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Environmental influences on fecundity, egg viability and egg cannibalism in the scale insect predator, *Chilocorus nigritus*

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Abstract. The effects of temperature on age-specific fecundity, egg viability and egg cannibalism were examined in the coccidophagous coccinellid, *Chilocorus nigritus* being fed on the cyanophyllum scale, *Abgrallaspis cyanophylli*. There were no significant differences in lifetime fecundity or oviposition rate at constant temperatures in the range of 20 to 30 °C although there was a trend for both parameters to increase with increasing temperatures. Total fecundity ranged from five to 1890 eggs per female whilst the oviposition rate varied from 0.2–12.1 eggs day^{-1}. Egg viability was significantly greater at 26 and 30 °C (63 and 74%, respectively) than at lower temperatures (18 to 30%) whilst egg cannibalism was highest at 24 and 26 °C (being the mid range of the temperatures tested). Mean pre-oviposition periods varied from 54 days at 20 °C to 8.2 days at 30 °C. The effect of relative humidities in the range of 33% to 75% on oviposition rate, egg viability and egg cannibalism was measured and found to have no significant effect on either parameter.

Résumé. Les effets de la température sur la fécondité, la viabilité des oeufs et le cannibalisme des oeufs ont été étudiés chez le Coccinelidé coccidiophage *Chilocorus nigritus*. Bien que les deux variables tendent à augmenter avec la température, il n'y a aucun effet statistiquement significatif sur la fécondité et le taux d'oviposition pour des températures constantes comprises entre 20 et 30 °C. La fécondité totale varie de 5 à 1890 oeufs par femelle tandis que le taux d'oviposition varie de 0.2 à 12.1 oeufs par jour. La fécondité des oeufs est significativement plus grande entre 26 et 30 °C (63 and 74%, respectivement) qu'aux températures plus basses (18 à 30%); le cannibalisme des oeufs est maximum entre 24 et 26 °C. La durée de la période d'oviposition varie de 54 jours à 20 °C à 8.2 jours à 30 °C. Les effets du taux d'humidité relative (entre 33% et 75%) ont été testés sur le taux d'oviposition, la viablilité des oeufs et le cannibalisme des oeufs et ne rélèvant aucune différence significative sur ces trois variables.

Key words: age-specific fecundity, Coccinellidae, Coleoptera

Introduction

Chilocorus nigritus (Fabricius) (Coleoptera: Coccinellidae) is an economically important natural enemy of scale insects, native to the Indian Sub-Continent and South-east Asia. However, throughout this century, it has been successfully utilized as a biocontrol agent of diaspids in numerous tropical and subtropical locations (Samways, 1984). Past studies on its fecundity have been inconclusive with estimates of total egg production ranging from 24 (Dorge et al., 1972) to 370+ (Greathead and Pope, 1977). Similarly, the pre-oviposition period ranged from one to three days (Dorge et al., 1972) to 24 (Greathead and Pope, 1977). In the current study, *C. nigritus* was being assessed as a potential biological control agent for use in temperate glasshouses and there was thus a need to clarify its reproductive ability, particularly in relation to varying temperatures and humidities. In a broader sense, any attempt to understand the population dynamics, or to assess the effectiveness of a biocontrol agent via its numerical reproductive response, obviously requires accurate estimations of not only pre-oviposition period, but also age-specific fecundity and egg viability. Whilst many studies on coccinellids have measured pre-oviposition periods and total fecundity, few have examined egg viability and, as far as the authors are aware, there have been no published studies on age-specific fecundity. The effect of temperature on developmental rate and survival in *C. nigritus* have been studied by Ponsonby and Copland (1996), but there have been no studies on the effects of humidity on any parameter in this species and accounts of its observed preferences are conflicting. Greathead and Pope (1977) felt that *C. nigritus* was better adapted to the dry savannahs of East Africa than the native *Chilocorus* species and Kinawy (1991) describes its introduction into the arid, subtropical desert region of Oman as successful. However, Samways (1989) in his work on its biogeography, suggested that it prefers hot, humid summers with cool dry winters. There was thus a need to clarify its requirements since glasshouse environments vary according to the plant species under cultivation. The aim of the following experiments was therefore to assess the reproductive tolerance of this species to a range of temperatures and humidities and to provide information that could be used to model its reproductive response.

Egg cannibalism is common amongst predatory insects in general and in coccinellids in particular (e.g. Heidari, 1989; Agarwala and Dixon, 1992). This experiment provided an ideal opportunity to gather data on the incidence of adult egg predation in *C. nigritus* which is thus presented below.

Materials and methods

Effects of temperature

Adult beetles were obtained from the International Institute of Biological Control, Rawalpindi, Pakistan and reared on the diaspid, *Abgrallaspis cyanophylli* (Signoret) (Homoptera: Diaspididae) cultured on potato tubers (*Solanum tuberosum* Linneaus) at temperatures of 27 °C ± 1 °C, a lighting regime of L12:D12 and an r.h. of 55% (± 10%). Adult beetles were allowed to oviposit into 100 × 100 mm eight ply surgical gauze pads laid on top of the potato cultures for a period of one week. The resulting eggs were reared in separate cages to adulthood and the emerging imagos were then removed on a daily basis, sexed according to the method of Samways and Tate (1984) and placed, one male and one female, into controlled humidity units (CHUs) under constant temperature regimes. CHUs consisted of two 1 lb honey jars in tandem, one upright containing a saturated salt solution to provide a constant humidity, the other inverted and containing the beetle eggs and larvae (along with a small potato tuber infested with all stages of *A. cyanophylli*). Tests using an electronic hygrometer showed that r.h. fluctuated by about ± 5% within the jars. CHUs containing a pair of beetles were incubated at constant temperatures of 20, 22, 24, 26, 30 °C and a further group was incubated at the cycling temperatures of 12 h at 14 °C and 12 h at 30 °C. The experiment was replicated five times at each temperature level and humidity was controlled at 59–68% r.h. (the exact level depending on temperature). All replicates were incubated in illuminated, cooled incubators at the temperatures stated, ± 1 °C. Illumination was via six 8 W fluorescent tubes providing a light intensity in the range of 15–25 W m^{-2}. Clean surgical gauze pads (as described above) were cut into quarters and placed inside the CHUs with the beetles in order to provide them with an ovipositing substrate. Gauze pads were removed daily throughout the experiment and the number of eggs were counted. At the same time, the CHU was examined for any eggs laid on the jar surface and the potato was searched for any eggs laid beneath dead scales, amongst the potato sprouts or on the surface of the potato tuber. These were counted and carefully removed, a process which usually resulted in their destruction. Eggs laid on the gauze and any that were successfully removed from the CHU were incubated at 26 °C in small, ventilated, transparent plastic boxes (173 × 155 × 65 mm) under constant light conditions and ambient humidity (approx. 30% ± 10%). Egg viability (%) was then estimated by counting the number of emerging larvae. Eggs were frequently cannibalized by the parents but these could be detected by the presence of the chorion which was never fully eaten (adult females were observed to lay eggs, turn, and immediately pierce the chorion and suck out the contents, on several occasions). Similarly,

damaged eggs could be detected by a lack of turgidity and whilst both these and eaten eggs were added to the total of eggs laid, they were removed from the egg viability calculations.

Effects of humidity

Emerging beetles (reared according to the method described above) were placed under constant light at a temperature of 26 °C for a period of 28 days. The beetles were sexed and placed, one female and one male, into CHUs with scale cultures and surgical gauze as described above. Relative humidity was controlled at 62% (±5%) and incubation was continued for a further seven days, thus enabling the beetles to become acclimated to the experimental conditions. Each pair was checked daily to ensure that oviposition was taking place. At the start of the experimental run, enough beetles were ovipositing for each of three levels of humidity to be replicated six times. Each replicate was then randomly assigned to one of the three treatments. From that stage onwards, the CHUs were sealed with Parafilm M to maintain humidities at more exact levels. During the course of the experiment, all pairs were kept at 26 °C under constant light and at an r.h. of 62% for a period of 10 days. After that period, six of the replicates were transferred to CHUs at 33% r.h., six were left in the original containers at 62% r.h. to act as a control and the remaining six were placed in CHUs at 75% r.h. This regime was continued for a further 10 days. The number of eggs on the gauzes and in the CHU and egg viability were determined daily as described above.

In both experiments, fresh scale-infested tubers were supplied every third day and the sex of the adult beetles in both experiments was confirmed by dissection and examination of the genitalia.

Statistical analysis

Effects of temperature

The pre-oviposition period, oviposition rate and the total number of eggs laid by individual females were analysed using one-way analysis of variance after first checking the data for an approximation to a normal distribution. The mean daily oviposition rate for each replicate was calculated by dividing the total number of eggs laid by an individual by the duration of its adult reproductive lifespan (i.e., eclosion to death minus the pre-oviposition period). Egg viability (temperature and humidity trials) and egg cannibalism data were analysed using the Kruskal–Wallis *k* sample test or the Wilcoxon–Mann–Whitney test on percentages relating to individual females, whilst a multivariate analysis of variance of oviposition rate over time was carried out using linear partitioning by the SAS ‘Repeated Time’ procedure. However,

the mean oviposition period varied with temperature and it was therefore necessary to standardize the data. This was achieved by dividing the oviposition period for each individual into ten periods of equal length. A mean oviposition rate was then derived for each period and compared with that of a similar period in other individuals at different temperatures. The relationship between the age of beetles and the daily oviposition rate was described using best fit polynomial regression analysis.

Effects of humidity

Data were analysed using the same methods as for the temperature trials with the following exceptions: between-treatment egg viability data were analysed using the Kruskal–Wallis *k* sample test (carried out on data from both before and after humidity changes were made). This ensured that any differences due to effects other than humidity were detected before humidity changes were made (e.g., experimental error, infertile males or natural variability in the females). Within-treatment analyses (before and after humidity changes) were carried out using Wilcoxon's signed rank test after first pairing the data.

Results

Effect of temperature

Pre-oviposition period, reproductive lifespan, total (life-time) fecundity and mean oviposition rate are presented in Table 1 and show that there were no significant differences in the total fecundity at any of the temperatures, despite the fact that means varied from 564 at 20 °C to 1361 eggs at 24 °C. However, variability was high and results were complicated by the fact that at three of the six temperature levels, one of the females died before any eggs were laid and at 24 °C, two of the females did not oviposit. The pre-oviposition period decreased with increasing temperature whilst the mean oviposition rate tended to increase under similar conditions. However, this latter result was not significant at the 95% level. At lower temperatures, the oviposition rate remained relatively constant throughout the entire reproductive period but as temperatures increased, the overall trend was for oviposition to peak at approximately one third of the way through the reproductive period and then to slowly decline (see Figure 1). Regression analysis between oviposition rate and age at 20 °C was not significant whilst at all other temperatures, second order polynomials gave the best fit to the data (Table 2). However, repeated time analysis showed that whilst oviposition rate varied significantly with time ($p < 0.0001$), linear partitioning indicated that there was no significant

Table 1. Preoviposition period, reproductive lifespan, oviposition rate and total fecundity in *Chilocorus nigritus* when fed on all stages of *Abgrallaspis cyanophylli* at various constant and one cycling temperature (r.h. in the range of 62–65%)

Temperature (°C)	N	Pre-oviposition period (days)			Reproductive lifespan (days)			Oviposition rate (eggs day^{-1})			Total fecundity (eggs laid female^{-1})		
		Mean	Range	S.D.	Mean	Range	S.D.	Mean	Range	S.D.	Mean	Range	S.D.
20	4	54.0 a	18–137	56.0	114 a	58–238	102.1	2.87 a	0.1–5.6	3.11	564 a	5–1230	652
22	4	23.8 a b	10–65	27.5	166 a	50–291	110.8	2.89 a	0.2–4.5	1.94	633 a	9–1257	579
24	3	15.3 a b	9–25	8.5	180 a	172–257	31.0	6.25 a	3.8–8.9	2.53	1361 a	989–1733	372
26	5	8.8 b	5–11	2.5	147 a	57–234	62.7	5.92 a	0.2–9.0	3.45	1008 a	9–1890	683
30	5	8.2 b	6–11	2.2	123 a	25–219	80.6	7.76 a	5.2–12.1	2.86	827 a	303–1503	508
14/30	4	15.5 b	8–34	12.4	144 a	41–211	37.2	4.81 a	3.4–6.8	1.5	782 a	508–889	184
Pooled data	25	20.2	6–137	25.4	146	25–291	77.3	4.72	0.2–12.1	2.42	847	5–1890	541

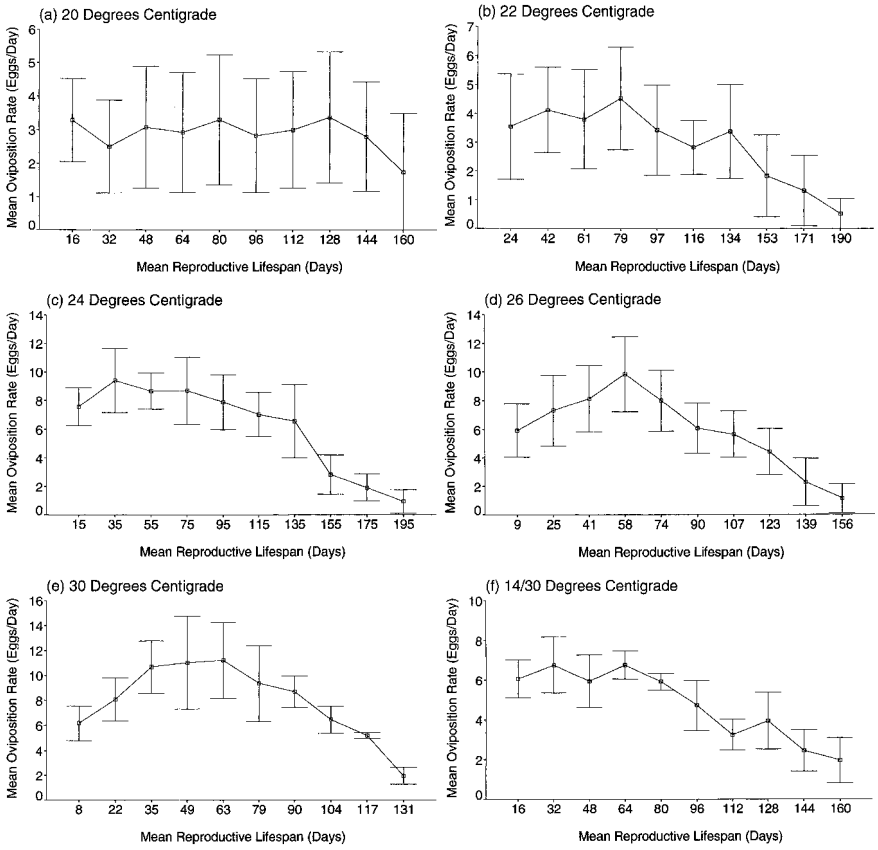

Figure 1. Effect of various constant and one cycling temperature on age specific fecundity in *Chilocorus nigritus* at 62–68% r.h.. Range bars = mean ± s.e., n = 5 (26 and 30 °C), 4 (20, 22 and 14/30 °C) or 3 (24 °C).

difference in the oviposition rate at each temperature in relation to time. Polynomial regression analysis was therefore also carried out on the pooled data, with a third order polynomial producing the best overall fit ($p < 0.0001$, $r^2 = 0.9832$; see Figure 2).

Egg viability increased with increasing temperature (Table 3) whilst at 14/30 °C, it was equivalent to that at 20 °C. The level of egg cannibalism varied considerably at the different temperature levels (Table 3), tending to be highest at those in the mid range.

Table 2. Best fit Regression equations for predicting age-specific fecundity (eggs/day) in *Chilocorus nigritus* when fed on all stages of *Abgrallaspis cyanophylli* at constant temperatures in the range of 20 to 30 °C (± 1 °C) and humidities in the range of 62–68% r.h.

Temperature (°C)	No. females	Regression equation	r^2	$p > F$
20	4	$y = 2.773589+0.008514x–0.000058124x^2$	0.0018	0.9683
22	4	$y = 3.253173+0.024919x–0.000210x^2$	0.1751	0.0284
24	3	$y = 7.192629+0.039985x–0.000385x^2$	0.4398	0.0003
26	5	$y = 5.797356+0.083881x–0.000761x^2$	0.2722	0.0006
30	5	$y = 4.993271+0.198921x–0.001713x^2$	0.2950	0.0003
14/30	4	$y = 6.423750+0.007823x–0.000236x^2$	0.4005	0.0001
Pooled data	25	$y = 3.652600+2.050806x–0.360677x^2+0.013305x^3$	0.9832	0.0001

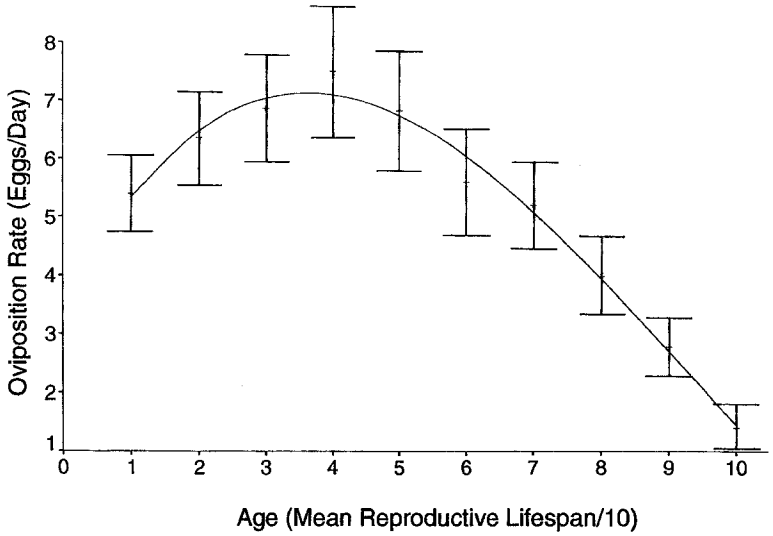

Figure 2. Age specific fecundity at temperatures between 20 and 30 °C and r.h. 62% to 65% in *Chilocorus nigritus* (pooled temperature data). Range bars = mean ± s.e., $y = 3.6526 + 2.050806x – 0.360677x^2 + 0.013305x^3$, $r^2 = 0.98$, $p < 0.0001$ (n = 25).

Effect of humidity

Analysis of variance and linear partitioning showed that there were no significant differences in the mean daily oviposition rate for each humidity treatment at any point during the experiment (Figure 3).

Table 3. Effect of differing temperatures on egg viability and egg cannibalism amongst individual pairs of male and female *Chilocorus nigritus* when fed on all stages of *Abgrallaspis cyanophylli* at 62 to 65% r.h. (% hatched = proportion hatched of the total laid by all females at any temperature level)

Temperature (°C)	No. of pairs	% hatched[1]	% cannibalised (mean)[2]
20	4	27 a	11 a
22	4	18 a	7 a
24	3	30 a	27 b
26	5	63 b	28 b
30	5	74 b	10 a
14/30	4	28 a	11 a

[1]Comparison between all temperatures (5 degrees of freedom) – $p < 0.05$ (Kruskall–Wallis test).
[2] Comparison between all temperatures (5 degrees of freedom) – $p < 0.025$ (Kruskal–Wallis test).
Treatments within a column followed by the same letter are not significantly different.

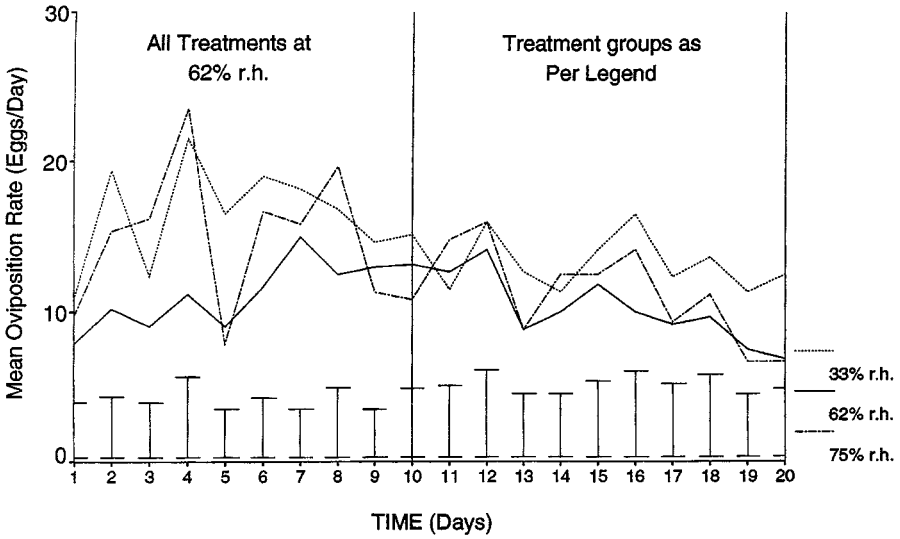

Figure 3. Effect of a change in humidity on fecundity in *Chilocorus nigritus* at 26 °C (n = 6). Range bars = least significant difference at the 5% level.

Mean daily egg viability over time for each treatment varied from 45 to 72% but between treatment analysis showed that there were no significant differences before or after changes in humidity were made (Table 4). Similarly, within-treatment analysis revealed no significant differences between the first 10 days at 62% and the second 10 days at the respective humidities (Table 4).

Egg cannibalism was not significantly altered by the humidity changes (Table 4) and the pooled data revealed an overall level of 16.1%.

Table 4. Between treatment and within treatment effects of a change in humidity on mean total egg production and mean egg viability in *Chilocorus nigritus* fed on all stages of *Abgrallaspis cyanophylli* at 26 °C after seven days acclimatization at 62% r.h. (10 days at 62% r.h. followed by 10 days at treatment r.h.) (n = 6)

Relative humidity	No. eggs laid (± S.D.)[1]	% hatched[2]	% cannibalised[2]
Treatment 1			
10 days @ 62%	114.7 (36.72)	53 a	5.5 a
10 days @ 33%	100.7 (84.22)	65 a	4.3 a
Treatment 2			
10 days @ 62%	164.3 (27.7)	44 a	21.2 b
10 days @ 62%	132.0 (19.63)	46 a	13.6 b
Treatment 3			
10 days @ 62%	148.5 (61.56)	46 a	28.2 b
10 days @ 75%	112.7 (84.27)	45 a	18.2 b

[1]See Figure 3 and text for statistical analysis.
[2]Means within a column with the same letter are not significantly different at p = 0.05 (Kruskal–Wallis test (between-treatment means) and Wilcoxon's signed rank test (within-treatment means).

Discussion

Effects of temperature

High variability may have been the reason that total fecundity and oviposition rate were found not to be significantly different at differing temperatures since there was a trend for total fecundity to increase up to 26 °C (slightly declining at 30 °C). This high variability was maintained throughout the measured range (note the standard deviations for the total fecundity data at constant

temperatures in Table 1), a trait which appears to be shared by all coccinellids (Hodek, 1973). In order to reduce the statistical problems associated with this high variability, larger numbers of replicates are indicated in future experiments of this type. Despite the statistical problems encountered, of major importance is the fact that (a) for the first time, a pattern of age-specific oviposition has been measured for an economically important coccinellid species and (b) a mean of 1008 eggs was laid at 26 °C, with one individual laying 1890 eggs (1520 more than in any other published study on this species, i.e. 370+ in Greathead and Pope, 1977). The reasons for this difference between the two studies are unclear but the implications are that (a) *A. cyanophylli* is a highly suitable host for rearing the species and (b) temperatures in the range of 26–30 °C not only produce the most favourable survival and developmental rates for *C. nigritus* (see Ponsonby and Copland, 1996), but also the highest level of viable offspring.

The pre-oviposition period was found to closely match that of Ahmad (1970) (15.4 days at 24 °C), Greathead and Pope (1977) (23 days at 21 °C) and Hattingh and Samways (1994) 14 days at 25–26 °C but to differ from that found by Dorge et al. (1972) and Jalali and Singh (1989) (1–3 and 14.4 days at 27 °C, respectively). The 2.2 eggs day^{-1} found by Greathead and Pope (1977) at 21 °C when *Aulacaspis tegalensis* (Zhnt.) was the prey agrees with the 2.89 eggs day^{-1} at 22 °C in the current study but the oviposition rate at 26 °C (5.92 eggs day^{-1}) differs from the 4.6 eggs day^{-1} found by Hattingh and Samways (1993) at a similar temperature when *Aspidiotus nerii* (Bouché) was the host. Similarly, the 3.1 eggs day^{-1} found by Ahmad (1970) at 24 °C when the beetles were fed *Aonidiella orientalis* (Newstead) was much lower than the 6.25 eggs day^{-1} in the current study.

Although age-specific oviposition rate was not significantly different at any of the temperatures, the high variability and trend associated with this parameter may not justify the pooling of the data. However, the fitted curve (Figure 2) was highly correlated and compares well with the graph of the means (Figure 1), suggesting that it gives an accurate qualitative indication of oviposition rate throughout the reproductive era, but that its quantitative use would be better restricted to temperatures in the mid-range (i.e. 24–28 °C). At 20 and 22 °C, the oviposition rate was almost constant throughout the reproductive era whilst at 30 °C and under the cycling regime of 14/30, the regression equations shown for these temperatures in Table 2 would probably give a more accurate estimation of oviposition rate at a given stage in the adult reproductive period than that of the pooled data.

Egg viability was significantly lowered by temperatures towards the lower end of the range. The reasons for this are unclear but it is possible that spermatogenesis was affected or that sperm mortality in the spermatheca of the

mated females was increased. Egg viability under the cycling regime was similar to those in the lower temperature range, further implying that exposure to cold temperatures is the cause of lowered fertility rather than (e.g.) the effect of temperature on voracity (adult beetles were found to eat relatively more food at cycling temperatures than they were at constant temperatures; Ponsonby and Copland (in preparation).

Egg cannibalism was extremely variable amongst the individual pairs with some eating none at all, whilst others consumed up to two thirds of the total laid. Thus comparisons of cannibalism at different temperature may not be justified with the low number of replicates (see Table 3) although the proportion of eggs eaten at 20, 22 and 30 °C was consistently low, suggesting that there was a trend for cannibalism to be reduced where conditions were less than optimum. The overall level of 20% was generally on the same level of egg cannibalism as that of adult aphidophagous species (Agarwala and Dixon, 1992) and similar to that of ladybird species in general (Hagen, 1962; Heidari, 1989; Hodek, 1973).

Effects of humidity

Results of this experiment showed that sudden changes in r.h. in the range of 33 to 75% had no detectable effect on fecundity, at least in the short term. High variability was again a feature of the different treatments but the means showed no evidence of any trend until the last five days of the trial when there appeared to be a more rapid decline in daily oviposition rate at 33 and 75% r.h. than there was at 62%. However, differences were not significant. Egg viability levels showed no overall trend before or after the change in humidity. In this experiment, egg viability levels were a little lower than those at 26 °C in the temperature trials (52 compared to 63% in the latter), although mean oviposition rates were a little higher (12.88 eggs day^{-1} in the current experiment compared to 11.9 at a corresponding period in the adult lifespan during the temperature trials).

General discussion

C. nigritus was found to be much more fecund than has been previously recorded in studies on both this and closely related species (*C. schioedtei* Mulsant laid 856 eggs (Greathead and Pope, 1977) whilst *C. bipustulatus* Linneaus has been found to lay in the region of 600 eggs (Kaufmann (1977) quoted in Drea and Gordon, 1990), indicating that *A. cyanophylli* is a highly suitable host for mass rearing. *C. nigritus* was able to tolerate a wide temperature range with some individuals laying as many eggs at 20 °C as those at 30 °C. Similarly, egg-laying activity was not affected by extremes of humid-

ity at 26 °C although interaction between temperature and humidity was not examined. However, egg viability data suggests that temperatures in the range of 26–30 °C are the most favoured.

In conclusion, this study has shown that although temperatures between 26 and 30 °C led to increased egg viability, the reproductive performance of *C. nigritus* was largely unaffected by a wide range of temperatures and humidities. This might account for the uncertainties in the literature relating to 'preferred' climate types and perhaps suggests that the reasons for the failure to establish the species in apparently favourable climates (e.g., Bermuda (Bennett and Hughes, 1959), and (initially) Hawaii (Davis, 1972)) may be due to other factors such as prey suitability, the presence of natural enemies, or pathogens to which the species has no resistance. However, the results of this study lend weight to other experiments (Ponsonby, 1995; Ponsonby and Copland, 1996; Ponsonby and Copland, in preparation) which indicate that *C. nigritus* would be a suitable biocontrol agent in UK glasshouses during a typical summer, when mean daily temperatures would be expected to be in excess of 20 °C.

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