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Absence of intraspecific interference during feeding by the predatory ladybirds *Chilocorus* spp. (Coleoptera: Coccinellidae)

VAUGHAN HATTINGH and MICHAEL J. SAMWAYS
Department of Zoology and Entomology, University of Natal, Pietermaritzburg, Natal

Abstract. 1. The hypothesis was tested that intraspecific behavioural interference does not adversely affect the feeding behaviour of adults of three predatory coccinellid species, *Chilocorus nigritus* (F.), *C.bipustulatus* (L.) and *C.infernalis* Mulsant, at densities found under field conditions.

2. Feeding rates on mature oleander scale *Aspidiotus nerii* Bouché were evaluated by two methods at various predator densities. Proportion of the population dispersing was also measured for one of the species.

3. Feeding rate did not decrease and dispersal did not increase with increasing predator density. No significant behavioural interference that might have reduced predatory efficiency was observed, counter to assumptions on which published interference models are based.

4. Results here help to explain the relative importance of parasitoids and predators in the effective control of red scale *Aonidiella aurantii* (Mask.). The results also provide guidelines for release of these biocontrol agents.

Key words. Feeding, interference, predators, ladybirds, *Chilocorus*, Coccinellidae.

Introduction

Mutual interference between insect parasitoids and predators in reducing their foraging efficiency has received much attention. The work has mostly modelled the interaction between parasitoids, with little experimental verification. Also, in earlier studies, predators were often assumed to behave in the same way as parasitoids in terms of intraspecific interference. In early population models (Lotka, 1925; Volterra, 1926; Nicholson & Bailey, 1935) searching efficiency (E) was assumed to be constant through fluctuations in parasitoid (P) and host density (N).

$$E = N_a/NP \qquad (1)$$

N_a is the total number of attacks per unit time and area. This assumption was shown to be invalid when Holling (1959) described efficiency as a decreasing function of host density based on his functional response expression. The assumption was also considered incorrect by Watt (1959) and Hassell & Varley (1969), who showed that efficiency declined with an increase in parasitoid density expressed as

$$E = QP^{-m} \qquad (2)$$

where Q is quest constant (level of efficiency of an individual parasitoid) and m is the interference constant. This reduction in efficiency

Correspondence: Mr Vaughan Hattingh, Department of Entomology, University of Natal, P.O. Box 375, Pietermaritzburg 3200, Natal, South Africa.

was adopted in subsequent modelling of interference (Hassell, 1971a, b; Royama, 1971; Hassell & Rogers, 1972; Hassell & May, 1973; Rogers & Hassell, 1974; Beddington, 1975; Hassell *et al.*, 1976; Free *et al.*, 1977). Rogers & Hassell (1974) attributed the reduced efficiency to temporary cessation of searching for hosts by a parasitoid following an encounter with another parasitoid. They described efficiency as

$$E = QP_s/P \qquad (3)$$

where Q is the searching capacity of a single parasitoid without interference, P is the total population size of parasitoids, and P_s is the number of parasitoids searching. This was expressed by Beddington (1975) as

$$E = a/(1 + at_hN + bt_wR) \qquad (4)$$

where a is the 'attack rate', t_h is the handling time, b is rate of encounters between parasitoids, t_w is the time wasted per encounter, and $R=P-1$. Hassell *et al.* (1976) included in their explanation an increase in dispersal following an increase in parasitoid density.

Free *et al.* (1977), in turn, described these responses as behavioural interference and defined a further component called pseudo-interference. This they ascribed to a differential exploitation of hosts in areas of high density. Free *et al.* (1977) drew attention to the possibility of important differences between intraspecific parasitoid and predator interference relationship. Behavioural interference was also considered to be less important under natural conditions than previous work had suggested. Since the work of Free *et al.* (1977) attention has been focused on functional and numerical responses, leaving the question of the relevance of this work to predators unanswered.

In this study we investigated mutual interference in three ladybird species (Coleoptera: Coccinellidae): (1) *Chilocorus bipustulatus* (L.), the well-known biocontrol agent of problem scale insects (Diaspididae) in Israel (Nadel & Biron, 1964), (2) *C.nigritus* (F.), an effective predator of red scale *Aonidiella aurantii* (Mask.) on citrus in certain climatic areas of southern Africa (Samways, 1984, 1986, 1989), and (3) *C.infernalis* Muls., which has been imported recently into South Africa from Pakistan as a further biocontrol agent of red scale in other climatic areas.

During routine laboratory rearing of *C.nigritus*, *C.bipustulatus* and *C.infernalis*, there was no indication of intraspecific behavioural interference. These observations prompted experimental evaluation of whether or not this interference occurred at densities similar to and greater than those found in the field.

Materials and Methods

Predator culture. All three ladybird species were reared on oleander scale *Aspidiotus nerii* Bouché on potatoes *Solanum tuberosum* L. and butternuts *Cucurbita moschata* (Turnhalle) at 26°C, 50–60% r.h. and a 14 h/day light period. Experiments were under the same conditions, which were similar to optimal field conditions. Individuals were randomly selected from those individuals on the surfaces of scale bearing vegetables in the rearing cages and transferred directly to experimental arenas. Thereby beetles on the sides of the rearing cages which often appeared to be in a semi-torpid state were avoided. Each insect was used only once.

Experiment I. The first experiment determined the feeding rate of *C.nigritus*, *C.bipustulatus* and *C.infernalis* adults. The prey were mature female oleander scale of equal age (approximately 1 week before crawler production commenced), reared on potatoes. The seeding arenas were circular plastic collars, 3 cm in diameter, 1 cm high, attached to the surface of the potatoes with apparently inert 'Prestik'. The beetles were placed onto the surface of the potatoes and the arenas closed with fine nylon gauze clamped around the collars with elastic bands. The prey density per arena was sampled.

Ladybirds fed for 4 h at densities of one, two, four or eight beetles per arena, six to twenty replicates per density. Trials were run from the seventh to the eleventh hour of the light phase. The trial was re-run with *C.nigritus* using ten replicates per density. The number of prey eaten were counted using a dissecting microscope. With their sharp mandibles (Samways & Wilson, 1988), the ladybirds make an incision through the dorsal surface of the scale covering and remove the soft body, leaving behind the empty scale covering. For each replicate, the total number of prey eaten was determined and divided by the number of predators in the arena. The mean of these figures for each species and density class was determined.

Experiment II. A limitation of design of Experiment I prompted a second experiment with adult *C.nigritus*. The small volume of the arena greatly restricted dispersal, and the search time was reduced by the very high prey density. The duration of the experiment may have been too short, further reducing the amount of available search time. If interference occurs primarily during searching, as suggested in the literature, these results would have underestimated the importance of interference. In the second experiment the arenas were made much larger, allowing relatively free dispersal. The duration of the experiment was increased, and the density of the prey was reduced. The total number of prey was not reduced, so avoiding any functional response due to a reduction in prey density.

The arenas in this second experiment were small cages in the shape of cubes with 20 × 20 cm sides. The floor was wooden, the sides and roof were fine nylon gauze attached to a wooden frame. The prey were mature female oleander scale (1 week before crawler production commenced), at approximately equal densities on potatoes of approximately equal size. The number of prey per potato was sampled. Each potato had a two-pronged wire fork on either side for handling, and rested on a collar to minimize scale damage. One potato was placed in each small cage and one, eight or fifteen individuals placed onto the surface of the potato.

Ten replicates of each predator density were run over the last 10 h of the light phase. These results were processed in the same way as the previous experiment. To determine dispersal, four counts at approximately 2 h intervals were made of the number of ladybirds not on the potatoes. For each 2-hourly count, the sum of dispersing individuals in the ten replicates for each density class, was divided by the total number of individuals per arena. The mean of these four values per class was then calculated.

Results

Experiment I

The mean number of oleander scale per small circular arena was 179 ($n=15$, ±1 SE=20). There was no significant difference between the number of prey eaten per predator in 4 h, at the various densities, for any of the three species (Kruskal-Wallis one-way analysis of variance by

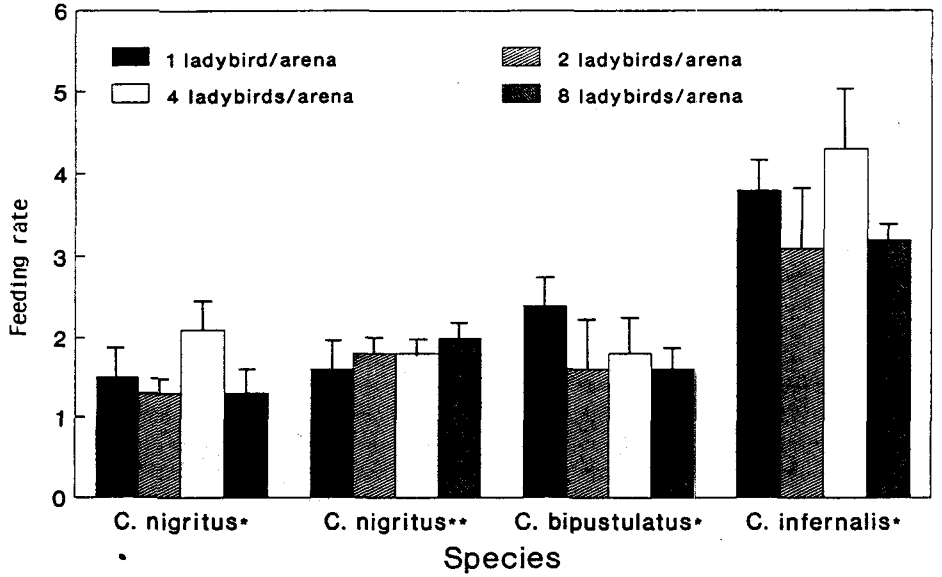

Fig. 1. Mean (+1 SE, presented parametrically for visual clarity) number of prey (Oleander scale, *Aspidiotus nerii*) consumed by *Chilocorus* spp. predators in 4 h at various predator densities in circular arenas. *Trial 1; **Trial 2.

Table 1. Mean (±1 SE, presented parametrically for clarity) number of prey (Oleander scale, *Aspidiotus nerii*) consumed per *Chilocorus nigritus* in 10 h at various *C.nigritus* densities in net cages, and mean percentage of predators dispersed from feeding sites.

Predator density	Mean consumption rate ±1 SE (*n*)	Mean percentage dispersal (*n*)
1	4.7±0.6 (10)	8 (4)
8	4.7±0.5 (10)	10 (4)
15	4.9±0.2 (10)	4 (4)

ranks, n.s.) (Fig. 1). Thus the ratio N_a/P in equation (1) was constant, and since the prey density (N) was practically constant, efficiency (E) could be considered constant through the range of predator densities (P) tested.

Experiment II

The mean number of scale insects per potato sampled was 320 ($n=10$, ±1 SE=21). There was no significant increase in dispersal with an increase in predator density (Table 1). Therefore, the ratio P_s/P in equation (3) was constant, making efficiency as expressed in this equation a constant at all predator densities. There were also no significant differences between the feeding rates at the various densities (Kruskal-Wallis one-way analysis of variance by ranks, n.s.) (Table 1). This can again be expressed as constant efficiency.

Discussion

Congregations of *C.nigritus* adults on banyan trees *Ficus benghalensis* during periods of unfavourable climatic conditions have been reported from Pakistan and India (Tirumala Rao *et al.*, 1954; Ketkar, 1959; Ahmad, 1970). However, no feeding takes place during such aggregations because there are no suitable prey on these trees (Tirumala Rao *et al.*, 1954; Ketkar, 1959). During several years of field observations of *C.nigritus* population levels on citrus in southern Africa, the highest density of feeding beetles encountered was two per leaf or four per orange, which, in some cases, were completely encrusted by red scale (Samways, pers. obs.). Interference may occur at predator densities higher than those used in our experiments. However, such extremely high densities would be of little relevance to their feeding under field conditions, particularly in citrus orchards where they are utilized for biocontrol.

These results support Free *et al.* (1977) in that behavioural interference is less important in predators than parasitoids. This difference may help to explain why predators are more important than parasitoids in the field control of red scale at high population densities on citrus. Predators, particularly *C.nigritus*, become increasingly important at high scale densities (Samways, 1984), and the shift in relative importance of different biocontrol agents with increasing host/prey population levels, is integral to the efficient functioning of this complex of biocontrol agents (Samways, 1986, 1988).

Podoler & Henen (1986) have shown that *C.bipustulatus* adopts an area-concentrated foraging mode for a short period after consumption of a prey item. *C.nigritus* and *C.infernalis* show the same response to prey encounters (Hattingh, 1989), which concentrates the foraging predators in areas of high prey density. This behaviour has been considered general of insects searching for patchily distributed resources (Nakamuta, 1985). Such aggregation would be counteracted (through interference induced dispersal), or the effectiveness of the foraging mechanism reduced (through repeated temporary cessation of searching behaviour), by the existence of strong behavioural interference.

These results caution against lumping predator and parasitoid behaviours together as framed by interference models. These ladybirds show no interference behaviour akin to that for parasitoids: they do not disperse with increased crowding, and there is no temporary cessation of searching behaviour following an encounter with another predator. These results do not invalidate the models for predators, provided appropriate values are given to certain parameters: $m=0$, eq. (2), and $t_w=0$, eq. (4). However, criticism of early models, for assuming that efficiency is constant through fluctuations in predator density, is invalidated when applied to these predator–prey interactions.

The results here have a bearing on the use of these insects as biocontrol agents. The absence of severe intraspecific behavioural interference means that these insects can be reared, transported and released in the field at high densities without interference problems. Other biotic or even abiotic factors however, may be limiting, and require further research.

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