

Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae)ANDRÉ FERRAN¹ and ANTHONY F.G. DIXON²¹Laboratoire de Biologie des Invertébrés, I.N.R.A.,
37 Bd du Cap, 06606 Antibes, France²School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK**Coccinellidae, predator, Aphidae, foraging behaviour, search strategy, prey detection, learning, environmental factor, predatory efficiency**

Abstract. Coccinellids, particularly their larvae are very voracious. Their foraging behaviour has been extensively studied in an attempt to determine their potential for controlling pest aphids, which occur in patches that are relatively short lived and within which the aphids are not uniformly distributed but clumped. In seeking aphid prey ladybirds like other insect predators forage both extensively and intensively, and use visual and olfactory cues for orientation. Intensive search follows an encounter with an aphid and serves to keep the predator in the vicinity of a cluster of prey. The success of larvae in capturing prey is dependent on abiotic and biotic factors such as plant structure, species of aphid attacked, the predator, in particular its age, level of hunger and genetic characteristics, and intra- and interspecific competition.

It is suggested that the poor progress in developing a foraging theory for insect predators, and ladybirds in particular, is a consequence of having mainly concentrated on the foraging behaviour of the most voracious stage, the larva. The behaviour of larvae serves to keep them within the patch selected by the adult. Thus for a better understanding we need information on the cues used by ladybird adults to assess the quality of patches of prey.

INTRODUCTION

Predators forage both between and within patches: where a patch is a spatial unit of the environment within which resources are aggregated (Hassell & Southwood, 1978). Prey is rarely uniformly distributed within a patch, but is much more abundant within than between patches. In the case of ladybirds in summer the patches are aggregations of aphids. The aphids in each patch are only abundant for a very short period, i.e., even in the absence of natural enemies the number of aphids fluctuate (Dixon, 1985). Therefore, the larvae of ladybirds risk starvation if the aphids they are attacking become rare or extinct before they can complete their development. In order to maximize their fitness in terms of resulting offspring biomass optimal foraging theory predicts that adults should lay a relatively low number of eggs in a patch and cease oviposition as soon as a critical number of eggs are laid and/or larvae are present, even though the aphids in the patch may still be increasing in abundance, i.e. it is the future quality of the patch for the larvae that is important (Kindlmann & Dixon, 1993). Studies on two species of ladybird beetles have revealed that adults can respond to cues indicating the long term quality of the aphid patch they are attacking and so forage in a way that is consistent with optimal foraging theory (Hemptinne et al., 1992; Hemptinne et al., 1993). In autumn the patches sought are hibernation sites. The physiological state and flight activity of adult ladybirds migrating to and dispersing from their hibernation sites is reviewed by Hodek et al. (1993).

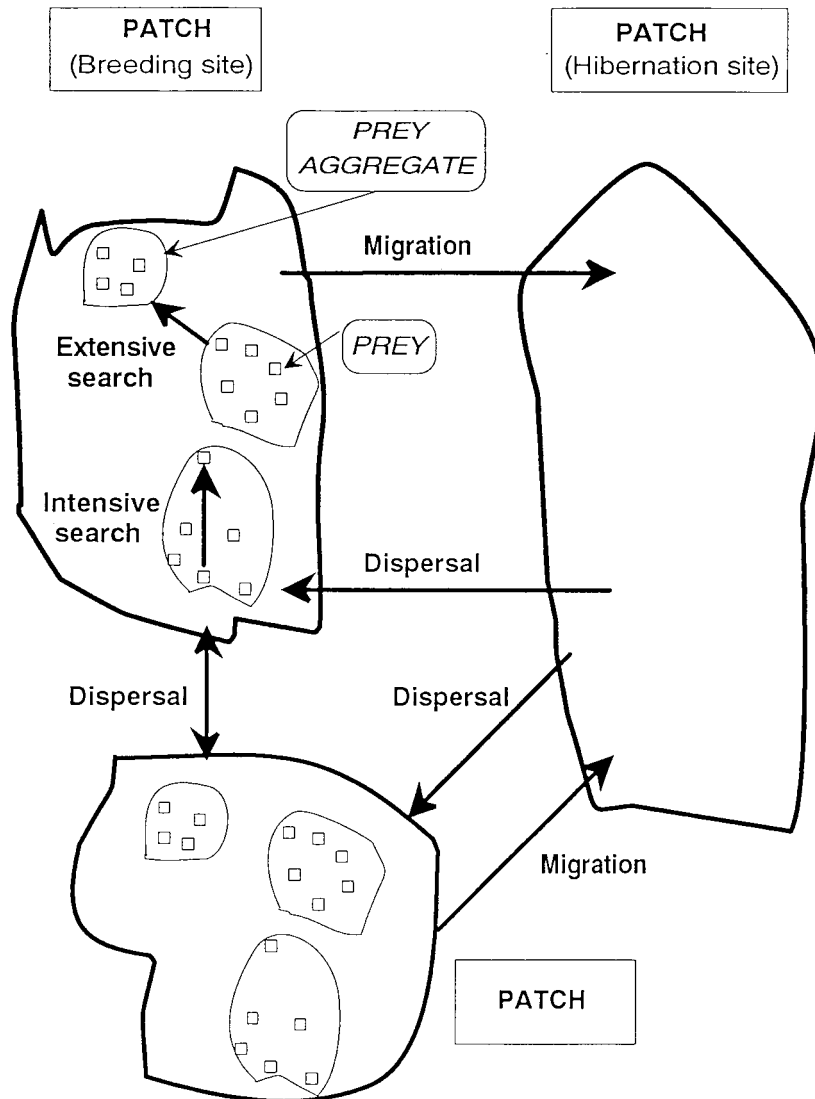


Fig. 1. Diagram illustrating how a ladybird might perceive its environment and forage for resources (modified after Hassell & Southwood, 1978 and Hodek et al., 1984).

In contrast to parasitoids both the larvae and adults of insect predators actively seek out and capture prey. This review, however, mainly considers behavioural responses of ladybird larvae that tend to keep them foraging within a patch. In the first section the movements of coccinellids are interpreted in the context of the environmental levels apparent to a forager, the second reviews larval orientation and prey recognition, the third the

possibility that larvae change their foraging behaviour as a consequence of previous experience and the fourth the effect of microclimatic conditions, plant structure, predator size and competitors on foraging behaviour.

FORAGING BEHAVIOUR

Hassell & Southwood (1978) classify the environmental levels apparent to foragers in terms of prey, patches, and habitats (Fig. 1). This provides a framework for discussing the foraging behaviour of ladybirds. The adults locate patches of aphids and their larvae feed on the aphids in these patches. A patch is an area where the probability of encountering prey is relatively high and is surrounded by areas where this probability is at or near zero. As aphids tend to aggregate patches of aphids usually consist of clusters of aggregations of aphids in which each aggregation is usually associated with a growing point of the host plant.

Movement between prey within aggregates of aphids is referred to as **local** or **intensive search** (Bond, 1980) or **area-restricted search** (Curio, 1976), between aggregates within patches **ranging or extensive search**, between patches **dispersal**, from patches to hibernation sites **migration** (Figure 1).

Pattern of foraging

Predators locate prey by extensive search and switch to intensive search after feeding (Jander, 1975). If no further prey are captured the predator gradually changes from the intensive to the extensive search mode. The length of time spent in intensive search is called 'giving-up time'. Extensive search is characterized by a relatively linear and fast movement, local search by sinuous slow tracks interrupted by numerous stops (Fig. 2). During a stop, larvae of Coccinellidae, Syrphidae and Chrysopidae 'cast' their body upwards and sideways thereby increasing the area within which prey may be located (Banks, 1957; Chandler, 1969). Intensive search is considered to be adaptive when predators hunt clumped prey, as it increases the chances of finding prey (Dixon, 1959).

The movement of predators can be described in terms of the parameters indicated in (Fig. 2):

- frequency, number and duration of stops (per second),
- distance travelled (in mm),
- rate of locomotion (mm per second),
- turning rate (degrees per second),
- turn bias. This parameter measures bias to turn to the left or to the right and is obtained by designating left turns as (-) and right turns as (+), summing these for each time period, and taking the average,
- path straightness is the ratio between beeline distance and the total path length,
- thoroughness index, T (Bond, 1980):

$$T = 1 - \exp \frac{4LW}{3.14r^2}$$

where

L = path length,

W = path width,

r = radius of minimum circumscriptive circle that encloses the path.

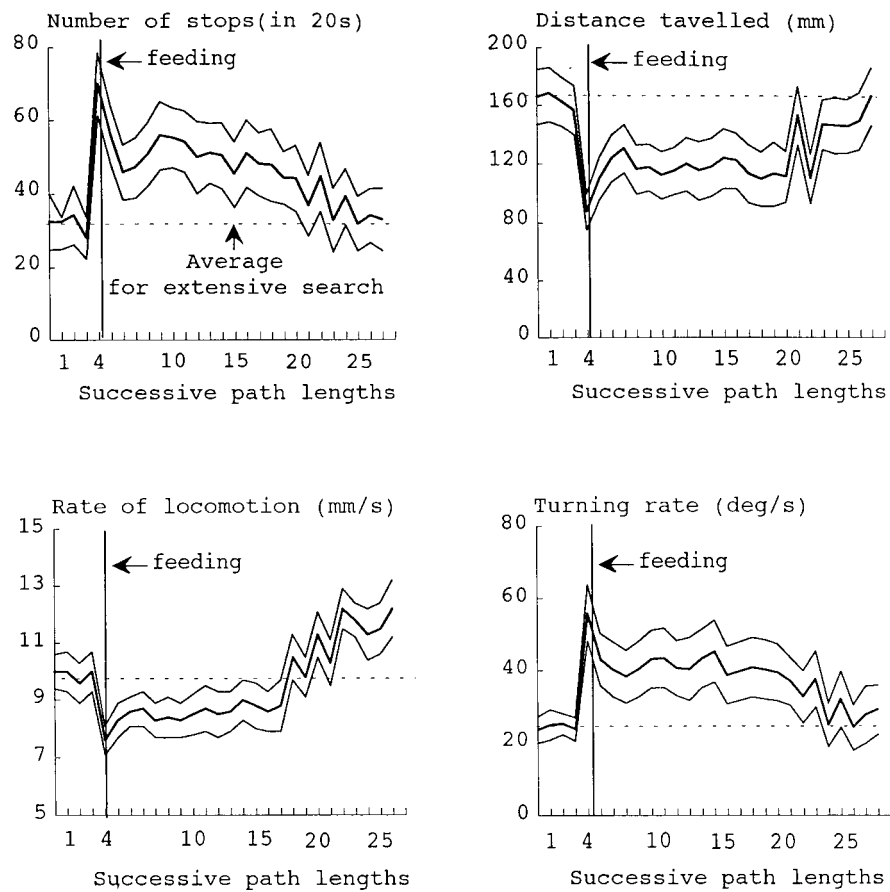


Fig. 2. Variation in the number of stops, distance travelled, rate of locomotion and turning rate shown by larvae of *Semiadalia undecimnotata* before and after feeding (average \pm SD).

For example, Carter & Dixon (1982) used the above parameter to show that each time a larva of *Coccinella septempunctata* L. ingests an aphid, its rate of locomotion decreases and its turn rate increases, followed by a decline in both measures to the prefeeding value over a period of 30 to 40 s. The return to a relatively straight pattern of movement results in a larva leaving the area.

Previously, the movement of searching predators was described by manually recording their position in space at successive points in time and then calculating the above parameters. In the laboratory, this movement can now be filmed and recorded on a magnetoscope (Fig. 3). Specific software then automatically computes the search parameters.

PATH RECORDING APPARATUS

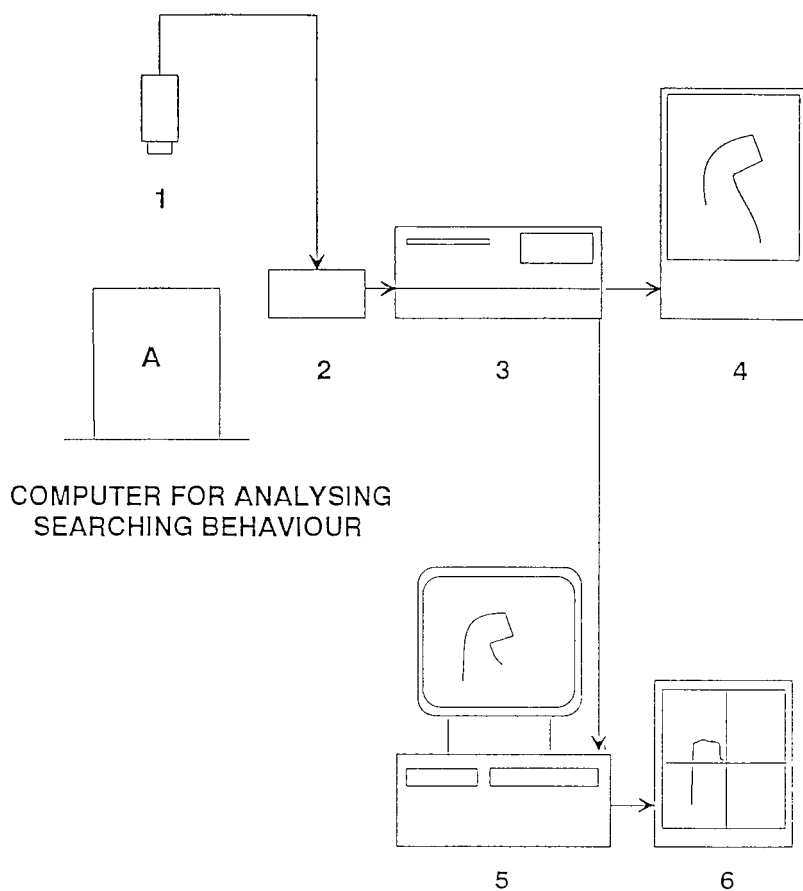


Fig. 3. An automatic method of quantifying search parameters (A – white arena, 1 – camera, 2 – apparatus for image binarisation, 3 – video recorder, 4 – control screen, 5 – computer with special card and software, 6 – screen for the initialisation of path analysis).

Optimal foraging

Many authors have attempted to explain and predict foraging behaviour using optimal foraging theory, which is based on four assumptions:

- foraging behaviour shows heritable variations,
- there is a range of possible behaviours,
- natural selection favours those individuals that contribute most to subsequent generations, and

- natural selection results in a change in the average foraging behaviour towards that which maximizes fitness.

From these assumptions mathematical or graphical models have been developed to account for the choice of diet and patch, the time spent in a patch, and the pattern of movement of foraging animals (Krebs & Davies, 1986; Pyke et al., 1977).

Within a patch, prey availability decreases as a result of predatory activity. The central concept is that the time spent by a predator in a patch depends on the initial density of prey and the average travel time between patches. The time spent in a patch is greater when the

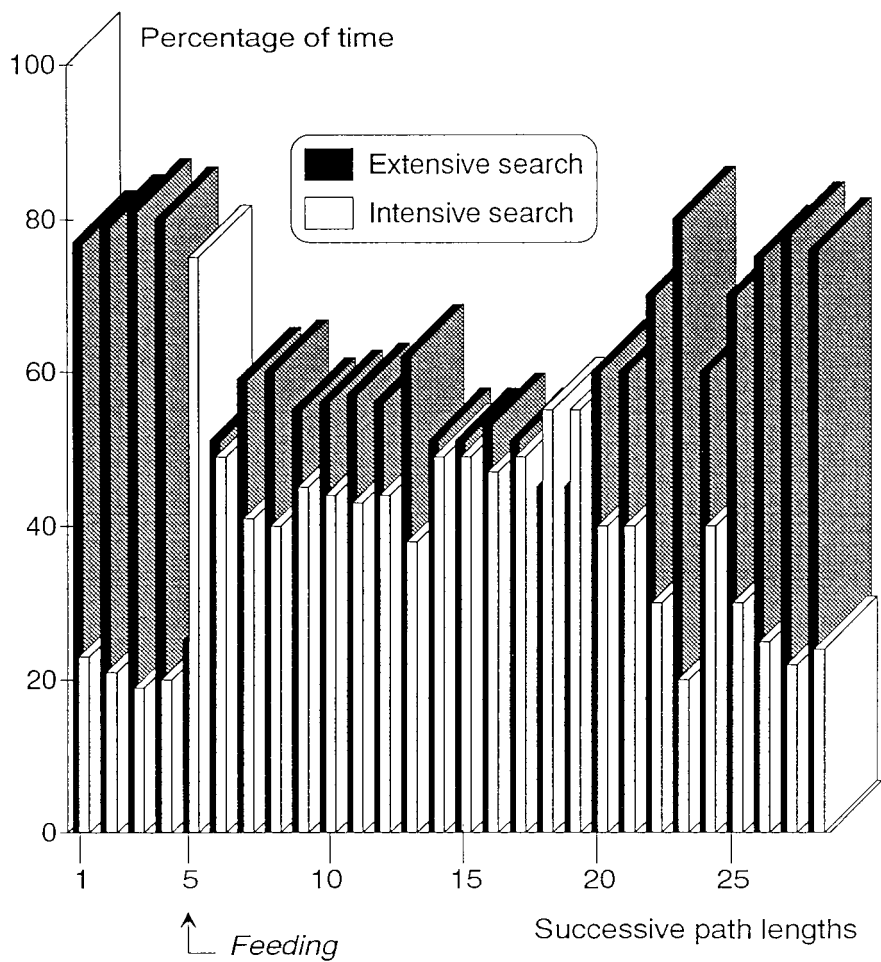


Fig. 4. Average percentage of time spent in intensive search by larvae of *Semiadalia undecimnotata* Schneid. before and after feeding (individual paths are divided into successive lengths of the same duration and classified as being in the extensive or intensive search mode).

travel time (patches are further apart) or the initial density of prey is high. This also applies to larvae moving between aggregates of aphids within a patch.

Optimal foraging theory has been criticized because it does not take into account inter-individual variability in foraging behaviour, which is important in the long term selection of an optimal foraging strategy (Bell, 1990). In *Semiadalia undecimnotata* Schneid., the temporal organization of larval movement is more complicated than the generally accepted succession of extensive search, feeding and intensive search (Ferran et al., 1993). Larvae can show periods of intensive search before feeding and a highly variable response to prey consumption, adopting intensive search immediately, later or never after prey capture. After capturing prey a typical pattern is an alternation of periods of extensive and intensive search (Fig. 4). If no further prey are captured, the number and the duration of the periods of intensive search progressively decrease.

In addition, many of the components of foraging behaviour of ladybird larvae have been shown to be hunger-dependent, an aspect largely ignored in the development of optimal foraging theory. In the desire to establish general strategic rules the consideration of detailed behavioural mechanisms and the constraints to which specific predators are subject have been sacrificed in favour of generalised assumptions. Although hunger-induced changes in foraging behaviour of coccinellid larvae enable them to forage in a manner consistent with the generalized strategic rules, no comment can be made as to whether they are foraging optimally or not. Only by knowing all the environmental, morphological and physiological constraints of a particular ladybird, which is clearly impractical, can the optimal solution be defined (Carter & Dixon, 1982).

For coccinellids, there are a few studies on optimal foraging behaviour and genetical variability in foraging behaviour of larvae. More work on these aspects of foraging behaviour will improve our understanding of the predatory behaviour of ladybirds each of which feeds on a number of species of aphids, which differ in quality, abundance and distribution.

ORIENTATION AND PREY RECOGNITION

During extensive and intensive search, ladybirds like other insects (Papaj & Prokopy, 1989) receive environmental and internal information. Some of this information is used to orientate towards prey.

This information can be classified into two main groups (Bell, 1990):

- 1) External sensory information that is typically visual, chemical or tactile. This information may be directional (visual stimuli, a trail, veins and edge of leaves) or non directional (pheromone), and
- 2) Internally-derived or internally-stored information transmitted from proprioceptors in or near locomotory organs and stored as individuals move, or acquired through learning or heredity.

Internally-derived information include motor commands and proprioceptive signals stemming from motor activity, which are coupled to a predator's body position or change in body position. Genetically-stored information used in searching takes the form of a 'program' and may govern the switch from extensive to intensive search (Bell, 1985).

Extensive search

Many investigators have concluded that coccinellids do not perceive their prey before making contact (Banks, 1957; Fleschner, 1950; Kaddou, 1960; Kehat, 1968) and consider that the efficiency of this random search is enhanced by both coccinellids and aphids being negatively geotactic and positively phototactic.

Visual cues

That adults orientate visually to prey has been suggested by several authors (Allen et al., 1970; Nakamuta, 1984a; Stubb, 1980). Adults and larvae of coccinellids perceive colour contrast and orientate towards objects with the sharpest colour contrast with the background and prefer those with a complex shape (Said et al., 1985). Nakamuta (1985) suggests that coccinellids are able to discriminate prey from non-prey like objects visually by their size and shape. The range of perception recorded for adults varies from 1.04 cm (*C. septempunctata*) to 1.91 cm (*Anatis ocellata*). In an arena, adult *C. septempunctata* move towards vertical posts after making an abrupt turn towards such visual stimuli and when offered a choice between a near and a far object of equal image size, will orientate towards the closer (Collett, 1988). Obata (1986) suggests that *Harmonia axyridis* is capable of utilizing visual cues such as green leaves in locating prey. However, there is no evidence to indicate that larvae use visual cues when foraging for prey.

Olfactory cues

Little is known about the olfactory cues perceived by coccinellids when searching for prey. Aphids secrete alarm pheromone in response to attack by predators, which causes other aphids to disperse (Nault et al., 1973). Synthetic (E)-farnesene, a principal component of aphid alarm pheromone, however, is not an orientation cue for coccinellids (Nakamuta, 1991). Obata (1986) and Meidari & Copland (1992), however, have shown that *H. axyridis* and *Cryptolaemus montrouzieri* can detect prey by smell.

Gustatory cues

Larvae of *C. septempunctata* may mark a plant chemically while searching (Marks, 1977). This enables subsequent short term recognition and avoidance of areas that have previously been searched. This is claimed to be specific to a particular larva and does not affect the searching activity of other larvae. However, as several attempts to confirm these observations have been unsuccessful (Dixon, unpublished) this work needs to be repeated. Coccinellid larvae frequently touch the surface on which they are moving with their anal disk and their maxillary palps. A chemical marker, therefore, could be produced in the anal region of the abdomen and perceived through sensillae on the maxillary palps. The upper surface of the last segment of these appendages is a thin membrane covered with gustatory sensillae (Barbier et al., 1989).

Intensive search

The adoption of the intensive search mode by coccinellids after ingesting prey (Nakamuta, 1984b) but not after encountering aphid dummies (Ferran, unpublished) indicates that the switch from extensive to intensive search results from ingestion of prey. For

this reason intensive search has also been called "success motivated search" by Vinson (1977). Chemical components of prey, which stimulate changes in movement of coccinellids are not known. As most coccinellids feed on a large number of aphid species, substances common to many aphid species might play this role (Hodek, 1973). Whether they can choose between prey species is not clear. Blackman (1967) reported that *Adalia bipunctata* L. could not distinguish between the toxic aphid *Megoura viciae* and the non toxic *Acyrtosiphon pisum*. In contrast, Dixon (1958) noted that as soon as *A. decempunctata* penetrates the body wall of the aphid *Hyalopterus pruni* the prey was rejected. Thereafter, palpal contact is enough to reject this prey. Chemicals excreted by aphids however can induce intensive search. Carter & Dixon (1984) showed that the presence of aphid honeydew increased the time *C. septempunctata* spent searching for prey on plants. The most important internal factor affecting intensive search, however, appears to be hunger (Carter & Dixon, 1982).

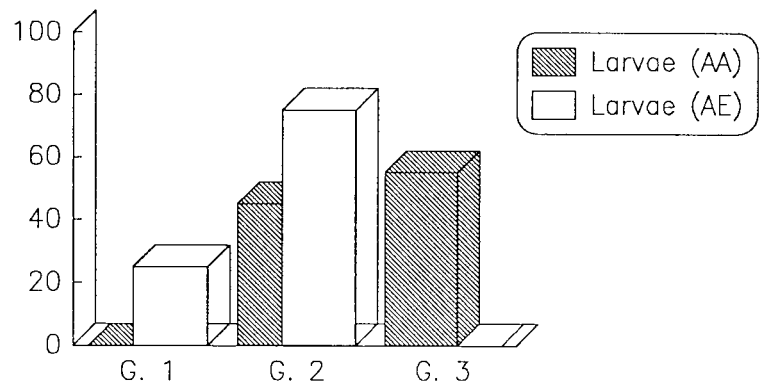
The sensory ability of ladybirds is poorly known. There are several reasons for this lack of knowledge. Up to 1980, searching for prey was considered a random process. Murdie (1971) in modelling predation assumed that these predators were 'blundering idiots'. It is widely believed that prey recognition by ladybirds only occurs after physical contact. This resulted from the fact that in most coccinellids, prey recognition does not markedly modify their behaviour, particularly their pattern of locomotion. However, adult *A. ocellata* (Allen et al., 1970) and *C. montrouzieri* (Meidari & Copland, 1992) stop when they see prey and then move forward to catch them. Environmental stimuli other than those associated with prey have been neglected. Plants may provide tactile and particularly chemical stimuli when infested with prey. The short range of perception of ladybirds, however, makes such studies difficult. Improved methods of monitoring using video cameras, olfactometry and electrophysiological recording may allow progress in this field.

LEARNING

If a species profits from experience, it can improve its foraging efficiency by responding appropriately to a changing environment (Drost et al., 1988). Conditioning is the most common type of learning and has been observed in six orders of insects, e.g. Orthoptera, Coleoptera and Hymenoptera (Papaj & Prokopy, 1989). Conditioning may bring about changes in feeding preferences or affect the way an insect forages.

Every species of coccinellid prefers a particular habitat (Iperti, 1966), e.g., *C. septempunctata* is found mainly on herbaceous plants and *A. bipunctata* on trees. In their specific habitat, these ladybirds eat all the species of aphids they encounter. Whether ladybirds can develop a preference for a particular species of aphid as a result of conditioning is unclear. Murdoch & Marks (1973) studied the predatory behaviour of *C. septempunctata* when attacking two species of aphid. These aphids were eaten in direct proportion to their relative abundance, i.e. no switching occurred in response to conditioning. Nevertheless, *Stethorus punctum*, a predator of tetranychid mites has a weak but consistent preference for *Tetranychus urticae* following preconditioning to this species (Houck, 1986). The aphidophagous coccinellid *H. axyridis* can be reared on eggs of *Ephestia kuehniella* (Lep.: Pyralidae) and on the aphid *A. pisum*. The foraging behaviour of the larvae varied according to the food they had previously eaten (Ettifouri & Ferran, 1993) (Fig. 5). When fed the same food, the larvae changed from an extensive to an intensive search mode. But when fed a different

Larvae reared on aphids(A) and fed subsequently on the same aphid (AA) or on eggs (AE)



Larvae reared on eggs (E) and feed subsequently on eggs (EE) or on aphids (EA)

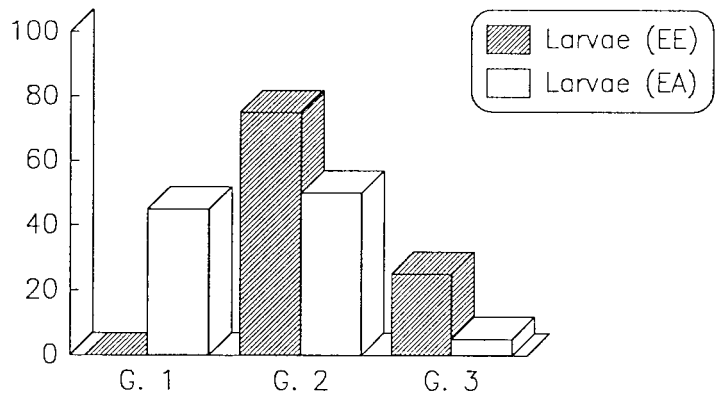


Fig. 5. Percentage of time spent just after feeding by larvae of *Harmonia axyridis* in G1 – extensive search, G2 – intermediate intensive search and G3 – intensive search.

food, the larvae either continue the extensive search mode or adopt a less sinuous path than in the typical intensive search mode. Thus, feeding larvae a particular species of prey conditions them to that prey as after capturing other kinds of prey they retain the extensive search mode, may quickly leave the area and are less effective at exploiting patches of this new prey.

These examples indicate the possibility of trophic conditioning in coccinellids, which could affect prey preferences and (or) searching activity. These changes, although temporary, could alter predatory efficiency.

THE EFFECT OF PHYSICAL AND BIOTIC FACTORS ON FORAGING BEHAVIOUR

Foraging behaviour is affected by abiotic and biotic factors of the environment, and the physiological state of the predator.

Abiotic factors

Environmental conditions (temperature, humidity, light intensity) affect the searching behaviour of ectotherms by modifying their rate of movement. Many predators depend on environmental sources of heat. Coccinellids, for example, warm up by absorbing solar radiation (Jankowsky, 1973). Rapid locomotion at high temperatures may be adaptative because predators need to find more prey to offset the depletion of their energy and water reserves. Desiccation often stimulates searching because prey are an important source of water.

Climate may also affect the distribution of predators on plants through its effect on the phototropic and geotropic responses. At the beginning of spring, larvae and adults of the thermophilic species *C. septempunctata* (Honěk, 1979) are found on the lower parts of wheat plants, the warmest region in this plant stratum (Honěk, 1983). This has two important consequences for predator-prey relationships. Aphids situated on the upper parts of wheat plants are not attacked by this coccinellid (Ferran et al., 1989). The adults mainly lay eggs on the soil, stones, and weeds, which is unfavourable for the survival of their progeny.

The foraging behaviour follows a rhythmical pattern controlled by a combination of endogenous factors and exogenous climatic components (Frazer & Gill, 1981). In wheat fields in spring, larvae and adults of *C. septempunctata* are most mobile in the middle of the day (Ferran et al., 1991). Later in the season, they search for most of each day and probably during the night (Nakamura, 1987). Curio (1976) suggested that the daily pattern in the search for prey is more or less dependent on the opportunities to feed rather than rigidly linked to circadian activity.

Biotic factors

Plant

The orientation towards prey and the predatory efficiency of coccinellids, which have limited sensory abilities, depend on the physical and maybe chemical characteristics of plants (Carter et al., 1984). Plant density, through its effect on the microclimate, affects both coccinellid abundance and species composition (Honěk, 1983). In cereal crops, the thermophilic *C. septempunctata* is the most abundant in low density stands and *Propylea*

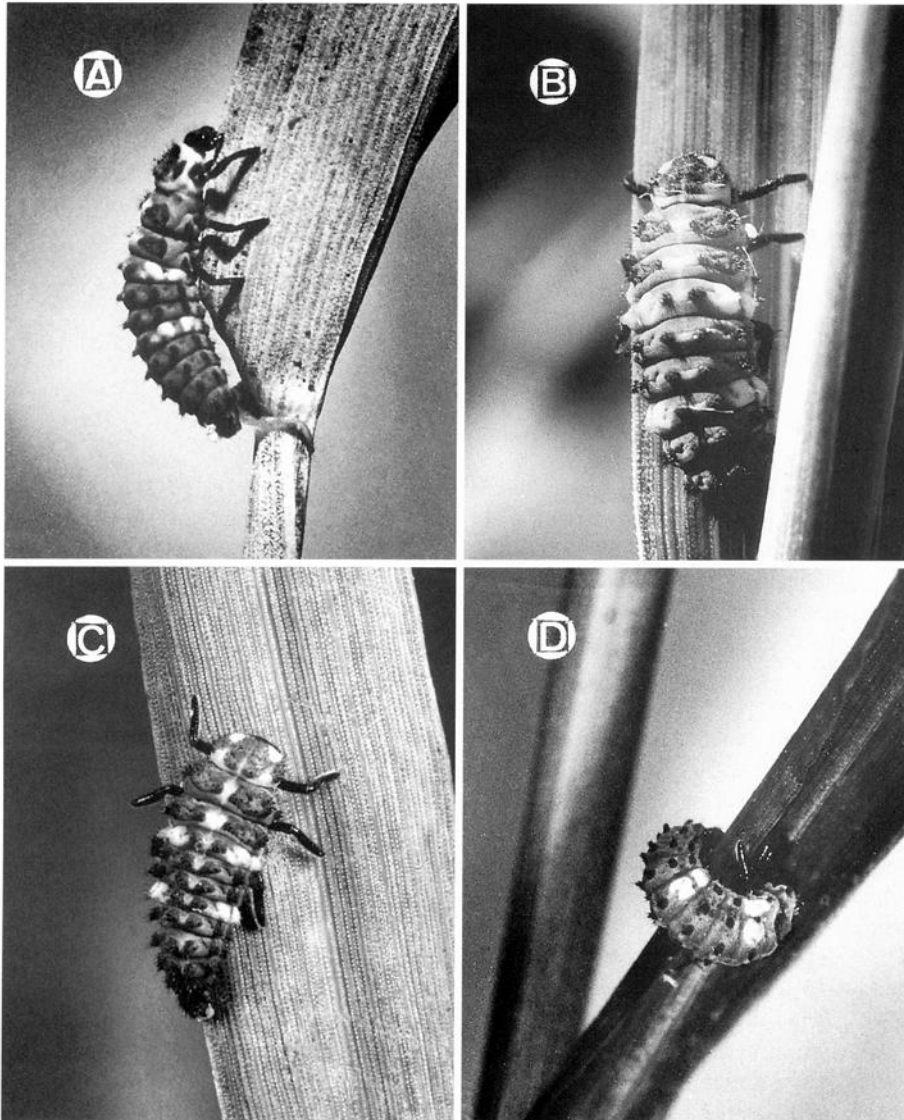


Fig. 6. The four positions adopted by *C. septempunctata* larvae on wheat leaves during extensive search: sagittal (A) and parallel (B), and intensive search: angular (C) and overlapping (D) (from Ferran & Deconchat, 1992).

quatuordecimpunctata L. prevails in dense stands.

The rate at which a predator encounters prey can be affected by the hairiness or waxiness of plants. Banks (1957) found that larvae of *P. quatuordecimpunctata* move more slowly on the hairy leaves of potato than on the glabrous leaves of bean. Coccinellids, like many other predators, concentrate their search along the veins of leaves where aphid density is generally highest (Dixon, 1959; Wratten, 1973). On leaves lacking prominent veins, coccinellids search the edge of leaves and the petiole. Thus coccinellids do not always search in areas of highest aphid density (Carter, 1982, Carter et al., 1984). The last instar larvae of *C. septempunctata* walk along the edges of wheat leaves clutching them with their legs and their anal pseudopod (Ferran & Deconchat, 1992) and when searching adopt one of four positions: sagittal, parallel, angular or overlapping (Fig. 6). Whatever position they adopt, the central area of the leaf is not searched and aphids there are not found.

The physiological state of a plant may also affect the foraging behaviour of a predator. Kesten (1969) reported that adult *Anatis ocellata* L. tested pine needles with their mandibles and only searched new needles, presumably to reduce the amount of time searching areas where prey are not likely to be present.

Plant structure may protect aphids from predators. For example, third and fourth instar larvae of *C. septempunctata*, unlike syrphid larvae are unable to enter the space between the stem and the ear of wheat, where the aphid *Rhopalosiphum padi* L. is often to be found (Ferran, unpublished).

Prey

In many insects, resource quality affects the duration and speed of search, capture rate, the run/stop ratio and the change from intensive to extensive search, which keep the insects longer in rich patches than in poor patches.

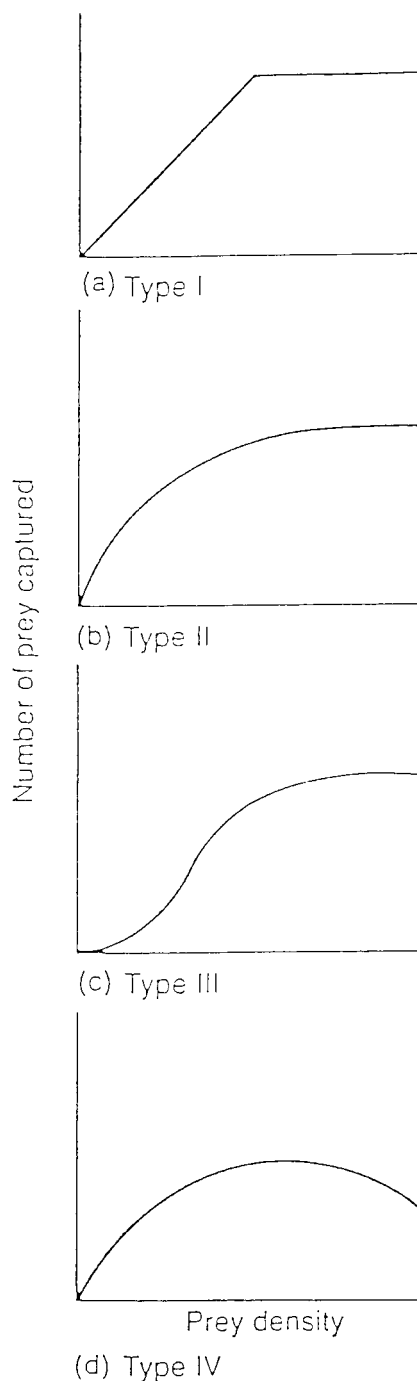


Fig. 7. Four types of functional response curve (from Holling, 1959).

Most research on prey quality is concerned with the nutritional value of various prey species. As the adoption of an intensive search mode follows the ingestion of suitable prey (Nakamuta, 1984b), the locomotory patterns of predators may be linked to aphid quality. This is confirmed by the results of Houck (1986) and Ettifouri & Ferran (1993, in press). The response to prey quality possibly depends on the food specificity of predators. The duration of intensive search is also related to the size of the prey consumed. *C. septempunctata brucki* showed significantly longer periods of intensive search when fed first a small then a large aphid, than vice versa (Nakamuta, 1985).

The consumption of prey per unit time usually increases along with prey density until the predator is satiated. This is known as the functional response (Holling, 1959) and can take one of four forms (Fig. 7). Type I and II responses are thought to reflect satiation and occur in one of two ways. The rate of feeding declines as a function of the filling of the gut. As prey becomes more abundant, predators initially feed more, but then handling time (capturing, eating and cleaning) soon takes up a sizable portion of the available time. The shape of the type III curve may result from one of several changes in predator behaviour. The forager may: 1. learn to find prey more readily at some critical prey encounter rate and then concentrate feeding on it, 2. spend less time in non-foraging activities at high prey encounter rates, or 3. emigrate from prey patches more readily at low prey densities. Coccinellids show a type II response to increase in prey density (Mogi, 1969; Kawauchi, 1979; Sinha et al., 1982; Hodek et al., 1984). However, Hassell et al. (1977) report that Cock's data (1977) reveal that *C. septempunctata* show a type III response.

Distance between patches and distribution of prey within patches may affect foraging behaviour and searching success. Murakami & Tsubaki (1984) conducted experiments on the searching efficiency of *C. septempunctata brucki* when attacking prey populations with different distributions and densities. They showed that searching efficiency depended on the prey distribution. At low prey density, the predator is most efficient when the prey is distributed uniformly whereas at high prey density, it is most efficient when prey is highly aggregated.

The response of prey to the presence of coccinellids can have an important effect on their foraging success (Dixon, 1958; Wratten, 1976; Hajek & Dahlsten, 1987). Many aphid species respond visually to walking coccinellids (Klingauf, 1967), to tactile stimuli, plant vibrations induced by predators (Brodsky & Barlow, 1986) and olfactory stimuli such as the alarm pheromone secreted by captured aphids (Ferran & Deconchat, 1992). The most active forms of avoidance shown by aphids are walking away, kicking and dropping. Dropping from plants is a fairly common response but is not without risks (Dixon, 1958) as aphids frequently fail to find another plant (Roitberg et al., 1979) and may be captured by coccinellids walking on the ground. In wheat fields, 30% of the prey captured by *C. septempunctata* are aphids walking on the ground (Ferran et al., 1991).

Predator

All species show changes in their pattern of movement following feeding and the area they traverse per unit time depends on size/age. The first instar, which only search a very small area is poor at capturing prey, and is a critical period in coccinellid development (Dixon, 1958, 1959; Brown, 1972). Newly hatched larvae remain on the egg cluster for some time after hatching and feed on the unhatched eggs. It is generally believed that such

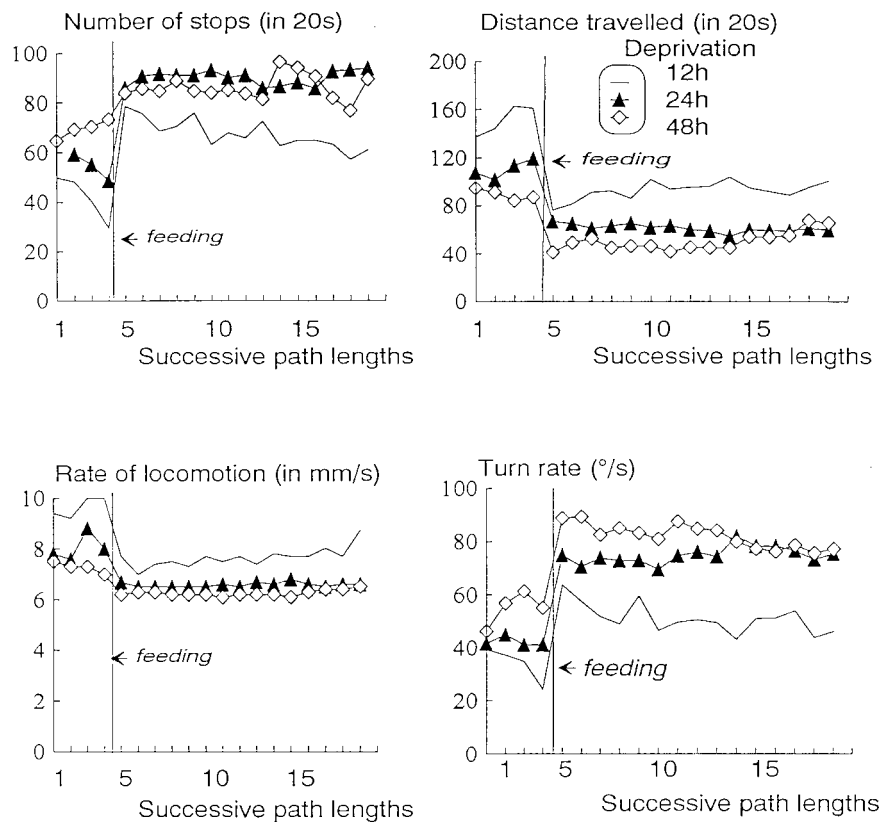


Fig. 8. Variation in the number of stops, distance travelled, rate of locomotion and turn rate of larvae of *Harmonia axyridis* deprived of food for 12, 24, or 48 hours.

sibling cannibalism benefits the survival of the remaining individuals enabling them to make a more prolonged search for aphids (Banks, 1956; Dixon, 1959). Track width and locomotory rate increase with body length while handling time is inversely proportional to size (Dixon & Stewart, 1991).

Starvation causes predators to adopt an intensive search mode before feeding and after feeding to search more intensively (Fig. 8) and to be less prey specific. The search becomes more and more intensive as shown by an increase in the number of stops, turn rate and a decrease in the rate of locomotion with starvation (Fig. 8). But, too long a period without food leads to a gradual decrease in activity and death (Nakamura, 1987).

Several foraging traits have been shown to be genetically determined in insects, such as circadian rhythms, the time of switching from extensive to intensive search, sensory and scanning abilities, dispersal tendency, and food and habitat preferences. In coccinellids, little is known about the genetic variability in searching behaviour. Larvae of *S.*

undecimnotata adopt intensive search immediately, after a delay or never after prey ingestion: this variability may be of genetic origin (Ferran et al., 1993).

Intraspecific competition

Predators aggregate on plants where prey is abundant. The numerical response of predators to increase in prey density is important in determining the effectiveness of these natural enemies and is often responsible for suppressing prey populations (Huffaker et al., 1971). This response to prey density results from egg-laying and the accumulation of larvae and adults (Hemptinne et al., 1992; Mills, 1982). Intensive search mode and inactivity when satiated result in the aggregation of these mobile predators in areas of aphid abundance (Dixon, 1959; Kareiva & Odell, 1987).

Following the rise in the density of predators, the total number of prey consumed increases at a decreasing rate while the rate of consumption per individual, which is at a maximum when few predators are present, decreases (Pandey et al., 1984). This results from rapid prey depletion and mutual interference between predators, which induces them to scatter (Eveleigh & Chant, 1982). Mutual interference causes the ladybirds to fall off a plant, switch from intensive to extensive search and stop feeding.

Abiotic and biotic factors affect the foraging behaviour of predators and contribute to variability through variation in the temporal and spatial availability of prey. Plants influence predator distribution, orientate their searching and in part determine the prey density actually available to them. In biological control programs, the response of mass reared predators to plants and the effect of plant structure on the predator's searching efficiency must be considered. Predators respond to the spatial distribution of prey by remaining in areas where prey is abundant. Starvation causes them to adopt an intensive search mode. The variability in their response to prey ingestion is advantageous as an insurance against temporal and spatial changes in prey number and distribution. The presence of other individuals generally has a negative effect on searching success. However, if adults assess the quality of aphid colonies accurately before laying eggs then there will be relatively little competition for food (Kindlmann & Dixon, 1993; Hemptinne et al., 1993) and the level of mutual interference will be slight.

Many authors like Jones (1977), Cain (1985), Kareiva & Odell (1987), Kindlmann & Dixon (1993) and Turchin (1991) propose models for quantifying insect movements, which incorporate some of the factors mentioned above. Such models have and will continue to give us a better understanding of ladybird foraging strategies.

CONCLUSION

Coccinellids tend to lay eggs close to aphids and their larvae, especially the very mobile last instar, actively seek out colonies of aphids. Thus, for a better understanding of their effectiveness as predators we need to understand their foraging behaviour.

Very little progress has been made in understanding the foraging behaviour of insect predators compared with parasites. This is mainly because few studies have been made of the searching behaviour of adults, which select the patches of prey the larvae exploit.

To fill this gap in our understanding we need to:

- 1) study the effect of change in environmental conditions (mainly plant, prey density and distribution, predator number) on locomotory and egg laying patterns,

- 2) model the foraging behaviour with a view to achieve a better understanding of how the predators maximize their fitness,
- 3) study the sensory abilities of these predators,
- 4) determine the role learning plays in foraging behaviour.

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