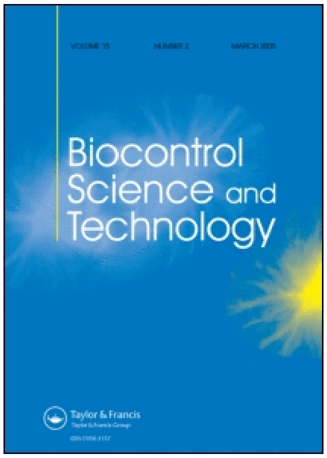

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Effect of Temperature on Development and Immature Survival in the Scale Insect Predator, *Chilocorus nigritus* (F.) (Coleoptera: Coccinellidae)

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Developmental and immature survival rates of the coccidophagous coccinellid Chilocorus nigritus *(F.) were examined under constant, cycling and glasshouse temperatures in order to determine its suitability for use as a biological control agent in temperature glasshouses. First instar larvae did not complete development at 18°C. However, within the range 20–30°C, the developmental rate increased with rising temperature. The theoretical lower thermal threshold for development was found to be 16.6°C. Thermal summation and polynomial regression methods were used to predict developmental periods under glasshouse conditions. The predictions were accurate to within a mean of 10% in relation to observed data. Under laboratory conditions, immature survival rates were highest 28°C (52%) and lowest at (and below) 20°C (17%). First instar larvae suffered the highest mortality rates, while pupae had the lowest. Under glasshouse conditions, the survival rates were much lower (9% in the winter months and 20% throughout the remainder of the year), but the species was considered to be a suitable biocontrol agent if mean daily temperatures were maintained at levels above 20°C.*

Keywords: Chilocorus nigritus*, temperature, thermal requirements, immature survival*

INTRODUCTION

Chilocorus nigritus (F.) is an economically important predator of a wide range of scale insect species on citrus, sugar cane, coconut and other crops in tropical and subtropical regions (e.g. Tirumala Rao *et al.*, 1954; Samways, 1984). During the course of this century, it has been exported from its native region (the Indian subcontinent and South-East Asia) to numerous locations around the world as a biological control agent. It has achieved complete and spectacular success against the target pest in a number of locations, such as the Seychelles (Vesey-Fitzgerald, 1953) and Oman (Kinawy, 1991)). In other areas, such as the New Hebrides (Chazeau, 1981) and South Africa (Samways, 1986), it has become a valuable addition to the local natural enemy complex. Despite these and numerous other (not always successful) attempts at utilization, little work has been carried out on the thermal requirements of the species. Several studies have reported development at a single temperature within the favourable range (e.g. Moutia & Mamet, 1946; Chazeau, 1981; Hattingh & Samways, 1993) but in order to prevent introductions into

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unsuitable climates, and to provide data for predicting development, it is essential that more detailed information across a wider temperature range is readily available to biological control researchers. The current work was undertaken when *C. nigritus* was being considered as a potential natural enemy of scale insects in UK glasshouses.

The effect of temperature on development has been widely studied for many insects. Where accurate, regular measurement of temperature is not possible, the linear, day-degree (thermal summation or accumulated heat) description of the relationship provides an acceptable model as long as temperatures remain in the mid-range (Kitching, 1977; Tingle & Copland. 1988). However, where regular and accurate measurement of temperature is achievable, a more complex description of the relationship is possible. In this case, an algorithm or an *n*th order polynomial can be fitted to the empirical data in order to improve accuracy, particularly where temperatures remain at the extremes of the favourable range for significant periods of time (Howe, 1967; Kitching, 1977). Polynomial regression analysis was found to describe the relationship between development and temperature accurately in *Scirtothrips citri* (Moulton) (Tanigoshi *et al.*, 1980), *Diglyphus intermedius* Girault (Patel & Schuster, 1983) and three mealybug parasitoids (Tingle & Copland, 1988), and is the model used in this study for comparisons with the accumulated heat method.

Immature survival will have a profound influence on the reproductive numerical response of a predator. It is thus an important factor to consider under glasshouse situations (where temperatures may be manipulated in order to improve survival of vulnerable stages of the life cycle). This study was, therefore, used as an opportunity to examine the influence of temperature on immature survival.

MATERIALS AND METHODS

Development Under Constant and Cycling Temperatures in the Laboratory

Adult beetles were obtained from the International Institute of Biological Control, Rawalpindi, Pakistan and reared on the diaspid, *Abgrallaspis cyanophylli* (Signoret) cultured on potato tubers (*Solanum tuberosum* L.) at temperatures of 27°C ± 1°C, with a 12 h/12 h light:dark photoperiod and 55% (±10%) relative humidity (RH). Adult beetles were allowed to oviposit into 100 × 100 mm 8-ply surgical gauzes laid on top of the potato cultures for up to 5 h. The gauzes were then removed, the number of eggs was counted and their position marked with a waterproof pen. They were then placed into controlled humidity units (CHUs) consisting of two 1-lb honey jars. In one of the lids, a 50-mm hole was drilled and covered with 30 mesh/cm nylon. The other lid had five small ventilation holes drilled in it and the two were then taped back-to-back using clear adhesive tape. Thus, two jars were used in tandem, one upright containing a saturated salt solution to provide a constant humidity and the other inverted and containing the beetle eggs and larvae (along with a small potato tuber infested with all stages of *A. cyanopllylli*). Tests using an electronic hygrometer showed that the RH fluctuated by about ±5% within the jars. CHUs containing a minimum of 10 eggs were incubated at constant temperatures of 18, 20, 22, 24, 28 and 30°C and a further group were incubated at the cycling temperatures of 12 h/12 h at 14/30°C. The experiment was replicated six times at each temperature level. The RH was controlled at temperatures from 18 to 28°C by placing saturated salt solutions of ammonium nitrate in the lower jar (66–60% RH respectively). Those at 30°C contained sodium nitrite to provide a RH of 63%, while those under the cycling regime were held at a RH of 59–68% by ammonium nitrate solutions. All replicates were incubated in illuminated incubators at the temperatures stated (±1°C). Illumination was via six 8-W fluorescent tubes, providing a light intensity in the range 15–25 W m^{-2}.

Observations were made twice daily until the eggs hatched, and then at daily intervals until adult emergence was complete. At egg eclosion, emerging larvae were counted. During larval development, cast exuviae were noted and removed daily in order to determine the number of moults, the duration of each stage and the survival rates of the various developmental stages.

The different stages were easily distinguished by the size of the exuviae, but because the process of finding and removing them was time consuming, it was carried out on only three of the six replicates. Emerging adult beetles were sexed in order to provide data on gender differences. Since first and second instars are restricted to preying on the early instars of the host insect (Samways & Wilson, 1988), larvae and adult beetles were provided throughout the experiment with potato tubers upon which were all stages of *A. cyanophylli.*

Development under Glasshouse Conditions

Eggs of *C. nigritus* were produced on surgical gauzes as described above and placed in a transparent plastic box (173 × 155 × 65 mm) from which the top and bottom had been removed and replaced with 40 mesh/cm nylon gauze. Emerging larvae were fed on cultures of *A. cyanophylli* as described above (renewed on a 2-weekly basis). The boxes were suspended from the branches of small trees (close to the temperature sensors) in both the northern and central sections of the conservatory at Wye College, UK. Care was taken to ensure that the boxes were never in direct sunlight and that air flow was not restricted, thus ensuring that the temperature was similar to that being recorded. Temperature sensors were housed in aspirated screens and the mean hourly temperatures were recorded and stored on floppy disk using a microcomputer. Developmental data (egg eclosion, pupation and adult emergence) were recorded daily. The experiment was repeated on a 4-weekly basis from 20 August 1992 to 24 September 1993. However, some data were lost due to a malfunction of the temperature sensors. The minimum temperature recorded during that period was 17°C and the maximum was 36°C. The RH was held constantly high (i.e. $>60\%$ RH).

In each of the above trials, the developmental period was deemed to be the number of days from oviposition to adult emergence.

Data Analysis

Developmental data were analyzed initially by one-way analysis of variance and the developmental rate (1/developmental period) was then subjected to polynomial regression. From the latter, temperatures in the mid- (linear) range were selected and used to carry out linear regression. The theoretical lower threshold for development ($T1$) was calculated by extrapolation, using the formula $T1 = -a/b$. The thermal constant (K) was calculated using the equation $K = 1/b$ and day-degree predictions for the glasshouse trials were carried out using the data stored on disk. The equation derived from the polynomial regression analysis was used in conjunction with the stored temperature data to compute the proportion of the total life cycle completed in 1 hour at any given temperature and the increments were summed until they reached unity (i.e. until development was complete). Since the equation was based on constant temperature data in the range 20–30°C, glasshouse data outside this range were not included in the polynomial analysis. Differences in the accuracy of each method of prediction were tested using a two-sample *t*-test on the residuals. Cycling temperature data were used to assess the accuracy of predictions based on the thermal summation method and to provide information on the actual thermal threshold. (It was assumed that no development would occur if the lower temperature was below the thermal threshold, and thus development would take twice as long as constant temperatures which were identical to the upper cycling temperature.)

Overall mortality data and differential survival data among the various stages and between the two sexes were analyzed using a χ^2 contingency table. Survival data are presented as percentages for ease of interpretation but were analyzed using the original frequencies.

RESULTS

Development

The effect of temperature on the development of the various immature stages of *C. nigritus* is presented in Table 1 and shows that the developmental period decreased with increasing temperature. Regression analysis of the developmental rate showed that a first-order polynomial gave the best theoretical fit ($r^2 = 0.99$), although from numerous other studies on insects (e.g.

TABLE 1. Mean developmental period (days (±) standard deviation (SD)) and pooled survival data (%) of the immature stages of *C. nigritus* at different constant and cycling temperatures and RH in the range 60–66% (number of replicates = three {larval stages} or six {egg and pupal stages}, each with 10–48 eggs at the start of the experiment)

Stage of development	Temperature (°C)[a]								LSD	Pooled survival data[b]
	18	20	22	24	26	28	30	14/30		
Egg	20.2a	14.5b	11.3c	9.8d	6.6e	6.4e	5.5e	10.0d	1.2	87
(SD)	(2.6)	(2.2)	(0.5)	(1.2)	(0.6)	(0.4)	(0.2)	(0.1)		(606)[c]
First Instar	4.0	14.6a	13.9a	10.5b	7.5bc	7.0c	4.9c	—	2.5	56
(SD)	—	(2.9)	(1.0)	(1.1)	(0.8)	(1.3)	(1.3)	—		(227)
Second Instar	—	5.0a	9.2b	7.2ab	5.2ab	3.5a	3.5a	—	4.1	92
(SD)	—	(1.2)	(4.5)	(3.9)	(0.6)	(0.5)	(0.7)	—		(127)
Third Instar	—	13.6a	10.0a	6.0bc	5.4bc	2.5c	2.9c	—	4.9	90
SD)	—	(1.7)	(7.8)	(2.9)	(2.5)	(1.7)	(0.9)	—		(117)
Fourth Instar	—	13.9a	13.7a	9.9a	9.9a	6.0a	5.6a	—	10.9	75
(SD)	—	(9.9)	(4.3)	(1.6)	(1.6)	(0.6)	(1.0)	—		(105)
Pupa	—	11.0a	9.9b	7.8c	6.1d	5.3de	4.8e	9.9b	0.8	94
(SD)	—	(1.6)	(0.7)	(0.6)	(0.2)	(0.3)	(0.3)	(0.4)		(268)
Egg–adult	—	74.5a	57.9b	48.0c	34.0d	28.6de	25.2e	47.0c	6.6	—
(SD)	—	(8.2)	(8.0)	(7.6)	(3.7)	(3.1)	(2.5)	(2.3)		—
Survival (egg–adult)[d]	0	17	39	39	40	52	51	47	—	42
(Total no. of eggs)	(68)	(66)	(77)	(96)	(82)	(69)	(78)	(138)	—	(606)

[a] Means within rows with the same letter are not significantly different (least significant difference (LSD) at the 5% level).
[b] χ^2 (comparison between all immature stages—5 degrees of freedom) = 157.656 ($p < 0.0001$).
[c] Figures in parentheses for pooled survival data represent the numbers at the start of each stage.
[d] χ^2 (comparison between all temperature levels except 18°C—six degrees of freedom) = 25.370 ($P < 0.0001$).

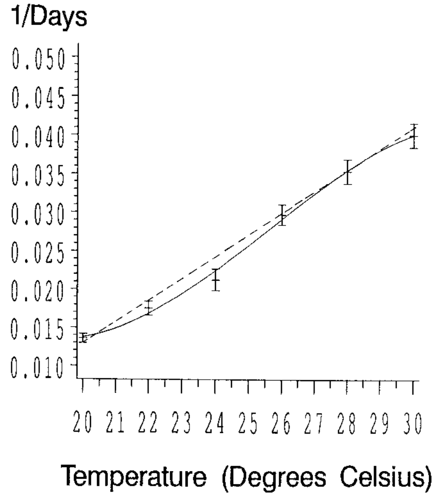

FIGURE 1. Best fit regression lines for predicting development in *C. nigritus* calculated from developmental rates (1/developmental period) at constant temperatures. ———, Best fit polynomial regression (all data points used); – – –, best fit linear regression (data for 22, 24, 26 and 28°C only). Range bars = mean ± standard error ($n = 6$, each with 10–48 eggs at the start of the trial).

Kitching, 1977; Tingle & Copland, 1988), a third-order polynomial is known to fit the actual biological situation more realistically and gave the best visual fit to the data in this instance. Since the r^2 value was only marginally smaller, the latter was therefore adopted and is presented in Figure 1 ($y = 0.4597770083 - 0.0557522239 9x + 0.0023808958 5x^2 - 0.0000310060162x^3$, $r^2 = 0.99$). Temperatures in the mid- (linear) range were judged from that curve to be 22, 24, 26 and 28°C, for which the regression equation was found to be $y = -0.050956 + 0.003079x$ ($r^2 = 0.84$). From this equation, the theoretical lower threshold for development was found to be 16.6°C and the thermal constant 324.8 degree-days. Prediction of the developmental period for cycling temperatures (12 h/12 h at 14/30°C) based on the thermal summation method was found to be 59.6 days. Using a two-sample *t*-test, the mean development under the cycling regime (47.03 days) was not found to be significantly different to twice that at 30°C (50.3 days). The proportion of the developmental period allocated to each immature stage was found to be similar at each temperature to the data for 26°C, as shown in Figure 2. Only four instars were observed during the course of this experiment.

A selection of results of the glasshouse trials are presented in Table 2, which shows that *C. nigritus* was able to complete its life cycle throughout the year under glasshouse conditions at Wye, although, as would be expected, the developmental period was much longer during the winter months. No significant differences were found between the accuracy of predictions from the accumulated heat method and that of the polynomial method ($t_{30} = 0.903$). However, there was a trend for the latter to be more accurate than the accumulated heat method. Mean differences from the predicted were +0.688 days for the polynomial ($n = 16$) and +3.50 days for the accumulated heat method ($n = 16$).

Survival

The analysis of overall mortality data and pooled data on the differential survival among the various stages under laboratory conditions is presented in Table 1 and shows that immature beetles were more likely to die at (and below) 20°C than at any other temperature. First instar larvae suffered the highest mortality levels, while the pupal stage had the highest survival rate. There were no significant differences in the sex ratios of surviving beetles at any of the

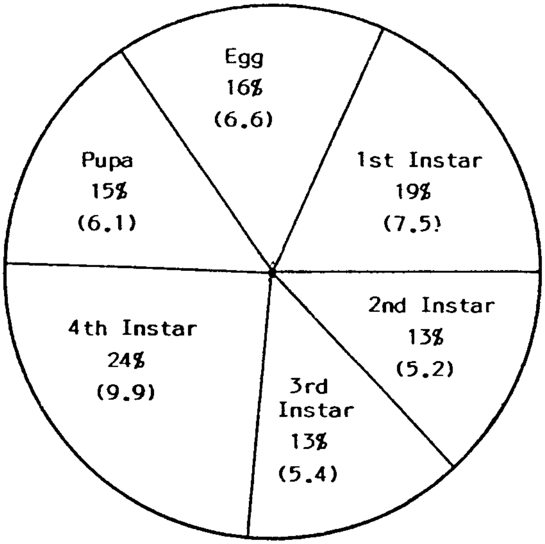

FIGURE 2. Mean developmental period (days) as a percentage of total development of the various immature stages of *C. nigritus* at 26°C and 62% RH ($n = 82$ at the start of the trial).

temperatures tested, although the overall sex ratio was significantly different to 1:1, favouring females at 1.47:1 (59.6%; $n = 178$) ($P < 0.025$ – χ^2 goodness-of-fit test).

DISCUSSION

As with numerous other studies on the effects of temperature on development, increasing constant temperatures led to an increase in developmental rate which was sigmoidal in shape (Figure 1). However, in this case, the shape of the curve suggested that the temperatures studied were largely within the mid- (linear) range. First instar larvae were unable to survive constant temperatures of 18°C, despite the fact that the theoretical lower threshold for development was found to be 1.4°C below that figure. At the upper extreme, a slowing in the developmental rate was detected at 30°C, but clearly the peak had not been passed and the beetle would certainly be able to tolerate constant temperatures above this level. Studies were not carried out at higher temperatures because the host scale could not survive under those conditions.

TABLE 2. Accumulated heat and polynomial predictions of developmental period (egg to adult) of *C. nigritus* under glasshouse conditions (Wye College Conservatory, August 1992–September 1993)—selected results only

Start date	No. of eggs at start of trial	Survival to adulthood (%)	Mean developmental period (days) (± SD)	Accumulated heat prediction (days) (± residual)	Polynomial prediction (days) (± residual)
20/8	27	26	55 (1.5)	(Sensors faulty)	(Sensors faulty)
18/11	54	12	96 (3.3)	(Sensors faulty)	(Sensors faulty)
25/2	31	32	57 (3.3)	60 (+3)	57 (0)
20/4	41	22	48 (1.9)	49 (+1)	49 (+1)
20/7	53	15	46 (2.3)	48 (+2)	47 (+1)
24/9	38	8	62 (1.0)	70 (+8)	68 (+6)

The fact that development at the cycling temperatures of 14/30°C was not significantly higher than twice that at a constant 30°C indicates that 14°C is at or below the thermal threshold for development. Predictions for this regime, based on the thermal summation method, showed that the theoretical figure was much higher than would be expected (59.6 days as opposed to the observed value of 47.03 days), indicating that 14°C is, indeed, below the thermal threshold and lending support to the theoretical figure of 16.6°C. If 16.6°C is substituted for 14°C in the thermal summation equation, the prediction for development becomes 48.3 days, closely matching the observed figure (although still tending to overpredict, as would be expected with this method which takes no account of the non-linear relationship between developmental rate and temperature at the upper and lower extremes).

The relative duration of the different instars was not affected by differing levels of temperature, and showed that the first instar had only a slightly shorter developmental period to the fourth, while the second and first instars were much shorter in comparison. This result disagrees with studies by Ahmad (1970) and Chazeau (1981), where the first instar duration was found to be much shorter than the fourth but similar to that of the second and third instars. The reasons for this difference may be dietary, since neither of those studies used *A. cyanaphylli* as a host. However, the overall developmental period (egg to adult) agreed closely with that found by Dorge *et al.* (1972) at 27°C, Chazeau (1981) at 28.3°C, Jajali and Singh (1989) at 27°C and Hattingh & Samways (1993) at 26°C, while disagreeing considerably with Moutia and Mamet (1946) at 24.5°C, Ahmad (1970) at 24°C and Greathead and Pope (1977) at 21°C. The reason for the differences in the latter studies is probably due to the fact that most of them were carried out at ambient temperatures with an overall daily mean being quoted, a situation which would not provide valid comparisons with a corresponding constant temperature.

The results of the glasshouse trials showed that both the accumulated heat method and the polynomial method gave predictions which were accurate to within a mean of approximately 10%, closely agreeing with the work of Allsopp (1981) using an algorithm on false wireworms and Tingle and Copland (1988) working with similar models on parasitoids. However, it was slightly more accurate than the results of Goodenough *et al.* (1983) using the accumulated heat and poikilotherm methods (19 and 11% respectively for *Trichogramma pretiosum* Riley reared on *Heliothis virescens* {F.} at 20°C). In the current study, both methods tended to underpredict in the winter months and overpredict during the hottest periods of the year. The accumulated heat method would normally tend towards the opposite of this observation if temperatures were outside the linear portion of the preferred range, overpredicting at lower temperatures and vice versa at the upper extremes. The reasons for the unexpected result in the current study are unclear, but may have been due to temperature differences caused by the juxtaposition of the experimental containers in relation to the temperature sensors. Overprediction in the polynomial method at high temperatures can almost certainly be related to a lack of data on development of *C. nigritus* above 30°C. Thus, where temperatures were above this level, contributions to the total development of the insects would not have been calculated. During a UK summer, temperatures in glasshouses would regularly be above 30°C (as they would be outdoors in tropical and subtropical regions where the beetle is utilized). Thus, any future work on the thermal requirements of the species should concentrate on gathering data at temperatures above this level. Since *A. cyanophylli* was unable to survive under constant temperature regimes above 30°C, either a different species of host scale is required which can survive such extremes, or cycling temperatures may be used to calculate the contribution that the higher temperature makes towards development.

Under laboratory conditions, first instar larvae were found to suffer the highest mortality amongst the immature stages with temperatures at the lower extreme tending to be more harmful (Table 1). Pupae had the highest survival rates, closely followed by second instars. These findings are in close agreement with numerous other studies on coccinellids (see e.g. Kehat, 1967; Hodek, 1973). However, egg survival was very high compared with other studies (e.g. Heidari (1989) where only 50% of *Nephus reunioni* Fürsch eggs were found to be viable), although overall immature survival, even at the most favourable temperature (28°C), was never more than 52%. This figure coincides closely with that of 57% found by Greathead and Pope (1977) for larval mortality in *C. nigritus*, while the overall pattern of survival rate (increasing towards the mid-range and declining at the extremes) is similar to that found for other *Chilocorus* species (Podoler & Henen, 1983).

Under glasshouse conditions, *C. nigritus*, was able to complete its development throughout the year (Table 2). However, survival rates were much lower than those found under laboratory conditions, reaching only 9% during the period October–January, but becoming significantly higher (20%) during the rest of the year ($P < 0.0001 - \chi^2$ contingency table). If *C. nigritus* were to be introduced into glasshouses as eggs (rather than adults), Table 1 suggests that overall mortality rates might be reduced if temperatures were to be maintained at 24–26°C for a short period when the first instar larvae were emerging. Whether higher temperatures were needed until the end of the first stage (10.5 days at 24°C) or whether they could be reduced once the first instars had found their first meal remains the subject of future research.

The female bias in the sex ratio found in this study closely agrees with the findings of Henderson and Albrecht (1988), who reported a similar bias in four Chilocorini (including *C. nigritus* from India) and one Coccinellini species. They hypothesized that since these species possess neo-XY chromosome systems, either the products of recombination are more lethal in males or there is an interaction between the Y-linked chromosomes of maternally inherited factors.

In conclusion, the most favourable constant temperature (in terms of developmental rate and overall immature survival) for *C. nigritus* was found to be in the region of 28 to 30°C, although survival was possible at temperatures of 20°C and above. This suggests that this species would be suitable for use as a biological control agent in temperate glasshouses provided the mean temperature was held at or above 20°C. Similarly, successful use of this predator in classical biological control programmes (or for inundative release in unprotected situations) is only indicated where mean daily temperatures are at or above this figure for a significant period of time during the period of peak pest activity.

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