

MECHANISM OF THE SWITCHOVER FROM EXTENSIVE TO AREA-CONCENTRATED SEARCH BEHAVIOUR OF THE LADYBIRD BEETLE, *COCCINELLA SEPTEMPUNCTATA BRUCKII*

KIYOSHI NAKAMUTA

Laboratory of Applied Entomology and Nematology, Faculty of Agriculture, Nagoya University,
Nagoya 464, Japan

Abstract—Area-concentrated search of predatory coccinellid adults, *Coccinella septempunctata bruckii*, is considered to be controlled by internal locomotory information, since the area-concentrated search is generated even if aphids are no longer present in the environment. To investigate what kind of cue elicits the switchover from extensive to area-concentrated search behaviour, the duration of area-concentrated search (giving-up time) was measured after each of the following five kinds of feeding stimuli was supplied: (a) contact with an aphid (*Myzus persicae*), (b) biting an aphid, (c) consumption of an aphid, (d) contact with an agar block of $ca\ 2 \times 2 \times 2$ mm, (e) consumption of an agar-block coated with a droplet of aphid body fluid. Switchover from extensive to area-concentrated search was observed as a response to all feeding stimuli. The cue to elicit the switchover is the contact with a prey rather than the consumption of it. The giving-up time is dependent on the intensity of feeding stimulus since giving-up time varied according to the type of feeding stimulus ($d \approx a < b < e < c$). The giving-up time was positively correlated with the duration of feeding on an aphid which represented the size of prey consumed. To test whether giving-up time is determined by the amount or by the size of prey consumed, it was measured after the ladybird beetle had fed first on a large then on a small aphid (Sequence A) and after it had fed first on a small then on a large aphid (Sequence B). Although the beetle consumed the same total amount of aphids in both sequences, the beetle showed the longer giving-up time in Sequence B than in Sequence A. Therefore, it can be concluded that giving-up time is determined by the size of prey most recently consumed rather than hunger level or prey capture rate.

Key Word Index: Prey search, area-concentrated search, eliciting cue, giving-up time, prey size. *Coccinella septempunctata bruckii*

INTRODUCTION

Many insect predators and parasitoids switch their search behaviour from extensive to area-concentrated or local search after having found a prey or a host item. This behaviour was first found in parasitoid wasps (Laing, 1937) and in predatory coccinellid larvae (Fleschner, 1950; Banks, 1957; Dixon, 1959). For instance, predatory coccinellids search in a relatively straight track within a broad area until the prey is captured (extensive search). After capturing the prey, however, the ladybird beetles localize the area searched for subsequent prey within the immediate vicinity of the prey capture site (area-concentrated search). If other prey are not found within a short period during area-concentrated search, the beetles return to extensive search (Marks, 1977; Carter and Dixon, 1982, 1984; Nakamuta, 1982).

Area-concentrated search has been considered to be characteristic of predators or parasitoids. However, Dethier (1957) found area-concentrated search for food items in the blowfly. Recently area-concentrated search was also found in male cockroaches seeking females (Schal *et al.*, 1983), in lepidopterous male moths seeking females (Ono, 1985) and in herbivorous insects searching for food plants (Jones, 1977).

Area-concentrated search may, therefore, be considered a general characteristic of insects searching for required resource items whose distributions are clumped. Area-concentrated search increases the probability of finding subsequent resource items (Evans, 1976; Murdie and Hassell, 1976; Murakami and Tsubaki, 1984).

The present paper deals with three questions on the behavioural mechanism controlling area-concentrated search of an adult ladybird beetle, *Coccinella septempunctata bruckii*: (i) what controls the locomotory pattern during area-concentrated search? (ii) what elicits the switchover in search behaviour? (iii) what determines the duration of area-concentrated search?

WHAT CONTROLS THE LOCOMOTORY PATTERN DURING AREA-CONCENTRATED SEARCH?

Figure 1 shows, to the same scale, a pre-feeding and a post-feeding search path of the same individual adult *C. septempunctata bruckii*. The search paths were recorded for 3 min in an experimental arena with a dia of 30 cm and a depth of 5 cm (Nakamuta, 1982). Locomotory rate was calculated every 15 s. The D_s/D_b ratio was calculated as a measure of straight-

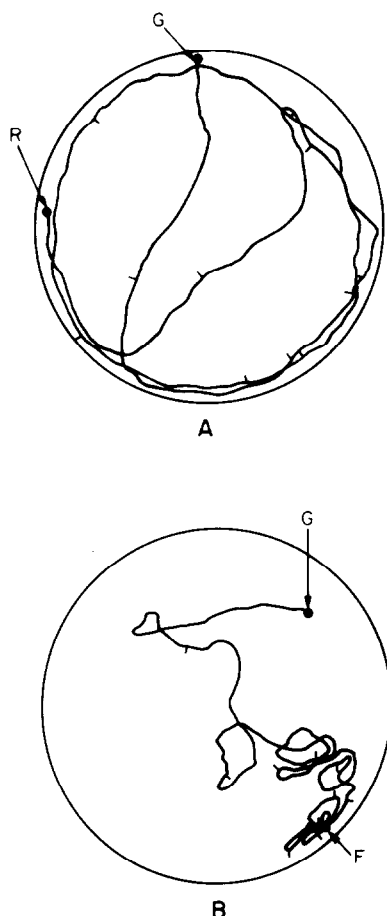


Fig. 1. Search paths of the same individual of *Coccinella septempunctata bruckii* in an experimental arena (A) before prey (an adult apterous *M. persicae*) capture and (B) after prey consumption. "R", "F" and "G" indicate the site where the tracing of the search paths was started, the site where the beetle consumed an aphid, and the site where the tracing was finished, respectively (from Nakamuta, 1982).

ness of search paths by the following formula: the length of the actual search path between a 15-s interval divided by the beeline distance between the intervals, a reciprocal of linearity index by Bell and Kramer (1979). The larger D_s/D_b ratio indicates that the search path is more tortuous. Before capturing an aphid, beetles moved in a relatively straight line (Fig. 1A). After consuming the prey, they localized their searching area (Fig. 1B); locomotory rate decreased (Fig. 2) and the D_s/D_b ratio increased significantly (Fig. 3). Within a short period locomotory rate increased and the D_s/D_b ratio decreased, resuming to the same level as before prey capture (Fig. 2 and 3). That the search area is localized is shown by a decrease in locomotory rate and an increase in the D_s/D_b ratio.

This feature of post-feeding locomotory pattern is similar to the search path recorded in other coccinellids (Banks, 1957; Rowlands and Chapin, 1978). In this experiment the locomotory pattern is generated even if aphids are no longer present in the environment. The ladybird beetle, therefore, might not use the external sensory cue to generate the

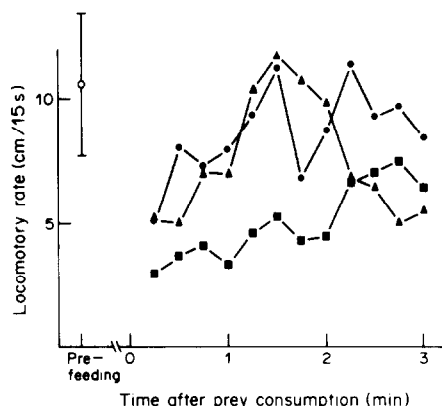


Fig. 2. Mean searching speeds (cm/15 s) before prey (an adult apterous *M. persicae*) capture (○), and after consumption of one prey (●—●), two prey (■—■) and four prey (▲—▲). Vertical bar indicates a \pm SD (from Nakamuta, 1982).

locomotory pattern of area-concentrated search, although it is uncertain from most studies whether or not the orientation pathway represents output of stored information or response to external sensory information (Bell and Tobin, 1982).

Ladybird beetles oriented the prey from the close proximity of the prey under light conditions though not orienting under dark conditions. Further, they oriented even dummy prey made of Parafilm[®] under light conditions. From these facts, the beetles are suggested to orient visually toward the aphid prey from the close proximity of the prey (Fig. 4). They, however, cannot orient with respect to landmarks or other cues in the environment, because no visual cues are present in the experimental arena.

Some insects utilize external chemical boundary information at the border of a resource patch (Waage, 1978; Tobin, 1981). For instance, the parasitic wasp, *Venturia canescens*, becomes "locked into" a resource patch by executing turn angles exceeding 90° relative to its track direction each time it approaches the outer limits of substrate prey odour

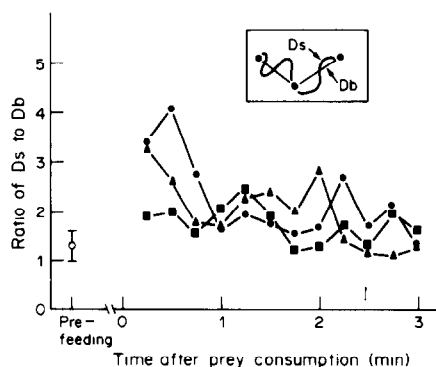


Fig. 3. Mean ratio of the length of an actual search path (D_s) to the beeline distance (D_b) during 15 s intervals before prey (an adult apterous *M. persicae*) capture (○), and after consumption of one prey (●—●), two prey (■—■) and four prey (▲—▲). Vertical bar indicates a \pm SD (from Nakamuta, 1982).

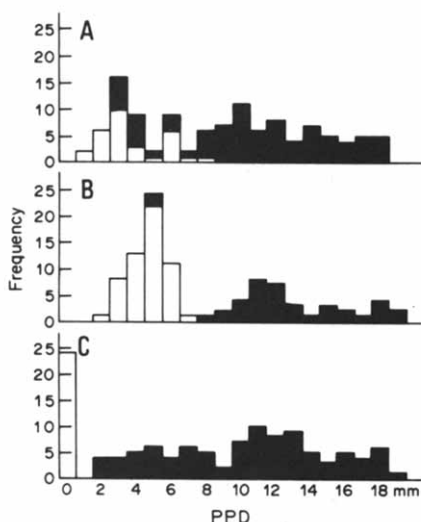


Fig. 4. Frequency distribution of the PPD (prey-predator distance) in successful (open column) and unsuccessful (solid column) orientation toward the prey. A: dummy prey under light conditions; B: aphid (*Myzus persicae*) prey under light conditions; C: aphid prey under dark conditions. PPD is defined as the distance between the point of turning toward the prey and the head of the prey in case of successful orientation. In unsuccessful orientation, PPD is the beeline distance between the trajectory of the centre of ladybird beetle's head and the aphid. PPDs in A, B and C are significantly different ($P < 0.01$, Mann-Whitney's U -test) [Modified from Nakamuta, 1984a].

(Waage, 1978). Males of the American cockroach, *Periplaneta americana*, turn when they encounter the edge of a female sex pheromone plume (Tobin, 1981). Although there may be a residue of prey odour in the experimental arena, it is unlikely that the ladybird beetles use it as an orientational cue since they do not show an olfactory response to the prey odour when tested in an olfactometer (Nakamuta, 1985a).

In conclusion, the locomotory pattern must be generated idiothetically by an internal mechanism or programme rather than allothetically by the perception of a change in the environmental cue. The internal mechanism controlling the locomotory pattern should be further studied.

WHAT ELICITS THE SWITCHOVER IN SEARCH BEHAVIOUR?

In most earlier studies, the locomotory pattern of ladybird beetles during area-concentrated search have been observed after the insects consumed prey and so despite of many studies on coccinellids search behaviour (cf. Hodek, 1973), the cues eliciting the switchover from extensive to area-concentrated search have not been delineated.

At what stage in the feeding sequence the switchover from extensive to area-concentrated search is elicited, is inquired by measuring the duration of area-concentrated search (giving-up time) after various feeding stimuli have been supplied for the ladybird beetle. Giving-up time has been originally defined as the time between the last capture of prey

and when an individual left a patch to go to another patch (Krebs *et al.*, 1974).

To measure giving-up time, a beetle was released into an experimental arena with a grid of 145 squares of 2×2 cm drawn on its base (Nakamuta, 1985b). Each feeding stimulus was presented to a searching ladybird beetle in one of these squares. When the beetle started searching after the completion of a stimulation, the duration of searching within the square where a stimulus was presented and adjacent 8 squares was measured (Fig. 5). Searching time within the 9-square area is defined here as the giving-up time.

It is difficult to clearly define a prey patch or the area where the ladybird beetles engage in area-concentrated search, so the prey patch is arbitrarily defined as mentioned above.

Although the area of patch seems to influence the absolute estimates of giving-up time, it probably does not influence the comparison of the relative values of giving-up time between different feeding stimuli using the same method.

Giving-up time was measured after each of following five feeding stimuli was supplied for a ladybird beetle which has starved for 24 h after satiation: (a) contact with a green peach aphid, *Myzus persicae*, with beetle's mouthparts, after which the aphid was removed; (b) biting an aphid, after which the aphid was removed. This or stimulus "a" simulated the unsuccessful capture of the prey; (c) complete consumption of an aphid; (d) contact with a $2 \times 2 \times 2$ mm agar block, after which the agar block was removed; (e) consumption of an agar block coated with aphid body fluid, which is known to stimulate feeding (Fig. 6).

Ladybird beetles exposed to any of the above stimuli searched in the area-concentrated mode

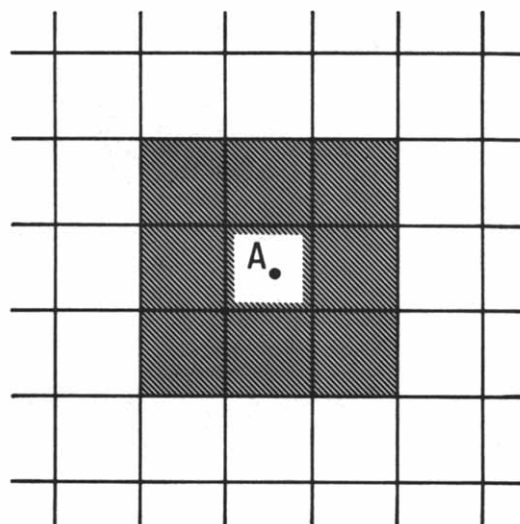


Fig. 5. Diagrammatic representation of "vicinity of prey detection", where the ladybird beetle engages in area-concentrated search. "A" indicates the site of prey detection. Hatched area represents the "vicinity" of prey detection. The duration of area-concentrated search (giving-up time) is defined as the duration of searching within the "vicinity" after prey detection. The size of each square is 2×2 cm (from Nakamuta, 1985b).

longer than those not exposed to any stimuli. The giving-up time was longest after the consumption of an aphid, some shorter after either the consumption of an agar block coated with aphid body fluid or biting an aphid and shortest after the contact with an aphid or an agar block but statistically significantly different from no stimulus (Table 1). Therefore, giving-up time may be dependent on the intensity of the feeding stimulus.

Switchover from extensive to area-concentrated search was observed as a response to all of feeding stimuli, suggesting that prey contact is sufficient to elicit the switchover. Giving-up time varied according to the intensity of feeding stimulus, with consumption of prey being the most intense stimulus. Coccinellid adults sometimes missed capturing prey after attacking them (Dixon, 1958; Brown, 1974) and even having contacted the prey the capture success rate of the beetle was less than 100% (Nakamuta, 1983). Considering these facts, it is more advantageous for the ladybird beetle to switch its search behaviour from extensive to area-concentrated one based on prey recognition (contact or biting) rather than consumption of prey.

WHAT DETERMINES THE DURATION OF AREA-CONCENTRATED SEARCH?

Since the giving-up time is likely to be dependent on the intensity of the feeding stimulus (Table 1), it is intriguing to ask if a larger aphid prey will initiate longer area-concentrated search than will a smaller aphid prey. To elucidate the relationship between the giving-up time and the size of prey consumed, an aphid (*Myzus persicae*) or an agar dummy coated with a droplet of aphid body fluid was fed to the ladybird beetle which was starved for 24 h after satiation. The time required to consume the prey and the giving-up time after consumption of the prey were measured.

Giving-up time was positively correlated with the time required to consume a 2nd or 3rd-instar *M. persicae* ($r = 0.66$, $P < 0.01$, Fig. 7B). Even by excluding the isolated point (longer feeding time) the positive relationship was significant ($r = 0.55$, $P < 0.05$). Even if an agar dummy coated with aphid body fluid was used instead of an aphid prey, the relationship between giving-up time and feeding time did not change. Giving-up time was also positively correlated with the feeding time ($r = 0.82$, $P < 0.001$,

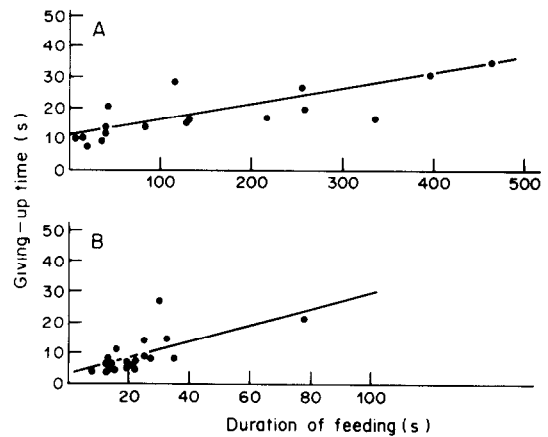


Fig. 7. The relationship between giving-up times in 24-h starved ladybird beetles and the feeding times on an agar block coated with a droplet of aphid body fluid (A) and on an aphid (a 2nd or 3rd-instar *Myzus persicae*) prey (B). Regressions are significant in both A ($r = 0.82$, $P < 0.001$, $N = 16$) and B ($r = 0.66$, $P < 0.01$, $N = 20$) (from Nakamuta, 1985b).

Fig. 7A). The variation in the volumes of aphid body fluid dropped on the agar block might be responsible for the variation in times required to consume an agar dummy coated with aphid body fluid. The slopes for the regression between giving-up time and feeding time were different between prey types. The slope for the regression in aphid prey was about 5 times as large as in agar dummy prey (Fig. 7), implying that a slight increase in feeding time on the aphid gives rise to much more increase in the giving-up time rather than increase in feeding time on the agar dummy. The live aphid is superior to the agar dummy coated with aphid body fluid as the stimulus to keep the beetles on being engaged in area-concentrated search. These results further suggested that giving-up time depends on not only feeding time but also the quality of prey.

To know whether the feeding time is a function of prey size, the time required to consume previously weighed aphid by a 24-h starved ladybird beetle was measured. Figure 8 shows that the feeding time is significantly correlated with the weight of the aphid consumed ($r = 0.83$, $P < 0.001$). It is, therefore, suggested that giving-up time is partly determined by the size of prey consumed.

There are two possible explanations for these results: (1) giving-up time is determined by the assessment of the size of prey consumed, or (2) giving-up time is inversely related to hunger level of the beetle, that is, it increases with decreasing hunger level. To test these hypotheses, giving-up time was measured after feeding the beetle on two aphids of different sizes in two different orders. The giving-up time was measured after a 24-h starved ladybird beetle was fed first on a large aphid (550 μg in weight) and then on a small aphid (250 μg , Sequence A). The beetle was fed to satiation on an excess of aphids. After 24 h following satiation, the beetle was fed first on a small and then on a large aphid (Sequence B) and the giving-up time was measured. Since the beetle consumes the same total amount of aphids in both sequences, if the giving-up time is different between

Table 1. Giving-up time of 24-h starved ladybird beetles, *Coccinella septempunctata bruckii*, exposed to different feeding stimuli

Types of feeding stimuli	Giving-up time: mean \pm SD in seconds
No stimulation	2.1 \pm 0.7**
Contact with an aphid	5.3 \pm 2.0 ^b
Biting an aphid	12.9 \pm 6.3 ^c
Consumption of an aphid	19.8 \pm 9.6 ^d
Contact with an agar block	5.4 \pm 2.1 ^b
Consumption of an agar block coated with aphid body fluid	16.7 \pm 7.3 ^c

*Values are mean \pm SD of ten different individuals. Means followed by different letters are significantly different at 0.05 level by Cochran-Cox's *t*-test (from Nakamuta, 1985b).

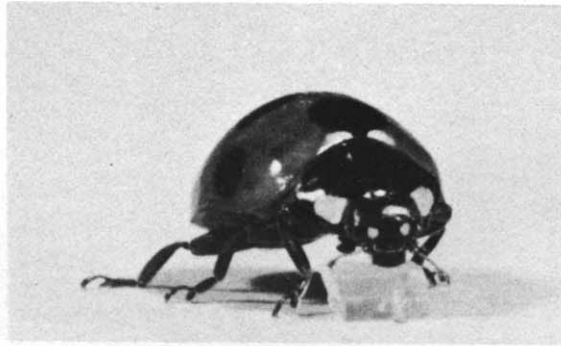


Fig. 6. An agar block coated with a droplet of aphid body fluid elicits feeding behaviour of the ladybird beetle, *Coccinella septempunctata bruckii* (from Nakamuta, 1984b).

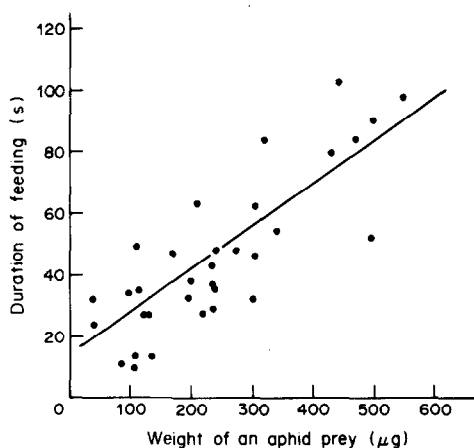


Fig. 8. Linear regression of time required for a 24 h starved ladybird beetle to consume an aphid of different weight vs the weight of an aphid ($r = 0.83$, $P < 0.001$, $N = 33$) (from Nakamuta, 1985b).

the two sequences it means that the giving-up time is determined by the size of prey most recently consumed.

The ladybird beetles showed significantly longer giving-up times in Sequence B than in Sequence A although they consumed the same total amount of aphids in both sequences (Fig. 9). Therefore, it is concluded that giving-up time is determined by the size of prey most recently consumed.

Two explanations have been proposed for the determination of giving-up time: (1) a fixed giving-up time and (2) a variable giving-up time mechanism. A predator leaves a patch when exploitation reduces the interval between prey capture to a period greater than the giving-up time, which is the fixed giving-up time mechanism (Hassell and May, 1974; Murdoch and Oaten, 1975). This is clearly inefficient where prey availability within a habitat changes in time. An optimal foraging model of patch use predicts that

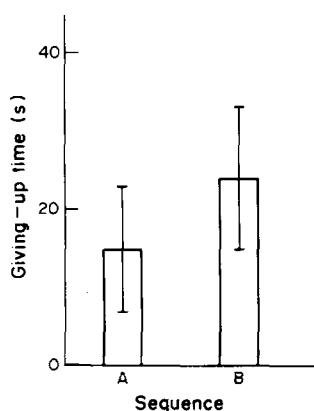


Fig. 9. Giving-up time of a 24-h starved ladybird beetle after consuming two aphids of different sizes. The beetle was fed in Sequence A: first on a large ($550 \mu\text{g}$) then on a small aphid ($250 \mu\text{g}$), and in Sequence B: vice versa. Vertical bar indicates a \pm SD. Mean giving-up times differed significantly between the sequences ($P < 0.05$, Wilcoxon signed-ranks test, $N = 10$) (from Nakamuta, 1985b).

(1) giving-up time should be a constant within an environment across patch types and (2) it should be shorter in the rich environment than in the poor environment (Charnov, 1976a). Experimental results consistent with Charnov's model are obtained in studies of the foraging behaviour of birds (Krebs *et al.*, 1974; Cowie, 1977). The critical assumption in these optimal foraging models, however, the predator should know the habitat quality before foraging, may not be realistic for any animal. In chrysopid larvae (Bond, 1980) and coccinellid larvae (Carter and Dixon, 1982) the giving-up time has been shown not to be a constant but to depend on feeding history (hunger level). If the hunger was the best estimate of the average feeding rate as suggested by Charnov (1976b), then, these results would be in accordance with the predictions of optimal patch use theory. In adult coccinellids, however, the giving-up times do not vary between the ladybird beetles which consumed different numbers of prey after 24 h of starvation (Nakamuta, 1982). It is suggested that the giving-up time tends to increase with the intensity of feeding stimulus provided for the beetle (Table 1). These results support the evidence giving-up time is determined by the size of prey.

From this study a new explanation for the behavioural mechanism of switchover from extensive to area-concentrated search behaviour of the ladybird beetle can be proposed. That is, giving-up time is determined by the size of prey most recently consumed. Similar findings were made on various species of insects searching for resource items by Chandler (1969), Dethier (1957), Etienne (1972), Nelson (1977) and Schal *et al.* (1983). For instance, the Syrphidae larvae also perform an area-concentrated search after consumption of the prey and the duration of area-concentrated search increased with increasing the duration of contact with an aphid prey (Chandler, 1969). The blowfly displayed dancing near the feeding site after feeding on a sucrose solution. In this case the duration of dance increased with the increasing concentration of sucrose solution (Dethier, 1957; Nelson, 1977). These results support the mechanism of giving-up time regulation reported here.

However, it is not clear how the decision making of giving-up time reported here in the ladybird beetle enhances the foraging efficiency of the beetle. That is, why decisions about prey size are so important to foraging efficiency. Does the prey size tell coccinellid anything about ages of other individuals in the colony? To answer these questions more detailed quantitative analyses are needed on the relationships between giving-up time and prey size. This is the objective for future studies.

Acknowledgements—I am grateful to Professor T. Saito for his general support during the times of this study. I would like to thank Drs W. J. Bell, Y. Tsubaki, T. Ono, R. D. Roitberg, K. D. Waddington and M. B. Sokolowski for their invaluable comments on the earlier draft of this paper. This study was in part supported by the postdoctoral fellowship from Japan Society for Promotion of Science.

REFERENCES

- Banks C. J. (1957) The behaviour of individual coccinellid larvae on plants. *Br. J. anim. Behav.* **5**, 12–24.

- Bell W. J. and Kramer E. (1979) Search and anemotaxis in cockroach. *J. Insect Physiol.* **25**, 631–640.
- Bell W. J. and Tobin T. R. (1982) Chemo-orientation. *Biol. Rev.* **57**, 219–260.
- Bond A. B. (1980) Optimal foraging in a uniform habitat: The search mechanism of the green lacewing. *Anim. Behav.* **28**, 10–19.
- Brown H. D. (1974) Defensive behaviour of the wheat aphid, *Schizaphis graminum* (Rondani) (Hemiptera:Aphididae), against Coccinellidae. *J. Ent.* **48**, 157–165.
- Carter M. C. and Dixon A. F. G. (1982) Habitat quality and the foraging behaviour of coccinellid larvae. *J. anim. Ecol.* **51**, 865–878.
- Carter M. C. and Dixon A. F. G. (1984) Foraging behaviour of coccinellid larvae: duration of intensive search. *Entomologia exp. appl.* **36**, 133–136.
- Chandler A. E. F. (1969) Locomotory behaviour of first instar larvae of aphidophagous Syrphidae (Diptera) after contact with aphids. *Anim. Behav.* **17**, 673–678.
- Charnov E. L. (1976a) Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.
- Charnov E. L. (1976b) Optimal foraging: Attack strategy of a mantid. *Am. Nat.* **110**, 141–151.
- Cowie R. J. (1977) Optimal foraging in great tits (*Parus major*). *Nature* **268**, 137–139.
- Dethier V. G. (1957) Communication by insects: Physiology of dancing. *Science* **125**, 331–336.
- Dixon A. F. G. (1958) The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). *Trans. R. ent. Soc. Lond.* **110**, 319–334.
- Dixon A. F. G. (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. anim. Ecol.* **28**, 259–281.
- Etienne A. S. (1972) The behaviour of the dragonfly larva, *Aeschna cyanea* M. after short presentation of a prey. *Anim. Behav.* **20**, 724–731.
- Evans H. F. (1976) The searching behaviour of *Anthocoris confusus* (Reuter) in relation to prey density and plant surface topography. *Ecol. Ent.* **1**, 163–169.
- Fleschner C. A. (1950) Studies on searching capacity of the larvae of three predators of the citrus red mite. *Hilgardia* **20**, 233–265.
- Hassell M. P. and May R. M. (1974) Aggregation of predators and insect parasites and its effect on stability. *J. anim. Ecol.* **43**, 567–594.
- Hodek I. (1973) *Biology of Coccinellidae*. Dr Wunk Publishers, The Hague.
- Jones R. E. (1977) Search behaviour: a study of three caterpillar species. *Behaviour* **60**, 237–259.
- Krebs J. R., Ryan J. C. and Charnov E. L. (1974) Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Anim. Behav.* **22**, 953–964.
- Laing J. (1937) Host finding of insects. I. Observations on the finding of hosts by *Alysia manducator*, *Mormoniella vitripennis*, and *Trichogramma evanescens*. *J. anim. Ecol.* **24**, 120–136.
- Marks R. J. (1977) Laboratory studies of plant searching behaviour by *Coccinella septempunctata* L. larvae. *Bull. ent. Res.* **67**, 235–241.
- Murakami Y. and Tsubaki Y. (1984) Searching efficiency of the lady beetle *Coccinella septempunctata* larvae in uniform and patchy environments. *J. Ethol.* **2**, 1–6.
- Murdie G. and Hassell M. P. (1976) Food distribution, searching success and predator-prey models. In *The Mathematical Theory of the Dynamics of Biological Populations* (Ed. by Bartlett M. S. and Hiorns R. W.), pp. 87–101. Academic Press, London.
- Murdoch W. W. and Oaten A. (1975) Predation and population stability. *Adv. Ecol. Res.* **9**, 2–131.
- Nakamuta K. (1982) Switchover in searching behavior of the ladybeetle, *Coccinella septempunctata* L. (Coleoptera:Coccinellidae) caused by prey consumption. *Appl. ent. Zool.* **17**, 501–506.
- Nakamuta K. (1983) Sequence of predatory behavior of the ladybeetle, *Coccinella septempunctata* L. (Coleoptera:Coccinellidae) on the green peach aphid, *Myzus persicae* Sulzer (Homoptera:Aphididae). *Appl. ent. Zool.* **18**, 559–561.
- Nakamuta K. (1984a) Visual orientation of a ladybeetle, *Coccinella septempunctata* L. (Coleoptera:Coccinellidae), toward its prey. *Appl. ent. Zool.* **19**, 82–86.
- Nakamuta K. (1984b) Aphid body fluid stimulates feeding of a predatory ladybeetle, *Coccinella septempunctata* (Coleoptera:Coccinellidae). *Appl. ent. Zool.* **19**, 123–125.
- Nakamuta K. (1985a) Experimental analysis of search behavior and prey recognition in a ladybeetle, *Coccinella septempunctata*. Unpublished Ph.D. Thesis, Nagoya University, Japan. (In Japanese).
- Nakamuta K. (1985b) Area-concentrated search in adult *Coccinella septempunctata* L. (Coleoptera:Coccinellidae): On releasing stimuli and the decision of giving-up time. *Jap. J. appl. Ent. Zool.* **29**, 55–60. (In Japanese with an English summary).
- Nelson M. (1977) The blowfly's dance: Role in the regulation of food intake. *J. Insect Physiol.* **23**, 603–611.
- Ono T. (1985) Search behavior of pheromone-stimulated potato tuber moth males (Lepidoptera:Gelechiidae). *J. Ethol.* **3**, 1–4.
- Rowlands M. L. J. and Chapin J. W. (1978) Prey searching behavior in adults of *Hippodamia convergens* (Coleoptera:Coccinellidae). *J. Ga ent. Soc.* **13**, 309–315.
- Schal C., Tobin T. R., Surber J. L., Vogel G., Tourtellot M. K., Leban R. A., Sizemore R. and Bell W. J. (1983) Search strategy of sex pheromone-stimulated male German cockroaches. *J. Insect Physiol.* **27**, 575–579.
- Tobin R. T. (1981) Pheromone orientation: Role of internal control mechanisms. *Science* **214**, 1147–1149.
- Waage J. K. (1978) Arrestment responses of the parasitoid, *Nemeritis canescens*, to a contact chemical produced by its host, *Plodia interpunctella*. *Physiol. Ent.* **3**, 135–146.