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Prey choice and substitution in *Chilocorus* spp. (Coleoptera: Coccinellidae)

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Abstract

Choice between prey species by *Chilocorus nigritus* (Fabricius) and *C. bipustulatus* (Linnaeus) adults and larvae was determined. Strong preferences were absent and differences in the predators' feeding histories, were not reflected in their choices. The deleterious effects of a prey substitution, during larval development and adult maintenance, were investigated using *C. nigritus* with supplementary work on *C. bipustulatus*. These diet changes significantly retarded larval development rate, and subsequent adults were smaller than control individuals. Prey substitutions in the adult diet, suppressed oviposition for several days and feeding rate was reduced at one day after substitution. Larvae were more sensitive than adults to such diet changes. This was not a case of classical unsuitability of the new prey, as the fecundity and feeding rate returned to the same levels as before the substitution after a few days of exposure to the new prey. Furthermore, both prey types were suitable for larval development of *C. nigritus* when they fed on one exclusively, but unsuitable when substitutions were made. The effects of prey substitutions may possibly be attributed to the presence, in the new prey, of plant toxins, which the predators are initially not physiologically capable of dealing with in large quantities. These results present difficulties for the concepts of monophagy and polyphagy, being less well defined than normally thought. In view of coccinellid foraging behaviour and larval habitat selection by adults, the temporary reduction in fitness following a diet change is considered to be adaptive.

Introduction

Chilocorus nigritus (Fabricius) and *Chilocorus bipustulatus* (Linnaeus) are well known as effective biocontrol agents of many scale insects (Nadel & Biron, 1964; Rosen & Gerson, 1965; Samways, 1984). These species have also been valuable in experimental investigation of the feeding and foraging behaviour of insect predators (Podoler & Henen, 1986; Samways & Wilson, 1988; Hattingh & Samways, 1990).

Chilocorus spp. were maintained in an insectary on oleander scale, *Aspidiotus nerii* Bouché (Homoptera: Diaspididae) on butternuts *Cucurbita moschata* (Cucurbitaceae) and potatoes *Solanum tuberosum* (Solanaceae), because of the ease with which these prey items can be cultured (Samways & Tate, 1986). Following an unexpected interruption in the supply of this prey, the scale insect *Asterolecanium miliaris* (Boisduval) (Homoptera: Diaspididae), which is plentiful on the exotic giant bamboo *Dendrocalamus giganteus* (Gramineae), and is a valuable alternative prey for *Chilocorus nigritus* in the field (Samways, 1984), was used as a substitute. A temporary, unquantified drop in the rate of oviposition was observed.

Debilitating effects have been observed in other coccinellids following a change in their diet from suitable to less suitable prey (Hodek, 1973; Iablokoff-Khnzorian, 1982; Hagen, 1987). However, there is a dearth of information on the effects of alternating between suitable prey types. Samways & Wilson (1988) reported that a change from *Aspidiotus nerii* to red scale, *Aonidiella aurantii* (Maskell) (Homoptera: Diaspididae), resulted in a drop in feeding rate of *C. nigritus* larvae, however the adult feeding rate was reported to increase. These responses are relevant to our understanding of their prey range, and could influence foraging theories.

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Field releases of *C. bipustulatus* aimed at establishment, and *C. nigritus* to increase the distribution and local population levels of this species, have been made in suitable climatic areas of southern Africa. These insectary reared specimens were released onto *A. aurantii* in citrus orchards or *Asterolecanium miliaris* on giant bamboo. The deleterious effects of prey substitutions have not been quantitatively assessed. This paper evaluates, through experimental manipulation in the laboratory, the significance of prey substitution.

Ability to choose and to alternate between prey types has an important bearing on the outcome of a biocontrol project using predatory insects. When one prey type becomes scarce, it may be important that the presence of another suitable local prey type will not only be suppressed by the agent, but may also be instrumental in stimulating the predator to stay in the area and not disperse. This phenomenon provides predatory insurance against a possible resurgence in numbers of the first pest. Another important consideration of prey substitution and subsequent suitability is in the insectary rearing of a predator. Often the target pest is not easy to rear, even though it may be notorious in the field. An alternative insectary prey may therefore determine whether the predator can be successfully maintained for later field release. The problem then is that such a secondary prey may or may not predispose the predator to switching to the target prey when released in the field.

Such prey substitution is intimately bound up with prey choice. Yet the ability of coccinellids to choose between prey types with different levels of suitability is not entirely clear. Earlier studies illustrate both the ability and inability to choose. Blackman (1967) reported that *Adalia bipunctata* (Linnaeus) could not distinguish between the toxic vetch aphid *Megoura viciae* Buckton and the non-toxic pea aphid, *Acyrthosiphon pisum* (Harris). In contrast, Dixon (1958) noted that as soon as *Adalia decempunctata* (Linnaeus) penetrated the body wall of the mealy plum-aphid, *Hyalopterus pruni* (Geoffroy), the prey was rejected. Thereafter, palpal contact was enough to reject this prey (Dixon, 1958). This study investigates the position of these *Chilocorus* spp. in this range of abilities.

Materials and methods

Beetle rearing

The experiments were conducted in an insectary at 25–26°C and 50–70% RH, with a L:D 14:10 photoperiod. The beetles were maintained on a biparental strain of *Aspidiotus nerii* on butternuts and potatoes (Samways & Tate, 1986). *Asterolecanium miliaris*, on internode sections of giant bamboo, were field collected as alternative prey.

Prey choice

Prey choice was evaluated by presenting *C. nigritus* and *C. bipustulatus* adults with *Aspidiotus nerii* and purple scale, *Chrysomphalus aonidum* (Linnaeus), on butternuts, *Asterolecanium miliaris* on short sections of bamboo stem, and *Aonidiella aurantii* on oranges *Citrus sinensis* cv Valencia (Rutaceae). The surface area of the different food substrates was the same, as were the densities of the various scale insects. The arena had a wooden floor 0.5 × 0.4 m covered with clean brown paper with 12 equal-sized rectangles drawn on it. The sides were also wood, with windows 0.24 × 0.24 m, and 0.34 × 0.24 m, covered with fine nylon netting. The lid was a 5 mm-thick glass plate resting on soft foam around the upper lip of the box, 0.42 m above the floor. Symmetrically positioned overhead lighting was provided.

The four prey types were each randomly allocated three rectangles on the floor of the arena. Twelve adults of each beetle species, reared on *Aspidiotus nerii* and not starved prior to the trial, were released on a cardboard platform, 0.12 × 0.12 m, suspended in the centre of the arena. Two-hourly counts were made of the beetles on the various prey types. A trial run showed that by 24 h, the total number of beetles found on the food substrates had reached a plateau, Friedman ANOVA, followed by a nonparametric multiple comparison (Siegel & Castellan, 1989), $\alpha = 0.05$. Thereafter, samples were taken at 24 h after release. The various prey types were randomly rearranged, and different individual predators were used for each of the six replicates. For each beetle species the counts on the three examples of each prey type were summed and analyzed by a Friedman ANOVA.

A similar trial was conducted with fourth-instar larvae of the two species. The butternuts, oranges and bamboo half-rings, were placed side by side so that larvae could move between them without having to cross an open space on the floor of the arena. Two larvae of each species, reared on *A. nerii*, were placed on each prey substrate with a soft paint brush.

The effect of the prey type previously eaten by adults and fourth-instar larvae of *C. nigritus*, on their choice between *Aspidiotus nerii* and *Asterolecanium miliaris* was determined. Potatoes were used that were infested with *Aspidiotus nerii* and short sections of bamboo stem infested with *Asterolecanium miliaris*, with approximately equal densities of scale insects and surface areas. One section of bamboo stem and one potato were used per replicate, and were placed in contact with each other in the centre of the arena. Controls were non-infested potatoes and bamboo sections, and beetles which had been reared on *A. miliaris*. The arenas had brown paper covered wooden floors 0.2 × 0.2 m. The sides which were 0.2 m high, and the roof consisted of a wooden frame covered in fine nylon netting.

Two beetle cultures were used, the one maintained on *Aspidiotus nerii* and the other on *Asterolecanium miliaris*. Three adults, or fourth instar larvae, were placed on each food substrate in separate trials. A trial run, using individuals from both feeding histories, indicated that after 24 h the ratio of predators on the two prey types had equilibrated. Thereafter, the number of predators on the surface of the potato or bamboo were recorded 24 h after being presented with the choice. There were six or seven replicates per developmental stage and feeding history category, and there were six control replicates with uninfested potatoes and bamboo. Counts were compared with permutation tests for related samples.

Prey substitution

The effect of prey substitution on the larval development rate and subsequent adult weight, was investigated

Table 1. Mean numbers of adults and fourth instar larvae of *Chilocorus bipustulatus* and *Chilocorus nigritus* on four prey species 24 h after being presented with the choice.

	Mean ± 1SE no. of individuals on prey spp.				
Predator	*Asterolecanium miliaris*	*Aspidiotus nerii*	*Chrysomphalus aonidum*	*Aonidiella aurantii*	Friedman ANOVA *P*
Adults					
C. bipustulatus	$2.3^a \pm 0.6$	$2.2^a \pm 0.3$	$0.7^a \pm 0.2$	$1.8^a \pm 0.5$	0.04
C. nigritus	1.8 ± 0.8	2.0 ± 0.4	2.0 ± 0.6	2.8 ± 0.8	>0.05
Larvae					
C. bipustulatus	$4.2^a \pm 1.0$	$7.8^a \pm 0.5$	$6.7^a \pm 0.8$	$4.2^a \pm 0.8$	0.03
C. nigritus	4.5 ± 0.4	6.7 ± 0.8	6.0 ± 0.4	4.2 ± 0.9	>0.05

Absence of a common superscript indicates a significant difference, nonparametric multiple comparison, $\alpha = 0.05$ (Siegel & Castellan, 1989)

with *C. nigritus*. Larvae were selected at the end of the first instar from a culture maintained on *Aspidiotus nerii*. As Treatment 1, these larvae were then reared on *Asterolecanium miliaris*, and as a control, larvae of the same age were selected from a culture maintained on *A. miliaris* and were further reared on it. Treatment 2 larvae, at the end of the first instar, were selected from the culture maintained on *A. miliaris* and then fed *Aspidiotus nerii*. The control larvae were maintained on *A. nerii* and after similar handling, continued feeding on *A. nerii*. The times taken for the adults to emerge were measured, and weighed one day after eclosion. A Kruskal Wallis ANOVA was performed, $\alpha = 0.05$, followed by a nonparametric multiple comparison, $\alpha = 0.05$ (Siegel & Castellan, 1989).

The effect of a prey substitution on the feeding rates of *C. nigritus* and *C. bipustulatus* adults was evaluated. Adult beetles which had previously been maintained on *Asterolecanium miliaris* were then fed *Aspidiotus nerii*. For the control, individuals reared and maintained on *A. nerii* were used. The feeding rates of individuals were recorded at various intervals after the switch, $n = 9$–11 individuals per species.

Consumption rate of *Asterolecanium miliaris* could not easily be measured. The entire scale covering was often removed and the presence or absence of the soft body beneath the remaining scales could not be determined without removal of the coverings. For this reason a reciprocal transfer from *Aspidiotus nerii* to *Asterolecanium miliaris* was not performed.

Circular plastic collars, 34 mm in diameter and 10 mm high, were attached with 'Prestik' (a soft putty used for attaching posters to walls) to the surface of potatoes, infested with approximately equal densities of equal aged (one week before crawler emergence) *Aspidiotus nerii* females. Individual beetles were enclosed in the arenas with nylon netting which was clamped around the arenas with elastic bands. After feeding on *A. nerii*, the beetles left behind an empty scale covering from which the soft body had been removed through a slit in the scale covering. The numbers of scale insects eaten were recorded after removal of the predators. For each species, a Friedman ANOVA was performed, followed by a nonparametric multiple comparison between treatments and controls, $\alpha = 0.05$ (Siegel & Castellan, 1989).

The rate of egg laying by individual pairs was determined by enclosure in arenas, with egg pads and prey. Arenas for enclosing coccinellids on potatoes with *A. nerii*, were circular plastic collars, 10 mm high and 35 mm in diameter. On bamboo with *Asterolecanium miliaris*, rectangular cardboard collars were used, 106 × 30 × 30 mm. The arenas were attached to the surfaces of scale bearing substrates, each enclosed with fine nylon gauze clamped around the sides with elastic bands. *C. nigritus* laid eggs in polyester fibre pads (Samways & Mapp, 1983) and *C. bipustulatus* between strands of frayed linen (Nadel & Biron, 1964).

C. bipustulatus and *C. nigritus* reared on *Aspidiotus nerii*, were enclosed on potatoes bearing *A. nerii*, their fecundity monitored, and then transferred to *Asterolecanium miliaris* on bamboo and their fecundity again monitored. *C. nigritus* adults within one day of eclosion from larvae reared on *Aspidiotus nerii*, were transferred to *Asterolecanium miliaris*. After 30 days their fecundity was measured, they were then transferred to *Aspidiotus nerii* and fecundity again monitored. Changes in fecundity were compared with a Friedman ANOVA, followed by a nonparametric multiple comparison, $\alpha = 0.05$ (Siegel & Castellan, 1989).

Results

Prey choice

The Friedman test indicated that there were significantly more *C. bipustulatus* adults and larvae on one or more of the four prey types than on the remaining prey types presented in the choice experiment (table 1). However, a nonparametric multiple comparison did not indicate a significant difference between any of the prey groups. These conflicting results can be attributed to differences in the power of the tests. Counts of *C. nigritus* adults and larvae on the four prey types were not significantly different, Friedman ANOVA.

The numbers of *C. nigritus* adults and larvae on uninfested butternuts and bamboo, between 1 h and 24 h after presentation with the choice, were not significantly different, Friedman ANOVA, $P > 0.05$. There were more *C. nigritus* adults on *A. nerii* than on *Asterolecanium miliaris* when presented with a choice

Table 2. Numbers of *Chilocorus nigritus* adults and larvae encountered on *Aspidiotus nerii* and *Asterolecanium miliaris* 24 h after presentation with the choice, mean ± 1 SE (*n*)

	Prey sp. on which reared			
	A. nerii counts after 24 h on		*A. miliaris* counts after 24 h on	
Predator	*A. nerii*	*A. miliaris*	*A. nerii*	*A. miliaris*
C. nigritus adults	$1.5^{a} \pm 0.5$ (6)	$0^{b} \pm 0$ (6)	$3.0^{a} \pm 0.6$ (6)	$0.7^{b} \pm 0.3$ (6)
C. nigritus larvae	$4.3^{a} \pm 0.4$ (6)	$1.5^{a} \pm 0.5$ (6)	$2.6^{a} \pm 0.3$ (5)	$3.0^{a} \pm 0.5$ (5)

Absence of a common superscript indicates a significant difference, permutation test for related samples, $\alpha = 0.05$.

between these two prey types and this was not affected by feeding history (table 2). There was no significant difference in the numbers of fourth-instar larvae on the two prey types, and this was not affected by feeding history (table 2).

Prey substitution

A substitution in prey type at the end of the first instar resulted in the time to adult eclosion being significantly longer than for those larvae reared continuously on only one prey type (fig. 1). Also, the weights of adults one day after eclosion were significantly lower when a prey substitution had taken place during larval development than without a substitution (fig. 1).

A substitution in prey type did not significantly affect the feeding rate of *C. bipustulatus* adults during the first four hours of exposure to the new prey (fig. 2). However, the feeding rate one day after the diet change was significantly lower than that of the control (fig. 2). Thereafter an increase in the feeding rate to a level similar to that of the control was observed. A similar trend was observed with the feeding rate of *C. nigritus* after exposure to a diet change (fig. 2).

The rates of egg laying by *C. bipustulatus* declined shortly after a prey substitution and then returned to a

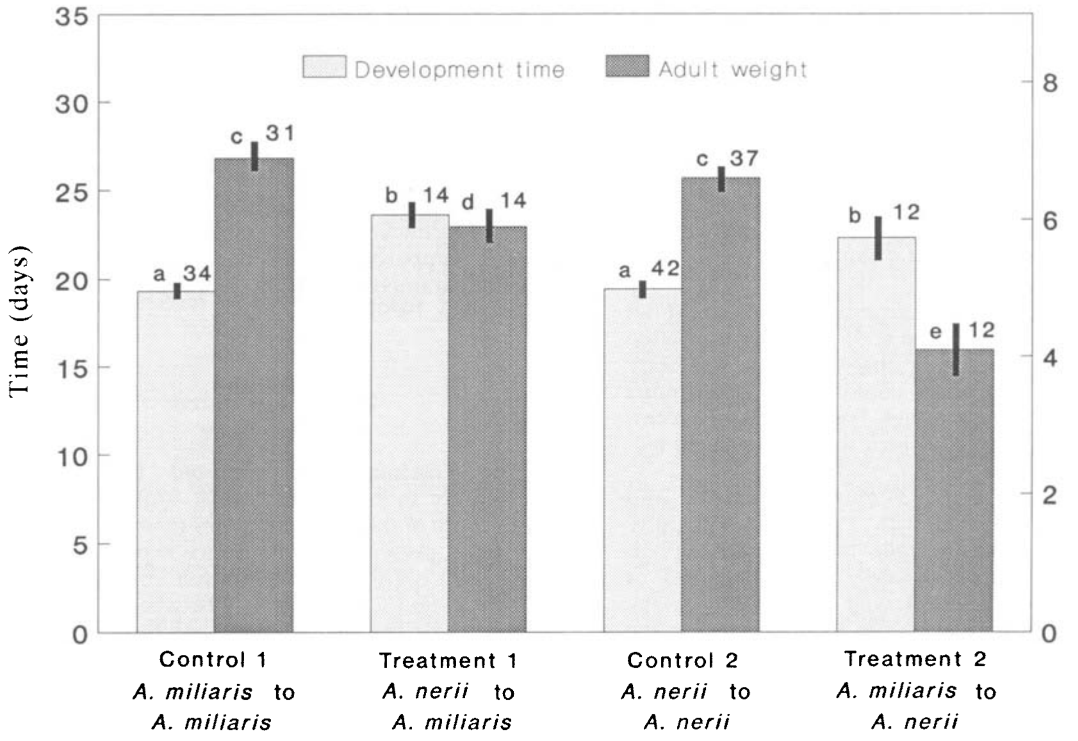

Fig. 1. Mean (± 1 SE), number of days from the end of the first larval instar to adult eclosion of *Chilocorus nigritus*, and mean weights of these adults, *n* to the right of SE bars. Control 1 reared continuously on *Asterolecanium miliaris*, Treatment 1 transferred from *Aspidiotus nerii* to *Asterolecanium miliaris*, Control 2 reared on *Aspidiotus nerii*, Treatment 2 transferred from *Asterolecanium miliaris* to *Aspidiotus nerii*. A common label indicates no significant difference, Kruskal Wallis ANOVA, followed by a nonparametric multiple comparison, $\alpha = 0.05$.

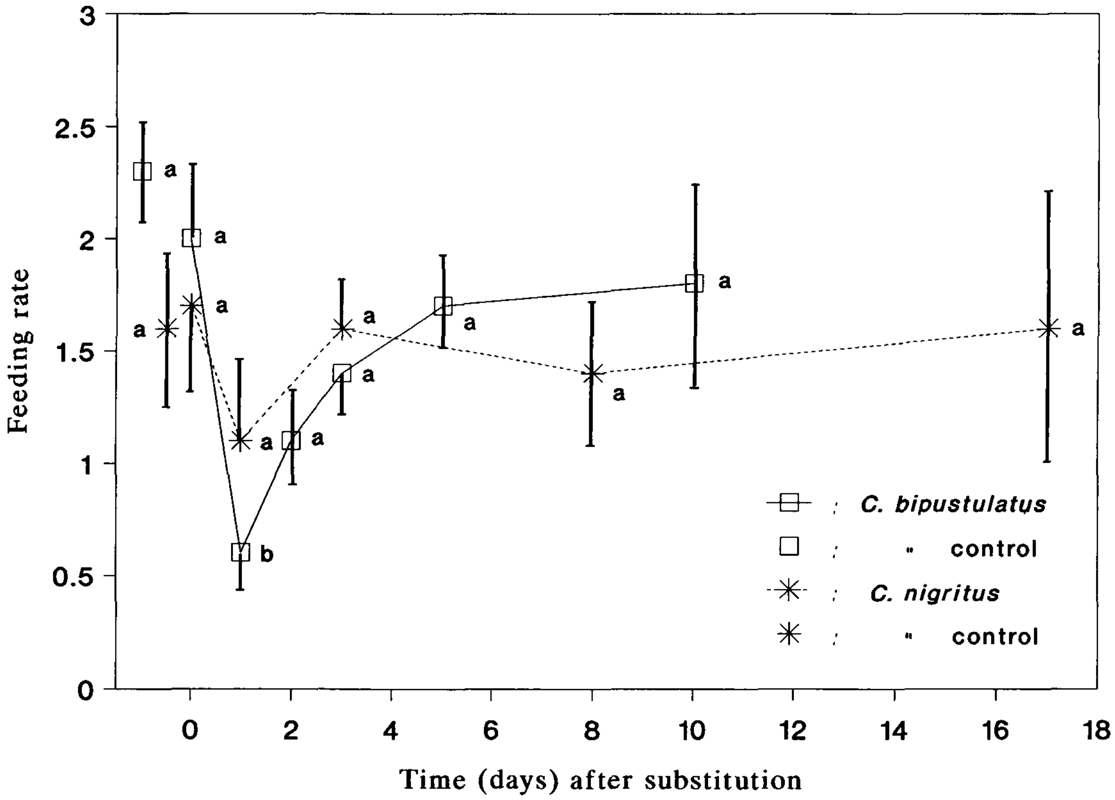

Fig. 2. Mean (± 1 SE) number of adult female *Aspidiotus nerii* eaten per individual adult *Chilocorus bipustulatus* or *C. nigritus* in 4 h, at various times after a change in diet from *Asterolecanium miliaris* $n = 9$ to 11. Controls were reared and maintained on *Aspidiotus nerii* exclusively. Common labels indicate no significant difference, Friedman ANOVA, followed by a nonparametric multiple comparison, $\alpha = 0.05$.

level equivalent to the rate prior to the substitution (fig. 3). Following a transfer of *C. nigritus* from *Aspidiotus nerii* to *Asterolecanium miliaris*, the fecundity dropped for a few days before returning to the same level as before the transfer. There was no reduction in fecundity following the transfer of *C. nigritus* from *A. miliaris* to *Aspidiotus nerii*.

Discussion

These *Chilocorus* spp. demonstrated only limited ability to choose between prey species. In the case of *C. nigritus* adults showing a preference for one of the two species provided in a choice experiment, the difference was only marginally significant. In these experiments, the prey types can be viewed as being in discrete patches with no species mixing. The beetles may be even less capable of choosing when prey species are intermixed. Blackman (1967) reported similar findings with *Adalia bipunctata* which could not avoid toxic *Aphis fabae* Scopoli and *Megoura viciae* when presented together with suitable prey. Also, slight preferences are not always for the more suitable prey, and *Aphis fabae* and *A. sambuci* Linnaeus, although natural prey for *Adalia bipunctata* in the field, are less suitable in the laboratory than some other prey (Blackman, 1967). This cautions against using prey choice alone to select suitable predator-prey relationships for biological control.

The reason why *C. nigritus* fecundity was not suppressed following a transfer from *Asterolecanium miliaris* to *Aspidiotus nerii* is not clear. It is possible that a particular prey substitution will adversely effect fecundity, but a substitution in the opposite direction may not have the same effect. Alternatively, having reared the larvae on *A. nerii* before transferring the adults to *Asterolecanium miliaris* at one day after eclosion, may have predisposed the adults to making the transition from *A. miliaris* to *Aspidiotus nerii* without a consequent reduction in the rate of egg laying.

The deleterious effects of prey substitution during adult coccinellid feeding are of short duration. The effects of a change during larval development are more serious, resulting in slower development and reduced adult size. Since fecundity in insects is generally proportional to female size (Beddington *et al.*, 1976; Slansky & Rodriguez, 1987) this translates into reduced fitness. The larval life stage is the most vulnerable in the coccinellid life cycle, and therefore extending the duration of this life stage may be an obstacle to risk avoidance. In view of the serious effects of such diet alterations, and the lack of

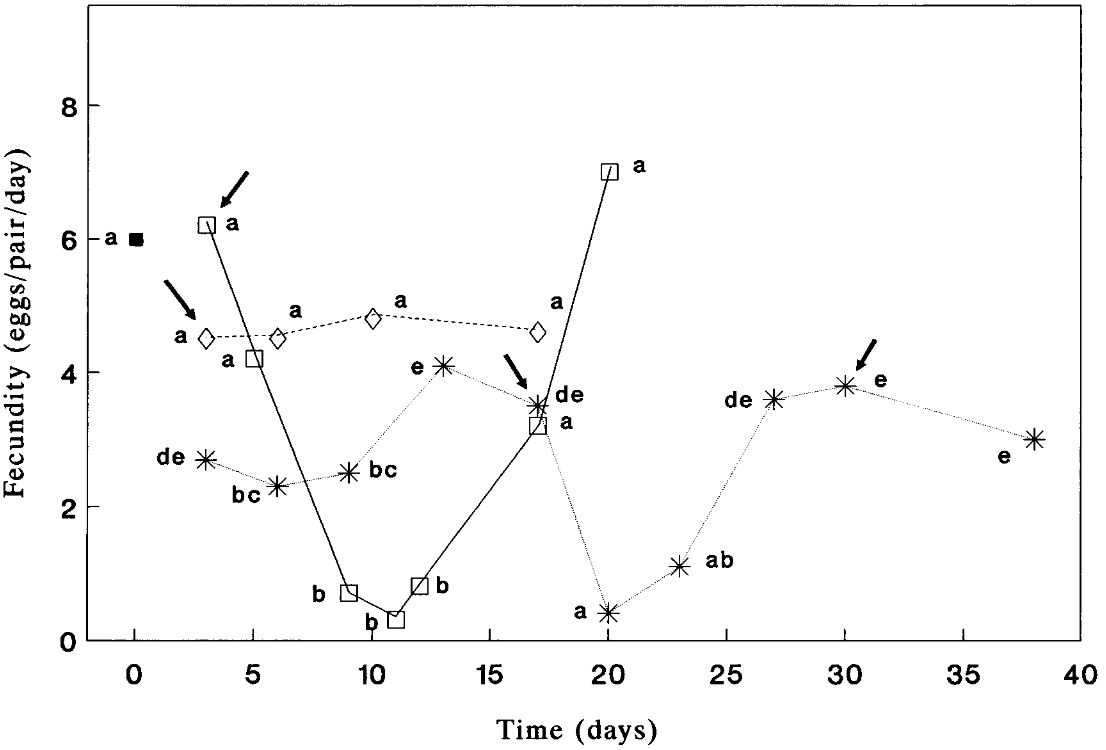

Fig. 3. Mean number of eggs laid per pair per day by *Chilocorus bipustulatus* and *C. nigritus*, before and after prey substitutions. The arrows indicate when the substitutions were made. *C. bipustulatus* were transferred from *Aspidiotus nerii* to *Asterolecanium miliaris* (□), $n = 6$, and fecundity was also measured when fed on *A. miliaris* continuously (■), $n = 12$. *C. nigritus* were transferred from *Aspidiotus nerii* to *Asterolecanium miliaris* (✳) after 17 d, and from *A. miliaris* to *Aspidiotus nerii* (◇), $n = 15$, and (✳) after 30 d. Absence of common letters in labels indicate a significant difference, Friedman ANOVA, followed by a nonparametric multiple comparison, $\alpha = 0.05$.

discrimination between prey types, a mechanism by which such situations are avoided can be expected, particularly in the case of larvae.

Since the adults are the dispersal life stage, they are likely to encounter unfamiliar prey in the new habitats following dispersal. In view of larval habitat selection being performed by adults via oviposition (Blackman, 1967; Hodek, 1973), this response of adults to encountering a novel prey may be considered adaptive. Commencement of extensive search in the foraging of coccinellids is dependent on the time since the last prey was consumed (Carter & Dixon, 1982) and this search mode results in dispersal from the patch (Krebs *et al.*, 1974; Nakamuta, 1985). Podoler & Henen (1986) and Hattingh & Samways (unpublished data) have found that these *Chilocorus* spp. forage in this way. On encountering a habitat where an unfamiliar prey type is encountered, the feeding rate of the adults would be suppressed. This reduced feeding rate would initiate the adoption of extensive foraging, resulting in dispersal from this habitat.

Simultaneously, fecundity would be suppressed and their progeny excluded from such a habitat, thus avoiding serious repercussions for the fitness of the next generation. Both *Aspidiotus nerii* and *Asterolecanium miliaris* are suitable for larval development of *C. nigritus* when fed exclusively on one of these species (Hattingh & Samways, unpublished data). This study however, shows that substitution of one of these species for the other, makes such a diet unsuitable for the larvae. If adults were to disperse to a new habitat with an unfamiliar prey type, but one which is suitable for larvae if fed on exclusively, it would be disadvantageous to exclude their progeny from this habitat through cessation of oviposition. Indeed, the temporary nature of suppressed fecundity on encountering such a habitat, would avoid this. Having primarily encountered only one prey type for several days, which would be suitable for larvae, egg laying would be resumed. The extensive search by adults induced by a reduction in feeding rate, would ensure sampling of a larger area of the new habitat.

The duration of intensive area concentrated search by coccinellids following a prey encounter increases with increasing hunger, and this increases the time spent in a patch (Carter & Dixon, 1982). The hunger level of dispersing beetles on encountering a new habitat with mixed prey or unfamiliar prey could affect their decision whether to remain or to disperse from the habitat. Hungry individuals might well tolerate the adverse effects of the unfamiliar prey, by means of longer periods of intensive search following prey encounters, rather than starve. This would provide advantageous flexibility for the dispersal response to encountering a habitat with less suitable prey and would be dependent on the hunger level of the dispersing beetles.

These *Chilocorus* spp. did not actively avoid unfamiliar prey, and their feeding rate on first encountering unfamiliar prey was not reduced. This indicates that the reduced feeding rate one day after exposure to the new prey was not due to the absence of cues used to locate and recognize prey, the absence of a phagostimulant, or the predators having greater difficulty in consuming the new prey.

The delayed and temporary deleterious effects of a change in diet probably have a physiological basis and are a result of a different chemical composition of the new prey type. Hagen (1987) states that either the proportion of nutrients, or the possession of sequestered secondary plant metabolites, determines the suitability of the prey for the predator. A different proportion of nutrients may require more of certain enzymes or symbiotic micro-organisms to be metabolized. This could take some time to achieve and could explain the temporary reduction in feeding rate and, consequently, fecundity.

Numerous authors have attributed unsuitability of particular prey types to toxins taken up from the host plant (Hodek, 1973; Hagen, 1987; Moraes & McMurty, 1987). The effects of feeding on prey which is unsuitable due to such toxins, are similar to those observed here (Hodek, 1973; Hagen, 1987). The temporary reduction in adult fitness on encountering such prey for the first time, could be a result of having to develop a mechanism to deal with such toxins. The high energy costs of maintaining detoxification enzymes make it advantageous for the animal to produce these only when required (Brattsten, 1979). The initial rapid feeding would provide the toxin required for induction of the necessary enzymes, and the ensuing period of reduced feeding would allow for production of sufficient enzyme to make consumption of large quantities of the new food possible. Induction can in cases be observed as rapidly as 30 minutes after exposure (Brattsten, 1979), but Terriere (1984) indicates that several hours is a more probable period, with maximal effect only evident after two or three days. This coincides with the duration of reduced feeding following exposure to unfamiliar prey in the study reported here.

There are a number of possible reasons why larvae are less capable of tolerating these diet changes than adults. In the field, larvae can be expected to encounter such diet changes less often than the adults which are responsible for dispersal. Also, larval habitat selection is performed by adults, and a mechanism whereby larvae are excluded from such habitats by the adults probably exists, as proposed earlier. The energetic costs of maintaining mechanisms to cope with such prey changes may be high, thus increasing the duration of the vulnerable life stage. Further, the area-concentrated search adopted by these predators reduces dispersal from a site as long as the prey remain plentiful, thereby ensuring that the larvae remain in the suitable habitat selected by their parents. These may be the underlying reasons why larvae are less capable of tolerating diet changes.

These results present difficulties for definitions of terms such as monophagy and polyphagy. Scriber (1979) stated that classification as polyphagous, requires qualification on the basis of whether the term applies to the species, a population, or an individual. These predators appear to be adapted to habitats in which predominantly monocultures of prey species occur. This appears to be a common feature of scale insect infestations in the field, although exceptions do occur (Hattingh & Samways, unpublished data). Coccinellids may be theoretically polyphagous, searching out high-density patches of preferred prey. In reality, the species may consist of populations with higher specificity, with the species as a whole having a far broader range of suitable prey.

It would be valuable to determine the duration of familiarity with the previous prey type, following a transfer to an unfamiliar prey species. This would relate to the success of these predators in controlling more than one prey species, following introduction into predominantly monoculture patches, or into mixtures of different prey species after familiarization. Also, how effectively can these natural enemies adjust to a diet of mixed prey types, or will fitness continuously be suppressed?

These results caution against exposing larvae to such diet alterations during insectary rearing of coccinellid biocontrol agents for field introduction. Maintenance of insectary cultures on prey species other than the target species is acceptable provided that larvae are not released into the field. Furthermore, a period of two weeks for familiarization of insectary adults with the target prey prior to release is advisable.

Acknowledgements

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