

# Life History of *Podisus maculiventris* (Heteroptera: Pentatomidae) Adult Females Under Different Constant Temperatures

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**ABSTRACT** Life table analysis was performed on *Podisus maculiventris* (Say) adult females at constant temperatures of 16, 26, 30, and 36°C. Survivorship curves were linear type II, with steeper rates of decline at higher temperatures. Longevity at 16°C (47.2 d) was significantly longer than that at 26°C (14.3 d) or 30°C (12 d). Adults under the 36°C survived only 4.9 d and laid no eggs. Percentage of eggs that hatched was relatively constant at  $\approx$  or about 40% at 16, 26, and 30°C. Numbers of egg clutches (ranging from 5.9 to 9.4), eggs per clutch (13.6–14.6), and eggs in the first clutch (9.0–15.1) did not differ significantly at these three temperatures. However, preoviposition period was significantly longer at 16°C (20.3 d) than at 26°C (6.3 d) and 30°C (4.9 d). Number of eggs laid was related to body weight by the equation  $E = -139.1 + 3.49w$ , where  $E$  is number of eggs laid per female lifetime, and  $w$  is the weight of the predator female. Life table analysis of *P. maculiventris* female adults showed that both net reproductive rate ( $R_0$ ) and gross reproductive rate ( $GRR$ ) were highest at 26°C, estimated at 47.8 and 156.0 females per female, respectively. However, the shorter generation times at 30°C ( $T = 42.2$  d) resulted in higher values for the intrinsic rate of increase ( $r = 0.09$ ), the finite rate of increase ( $\lambda = 1.09$ ), and doubling time ( $DT = 7.7$  d). Analysis of cumulative egg production suggests that 26°C may be more suitable for maintaining colonies of *P. maculiventris* because of the sustained levels of egg production over a longer period, compared with the 30°C treatment.

**KEY WORDS** *Podisus maculiventris*, life history, life table

THE SPINED SOLDIER BUG, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae), is endemic throughout North America and has been recorded in various crops, including soybean, *Glycine max* (L.) Merr.; alfalfa, *Medicago sativa* L.; and corn, *Zea mays* L. *P. maculiventris* is a polyphagous predator known to feed on >75 insect species (McPherson 1980, McPherson et al. 1982), several of which are important pests (Waddill and Shepard 1975, Lopez et al. 1976). A considerable body of knowledge has been developed on the effects of different feeding regimens on its life history, its reproduction, and trade-offs that occur under both laboratory and field conditions (Legaspi and O'Neil 1993, Wiedenmann et al. 1996, Legaspi and Legaspi 1998). Research has included both theoretical aspects of predator search and functional response (Wiedenmann and O'Neil 1991, 1992), as well as practical use of *P. maculiventris* in applied biological control programs (O'Neil et al. 1996, O'Neil 1997). However, limited information exists on life tables of this

predator, and how they may be affected by temperature.

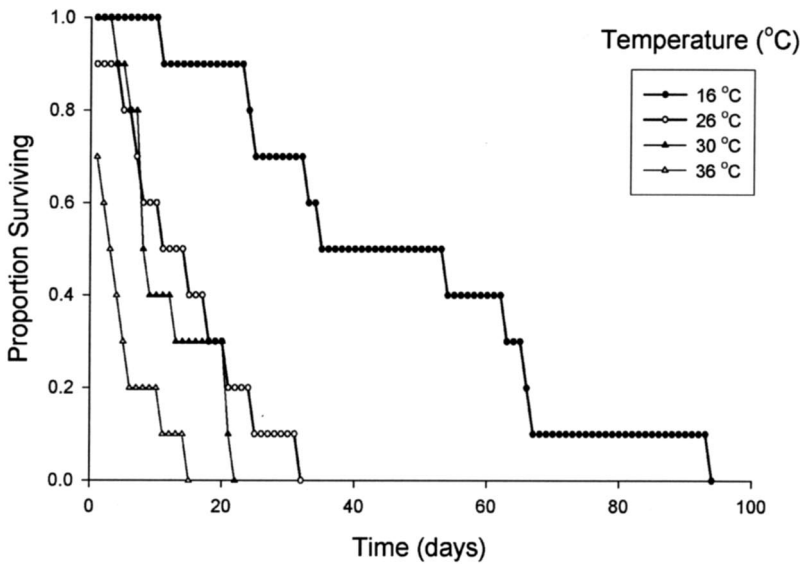
Life table analysis is a standard ecological method for estimating demographic parameters related to population dynamics. Computational methods for constructing life tables and estimating key reproductive parameters date back several decades (Birch 1948). Numerous published examples illustrate the practical use of life table analyses (Maia et al. 2000). More specifically, life tables facilitate the analysis and understanding of insect population dynamics and the effects of external factors, such as biological control agents (Wittmeyer and Coudron 2001). In this study, I present life table analyses of *P. maculiventris* female adults under four constant temperatures using as prey the greater wax moth, *Galleria mellonella* (L.) (Lepidoptera: Pyralidae).

## Materials and Methods

**Effects of Temperature on Survivorship and Longevity.** *P. maculiventris* used in the experiment were obtained from a laboratory colony at USDA-ARS-CMAVE/Florida A&M University Center for Biological Control in Tallahassee, FL. Newly emerged to 3-d-old *P. maculiventris* adult females were placed

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A: Survivorship Curves for *Podisus maculiventris*



B: Effect of temperature on longevity

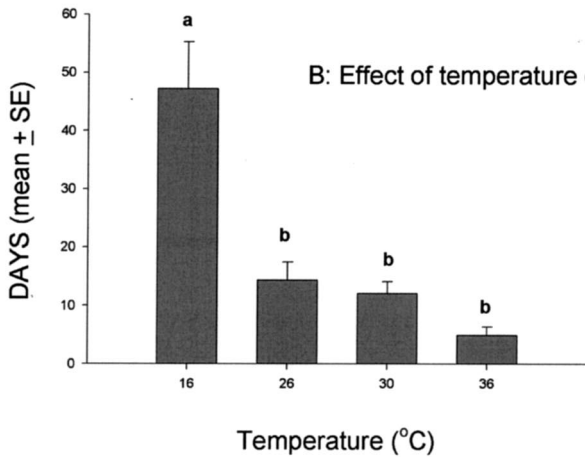


Fig. 1. (A) Survivorship curve of adult *P. maculiventris* as affected by temperature. (B) Effect of temperature on longevity ( $F = 17.3$ ;  $df = 3, 36$ ;  $R^2 = 0.59$ ;  $P < 0.01$ ). Different letters indicate means are significantly different at  $P = 0.05$  (Tukey's HSD).

individually into petri dishes (15 cm in diameter) lined with filter paper, and starved for 24 h before the start of the experiment. They were then provided daily with five fourth to fifth instars of *G. mellonella* (Rainbow Mealworms & Crickets Co., Compton, CA) as prey. The average weight of the prey was  $321.96 \pm 11.59$  (SE) mg and the mean length was  $2.62 \pm 0.05$  (SE) cm. A water source consisted of a cotton ball dipped in water and placed in a small dish (3.5 cm in diameter). Body weights were recorded at the start of the experiment by using a Sartorius analytical balance (model BP221S, Sartorius Corp., Edgewood, NY) with a precision of  $\pm 0.0001$  g, and weights were recorded at 5-d intervals until death. A young male (5–10 d old)

was placed into each dish for a period of 3–4 d each week to permit mating. Numbers of eggs laid and *P. maculiventris* females dying were recorded daily until all females had died. All egg masses were removed, counted, and held until hatching at laboratory ambient temperature of 24–25°C. Egg hatch occurred on average after 5 d. Numbers of eggs that hatched were recorded and percentage hatching was calculated. Each petri dish containing a single female was considered one replicate. Ten replicates were used for each of four temperatures: 16, 26, 30, and 36°C. Constant temperature conditions were maintained inside ThermoForma model 3740 growth chambers (ThermoForma, Marietta, OH) with a photoperiod of 14:10

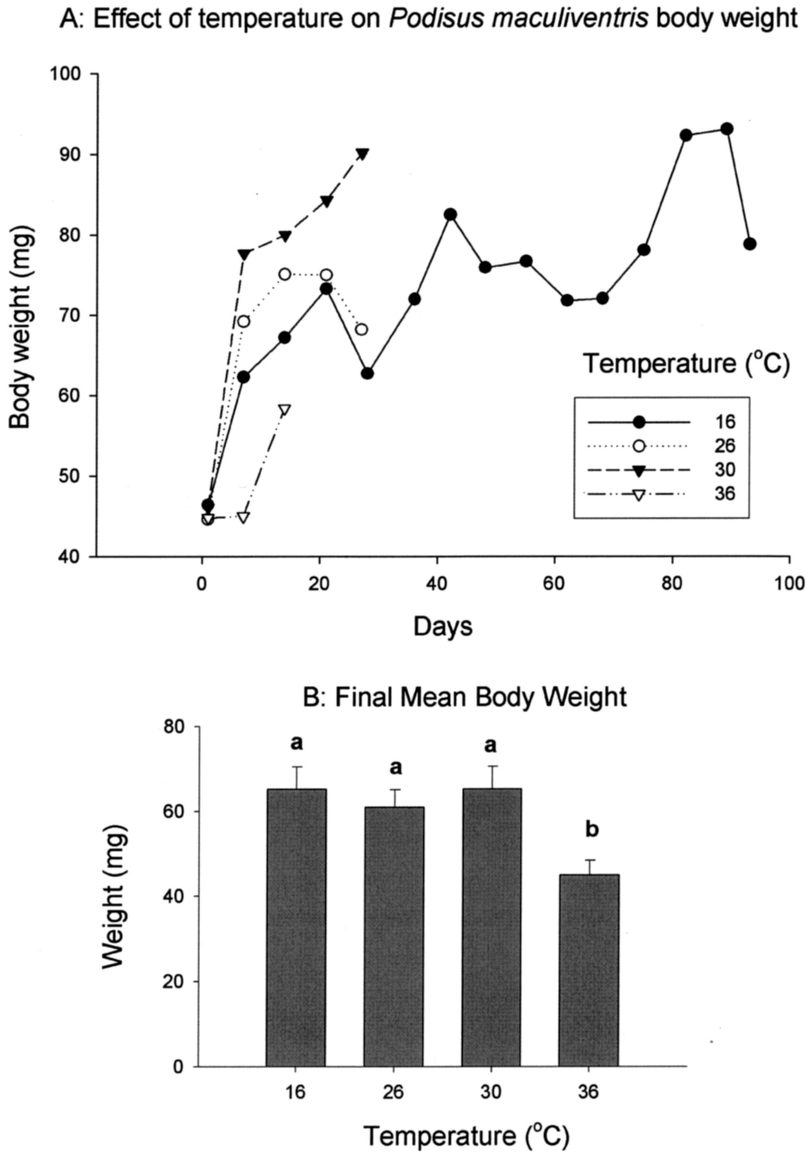


Fig. 2. (A) Effect of temperature (°C) on body weight (milligrams) of adult female *P. maculiventris*. (B) Final mean body weight ( $\pm$ SE) by temperature ( $F = 4.35$ ;  $df = 3, 36$ ;  $R^2 = 0.27$ ;  $P = 0.01$ ). Means with different letters are significantly different at  $P = 0.05$  (Tukey's HSD).

(L:D) h and mean of 60% RH. Temperature and relative humidity inside each chamber were monitored by HOBO recorders (Onset Computer Corp., Bourne, MA).

**Life Table Calculations.** Numerical methods for calculating life history parameters may be obtained from standard biological texts (Southwood and Henderson 2000, Begon et al. 1990) and have been applied for many insect species (Medeiros et al. 2000). The net reproductive rate ( $R_0$ ) is the mean number of female progeny produced by a single female during its mean lifetime and was calculated as follows:

$$R_0 = \sum_{x=0}^n l_x m_x \quad [1]$$

where  $x$  is age group,  $l_x$  is probability of surviving to age  $x$ ,  $m_x$  is age-specific fecundity, and  $n$  is the number of age groups. In this study, number of eggs laid at each age group was divided by 2, to estimate number of eggs that would result in females. This is probably a conservative estimate of female sex ratio, because field studies suggest that natural populations are  $\approx 65\%$  female (Legaspi et al. 1996). The Gross reproductive

rate (*GRR*), also expressed in units of number of females per female, was calculated as follows:

$$GRR = \sum_{x=0}^n m_x \quad [2]$$

The generation time (*T*) is an estimate in days of the mean period between birth of the parents and that of the offspring and was calculated as follows:

$$T = \left( \sum_{x=0}^n x l_x m_x \right) / R_0 \quad [3]$$

An approximate estimate for the intrinsic rate of increase (*r*), expressed in numbers of females per female per day, was calculated as follows:

$$r = \frac{\ln(R_0)}{T} \quad [4]$$

The finite rate of increase, also expressed in females per female per day, was estimated as follows:

$$\lambda = \exp(r) \quad [5]$$

Doubling time (*DT*) is the estimated time in days required for the population to double and was calculated as follows:

$$DT = \frac{\ln(2)}{r} \quad [6]$$

**Statistical Analyses.** All statistical tests were performed using Systat 10 software (Systat Software, Inc., Richmond, CA). The effects of temperature on longevity, numbers of egg clutches, eggs per clutch, eggs in the first clutch laid, preoviposition period, and percentage of egg hatch were analyzed using one-way analysis of variance. Means were separated using Tukey's honestly significant difference (HSD) test at *P* = 0.05. Percentage data were transformed using the angular transformation before statistical analysis, but they are presented as nontransformed means (Sokal and Rohlf 1995). Regression analysis was performed on total number of eggs laid as a function of female body weight.

**Results and Discussion**

**Effects of Temperature on Survivorship and Longevity.** *P. maculiventris* adult females displayed a typical type II linear survivorship curve, characteristic of organisms that die at a constant rate (Begon et al. 1990) (Fig. 1A). Higher temperatures were associated with steeper declines in adult survivorship, with longest survival at 16°C, and highest mortality rates at 36°C. Temperature had a highly significant effect on mean longevity of *P. maculiventris* females (*F* = 17.3; *df* = 3, 36; *R*<sup>2</sup> = 0.59; *P* < 0.01) (Fig. 1B). Longevity at 16°C was significantly longer than that at other temperatures (Tukey's HSD, *P* < 0.01).

The effect of temperature on mean body weight of *P. maculiventris* females is probably compounded by

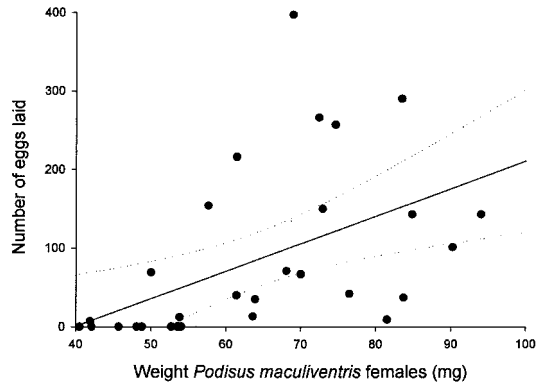


Fig. 3. Total number of eggs laid as a function of adult female body weight  $E = -139.1 + 3.49w$ , where *E* is number of eggs laid per female lifetime, and *w* is the weight of the predator female (*F* = 9.2; *df* = 1, 28; *R*<sup>2</sup> = 0.25; *P* < 0.01). Dotted lines represent 95% CL.

its effect on longevity and development. At 16°C, body weight increases slowly, but at a sustained rate because survival is longest at this temperature (Fig. 2A). In contrast, body weight seems to increase at a higher rate at 26°C and 30°C, but the increase is not sustained because individuals do not survive for as long at these temperatures. The slow and short duration increase in weight at 36°C indicates this temperature is too high for *P. maculiventris* females to either survive or develop for any significant period. Mean body weight at 36°C is significantly lower than the other temperature treatments because the females were not able to survive and develop at this temperature extreme (Fig. 2B).

The pooled data on numbers of eggs laid as a function of body weight shows that heavier females also lay the most eggs (Fig. 3), albeit with a low *R*<sup>2</sup> value. The regression equation for numbers of eggs as a function of body weight is  $E = -139.1 + 3.49w$ , where *E* is number of eggs laid per female lifetime, and *w* is the weight of the predator female (*F* = 9.2; *df* = 1, 28; *R*<sup>2</sup> = 0.25; *P* < 0.01). Zanuncio et al. (2000) found the same result using *Podisus rostralis* (Stål). Heavier females displayed shorter preoviposition periods, whereas the numbers of eggs produced per day was positively correlated with female weight. Therefore, mass rearing programs for *P. rostralis* should focus on the use of female parents weighing at least 60.0 mg (Zanuncio et al. 2000).

The effect of temperature on cumulative number of eggs laid is illustrated in Fig. 4A. At 16°C, egg laying is delayed by a prolonged preoviposition period of ≈2 wk. Eggs are laid at a lower rate compared with the higher temperature treatments, but the ovipositional period is longer due to the longer duration times at this temperature. Oviposition rates at 26 and 30°C are similar over the first 2-wk period, but they are sustained at higher rates at 26°C, which also exhibited a longer ovipositional period. No eggs were laid at 36°C, which was too high for *P. maculiventris* adult females to survive and reproduce. Mean cumulative numbers

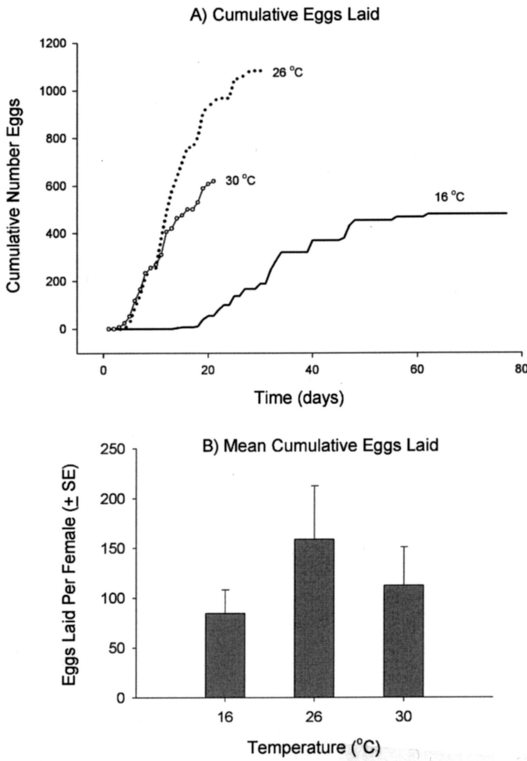


Fig. 4. (A) Cumulative number of eggs laid (summed across all replicates) as affected by temperature. (B) Mean cumulative numbers of eggs laid by temperature (excluding individuals that laid no eggs) ( $F = 0.75$ ;  $df = 2, 18$ ;  $R^2 = 0.08$ ;  $P = 0.49$ ).

of eggs per female ranged from 84.8 at 16°C to 158.9 at 26°C; however, treatment effects were not significantly different ( $F = 0.75$ ;  $df = 2, 18$ ;  $R^2 = 0.08$ ;  $P = 0.49$ ) (Fig. 4B).

Data on egg clutches and percentage egg hatch are summarized in Table 1. Numbers of egg clutches (ranging from 5.9 at 16°C to 9.4 at 26°C), eggs per clutch (13.6 at 16°C to 14.6 at 30°C), and eggs in the first clutch (9.0 at 16°C to 15.1 at 26°C) did not differ significantly at these three temperatures. Westich and Hough-Goldstein (2001) also found that percentage of egg hatch of *P. maculiventris* was not affected by temperature, averaging 70% at both 18°C and 25°C. Pre-

Table 2. Life table statistics for *P. maculiventris* adults under four constant temperatures

Parameter	Temp (°C)			
	16	26	30	36
$R_0^a$	25.14	47.8	44.4	0.0
$GRR^b$	41.3	156.0	117.7	0.0
$T^c$	64.2	44.8	42.2	
$r^{d1}$	0.05	0.08	0.09	
$\lambda^e$	1.05	1.08	1.09	
$DT^f$	13.9	8.6	7.7	

<sup>a</sup>  $R_0 = \sum l_x m_x$  expressed in units of females per female (assuming 1:1 sex ratio).

<sup>b</sup>  $GRR = \sum m_x$  in females per female.

<sup>c</sup>  $T = (\sum x l_x m_x) / R_0$  in days.

<sup>d</sup>  $r = \ln R_0 / T$  in females per female per day.

<sup>e</sup>  $\lambda = \exp(r)$  in females per female per day.

<sup>f</sup>  $DT = \ln(2) / r$  in days.

oviposition period was significantly longer at 16°C (20.3 d) than at 26°C (6.3 d) and 30°C (4.9 d).

**Life Table Calculations.** Life table statistics for *P. maculiventris* female adults are summarized in Table 2. Both  $R_0$  and  $GRR$  were highest at 26°C, estimated at 47.8 and 156.0 females per female, respectively. Generation time ( $T$ ) of 42.2 d was shortest at 30°C. Both  $r$  and  $\lambda$  were highest at 30°C, estimated at 0.09 and 1.09, respectively. Doubling time was fastest at 30°C and was estimated at 7.7 d. Reproductive parameters are marginally higher at 30°C compared with the other temperatures tested. The higher sustained oviposition rate displayed at 26°C is apparently offset by the shorter generation time at 30°C.

Wittmeyer and Coudron (2001) constructed life tables for *P. maculiventris* and tested for the effects of artificial diets fed to larvae and adult predators on the reproductive parameters at  $26 \pm 5^\circ\text{C}$ . Insect-free diets provided during both immature and adult stages resulted in longer developmental times and preoviposition periods, and significantly reduced  $R_0$  and  $r$  parameters. When fed an insect diet of cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), during both immature and adult stages, the reproductive parameters for *P. maculiventris* were calculated as follows ( $\bar{X} \pm \text{SD}$ ):  $R_0 = 42.2 \pm 2.9$ ,  $T = 34.9 \pm 1.9$ , and intrinsic rate of increase ( $r$ ) =  $0.11 \pm 0.002$ . In a similar study, the values were  $R_0 = 59.5$ ,  $T = 33.3$ , and  $r = 1.001$  (Coudron et al. 2002). Corresponding values for the 26°C treatment in this study were  $R_0 = 47.8$ ,  $T = 44.8$ , and  $r = 0.08$ , which indicated lower reproductive

Table 1. Mean egg clutch data ( $\pm \text{SE}$ )

Measurement	Temp (°C)			Statistics			
	16	26	30	$F$	$df$	$R^2$	$P$
Egg clutches	5.86 $\pm$ 1.34	9.43 $\pm$ 2.89	7.12 $\pm$ 2.2	0.63	2, 29	0.06	0.54
Eggs/clutch	13.578 $\pm$ 1.34	14.21 $\pm$ 1.58	14.62 $\pm$ 0.75	0.12	2, 18	0.013	0.89
Eggs in first clutch	9.0 $\pm$ 2.3	15.1 $\pm$ 2.54	10.25 $\pm$ 1.45	2.34	2, 18	0.21	0.12
Days first clutch laid	20.33 $\pm$ 2.08a	6.29 $\pm$ 1.11b	4.88 $\pm$ 0.61b	42.23	2, 18	0.82	<0.01
% Egg hatch	45.8 $\pm$ 14.1	42.3 $\pm$ 10.6	37.9 $\pm$ 8.9	0.22	2, 18	0.025	0.80

Data for the 36°C treatment was excluded from the analyses because no eggs were laid. Only nonzero replicates were included for other treatments. One-way analysis of variance was performed across rows for temperature effects on each factor. Different letters indicate means are significantly different (Tukey's HSD) where treatment effects are significant.



rates and longer generation times, suggesting that *G. mellonella* was an inferior food source. Furthermore, the following biological data were recorded by Wittmeyer and Coudron (2001): developmental time (second instar to adult) =  $17.8 \pm 0.3$ , weight (mg) =  $93.7 \pm 3.1$ , preoviposition period =  $7.3 \pm 0.3$ , and eggs per female =  $120.1 \pm 3.5$ .

Using a closely related species, Medeiros et al. (2000) constructed life fertility tables for *Podisus nigrispinus* (Dallas) at a constant temperature of 25°C. Each female oviposited a mean of 188.5 eggs, with a mean longevity of 31.2 d. The  $R_0$  was 31.9 females per female,  $T$  was 47.4 d,  $DT$  was 9.5 d,  $r$  was 0.073, and finite rate of increase ( $\lambda$ ) was 1.08. These values are similar to those obtained in this study for *P. maculiventris* at 26°C (Table 2). In a subsequent study (Medeiros et al. 2003), life table parameters of *P. nigrispinus* were measured at 20, 23, 25, 28, 30 and  $33 \pm 0.2^\circ\text{C}$  ( $60 \pm 10\%$  RH, photoperiod of 14:10 [L:D] h) by using *Alabama argillacea* (Hübner) (Lepidoptera: Noctuidae) as prey.  $GRR$  ranged from 1.6 (at 33°C) to 366.6 (28°C);  $R_0$  from 0.02 (33°C) to 189.5 (28°C) females per female;  $T$  from 33.3 (33°C) to 85.5 (20°C) days;  $DT$  from 0.82 (33°C) to 17.8 (20°C) d;  $r$  from 0.13 (33°C) to 0.12 (28°C) per day;  $\lambda$  from 0.88 (33°C) to 1.12 (28°C) females per female per day. Population growth rates were highest between 28 and 30°C, with 33°C proving detrimental to predator reproduction. As in this study, the higher temperature used was sub-optimal.

In published studies, previous workers maintained their laboratory colonies of *P. maculiventris* at close to 26°C, perhaps because this temperature may be optimal for insect growth and development in general. Examples of environmental conditions selected include  $23 \pm 1^\circ\text{C}$  ( $65 \pm 10\%$  RH, photoperiod of 16:8 [L:D] h; de Clercq et al. 2002);  $24 \pm 1^\circ\text{C}$  (40–70% RH, photoperiod of 14:10 [L:D] h; Legaspi and O'Neil 1993); 25°C (photoperiod of 18:6 [L:D] h; Westich and Hough-Goldstein 2001); 26°C (65% RH, photoperiod of 16:8 [L:D] h; Aldrich and Cantelo 1999);  $26 \pm 2^\circ\text{C}$  ( $60 \pm 10\%$  RH, photoperiod of 16:8 [L:D] h; Sant'Ana and Dickens 1998). Life table statistics such as those calculated in this study may provide useful values for summarizing the reproductive capacities of insects. However, they also may be misleading when applied to a situation, such as selecting an optimal temperature for mass rearing a test insect, or simply maintaining a colony for experimental purposes. Examination of the life table data indicates that 30°C yields the numerically best reproductive values. Inspection of cumulative eggs laid with time may indicate a more favorable reproductive trend of prolonged egg production over a longer period. Therefore, 26°C may indeed be a more suitable temperature for maintaining a colony of *P. maculiventris* than 30°C.

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