Foraging behaviour of Coccinellid larvae: duration of intensive search

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Keywords: Intensive searching behaviour, coccinellid larvae, search rate, unsuccessful prey encounter

Abstract

The duration of intensive searching behaviour of third-instar larvae of *Coccinella septempunctata* L. following feeding, and the searching behaviour of fourth instar larvae following an unsuccessful prey encounter, was determined. Even though the speed of search and track width of third instar larvae is less than that of fourth instar larvae and adults, their intensive searching behaviour was found to be of similar duration. Intensive searching behaviour was elicited even after an unsuccessful prey encounter, an important strategy for early instar larvae whose capture efficiency is low.

Introduction

As an adaptation to the clumped distribution of their prey, coccinellids, in common with many invertebrate predators, search more intensively after feeding (Curio, 1976; Hassell & Southwood, 1978). However, the duration of this intensive search varies from 15 s for fourth-instar larvae of *Adalia bipunctata* (L.) (Banks, 1957) to 7 min for *Anthocoris confusus* (Reuter) nymphs (Evans, 1976a). This is thought to be related to the predator's rate of search and the average patch size of its prey (Hassell & Southwood, 1978). Thus, the duration of intensive search should be longer in the early instars of a species because their short range of perception (track width) and low speed of movement results in them traversing a smaller area per unit time than later instars. Similarly, the capture efficiency of early instars is lower than in later instars in many insects (Dixon, 1959, 1970; Brown, 1972; Evans, 1976b), which in effect decreases the abundance of prey available to the earlier instars of a predator.

The duration of intensive search of adults of *Coccinella septempunctata*, starved for 24 h, is 30 s (Nakamuta, 1982) and is similar to that of fourth-instar larvae starved for 25 h, i.e., 23 s (Carter & Dixon, 1982). The aim of this study is to determine the duration of intensive search of third-instar larvae of *C. septempunctata* and to compare it with that for fourth-instar larvae. In addition, since coccinellids do not capture all the aphids they encounter, the searching behaviour of fourth-instar larvae after an unsuccessful encounter is also investigated.

Materials and methods

The track larvae followed after encountering prey was recorded using the pantograph recording equipment described by Carter & Dixon (1982). Experiments were conducted at 20 ± 1 °C, 70–75% r.h., and a photoperiod of 16 h.

Duration of intensive search of third-instar larvae. Fifteen larvae, which had moulted from the second instar the previous day, were each fed to satiation on pea aphids, *Acyrthosiphon pisum,* and then starved for 20 h. The prey used to initiate intensive searching behaviour were first-instar pea aphids, cut in half to ensure that larval hunger was not significantly reduced.

Entomol. exp. appl. 36, 133–136 (1984).

Searching behaviour following an unsuccessful prey encounter. Twenty fourth-instar larvae, which had moulted from the third instar the previous day, were fed to satiation on pea aphids and then starved for 25 h. These larvae were then allowed to encounter adult pea aphids, which usually escaped. If the aphid failed to escape it was gently pulled free before the larva started feeding.

Results

Duration of intensive search of third-instar larvae. The change in the speed of movement of third instar larvae following feeding is shown in Fig. 1. The duration of intensive search was calculated as the time to reach a speed of 4.5 mm s^{-1}, which is slightly lower than the 4.6 mm s^{-1} previously reported by McLean (1980) for extensively searching third-instar larvae. Third-instar larvae searched intensively for 28.8 ± 4.6 s (± s.e.), a similar period to that recorded for adults (Nakamuta, 1982) and not significantly different from the duration of intensive search of fourth-instar larvae (Mann-Whitney U = 125.5, $N_1 = 15$, $N_2 = 20$; data on fourth instars from Carter & Dixon, 1982).

Thus, although third-instar larvae traverse a smaller area per unit time than fourth-instar larvae and adults (Table 1), the duration of intensive search of all three stages is similar. This resulted in third instar larvae intensively searching a smaller area after encountering prey than is searched by fourth instar larvae or adults.

Table 1. Width of the track, speed of movement and area traversed when searching extensively, and duration of intensive search of third and fourth instar and adult seven spot coccinellids.

	Adults	4th inst.	3rd inst.
Width of track (mm)	5.9[d]	6.5[c]	4.0[c]
Speed of movement (mm s^{-1})	7.1[a]	6.5[b]	4.6[c]
Area traversed (mm s^{-1})	41.9	42.3	18.4
Duration of intensive search	30[a]	23[b]	29

[a] Nakamuta (1982); [b] Carter & Dixon (1982); [c] McLean (1980); [d] Stubbs (1980).

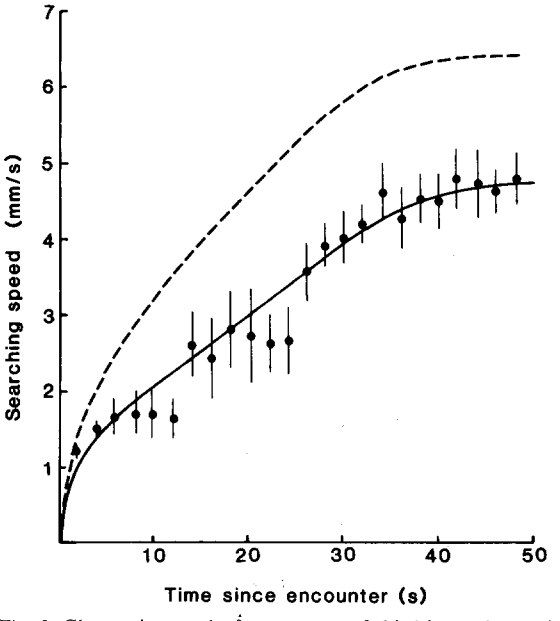

Fig. 1. Change in speed of movement of third-instar larvae in relation to time since feeding ± 1 SE (line fitted by eye). The change in speed of movement of fourth-instar larvae (---) is from Carter & Dixon (1982).

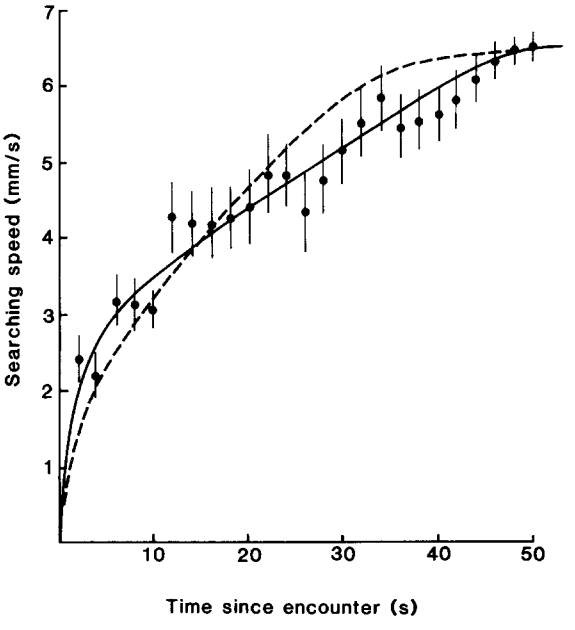

Fig. 2. Change in speed of movement of fourth-instar larvae in relation to time since unsuccessfully encountering an aphid ± 1 SE (line fitted by eye). The change in speed of movement of larvae after a successful encounter (---) is from Carter & Dixon (1982).

Searching behaviour following an unsuccessful prey encounter. The change in the speed of movement of fourth-instar larvae following an unsuccessful encounter was very similar to that which followed a successful encounter with prey (Fig. 2). The speed of movement immediately after losing contact with the prey item was, however, faster after an unsuccessful than a successful encounter.

The duration of intensive search, calculated as the time taken to reach a speed of 6.5 mm s^{-1}, the speed of extensively searching fourth-instar larvae (McLean, 1980; Carter & Dixon, 1982), was found to be 25.2 ± 3.2 s, which is not significantly different from the 23 s observed after a successful prey encounter ($U = 196.5$, $N_1 = 20$, $N_2 = 20$; data from Carter & Dixon, 1982).

Discussion

The time a predator spends searching intensively after a prey encounter is thought to be related to the predator's search rate and the average patch size of its prey (Hassell, 1978; Hassell & Southwood, 1978). However, the large difference in the searching ability of third-instar larvae compared with fourth-instar larvae and adults of *C. septempunctata* was not associated with a difference in the duration of intensive search.

In coccinellids, and several other insects, the duration of intensive search is not fixed for each instar but is variable and determined by hunger (Dethier, 1976; Bond, 1980; Carter & Dixon, 1982). Since a predator's rate of search, together with many other factors such as its capture efficiency, the relative gains from the prey and metabolic costs, will influence hunger, the duration of intensive search may not be the same in different instars even at the same prey density. However, as third- and fourth-instar larvae and adults starved for a day would have no food in their anterior midgut they would have maximum hunger as defined by Holling (1966) (Carter & Dixon, 1985). Thus even in maximally hungry seven spot coccinellids large differences in the rate of search between stadia are not reflected in differences in the duration of intensive search.

Intensive searching behaviour was also initiated by an unsuccessful encounter with prey. Similarly, Chandler (1969) found that the first instar larvae of *Syrphus balteatus* (Deeger) also searched intensively after encountering prey that subsequently escaped before feeding started. Since even a failed encounter is an indication that a clump of prey has been found, this behaviour is adaptive especially so for the early instars whose capture efficiencies are low. The reduction in searching speed after an unsuccessful encounter may also increase the efficiency with which larvae respond to the next prey they encounter as the larvae of fast moving coccinellid species rarely capture the first aphid they encounter whereas slow moving species were much more successful (Frazer *et al.*, 1981). Thus, by searching intensively after an unsuccessful encounter coccinellids increase the probability of locating and capturing aphids.

Acknowledgements

This work was supported by a Science and Engineering Research Council grant to M. C. Carter who is grateful for their assistance.

Résumé

Effet du stade sur le comportement intensif de prospection des Coccinelles

On a déterminé au laboratoire la durée du comportement intensif de prospection du 3è stade larvaire de *Coccinella septempunctata* après un repas, et le comportement de prospection du 4è stade après rencontre infructueuse avec une proie.

La durée de la recherche intensive pendant le 3è stade, après privation d'aliment pendant 20 h, était de 28,8 sec. Bien que l'aire parcourue par unité de temps pour ce stade ait été inférieure à la moitié de celles parcourues par des larves de 4è stade et des adultes, les durées de recherches intensives étaient voisines. Le comportement de recherche intensive a été provoqué même après une rencontre infructueuse avec une proie, et il durait autant qu'après une rencontre fructueuse. Ce comportement est particulièrement important pour les stades précoces dont l'efficacité de capture est faible, puisqu'une rencontre infructueuse est l'indication qu'un groupe de proies a été découvert. La recherche intensive succédant à un échec accroît les probabilités de localisation ultérieure de proies et ainsi augmente les probabilités de capture.

References

Banks, C. J., 1957. The behaviour of individual coccinellid larvae on plants. Anim. Behav. 5: 12–24.

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., 1972. Predacious behaviour of four species of Coccinellidae (Coleoptera) associated with the wheat aphid *Schizaphis graminum* (Rondami) in South Africa. Trans. R. ent. Soc. Lond. 124: 21–36.

Carter, M. C. & A. F. G. Dixon, 1982. Habitat quality and the foraging behaviour of coccinellid larvae. J. Anim. Ecol. 51: 865–878.

Carter, M. C. & A. F. G. Dixon, 1985. Assessment of habitat quality by coccinellid larvae. In: I. Hodek (ed.) Ecology of Aphidophagous Insects II. Dr W. Junk, The Hague (in press).

Chandler, A. E. F., 1969. Locomotory behaviour of first instar larvae of aphidophagous syrphidae (Diptera) after contact with aphids. Anim. Behav. 17: 673–678.

Curio, E., 1976. The Ethology of Predation. Springer-Verlag, Berlin.

Dethier, V. G., 1976. The Hungry Fly: A Physiological Study of the Behaviour Associated with Feeding. Harvard University Press, Cambridge, Mass.

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.

Dixon, A. F. G., 1970. Factors limiting the effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.) as a predator of the sycamore aphid, *Drepanosiphum platanoides* (Schr.). J. Anim. Ecol. 39: 739–751.

Evans, H. F., 1976a. The searching behaviour of *Anthocoris confusus* (Reuter) in relation to prey density and plant surface topography. Ecol. Ent. 1: 163–169.

Evans, H. F., 1976b. The role of predator-prey size ratio in determining the efficiency of capture by *Anthocoris nemorum* and the escape reactions of its prey, *Acyrthosiphon pisum*. Ecol. Ent. 1: 85–90.

Frazer, B. D., N. Gilbert, P. M. Ives & D. A. Raworth, 1981. Predation of aphids by coccinellid larvae. Can. Ent. 113: 1043–1046.

Hassell, M. P., 1978. The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press, Princeton.

Hassell, M. P. & T. R. E. Southwood, 1978. Foraging strategies of insects. Ann. Rev. Ecol. Syst. 9: 75–98.

McLean, I. F. G., 1980. Ecology of the Natural Enemies of Cereal Aphids. Unpublished PhD Thesis, University of East Anglia, Norwich.

Nakamuta, K., 1982. Switchover in searching behaviour of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) caused by prey consumption. Appl. Ent. Zool. 17: 501–506.

Stubbs, M., 1980. Another look at prey detection in coccinellids. Ecol. Ent. 5: 179–182.

Accepted: June 5, 1984.