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Temperature dependence for development of the whitefly predator *Clitostethus arcuatus* (Rossi)

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Abstract This work aimed to study the biology of *Clitostethus arcuatus* (Rossi) (Coleoptera: Coccinellidae) under different temperatures and evaluate the optimum temperature for its mass rearing. Studies were carried out in the laboratory at four constant temperatures (15°C, 20°C, 25°C and 30°C), 75 ± 5% relative humidity and a photoperiod of 16 h light:8 h dark, in which *C. arcuatus* was fed *ad libitum* with nymphs of all instar of *Aleyrodes proletella* L. (Homoptera: Aleyrodidae) on *Brassicae oleracea* L. (var. *Costata*). The following biological parameters were evaluated: development time and survival rates of pre-imaginal stages, adult longevity (female and male), length of the pre-oviposition and oviposition periods, fecundity, fertility and percentage of egg hatching. Population growth parameters, the lower development threshold and the sum of effective temperatures were estimated. Temperatures ranging from 20°C to 30°C were suitable for the development of *C. arcuatus*, suggesting that this species is well adapted to the temperatures usually found inside greenhouses or in open fields in temperate regions. Although the intrinsic rate of natural increase and doubling time were similar at 25°C and 30°C, the temperature of 25°C was shown to be the most suitable for mass rearing and development of populations under field conditions, since the percentage of egg hatching and the accumulated survival rates of the pre-imaginal stages were the highest. Considering the estimated lower threshold for pre-imaginal development (7.9°C) and the sum of effective temperatures [293.6 degree-days (°D)], it is predicted for Ponta Delgada (Azores, Portugal) that the first adults of *C. arcuatus* should emerge by the first fortnight of February and that up to 12 generations per year can occur.

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Introduction

Some whitefly species are considered to be major pests, by inflicting important crop losses worldwide, especially to horticultural plants in greenhouses (Mound and Halsey 1978; Evans and Castillo 1998; Katsoyannos et al. 1998; Martin 1999; Symondson et al. 1999; Liang and Liu 2002). The damages are caused by the insects' direct feeding, which implies the extraction of large amounts of phloem sap. In consequence, there is a decrease of plant vigour and a great excretion of honeydew that serves as a medium for the development of black sooty mould fungi, which, in turn, interfere with photosynthesis. In addition, those whiteflies are involved in transmission of several plant viruses (Drost et al. 1998; Symondson et al. 1999; Viscarret et al. 2000; Liang and Liu 2002).

Among the Aleyrodidae found in the Azores, the citrus whitefly *Aleurothrixus floccossus* (Maskell), the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) and the cabbage whitefly *Aleyrodes proletella* L. (Homoptera: Aleyrodidae), are the most abundant species. In the Azores *A. proletella* is only referred for S. Miguel and Terceira islands (Borges et al. 2005). This species is also present in mainland Portugal (Guimarães 1996) and in several European countries (Mound and Halsey 1978).

The strategy of using chemical control has been proven to be ineffective, due to the whiteflies' great reproductive potential, the difficulty of the growers to detect the small and translucent nymphs in the early stages of infestations and the negative impacts on biological control agents. Moreover, generally, the insecticides are not equally effective over all developmental stages of the insects (Wagner et al. 1991); therefore, it is very difficult to synchronize the spraying of insecticides with the specific developmental stage present on the crop. The increasing problems driven from chemical pesticides have led to a rising interest in classical biological control and integrated pest management (IPM) to control whitefly populations. The introduction of exotic natural enemies to control whitefly may be a possible strategy, but a number of studies have revealed that introduced species may affect the dynamics and the composition of native guilds, as the invaders may interact with them, directly or indirectly, including through intraguild predation (IGP) (Secord and Kareiva 1996; Evans 2004; Lucas 2005; Soares and Serpa 2007). Since biological invasions are considered to be the second greatest cause of global biodiversity loss after direct habitat destruction (Pimentel et al. 2000; Labrie et al. 2006), and, in small and isolated islands the lower species richness and abundance than in continental ecosystems increase the risk of biodiversity loss (Van Driesche and Hoddle 1997), the use of native natural enemies instead of the introduction of new species is strongly recommended.

Recent results on the suitability of the cabbage whitefly as prey for *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae), a predator present in the Azores, showed that this ladybird beetle did not thrive on *A. proletella* and, therefore, should not be used as a main biological control agent against this pest (Cabral et al. 2006).

Considering the above-mentioned reasons, we have selected another predator, also present in the Azores, that feeds primarily on whiteflies, the ladybird beetle *Clitostethus arcuatus* (Rossi) (Coleoptera: Coccinellidae) (Fürsch 1987; Soares et al. 2003; Borges et al. 2005). This species is widespread over central and meridional Europe, the Mediterranean region, Asia and North America (Raimundo and Alves 1986).

This study aimed to determine the effects of constant temperatures (15°C, 20°C, 25°C and 30°C) on biological and population growth parameters of the predator and to evaluate the optimum temperature for mass rearing of *C. arcuatus.* Thermal requirements for development were also determined so that we could estimate the annual number of generations that this species can achieve in its natural habitat.

Material and methods

Insects

Clitostethus arcuatus adults were collected on S. Miguel Island, Azores, Portugal, early in the summer before the experiments took place. Ladybird beetles were reared on a tritrophic system (host plant *Brassicae oleracea* L. (var. *Costata*); prey *A. proletella*; predator *C. arcuatus*), inside a climate chamber at 25 ± 1°C, 75 ± 5% relative humidity and a photoperiod of 16 h light:8 h dark (16L:8D) using fluorescent lamps (Phillips TDL 23W/54 and TDL18W/54).

Biological parameters

The methodology used in this study was adapted from Soares et al. (2001). All experiments were done inside climate chambers at constant temperatures of 15°C, 20°C, 25°C and 30°C. Photoperiod was maintained at 16L:8D, while relative humidity was kept at 75 ± 5% inside each climate chamber.

For each temperature, at least 20 eggs of *C. arcuatus* (obtained from adults of the tritrophic rearing system) were isolated inside Petri dishes (ø 5 cm, height 3 cm). Upon hatching, neonate larvae were fed *ad libitum* with mixed instar nymphs of *A. proletella* provided on cabbage leaves. Every 2 days, the food supply was replaced until adult emergence. To determine the pre-imaginal development times and accumulated survival rates, we observed individuals from egg to adult twice a day (09:00 h and 17:00 h).

To evaluate the longevity and reproductive parameters of the adults, we sexed and paired ($N = 20$) newly emerged individuals. Each pair was placed inside a 60 ml Petri dish (ø 5 cm, height 3 cm) and fed *ad libitum* with mixed instar nymphs of *A. proletella* provided on cabbage leaves. Every day, the food supply was replaced until the death of the adults. Each couple was observed daily so that we could record their longevity, the length of pre-oviposition and oviposition periods and the fecundity (number of laid eggs). The fertility (number of eggs with embryos) and percentage of egg hatching (percentage of eggs with embryos that hatched) were determined.

Population growth parameters

For each temperature, the following population growth parameters were estimated: the net reproductive rate ($R_0 = \Sigma\, l_x\, m_x$), the mean generation time (T), the intrinsic rate of natural increase ($r_m = \ln R_0 (T)^{-1}$), the finite rate of increase ($\lambda = e^{r}$) and the doubling time (DT

= $\ln 2/r_m$). The l_x corresponds to the age-specific survival of the females and the m_x to the age-specific fertility (= born larvae/female). The expected number of larvae produced per female each day ($l_x m_x$) was also estimated (Southwood and Henderson 2000; Vasicek et al. 2004; Kontodimas and Stathas 2005).

Thermal requirements

The lower development threshold (LDT) and the sum of effective temperatures (SET) were estimated using the development times of the pre-imaginal stages at each constant temperature (15°C, 20°C, 25°C and 30°C). It was assumed that, within the interval of temperatures favourable for the insects' development, the relationship between the inverse of the development time (development rate) and the temperature is nearly linear (Honěk and Kocourek 1990). According to this, the following linear relationship was considered:

$$1/DT = aT + b$$

where DT corresponds to the development time of the pre-imaginal, which is inversely proportional to the temperature (T), and a and b are the regression parameters. The LDT corresponds to T, when no development occurs, that is, when $1/DT = 0$ (Honěk and Kocourek 1988). The SET [degree-days (°D)] was calculated according to the following expression:

$$\begin{aligned} \mathrm{SET} = \{&[\mathrm{DT}_{15}(15 - \mathrm{LDT}_{15})] + [\mathrm{DT}_{20}(20 - \mathrm{LDT}_{20})] + [\mathrm{DT}_{25}(25 - \mathrm{LDT}_{25})] \\ &+ [\mathrm{DT}_{30}(30 - \mathrm{LDT}_{30})]\}/4 \end{aligned}$$

where DT_x is the development time at temperature x and LDT_X is the lower development threshold for the temperature x.

To estimate the number of generations of *C. arcuatus* that can occur in Ponta Delgada (Azores, Portugal), we used calendar monthly averages of temperature resulting from 12:00 GMT daily readings recorded during a 30-year period (1951–1980) provided by the Institute of Meteorology/Azores.

Statistical analysis

To correct heteroscedasticity, data regarding pre-imaginal development time, adult longevity, and pre-oviposition and oviposition periods were transformed by log (x), and fecundity and fertility data by log (x + 1) prior to analysis of variance (ANOVA) (Hill and Hill 2002). Where statistical differences existed between data sets ($P < 0.05$), Fisher's least significant difference (LSD) tests were used to separate the differing means. Accumulated survival rates (from egg to adulthood) and percentage of egg hatching were analysed by the multiple comparison test for proportions, where significant results are represented by giving a $q_{0.05,\infty,4}$ value > 3.633 (Zar 1996). All analyses were performed with SPSS, 12.0.1 for Windows (SPSS 2004). The values displayed are regular averages and standard errors.

Results

Biological parameters

Within the range of temperatures tested, and with the exception of the third and fourth larval stages reared at 25°C and 30°C, the pre-imaginal development times decreased significantly with temperature increase, the total time of development being longer at 15°C (44.3 ± 2.25 days) and shorter at 30°C (13.2 ± 0.58 days) (Table 1).

Accumulated survival rate was significantly higher at the temperature of 25°C (56%) than at the other temperatures ($q = 7.32$, $q = 6.15$ and $q = 9.15$, $P < 0.05$, respectively for 15/25°C, 20/25°C and 25/30°C comparisons). No significant differences (all $P > 0.05$) were observed between accumulated survival rates at 15°C (21%), 20°C (26%) and 30°C (14%) (Fig. 1).

Adult male mean longevity was significantly higher at 15°C, but it did not differ significantly between the other temperatures tested (Table 2). Adult female mean longevity also decreased with temperature increase, being significantly higher at 15°C than was the longevity observed at 25°C and 30°C (Fig. 2, Table 2). Independently of temperature and age, the age-specific survival curve of females (l_x) showed a constant rate of mortality corresponding to a typical type II hypothetical survivorship curve (Fig. 2).

The pre-oviposition period decreased significantly with temperature increase, while oviposition period was significantly higher at 20°C than at the other temperatures. Fecundity did not differ significantly between the temperatures of 20°C, 25°C and 30°C, but it was significantly lower at 15°C (Table 2). However, the expected number of larvae produced per female each day ($l_x m_x$) differed between all temperatures: at 15°C the females maintained a constant and low rate of larvae production, while at 25°C and 30°C the

Table 1 Pre-imaginal development times (days ± SE) of *C. arcuatus* under different constant temperatures (15°C, 20°C, 25°C and 30°C). *L1, L2, L3* and *L4* first, second, third and fourth larval stages, respectively, *PP* + *P* pre-pupa and pupa, *N* size of the cohort

Pre-imaginal stages	Temperature (°C)				ANOVA
	15 $N = 22$	20 $N = 24$	25 $N = 33$	30 $N = 42$	
Egg	11.1 ± 0.12a*	5.1 ± 0.08b	3.8 ± 0.07c	3.1 ± 0.04d	$F_{(3, 117)} = 1156.052$; $P \leq 0.0001$
L1	6.1 ± 0.31a	2.8 ± 0.11b	1.8 ± 0.06c	1.6 ± 0.08d	$F_{(3, 69)} = 154.897$; $P \leq 0.0001$
L2	3.3 ± 0.19a	2.1 ± 0.20b	1.3 ± 0.09c	1.0 ± 0.09d	$F_{(3, 53)} = 40.538$; $P \leq 0.0001$
L3	3.9 ± 0.1a	2.3 ± 0.12b	1.9 ± 0.16c	1.7 ± 0.37c	$F_{(3, 45)} = 13.302$; $P \leq 0.0001$
L4	8.9 ± 0.21a	5.2 ± 0.21b	3.8 ± 0.27c	3.1 ± 0.41c	$F_{(3, 38)} = 31.607$; $P \leq 0.0001$
PP + P	12.3 ± 0.25a	5.8 ± 0.11b	4.3 ± 0.06c	3.5 ± 0.22d	$F_{(3, 25)} = 152.465$; $P \leq 0.0001$
Total	44.3 ± 2.25a	22.3 ± 0.48b	17.2 ± 0.41c	13.2 ± 0.58d	$F_{(3, 25)} = 111.449$; $P \leq 0.0001$

* Means in each row followed by different letters are significantly different at $P < 0.05$ (LSD tests)

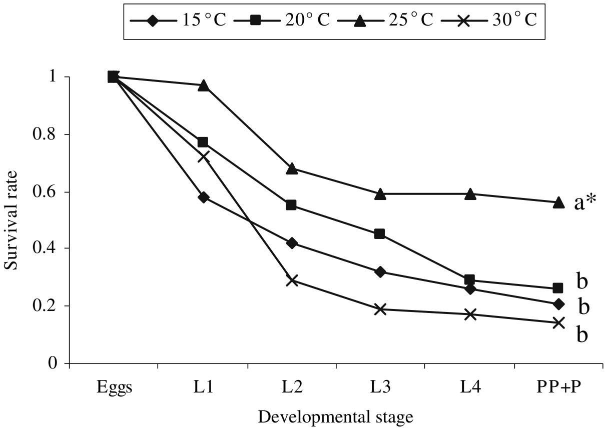


Fig. 1 Survival rates of *C. arcuatus* pre-imaginal stages under different constant temperatures (15°C, 20°C, 25°C and 30°C). *L1, L2, L3* and *L4* first, second, third and fourth larval stages, respectively, *PP + P* pre-pupa and pupa. *Values with different letters are significantly different at $P < 0.05$ (multiple comparison tests for proportions)

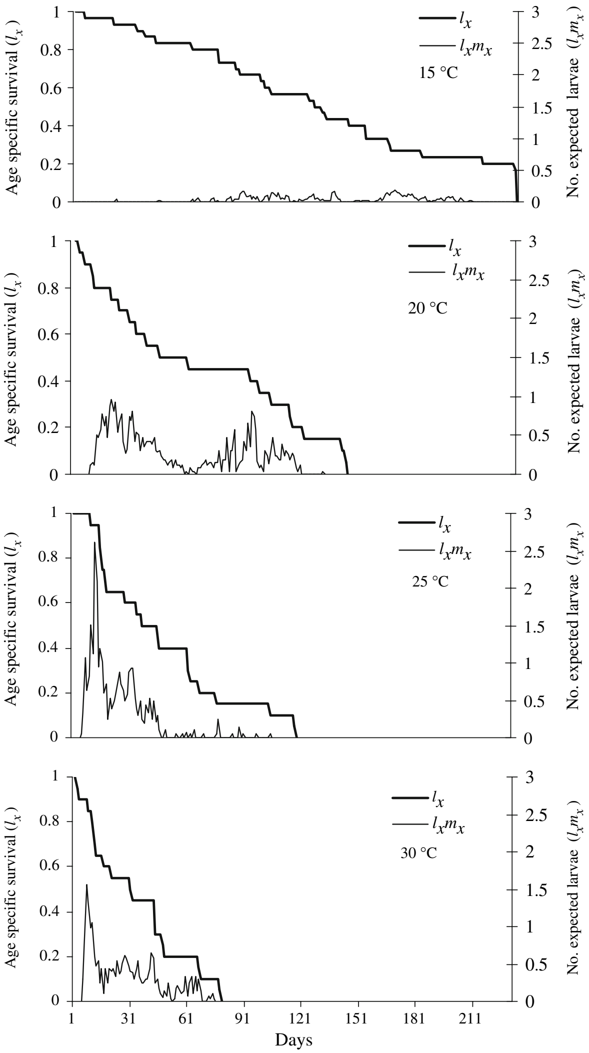
Table 2 Adult longevity and reproductive parameters of *C. arcuatus* under different constant temperatures (15°C, 20°C, 25°C and 30°C). $Fec_{(oviposition\ period/2)}$ and $Fer_{(oviposition\ period/2)}$ observed fecundity and fertility during half of the oviposition period, respectively, *fecundity* number of laid eggs ± SE, *fertility* number of hatched eggs ± SE and *percentage of egg hatching* percentage of eggs with embryos that hatched ± SE, *N* size of the cohort

Parameters	Temperature (°C)				ANOVA
	15 $N = 20$	20 $N = 20$	25 $N = 20$	30 $N = 20$	
Longevity					
Females	149.4 ± 22.2a*	86.7 ± 12.9ab	48.8 ± 8.0bc	33.6 ± 5.6c	$F_{(3,\ 61)} = 8.149$ $P \leq 0.0001$
Males	153.8 ± 21.3a	65.3 ± 15.4b	56.3 ± 8.9b	51.9 ± 7.4b	$F_{(3,\ 64)} = 5.48$; $P = 0.002$
Pre-oviposition period	81.8 ± 6.0a	20.2 ± 6.3b	9.2 ± 0.8c	5.7 ± 0.3d	$F_{(3,\ 69)} = 157.325$; $P \leq 0.0001$
Oviposition period	35.5 ± 9.6a	49.8 ± 10.1b	28.9 ± 5.6a	27.8 ± 5.0a	$F_{(3,\ 67)} = 2.155$; $P = 0.101$
Fecundity (Fec)					
Total	12.3 ± 4.4a	44.6 ± 12.7b	31.2 ± 5.6b	33.8 ± 7.6b	$\mathrm{F}_{(3,\ 86)} = 6.482$: $P = 0.001$
$\mathrm{Fec}_{(\mathrm{oviposition\ period/2})}$	3.9 ± 1.7a	21.9 ± 6.1b	17.7 ± 3.0b	16.1 ± 3.5b	$F_{(3,\ 86)} = 10.22$; $P \leq 0.0001$
Fertility (Fer)					
Total	7.2 ± 2.5a	34.5 ± 9.8b	30.3 ± 5.4b	24.5 ± 5.5b	$F_{(3,\ 86)} = 9.177$; $P \leq 0.0001$
$\mathrm{Fer}_{\ (\mathrm{oviposition\ period/2})}$	2.3 ± 1.0a	17.0 ± 4.7b	17.2 ± 2.9b	11.7 ± 2.5b	$F_{(3,\ 86)} = 13.471$; $P \leq 0.0001$
Percentage of egg hatching	57.89a	77.42b	97.06c	72.41ab	**

* Means in each row followed by different letters are significantly different at $P < 0.05$ (LSD tests)

** Percentages in this row followed by different letters are significantly different at $P < 0.05$ (multiple comparison test for proportions)

Fig. 2 Expected number of larvae of *C. arcuatus* produced per female each day ($l_x m_x$) under different constant temperatures (15°C, 20°C, 25°C and 30°C). l_x age survival rate, m_x age-specific fertility



number of expected larvae peaked during the first 15 days of their lives; at 20°C two peaks of larvae production were identified (Fig. 2).

Percentage of egg hatching was significantly higher at 25°C (97.06%) than at the other temperatures ($q = 10.46$, $q = 6.28$ and $q = 7.43$, $P < 0.05$, respectively for 15/25°C, 20/25°C and 25/30°C comparisons).

Population growth parameters

The net reproductive rate (R_0) was higher when *C. arcuatus* was maintained under 20°C; However, the intrinsic rate of natural increase (r_m) and the finite rate of increase (λ) were

Table 3 Population growth parameters of *C. arcuatus* fed on *A. proletella* under different constant temperatures (15°C, 20°C, 25°C and 30°C). R_0 net reproductive rate, r_m intrinsic rate of natural increase, λ finite rate of increase, *T* mean generation time, *DT* doubling time

Parameters	Temperature (°C)			
	15	20	25	30
R_0	7.08	34.07	29.64	23.74
r_m	0.02	0.08	0.14	0.16
λ	1.02	1.08	1.15	1.18
T	99.57	45.05	23.61	19.62
DT	35.26	8.85	4.83	4.29

higher and the doubling time (DT) was lower at the rearing temperatures of 25°C and 30°C (Table 3).

Thermal requirements

Within the range of temperatures tested, the LDT (°C) and the SET (°D) for *C. arcuatus* were effectively determined by the linear model, as shown by the high coefficients of determination obtained for all the developmental stages (all $R^2 > 0.94$) (Table 4). The lower development thresholds of *C. arcuatus* pre-imaginal stages ranged from 1.7°C (third larval stage) to 9.1°C (first and second larval stages); for the total pre-imaginal development it was 7.9°C (Table 4).

The number of degree-days required for the development of each pre-imaginal stage ranged from 20.9°D (second larval stage) to 75.5°D (pre-pupa and pupa), and to complete the development from egg to adult emergence it was 293.6°D (Table 4).

Table 4 Lower development threshold (*LDT*) and sum of effective temperatures (*SET*) required for the development of the different pre-imaginal stages of *C. arcuatus*, with the respective coefficient of determination (R^2), slope (*a*) and intercept (*b*). *L1, L2, L3* and *L4* first, second, third and fourth larval stages, respectively, *PP* + *P* pre-pupa and pupa

Pre-imaginal stages	Td = a temperature + b		R^2	LDT (°C)	SET (°D)
	a	b			
Egg	0.0153	−0.1261	0.98	8.2	66.5 ± 3.2
L1	0.0316	−0.2863	0.96	9.1	32.3 ± 1.7
L2	0.0477	−0.4357	0.99	9.1	20.9 ± 0.7
L3	0.0217	−0.0377	0.94	1.7	46.5 ± 2.1
L4	0.014	−0.0931	0.99	6.7	71.5 ± 1.2
PP + P	0.0135	−0.11	0.98	8.1	75.5 ± 3.3
Total pre-imaginal	0.0035	−0.0275	0.99	7.9	293.6 ± 9.3

Discussion

Environmental temperature is one of the most important factors determining physiological process on poikilothermic species (Honěk and Kocourek 1990; Chapman 1998). Temperature determines the biological performances of insects, such as development time of pre-imaginal stages, life expectation and reproductive parameters of the adults (e.g. fecundity, fertility and percentage of egg hatching), having by this way a differential contribution of each single individual for the population growth (Perdikis and Lykouressis 2002; Kontodimas and Stathas 2005; Cabral et al. 2006). The estimation of the performances of natural enemies, including development time, temperature thresholds, thermal constant and population growth parameters, can contribute to the selection of the most suitable biological control agent to be used under different environmental conditions (Perdikis and Lykouressis 2002), as well to set the best thermal condition for insect mass rearing.

Our results showed that total development time of *C. arcuatus* pre-imaginal stages significantly decreased with increasing temperature, as expected within the range of favourable temperatures. Furthermore, regardless of temperature, the proportion of the development time of eggs ranged between 22% and 25%, of L1–L4 it ranged between 50% and 56% and of pre-pupa and pupa it ranged between 25% and 29%. These results are consistent with the suggestion that the proportion of the development time of pre-imaginal stages for ladybird beetles is typical of each stage and independent of temperature (Hodek and Honěk 1996; Dixon 2000).

The development times of pre-pupa and pupa and of the fourth larval stage were higher than those of the other pre-imaginal stages. Liotta (1981) obtained similar results when studying this species under field conditions in Sicily. Bellows et al. (1992), using a population from Israel fed with *Siphoninus phillyreae* (Haliday) (Homoptera: Aleyrodidae) nymphs and the experimental temperatures of 21.1°C, 28.2°C and 32.2°C, also achieved similar results. The same trend of pre-imaginal development time was observed for other Coccinellidae (Coleoptera), such as *Harmonia axyridis* Pallas (Schanderl et al. 1985), *Coccinella septempunctata* L. and *Hippodamia convergens* Guerin-Meneville (Michels and Behle 1991) and *Coccinella trifasciata* LeConte (Harris) (Miller and LaMana 1995).

Accumulated survival rates of *C. arcuatus* pre-imaginal stages were higher at 25°C and lower at 15°C and 30°C. Bellows et al. (1992) reported for *C. arcuatus* higher rates of survival at 28.2°C (~80%) and 32.2°C (~40%) in contrast to our results at 30°C (14%). Although the diets provided in both studies are distinct, the results obtained suggest a possible acclimation of the Azorean populations to the mild environmental temperatures of this archipelago, since the highest survival rate was observed at 25°C.

The fecundity of *C. arcuatus* was higher at 20°C, while Bellows et al. (1992) observed that the fecundity of this species peaked at 28.2°C. Furthermore, although the percentage of egg hatching varied among the temperature tested, no trend in the variation was observed in the current study, while Bellows et al. (1992) reported a decrease in egg hatching rates with increasing temperatures. Again, these discrepancies could be explained by the possible acclimation of the Azorean populations to the temperatures usually found in their natural habitats that fall into the range of temperatures tested in this study.

According to Hodek and Honěk (1996), the decrease of the pre-oviposition period with temperature increase is a common trend among coccinellid females that do not undergo diapause. The pre-oviposition period of *C. arcuatus* at 15°C was much longer than at the other temperatures. One possible explanation for this fact may be related to the thermal requirements for egg maturation in *C. arcuatus*, suggesting that oviposition and reproduction may be negatively affected at temperatures beneath 15°C.

Considering the estimated lower threshold for pre-imaginal development (7.9°C) and the sum of effective temperatures (293.6°D), we predict for Ponta Delgada (Azores, Portugal) that the first adults of *C. arcuatus* should emerge during the first fortnight of February and that up to 12 generations per year can occur.

The intrinsic rate of natural increase (r_m) and the finite rate of increase (λ) were higher at 30°C and lower at 15°C; nevertheless, the values of these rates were quite similar at 25°C and 30°C. The net reproductive rate (R_0) was higher at 20°C and much lower at 15°C. Bellows et al. (1992) estimated for *C. arcuatus* a maximum net reproductive rate (R_0) at 28.2°C (79.18 descendants per female in each generation), which is higher than the obtained in the current study. This discrepancy can be explained by the different nutritional quality of diets provided in both studies. According to several studies, essential foods show varying degrees of favourability to coccinellids, enabling different development rates, survival and fecundity, factors that limit the capacity of a population to grow (Dixon 2000; Soares et al. 2004; Cabral et al. 2006).

Despite r_m, T, λ and DT values being quite similar at 25°C and 30°C, the fact is that *C. arcuatus* at 25°C displays higher larval survival rates, male and female longevities, percentage of egg hatching and number of expected larvae during the first 15 days of its life. For these reasons the optimum temperature for mass rearing of *C. arcuatus*, using *A. proletella* as prey and *B. oleracea* as host plant, is considered to be 25°C. In general the results obtained reveal that *C. arcuatus* is well adapted to temperatures between 20°C and 30°C, which are quite frequent inside greenhouses and open horticultural crops in Azores.

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