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Maximum feeding potential of larvae and adults of the scale insect predator, *Chilocorus nigritus* with a new method of estimating food intake

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Abstract. A method of estimating the weight of individual *Abgrallaspis cyanophylli* (Signoret) without the need for removal from the host plant is described. Using this method, which enables accurate estimations of scale insect weight by measuring length and relating it to a previously determined regression model, maximum feeding potential in male and female *Chilocorus nigritus* (F.) adults was examined at various constant temperatures over the range of 13 to 30 °C and at a cycling temperature of 12 h/12 h at 14/30 °C (r.h. in the range of 62 to 68%). Mean daily potential food intake varied from 0.097 mg/day at 13 °C to 1.432 mg/day at 30 °C. However, intake at the cycling temperature was significantly higher than that at constant temperatures (1.98 mg/day). At 15, 20 and 30 °C there were no significant differences between male and female potential food requirements whilst at temperatures in the mid range, there was a considerable increase in female potential voracity when compared to that of the males. Maximum potential larval food requirement for development at 26 °C and 62% r.h. in *C. nigritus* was also estimated using the above method. A mean of 16.24 mg of *Abgrallaspis cyanophylli* (Signoret) was required for larvae of both sexes to complete development. This study suggests that *C. nigritus* would be most efficient as a biological control agent if used in glasshouses with a mean daily temperature above 22 °C.

Key words: Biological control, Coccinellidae, Coleoptera, Diaspididae, *Abgrallaspis cyanophylli*, *Chilocorus nigritus*

Introduction

Chilocorus nigritus (F.) (Coleoptera: Coccinellidae) is native to the Indian sub-continent and southeast Asia. It is an economically important natural enemy of scale insects, having been successfully used as a biological control agent of species of Diaspididae in numerous tropical and subtropical locations (Samways, 1984). Adult and larval consumption of scales by *C. nigritus* has been the subject of five studies (Tirumala Rao et al., 1954; Ahmad, 1970;

Samways and Wilson, 1988; Jalali and Singh, 1989; Hattingh and Samways, 1993) but in all of them, host species have varied and developmental stage and/or numbers of consumed scale were reported rather than their mean scale weight. Similarly, temperatures varied between studies or were not reported. Since diaspidids vary in their weight depending on species, stage, plant host, and temperature (Ponsonby, 1995), comparisons between studies are difficult. A lack of such information also prevents accurate interspecific comparisons of voracity and has been viewed by many as a serious impediment to population modelling (e.g., Frazer, 1987). However, problems exist with measuring the weight of sessile insects such as diaspidids because removal of individuals from the host plant results in rapid dehydration and weight loss (Foldi, 1990). It also requires removing the scale cover. Since predators spend time and energy removing or penetrating scale covers, artificially removing them results in unrealistic estimations of predation rate and is thus of little value for modelling.

A similar problem exists when estimating total larval food requirement for diaspidid-feeding coccinellids. This parameter has traditionally been based on numbers of scales eaten rather than weight. Moreover, since first instar larvae mostly consume only first instar prey of some species (e.g., Samways and Wilson, 1988), comparing total prey consumption between studies is difficult unless the larvae were fed on first instar prey of the same species throughout development to pupation. When the weight of prey has been used, larval food intake in acarophagous, aphidophagous and coccidophagous coccinellids varied little for a given species when temperatures were constant and in the favourable range (for summary see Hodek, 1973). Hodek (1973) and other authors (e.g., Gawande, 1966) also concluded that fluctuating temperatures stimulated an overall increase in larval food consumption varying from 10.6% to 100%. In the current study we aimed to accurately estimate the weight of diaspidids consumed by *C. nigritus*, quantify the daily maximum feeding potential of adult *C. nigritus* over a range of temperatures, and accurately estimate total larval food requirement. Of particular interest was the relative consumption at lower and cycling temperatures since this would reflect the ability of *C. nigritus* to suppress scale insects in temperate glasshouses and indicate its seasonal use.

Materials and methods

Adult *C. nigritus* were obtained from the International Institute of Biological Control, Rawalpindi, Pakistan and unless otherwise stated, were reared on the cyanophyllum scale, *Abgrallaspis cyanophylli* (Signoret) cultured on potato tubers (*Solanum tuberosum* L.) at temperatures of $26 \pm 1\,^{\circ}C$, 12 h/12 h

light/dark cycle and 55% r.h. (± 10%). Initial cultures of *A. cyanophylli* were obtained from an *Opuntia maxima* lobe in the Princess of Wales Conservatory at the Royal Botanic Gardens, Kew. Crawlers from the lobe were allowed to infest potato tubers (*Solanum tuberosum* L. cv. 'Romano') which, after a period of screening in order to remove infestations of the parasitoid *Encarsia citrina* Craw, were used to form the stock culture. Unless otherwise stated, the scale insects were then subsequently cultured on potato tubers incubated at 26 ± 2 °C and 55% r.h. (± 10%) under constant light.

Experiment 1 – Estimating host weight

S. tuberosum tubers (cv 'Romano') (40 to 70 mm) were inoculated with *A. cyanophylli* under the culture conditions described above by placing them on top of scale infested tubers when crawlers were abundant. The newly infested tubers were removed the following day and ten first instar nymphs were randomly selected by using a random number generator to provide co-ordinates on a 5 mm × 5 mm grid square photocopied onto acetate and placed over the tuber. The length of the nymph (anterior apex to the pygidium) was measured using a stereo microscope (×10) with a graticule eyepiece. The ten nymphs were then carefully removed and weighed collectively on a Sartorius 4503 Microbalance (accurate to within 0.001 mg) in order to derive a mean individual weight. This process was repeated 10 times, providing a sample size of 100 insects. The tubers with the remaining scale insects were then placed under constant light in an incubator at 26 ± 1 °C. After seven days, another ten groups of ten scales were selected at random, measured and collectively weighed. This process was repeated at seven day intervals until three weeks after the scales had begun ovipositing. The SAS GLM procedure was then used to determine the relationship between mean weight and length using best-fit polynomial regression analysis (Zar, 1984).

Experiment 2 – Larval food requirement

Larval consumption of scale was measured at only one constant temperature because of resource and time constraints. Since the most favourable temperatures for both *A. cyanophylli* and *C. nigritus* ranged from 26 to 28 °C (Ponsonby, 1995; Ponsonby and Copland, 1996, 1998), a temperature of 26 °C was selected for this experiment.

Medium to large potato tubers (cvs 'Desiree' and 'Cara') were inoculated with *A. cyanophylli* as in Experiment 1. Cultures were initiated on a weekly basis over several weeks to provide uniformly aged scale at all stages of development during the experimental period. This was timed to coincide

with hatching *C. nigritus* eggs, which had been produced by allowing adults (reared as described above) to oviposit into clean surgical gauze (100 mm × 100 mm 8 ply). The gauze was removed daily and incubated at 26 °C and 62% r.h. using a saturated salt solution of ammonium nitrate. Emerging larvae were then placed into small cages constructed from 15 mm internal diameter plexiglass tube cut to 5 mm lengths. Forty mesh/cm polyester netting had been glued to the top of the tube whilst a strip of foam rubber had been glued around the base to provide a flexible fit to the contours of the tuber. The cages were attached to the tubers using wire staples and rubber bands. Before the test cage was attached to a group of scales, the surface of the tuber was lightly cleaned with a fine, soft brush to remove any loose soil or crawlers which had not settled. Scales were also examined with a 10× stereo microscope to ensure that they were of uniform size and that none were dead or damaged. At this stage, a sample of 10 scales on each of 10 potatoes were randomly selected using the method described in Experiment 1 and their size (as seen beneath the scale cover) measured with a graticule eyepiece. The regression equation obtained in Experiment 1 was then used to estimate mean scale weight. This procedure was carried out at the start of the run and thereafter at every change in host instar throughout the experimental run (or on a weekly basis, whichever came sooner).

Once the cages were attached to the tuber, a line was drawn around them with a waterproof marker to indicate their position after removal. Several cages were attached to each tuber (the exact number depending on the tuber size). Tubers with cages attached were then placed into unventilated polystyrene boxes (270 mm × 160 mm × 100 mm) to which a saturated salt solution of ammonium nitrate had been added before incubation at 26 ± 1 °C. This ensured a constant r.h. of 62% during the experimental run. Cages were removed on a daily basis and scales that had been killed or eaten were counted. At the same time, beetle exuviae were removed and their presence noted. First instar beetle larvae were provided with first instar scale insects, which had settled on the potato surface and begun to secrete their scale cover. The host stage was changed with each larval moult of the beetle so that first instar larvae were fed first instar scale, second instar larvae fed on first or second instar scale whilst third and fourth instar larvae were fed on second instar scales, pre-ovipositing adult females and pre-emergent puparial males. Once adult male scales began to emerge, all male scales were removed from the test arenas since it became impossible to determine whether they had eclosed naturally or been eaten.

Once beetles pupated, daily observations were suspended for a week, after which, pupae were checked daily for eclosion. Emerging adults were sexed by dissection. Beetle larvae which died prematurely were eliminated from the

study and the replicate was repeated using a newly emerged first instar. This process continued until the number of replicates reached 20.

Students two-sample *t*-test was used to analyse the differences between total prey killed (estimated weight) and development period of male and female beetle larvae at all stages of larval growth whilst regression analysis was used to examine the relationship between total prey killed and developmental period of the larvae (egg hatch to pupation).

Experiment 3 – Temperature effects on adult voracity in C. nigritus

Newly emerged adults, reared by the method described above, were placed in incubators under continuous light conditions at temperatures of 13, 15, 20, 26, 30 and 14/30 °C (the latter cycling at 12 h/12 h). Beetles placed at 13 and 15 °C were first acclimated at 20 °C for seven days. All cultures were kept in transparent polystyrene boxes (270 mm × 160 mm × 100 mm) in which two holes (70 mm in diameter) had been cut and covered with 30 mesh/cm for ventilation. Food intake in coccidophagous coccinellids is known to be very low after eclosion, increasing gradually to a peak at the end of the first week and then declining to a stable level after two weeks (e.g., Yinon, 1969). In order to avoid instability in food intake during this period we used adults that had been acclimated at treatment temperatures for a minimum of two weeks (i.e., from two to six weeks after eclosion). These were sexed using the method described by Samways and Tate (1984). To provide scale for the adult beetles during the experiment, we used medium to large *S. tuberosum* tubers (cvs 'Desiree' and 'Cara') infested with five week old *A. cyanophylli* that were evenly spaced and of uniform size. At that stage, most male scales had emerged and the female scales had not yet begun to oviposit. To ensure homogeneity of the host insects, all male cases and unhatched puparia were removed as were small, large and dead females. A sample of 10 to 15 remaining scales were randomly selected using the method described in Experiment 1 and their size (as seen beneath the scale cover) measured using a 10× stereo microscope with a graticule eyepiece. The regression equation obtained in Experiment 1 was then used to estimate mean scale weight. Adult beetles (3 of each sex) were then placed into small cages constructed from 15 mm internal diameter plexiglass tube and attached to the tuber as described in Experiment 2.

Tubers with cages attached were then placed into unventilated polystyrene boxes (270 mm × 160 mm × 100 mm) to which a saturated salt solution of ammonium nitrate (temperatures 13 to 26 °C) or sodium nitrite (30 °C) had been added before incubation at the desired temperature. This ensured a constant r.h. in the range of 62 to 68% during the experimental run.

After 24 hours, the cages were carefully removed and the number of scale insects that had been killed or eaten were recorded. The weight of scale killed or eaten was then calculated using the regression equation determined in Experiment 1.

The experiment was repeated every other day for 12 days at each temperature level (i.e., a total of 6 replicates, all treatments running concurrently) with no beetle being tested more than once. Data were analysed as a completely randomized factorial design (each run being treated as a block) using ANOVA (SAS GLM and LSMEANS procedure) after first checking data for an approximation to a normal distribution. Because steps had been taken to standardize the prey, the data were analysed using numbers eaten but are presented as both number eaten and as an estimate of total potential weight eaten.

Results

Experiment 1 – Estimating host weight

Regression analysis revealed that the relationship between scale body weight against length was best described by a quadratic equation ($F_{2,87} = 762.3$, $p < 0.0001$; $r^2 = 0.95$) (Figure 1a). Whilst there was good correlation overall, it was obvious from the plots that there was poor correlation at the highest values. Analysis of the relationship between length or weight against time (Figures 2a and 2b) found that both length and weight reached a peak followed by a short period of decline which coincided with the onset of oviposition. Thus, although quadratic regression gave the best fit to the entire data set, the accuracy was diminished once the insects began to oviposit. By using data only from pre-ovipositing females, a much more accurate fit was achieved ($F_{2,67} = 3478$, $p < 0.0001$; $r^2 = 0.99$ (Figure 1b).

Male *A. cyanophylli* are morphologically similar to the females up to the second moult and, as with the females, a quadratic equation gave the best fit to the data ($F_{2,27} = 147.8$, $p < 0.0001$; $r^2 = 0.94$) (Figure 1c).

Experiment 2 – Larval food requirement

One insect died just prior to pupation and was excluded from the analyses. With the exception of the first instars, the method of feeding varied considerably between individual larvae. First instars chewed through the newly formed scale cover and sucked out the body juices, leaving the cuticle behind. Of some interest is the fact that some first instar beetle larvae were able to feed on second instar scale nymphs. Second, third or fourth instars either

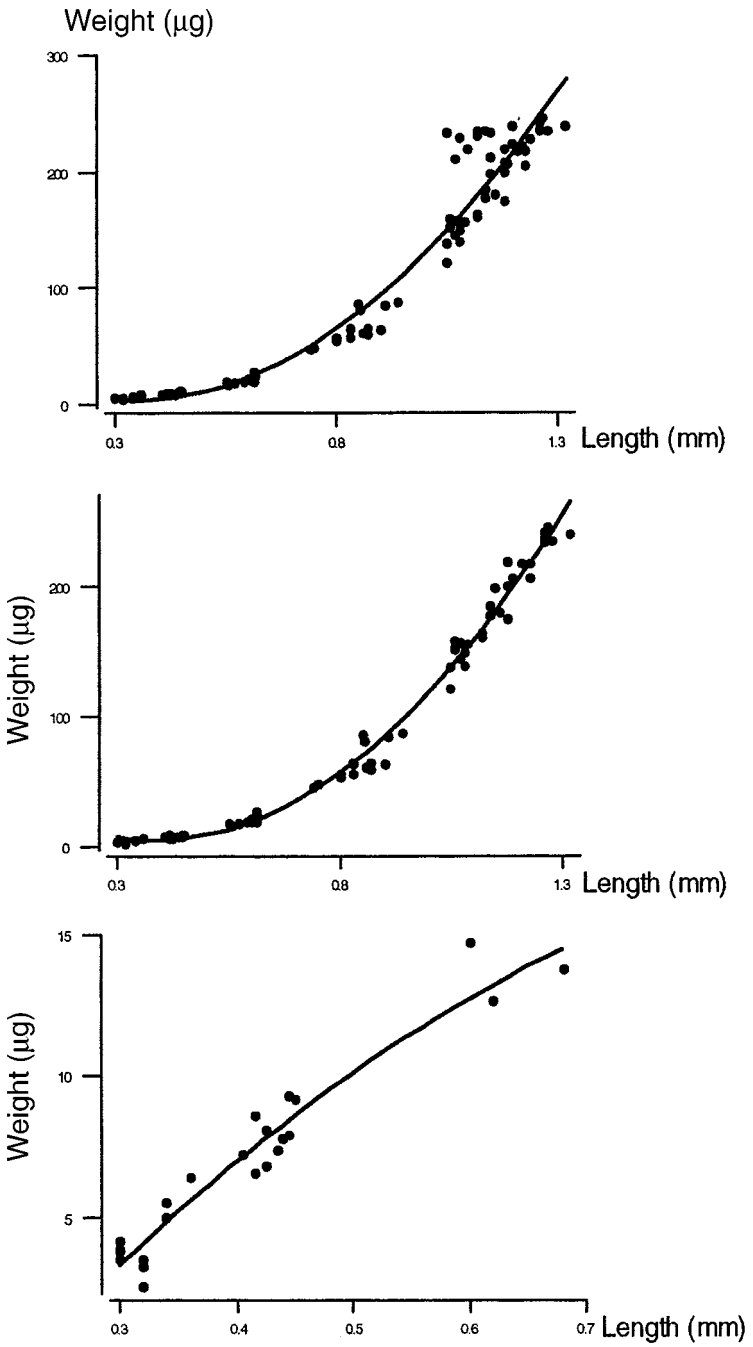

Figure 1. Relationship between weight and length at 26 °C in (a) female *Abgrallaspis cyanophylli*. Y = 34.12 – 189.07 X + 283.97 X^2, r^2 = 0.95 (n = 90), (b) female *Abgrallaspis cyanophylli* up to oviposition. Y = 47.42 – 224.29 X + 295.23 X^2, r^2 = 0.99 (n = 70) and (c) immature male *Abgrallaspis cyanophylli*. Y = –10.85 + 55.30 X – 26.54 X^2, r^2 = 0.94 (n = 30).

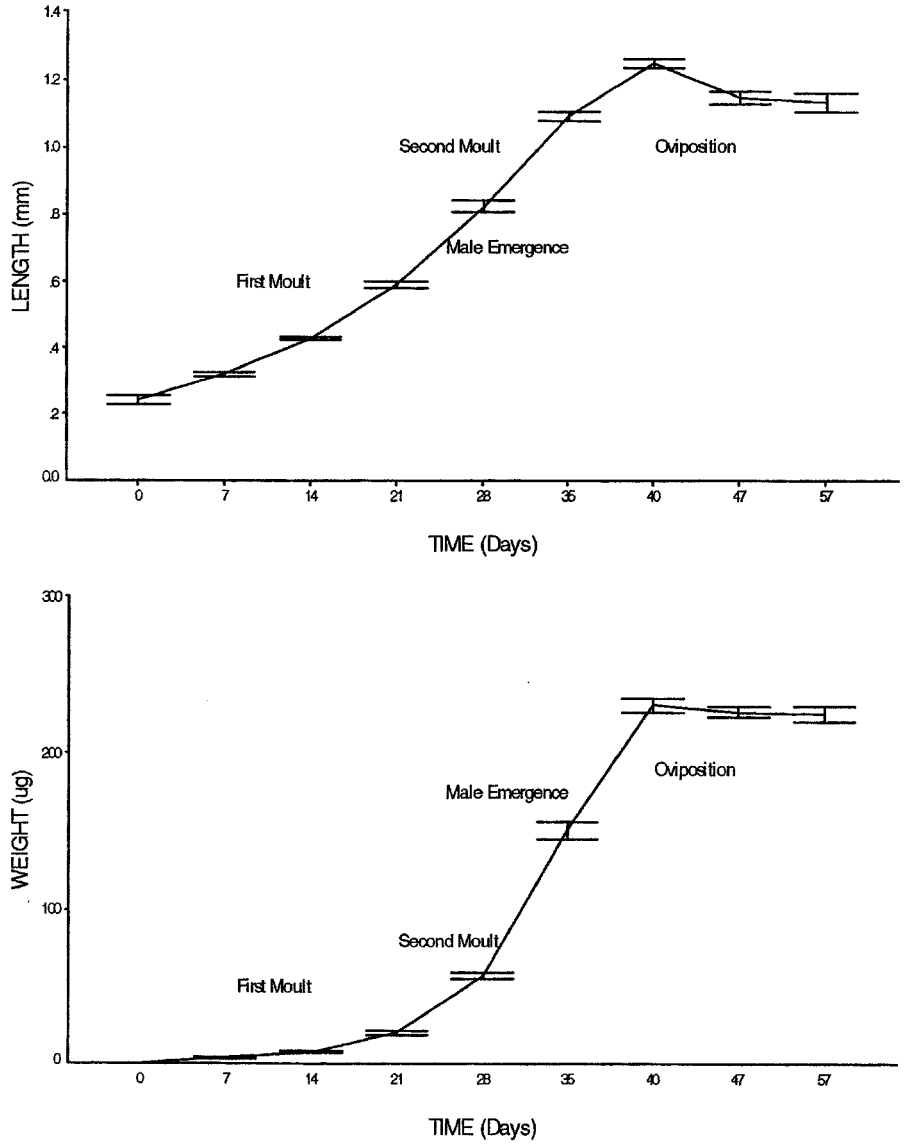

Figure 2. Relationship between (a) length and time, and (b) weight and time at 26 °C in female *Abgrallaspis cyanophylli* (range bars = mean ± s.e.).

Table 1. Mean total number of *Abgrallaspis cyanophylli* killed by the various larval instars of *Chilocorus nigritus* at 26 ± 1 °C and 62% r.h. (n = 9 females, 10 males). Numbers in parentheses represent the estimated weight of *A. cyanophylli* killed (mg)

C. nigritus	Number and stage of *A. cyanophylli* killed					
Instar/Gender	1st instar	2nd instar	Puparial males	Adult females	Total	SD
First instar						
Male	108 (0.45)	14 (0.11)	—	—	122 (0.56) a	18.9 (0.11)
Female	96 (0.40)	8 (0.06)	—	—	104 (0.46) a	27.3 (0.15)
Second instar						
Male	4 (0.02)	90 (0.85)	2 (0.02)	—	96 (0.89) a	30.6 (0.32)
Female	18 (0.07)	85 (0.83)	5 (0.06)	—	107 (0.97) a	31.4 (0.54)
Third instar						
Male	—	86 (1.50)	34 (0.46)	14 (0.89)	135 (2.88) a	50.6 (0.49)
Female	—	92 (1.82)	17 (0.24)	18 (1.00)	127 (3.05) a	19.6 (0.60)
Fourth instar						
Male	—	18 (0.35)	13 (0.18)	130 (10.93)	160 (11.40) a	64.5 (3.11)
Female	—	14 (0.27)	3 (0.04)	153 (12.01)	170 (12.32) a	57.3 (2.39)
Total						
Male	112 (0.47)	208 (2.81)	49 (0.66)	144 (11.82)	512 (15.78) a	122.4 (3.16)
Female	114 (0.47)	199 (2.98)	25 (0.34)	171 (13.01)	508 (16.75) a	39.3 (2.37)
Pooled sexes	113 (0.47)	204 (2.86)	37 (0.50)	158 (12.42)	510 (16.24)	90.5 (2.78)

Means with the same letter in any *C. nigritus* instar group are not significant at $p = 0.05$ (Student's two sample *t*-test).

completely removed the scale cover, chewed a small to large hole in the dorsum, chewed a parallel line to the scale margin and lifted the top off (in the same manner as a tin-opener) or chewed a small hole close to the scale margin. In the latter case, the body of the scale was sucked dry (with the cuticle left partially showing through the hole in the scale cover); whilst in all other cases, the body contents were sucked out, the larvae variously leaving the cuticle behind or partially eating it. Only very rarely was the entire insect eaten. The duration of development of the various instars did not differ significantly between the sexes (Figure 3) and whilst there was a significant

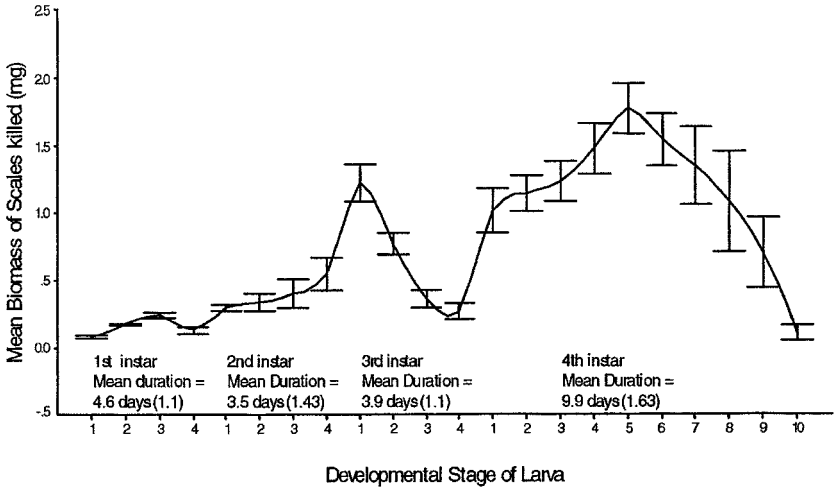

Figure 3. Standardized data (based on mean daily weight of insects killed) of potential food consumption in *Chilocorus nigritus* larvae for each quarter (first, second and third instars) or tenth (fourth instar) of each developmental stage (range bars = mean ± s.e.). Figures in parentheses represent standard deviations.

trend for overall consumption to increase with duration of development, the result was poorly correlated ($p = 0.01$, $r^2 = 0.28$).

Male and female *C. nigritus* larvae killed similar numbers of scale insects per day and required similar amounts of prey to complete development (Table 1).

With the exception of 2nd ecdysis, the general pattern of food consumption was a gradual increase soon after each moult but with a decline as larvae approached the next ecdysis (Figure 3).

Experiment 3 – Effect of temperature on voracity in adult C. nigritus

Too few beetles survived at 13 °C (5 females, 1 male) for these data to be included in the analysis. Analysis of variance showed that the main effects of temperature regime and gender were highly significant ($F_{4,165} = 41.6$, $p \leqslant 0.0001$ and $F_{1,165} = 19.4$, $p \leqslant 0.0001$ respectively) as was the interaction between gender and temperature ($F_{4,165} = 5.7$, $p < 0.0001$). Analysis of the means showed that female beetles killed significantly fewer scale insects at 20 °C than they did at 26 or 30 °C although there was no significant difference in voracity at the two latter temperatures (Table 2). Female beetles under the cycling regime of 14/30 °C killed significantly more insects than did beetles of either sex at any other temperature. Males killed most insects at 30 °C and at the cycling regime of 14/30 °C but were generally less voracious than

Table 2. Effect of temperature on number and estimated weight of pre-ovipositing adult female *Abgrallaspis cyanophylli* eaten in a 24 hour period by adult male and female *Chilocorus nigritus* two to six weeks after eclosion (n = 18 males and 18 females at each temperature level)

Temperature	Sex	Mean number eaten (± SD)[1]	Estimated weight eaten (mg)	Mean number eaten (pooled sexes) (± SD)[2]	Estimated weight eaten (pooled sexes)
13*	pooled	—	—	0.48 (0.73)	0.097
15	Female	1.94 (2.89) a	0.394	1.61 (1.69) a	0.327
	Male	1.28 (1.45) a	0.259		
20	Female	3.94 (1.83) b	0.801	3.97 (2.01) b	0.806
	Male	4.00 (2.22) b	0.812		
26	Female	8.83 (4.11) c	1.793	7.00 (3.76) c	1.421
	Male	5.17 (2.28) b d	1.049		
30	Female	7.17 (3.31) c	1.455	7.06 (3.33) c	1.432
	Male	6.94 (3.44) c d	1.409		
14/30	Female	12.33 (4.92) e	2.504	9.78 (4.64) d	1.985
	Male	7.22 (2.49) c	1.466		
Overall Mean[3]	Female	6.84 (4.97)[3]	1.389	5.88 (2.99)[3]	1.194
	Male	4.92 (3.25)[3]	0.999		

*Too few males survived for statistical comparisons to be made.
[1]Means with the same letter within the column are not significantly different (LSD at 5% level = 1.9616).
[2]Means with the same letter within the column are not significantly different (LSD at 5% level = 1.3899).
[3]Comparison between female and male was significant at $p = 0.05$ (LSD = 0.8791).

females (Table 2). No differences in the number of scales killed by males and females occurred at 15, 20 and 30 °C but at 26 °C and 14/30 °C, females killed more than males (Table 2).

Discussion

Experiment 1 – Estimating host weight

Decline in scale insect body weight and length after the onset of oviposition in the current study (Figure 2) agrees with Koteja (1990) who also reported this phenomenon in other diaspidid species. Since evidence of egg-laying can be seen through the scale cover in this species, ovipositing females are easily separated from those at the pre-oviposition stage, thus enabling accurate estimations of body mass in the latter group. The curve estimating the relationship between weight and length in male scale insects was a different shape to that of the females, presumably reflecting the fact that growth and feeding rates decline towards zero as the developing insect moults and enters the non-feeding pre-pupal stage.

Experiment 2 – Larval food requirement

Of some importance is the fact that because of rapid dehydration of the insects once the scale cover is pierced (Foldi, 1990), and the even more rapid dehydration of insects which have been punctured and killed but not eaten, it was impossible in both larval and adult trials to distinguish between insects which had been killed and eaten, and those killed but not eaten. Thus, observations of feeding behaviour and poor correlation between duration of development and larval 'consumption' (which may have been due to an increase in killing but not eating insects rather than an increased food consumption or requirement) suggest that the estimated weight of scale 'eaten' as presented in this study more accurately describes the maximum feeding potential of the larvae than the larval food requirement. However, although the accurate estimation of scale insect consumption by *C. nigritus* and other coccidophagous insects remains difficult, the low variability of the estimated scale insect data in this experiment suggests that qualitative comparisons of maximum food intake amongst morphologically similar prey species would be possible using this method.

That *C. nigritus* larvae were able to feed on second instar scale insects was discovered during a temporary shortage of first instar *A. cyanophylli* and disagrees with the work of Samways and Wilson (1988) who found that only first instar *Aspidiotus nerii* Bouché (a morphologically similar species to

A. cyanophylli) could be attacked by this beetle stage. This is further evidence that *A. cyanophylli* is a superior host when compared to *A. nerii* for the mass rearing of *C. nigritus* (see Ponsonby and Copland, 1998) because it allows more flexibility in the foraging behaviour of the first instar larvae. Also of considerable interest is that a mean of 510 *A. cyanophylli* of varying stages were required for the development of a single *C. nigritus* larva from eclosion to pupation. This compares with a mean total of 131 mature, pre-ovipositing *Chrysomphalus aonidium* L. consumed by larvae of *Chilocorus bipustulatus* L. (Yinon, 1969).

The similarity found in the duration of larval instar development of male and female larvae and in the biomass killed by each sex, supports the suggestion below that the increase in female imaginal intake reflects the higher energy demands for producing eggs than sperm, rather than any inherent difference in voracity between the sexes.

The mean duration of the total larval development was 3.3 days shorter in the current experiment when compared to earlier work by Ponsonby and Copland (1996). This difference may be due in part to the fact that in the current experiment, emerging larvae were placed in isolation and in contact with a ready supply of suitable food, whilst in the former study, they were in competition with conspecifics and forced to search for a suitable host stage amongst an abundance of all host stages.

The temporal pattern of larval consumption agrees with that found by Yinon (1969) in developing larvae of *C. bipustulatus*. First instar larvae consumed 3%, second instars 6%, third instars 18% and fourth instars 73% of the total larval intake. The first instar intake was generally low and the fourth very high when compared to some other species – e.g., 11 and 44% in *C. bipustulatus* (Yinon, 1969) and 4 and 50% in *Cryptolaemus montrouzieri* Mulsant (Heidari, 1989) – but similar to *Coccinella septempunctata bruckii* Mulsant (8 and 72%) and *Exochomus flavipes* Thunberg (4 and 73%) (Hodek, 1973). Reasons for such differences remain unclear but may be due to differing functional responses or to the fact that all of these studies recorded results as numbers of prey killed rather than prey weight.

Experiment 3 – Effect of temperature on voracity in adult C. nigritus

Higher female consumption has been reported in most studies on adult coccinellids (e.g., Hagen, 1962; Gawande, 1966; Smith, 1966; Hodek, 1973; Heidari, 1989). However, no other study has suggested a feeding rate interaction between gender and temperature with respect to this parameter, perhaps because the insects examined were not generally exposed to constant temperatures at or near the extremes for the species. The reason for such an interaction in the current study is unclear but since male and female

C. nigritus are morphologically similar, it is probably related to the energy requirements for egg production as oviposition rates were found to be relatively low in *C. nigritus* at 20 °C when compared to those at 26, 30 and 14/30 °C (Ponsonby and Copland, 1998). In the current study, beetles did not oviposit at 15 °C. However, this does not explain the similarity between male and female voracity at 30 °C.

Number of prey killed (pooled sexes) was 38.5% higher under the cycling regime than the next highest intake at 30 °C. This indicates that the increased voracity observed in coccinellid larvae during development at such temperatures (numerous studies, e.g., Gawande, 1966; Hodek, 1973) is also true of the adults. Reasons for this phenomenon remain unclear.

Effective comparisons between the results of this study and findings in similar studies on *C. nigritus* were difficult due to the differences in host species and stages. However, work carried out by Samways and Wilson (1988) using adult female *A. nerii* was qualitatively comparable but showed a much higher voracity than adults in the current study (mean consumption of 11.4 insects at 26 °C over a 12 hour period compared to 7 over a 24 hour period in this experiment), possibly because they starved the beetles for 24 hours before the experimental run. This pre-treatment was attempted in the current study during trial runs and was indeed found to significantly inflate the numbers eaten by an average of 351% across the temperature range examined. Variability (SD) also increased by an average of 590% when starved beetles were compared to those not starved. Since one of the main objectives of this experiment was to derive a realistic estimate of daily food intake under field conditions of medium to high host density, a starvation pre-treatment was not adopted. However, it is recognised by the authors that starvation may be an important factor in host location behaviour and in field releases where rapid dispersal of adults is to be avoided.

General discussion

C. nigritus was found to be a highly voracious species with a total requirement of over 500 scale insect prey to complete the larval development (more than 100 first instar scales being required for the first larval stage alone). Thus, like most coccinellids, a high host density is required to allow *C. nigritus* larvae to mature and their successful use in biocontrol programmes will depend heavily on the density of the target pest species in general, and on the first instar (and early second instar) in particular.

In conclusion, reduced adult voracity at the lower temperatures would suggest that *C. nigritus* would be most efficient as a biological control agent if used in glasshouses with a mean daily temperature above 22 °C. This

agrees with the optimum conditions required for development (Ponsonby and Copland, 1996) and fecundity (Ponsonby and Copland, 1998). Based on temperature data supplied by the Royal Botanic Gardens, Kew, this would tend to restrict its use in the UK in cool (temperate) glasshouses to the period from early May to early October. However, under hothouse (tropical) conditions, its use could be extended from early March to late October.

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