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Aspects of prey relations in the coccidophagous ladybird *Chilocorus nigritus* relevant to its use as a biological control agent of scale insects in temperate glasshouses

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Abstract The armoured scale insects *Acutaspis umbonifera* (Newstead), *Pinnaspis buxi* (Bouché) (Homoptera: Diaspididae) and the soft scale insects *Saissetia coffeae* (Walker) and *Coccus hesperidum* L. (Homoptera: Coccidae) were tested as suitable prey for the ladybird *Chilocorus nigritus* (F.) (Coleoptera: Coccinellidae), with a view to using the beetle as a biological control agent in UK glasshouses. *C. nigritus* larvae were able to complete development on all prey species tested and adults were also able to mature eggs on *P. buxi*, *S. coffeae* and *C. hesperidum* (*A. umbonifera* was not tested in this respect). Prey in ornamental glasshouses and interior landscapes are often diverse and patchily distributed. Thus the effect on the beetle larvae of switching between diaspidid and coccid prey was also examined. Larvae were able to switch from feeding on *C. hesperidum* to *Abgrallaspis cyanophylli* (Signoret) (Homoptera: Diaspididae) and vice versa with only minor detrimental effects when compared to those beetles reared throughout on one prey species. Introductions of *C. nigritus* as eggs, rather than adults are indicated for the control of soft scale species.

Keywords Coccidae · Coccinellidae · Coleoptera · Diaspididae greenhouses · Homoptera · Plantscapes · Prey-switching

Introduction

Until February 1992, 306 species in 12 families of the Coccoidea had been recorded in the United Kingdom, 90 species being described as indigenous and 216 as exotic (C. Malumphy, personal communication). Most species were from three families,

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viz. the Diaspididae (128 species), the Pseudococcidae (78 species) and the Coccidae (63 species). Members of these groups rarely cause economic losses in outdoor or protected edible crops in the United Kingdom but are often serious pests of ornamentals in glasshouses and indoor landscapes (Copland and Ibrahim 1985; Kosztarab 1997). Until recently, there had been no commercially available controls for the Diaspididae whilst in the Coccidae, just one parasitoid, *Metaphycus helvolus* Compere (Hymenoptera: Encyrtidae), was available. Thus the economically important ladybird *Chilocorus nigritus* (Fabricius) (Coleoptera: Coccinellidae), a native to the Indian sub-continent and South East Asia, was evaluated as a potential biological control against diaspidid and coccid pests in UK glasshouses. Samways (1984) lists records of it feeding on 46 species of Homoptera in eight different families, which suggests it to be a generalist predator. The same author suggested that the preferred prey were Asterolecanidae, Coccidae and Diaspididae but some reports in the literature were contradictory or inconclusive, suggesting the presence of varying biotypes. For example, Vesey-Fitzgerald (1953) found the larvae on the Seychelles feeding on a 'great variety of diaspids but were not definitely observed feeding on lecaniids' but where the two groups were found together, some members of the Coccidae had been eaten. Tirumala Rao et al. (1954) reported poor reproduction rates when beetles from Madras were reared on the coccid, *Megapulvinaria maxima* (Green) (Homoptera: Coccidae), concluding that diaspidid scales are specially favoured as prey. Conversely, Chazeau (1981) noted that on the New Hebrides, the beetle had a similar development period on the coccid, *Coccus viridis* (Green) as it did on the diaspidid, *Aspidiotus destructor* Signoret, and was able to mature eggs on either species. In South Africa, the beetle has rarely been seen feeding on Coccidae and did not feed on *Protopulvinaria pyriformis* (Cockerell) on avocado even when confined with them (Samways 1984). However, it showed a marked ability to survive on *Asterolecanium miliaris* (Boisduval) (Hattingh and Samways 1991a). Target pests for control in UK glasshouses included the diaspidids *Hemiberlesia lataniae* (Signoret), *Pinnaspis buxi* (Bouché), *Abgrallaspis cyanophylli* (Signoret), *Chrysomphalus aonidum* L., *Diaspis boisduvallii* (Signoret), *Acutaspis umbonifera* (Newstead) and *Ichnaspis longirostris* (Signoret) (Ponsonby 1995). Probably of more general concern were, and remain, two members of the Coccidae, viz., *Coccus hesperidum* L. and *Saissetia coffeae* (Walker) (Ponsonby 1995; Kosztarab 1997). However, apart from one record in the literature of *C. nigritus* being associated with *C. hesperidum* (Jalaluddin et al. 1991), neither species had been reported as an acceptable prey. Thus there was a need to determine whether *S. coffeae* or *C. hesperidum* were prey species that could support the development and reproduction of *C. nigritus*.

Numerous studies on the host relations of predatory coccinellids have shown that there may be important differences between 'essential' or 'suitable' prey (i.e. those that allow larval development with high oviposition and survival rates amongst adult females) and 'accepted', 'supplementary' or 'marginal' prey which serves as an energy and nutrient source but does not support oviposition or permit development of immatures (e.g. see Hodek and Honěk 1996; Dixon 2000 and Michaud 2005 for detailed discussions on this topic). However, it is clear from a substantial literature that host relations are very complex since large differences occur in the 'quality' of essential prey in terms of larval survival and development, adult fecundity and longevity and in the weight of all stages. Host plant effects may also play a distinct role in prey suitability (e.g. Nishida and Fukami 1989) and more recently, much attention has been given to the benefits of mixed diets (e.g. Evans et al. 1999).

Hodek and Honěk (1996, p. 167) suggest that in most cases, only experimental evidence is 'adequately unequivocal and precise' and thus it has become the norm to note not only the completion of development by larvae when host range testing, but also to collect data on the resulting generation of adults. This study aimed to assess the suitability of a range of diaspidid and coccid hosts for *C. nigritus* that had not hitherto been studied but were directly relevant to a range of glasshouse environments in the United Kingdom.

Prey distribution in ornamental glasshouses (botanic gardens, butterfly farms, etc.), as opposed to commercial houseplant production, tends to be patchy with suitable host plants occurring as individuals or in relatively small groups. Such conditions favour switching behaviour in the predaceous Coccinellidae (Dixon 2000). Evidence from field studies on the mid-gut contents of the closely related *Chilocorus bipustulatus* L. in Israel (Mendel et al. 1985) have shown that the adult beetles switched between diaspidid prey and the coccid, *Saissetia oleae* (Olivier) when suitable stages of the latter became relatively more abundant. However, Samways and Wilson (1988) reported that third and fourth instar *C. nigritus* larvae were unable to adapt to a switch in prey from *Aspidiotus nerii* Bouché to *Aonidiella aurantii* (Maskell) and entered premature pupation as a result. Conversely, the adults readily switched species and even increased their feeding rate when subjected to the same treatments as the larvae. Similarly, Hattingh and Samways (1991b) also reported that when first instar larvae were forced to change from a diet of *Asterolecanium* sp. to one of *A. nerii* or vice versa, developmental period was longer and adults weighed less when compared to controls reared on either species throughout development. Dixon (2000, p. 95) suggested that ladybird larvae could not be conditioned to a particular prey type but 'simply tend to grasp and attempt to consume whatever the size or species of prey they encounter'. During semi-field trials in the current study it was observed that *C. nigritus* larvae, which had been feeding on *A. cyanophylli* infesting an *Opuntia* sp., moved of their own accord to nearby *Ficus benjamina* L. plants infested with *C. hesperidum* when *A. cyanophylli* became scarce (Ponsonby 1995). Since *C. nigritus* can be effectively introduced as eggs (Samways and Mapp 1983), an experiment was carried out in order to assess any adverse effects on larvae when forced to switch from a diaspidid to a coccid prey during development.

Materials and methods

Experiment 1—prey suitability trials in *C. nigritus*

Scale insects from the Coccidae were cultured as follows:

Coccus hesperidum: 'Hubbard' squashes (*Cucurbita maxima* Duchesne) were placed in close contact with heavily infested *Hibiscus* sp. from Imperial College Wye Campus conservatory in a controlled temperature (CT) room at 26°C (±1°C), a lighting regime of L16:D8 and 55% r.h. (±10%). Crawlers were allowed to infest the squashes, after which the plants were removed. Colonisation of the squashes by the scale insects usually took two generations. Additional 'Hubbard' squashes were thereafter infested at regular intervals in order to maintain a mother culture. 'Butternut' squashes (*Cucurbita moschata* Duchesne ex Lamarck) were used for all experiments and were inoculated by placing them on the mother culture and allowing two generations of scale

to develop. Only when the crawlers of the third generation were beginning to emerge were the squashes used for trials.

Saissetia coffeae: These insects were reared on green potato shoots (*Solanum tuberosum* L.) according to the method of Blumberg and Swirski (1977). Each shoot was inoculated by placing a single gravid female bearing unhatched or hatching eggs onto a leaf or stem. Inoculated shoots were cultured in transparent plastic boxes measuring 270 mm × 160 mm × 100 mm with two 70-mm diameter ventilation holes in the lid (covered with 30 mesh cm^{-1} polyester). These were placed in a CT room at 27°C (±1°C), a lighting regime of L12:D12 and 55% r.h. (±10%). Emerging crawlers settled on the leaves or stem and were allowed to grow to the appropriate stage for the beetles' requirements. Thus first instar scale were supplied to first instar beetle larvae whilst second and early third instars were fed to all other beetle stages.

Diaspididae: Some diaspidid scales are easily reared on 'butternut' and 'Hubbard' squashes but these were expensive and it was often difficult to ensure continuity of supply in the United Kingdom. Hence, *P. buxi* and *A. umbonifera* were reared on *Ctenanthe oppenheimiana* 'Tricolor' (E. Morren) plants grown in 610 mm × 530 mm × 400 mm Perspex insect cages ventilated by a 100-mm diameter opening covered by 30 mesh cm^{-1} polyester. Access to the cage was via an opening 380 mm × 300 mm covered by 30 mesh cm^{-1} polyester held in place by Velcro strips. The cages were placed in 650 mm × 450 mm × 55 mm galvanised steel trays, into which was laid a sheet of capillary matting. The plants were inoculated by placing heavily infested *Sarcophrynium brachystachys* (Bentham) (*P. buxi*) and *Thaumatococcus daniellii* (Bennett) leaves (*A. umbonifera*) from the Princess of Wales Conservatory, Royal Botanic Gardens, Kew in close contact with the leaves. Cages were incubated in the glasshouse in ambient daylight at 22°C minimum day temperature, 18°C minimum night temperature until they were heavily infested with overlapping generations of all stages. This technique was also suitable for rearing *Hemiberlesia palmae* (Cockerell) and *I. longirostris*, the latter on *F. benjamina* plants. However, numbers of these species were too few for use in experiments at the time of the experimental runs.

Where scale insects were successfully reared on squashes or potato shoots, developmental periods and evidence of oviposition in *C. nigritus* were obtained by the following method:

Adult beetles were obtained from the International Institute of Biological Control, Rawalpindi, Pakistan and reared on *A. cyanophylli* cultured on potato tubers at temperatures of 27 ± 1°C, 12 h/12 h light/dark cycle and 55% (±10%) r.h. The beetles were allowed to oviposit into 100 mm × 100 mm eight ply surgical gauzes laid on top of the potato cultures for up to 5 h. The gauzes were then removed, the numbers of eggs were counted and their position was marked with a waterproof pen. The gauzes were then placed in transparent boxes containing the relevant scale insect cultures as described above. Particular attention was given to the presence of first instar scales, which are required by the emerging larvae.

Cultures were incubated at 26° ± 1°C (*C. hesperidum*) or 24° ± 1°C (*S. coffeae*) in illuminated, cooled incubators at ambient humidity of 28 ± 10% until adult beetle emergence was observed. Illumination was via six 8-W fluorescent tubes providing a light intensity in the range of 15–25 W m^{-1}.

Emerging adult beetles of the F_1 generation were immediately removed from the cultures and placed under similar conditions with fresh scale cultures until oviposition had begun and larvae of the F_2 generation were preparing to pupate.

All adults of the F_1 generation were then removed and the emergence of the F_2 adults noted.

Emerging adults of the F_2 were then removed and steps 3 to 4 were repeated. This process was continued as long as possible and in each generation, developmental period and numbers of surviving adults were noted.

Where scale insects were reared on plants other than squashes or potato shoots, trials were carried out under glasshouse conditions with a minimum temperature of 24°C day and night and a minimum lighting regime of L12:D12 (light supplied by a 400-W mercury vapour lamp). Scale cultures under these conditions were inoculated with *C. nigritus* eggs either by using the method described above (*A. umbonifera*) or by introducing three ovipositing adult females and two males (previously reared on *A. cyanophylli* cultures) for a period of 15 days (*P. buxi*). In the latter case, cultures were examined for signs of oviposition on a daily basis. Developmental period and numbers of surviving adults were noted in both trials.

Fluctuating day temperatures under these conditions made direct comparisons of developmental period impossible and thus thermal summation methods were used to compare this variable in the various species. Temperature data were gathered with a Grant Squirrel data logger and accumulated heat (day-degrees) was calculated according to the formula: Σ((maximum temperature + minimum temperature)/2-thermal threshold for development). The thermal threshold for development in *C. nigritus* was previously determined to be 16.6°C (Ponsonby and Copland 1996).

Experiment 2—effect of switch in prey species on larval development and adult weight in *C. nigritus*

Coccus hesperidum and *A. cyanophylli* were reared on 'butternut' squashes and potato tubers (respectively) and *C. nigritus* eggs of uniform age were obtained as described in Experiment 1. Throughout the experiment, both scale insect species were supplied to the appropriate treatments as cultures with two overlapping generations. All treatments were carried out at 28°C (±1°C) and 55% r.h. (±10%) in illuminated, cooled incubators in transparent, ventilated plastic boxes as described for the culture of *S. coffeae* above. The developmental period of beetle larvae fed on *A. cyanophylli* was known to be approximately 16 days at 28°C whilst that of the first instars was approximately 7 days (Ponsonby and Copland 1996). Thus each box was inoculated with a minimum of 18 *C. nigritus* eggs and the emerging larvae were subjected to the following treatments:

Treatment 1—reared throughout on *A. cyanophylli*;

Treatment 2—reared throughout on *C. hesperidum*;

Treatment 3—reared for 7 days after egg eclosion on *A. cyanophylli* and then transferred to *C. hesperidum* for the remaining period of development;

Treatment 4—reared for 7 days after egg eclosion on *C. hesperidum* and then transferred to *A. cyanophylli* for the remaining period of development.

In each case, the time and number of eggs eclosing, number of larvae transferred, number of larvae pupating and numbers of adults emerging were noted. Food deprivation amongst coccinellid larvae is known to increase developmental period and larval mortality but decrease adult size (e.g. Kehat 1968; Heidari 1989). Undersized adults resulting from such deprivation tend to be less fecund and suffer from reduced longevity (Heidari 1989; Hodek and Honěk 1996). Thus

developmental period and weight of emerging adults were also noted in order to detect any reluctance to feed on the prey. Beetles were weighed on a Sartorius 4503 microbalance (accurate to within 0.001 mg) after first anaesthetising them with CO_2. The experiment was replicated three times at each level, each with an average of 27 eggs at the start of the trial.

Statistical Analysis

For experiment 1, insufficient data were gathered for statistical analysis. In experiment 2, within-treatment analysis of variance did not detect differences between replicates for any parameter and so data were pooled for the following analyses. Differences in larval development period and adult weight were analysed using a completely randomised one-way analysis of variance (SAS® ANOVA procedure, SAS Institute 1992). Means were further separated using the Bonferroni/Dunn test. Mortality data (as measured by the number of larvae reaching the adult stage out of the number of eggs which hatched) were analysed using a Chi-square 4×2 contingency table. Results of this variable were tested using the original data but presented as percentages for ease of interpretation. It is generally accepted that the highest levels of coccinellid larval mortality occur at the first instar stage (e.g. Hodek and Honěk 1996; Ponsonby and Copland 1996). Thus direct comparisons of mortality before the switch in prey (first, or newly emerged second instar stage) with that recorded after (second to fourth instar stage), would not be valid. Consequently, empirical data from an earlier experiment (Ponsonby and Copland 1996) were used to generate a Chi-square goodness of fit table that assumed a null hypothesis of 2.16:1 between mortality of the larvae during the first 7 days and that of the remaining period of development.

Results

Experiment 1—prey suitability trials in *C. nigritus*

Results are presented in Table 1 and show that in all trials continuity in supply of suitable prey was restricted due to the unexpectedly high voracity of the beetle larvae and adults. High summer temperatures and a failure in the data logger disrupted *A. umbonifera* trials. Despite these problems, it was determined that larvae could complete development on all species tested. Furthermore, beetles reared on *S. coffeae* were able to mature eggs and rear larvae through two further generations. Adult females reared on *C. hesperidum* also matured eggs and produced a second generation of larvae before trials were stopped due to a shortage of scale cultures. Female beetles readily oviposited on *P. buxi.*

Accumulated heat data could not be compared statistically but varied from 477 degree-days in the F_1 generation on *S. coffeae* to 283 degree-days in the F_3 generation reared on the same species.

Experiment 2—effect of switch in prey species on larval development and adult weight in *C. nigritus*

Results are presented in Table 2 and show that there were no significant differences in developmental period when beetles were reared on *A. cyanophylli* throughout

Table 1 Results of host range testing in *Chilocorus nigritus* carried out on two species of Coccidae and two species of Diaspididae

Host insect species	Host plant species	Generation	N[a]	Developmental period (egg to adult) (days)			Generation time (adult to adult) (days)	Mean temperature (°C)	Accumulated heat (degree-days)
				Mean	Range	SD			
Coccidae									
Saissetia coffeae	*Solanum tuberosum*	F_1	14/64	64	61–75	5.53	–	24	477
		F_2	14	–	45–?[b]	–	63	24	336
		F_3	2	–	38–?[b]	–	101	24	283
Coccus hesperidum	*Cucurbita moschata*	F_1	18/138	34	27–40	4.88	–	26	321
		F_2	Eggs laid 15 days after adult emergence and 38 larvae hatched but did not complete development due to insufficient quantities of *C. hesperidum*						
Diaspididae									
Acutaspis umbonifera	*Ctenanthe oppenheimiana* 'Tricolor'	F_1	5/77	–	25–?[c]	–	–	?[c]	?[c]
Pinnaspis buxi	*Ctenanthe oppenheimiana* 'Tricolor'	F_1	2/10[d]	36.5	35–38	–	–	24	308

[a] Number of adults completing development/number of eggs introduced

[b] Interruptions in supply of host scale delayed development of some larvae

[c] Plants desiccated by high temperatures, no temperature data

[d] Indicates number of larvae detected rather than eggs introduced. Scales on ten heavily infested plants were completely eliminated before remaining eight larvae could complete development

Table 2 Effect of enforced change in host from *Abgrallaspis cyanophylli* to *Coccus hesperidum* (and vice versa) on developmental period, adult weight and immature mortality in *Chilocorus nigritus*, when compared to being reared throughout larval development on a single host species

Treatment[a]	No. of adults	Developmental period (days)			Adult weight (mg)			Larval survival (%)[c]
		Mean[a]	Range	SD	Mean[b]	Range	SD	
Treatment 1: reared throughout on *A. cyanophylli*	38	25.1 a	22–28	2.1	6.3 a	3.8–8.2	1.0	72
Treatment 2: reared throughout on *C. hesperidum*	36	26.1 b	24–28	1.1	6.1 ab	4.8–7.7	0.7	75
Treatment 3: 7 days on *A. cyanophylli*, remainder on *C. hesperidum*	47	25.4 ab	23–27	1.4	5.7 b	4.1–8.8	0.9	70
Treatment 4: 7 days on *C. hesperidum*, remainder on *A. cyanophylli*	36	25.2 ab	24–28	0.8	5.8 ab	3.9–7.5	1.1	56

[a] All treatments carried out at 28°C (±1°C) and 55% r.h. (±10%) (three replicates of each treatment, each with 18–46 eggs at the start of the trial)

[b] Means within a column followed by the same letter are not significantly different (Bonferroni/Dunn test)

[c] Chi-square (3 *df*) = 5.7 (not significant at the 5% level)

(Treatment 1) and those that were forced to change their diet after 7 days (Treatments 3 and 4). Beetles reared entirely on *C. hesperidum* underwent a significantly longer developmental period but the mean duration was less than 1 day more than the other treatments and the range was very similar ($P \leq 0.05$—Bonferroni/Dunn test). There was a significant trend for one group of beetles that were forced to change diet (Treatment 3) to weigh less on adult eclosion than those reared on *A. cyanophylli* throughout (even though the largest individuals were recorded in this group). Similarly, there was an increase in overall mortality in Treatment 4 but this was not significant (Chi-square contingency table). Mortality data of larvae during the first 7 days of the trial compared to that of the remaining developmental period are presented in Table 3 and show that in all cases the null hypothesis could not be rejected because numbers of larvae dying in respective groups closely matched the expected values.

Discussion

Experiment 1—prey suitability trials in *C. nigritus*

When fed on either *S. coffeae* or *C. hesperidum*, *C. nigritus* larvae were able to complete development and the subsequent F_1 generation females (and, in the case of *S. coffeae*, those of the F_2 generation) were also able to mature viable eggs. Thus both of these species can be tentatively considered as 'essential' prey according to

Table 3 Observed and expected differential mortality of emerging *Chilocorus nigritus* larvae at 28°C (±1°C) and 55% r.h. (±10%) when fed for 7 days on one prey species (mean duration of first instar) and the remainder of the developmental period on another prey species

Treatment	Frequency	No.	Mortality (first 7 days)	Mortality (remaining period)	χ^2(1 *df*)
Treatment 1—*Abgrallaspis cyanophylli* throughout	O	53	11	4	0.152
	E		10.3	4.7	
Treatment 2—*Coccus hesperidum* throughout	O	48	9	3	0.246
	E		8.2	3.8	
Treatment 3—*A. cyanophylli* to *C. hesperidum*	O	71	16	6	0.193
	E		15	7	
Treatment 4—*C. hesperidum* to *A. cyanophylli*	O	64	20	9	0.036
	E		19.8	9.2	

O observed frequency, *E* expected frequency based on empirical data which indicates a differential mortality of 2.16:1 amongst first instar larvae when compared to mortality amongst second, third and fourth larval instars combined (*A. cyanophylli* fed throughout)

the criteria suggested by Hodek and Honěk (1996). However, it should be noted that the beetles killed large numbers of the soft scale species but appeared only to consume a very small part of the total biomass, mainly because the method of feeding was to pierce the dorsum and then suck out part of the body fluids, leaving the rest of the scale intact. This occurred even amongst the very early instars of the scale, which were quickly depleted as a consequence. These findings indicate that large numbers of soft scale would be required to feed relatively few beetles. All stages of both scale species were consumed by the beetles with the exception of sclerotised, gravid female *S. coffeae* that were not attacked unless they were removed from the stems before being fed to the beetles. In the latter case, adult beetles and all larval stages quickly consumed the eggs or emerging crawlers. Beetles were not weighed in this experiment for logistical reasons but it was noted that adults emerging from both species appeared to be generally smaller than those reared on *A. cyanophylli*. However, this was possibly due to the difficulty in maintaining an adequate food supply, a situation known to lead to undersized adults in other coccinellid species (e.g. Kehat 1968; Heidari 1989; Hodek and Honěk 1996).

Adult females readily oviposited when restricted to a diet of *P. buxi*. However, these relatively small prey were eaten in such large quantities by the adults and their offspring that only two of the latter had sufficient food to complete development, despite the fact that they were provided with ten 300-mm high plants, all heavily infested with scale (leaf densities were measured at eight adult female scale cm^{-2} at the start of the trial). As with the two soft scale species studied, this species would need to be present in very large numbers to support reproductive activity in *C. nigritus*. The culture plants were kept for a further 6 months, during which period, no re-infestation of *P. buxi* occurred.

Five *C. nigritus* larvae were able to complete development on *A. umbonifera* but excessively high summer temperatures caused the plants to dry out and desiccate before any more larvae could mature and thus it was not possible to determine whether oviposition in *C. nigritus* could be supported by this species. However,

during field trials in the Palm House, Royal Botanic Gardens, Kew, *C. nigritus* eggs, larvae, pupae and adults were found on a *Sabal bermudana* LH Bailey plant heavily infested with *A. umbonifera* (Ponsonby 1995), suggesting that this species can be considered 'essential' prey.

Although accumulated heat data could not be compared statistically because of a lack of replication, all results were similar to the thermal constant of 325 degree-days found in an earlier study by Ponsonby and Copland (1996) when beetles were reared on *A. cyanophylli*, apart from the F_1 generation reared on *S. coffeae*, suggesting that none of the prey species had a detrimental effect on development. The exceptionally long developmental period in the first generation on *S. coffeae* was almost certainly due to difficulties in maintaining an adequate food supply.

Experiment 2—effect of switch in prey species on larval development and adult weight in *C. nigritus*

Unlike the findings of Samways and Wilson (1988), where third and fourth instar *C. nigritus* larvae of South African origin entered premature pupation when switching between the diaspidids *A. nerii* and *A. aurantii*, first and second instar larvae in this study experienced only minor detrimental effects when switching in either direction from soft scales to armoured scales. These results also differ from the study by Hattingh and Samways (1991b), where *C. nigritus* larvae underwent significantly longer developmental periods, resulting in smaller adults, after first instars were switched from an *Asterolecanium* sp. to *A. nerii*, or vice versa. However, in the latter study, the larvae were able to complete development and thus further work is indicated to examine the possibility that larval switching may occur only early in the developmental period or whether different prey species elicit different effects in this respect. It is also possible that, as with some aphidophagous coccinellid species (Hodek and Honěk 1996), *C. nigritus* populations from varying geographical locations respond differently to varying prey species. The proportion of first instar larvae surviving in all treatments in the current study was remarkably close to levels observed in earlier experiments (Ponsonby and Copland 1996). However, the overall level of larval survival in the current experiment averaged 70% as opposed to 52% at 28°C in Ponsonby and Copland (1996) and 57% in Greathead and Pope (1977), further suggesting that this particular prey combination is suitable for larval development in *C. nigritus*.

General Discussion

The findings of this study together with that of Samways and Wilson (1988), Hattingh and Samways (1991b) and others such as Greathead and Pope (1977) and Jalali and Singh (1989) suggest that the prey relations of *C. nigritus* are very complex and therefore broad generalisations are not possible. However, evidence from the literature and from the testing carried out here support the assumption that the beetle would be suitable for introduction into glasshouse environments as a biological control agent when a wide range of prey are present. All of the scale species tested showed indications of being 'essential' prey (with the possible exception of *A. umbonifera*) but as Hodek and Honěk (1996, p. 168) caution, 'prey may be also found to be essential, which is only seldom preyed upon under natural conditions...'. Indeed,

full glasshouse trials at the Royal Botanic Gardens, Kew generally indicated that adult *C. nigritus* gradually dispersed when released against heavy populations of *C. hesperidum* and moderate populations of *A. umbonifera* before populations were significantly reduced, although there was strong evidence that it was able to play a major role in controlling *S. coffeae* on some plant species (Ponsonby 1995). Of particular importance in this study is the considerable voracity demonstrated by *C. nigritus* and it seems likely that, unless prey are present in extreme abundance, adults will tend to disperse from any host. Thus introductions as either eggs or larvae are indicated for control of soft scale species or where only light to moderate infestations of armoured scales are present.

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