of a magnetic tablet. The walking patterns along the borders of the arena were excluded for analysis to prevent edge effects. The walking of the beetles was frequently interrupted by short or long stops. Stops lasting less than one second were included into the walking time. The duration of a walking pattern (a path or a track) varied from a few minutes to a quarter of an hour depending on the activity of the beetle).

A path (or a track) can be represented by a sequence of points $(X_0, Y_0), (X_1, Y_1), \dots, (X_N, Y_N)$ such that for any i (INTEGER, $1 \leq i \leq N$), the i th step is a vector $P_i = (X_i - X_{i-1}, Y_i - Y_{i-1})$ with length P_i . Because these points are measured at constant time intervals P_i also represents the velocity of the beetle during that period.

The value of the change of direction between vectors P_i and P_{i+1} is measured algebraically by the turning angle α_i ($1 \leq i \leq N-1$). The distribution of changes of direction is characterized by a mean vector M (Batschelet, 1981). Its orientation, $M = \arctg(\Sigma \sin \alpha_i / \Sigma \cos \alpha_i)$, defines the angular mean of the distribution. To take into account the forward tendency of locomotion of most animals, the distribution of changes of direction is taken to be symmetrical and have an angular mean $M = 0$. The mean vector length r is defined as $r = (\Sigma 2 \cos \alpha_i + \Sigma 2 \sin \alpha_i)^{1/2} / (N-1)$. It ranges between 0 and 1 and expresses the concentration of the distribution around M and it offers a measure of correlations between the directions of successive steps. When this correlation is zero one obtains the random walk model, when the correlation is one a straight line movement is obtained.

Thus to characterize the tracks the following variables were estimated from the experiments:

1. The turning rate in degrees per time unit and turning angle per length unit respectively.
2. The mean, standard deviation and kurtosis of the frequency distribution of the turning rates according to the TUKEY distribution (Montford & Otten, 1976). This is a theoretical distribution which can be fitted to a range of experimentally observed frequency distributions, from uniform to contagious. It is a symmetrical distribution and it is characterized by three parameters: The mean (M), the standard deviation (σ), and a kurtosis related parameter (K). In its cumulative form the distribution can be described by:

$$\begin{aligned}
 X_p &= M + \sigma * Y_p && (4) \\
 Y_p &= (p^K - (1-p)^K) / K && \text{if } K \neq 0 \\
 Y_p &= \ln(p / (1-p)) && \text{if } K = 0 \\
 p &= \text{cumulative frequency of the turning rates } \{p = P(\Phi < x)\}
 \end{aligned}$$

Calculation of the parameters is done according to Sabelis (1981). The standard deviation of the frequency distribution offers information on the windingness of the track. The higher the standard deviation the more winding the track. The kurtosis tells us more about the form of the distribution curve, whether it is relatively 'flat' or 'sharply peaked' at its mode. According the value of k the following distributions can be obtained:

k = -0.85	:Cauchy
k = 0	:logistic
k = 0.14	:normal
k = 1 or 2	:uniform

3. The velocity, expressed in cm/sec. To obtain information more rapidly a part of the tracks were divided in 10 second parts and analysed by hand for the walking velocity only.
4. The concentration around M according to the length of vector r.
All these variables were analysed for the whole range of RSATL to examine possible relationships.

2.2.2 Results.

General observations.

Visual observations on the walking tracks of beetles in different motivational states soon revealed that there were three distinct types of walking. Hungry beetles walked more straight and at a higher speed. Beetles with some food in their stomach up to satiated walked more winding and also slower, while beetles that had consumed a prey showed a very winding walking pattern at a speed that gradually increased. When no other prey were found these walking patterns have been given the indications of straight (also sometimes called high speed

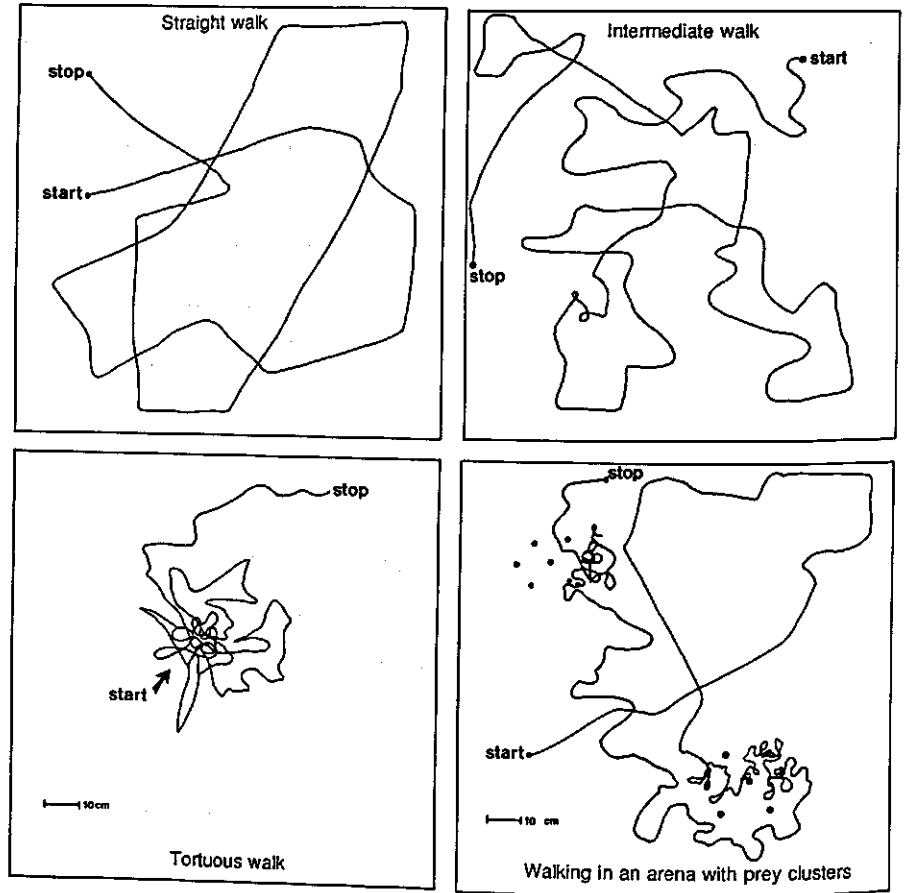


FIG. 2.7 Types of walking patterns observed in *P. coerulea*.

walking), intermediate and tortuous (TW) walk, respectively. These patterns are shown in fig 2.7. The characterisation of these patterns in turning rate and speed is given in table 2.2. When more prey items are found in a prey cluster tortuous walk continues and remains very winding at a low walking speed.

Turning rates.

The average turning rate expressed in degrees/second and the turning angle in degrees per cm. of the different tracks increase with the windingness of the track. Although hungry beetles which perform straight walk showed a smaller average turning rate than those having a RSATL > 5% this difference was not significant. However, the average turning angle per cm is significantly smaller for straight walking beetles than for intermediate walking ones.

The average turning rate of tortuous walk is larger than that of an intermediate walking pattern. If the beetle walks in a prey cluster after each consumption

TABLE 2.2 Speed (cm/sec), turning rate (degr/sec), turning angle (degr/cm) and concentration grouped according to walking pattern and motivation level (RSATL < 5% and RSATL > 5%) and for tortuous walk in and outside a prey cluster (n= number of beetles, SE is the standard error of the mean)

	n	Speed		Turning rate		Turning angle		Concentration	
		cm/sec	SE	degr/sec	SE	degr/cm	SE	mean	SD
Straight (RSATL < 5%)	20	4.66	0.71	16.00	4.7	3.51	0.97	0.76	0.1
Intermediate (RSATL > 5%)	20	2.2	0.33	19.64	2.91	9.34	1.32	0.68	0.07
Tortuous walk	23	1.04	0.22	23.5	2.77	23.33	2.65	0.59	0.08
TW in prey cluster	4	1.03	0.34	30.2	3.16	30.1	3.08	0.43	0.08

the tortuous pattern starts over again, this results in an even larger average turning rate and turning angle.

The turning rates per 2 seconds of all the tracks grouped for the three walking types were summarized in frequency distributions, which appear to be symmetrical around zero and extend from -180 degrees to +180 degrees (fig. 2.8). The

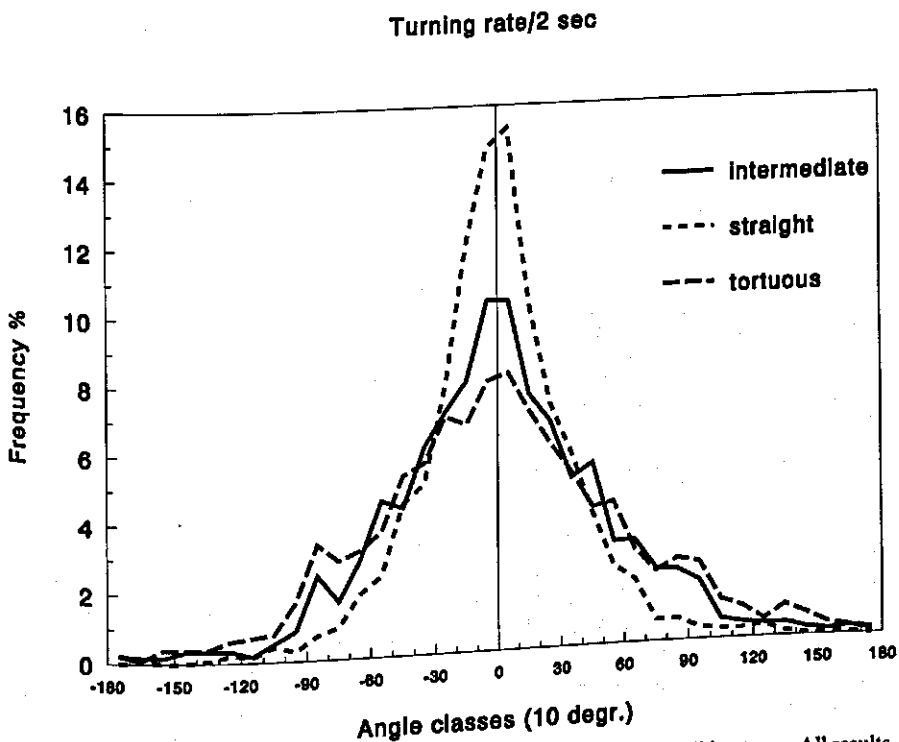


FIG. 2.8 Frequency distribution of turning rate (2 sec. periods) for the three walking types. All results of observations combined.

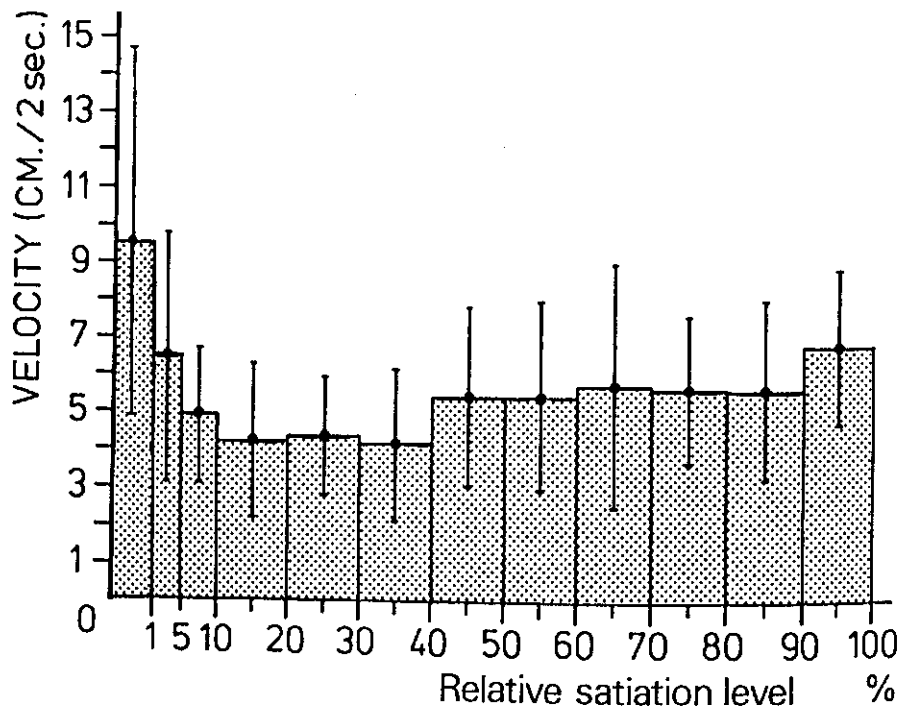


FIG. 2.9 Walking velocity at different relative satiation levels at 20°C

more winding the walking type the larger the standard deviation of the distribution.

Velocity

The relationship between walking speed and relative satiation level, with exclusion of tortuous walk, is shown in fig. 2.9. In this figure both the results of completely analysed tracks and those of tracks which were only analysed for speed are combined. The figure shows a breakpoint around a satiation level of 5%. Above 5% satiation the average velocity is almost constant having a tendency to increase a little at the higher satiation levels. But in general the velocity is approximately 2.5 cm/sec, which is a little bit higher than the speed found in the completely analysed tracks. Below a relative satiation level of 5% walking velocity increases rapidly to approximately 5 cm/sec. Thus using velocity as a criterium 2 types of walking patterns could be distinguished. After prey consumption the beetle resumed walking at a very low speed. Gradually the speed increased until it reached a velocity of approximately 2-3 cm/sec. The average walking velocity after consumption of a prey was approximately 1 cm/sec.

When the speeds of all the time steps of all the tracks of these different walking patterns were grouped according to the three walking types this gives fig. 2.10. The frequency of these distributions of velocities per 2 sec. time steps shows

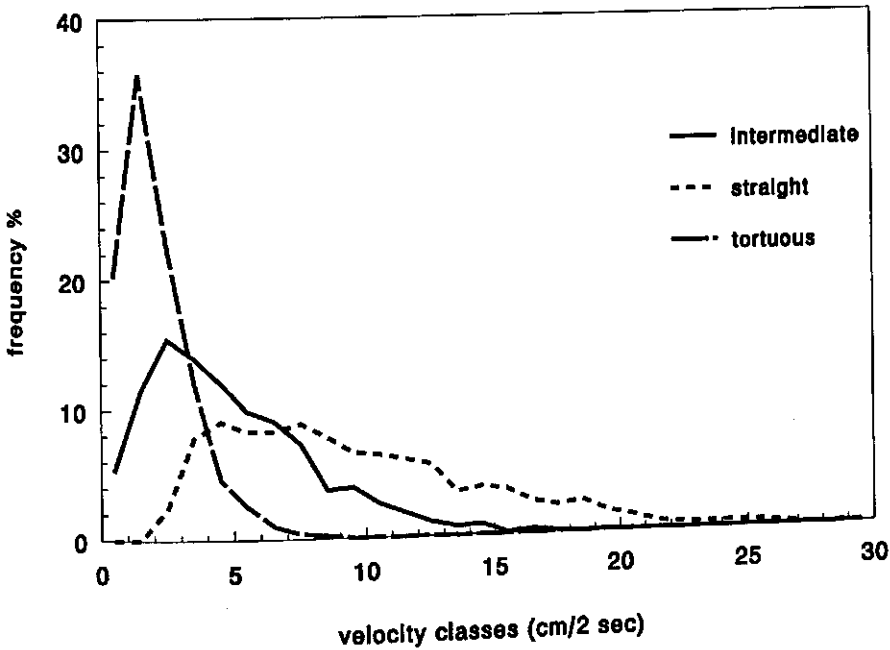


FIG. 2.10 Frequency distribution of walking velocity for three walking types.

that tortuous walk appears to have the narrowest distribution. The frequency distribution of the other types are highly leptokurtic and largely overlap, straight walk showing more time steps with a high speed than intermediate walk.

Relationship between velocity and windingness.

When the velocity is correlated with the turning rate, it appears that the mean turning rate decreases significantly ($r=0.65$, $P < 0.01$) with increasing speed. However, the variation is high (fig 2.11). The relationship between velocity and average turning angle per cm shows less variation. The relationship would be a perfect hyperbole, if the turning rate was constant for all velocities. In fig. 2.12 a hyperbole (Y1) with $x=0.55$ as limit is not fitting well through all the points. Most of the turning angles of tortuous walk are positioned left of the curve. This may be an indication that tortuous walk is another walking type. A power curve (Y2) offers the best fit through all the points. This curve has a limit at $x=0$ which indicates that the beetle turns around on the spot. The turning angle changes gradually and continues from 360 to almost zero degrees with increasing speed.

From each track the frequency distribution of the turning rate per 2 sec. time step was made. A Tukey distribution was fitted to the angle frequency distribution and thus for each track the appropriate standard deviation and the kurtosis were calculated (according to Sabelis, 1981). Using all the analysed tracks, relationships were estimated between walking velocity per 2 seconds (V) of the beetle

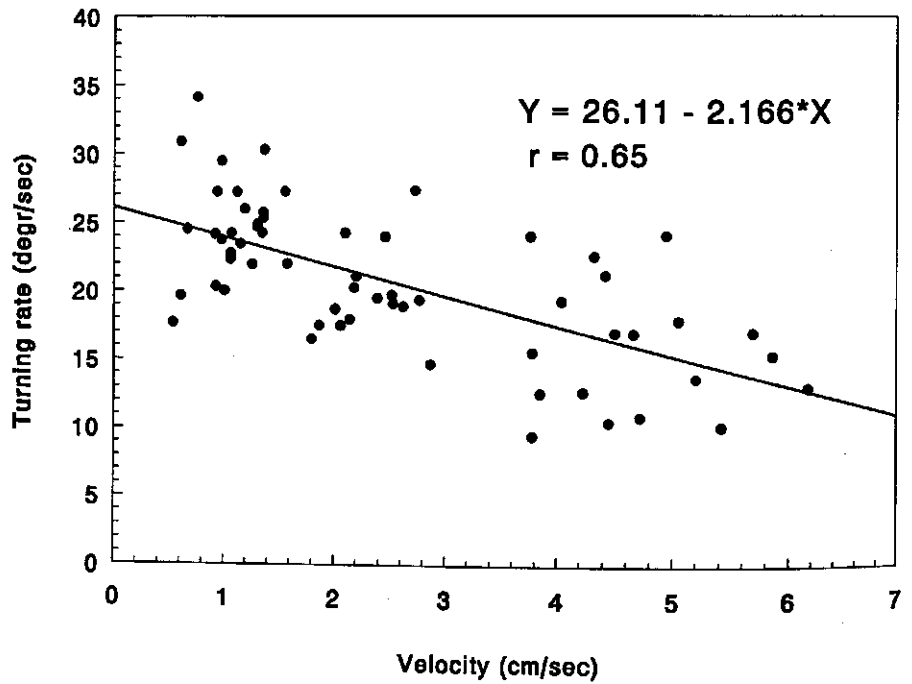


FIG. 2.11 Relationship between walking velocity and turning rate.

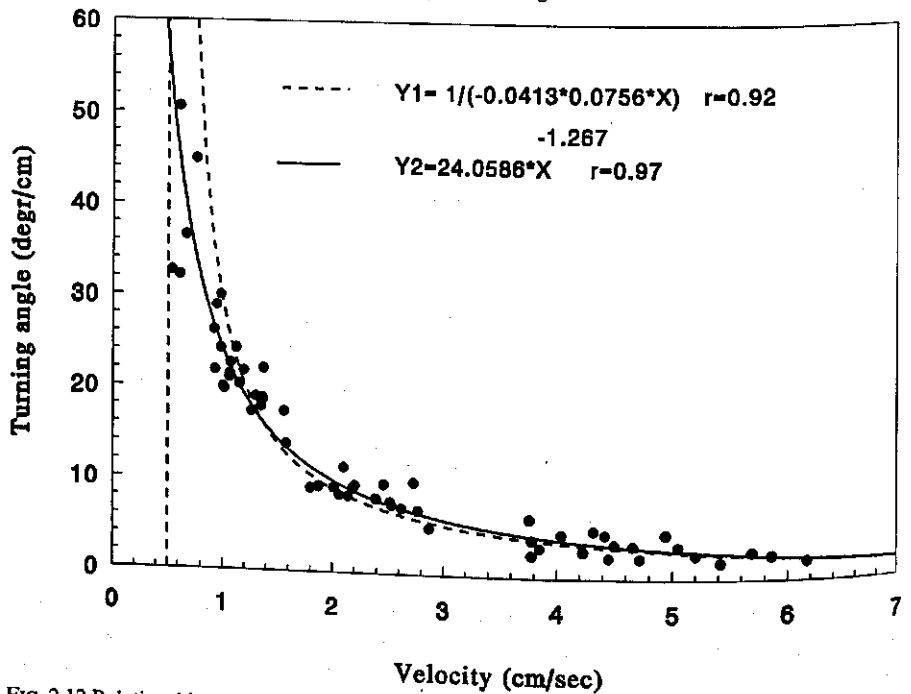


FIG. 2.12 Relationship between turning angle (degrees/cm) and walking velocity.

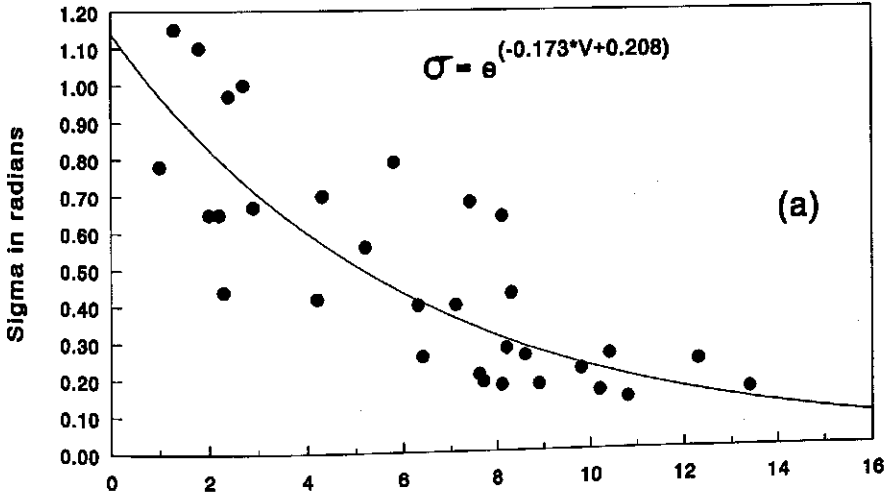


FIG. 2.13a Relationship between the SD of the frequency distribution of the turning rate of a walking track (fitted with the Tukey distribution) and average walking velocity.

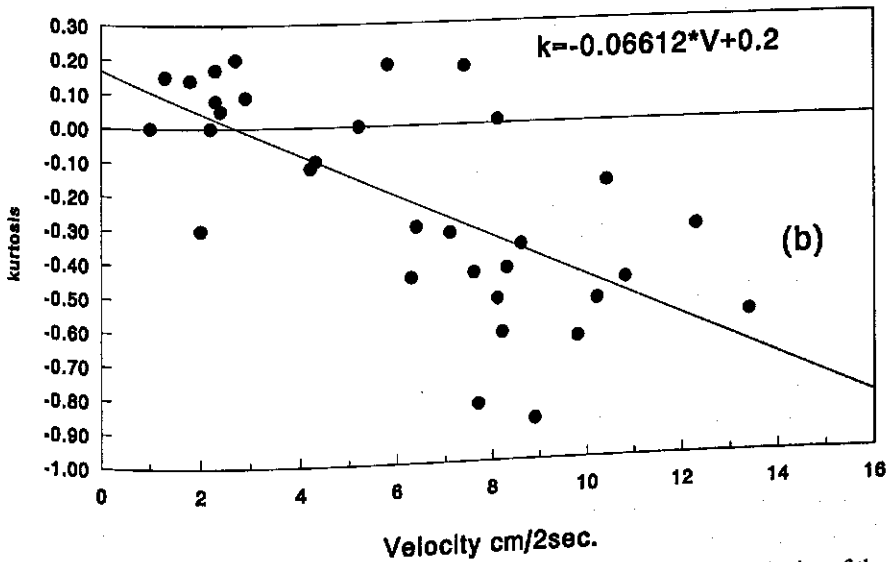


FIG. 2.13b Relationship between kurtosis related parameter K of the frequency distribution of the turning rate (fitted with the Tukey distribution) and walking velocity.

and its standard deviation (σ) and kurtosis (K) of the turning rates frequency distribution. A significant relationship was found (fig 2.13 a + b). The faster the beetle moves the narrower the distribution and the smaller the standard deviation of it, and the more negative kurtosis.

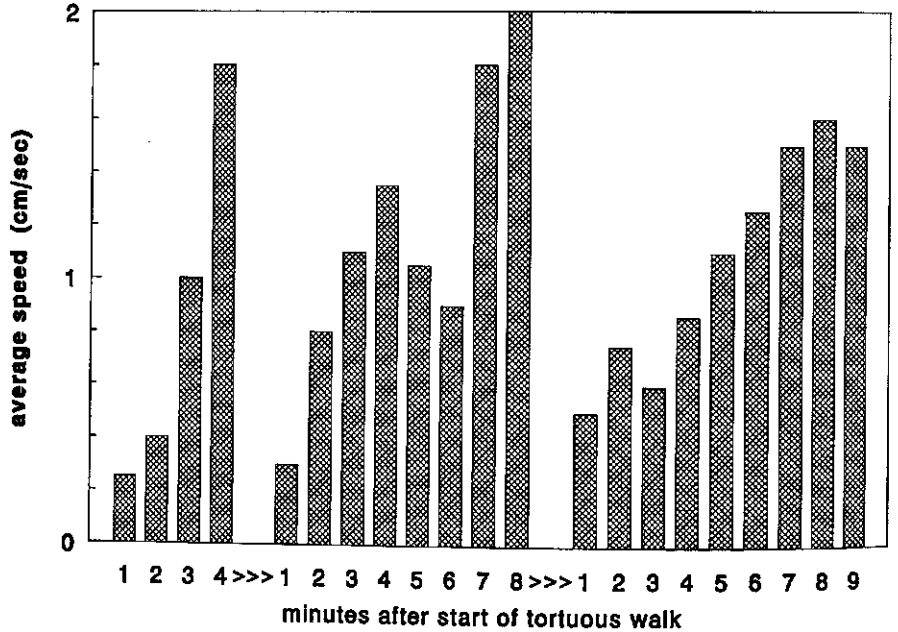


Fig. 2.14 Example of increase of walking speed in tortuous walk after prey consumption.

This gives the following expressions:

$$\sigma = \exp(-0.173*V+0.208) \quad r^2=.7 \quad (p < 0.01) \quad (5)$$

$$K = -0.0661*V+0.2 \quad r^2=.49 \quad (p < 0.01) \quad (6)$$

Duration of tortuous walk.

After prey consumption the velocity of the beetle gradually increases and when no other prey is found rapidly the track straightens out and either becomes intermediate walk or the beetle stops walking or reaches the edge of the arena. An example of such an increase of speed during the course of a typical tortuous walk track is given in fig. 2.14. The time span of tortuous walk appeared to be a function of the relative satiation level (fig. 2.15). When the gut is almost empty this behaviour may last for about 11 minutes, but when the relative satiation level exceeds 80% it does not occur anymore.

Concentration

The concentration parameter r decreases with the tortuosity of the track (fig. 2.16). When all the walking tracks are taken for estimation of the correlation between walking velocity and concentration this relationship shows to be significant ($r = .61$ for $n = 67$, $p < 0.01$). The combined walking patterns (table 2.2) show no significant difference between the mean values of straight and interme-

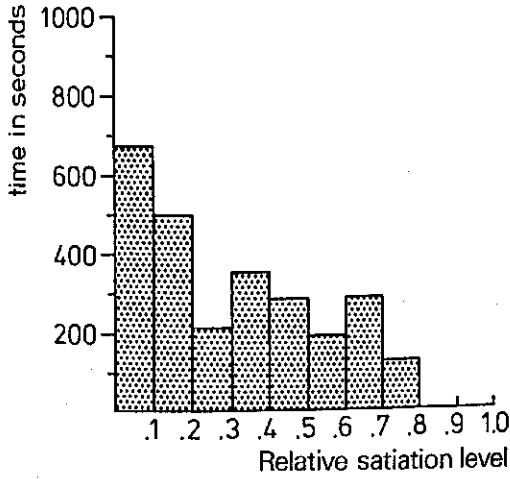


FIG. 2.15 Relationship between duration of tortuous walk and relative satiation level.

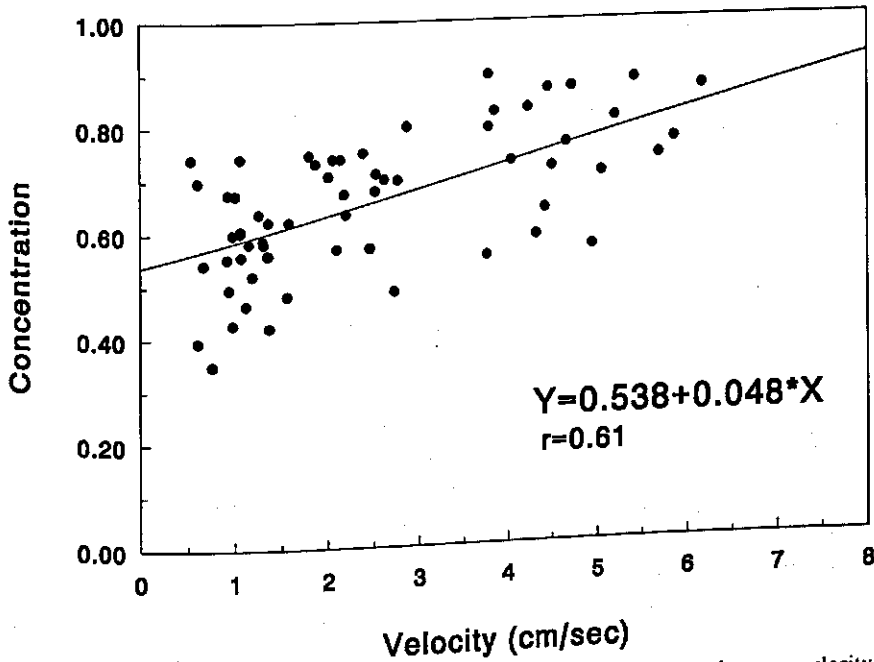


FIG. 2.16 Relationship between concentration parameter of walking patterns and average velocity.

diate and between intermediate and tortuous walk but it does between straight and tortuous walk.

Field observations.

Beetles walking in the arena could be observed rather easily by eye. On the

video they were more difficult to follow, especially when they walked in the vegetation. This hampered the registration of the tracks and limited the number of tracks which could be followed. At least one track per beetle was analysed. The results are given in table 2.3. The speed of walking in the field was usually lower than found in the laboratory, both for hungry beetles and for those with some gut filling. After prey consumption in the field, tortuous walk occurred also but at a lower velocity.

When a beetle was placed in the arena together with prey clusters of ± 10 maggots, it could be observed also that during sunny weather the beetles took the maggots from the cluster and dragged them to a shaded place in the vegetation. After prey consumption they returned in a rather straight way to the prey cluster to capture another prey. This process was repeated until satiation. When it was cloudy the beetles stayed in the cluster until satiation. When more beetles were placed in the arena in the prey clusters often fights between beetles could be observed. Then dragging away of prey from the prey clusters occurred more often.

TABLE 2.3. Observations on velocity (cm/sec), turning rate (degr.sec), turning angle (degr/cm) and concentration of beetles walking in the field. The temperature varied between 17-23 °C. The results are grouped for two satiation levels: hungry beetles (RSATL < 5%, straight walk) and beetles with some gut filling (RSATL > 5%, intermediate walk), and for tortuous walk. (n = number of beetles, SD = standard deviation between the tracks, SE = standard error of the mean of the tracks).

	n	Speed		Turning rate		Turning angle		Concentration	
		cm/sec	SE	degr/sec	SE	degr/cm	SE	mean	SD
RSATL < 5% (straight)	9	4.3	0.4	16.2	5.1	4.8	1.2	0.74	0.15
RSATL > 5% (intermediate)	8	1.6	0.25	22.2	7.0	13.8	4.2	0.63	0.10
Tortuous walk	6	0.9	0.15	28.5	10.0	32.4	11.2	0.55	0.12

2.2.3 Discussion

Observation of walking tracks with the help of video equipment is a nice but also a very laborious technique. In the laboratory the tracks could be followed rather easily. The field observations gave more problems. It was especially difficult to indicate the timesteps correctly. The time lag between the moment of hearing the time signal and drawing the time mark on the plastic sheet attached to the monitor was a source of errors. This time lag is in the order of 0.3-0.5 sec. If the time lag would be constant there is no problem, but because of its variability it may result in an error of about 10-20% of speed estimates. At low velocities marking give other problems, because distances are small and the marks come too close together by which the velocities estimated have to be considered cautiously.

Pauses smaller than 2 seconds have been omitted. They occurred irregularly and in fact do decrease the calculated average velocity of the track. Brunsting

(1983) got the same problems during his observations of displacement of *P.oblongopunctatus* in the laboratory, but he even included pauses up to 30 seconds into the activity pattern.

When we correct his measurements adequately the speed of active, well fed beetles appeared to be: at 7°C 0.85 cm/sec, 10°C 1.1 cm/sec, 16°C, 1.9 cm/sec, 20°C 2.2 cm/sec. and at 25°C 3.4 cm/sec. These velocities are about the same for fed beetles of *P.coerulescens*. As beetles of both species are of about the same size this could be expected (Evans, 1977). Just as in *P.oblongopunctatus* also in *P. coerulescens* a raise of temperature increases the speed of locomotion as was observed by Mossakowski and Stier (1983). They did experiments with hungry beetles and forced them through a tunnel and found at 10°C 1 ± 0.2 cm/sec, at 15°C 3 ± 0.5 cm/sec, at 20°C 5.8 ± 1 cm/sec, at 25°C 8.5 ± 1 cm/sec and at 30°C 9 ± 1.5 cm/sec. The velocity at $\pm 20^\circ\text{C}$ is about similar to that found in my observations for hungry beetles.

In this analysis of the walking pattern spatial and temporal components of the walking pattern are blended. To get insight in the effect of velocity on the structure of the path both its relationship with the turning rate (degrees/sec) and the turning angle (degrees/cm) have been considered. From the observations it is quite clear that the turning angle depends on the speed of walking. The turning rate on the other hand is for most of the tracks almost constant. But at extreme low and high velocities the rate is respectively higher or lower. This results in a significant negative correlation between turning rate and velocity (fig. 2.11). when all the tracks are involved. Therefore, the turning angle (= turning rate/speed) becomes relatively smaller as the speed increases, otherwise the product of turning angle and velocity would result in a constant value (= angle/sec). This is mainly due to the relative high turning rate made at a low speed and the low turning rate at high speed. At low speed this results in a strong winding searching pattern. This is what is usually referred to as 'area restricted search'. This offers an argument for the hypothesis that the tortuosity of the track may be determined by more factors than by low speed alone. It may also be that at low velocities, after prey consumption, both an extra internal or external stimulus makes that the the distribution of the turning rate becomes wider and the average rate becomes higher. This extra high turning rates may be initiated by the remains of the prey (external stimulus) or by a stimulus from the crop expansion. When no other prey is discovered this stimulus may wane so that the beetle returns to the speed it had before the previous feeding.

Differences between field and laboratory observations in *P.coerulescens* especially hold for the walking velocity. This was most probably caused by the vegetation density which was much higher in the field than in the laboratory experiments. Structure and density of vegetation together with the roughness of the soil surface (Mossakowski and Stier, 1983) are important factors that influence the speed and thus the walking pattern of the beetles. Although velocity in the field was lower than in the laboratory the same three walking patterns could be observed both in laboratory and field. This is a valid indication that in this beetle these walking patterns are general, and that walking speed is mainly gov-

erned by the hunger level in combination with temperature, soil surface and vegetation structure.

2.3 REACTION DISTANCE

2.3.1 Method

Reactions of beetles towards prey were observed in an arena. These reactions could be: a sudden stop with distinct waving of the antennae, a sharp change in direction towards the prey, biting the prey or just investigating the prey with antennae and maxillae. When a beetle showed a reaction towards a prey this was called a discovery.

2.3.2 Results

In an arena most hungry beetles observed showed reactions when they touched a prey item (maggots of 2 mg). The percentage of beetles being in the immediate vicinity of a prey and reacting with a sharp turn or with distinct antenna waving decreased with increasing distance. Between a distance greater than zero but smaller than 1 cm, 75% showed reactions. Between 1 and 2 cm, 40% reacted, and this decreased to 30% when the distance between prey and predator was between 2 and 4 cm. When the distance exceeded 4 cm no reaction of the beetles was observed (fig 2.17).

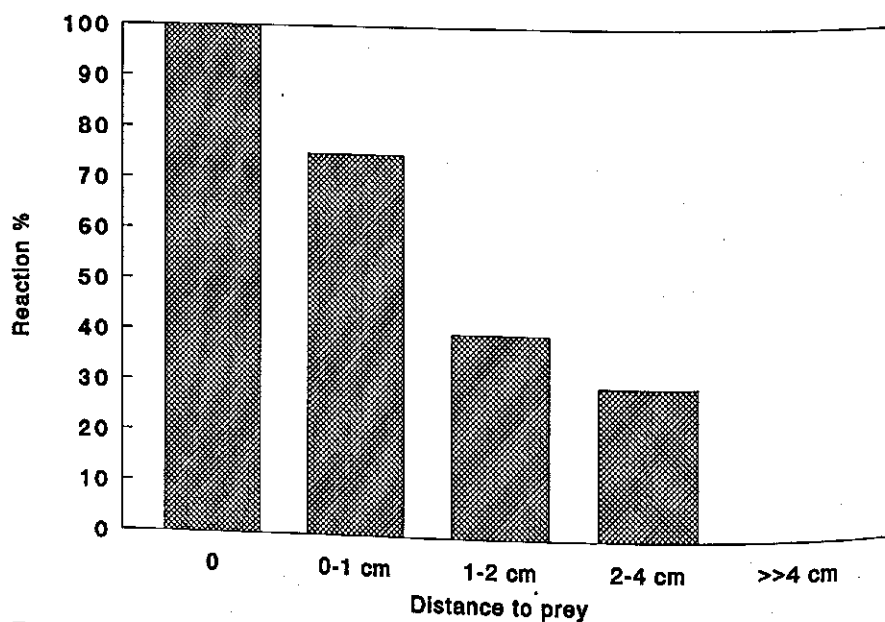


FIG. 2.17 Distribution of % of beetles reacting to prey depending on distance to the prey.

2.3.3 Discussion

P.coerulescens is a diurnal beetle with reasonably developed eyes which are able to observe movements of objects in its neighbourhood (Pers. observations). This suggests that hunting by eye may be a means of tracing prey. Antenna waving is often observed in the immediate vicinity of the prey, which suggests that odours may also be involved in prey searching. However, preliminary experiments on the walking sphere at the Department of Entomology (for description of apparatus see Thiery & Visser, 1986) with *P.coerulescens*, did not show reactions to odours of maggots, contrary to the carabid *P. madidus* that immediately reacted by changing its walking direction. The observation of small prey seems to be restricted to distances up to 4 cm, but from 0 to 4 cm the proportion of beetles reacting decreased sharply. Although the beetle often changed direction in the immediate vicinity of a prey it is difficult to distinguish this from an accidental turn, which is also possible, of course. The number of observations is not high enough to give a clear picture. The chance to make such a turn by accident must be known. This can be computed from the observed turning rate frequency distribution. The observed angle directed to the prey must be compared with the chance to make the same turn by accident.

Reaction distance may be influenced by size and movement of the prey, but the latter factor has not been investigated. The beetle surely is not a specific eye hunter such as the carabid *Notiophilus biguttatus* (Bauer, 1975, 1981, Bauer et al., 1977, Ernsting, 1977, 1978). If vegetation hampers sight only short vision is important, and running into a prey just by random movement and making contact with mouthparts and antennae may be an obvious way of prey discovery. Nevertheless, it must be stressed that each enlargement of the reaction distance will have a positive effect on the discovery rate with prey. Each observation of prey by eye at a greater distance than the prey diameter is increasing the efficiency of searching. In the case of *P. coerulescens* doubling the reaction distance should theoretically double the rate of discovery. But this also depends on the satiation level, because this determines the speed and thus whether the beetle will walk more or less winding, which in its turn determines the degree of recrossing of the walking path and therefore the effectiveness of the searching expressed as the encounter rate.

The reaction distance was measured from the head of the beetle to the outside of the prey. When predator and prey are considered objects with a specific diameter the real reaction distance of a predator to a prey consists of the prey radius plus the predator radius plus the above mentioned distance (see also Skellam, 1958). The predator has a length of about 1 cm and a width of 0.5 cm, a 2 mg maggot measures about 0.5 cm in length and is 0.25 cm wide. As an average for the distance of discovery between prey and predator another cm can be added. Instead of the beetle diameter (1 cm) one can also think about taking the maximum distance between the antennae tips but the average reaction distance then will also be between 1 and 2 cm.

It is not known whether or not hunger elicits an effect on the reaction distance. The results of the few experiments do not give substantial evidence that hunger

is involved. It seems a matter of chance whether or not within a distance of 0-4 cm a beetle discovers a prey.

2.4 SUCCESS RATIO

Experiments were executed in the laboratory with *P. coerulescens* to assess the relationship of RSATL of the beetle with a few prey types it may encounter in the field.

2.4.1 Method

The observations were executed in large Petri dishes (diam 20 cm) with loamy sand on the bottom. A beetle of known weight and satiation level was placed in the dish with a specific prey item. The following prey types were tested: maggots of the blow fly (*Calliphora* sp.) (2-4 mg), larvae of the Heather beetle *Lochmea suturalis*, earthworms (2 cm long) and Leather jackets (larva of *Tipula* sp., 1 cm long). When the beetle didn't react to the prey after 40 contacts with prey the observations were stopped. Then the discovery rate was considered to be close to zero (smaller than 1/40). After consumption of the prey the beetles were weighed. Later on they were used again. Maggots and Heather beetle larvae were tested over more levels of satiation than earthworms and Leather jackets.

To get an impression of the eagerness of a beetle trying to kill a prey also the attack ratio was measured. The attack ratio differs from the success ratio by that only those discoveries are involved in which the beetle tries to kill the prey by biting. Some observations were also executed with wolfspiders (*Lycosidae*) and ants (*Myrmica* sp.) as prey because they were often found in the gut of *P. coerulescens* (Hengeveld, 1980).

2.4.2 Results

The success ratio of the beetle with the maggots is found to be clearly related to the relative satiation level. Maggots appear to be very attractive to the beetles even at a high relative satiation level. The attack and the success ratio are high and run similar even at high satiation levels (fig 2.18a). An attacked maggot is always successfully attacked. The Heather beetle larvae are also attractive at high satiation levels but an attack is not always followed by subsequent killing of the prey (fig 2.18b).

When earthworms and Leather jackets are encountered a different result is found (fig. 2.18c and d). Earthworms are attacked heavily, they seem to be rather attractive but in most cases the earthworms escape from the attack by giving a strong lash with their body, while also the slime gives problems to the beetle. This behaviour results in a low success ratio. Leather jackets are also easily attacked, but the skin of the larva is so tough that only with the highest effort, the mandibles of the beetle can penetrate. After a few fruitless attacks the beetle mostly leaves this prey almost unharmed, thus resulting in a low success ratio.

Wolfspiders are too rapid for the beetle, they always escape and cannot be

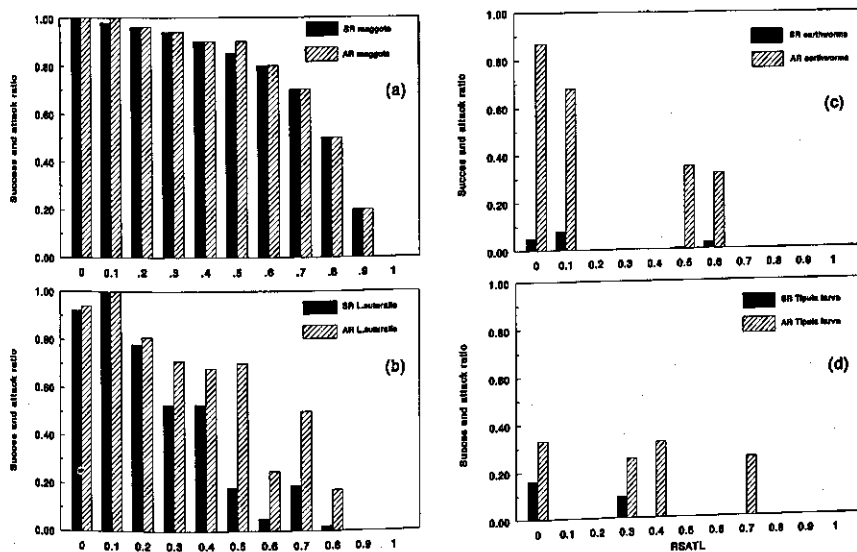


Fig. 2.18 Relationship between both success and attack ratio with relative satiation level of *P. coerulescens* when A) maggots, B) Heather beetle (*L. suturalis*), C) earthworms, D) leatherjackets (*Tipula* sp.) were offered as prey.

captured. The same holds for the ants. The latter attack the beetle furiously, which tries to get rid of them as soon as possible.

2.4.3 Discussion

P. coerulescens is a general predator of all kind of prey (Hengeveld, 1980). Aphids, lepidopterous larvae and diptera form an important part of its diet but also remains of Lycosidae and ants were found. Lepidopterous larvae, maggots and aphids are prey types with a soft body that hardly can defend themselves, which will result in high success ratios when discovered by a beetle. This is supported by the experiments with the maggots and with the heather beetle larvae. The experiments show that defense reactions of prey are important esp. in earthworms and that counterattack of ants is even more effective. The rapid wolfspiders escaped by their higher speed. The observation of remains of these two prey types in the gut of *P. coerulescens* must therefore be from dead or injured specimens. Other less rapidly moving spider species may be an easier prey to get by the beetle.

2.5 VALIDATION OF PREDATION IN AN ARENA

Validation of predation and egg production of this carabid under field conditions is hardly possible, because of experimental difficulties. For instance to

get a reliable average of predation a great number of repetitions is necessary and since field conditions change continuously this cannot be reached by direct observations. Egg production can be measured directly by sieving of the soil, but therefore the beetle has to be disturbed by placing it in another arena and this may influence the predatory behaviour negatively. Nevertheless, to get at least some observations of predation in aggregated prey distributions these were made under constant environmental conditions in an artificial arena in the laboratory.

2.5.1 Methods

Observations were carried out in an arena of 100*150 cm. The soil consisted of loamy sand with light vegetation and some leaves and small pieces of bark under which the beetles could hide. The temperature was about 22°C and the observations were recorded with video (see chapter 2). Only laboratory-reared female beetles, which hatched in late summer and were kept cool at 12°C and which were not fed before in their adult stage were used in the experiment. A single beetle was used per observation. Before each observation the beetle was set at 20°C for one day and weighed just before it was placed in the arena. The observational period lasted 1½ hour. The observations occurred between 10:00 and 14:00 o'clock, because of diurnal rhythm in locomotory activity of the beetle (chapter 2). Each day one beetle was observed. The prey was *Drosophila* maggots of 2 mg each, which were arranged in two clusters of 7 prey in a hexagonal way with one prey in the centre and placed 10 cm apart. The place of the clusters was randomly chosen but more then 50 cm apart. The maggots were kept at their place in the cluster by a microneedle through the outer parts of their skin.

2.5.2 Results

In the beginning it usually took half an hour before the beetles found the first prey. They walked rather straight and spent a lot of time running around the edge. Capture of the first prey took 36.7 ± 32.5 minutes ($X \pm SD$). After capture and consumption of the first prey others followed rapidly. The beetle changed its walking behaviour into an intensive search by walking tortuously and 'border running' did hardly occur anymore. The time between captures without the time needed for consumption (the handling time) in the same cluster was about 4.3 ± 4.6 minutes ($X \pm SD$ n=42). The interval time between prey capture in another cluster was 7.5 ± 5.7 minutes ($X \pm SD$ n=7). The handling time took 171 ± 38 sec per prey (n=57). No relationship between handling time and hunger level could be found. The average prey capture per beetle for the observation period was 5.7 ± 3.7 ($X \pm SD$).

2.5.3 Discussion

For most beetles the time needed to capture the first prey is extremely long compared to the following periods needed for the successive captures. This was mostly due to running behaviour along the borders of the arena and to the

straight walking behaviour in that period. This border behaviour may be a consequence of straight walking on such a small surface. It is striking to see that the border behaviour disappears after capture of the first prey. The increase of windingness appeared to be very effective in capturing successive prey even in another prey cluster. Another point is the individual difference in capture succes between the beetles, it varied from zero to 11 prey captured. Whether this occurs by accident or depends on individual differences in behaviour can be solved by simulation of predatory behaviour in an arena as has been done in the next chapter.

3.0 SIMULATION

3.1 DEVELOPMENT OF SIMULATION MODELS

To simulate predation rate and the resulting egg production at different densities and distributions of the prey a model was constructed that integrates the most important components of predation and egg production of the beetle. To analyse the effect of the various components of behaviour this was done in three steps.

1. A model of walking behaviour and prey encounter was developed that simulates the walking patterns and prey discovery at different prey densities and distributions. With this model the importance for the searching efficiency of various components of walking behaviour, resulting in the three observed walking patterns, can be studied. This also offered the possibility to investigate at which prey distribution the various types of walking behaviour are most profitable for the beetle.
2. Integration of the relationship between relative satiation level (without the influence of ovary size) and locomotory activity, succes ratio, walking speed and duration of tortuous walk into the previous model, to study the effect of satiation on predatory behaviour.
3. Integration of ovary growth and egg production into the relative satiation model, resulting in a complete model that, for one beetle at several distributions and densities of the prey, simulates predation and egg production over a season.

3.1.1 Simulation of walking behaviour and prey discovery

A general description of the simulation model of walking behaviour and prey discovery is given below. An annotated computer program listing is given in appendix I.

The following aspects are incorporated in the model:

- a) Walking velocity.
- b) Standard deviation and kurtosis of the frequency distribution of the turning rate and their relationship with walking velocity.
- c) Duration of tortuous walk.
- d) Prey cluster scanning and individual prey scanning.
- e) Reaction distance to prey.
- f) Prey density and prey distribution.

The aspects from (a) to (d) are properties of the beetle, (f) concerns prey pro-

properties and (e) concerns properties of both. In this model satiation effects are not yet incorporated.

Velocity and turning rate.

The average speed of the beetle is introduced as a forcing variable at the beginning of the simulation. Beetles do not walk with a constant speed but show variations in velocity. Therefore each time step a value is taken at random from a uniform distribution around this average value (the speed in a track varied randomly around the average speed with a standard deviation of 50% of the mean as this was observed to occur in the individual tracks of the beetles (chap. 2)). The direction of walking is calculated by drawing randomly a direction from the experimentally established distribution of the turning rate. This is done again at each timestep, and the next angle is added to the former direction which then gives the new direction (fig.3.1).

As the speed (V) of the beetle is known (for each time step this is the distance between two sets of coordinates XP_1, YP_1 and XP_2, YP_2 it is possible to calculate the new coordinates of the beetle with the cosine rule.

$$XP = XP + \text{COS}(\text{DIR}) * V$$

$$YP = YP + \text{SIN}(\text{DIR}) * V$$

The walking direction (DIR) of the beetle depends both on the former direction and on the turning rate (A) drawn randomly from the Tukey distribution.

$$\text{DIR} = \text{DIR} + A$$

$$A = AV + \text{SIGMA} * (P^{\text{KURT}} - (1-P)^{\text{KURT}}) / \text{KURT}$$

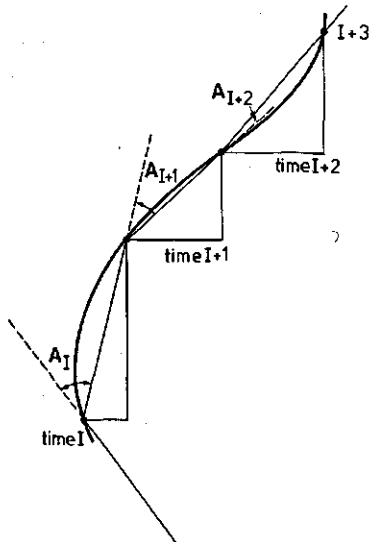


FIG. 3.1 Turning rate (A_I, A_{I+1}, A_{I+2}) at consecutive timesteps.

This formula calculates the turning rate/2 sec as a function of the average (AV), the standard deviation (SIGMA) and kurtosis (KURT) of the turning rate distribution (see Chapter 2.).

The model simulates the walking of beetles in an arena of a specific size. The moment the beetle reaches the border of the arena it will rebound into the field.

Duration of tortuous walk.

Just after consumption of a prey, the beetle resumes searching at a very low speed. When no new prey is encountered the speed increases gradually to the speed before consumption or to a level that corresponds with a specific level of satiation. In the discovery model the duration of tortuous walk is kept constant at 300 seconds being the average duration of tortuous walk. During this period the speed gradually increases to the speed at which the beetle was walking before prey consumption. Parallel with the increase of speed the distribution of the turning rate changes from wide to narrow because the speed determines the SIGMA and Kurtosis parameter of the TUKEY distribution.

Prey distribution and prey encounter.

In the program the distribution of the prey can be arranged such that it may vary from random to very aggregated. This is done by putting the prey in discrete prey clusters of a specific size. The numbers of prey in each cluster, the number of clusters and the size of the clusters can be varied. The prey is considered to be immobile. In the clusters they are randomly distributed, and the clusters themselves are also randomly distributed in the arena. The arena is a square which can be varied in size. The clusters are circular.

The area of discovery.

In the model, the beetle is represented as a circular object with a specific radius. The prey is considered in the same way. Together with the distance of prey discovery they constitute the reaction distance (radius predator + radius prey + discovery distance) which varies between 1 and 2 cm. When the beetle is walking it covers a path with a width of 2 times the reaction distance in which it can discover a prey (the area of discovery). In the model prey discovery in the area of discovery is calculated by giving each prey in the cluster coordinates relative to a new coordinate frame. This frame is perpendicular on the moving direction of the beetle during the time step (fig 3.2).

When a beetle moves from one position to the next an area is covered consisting of a strip of 2 times the reaction distance in width but also consisting of the half of a circle at the start and end of the step. When the beetle moves to the next position with a change in direction a portion of the area is covered twice (fig 3.3). Double counting of prey present in that area has to be avoided.

Two situations can be distinguished (fig 3.4, I and II)

I) The distance a beetle covers during one time step ($V =$ the speed per timestep) is larger than its reaction distance.

In this case three area's can be distinguished (fig 3.4, I).

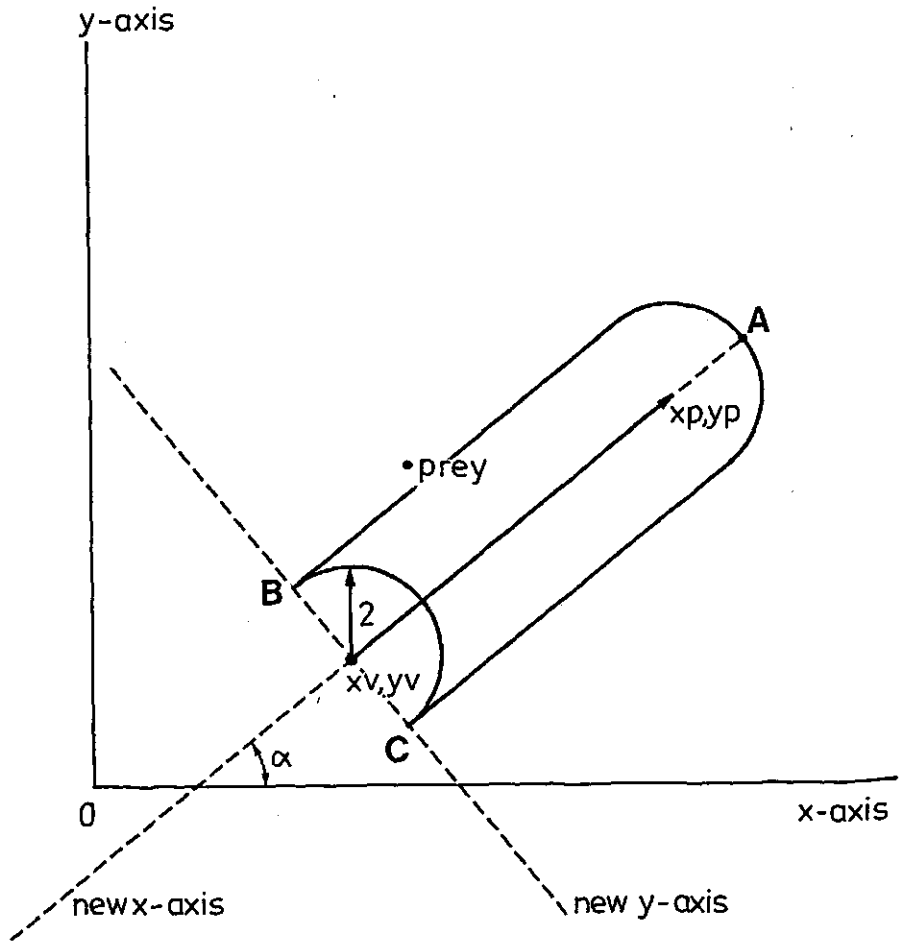


FIG. 3.2 A new coordinate frame is constructed, to determine whether a prey is in the beetles area of discovery. For a number of points the coordinates are given in this new frame. $x_v, y_v = (0, 0)$. $x_p, y_p = (V, 0)$. $A = (V + \text{radius}, 0)$. $B = (0, \text{radius})$. $C = (0, -\text{radius})$.

- A) X-coordinate is smaller than reaction distance
- B) X-coordinate is larger than reaction distance but smaller than V
- C) X-coordinate larger than V

The prey items located in each part of the area of discovery must be scanned separately to see which one has already been discovered in the previous time step (for details of the program see appendix I).

II) The distance a beetle covers during one time step is less than its reaction distance (fig. 3.4.II). In this case only those prey items further away than the reaction distance from XV, YV and closer to XP, YP than the reaction distance (the white area in the figure) are considered to be discovered.

In this model the discovered prey are put back into the cluster with a new

• II

• III

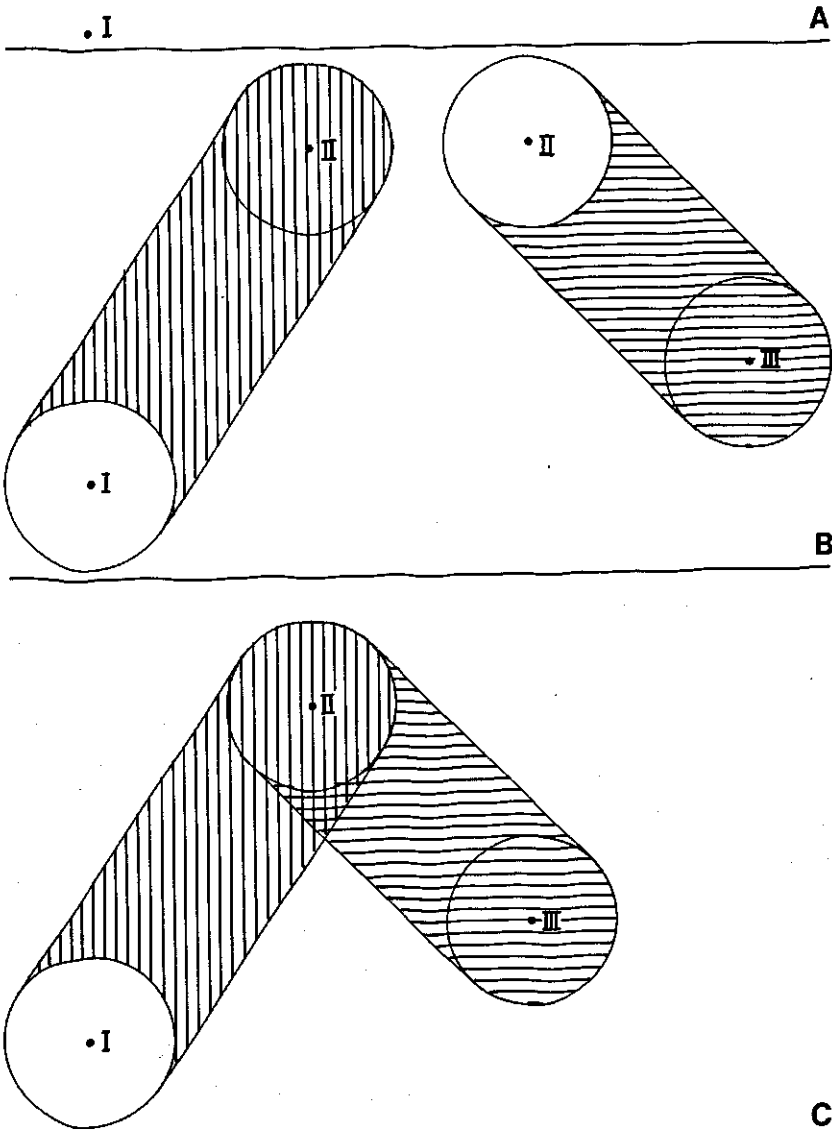


FIG. 3.3 A, location of the beetle at three consecutive timesteps I,II,III. B, area searched from times I to II and II to III. C, area searched from time I to III. The double hatched area is covered twice.

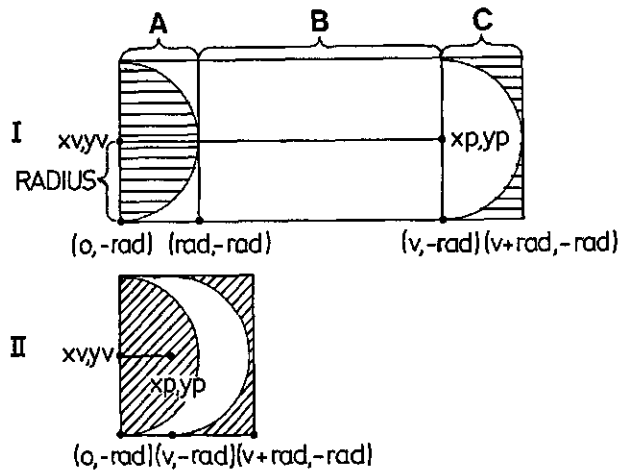


FIG. 3.4 Prey located in non-hatched areas is encountered by the beetle. Two situations are shown: I) The speed $>$ RADIUS, II) The speed $<$ RADIUS. xv, yv is the former position of the beetle and xp, yp is its new position of the beetle. Coordinates given in the figure are the new coordinate frame (see text).

set of coordinates if the prey density has to remain constant, or they are removed from the cluster when this is not necessary. For the calculation of a functional response of a predator to prey density the average density in the field has to remain constant. If the prey remains at the same spot the chance of encountering the same prey twice or more is very high especially when the speed is low and the prey density in the cluster high. This may give erroneous high rates of discovery.

Cluster scanning.

It is less laborious to first determine which cluster is within the reaction distance of the beetle and subsequently to scan only the prey of that cluster than to scan all prey in the field each time step. To determine whether or not a cluster is within the reaction distance of the beetle the coordinates of the centrally located prey of a cluster are used. If the distance measured between the center of the beetle and the center of the cluster is smaller than the sum of the reaction distance of the beetle and the cluster radius, only then the distance to each individual prey in that nearest cluster will be measured. If this condition is not fulfilled the next walking step will be taken and cluster scanning will start over again.

3.1.2 Coupling motivational state and searching behaviour

To analyse the searching behaviour in relationship to the motivational state of the beetle the following relationships were integrated into the searching model:

a) Locomotory activity (TWALK), b) Success ratio (SR) and c) Walking velocity

(V) all with respect to the relative satiation level (for the appropriate values see chapter 2).

In this simplified model a fixed maximum gut capacity is used and RSATL is only determined by ingestion and by gut-emptying. Prey size is given as a fraction of the maximum gut capacity. Thus each time a prey is consumed RSATL is increased with that fraction. Gut emptying is simulated with the relative gut emptying rate found at 20°C (Mols, 1988).

a) Calculation of the level of locomotory activity.

The time a beetle spends walking during a specific timestep can be calculated from the relations found in the experiments concerning the relationship between the relative activity coefficient ($AC = (\text{actual activity}) / (\text{maximum activity of hungry beetles per time period})$) and RSATL (chapter 2). Per timestep the activity period can be calculated with:

$$WALK = AC * \text{FREQ} * \text{MAXACT}$$

WALK = The total time a beetle is locomotory active during a timestep.
AC = The relative activity coefficient related to the relative satiation level.
FREQ = The fraction of the total daily locomotory activity realized during that timestep.
MAXACT = The duration of locomotory activity of a hungry beetle expressed in hours per day at 20°C

In the motivational model the timestep of integration (DELTA) is a quarter of an hour, which is sufficient to calculate the decrease of RSATL by digestion. The walking part of the program is running during that quarter for TWALK seconds.

b) Success ratio and RSATL

The relationship between the success ratio and RSATL determines the chance of a discovered prey to be captured. The relationship found for maggots is used in the model (see chap 2.)

c) Velocity and RSATL

When RSATL exceeds 5% the average walking velocity decreases from about 5 cm/sec to an average of 2.5 cm per sec (fig 2.12). This is included into the model.

d) Duration of tortuous walk.

Each prey consumption is followed by tortuous walk. During that period the velocity is adapted to the value that corresponds with the actual RSATL. The duration depends on RSATL according to figure 2.19. Thus when the beetle is still very hungry after consumption of a small prey tortuous walk may last

11 minutes during which the speed increases slowly to the level of 5 cm/sec. When RSATL is about 50% tortuous walk is shorter (about 4 minutes) and than speed returns sooner to the level of 2.5 cm/sec. When RSATL exceeds 80% tortuous walk does not occur any longer.

3.1.3 Simulation of searching, predation and egg production

In this extended model the relationship of locomotory activity with RSATL and with the diurnal rhythmicity is combined with the complete motivational part including egg production and with the searching and predation part. RSATL is governed by ingestion and egestion and by the egg load. One run of the model concerns the simulation of searching, predation and egg production during a whole season, which takes about 35 days at 20°C.

3.2 SIMULATION EXPERIMENTS

I) Simulation of searching independent of motivation.

Simulations were done with the searching model (appendix 1) in which only walking behaviour was incorporated. The goal was to investigate the range of prey distributions and densities at which the walking behaviour of *P. coeruleus* is most profitable. The distributions varied from random to extremely aggregated. The overall prey density per arena was varied over a wide range depending on the simulation experiment. Prey cluster size was investigated from 5, 10, 20, 30, 40, 80, 160 to 320 cm diameter. Prey number in the cluster was varied from 5, 10, 20, 40 to 80. All different combinations of cluster diameter and prey/cluster were tested.

The effect of the following characteristics of walking behaviour were analysed in the simulations:

- 1) Speed in a range varying from 1 to 5 cm per sec in the random prey distributions, and average speeds of 2.5 and 5 cm per sec in the aggregated distributions. The latter were chosen because they resemble the average speeds found in beetles with food in the gut and in hungry beetles respectively.
- 2) The effect of having tortuous walk after consumption of a prey item.

The beetle's discovery rate with prey per hour was used as output variable of the simulations.

The number of repetitions of the simulations was dependent on the aggregation of prey. The stronger the aggregation the more simulations were needed to obtain reliable values of the discovery. For 5-20 prey/cluster 50 runs were necessary and for more than 20 prey/cluster 100 runs, because in the latter case only few clusters were present in the arena when the overall prey densities were kept low.

II) Simulation of searching and predation coupled to motivation.

Simulation runs were made for periods of one hour. For each run in sequence prey was replaced in the arena with the same density and distribution, but not

at the same place. In the simulations the beetles were considered to be active during the whole period. With the results of the simulations functional response curves could be constructed. This is done for different prey densities and prey distributions, varying from random to strongly aggregated with the same cluster diameters and prey number per cluster as mentioned before.

In aggregated prey distributions simulations were done with:

- a) Constant prey density. A captured prey was randomly replaced at another place in the cluster.
- b) Decreasing prey density by removal of captured prey. By this procedure local depletion of prey occurs, which is a natural phenomenon in predators. As a consequence prey density in the arena does not remain constant. Thus no normal functional response curves can be constructed in this way. It is to be expected that at locally high prey densities the average density/m² will not change much after a capture but at locally low prey densities local removal of prey may exert a negative influence both on the discovery rate and on the predation rate.

III) Simulation of searching, predation and egg production.

Simulations were done at constant temperatures with random as well as with aggregated prey distributions. The prey is replaced every day. The overall prey density varied from 0.125 to 16 prey/m² for random prey distributions and from 0.125 to 8 for aggregated prey distributions. The aggregated distributions were done with 20 prey/cluster, and the cluster diameters used were: 5, 10, 20, 30, 40, 80, 160, 320 cm. The prey density in the clusters with 20 prey per cluster depends on cluster surface and is respectively: 11088, 2546, 636, 283, 159, 39.8, 9.94, and 2.48 prey/m². Reaction distances of 1 and 2 cm. were tested in the simulations. The effect of TW and of prey depletion was tested in random prey distributions and in aggregated distributions at prey densities ranging from 0.25, 0.5 and 1 prey/m².

IV) Simulation of dispersal.

The beetle *P.coerulescens* only rarely flies, thus dispersal almost exclusively occurs by walking. Therefore, dispersal of the beetle depends both on walking speed, on windingness of the walking track, and on the duration of locomotory activity. These are determined again by the motivation of the beetle, which in turn depends on prey density and distribution. With the help of the searching model it is possible for each walking speed to simulate dispersal of the beetle from a fixed point in the environment. The dispersal is measured as the linear displacement from the starting point. This linear displacement is simulated for the walking velocities ranging from 1 to 6 cm/sec for the time periods 1, 2, 4, 8, 16, 32 and 64 minutes and for 5.4 hours as the latter is the maximum period of activity per day for a hungry beetle. Each velocity-time combination is repeated 100 times.

V) Simulation of the validation experiment.

Simulation was done in an area with the same surface as in the experiment (see chapter 2.5). Two clusters with 7 prey, each were placed at random in the arena. The complete model was run for the appropriate part of the day: Start at 11 pm for 90 minutes. As a comparison the model was also run with 14 prey placed at random in the arena. The captured prey items were not replaced. The simulation model was adapted for this small arena by including walking along the border of the arena into it. The moment the beetle reaches the border of the field it was not rebounded into the field but it followed the border depending on the choice of the subsequent angle. When an angle is chosen that should lead the beetle outside the field the border will be followed, other angles will bring the beetle back into the field again. This approach is an assumption, but as no quantitative information was available about behaviour of the beetle in the field to borders this was chosen. It results in patterns that resemble the walking behaviour observed in the neighbourhood of borders and obstacles.

3.3 SIMULATION RESULTS

The simulated walking pattern was analysed in the same manner as the real walking patterns. The turning rate at different walking speeds obtained in this way were the same as those found for the real tracks. This was also the case with the concentration parameter. It was concluded that the model simulated the walking patterns correctly. Therefore, the simulation experiments were carried out as planned.

3.3.1 Searching without motivation.

a) Random prey distributions.

The discovery rate per hour of the beetle with randomly distributed prey with and without performance of tortuous walk after each discovery is shown in fig 3.5 (a and b). In both cases the discovery rate increases steadily both with increasing velocity and with increasing density of the prey. When the velocity exceeds 2.5 cm/sec the discovery rate increases strongly because of the decrease of windingness. When prey is randomly distributed tortuous walk has an inhibiting effect on the discovery rate. This effect becomes stronger both when prey density and walking velocity increases. At low velocities (< 1 cm/sec) the path is so winding that a further decrease of speed caused by tortuous walk, and consequently followed by an increase in windingness has hardly any influence on the discovery rate anymore since the linear displacement is very low. The difference in discovery rate between walks with and without tortuous walk increases with prey density and depends on walking velocity. At a speed of 5 cm/sec the difference at a prey density of 1 prey/m² is about 11% and increases up to 45% at 5 prey/m² and becomes greater at higher prey densities. In table 3.4.1 the simulations are given for $V = 5$ and 2.5 cm/sec at an increasing range of prey densities. The

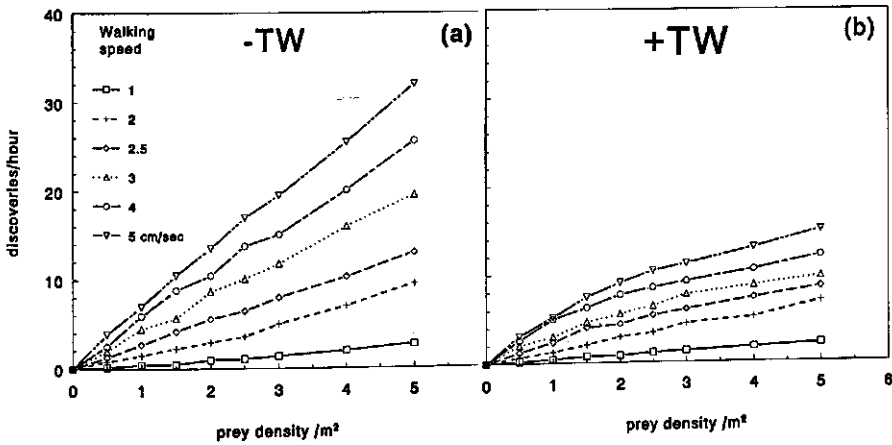


FIG. 3.5 Discovery rate (discoveries/hour) with randomly distributed prey, simulated for different walking velocities (cm/sec) of the beetle, a) without and b) with tortuous walk after prey encounter.

coefficient of variation (SD/mean) is about similar for tracks with and without TW.

The efficiency of the walking track can be expressed as the distance covered per discovered prey (= path length/discoveries). When a comparison is made per tracks with and without tortuous walk than it appears that up till a prey density of 8 prey/m² the efficiency is approximately the same for both tracks. Above this prey density TW becomes more and more inefficient, because by the high discovery rate the amount of time spent in TW increases, thus the average walking speed decreases more and more resulting in a walking pattern that becomes more and more winding. Recrossing occurs more often and this decreases the efficiency of the track.

b) Aggregated prey distributions.

If in aggregated prey distributions a discovery is *not* followed by tortuous walk the mean discovery rate is the same as in random prey distributions. Only the standard deviation of the discovery rate per hour depends on the cluster type (prey density in the cluster and cluster size). The coefficient of variation increases both with a decreasing number of clusters and with increasing prey density per cluster (for an example see fig.3.6). The smaller the cluster and the higher prey density in the cluster the higher the standard deviation of the discovery rate. At a high prey density in the cluster the number of clusters per area decreases (because the overall prey density per m² in these simulations remains constant), thus the distance between the clusters increases and therefore a beetle needs more time to cover this distance. Therefore, long periods between discoveries will be followed by series of short periods when the beetle is in a prey cluster. Tortuous walk after prey discovery increases the discovery rate, but the

TABLE 3.4.1. The effect of tortuous walk on the discoveries per hour at two walking velocities ($V = 5$ and 2.5 cm/sec). Simulations without motivation and and success ratio. Prey is randomly distributed and the density is kept constant. A discovered prey is placed elsewhere in the arena. Reaction distance = 2 cm. Averages are based on 50 runs; path+ /path is the ratio of the pathlength with and without TW; disc+ /disc- is the ratio of discoveries with and without TW.

prey density/m ²	coefficient						
	Disc- overies	variation		pathlength		path/ discoveries	ratio disc+ /disc-
		average	SD	sd/disc	average		
V = 5 cm/sec -TW							
0.05	0.30	0.51	1.70	18000	100	60000	1
0.1	0.74	0.72	0.97	18000	100	24324	0.97
0.25	1.60	1.25	0.78	18000	100	11250	0.97
0.5	3.36	2.00	0.60	18000	100	5357	0.93
1	6.60	3.12	0.47	18000	100	2727	0.89
2	13.39	3.16	0.24	18000	100	1344	0.61
4	25.74	4.72	0.18	18000	100	699	0.50
8	49.00	6.97	0.14	18000	100	367	0.38
16	98.00	13.6	0.14	18000	100	184	0.26
32	191.70	12.9	0.07	18000	100	94	0.18
V = 5 cm/sec +TW							
0.05	0.30	0.58	1.93	17779	459	59263	path+ /path-
0.1	0.72	1	1.39	17505	706	24313	0.99
0.25	1.56	1.1	0.71	16891	756	10828	0.96
0.5	3.12	1.42	0.46	15795	1002	5063	0.94
1	5.86	1.73	0.30	13940	1124	2379	0.87
2	8.16	1.43	0.18	12501	917	1532	1.14
4	12.82	2.51	0.20	9974	1208	778	1.11
8	18.72	2.55	0.14	7881	919	421	1.15
16	25.24	2.76	0.11	5798	600	230	1.25
32	33.70	3.21	0.12	4347	353	129	1.37
V = 2.5 cm/sec -TW							
0.05	0.15	0.27	1.80	9000	60	60000	disc+ /disc-
0.1	0.26	0.56	2.15	9000	80	34615	0.85
0.25	0.76	0.89	1.17	9000	80	11842	0.87
0.5	1.48	1.13	0.76	9000	80	6081	0.80
1	2.62	1.66	0.63	9000	80	3435	0.85
2	5.32	2.65	0.50	9000	80	1692	0.76
4	10.28	3.30	0.32	9000	80	875	0.70
8	20.50	5.14	0.25	9000	80	439	0.53
16	43.78	8.19	0.19	9000	80	206	0.37
32	85.78	11.11	0.13	9000	80	105	0.25
V = 2.5 cm/sec +TW							
0.05	0.15	0.44	2.93	8933	194	59553	pathd+ /path-
0.1	0.22	0.42	1.91	8905	159	40477	0.99
0.25	0.66	0.74	1.12	8756	261	13267	1.12
0.5	1.18	1.06	0.90	8548	399	7244	1.19
1	2.22	1.33	0.60	8233	444	3709	1.08
2	4.06	1.52	0.37	7547	532	1859	1.10
4	7.20	1.94	0.27	6591	585	915	1.05
8	10.96	2.50	0.23	5647	577	515	1.17
16	16.22	2.16	0.13	4335	395	267	1.30
32	21.38	2.86	0.13	3410	346	159	1.52

coefficient of variation (SD/mean)

$v=2.5$ cm/sec, No tortuous walk

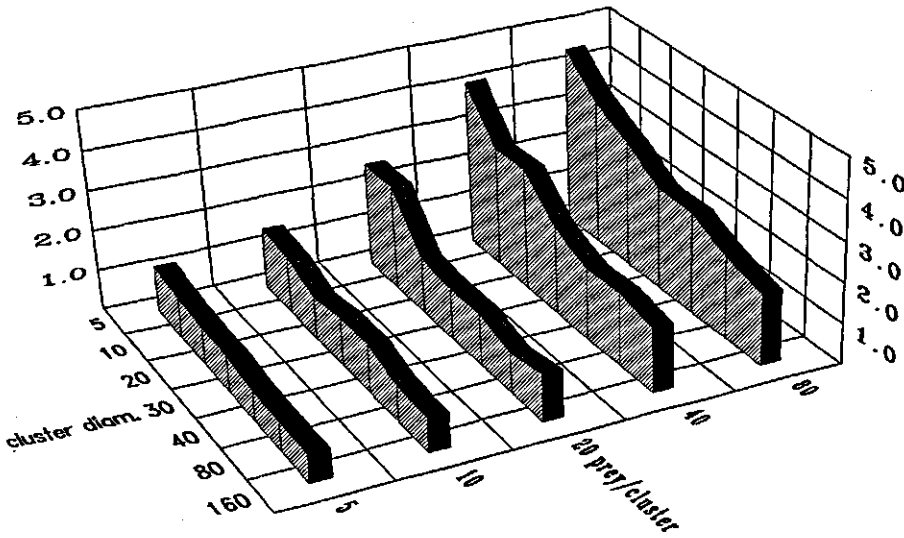


FIG. 3.6 Coefficient of variation (SD/mean), without tortuous walk, of prey discoveries when prey is distributed aggregated. In that case the mean discovery rate equals that with random prey distributions. Overall prey density is 1 prey/m².

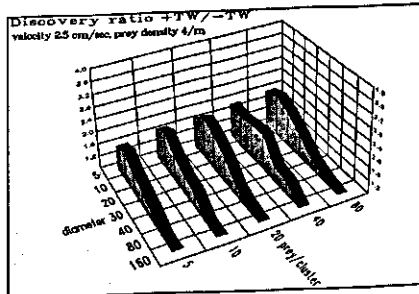
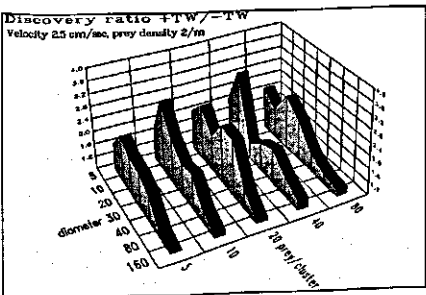
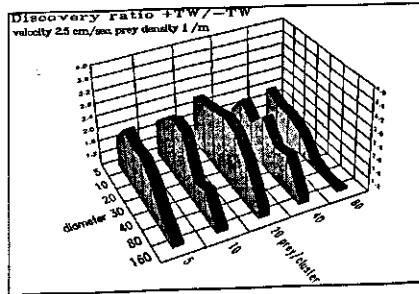
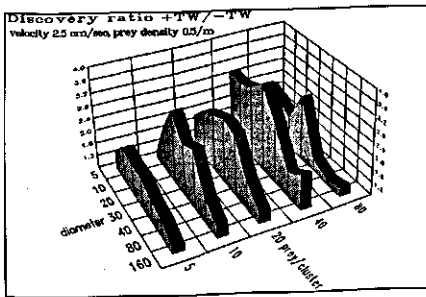


FIG. 3.7 Effect of tortuous walk in different aggregated prey distributions and overall prey densities, expressed as a ratio of the discoveries with and without tortuous walk after prey encounter.

size of the effect depends both on walking velocity, on cluster size, and on prey density in the cluster. To show the positive effect of tortuous walk in aggregated prey distributions, the ratios of discovery rates per hour between walking tracks with (+TW) and without tortuous walk (-TW) are given in figures (3.7 a to d) for 4 different prey densities.

The figures show an optimum for the positive effect of tortuous walk that depends on the walking velocity as well as on the cluster size and prey density in the clusters. In general, increase of the average prey density decreases the positive effect of tortuous walk, because after each discovery the walking speed decreases thus decreasing the average walking speed over the whole searching period. When $V = 2.5$ cm/sec tortuous walk shows its highest profit at intermediate cluster diameters from 10 to 40 cm.

The efficiency of the walking pattern (path length/discovery rate) is demonstrated in fig 3.8.a,b for $V = 5$ and 2.5 cm/sec. These figures show that at the average prey density of 0.5 prey/m² the effort for the beetle to discover a prey is minimal between small clusters crowded with prey and large clusters that almost approach a random prey distribution. In small crowded clusters it takes a longer walk to reach a cluster, because the distance between the clusters is long. In large clusters the prey density in the clusters is so low that tortuous walk becomes less profitable also. Both for walking speeds of 5 and 2.5 cm/sec it shows that prey in clusters of an intermediate size are discovered with the lowest cost in terms of walking distance. Simulations done at higher average prey density show that the lowest effort shifts more to the smaller clusters and to the higher number of clusters per arena.

3.3.2 *Searching and predation coupled to motivation*

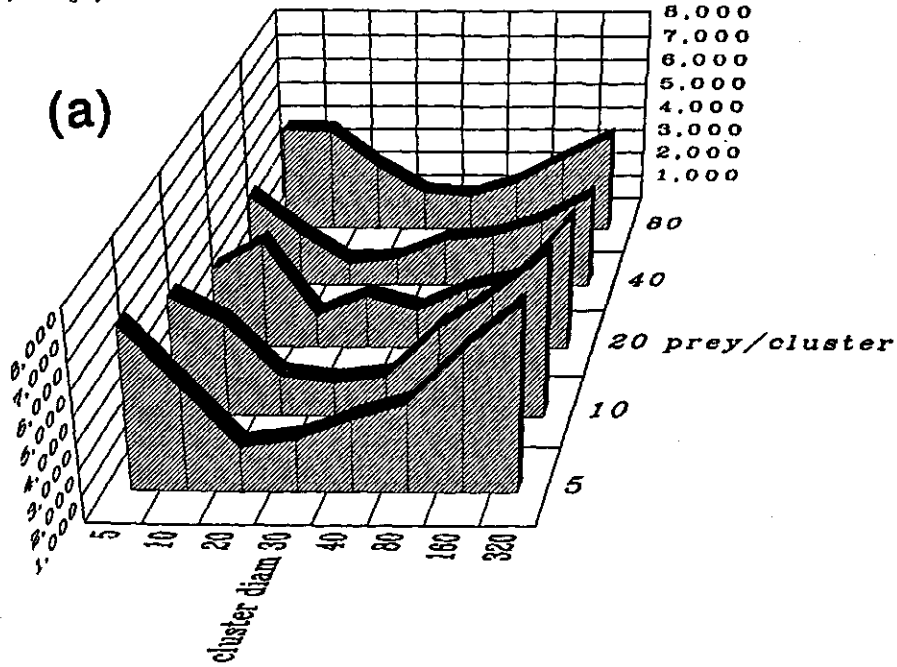
1) **Random prey distributions.**

The effect of the success ratio on predation is clearly shown in fig (3.9 a and b). At increasing prey density the discovery rate steadily increases, while the predation rate is levelling off to approximately 12 captures per hour at the highest prey density. This effect is mainly caused by a decreasing success ratio when satiation level increases, although at low prey densities the walking speed also influences the form of the curve. At the start of the simulation walking velocity is 5 cm/sec but after capture of the first prey the velocity decreases to 2.5 cm/sec. Therefore the first prey will be captured at a rate which is twice that of the second prey. At prey densities below 1 prey/m² no difference can be found between the discovery rate and the capture rate as almost each discovered prey will be captured. At prey density 4 /m² the discovery rate curve seems to bend upwards when TW is involved. This is caused by the decrease of the duration of tortuous walk when the beetle becomes more and more satiated, and which is absent above 80% of RSATL. Above this satiation level the walking speed remains constant thus from that prey density the discovery rate increases linearly with prey density.

When prey density is not kept constant after capture of a prey it decreases

pathlength/discoveries

prey density 0.5 prey/m, v=5 cm/sec



pathlength/discoveries

Prey density 0.5/m, v=2.5 cm/sec

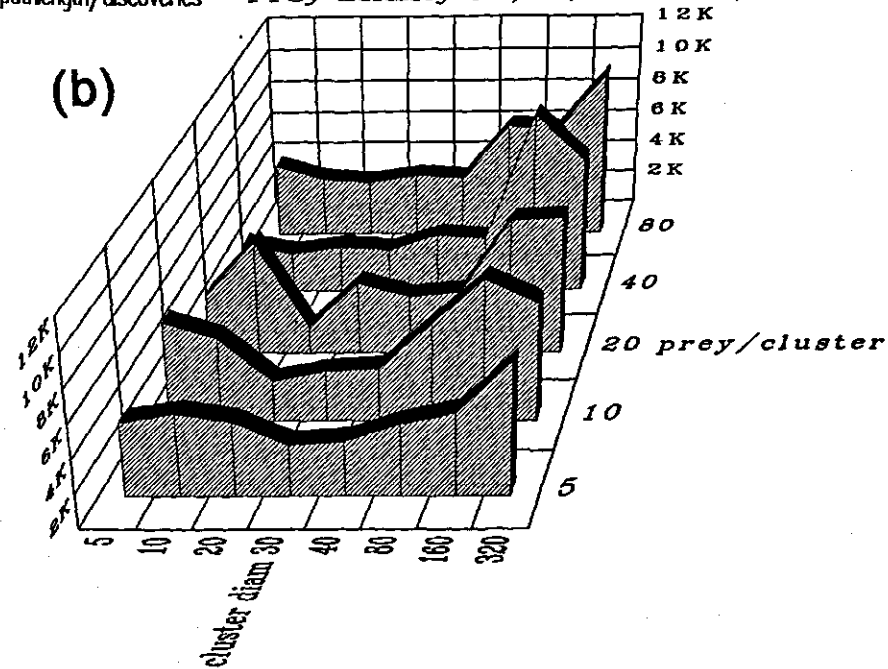


FIG. 3.8 Distance walked by the beetle per prey discovered in aggregated prey distributions for two walking velocities: a) 5 cm/sec, b) 2.5 cm/sec. Overall prey density is 0.5 prey/m².

slowly after each capture, which leads to a slightly lower discovery rate, but it hardly influences the capture rate (fig. 3.9 a and b), because the prey is replaced every hour.

When the reaction distance is halved from 2 to one this decreases the discovery rate also with 50%, but as the capture rate levels off at increasing prey density the effect of decreasing relative distance becomes smaller at increasing prey density.

2) Aggregated prey distributions.

Figures 3.10 (a to d) and 3.11 (a to d) show the effect of walking behaviour in situations of constant and decreasing prey densities respectively caused by predation in relation to cluster diameter, and prey number per cluster, at two average prey densities viz. 0.5 and 1 prey/m². To illustrate the difference between random prey distributions and aggregated distributions the discovery and the capture rate of random prey distributions for these two prey densities are given by the horizontal lines. It shows clearly that both discovery rate and capture rate at these two prey densities are significantly higher when the prey is aggregated. It also shows that this strongly depends on the cluster diameter as small, but larger than 5 cm diameter, clusters, result in higher discovery rates than large clusters and extremely small clusters. Prey depletion does affect the discovery rate at cluster diameter up to 80 cm and when the prey density per cluster is high. This can be explained by the increase of the distance between the clusters. The capture rate is much lower than the discovery rate and seems only affected by local prey depletion when prey number per cluster is low. This is because the discovery rate remains sufficiently high. This is only the case when the arena is sufficiently large in relation to prey density (> 100 m²) to overcome a serious decrease in overall prey density. When the clusters have a high prey number (thus only a few clusters per arena) the capture rate decreases to the average

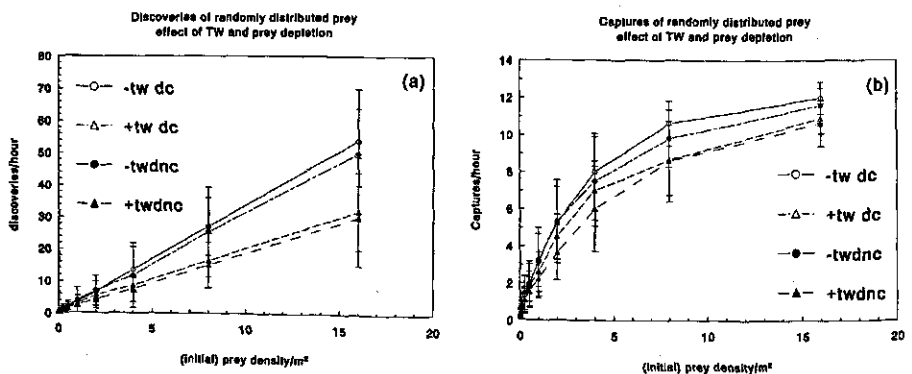


FIG. 3.9 Discoveries (a) and captures (b) when prey is randomly distributed. Effect of tortuous walk (+ or -TW), and effect of prey depletion (density constant = dc, density not constant = dnc) are shown.

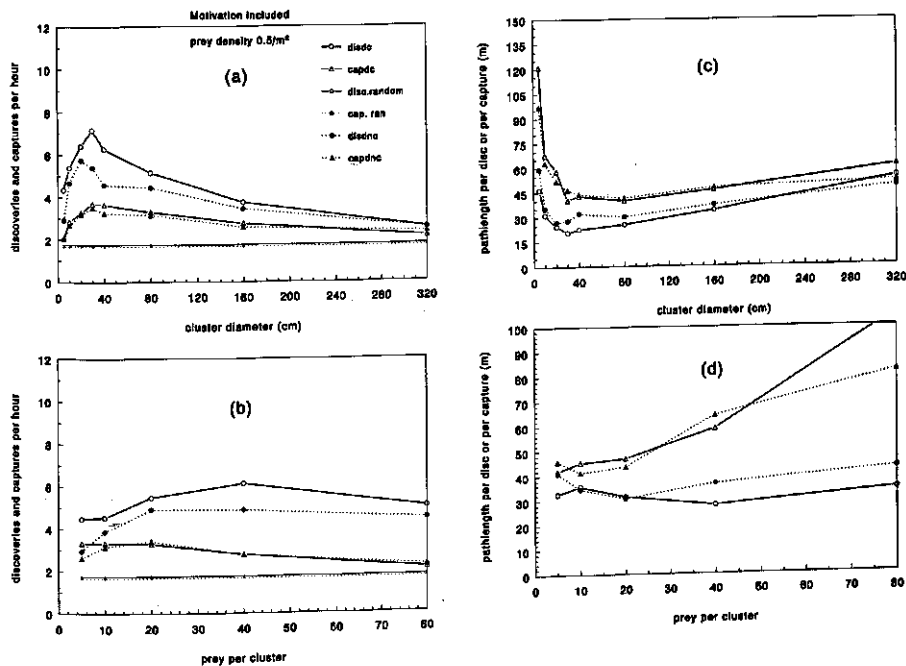


FIG. 3.10 Effect of cluster diameter (a,c) and prey/cluster (b,d) on discoveries, captures and the distance walked per prey in aggregated prey distributions at an overall prey density of 0.5 prey /m² at constant prey density (dc) and with depletion of prey (dnc) by the beetle. The values for the random prey distribution are given for comparison.

value of the random prey distribution, because of the satiation of the beetle and of the long distance between the clusters. Once a prey cluster is reached the beetle cannot eat more than up to satiation, the success ratio decreases strongly and although more prey are discovered they will not be captured. The same can be said for the pathlength walked per prey discovery or per prey capture (fig 3.10 and 3.11 c and d). The searching is most effective at intermediate cluster sizes (10-80 cm diameter). When clusters are smaller and heavily crowded long distances have to be walked per prey discovery or per prey capture, and above 80 cm the distance increases to the distance walked as for random prey distributions

3.3.3 Searching, predation and egg production

Random prey distributions.

Prey density.

The discovery rate in relationship to prey density is shown in fig 3.12. Whether or not prey density is kept constant after predation of a prey seems

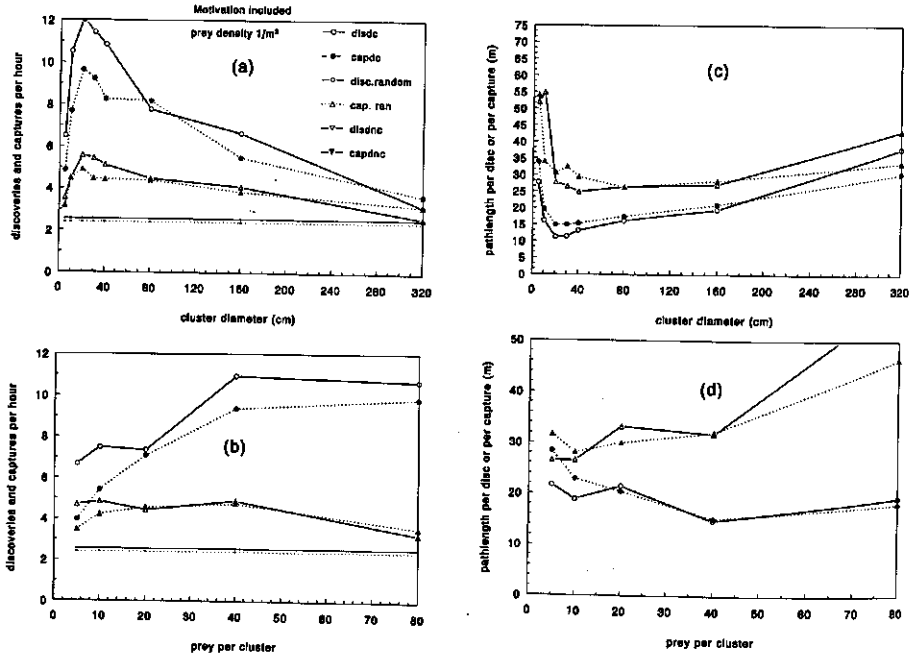


FIG. 3.11 Same as Fig 3.10 but with overall prey density of 1 prey/m².

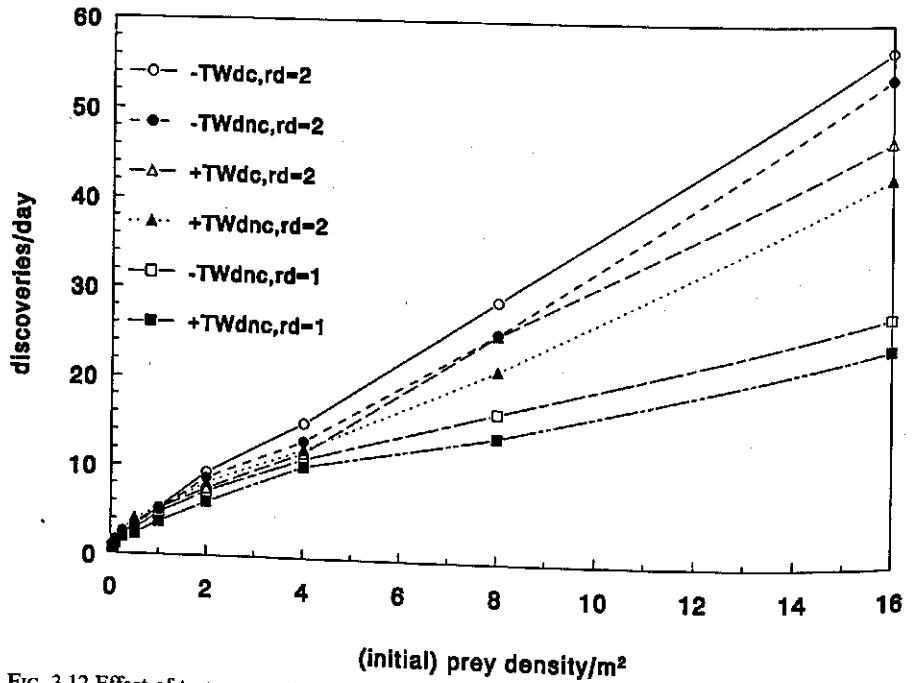


FIG. 3.12 Effect of tortuous walk (+ or -TW), prey depletion (dc or dnc) and reaction distance (rd = 1 or 2 cm) on number of discoveries per day for random prey distributions of increasing density.

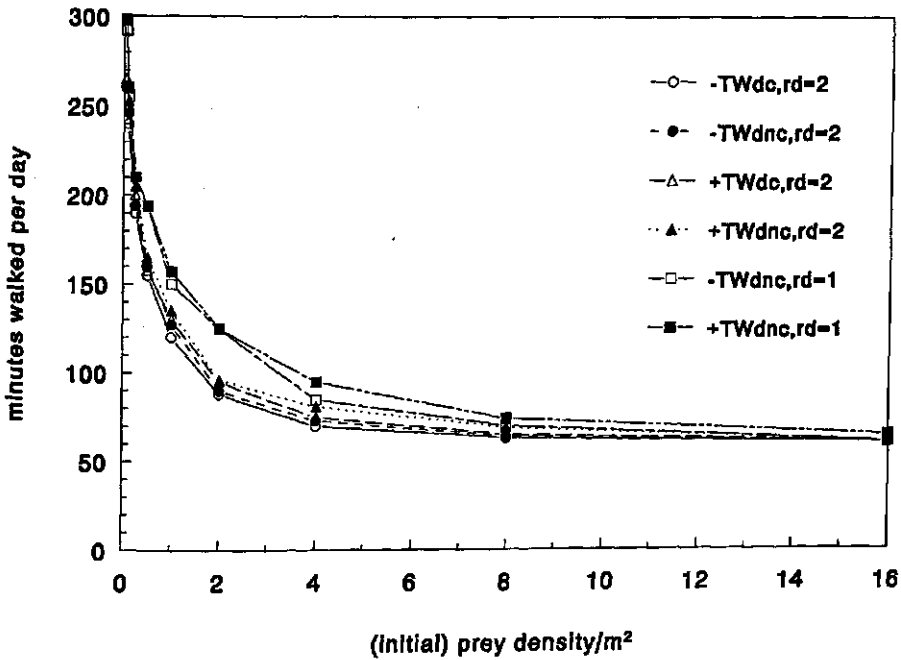


FIG. 3.13 Effect of tortuous walk (+ or -TW), prey depletion (dc or dnc) and reaction distance (rd = 1 or 2 cm) on locomotory activity, expressed in minutes per day, for random prey distributions of increasing density.

hardly to affect the discovery rate when prey is replaced daily. Even on this time scale local prey depletion does not seem to play an important role. At low prey densities (smaller than 4 prey/m²) the curves increase like a power curve. Above this density the discoveries increase almost linearly with prey density. This can be explained by the switch of the walking speed from 5 to 2.5 cm/sec when RSATL exceeds 5%. after the first prey capture. At low densities more time is spent by walking at high speed. As prey density increases this high speed is replaced by intermediate speed and in the mean time the total locomotory activity is decreasing. Above 4 prey/m², almost all the walking is done at an average speed of 2.5 cm/sec. and locomotory activity does not decrease much anymore (fig. 3.13).

Capture and consumption rate per day follow a Holling 2 curve (fig 3.14 a and b) and the same can be observed for the egg production per season (fig.3.14 c). No strong effect of prey depletion either on capture and consumption rate as on egg production can be observed. The interval of prey replacement is too short for that.

Tortuous walk: Tortuous walking has only a small influence on the discovery rate when prey density is below 1 prey/m². Above this density the negative effect

Random prey distribution, captures/day
effect TW, reactive dist., prey density

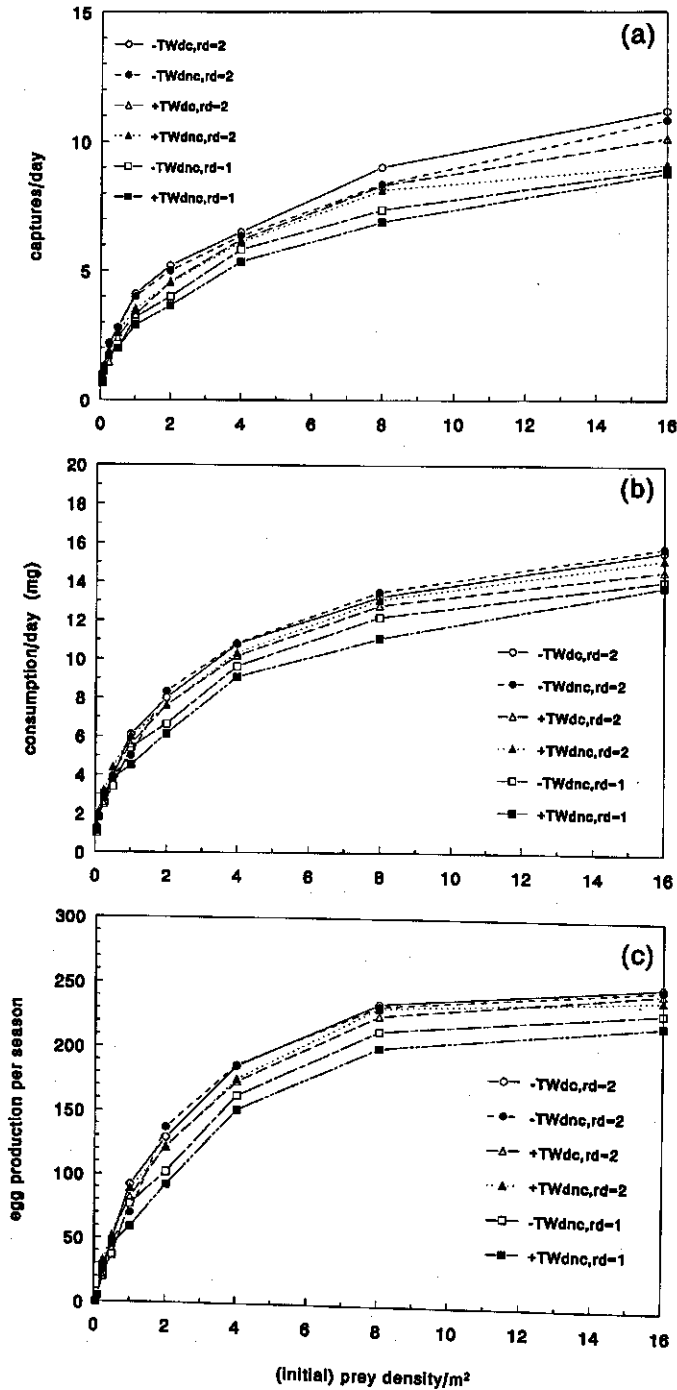


FIG. 3.14 Effect of tortuous walk (+ or -TW), prey depletion (dc or dnc) and reaction distance (rd = 1 or 2 cm) on captures per day (a), on the consumption/day (b), and on the egg production per season (c) for random prey distributions of increasing density.

of tortuous walk is increasing up to 20%. With tortuous walk the pathlength per day is shorter and locomotory activity is approximately 5% higher than in behaviour without tortuous walk. Thus locomotor activity is only partially compensating the effect of lower prey capture when tortuous walk is performed.

Concerning predation, consumption and egg production the difference resulting from behaviour with and without TW is small. Generally having TW in random prey distributions results in a lower predation rate. Per prey density the effect is not significant. The negative effect of TW on egg production is greatest between 1 and 8 prey/m²

Reaction distance. Up to prey density 4 prey/m² halving the reaction distance from 1 to 2 cm has only a small effect on the discovery rate. Up till this density locomotory activity is almost complete compensating the effect of the decreased reaction distance. Above this density the effect of reaction distance becomes more and more important up till about 50% at 16 prey/m². This effect can be explained by the form of the locomotory activity curve in relationship to prey density (fig. 3.13). Compensatory effects are strong up to 4 prey/m², above this prey density locomotory activity remains almost constant.

Above prey density of 1 prey/m² the effect of halving the reaction distance on the capture rate is about 15%. Below this density no difference can be observed. For consumption and egg production (fig.3.14 b and c) the same effects can be observed because they are a direct result of prey capture.

Aggregated prey distributions.

Since predation rate is hardly affected by local prey depletion when prey is replaced once per day this schedule is used further on for the simulations of searching and predation in aggregated prey distributions.

Cluster diameter: In fig 3.15 the influence of cluster diameter is given on discovery rate, capture rate and consumption per day for 20 prey/cluster and a reaction distance of 2 cm.

Prey discovery is clearly influenced by the cluster diameter. The discovery rate is always higher in clustered than in random prey distributions. The lower prey densities show the highest discovery rate in clusters with 30 cm diameter, but when the prey density increases this shifts to clusters with a smaller diameter.

Generally it can be stated that at low overall prey densities (< 1 prey/m²) prey clustering results in higher capture rates compared to random prey distributions. At higher prey densities only the very small clusters result in a higher capture rate than the others and random prey distribution. At higher overall prey densities the intercluster distance is shorter which makes the small (high density) clusters becoming better attainable. The larger clusters give capture rates that are similar to those found at a random prey distribution. Up till an overall prey density of 1 prey/m² prey clusters of 20, 30 and 40 cm diameter prey are utilized better resulting in higher consumption rates. Above this overall density the capture, consumption (fig 3.15) and egg production rates (fig 3.16)

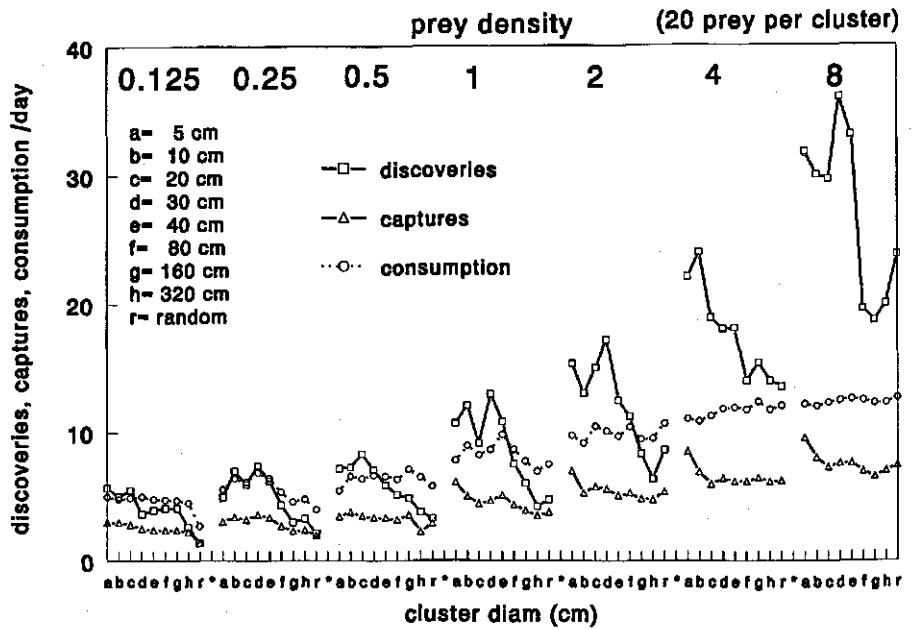


FIG. 3.15 Effect of prey cluster diameter on discoveries, captures and prey consumption (mg) per day for different overall prey densities. The number of prey/cluster is 20. The captured prey was removed from the field.

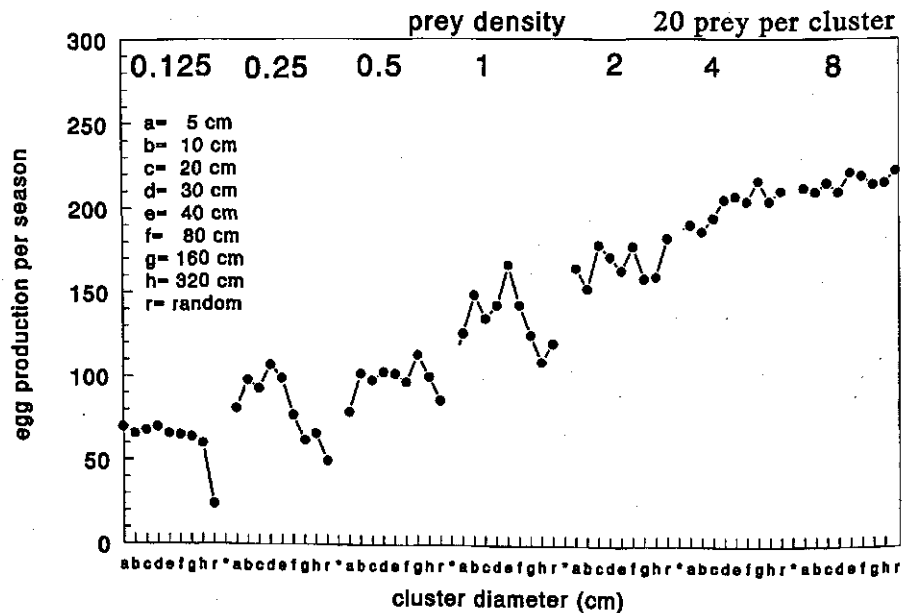


FIG. 3.16 Effect of prey cluster diameter on total egg production per season for different overall prey densities. The number of prey/cluster is 20. The captured prey was removed from the field.

are not different from those in random prey distributions. The high capture rate in the very small clusters at high prey densities do not result in high consumption rate because of rapid satiation in those clusters. Thus profitability, expressed in capture rate, consumption and egg production, of the beetle's behaviour occurs only in aggregated prey distributions at low overall prey densities (smaller than 1 prey/m²).

Walking behaviour: When walking behaviour is considered (spending of time and walking types fig 3.17), it is found that in aggregated prey distributions at low overall densities high activity and much high speed walking is alternated with days with low activity spent in a prey cluster. High speed walking occurs especially at low overall densities and when clusters with small diameters are available. The time spent in high speed walking not only decreases with overall prey density, because the chance to discover and capture a prey increases, but also with increasing cluster diameter, because the distance between prey clusters is shorter. The fraction of time spent in tortuous walk is very short when the prey density in the cluster is high, because once in a prey cluster captures follow each other rapidly, thus leaving less time to complete the whole duration of TW. When prey clusters with the same amount of prey items become larger the distance between the prey in the cluster increases thus giving the beetle more space and time to complete its tortuous walk. Therefore more time will be spent walking tortuously when the clusters are larger. When the prey distribution

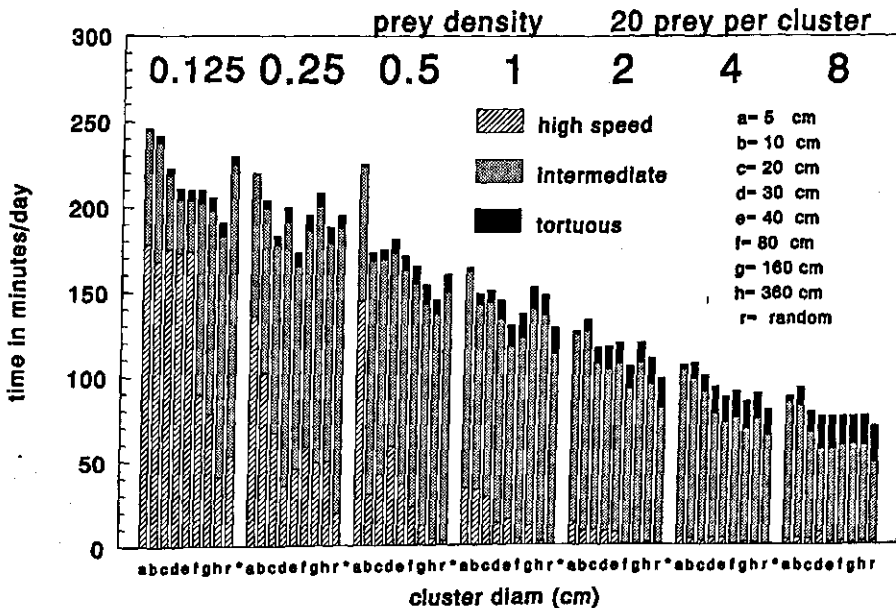


FIG. 3.17 Time (in minutes) per day spent on the three walking types depending on prey cluster diameter (with 20 prey/cluster) and overall prey density.

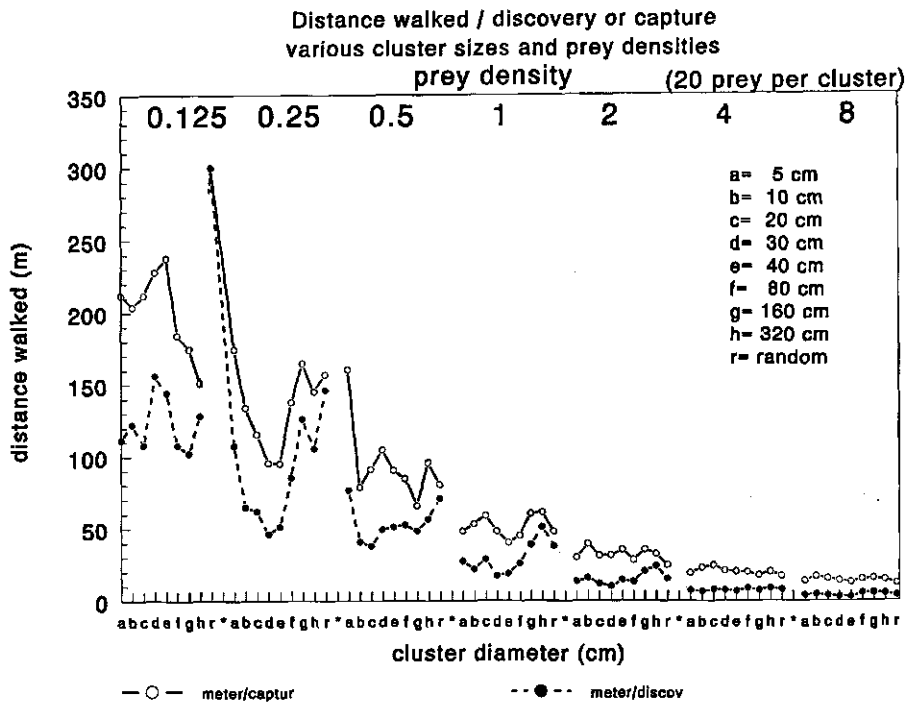


FIG. 3.18 Distance walked (m.) per discovery or per capture depending on prey cluster diameter (20 prey/cluster) and on overall prey density.

approaches randomness the fraction of time spent in tortuous walk is generally longer compared to aggregated prey distributions.

Simulations with the complete model have also been done without performance of tortuous walk to see to what extent having this behaviour is advantageous with respect to prey discovery and prey capture and to egg production in aggregated prey distributions. The results are that the positive effect of TW is only present at very low overall prey densities (< 1 prey/m²) and that it is inversely related to prey density. For prey densities 0.25, 0.5 and 1 prey/m² performance of TW compared to non-performance gives resp 38%, 23% and 2% higher number of discoveries per day, this resulted in resp 32%, 18% and 0% increase in captures/day and a 120%, 16% and 3% higher egg production. The strong effect on egg production at the lowest prey density is because performance of tortuous walk in such poor food situations leads to such an increase of the capture rate that the metabolic threshold (a consumption of 2 mg/day) leading to egg production is exceeded. Therefore, in such poor food situations walking tortuously after prey capture is extremely important.

The average distance which has to be covered by the beetle between two discoveries or two captures depends both on the cluster diameter and on the overall prey density (fig 3.18). The figure shows that only at low densities to 1 prey/m²

discovery rate in relation to
various clustersizes and prey densities

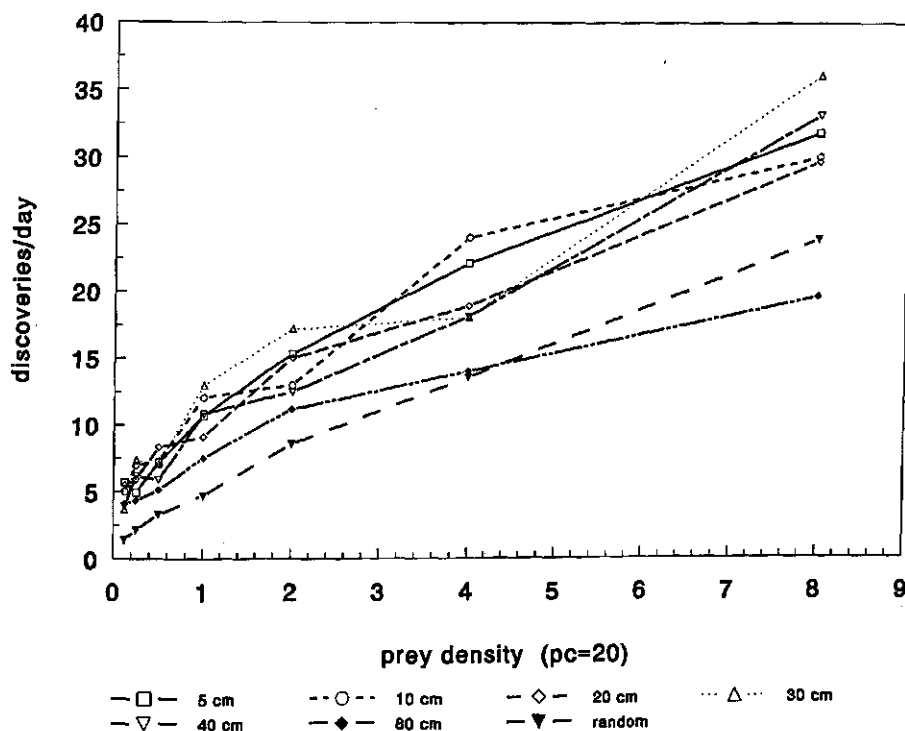


FIG. 3.19 Discoveries per day in relation to overall prey density and prey cluster diameter (20 prey/cluster). The largest clusters (160 and 320 cm diameter) are omitted because their results are the same as for random prey distribution.

and with small cluster diameters between 10 and 40 cm the behaviour is most profitable because than the shortest distance has to be covered. At higher prey densities such a minimum is not observed anymore.

Prey density: To show the positive effects of the combined behavioural components of discovery and predation in clustered prey distributions as compared to random prey distributions the functional (fig 3.19 and 3.20) and numerical respons curves fig 3.21 are given. These show that especially at overall low prey densities the behaviour of the beetle shows its greatest profitability in clustered prey distributions. Small clusters are more heavily attacked than larger ones, which leads to a higher consumption and egg production. When overall prey density exceeds 1 prey/m² it depends on the cluster size whether the prey clustering offers still any advantage for the beetle.

Reaction distance: Decreasing the reaction distance from 2 to 1 cm when prey

capture rate in relation to
various clustersizes and prey densities

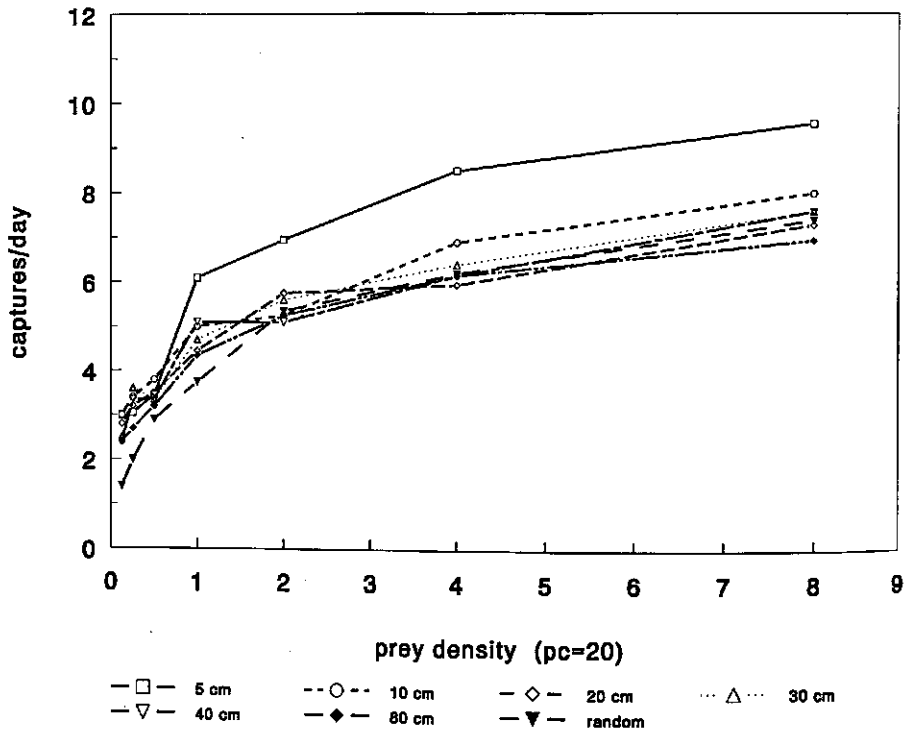


FIG. 3.20 Captures per day in relation to overall prey density/m² (functional response) and prey cluster diameter (20 prey/cluster). The largest clusters (160 and 320 cm diameter) are omitted because their results are the same as for random prey distribution.

is aggregated highly decreases discovery rate (30%) but less so predation rate (15%) and egg production (13%). The greatest effect is found at low overall prey densities in small clusters. This is in contrast with random prey distributions where no effects of changing reaction distance could be observed at such low overall prey densities. In aggregated prey distributions and low overall prey densities more time is spent in straight walk, which is effective because of the smaller amount of recrossings as compared to intermediate walk. But it also results from the fact that in clustered situations the most important capture is the first one. Then the chance to find the first prey is the chance to find a cluster and because behaviour changes and the prey density in a cluster is higher than the overall prey density the next prey will be discovered sooner. Therefore, because of this phenomenon, reaction distance must be considered relative to the cluster size and thus a change of reaction distance from 2 to 1 is relatively small with respect of the size of a cluster. A constraint in this predatory behaviour is that, once a cluster is discovered, satiation is reached soon, because of the high prey

Egg production per season in relation to various cluster sizes and prey densities

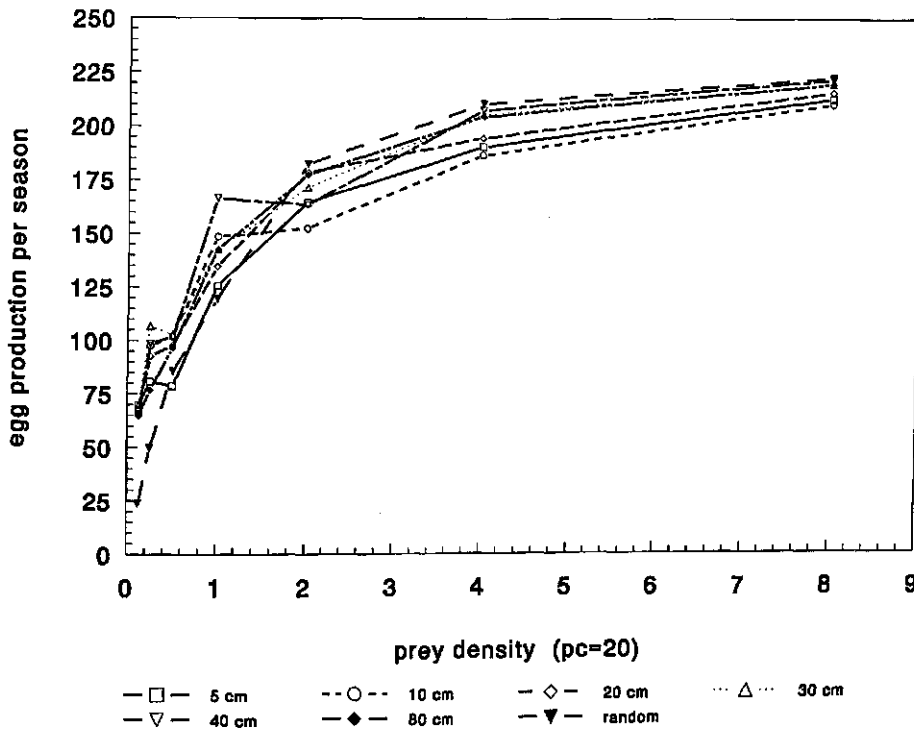


FIG. 3.21 Egg production per season in relation overall prey density (numerical response) and prey cluster diameter (20 prey/cluster). The largest clusters (160 and 320 cm diameter) are omitted because their results are the same as for random prey distribution.

density in a cluster, leading to a relative small effect on capture rate, when reaction distance is halved. When prey clusters are very large, residence time in such clusters becomes longer. In such cases reaction distance becomes more important because the longer the beetle has to deal with the prey density and prey distribution in that cluster, the more the daily capture rate will be determined by the local situation instead of by the overall prey density.

3.3.4 Dispersal of beetles as a result of walking behaviour

The relationship between velocity and linear displacement (Ld) is given in fig.3.22 This figure shows that linear displacement strongly depends on the speed and therefore on the windingness of the track. Tortuous walk keeps the beetle almost on the spot, while intermediate walk gives a linear displacement of approximately 2-3 meters/hour, and high speed walking leads to a displacement of about 6-12 meters/hour. According to the figure linear displacement is dependent on the velocity and is proportional with the square root of the

linear displacement in time
for different velocities

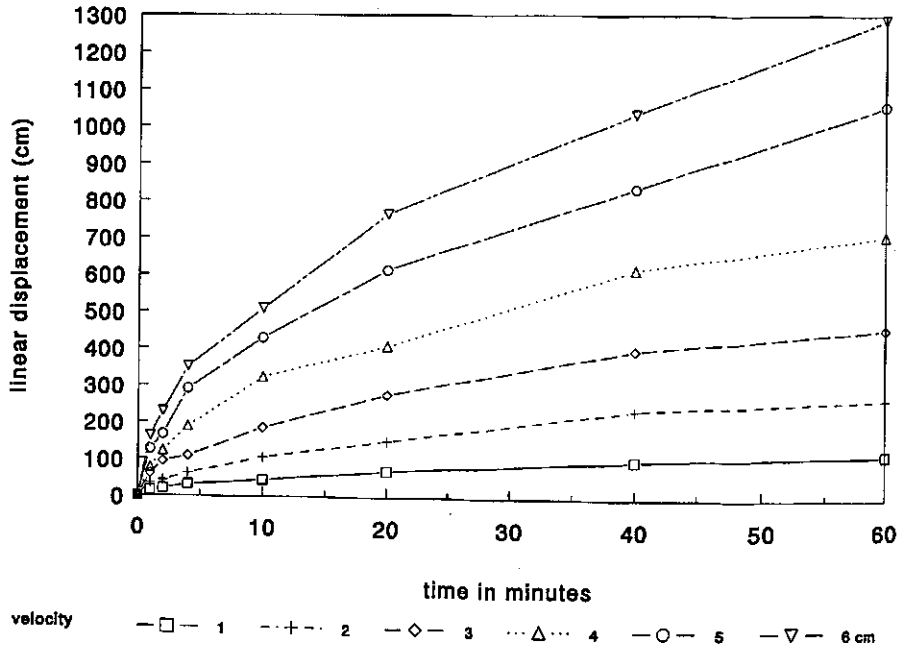


FIG. 3.22 Linear displacement of the beetle in time for different walking speeds. (cm/sec)

walking time according to:

$$Ld = a\sqrt{t} \tag{1}$$

For each velocity the constant (a) is calculated with linear regression. The relationship between the walking velocity (V in cm/sec) and the constant (a) follows closely a power curve according to:

$$a = 1.82 V^{1.385} \quad r^2 = .99 \tag{2}$$

Combining equations (1) and (2) results in a general equation with which the linear displacement of the beetle can be calculated for each walking velocity and for each time period (in seconds):

$$Ld = 1.82 V^{1.385} * \sqrt{t} \quad (\text{cm})$$

With this relationship it is possible to calculate the daily linear displacement of the beetle for each relative satiation level as this results in a specific duration of the locomotory period (see fig.2.4) and in a specific walking speed (fig 3.23)

**linear displacement per day (m)
depending on satiation level at 20 C**

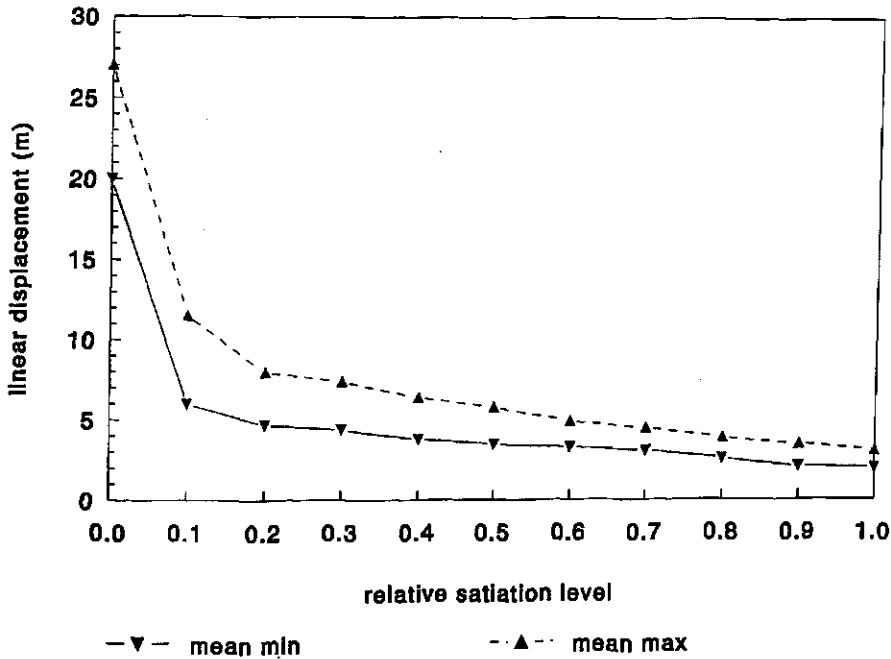


FIG. 3.23 Range of linear displacement per day (min and max) depending on RSATL at 20 °C.
Calculated with formula using $v \pm 0.5$ (resulting in min. and max ld)

In this figure it is shown that hungry beetles have an average daily linear displacement that varies between 17 and 23.5 meter. From $0.1 < \text{RSATL} < 0.6$ this distance varies between 4-9.5 meter and well fed beetles show a displacement of 2-4 meter.

Discussion.

The dispersal of the beetle is determined by its walking behaviour. In areas with a low prey density more time will be spent in high speed walking thus this will lead to leaving an area which is unsuitable and reaching another one that is more profitable in the fastest way. The moment a more profitable area is reached both locomotory activity and speed decrease because the RSATL decreases, resulting in a longer stay in the profitable area. This supports the work of Baars(1979) who measured daily distances covered by radioactively labeled *P.coerulescens* in two different habitats: a poor *Molinia* field and a mosaic type of heathland. He found two distinct patterns of movement in individual beetles. There were periods, sometimes very prolonged, during which the beetles only covered small distances (average 2.5 m ranging from 0-13 meter) in continually

changing directions which he called 'random walk' that alternated with periods in which long distances were covered (average 22 m ranging from 2-87 m) in a more or less constant direction, which he called 'directed movement'. In the Molinia field the beetles performed shorter periods of 'random walk' than in the mosaic field. The duration of 'directed movement' was about equal, but the distances covered during 'directed movement' were larger in the Molinia field nl. 28 m compared to 17 m in the mosaic field. These distances measured at warm days (maximum temp. 24-28 °C) come closely to those calculated for hungry beetles with an average temperature of 20 °C. The alternation of periods with short distances to periods with long distances supports the idea of the beetles reacting to clustered prey in the field. In this view the Molinia field should have prey clusters that are smaller or occupied by lower prey densities than those in the mosaic field. Although alternating periods of low and high temperature may give the same results, the observation that at the same day beetles could be observed that only covered short distances while others walked large distances is not in agreement with that. Simulations of searching behaviour with clustered prey at constant temperatures show the same alternation of long and short distances at low overall prey densities. This also supports the hypothesis that daily linear displacement to an important level is determined by the prey distribution and prey density in the field.

By Okubo (1980) much attention is given to the relationship between the dispersal of organisms and diffusion processes. Diffusion is defined as a ' basically irreversible phenomenon by which matter, particle groups, population, etc spread out within a given space according to individual random motion. When this theory is applied to the beetles it can get the following meaning:

1. The netflux of beetles over a line of one meter and per time unit (for example the border between an unprofitable and a profitable area) equals the diffusionconstant multiplied with the difference in beetle density over that distance.
2. The difference in density is determined by the immi- and emigration of the beetles.
3. If the diffusion constant is different for the 2 areas this will lead to a concentration of beetles in that area with the lowest diffusionconstant.

With the information above and assuming that walking is at random it is possible to calculate the diffusion constant D from the walking behaviour in the following indirect way:

$D = \lim_{t \rightarrow \infty} (Ldis)^2 / (2t)$ This holds when a track is simulated long enough such that the D is constant in the end. This leads to the following equation for the diffusion constant in relation to the walking velocity:

$$D = 5840 * V^{2.738} \quad (\text{cm}^2/\text{hour})$$

With the diffusion constant the general spread of a population beetles over an area can be calculated. This offers a tool to estimate the exchange of individuals of different local populations in dependence of walking characteristics, food

TABLE 3.2. Calculation of diffusion constant D with help of the walking program at different walking speeds.

v cm/sec	D (m ² /hour)	SD
1	0.6	.025
2	3.7	.15
3	10.6	.43
4	26.6	.97
5	51.7	1.9

level and temperature as these determine mainly the walking behaviour. It can also be used the other way around to estimate the general food level of a location once the individual walking characteristics of a species are known in relationship to surface structure and temperature by measuring the immi- and emigration.

Simulation of validation experiment(2.5)
number of captures in 90 minutes

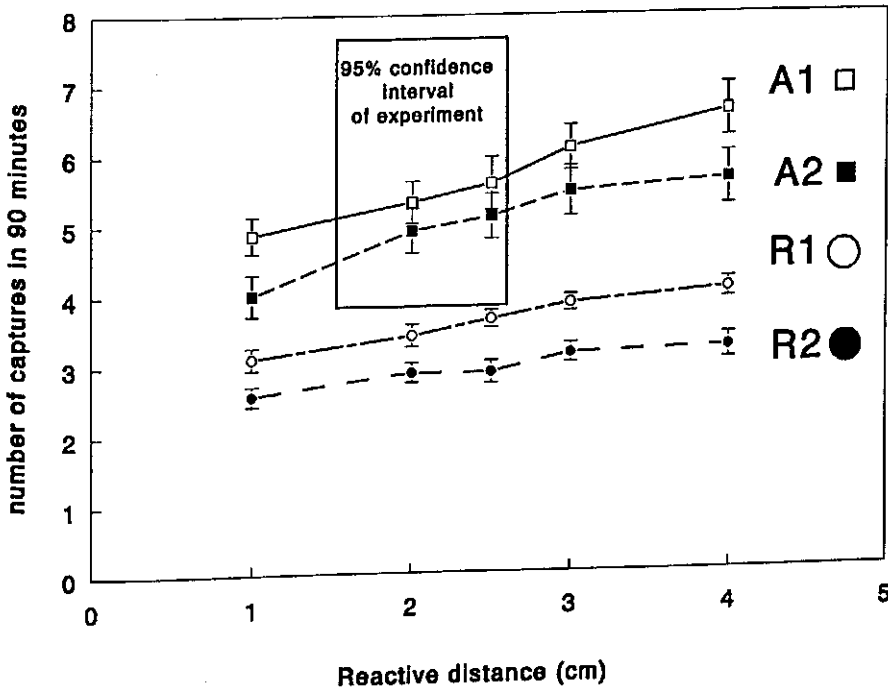


FIG. 3.24 Results of the validation experiment (\pm 95% confidence interval) in an arena of 100*150 cm.(chapter 2.5) compared to results of simulation for aggregated prey (A) and randomly distributed prey (R) related to reaction distance. Prey content is 5% (A1,R1) or 10% (A2,R2) of MAXGUT respectively.

3.3.5 Comparison of validation experiment and its simulation

The mean result of the observations, 5.7 ± 3.7 prey captured/period (10 beetles) (see chapter 2.5) and its 95% confidence interval of the mean are given in fig. 3.24 together with the results of the simulation (average of 100 runs). Because only 10 beetles were observed the confidence interval is quite large. Nevertheless, the results of simulations with clustered prey agree rather well with the observations. Simulations with randomly placed prey show a significantly lower predation rate. Since the maggots offered in the experiment differed slightly in weight, effects of variations in prey weight on the capture rate were simulated by offering prey with a weight of 5% or 10% of the maximum gut capacity of the beetle. By feeding on heavier prey satiation occurs sooner resulting in a lower capture rate, but even this remained within the 95% confidence interval of the experimental results.

Reaction distance of the beetle is not exactly known therefore simulations have been carried out on a range of reaction distances (ranging from 1 to 4 cm) to test the effect of it on predation rate. Changing reaction distance has only a minor effect on predation rate. Probably this is mainly due to prey depletion in such a small arena, because after each prey capture it is more difficult to get the next one. The type of prey distribution has a much stronger effect on predation rate than the reaction distance. Concerning prey depletion, the difference with the results of previous simulations, where effects on capture rate by prey depletion hardly occurred, is due to the size of the arena. In a large arena local lower densities of prey are easily compensated for by the beetle as it walks relatively large distances. In a small arena the beetle is kept at the same location where prey density decreases rapidly by predation.

4.0 GENERAL DISCUSSION

The ultimate aim of this study was to investigate the impact of spatial distribution and density of prey on the predatory behaviour and resulting egg production of the carabid beetle *Pterostichus coerulescens* L. Firstly the driving force ('the motivation') behind foraging behaviour was studied, secondly the most important components of foraging behaviour were identified, and thirdly the relationships between the behavioural components and motivation were quantified. Mols (1988) showed that in addition to the emptiness of the gut the size of the ovaries and of the ripening eggs had to be taken into account, because they limits gut expansion and thus determine the relative satiation level of the beetle and also the rate of change of the satiation level. The latter depends both on the gut-emptying rate and on the egg deposition rate, because egg laying has an effect on the extent of expansion of the gut. Because of the clear influence of the size of ovaries and eggs in *P. coerulescens* the definition of motivation differs from that found for predatory mites (Fransz, 1974; Rabbinge, 1976, Sabelis, 1981), where gut size was considered to be constant. Next, the relative satiation level was related to the components of predatory behaviour. The most important components are: locomotory activity, walking velocity and turning rate, reaction distance to the prey, and success ratio. The implications of the relationships found for predation and egg production in relation to the spatial distribution of the prey, are discussed below.

4.1 PREDATORY BEHAVIOUR AND PREY DISTRIBUTIONS

An important factor determining the predation rate of a predator is the way it searches for its prey. Firstly, the prey habitat has to be located, and then the prey itself has to be found. In *P. coerulescens* this takes place by walking as the beetle rarely flies. Lastly the suitability of the prey has to be established once it has been encountered. However, *P. coerulescens* is a polyphagous predator accepting all kinds of prey (Hengeveld, 1980). Therefore, search for a specific prey habitat is hardly necessary. Its preference for a specific locality will mainly be influenced by other factors such as soil type and structure, vegetation and microclimate (Heydemann, 1955). Sandy soils with a low humus content, open and dry localities with sparse vegetation where sunlight can easily reach the soil, are preferred. When it has found such a habitat it will look for food. This food may include aphids (mostly highly aggregated), larvae of Diptera feeding in the litter (random to aggregated), caterpillars (random to aggregated) and also larvae of the heather beetle (*Lochmea suturalis*), usually highly aggregated.

Thus, the beetle has to deal with prey with all kinds of spatial distributions. Prey density in the beetle's habitat, may be temporarily very low, as in poor heathland and moorland, or sometimes excessively high as during heather beetle outbreaks. In previously cultivated land prey density may be moderate to high depending on the nitrogen content of the soil. From experiments and simulations, it appeared that the beetle was adapted to such varying prey distributions, and can respond to them by changing its behaviour.

4.1.1 The advantage of specific walking behaviour

In the experiments we observed that the beetle may show three distinct types of walking. A) Walking at high speed when it is hungry, B) walking at an intermediate speed when it has something in its stomach and C) a slow very winding walk after eating of a prey. High-speed walking is very useful when large distances have to be covered. It only occurs when the beetle is hungry, disturbed, or when trying to escape from enemies. It is profitable when prey is aggregated or when large prey is randomly distributed at a low density. In these situations high-speed walking between the clusters results in a substantial increase in predation because the distance between them is covered in the shortest time. The time between encounters with clusters is more than halved, because at higher speed the beetle walks straighter. Intermediate speed is advantageous in prey clusters, because it results in a longer stay in the clusters where there is a good chance of meeting the next prey. Tortuous walk (TW) is only profitable if prey are aggregated (Chapter 3.3.1); with randomly distributed prey it is disadvantageous as it decreases the discovery rate because the high degree of recrossing results in a low linear displacement. If the duration of TW could remain constant it would have more effect as the prey density increased. However, the duration of TW is not constant, rather it depends on RSATL and decreases as the satiation level increases. This means that at increasing prey densities it will have less and less effect until it disappears above a RSATL of 80%.

Considering the rate of discovery that results from the walking behaviour without the feedback of the motivational part, sizes of clusters can be found in which TW behaviour is more useful. Tortuous walk was of most use within clusters smaller than 30 cm diameter. The high degree of recrossing at velocities of below 3 cm/sec decreases the effectiveness of the search (area searched/distance walked). On the other hand, because of this intensive search, a small area will be inspected very thoroughly. Of course, this is only profitable when prey is aggregated.

The effectiveness of this walking pattern can be estimated by simulating the discovery rate of the beetle at different walking speeds and with randomly distributed prey. The outcomes of these simulations can be compared with estimations calculated with the Skellam formula (Chapter 1.1), where the effect of turning resulting in recrossing is not included. The differences between the results of simulation and of calculation with this formula gives an estimate for the effect of recrossing. The more winding the path, the more recrossings and the lower the effectiveness. The effectiveness is estimated by dividing the simu-

Efficiency of walking depending on walking velocity

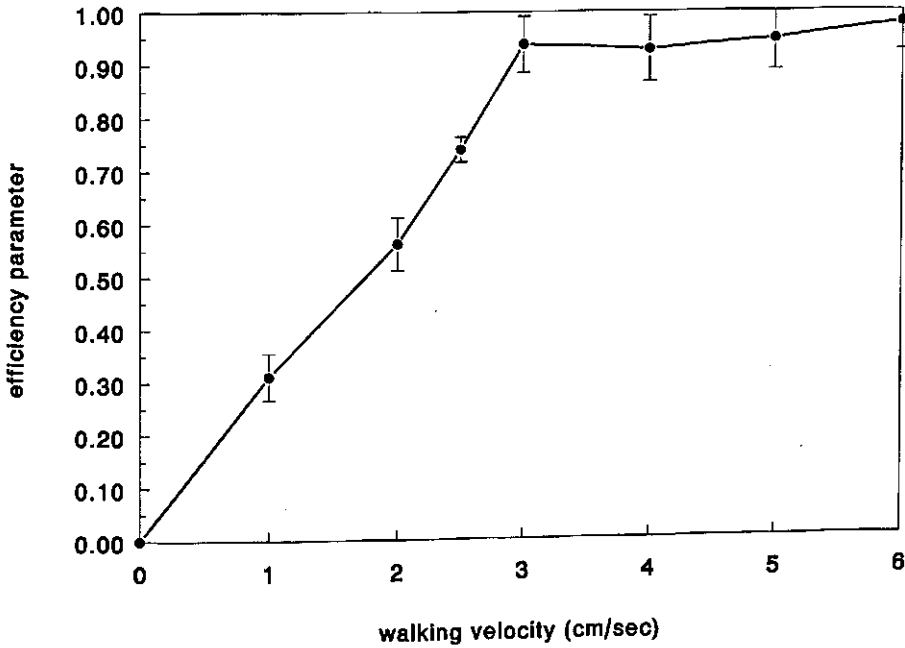


FIG. 4.1 Searching efficiency parameter (E_{ff}) calculated from results of the stochastic searching model and the Skellam model (see text) offers a correction factor for the windingness of the walking track.

lated results by those calculated with the Skellam formula. This is illustrated in fig 4.1, which shows that the effectiveness of the walking pattern depends on the speed of walking. Therefore, the efficiency of tortuous walk is very low. That, nevertheless, it is profitable in clustered prey distributions must be attributed wholly to the compensation by the increased time spent in prey clusters, only then does it result in a higher predation rate and in a higher egg production.

When no motivation is included Skellam's formula provides an easy way of estimating discovery rates, but for the beetle it highly overestimates the discovery rate below a speed of 3 cm/sec. This effect shows that Skellam's formula can only be used for rather straight walking patterns, unless a necessary correction for recrossing, depending on turning rate and thus on speed, is included. The second restriction is that it only can be used for the estimation of predation for periods with constant behaviour, because changes in behaviour are not included in it.

When walking behaviour is coupled to motivation, it may be concluded that the searching behaviour of *P.coerulescens* is adapted to various types of prey distribution, but that it shows its greatest profitability at overall low prey densities with aggregated prey. Especially when the prey is small, i.e. 5-10% of the maximum gut size, tortuous walk is very profitable.

But how will the situation be in the field with varying temperatures, rain, and varying structures of both soil surface and vegetation? Walking velocity is positively related to temperature (Mossakowski & Stier, 1983). If the relationship between velocity and turning rate remains the same at different temperatures, the model takes care of the effect of fluctuating temperatures. But if the relationship changes this has to be carefully studied before reliable statements about the the field situation can be given.

The influence of soil surface structure and vegetation was only incorporated to a small extent into the experiments. Dense vegetation and a rough surface hamper walking speed and increase the turning rate so that these may deviate a lot from the relationship established experimentally between velocity and turning rate. On the other hand, the agreement between the dispersal found in the field (Baars, 1979) and that found by simulation indicates that this effect could be less important than that of the temperature.

By sampling, we can estimate prey density and prey distribution in the field, but what we assess, may differ completely from what the beetle experiences. Also between various prey species differences in availability will be very difficult to assess, if not impossible. This makes it difficult to make a direct comparison between the results obtained by simulation and those estimated from the field, and also to predict predation rates in relation to 'real' prey densities and distributions. However, a rough estimate of the total prey situation may be obtained using the state variables of the beetle, such as weight of the adult beetle and number of eggs in the ovaries, to calculate at which overall prey consumption the values of these state variables can be reached. The mean and variance of these individual state variables of the beetles in relationship to the locality where they were caught represents the food available at that particular time and place. The variation in beetle weight in the field may thus give an indication of prey consumption and consequently of prey availability and prey clustering. Prey quality is an essential element in food availability as it is difficult to consider apart. But it may obscure the interpretations of the beetle weight, because prey quality influences the motivation and egg production. Nevertheless, the model may be used as a tool to illustrate how the different prey densities and distributions led to the distribution of the internal states of the beetles in the field.

4.1.2 The effect of locomotory activity

Two factors significantly influence the locomotory activity, namely temperature (Thiele, 1977), and the hunger level of the beetle. As the locomotory activity of the beetle decreases like a hyperbole with the increase of the satiation level, thus decreasing strongest at low satiation levels, this points to an adaptation to clustered prey. By decreasing its locomotory activity after consuming a prey (even a small one), the beetle stays longer in a location profitable for feeding. While resting it digests the prey and produces eggs of it. In combination with the slow and tortuous walk this is highly profitable. In contrast, long periods of locomotory activity together with high speed walking during periods of hunger increase the chance of finding places where food is more abundant.

In the experiments, locomotory activity differed highly between individuals. This variation was strongly correlated with egg production. Because high egg production results from a high intake of food and its rapid and efficient conversion, it may be hypothesized that the relative rate of gut emptying (RRGE) and the efficiency of food conversion (EFF) (See Mols, 1988) are the most important variables on an individual level. The energy used by the beetle for walking depends on its locomotory activity and walking speed (Alexander et al, 1977, Delcomyn, 1981, 1984, 1985, Heath et al.1982, Herreid et al., 1981) thus an increase of activity and speed is only advantageous, if it enhances the discovery rate of prey. We have no information about the difference in energy usage between high-speed walkers and intermediate-speed walkers. Respiration experiments showed no difference in relative weight loss between starved and non-starved beetles, so that these differences may be small. Egg production as a result of ingestion, digestion and respiration is a good measure of energy surplus. Therefore it can be used to show the differences between the beetle's searching effort in randomly and aggregated prey distributions.

Because of differences in individual locomotory activity, we may also talk about 'active' and 'lazy' beetles as high and low egg producers respectively. A 'lazy' beetle may remain longer under the cover of litter etc and thus may have a lower chance of being victim to a predator. Different strategies of survival may be represented: a) Being active and thus increasing the chance of finding extra prey and increasing egg production but with a higher risk of being discovered by an enemy and being eaten itself, or b) being lazy resulting in a lower egg production, but having the chance of surviving longer. Which of these strategies is most successful will depend on the predation pressure. It could also be hypothesized that 'lazy' beetles, because of a lower metabolic rate, can better survive periods with an extremely low prey availability (during a dry spell) than 'active' beetles.

Locomotory activity and temperature.

To simulate locomotory activity at field temperatures, its relationship with temperature must be known. From the results of the experiments in Chapter 2 and from field data (Baars, 1979) the following reasoning can be used to get an estimation of this relationship.

In the observations done at 12°C the beetles hardly showed any activity. Although locomotory activity was very low, feeding and egg production still occurred at a low level (Mols, 1988). Therefore, not 12 but 10°C was considered to be the thermal threshold for locomotory activity.

To estimate the maximum locomotory activity at other temperatures, the maximum locomotory activity at 20°C is taken as a reference, and the factor ACTEMP was introduced. ACTEMP is the locomotory activity relative to the maximum locomotory activity at 20°C, which is given the value of ACTEMP = 1. At 10°C ACTEMP = 0. Above 20°C ACTEMP was not known because observations were lacking. Therefore, to get rough estimates of the relative activity at other temperatures, we used the catches of pitfall traps set in springtime,

when no young beetles emerge, and correlated them to air temperature (Baars, 1979). The catches at different temperatures were scaled to those of 20°C, and thus the estimates of ACTEMP were obtained (table 4.1). At temperatures above 22°C pitfall catches decreased and above 30°C became zero. This is a rough estimate of course, because we only related trap catches to temperature, assuming that other factors have the same effect on activity.

TABLE 4.1 Relative locomotory activity (ACTEMP) estimated as a function of temperature (degrees Celcius).

Temperature	ACTEMP	Temperature	ACTEMP
10	0	22	1.2
12	0.1	25	0.75
15	0.5	30	0.15
20	1.0	35	0

Observations showed that locomotory activity of the beetles in the arena in the field almost decreased to zero when temperature was near to or above 30°C.

Locomotory activity and pitfall trapping

Another field of interest is the estimation of population density by means of pitfall trapping, where the locomotory activity of a beetle plays an especially important role; the number of beetles captured reflects their locomotory activity. As stated earlier we learned that the change of locomotory activity is governed by temperature and by satiation level. Beetles with a high locomotory activity are caught sooner than beetles with a low one. Hungry beetles have therefore a higher chance of being caught by a pitfall trap than those who are full. In good feeding areas, pitfall captures will underestimate the real population density, while in poor feeding areas they will overestimate it. This hypothesis is supported by Chiverton (1984), who found that significantly more female *P. melanarius* were caught in plots treated with insecticides than in the untreated control plots. The females from the treated plots had a lower gut content than females from untreated plots.

Estimations of state variables based on dissection of beetles caught in pitfall traps, such as gut content and the number of eggs in the ovaries, both of which are highly related to how much food they can get, will severely underestimate the beetle's weight, average gut content and the average number of eggs number in the females of the population. Estimations of the quantity of food available in the field, based on the condition of the beetles caught in pitfall traps underestimate the real food situation. To get an impression of the real distribution of the different feeding conditions of beetles in a field population, the frequency distribution of the numbers caught over specific feeding conditions, needs to be corrected for their chance of being captured, which for hungry beetles is 5 times higher than for satiated beetles.

4.1.3 The effect of success ratio

The success ratio for different kinds of prey, depends on the satiation level of the beetle. As this ratio decreases with increasing level of satiation it largely determines the shape and level of the functional response curve (especially when prey handling time is relatively short with respect to the total searching time). This is also found with other predators (Fransz, 1974; Rabbinge, 1976; Sabelis, 1981). The relationship between success ratio and RSATL is specific for each kind of prey. Preferences for different kinds of prey may be found by comparing the success ratio – RSATL curves, as these are hunger dependent. Thus, for polyphagous predators the difference in the success ratio -RSATL relationship between different kind of prey may explain the preference for particular kind of prey at a specific satiation level.

4.1.4 The effect of reaction distance

In the simulations, reaction distances are 1 and 2 cm. The simulations show that in random prey distributions reaction distance plays a substantial role, because discovery rate is linearly related to it. When the prey distribution is aggregated, differences in reaction distance do not result in the same change in discovery rate. Simulations showed that doubling the reaction distance from 1 to 2 cm results neither in a doubling of discovery rate (42%), nor in doubling of captures/day (17%). When the prey is clustered, it is only profitable for the beetle to increase its reaction distance to about the radius of the prey cluster. *P.coerulescens* is diurnal and hunts by eye and it does not seem to orient itself from a distance by olfactory queues. In preliminary experiments on a walking sphere it showed no reactions to a stream of air with maggot odour, while a nocturnal hunting species (*Pterostichus madidus*) reacted immediately. Hunger may have an effect on reaction distance in *P.coerulescens*; however, the results of a few experiments, give no reliable evidence of this.

4.2 PREDATION AND EGG PRODUCTION

From the results of simulations using models in which all the important behavioural components were included and connected with the motivation model, the following can be concluded concerning daily predation and egg production:

- (1) In random prey distributions, the predation per day is about the same whether the beetles perform tortuous walk after prey consumption or not. Although tortuous walk normally will lead to a lower predation rate this is partly compensated for by a small increase in locomotory activity.
- (2) In aggregated prey distributions, the advantage of the walking behaviour is much more striking when the discovery rate is considered alone than when predation rate is taken into account.

Predation and egg production are only higher when the prey density is low and prey is aggregated. With more than 1 prey/m² no difference could be found between aggregated and random prey distributions. It may be hypothesized that

predatory behaviour of the beetle is adapted to clustered prey occurring at low densities.

- (3) Below overall prey densities of 1 prey/m² the beetle is most adapted to small prey clusters (up to 40 cm), resulting in higher prey capture, consumption and egg production. However, within this range of small cluster diameters the beetle can reach a similar rate of predation and egg production. In the simulations the distance between the clusters decreases with the decrease of the prey density in the clusters, so that over this range of cluster sizes, differences in prey density and distance are more or less compensated for by the change of the beetle's searching behaviour.
- (4) Although prey capture is always higher when the clusters are very small (< 10 cm) (fig. 3.15), this does not result in a higher prey consumption and egg production. In small prey clusters, prey is encountered rapidly after each other, therefore satiation is reached very soon, and as a result only a small part of each captured prey is consumed. This decrease in prey utilisation has a negative feedback on egg production.

By its wide range of behavioural reactions in relation to the relative satiation level, the beetle is able to adapt to the prey distribution encountered. At low prey densities and small cluster sizes (smaller than 40 cm) a high locomotory activity, straight walk alternating with tortuous walk, are responsible for an optimal result. When prey density as well as cluster size increase, intermediate walk replaces straight walk more and more, locomotory activity decreases and tortuous walk becomes less important.

It is of interest to compare this simulated behaviour with that found in the field by Baars (1979) for the same species. He observed periods in which beetles day after day covered long distances (straight walk) alternating with periods in which only short distances were covered. To a great extent this behaviour can now be explained by the relationships between behavioural components of the beetle and its motivation; because in simulations the same pattern is found for low overall prey densities and aggregated prey distributions.

4.3 DISPERSAL

In poor habitats, such as those of *P.coerulescens* dispersal is important, leading to the exchange of individuals between subpopulations. From experiments and by simulation we learned how *P.coerulescens* can cope with a low prey density in a mozaic landscape with alternating rich and poor prey patches.

Both from Baars' (1979) field experiments and the results of calculations using walking behaviour components, such as velocity, turning rate and locomotory activity, we can predict the dispersal power of this species. Linear displacement calculations agree rather well with Baars' field observations (Chapter 3.3.4). Dispersal is governed by temperature and food; temperature has a direct influence (Massakowski et al., 1983) on walking speed and locomotory activity (Chapter 2.2), but also an indirect influence via the rate of change of the motiva-

tional state. The relative amount of food in the gut has a direct effect on walking speed and locomotory activity. When the beetle is in a prey cluster linear displacement of the beetle is low (2-4 meter), outside prey clusters it increases and when no prey is found, daily distances can vary between 17 and 24 metres. This high-speed walking behaviour may last only for a few days e.g. depending on temperature for about a week in June, because after that period eggs are resorbed and the beetles become 'spent' (van Dijk, 1979) producing no more eggs for the rest of the season. Roughly, this implies that distances between clusters must not be more than about 45 metres. If there is food available between clusters, the distances may be much larger.

Fieldwork and simulations may help to derive guidelines for nature conservation to predict for this and other species how far they can walk between suitable pieces of landscape or habitats, and whether it is necessary to help them by constructing corridors or stepping stones between such areas. Such information can thus help to increase the attainability of suitable sites for certain species and increase exchange between subpopulations.

4.4 COUPLING PREDATION TO POPULATION MODELS

In predator-prey population models, the interaction between the growth of the prey population and the predator population is obtained by the functional and numerical response of the predator to its prey. According to Solomon (1949), functional response is defined as the number of hosts successfully attacked per natural enemy (a predator or a parasitoid) as a function of host density. Thus it describes the way a predator or parasitoid responds to the changing abundance of its prey by killing or parasitizing more or fewer prey as it becomes respectively easier or more difficult to find.

The numerical response is defined as the reaction of a predator/parasitoid to the changing abundance of the prey by: (1) Producing more or fewer off-spring when the prey is respectively easier or harder to find and to consume. (2) Migrating to or aggregating in areas with higher prey densities.

The functional response is also a numerical response, if the eggs are laid in or near a host, as occurs with most parasitoids, the adults of which do not consume the prey. In predator models, a factor is used that converts the number of prey consumed into the number of offspring produced. In agricultural systems, the functional response is a commonly measured characteristic of natural enemies of crop pests. The failure of natural enemies to keep pest density below the economic threshold has been associated with a rapid increase in pest density which overwhelms the enemies functional and numerical response (Murdoch et al., 1985). This may be due to the satiation of the predator, or to limitations of the handling time, or the time-lag in the egg production in the case of predators. Therefore, by knowing the functional and numerical responses of a natural enemy, it is theoretically possible to predict its contribution to the dynamics of a pest population, and identify the density at which the pest would escape control by the beneficial enemy (O'Neil, 1990).

4.4.1 Functional response models

In predator-prey population models, simple descriptive models of the functional response are preferable as they are easy to understand and, unlike the stochastic models, do not need much computer time. One may ask, what models are available to describe the functional response of a general predator like *P.coerulescens* appropriately, and is it possible to apply them?

Holling (1966) describes 3 types of functional response models for random prey distributions (see appendix II).

Type 1 response: When a predator kills a constant proportion of the prey the relationship between prey density and number of prey killed is linear until a plateau is reached where the number of successful attacks remains constant. The plateau represents the maximum predation rate. That rate is physically determined.

Type 2 response: Just as in the type 1 response a saturation level is reached, but in a gradual way. This is probably the most widespread type of response. If we realise that a predator or parasitoid only has a limited amount of time, this type is easy to understand. Some of this total time (T) is needed for searching for prey while another part, collectively referred to as 'handling time', is used for the pursuit, attack and consumption of prey. At increasing prey densities (N_0) the time available for searching (T_s) decreases as more time is used for the handling of prey (T_h). This leads to Holling's 'disc equation' for the calculation of the number of prey killed (N_c)

$$N_c = a' * T * N_0 / (1 + a' * T_h * N_0)$$

a' = the searching efficiency or relative rate of successful attack.

Holling assumes that when a predator or parasitoid searches for prey it does not change its behaviour during the whole searching period. The number of prey encountered is an instantaneous rate which only holds for short periods when the prey density remains constant. In case of predators, this is not true because when prey is killed it is removed from the population. In case of parasitoids, it is assumed the parasitoid searches in such a way that a host is only encountered once, thus the number of prey encountered equals the number of prey parasitized. This only holds for a short observation period. It can also be said that the parasitoid searches systematically. What we see in most experiments is that parasitoids do not avoid previous parasitized hosts thus that they encounter a host more than once. To account for this effect, the approach of Nicholson and Bailey (1935) can be used (see Rogers, 1972). They assume that:

- Searching is random and does not change during the observation period, thus each prey has an equal chance of getting parasitized in a certain period.
- Parasitoids do not discriminate between parasitized and unparasitized hosts.
- Parasitoids do not interfere with each other.
- The parasitization time is zero (i.e. no handling time)

then the chance of a host being encountered is a Poisson process. The chance

of having no encounters (and thus no parasitization) equals the zero term of the Poisson distribution. Including the 'Disc equation' in the Nicholson's competition equation leads to the 'random parasite' or to the 'random predator equation'. (See appendix II).

Type 3 response: If a predator reacts to an increase in prey density by increasing the proportion of prey it kills over a specific range of prey densities, this results in a sigmoid curve. This type of response is caused by a number of predatory characteristics, and it may be found in predators which are capable of learning.

Prey aggregation

Prey often has an aggregated distribution, resulting in predators that search for them in an adapted way. In functional response models instead of using the zero term of the Poisson distribution the zero term of the negative binomial distribution is used for expressing the proportion of prey that escapes from predation (Crawley, 1992): $P_0 = (1 + 1/k)^{-k}$ thus $1 - P_0$ is the proportion that will be predated. k is the aggregation parameter. As k gets large (> 10) the negative binomial approaches the Poisson distribution. For small values of k (< 1) the distribution of predator attacks is highly aggregated. As the degree of aggregation increases, the value of k decreases and the zero term gets bigger. This means that a larger proportion of the prey escapes predator attack.

The type II and III functional response models and the random parasite and predator equations (see appendix II) predict that the number of hosts or prey attacked increases at a diminishing rate as the prey density increases. It is possible to use these models to describe the same experimental results, although in this way different estimates of the searching efficiency and the handling time will be obtained. This is because the disc equation assumes that the predator searches systematically for its prey and does not waste any time in re-searching part of the arena, whilst the random predator equation assumes that the predator searches at random. The values of the parameters can be obtained by linear regression of the experimental results. Although this all seems clear we soon get into trouble when the real handling time is measured experimentally. It may appear to deviate substantially from the calculated value which shows that searching efficiency (a') and handling time (T_h) stand for more than they are meant to. This may imply that the predator or parasitoid does not search randomly, that T_h is not constant, that the locomotory activity changes with prey density, or that the searching velocity changes with prey density etc. In such cases it is better not to estimate a' and T_h from the data of the functional response experiments, because they apply only to these specific experimental conditions. When conditions are changed, the functional response changes. It is better to estimate their value from behavioural observations of the predator or parasitoid during the process of searching and predation or parasitization.

From the stochastic simulations, we learned that for *P. coerulescens*, especially at low prey densities, different Holling II response curves can be constructed

for each prey distribution. Using the negative binomial zero term for aggregated prey in the Random predator equation model seems not to be appropriate, because it results in a lower predation when prey is aggregated than when prey is randomly distributed. This result is in complete contradiction with the stochastic simulation experiments of *P. coerulescens* (Chapter 3), where it was found that the functional response of the beetle, which, both for random and aggregated prey distributions looks like a Holling II response curve, is steeper when prey was aggregated, and thus predation higher, than when it was randomly distributed. Therefore, using the $(1-P_0)$ term of the negative binomial, seems not to be appropriate for estimation of predation in aggregated prey distributions, because changes in behaviour are not accounted for. This agrees with Murdoch et al. (1989, 1990) who say, that rearrangement of predators to prey aggregations during the season makes the functional response curve steeper. That result is good for biological control but not for the stability of the predator-prey system.

For aggregated distributions a solution can be found by dividing the searching time into periods when the predator is either present inside or outside a prey cluster, because of possible changes in behaviour of a predator/parasitoid. This mostly results in complex models involving the behaviour of both predator and prey.

4.4.2 From behavioural components to functional response

To include real behavioural components in the functional response models, Skellam's extended formula for calculation of the predation rate offers a solution (Chapter 1.1; Sabelis, 1981). This model uses behavioural components for the calculation of predation, which can be measured separately, such as: the walking velocity, the effectiveness of walking depending on windingness, locomotory activity, reaction distance and success ratio; all in relation to external and internal conditions. If the handling time (T_h) is included in the searching time (T_s) the equation can be extended to:

$$N_{\text{pred}} = T_s / \{1 / (a' * N_o) - T_h\}$$

$$a' = V * D * E_{\text{ff}} * S_r$$

If the handling time is included in the resting time

$$N_{\text{pred}} = a' * N_o * T_s = a' * N_o * A * T$$

The assumptions are:

- The predator walks randomly with respect to the prey
- The velocities of prey and predator are mutually independent and the resultant velocity is $V = \sqrt{(V^2_{\text{pred}} + V^2_{\text{prey}})}$. If this is not the case (for example when the predator follows the trail of a prey) the formula is not applicable.
- The behaviour does not change.

If the handling time is difficult to measure and relatively short with respect to the exposure time (T), it is easier to measure the active searching period T_s ,

directly and ignore T_h . If T_h is relatively long (and therefore strongly influences T_s) it is better to measure both. In predators handling time may be very variable as it may depend on satiation level and prey size (Mols, 1988) and sometimes also on a digestive pause (Holling, 1966).

For inclusion of specific searching behaviour, like tortuous walk, searching time should be divided into periods with and without tortuous walk.

As these are instantaneous rates they can be substituted in The Nicholson & Bailey equation to get a Random predator or Random Parasite equation.

Then we obtain equations in which behavioural characteristics are included, thus the vague variable 'a' is now replaced by biologically clear variables. The problem remains that predator behaviour (especially walking speed, locomotory activity and prey acceptance) changes according to local differences in prey density. Therefore this approach is only applied to short periods when it can be assumed that behaviour is constant. A disadvantage is also that population models including these functional response models with changing behaviour cannot be solved analytically but only numerically.

4.4.3 *From individual predator models to population models*

The stochastic searching model (Chapter 3) may be useful for analysing the effect of walking behaviour at different prey densities and prey distributions at the individual predator level. The model can be extended to population level by bringing in more beetles and by making the stationary prey distribution and prey density dynamic. This will lead to a complete stochastic model which can be used to estimate the effect of the beetle as a control agent of a specific pest, for example, aphids in cereals. However, many simulation runs and a large amount of computer time are needed, due to the stochastic nature of the model for walking behaviour and the small time step (2 sec). Another approach uses the average predation values for individual beetles, calculated with the stochastic model as input for the predator-pest model; assuming that the outcome from average input values is identical to the average outcome with variable input values. This is generally only true when the variation in input parameters is small or when the model has linear relationships between its variables. However, there is a large variation between individual beetles, especially at low prey densities, while several relationships (e.g. the functional response) in the model are non-linear and depend on prey distribution. Thus averages cannot be used as inputs in the simulation. A solution for this problem is offered by compound simulation (Fransz, 1974; Rabbinge et al, 1989). Therefore, the beetle population is divided into three classes according to the types of walking behaviour. Each class is split into two subclasses, for beetles inside and outside a prey cluster. Thus beetles belong to one of six classes. Within a walking class the beetles are assumed to behave identically. The stochastic model of the individual beetle is replaced by relationships, calculated from a large number of runs with this model, which estimate time spent within a prey cluster as a function of walking velocity and cluster diameter (fig 4.2). The discovery rate with prey clusters and with prey within a cluster can be approximated with the extended Skellam model.

residence time of predator in prey
cluster in relation to walking speed

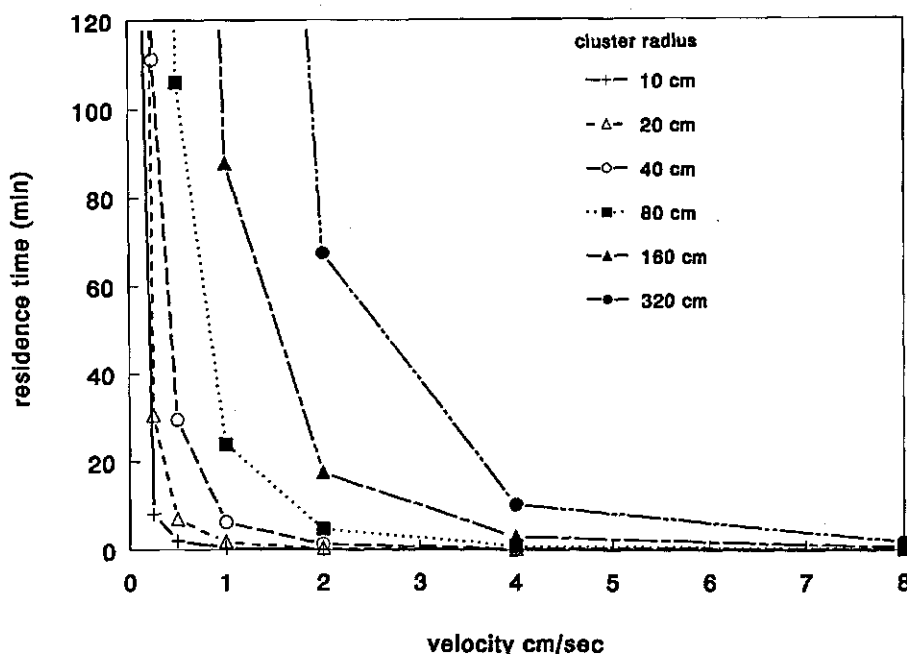


FIG. 4.2 Residence time of the beetle in a prey cluster depending on walking speed and prey cluster size.

Each time step, the population model is run for each class of beetles separately and beetle numbers in each class are adjusted according to motivation dependent behaviour and the residence time in the cluster. When beetles (or fractions of the beetle population) shift from one class to another also all contents of the state variables of the motivational part also shift to the next class, and are averaged with those that are still there (fig 4.3). In this way, a stochastic model of an individual beetle is replaced by a deterministic model in which the motivational state of all beetles in a class changes by the average state in that class. Prey numbers may be distributed randomly or clustered and can be calculated with a population growth model. For example an aphid growth model in cereals (Rabbinge et al., 1979, Rabbinge & Carter, 1984, Carter, 1985). Preliminary simulations with this model show that *Pterostichus cupreus*, the dominant carabid species in cereals on clay soil, which is very closely related, and similar in size to *P.coerulescens*, may have a considerable impact on aphid population growth. The relationships found for *P.coerulescens* were used in the model, therefore the conclusions were based on the assumption that *P.cupreus* behaves similar to *P. coerulescens*.

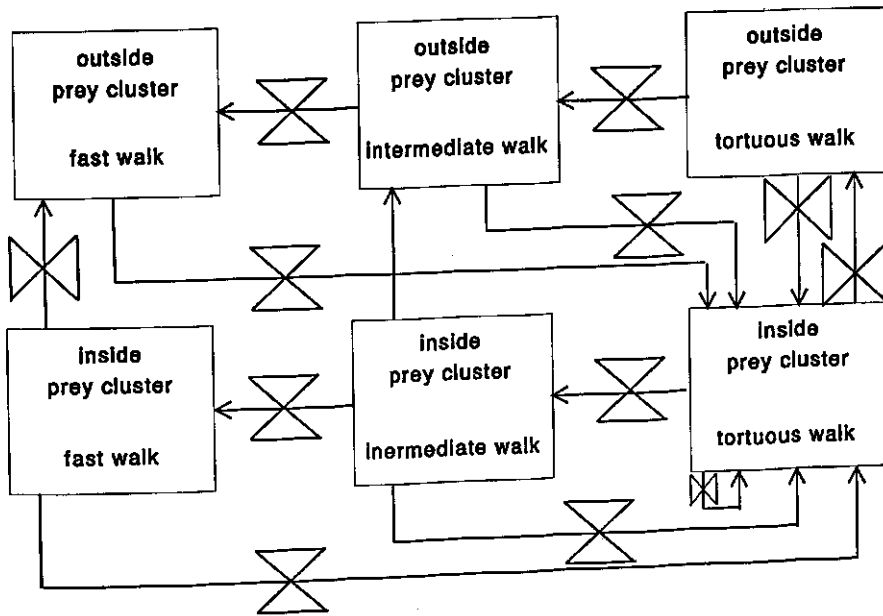


FIG. 4.3 Division of the states of the beetle according the type of walking behaviour and being inside or outside a prey cluster used in the compound model of the beetle population.

4.5 METHODOLOGY OF EVALUATION OF POTENTIAL PREDATORS FOR BIOLOGICAL CONTROL

The relationships found in *P.coerulescens* between both motivational state and behaviour and the prey density and distributions of its prey may lead to a list of recommendations on how observations and experiments should be carried out when a potential predator is evaluated for use in biological control and which factors have to be taken into account.

1. From the research on the motivational state of the beetle in Part I of this study (Mols, 1988), it is clear that we need to quantify the physical and physiological properties of a predator.
 - a) Gut capacity in relation to predator size and room in the abdomen,
 - b) Satiation level for different physiological stages of the predator (reproductive or not),
 - c) Gut emptying rate.
 - d) Metabolic needs, both in reproductive and non-reproductive state.

- e) Uptake and conversion efficiency in relation to prey type.
 - f) Egg weight
2. For the estimation of searching and predation rate the following behavioural components are necessary.
 - a) Walking behaviour (walking speed and turning rate) and duration of specific walking behaviour (e.g. intensive search)
 - b) Relationships of behavioural components, like locomotory activity, success ratio and reaction distance with internal variables like the satiation level.
 3. Validation experiments concerning the motivational part and the functional response.
 - a) Independent egg production experiments under controlled food conditions.
 - b) For functional response experiments, the area of observation must be related to the radius of action (walking distance per day) of the predator. If this is not the case, border effects will strongly influence the outcome of the experiments.
 - c) The experiment must be long enough for the predators to adapt to the prey density and prey distribution such that feedback mechanisms show their effect. Historical effects like gut content, fat quantity, ovary size and number of eggs in the oviduct strongly determine the predatory capacity (e.g. effect of egg load on the expansion of the gut). Not doing this overestimates the advantage of the predator. As the predator becomes older, the responses to internal and environmental stimuli may change, resulting in a difference in predation.
 - d) Experiments to find out the functional response of a predator, especially at low prey densities and also when the prey is clustered need many repetitions. To obtain confident averages the number of repetitions required is often so high that this is not practical, because of the time and space needed and above all the stochastic nature of the material. Nevertheless, if they are carried out, results will be very arguable. Functional response curves carried out with standardized predators only hold for that type of standardization, meaning that different standardizations result in different functional responses. The results of an experimentally established specific functional response of a predator are only indicative for its predatory capacity. Therefore simulation models incorporating the behaviour of the natural enemy may be a better tool for estimating its functional responses.

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APPENDIX I THE SEARCH MODEL

APPENDIX I

Simulation of walking behaviour and discovery.

The direction of walking is calculated by drawing randomly a direction out of the turning rate distribution. Each timestep this is done again and the next angle is added to the former direction which then gives the new direction. This is accomplished by drawing a random number out of a uniform distribution between 0 and 1.

$P = \text{RAN}(IS)$

IS is a seed number needed for the random generator. P is used in the following equation:

$A = AV + \text{SIGMA} * (P^{**KURT} - (1. - P)^{**KURT}) / KURT$

Which is the Tukey distribution (Montfort et al. 1976) given in chapter 2.
The angle is now added to the former direction giving the new direction of the beetle.

$DIR = DIR + A$

As the speed of the beetle is known it is possible to calculate the new coordinates of the beetle (XP, YP)

$XP = XP + \text{COS}(DIR) * V$
 $YP = YP + \text{SIN}(DIR) * V$

The moment the beetle reaches the border of the field it will follow it when angles are chosen that should lead the beetle outside the field, other angles lead the beetle back into the field again.

Duration of tortuous walk.

Just after consumption of a prey, the beetle resumes searching at a very low speed. If no new prey is discovered the speed increases gradually to the speed given at the start of the simulation. In reality this will be the speed belonging to a specific level of satiation. The duration of tortuous walk is thus the time from the end of consumption when searching is started until the speed equals the value before the prey was discovered. Parallel with the increase of speed the turning rate distribution changes from wide to narrow, as the speed determines the SIGMA and Kurtosis parameter of the TUKEY distribution.

Prey distribution and prey discovery.

In the program the distribution of the prey can be arranged such that it may vary from random to very aggregated. This done by putting the prey in discrete prey clusters of a specific size. The numbers of prey in the cluster, the number of clusters and the size of the clusters can be given a specific value. The immobile preys are located in NC clusters, which are randomly distributed through the model field. Within a cluster IC preys are randomly located. Therefore, NC*IC preys are present in the field. The model field is a square with sides of UNIT length (expressed in cm.). The clusters are circular with a diameter of CLUNIT.

The distribution of prey through the field can be arranged as follows:
 Random distribution: 1) Put one cluster in the field with the same diameter as the field length and place all the prey randomly in that cluster or 2) take as many clusters as prey are needed and place one prey in each cluster.

Aggregated distributions: Aggregation of prey increases by both decrease of the number of clusters per field and by decrease of the cluster size and consequently increase of the number of prey per cluster.

Procedure of prey location.

First the centers of the clusters are randomly placed in the field, and stored in two arrays. The X(L) and Y(L) memories, with the L being a multiple of IC, and in the CCX(I) and CCY(I), with I running from 1 to NC. The coordinates stored in the latter arrays are used to determine the distance from the beetle to the cluster centre. This procedure is needed for cluster scanning. Obviously it is less laborious if firstly the nearest cluster is determined and subsequently the prey of that cluster have to be scanned than to scan all the preys in the total field each time step. To determine which cluster is nearest, it is necessary to identify that cluster. The centrally located prey of a cluster is used as identification mark. Subsequently the preys are randomly located around the center of the cluster in a square with dimensions CLUNI*CLUNIT. To acquire a circular cluster, the preys located in this square are checked to see if they are within a distance of 0.5*CLUNIT from the center. This is tested by calculating the distance from the prey to the center. If this distance is greater than 0.5*CLUNIT the prey is discarded and a new prey is selected. The prey distribution is accomplished in the following program section:

```

DO 1 I = 1, NC
L = IC*I
X(L) = RAN( IS ) * UNIT
Y(L) = RAN( IS ) * UNIT
CCX(I) = X(L)
CCY(I) = Y(L)
DO 1 J = 1, (IC-1)
M = IC*(I-1) + J
11 XM = RAN( IS )
YM = RAN( IS )
X(M) = X(L) + (XM-0.5) * CLUNIT
Y(M) = Y(L) + (YM-0.5) * CLUNIT
DIST = SQRT( (X(M)-X(L)) * (X(M)-X(L)) + (Y(M)-Y(L)) * (Y(M)-Y(L)) )
HCLUNI = 0.5 * CLUNIT
IF (DIST. GT. HCLUNI) GO TO 11
1 CONTINUE

```

Cluster scanning.

First the program determines which prey cluster is nearest to the beetle.

```

DO 4 L = 1, NC
DIST1 = SQRT( (CCX(L)-XP) * (CCX(L)-XP) + (CCY(L)-YP) *
(CCY(L)-YP) )
DIST = AMIN1( DIST1, DIST )
IF (DIST. EQ. DIST1) L1 = L * IC
T4 CONTINUE

```

Prey is only located in the clusters, thus the beetle can only discover a prey within a certain distance from the cluster center. The sum of the reaction distance of the beetle and the cluster radius form this distance (CLDIST). As standard reaction distance 2 cm is taken.

```

RADIUS = 2.0
CLDIST = 0.5 * CLUNIT + RADIUS
IF (DIST. GT. CLDIST) GO TO 6

```

If the distance is greater than CLDIST, for all clustres, the beetle did not find any cluster. Hence, the program will skip the next section in which the individual prey in the neares cluster are scanned.

The area of discovery.

In the model, the beetle is represented as a round object with a radius of 2 cm. When a beetle moves from one position to the next an area is covered consisting of a strip of 4 cm width but also consisting of a halve circular start and end area. When the beetle moves to the third position with a change in direction a part of the area is covered twice (fig 3.3). This indicates already that a winding walking track never reaches 100% searching efficiency even if they do not seem to cross.

Prey discovery in the area of discovery is calculated in the model by giving all the prey in the cluster coordinates relative to a new coordinate frame. This frame is perpendicular on the moving direction of the beetle during the time step.

The coordinates of the preys can be determind with the formula's:

$$X_{new} = (X_{old} - XV) * \cos(\alpha) + (Y_{old} - YV) * \sin(\alpha)$$

$$Y_{new} = (Y_{old} - YV) * \cos(\alpha) + (X_{old} - XV) * \sin(\alpha)$$

These new coordinates given to the preys in a specific prey cluster and the scanning of preys located in the area is programmed as:

```

DO 5 J      =1, IC
I          =L1-IC+J
DX        =X(I)-XV
DY        =Y(I)-YV
CX(J)     =DX*CSDR+DY*SNDR
CY(J)     =DY*CSDR-DX*SVDR
IF(CX(J).LE.(V+RADIUS).AND.CX(J).GE.0.)GO TO 15
GO TO 5
15 IF(ABS(CY(J)).LE.RADIUS)GO TO 16
GO TO 5
16 NL      =NL+1
B(NL)     =J
5  CONTINUE

```

Two situations can be distinguished.

a) The distance a beetle covers during one time step is larger than its reaction distance.

In this case three area's can be distinguished.

- A) X-coordinate is smaller than reaction distance
- B) X-coordinate is larger than reaction distance but smaller than V
- C) X-coordinate larger than V

The prey located in area A must be scanned to see which ones have already been discovered in the previous time step; viz. all the prey located in the half circle. The selection takes place by determining the distance from the prey tp the XV, YV. If the distance is smaller than reaction distance the prey is discarded. From the prey located in area C, only those within a distance reaction distance from XV, YV are retained, whereas all prey in area B are saved.

Determination whether a prey is located in area A,B or C

```
DO 71 =1, NL
AM =B(J)
IF(CX(AM). LE. RADIUS) GO TO 17
GO TO 18
17 D =AM
GO TO 71
18 IF(CX(AM). GT. V) GO TO 19
GO TO 20
19 E =AM
GO TO 71
20 NF =NF+1
F(NF) =AM
71 CONTINUE
```

The chance that a prey will be located in B is much greater than the chance to locate a prey in sector A or C. The preys located in B are stored in the F(NF) memory. A and C can maximally contain 1 prey each.

In the next section of the program it is prevented that in two consecutive time steps the same prey is scored in part A and C. This part of the program may be omitted if the prey is removed after an discovery or when it is not sessile.

```
IF(D. EQ. 0) GO TO 21
DIST1 =SQRT(CX(D)*CX(D)+CY(D)*CY(D))
IF(DIST1. LT. RADIUS) GO TO 21
G =D
21 CONTINUE
IF(E. EQ. 0) GO TO 22
DIST2 =SQRT((CX(E)-V)*(CX(E)-V)+CY(E)*CY(E))
IF(DIST2. GT. RADIUS) GO TO 22
H =E
```

The selected prey from sectors A, B and C are potential prey, and they are put in memory POT(CNT). In fact these are all the prey discovered by the beetle in one time step.

```
22 CONTINUE
IF(G. EQ. 0) GO TO 23
I =L1-IC+G
CNT =CNT+1
POT(CNT)=I
23 CONTINUE
IF(NF. EQ. 0) GO TO 24
DO 24 J =1, NF
I =L1-IC+F(J)
CNT =CNT+1
POT(CNT) =I
24 CONTINUE
IF(H. EQ. 0) GO TO 25
I =L1-IC+H
CNT =CNT+1
POT(CNT) =I
25 CONTINUE
```

b) The distance a beetle covers during one time step is less than its reaction distance.

In this case only those prey at larger distance than the reaction distance from XV, YV and closer to XP, YP than reaction distance are also put in memory POT(CNT) and can also be considered as discovered.

```
DO 8 I      =1, NL
AM          =B(I)
DIST3      =SQRT(CX(AM)*CX(AM)+CY(AM)*CY(AM))
DIST4      =SQRT((CX(AM)-V)*(CX(AM)-V)+CY(AM)*CY(AM))
IF(DIST3. GT. RADIUS. AND. DIST4. LE. RADIUS) GO TO 41
GO TO 8
41  NF      =NF+1
      F(NF)  =AM
8    CONTINUE
      IF(NF. EQ. 0) GOTO 43
DO 43 J    =1, NF
      I      =L1-IC+F(J)
      CNT    =CNT+1

      POT(CNT) =I
43  CONTINUE
```

In the discovery model the discovered prey are given new coordinates in the cluster. The average density in the fields remains constant. If this is not done the chance of discovering the same prey in sector B is very high when the speed is low and the prey density in the cluster high. This may give erroneous high rates of discovery.

APPENDIX II

Functional response models.

Holling (1959, 1966) describes 3 types of functional response models derived from different types of predators.

Type 1 response: When a predator kills a constant proportion of the prey the relationship between prey density and number of prey killed is linear until a plateau is reached where the number of successful attacks remains constant.

The number of prey encountered (N_e) is linearly related to prey density (N_0) and to the searching time (T_s):

$$N_e = a' * N_0 * T_s \quad (1)$$

a' = relative rate of successful attack, also called the searching efficiency.

When the plateau is reached $N_e = \text{constant}$

Type 2 response: Just as in the type 1 response a saturation level is reached but now in a gradual way. If a part of the total time available (T) is used for prey handling (T_h) the searching time equals:

$$T_s = T - T_h * N_e$$

Formula of Holling for type 2 response curve:

$$N_e = a' * T_s * N_0 \quad \text{where } T_s = T - T_h * N_e \text{ thus:}$$

$$N_e = a' * (T - T_h * N_e) * N_0$$

If N_e is brought to the left hand side the formula becomes:

$$N_e = a' * T * N_0 / (1 + a' * T_h * N_0) \quad \text{the 'disc equation'} \quad (2)$$

This only holds for a short observation period. It can also be said that the parasitoid searches systematically. What we see in most experiments is that parasitoids do not avoid previous parasitized hosts thus that they encounter a host more than once. To account for this effect the approach of *Nicholson & Bailey (1935)* is used (see *Rogers, 1972*). The chance of a host being encountered is a Poisson process. The chance having no encounters (thus no parasitization) equals the zero term of the Poisson distribution:

$$P_0 = \exp(-N_e/N_0)$$

The fraction that a host is encountered once or more is thus $(1 - P_0)$

The number of prey attacked by one predator or parasitoid is:

$$N_e = N_0(1 - \exp(-N_e/N_0)) \quad (3)$$

substitution of equation (1) for N_e gives the Nicholson's 'competition curve' for a single enemy

$$N_e = N_0(1 - \exp(-a' * T_s)) \quad (4)$$

The relative rate of successful attack $a' = (\ln(N_0/(N_0 - N_e)))/T_s$

Thus we can calculate a' from the results of a parasitization experiment, because we know the density N_0 and count $N_{par} = N_e$ as the number of hosts parasitized in time T_s .

If it is assumed that the parasitoid searches at random, equation (2) can be built into equation (3), then we get the so called '**Random Parasite Equation**':

$$N_{par} = N_0 \{ 1 - \exp(-a' * T_s / (1 + a' * T_h * N_0)) \} \quad (5)$$

Equation (5) can not be applied for most predators because they remove their prey as they find one, at the first encounter. No time is wasted in repeated encounter (re-handling) with prey, and more time is available for searching. Thus for a predator

$$T_s = T - N_{pred} * T_h$$

For the equation of Holling this leads to the same 'disc equation' if it is assumed that $N_{pred} = N_e$ which also holds for a short period. The parameter N_e in equation (3) describes the number of

encounters that the predator would have with the prey if the predator did not consume its prey or if the prey density remained constant. Had these encounters been distributed at random, the number of prey that would have been encountered once or more times (and therefore the number of prey eaten) was the same as in equation (4). Substituting for T_s , equation (4) gives the '**Random Predator Equation**'

$$N_{\text{pred}} = N_0 \{1 - \exp(-a'(T - N_{\text{pred}} * T_h))\} \quad (6)$$

The Random Parasite Equation can be adapted for parasites that do discriminate between parasitized and non-parasitized hosts by taking different handling times for both types of hosts (*Arditi, 1983*).

Type 3 response: If a predator reacts to an increase of prey density by increasing its proportion of prey killed over a specific range of prey density this will result in a sigmoid curve.

If it is found that the relative rate of encounter a' or the searching time T_s increases with (N_0) or that T_h decreases with N_0 , then a sigmoid relationship between predation or parasitism and prey density may be found. For example, the parameter a' can be assumed to increase with N_0 in the following way (*Hassell, Lawton & Beddington, 1977*).

$$a' = b * N_0 / (1 + c * N_0) \quad (\text{b and c are constants}) \quad (7)$$

a' rises from 0 when no hosts are present to a maximum b/c . This relationship can be substituted in (5) or (6) and gives a sigmoid functional response for a predator or a parasitoid.