Life Table Analysis for *Podisus maculiventris* Immatures and Female Adults Under Four Constant Temperatures

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ABSTRACT   Detailed life tables and reproduction were studied in nymphs and adult females of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) fed larvae of *Galleria mellonella* L. (Lepidoptera: Pyralidae) at constant temperatures of 18, 22, 26, and 30°C. Development rates were fitted to the equation $Y = a + b \ln x$. The theoretical development threshold was calculated as $T_0 = \exp(-a/b)$, resulting in $T_0 = 12.48$ and 12.78°C for females and males, respectively. Degree-days for development ranged from 233.92 in males at 18°C to 338.73 in females at 30°C. In all temperature treatments, *P. maculiventris* immatures consumed a mean of approximately eight prey items. Mean immature body weights were higher at higher temperatures, but females were heavier than males only at the fifth instar. In adult female *P. maculiventris*, age at first oviposition ranged from 2.7 d at 30°C to 13.4 d at 18°C. Percentage of egg hatch was lowest at 18°C (11%) and highest at 30°C (36.4%). Survivorship curves showed a linear decline with time, the steepest curves at the highest temperatures. Total number of eggs laid per female ranged from 429.4 at 18°C to 755.4 at 26°C. Mean egg numbers were fitted to a surface equation as eggs $= (-6.658 + 0.432T) d \exp(-0.002Td)$ where d and T are age (days) and temperature (°C), respectively. Net and gross reproductive rates were highest at 26°C ($R_0 = 379.126$; gross reproductive rate [GRR] $= 491.273$ ♀/♀) and lowest at 18°C ($R_0 = 207.873$; GRR $= 294.972$). Generation and doubling times were shortest at 30°C (T $= 35.021$ and DT $= 4.270$ d). Intrinsic and finite rates of increase were also highest at 30°C ($r = 0.1623$; $\lambda = 1.1763$). Reproductive parameters were recalculated using numbers of eggs that actually hatched, resulting in lower values, although the effects of temperature did not change. In the context of mass rearing *P. maculiventris*, 26°C is the optimal temperature tested, but female predators >21 d should be not be used because they may not be capable of laying viable eggs.

KEY WORDS   life history, reproduction, development, survivorship

THE USE OF LIFE tables was pioneered by Pearl and Parker (1921) to study populations of *Drosophila.* Currently, life tables are generally constructed for two purposes: (1) to calculate reproductive parameters relating to the intrinsic rate of increase or (2) to analyze the effects of specific mortality factors, such as biological control agents, on insect population dynamics (Jervis and Copland 1996, Kidd and Jervis 1996). Reproductive parameters commonly calculated include net reproductive rate (R_0; mean number of female progeny produced by a single female during its mean lifetime, expressed in ♀/♀); gross reproductive rate (GRR; also females produced per female, excluding effects of parental survivorship, in ♀/♀); generation time (T; mean period between birth of the parents and that of the offspring, in days); intrinsic rate of increase (r; increate rate in ♀/♀/d); finite rate of increase (λ; in ♀/♀/d); and doubling time (DT; time for population to double, in days).

Life tables have been constructed for *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) and other related species for the purposes of estimating reproductive parameters, often in the context of mass rearing. Medeiros et al. (2000) used life table analysis for *Podisus nigrispinus* (Dallas) to calculate reproductive parameters at 25°C. Females laid ≈188.5 eggs each and lived 31.2 d. Reproductive parameters were $R_0 = 31.9$ ♀/♀, T $= 47.4$ d, DT $= 9.5$ d, $r = 0.073$ ♀/♀/d, and $\lambda = 1.08$ ♀/♀/d. In a subsequent study, life table parameters of this species were measured at 20, 23, 25, 28, 30, and 33 ± 0.2°C (60 ± 10% RH, 14:10 L:D) using *Alabama argillacea* (Hübner) (Lepidoptera: Noctuidae) as prey (Medeiros et al. 2003). GRR was found to range from 1.6 (at 33°C) to 366.6 (28°C); R_0 from 0.02 (33°C) to 189.5 (28°C) ♀/♀; T from 33.3 (33°C) to 85.5 (20°C) d; DT from 0.82 (33°C) to 17.8 (20°C) d; r from 0.13 (33°C) to 0.12 (28°C)/d; and λ from 0.88

$(33°C)$ to 1.12 $(28°C)$ ♀/♀/d. Population growth rates were highest between 28 and 30°C, with the highest temperature of 33°C proving detrimental to predator reproduction.

Life table analysis of *P. maculiventris* showed that insect-free diets in both immature and adult stages caused longer developmental times and preoviposition periods and significantly reduced R_0 and r at $26 \pm 5°C$ (Wittmeyer and Coudron 2001). When fed cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), during both immature and adult stages, the reproductive parameters for *P. maculiventris* were $R_0 = 42.2 \pm 2.9$ (SD); $T = 34.9 \pm 1.9$; and $r = 0.11 \pm 0.002$. In a subsequent study, Coudron et al. (2002) reported values of $R_0 = 59.5$, $T = 33.3$, and $r = 1.001$. In their 26°C treatment, $R_0 = 47.8$, $T = 44.8$, and $r = 0.08$, indicating lower reproductive rates and longer generation times, thereby suggesting that *Galleria mellonella* L. larvae (Lepidoptera: Pyralidae) was an inferior food source. Legaspi (2004) found that *P. maculiventris* female adults fed *G. mellonella* exhibited the highest R_0 and GRR at 26°C (estimated at 47.8 and 156.0 ♀/♀, respectively) but that shorter generation times at 30°C $(T = 42.2$ d) resulted in higher values of r (0.09) and λ (1.09). Although much work has been done on the life history of *Podisus* spp. adults, there is a lack of information on biology of immatures, especially at different constant temperatures. In this study, we studied development in nymphs and constructed life tables for adult females in *P. maculiventris* at 18, 22, 26, and 30°C.

Materials and Methods

Temperature Treatments

Podisus maculiventris immatures and female adults were studied under four constant temperatures: 18, 22, 26, and 36°C. Constant temperature conditions were maintained inside ThermoForma model 3740 growth chambers (ThermoForma, Marietta, OH) with a 14:10 (L:D)-h photoperiod and a mean of 60% RH. Temperature and relative humidity inside each chamber were monitored by HOBO recorders (Onset Computer, Bourne, MA).

Podisus maculiventris **Immatures.** *Podisus maculiventris* used in this study were obtained from a laboratory colony at USDA-ARS-CMAVE/FAMU-CBC in Tallahassee, FL. For each temperature treatment, 60 eggs from different females were placed collectively into a single petri dish (9 cm diameter) lined with filter paper. A damp cotton ball in a small dish was placed inside each petri dish to provide moisture. From the eggs that hatched, 30 nymphs for each temperature treatment were placed individually into petri dishes lined with filter paper. Nymphs were fed larvae of *G. mellonella* (321.9 ± 57.9 [SD] mg; 2.62 ± 0.24 cm length; $n = 25$; Rainbow Mealworms & Crickets, Compton, CA). Body weights of nymphs were recorded at the beginning of each instar (BP221S Balance; Sartorius, Egdewood, NY), starting from the third instar.

Podisus maculiventris **Adult Females.** Newly emerged to 3-d-old *P. maculiventris* adult females that emerged from the immatures described above were placed individually into petri dishes (15 cm diameter) lined with filter paper and starved for 24 h before the start of the experiment. They were provided daily with five fourth- to fifth-instar larvae of *G. mellonella* as prey. Body 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 adult females dying were recorded daily until all *P. maculiventris* females died. All egg masses were removed, counted, and held at ambient laboratory temperatures (24–25°C) for 5 d to record numbers of eggs that hatched. Numbers of eggs that hatched were recorded and percentage hatching was calculated. The following were also recorded: number of egg clutches per female, number of eggs per clutch, number of eggs in the first clutch laid, and preoviposition period. Each petri dish containing a single female comprised one replicate. Ten replicates were used for each of four temperatures, 18, 22, 26, and 36°C, maintained in growth chambers (60% RH, 14:10 L:D).

Life Table Calculations

The reproductive parameters of adult female *P. maculiventris* calculated were R_0, GRR, T, r, λ, and DT. Age of adult females (x) was estimated by adding the mean duration times of the immatures at the appropriate temperature treatment. Eggs were not reared to adulthood; therefore, sex could not be determined. Instead, numbers of eggs laid were divided by two under the assumption of a 1:1 sex ratio (Wittmeyer and Coudron 2001). Reproductive parameters were also calculated using numbers of eggs that hatched (divided by 2) to allow comparisons against calculations based on egg numbers laid.

Statistical Analyses

In *P. maculiventris* immatures, the effect of temperature on development rate (1/duration of life stage) was analyzed by nonlinear regression using a simple logarithmic model $Y = a + b \ln x$, where Y is development rate, x is temperature (°C), and a and b are constants (Systat NONLIN procedure using least squares estimation and Gauss-Newton method). Separate analyses were performed on the egg stage, nymphs (first through fifth instars), and all immature stages (egg to fifth instars). Theoretical temperature development thresholds were calculated as the x-intercept of the regression curve of development and temperature (Jervis and Copland 1996). In linear regressions, $Y = a + bT$ and $T_0 = -a/b$. When $Y = a + b \ln T$, then $T_0 = \exp(-a/b)$. Degree days for development were calculated as degree-days $= (T - T_0)D$, where T is the constant temperature used in the treatment, T_0 is the theoretical development threshold, and D is mean development time at that temperature

Table 1. Parameter estimates for effects of temperature on development rate of *P. maculiventris* immature lifestages using Y = a + b ln x

Life stages	A	B	R^2
Females: egg to fifth instar	−0.154 ± 0.006	0.061 ± 0.002	0.953
Males: egg to fifth instar	−0.158 ± 0.006	0.062 ± 0.002	0.955
Female eggs	−0.691 ± 0.068	0.289 ± 0.022	0.786
Male eggs	−0.780 ± 0.061	0.318 ± 0.019	0.843
Females: first to fifth	−0.195 ± 0.008	0.076 ± 0.003	0.945
Males: first to fifth	−0.198 ± 0.009	0.078 ± 0.003	0.941

Parameter estimates are shown as asymptotic SEs.

(Greenberg et al. 2000). Sex was determined on emergence of adults, and development rates were separated by sex. Two-way analysis of variance (ANOVA) was used to examine the effects of sex and temperature on immature lifestage duration, number of prey consumed, and body weights.

In adults, one-way ANOVA was performed to analyze the effects of temperature on total number of eggs, number of egg clutches, numbers of eggs per clutch, age at first oviposition, number of eggs in the first clutch, number of eggs hatched, percentage of eggs hatched, and body weight. Percentage data were converted by arcsine transformation before analysis but are presented as untransformed means (Sokal and Rohlf 1995). Nonlinear regression was used to create a surface describing the effects of temperature and age on daily oviposition rate. Numbers of eggs laid was fitted to the model: eggs = $(p + qT)d \exp(-wTd)$, where T is temperature and d is days (Enkegaard 1993). Parameters p and q describe the effects of temperature on how quickly maximal oviposition is reached and w on how quickly it declines back to zero (Drost et al. 1998, Greenberg et al. 2000).

Results and Discussion

Podisus maculiventris Immatures

Development Rates. Higher temperatures resulted in higher development rates, adequately described by the logarithmic equation Y = a + b ln x (Table 1; Fig. 1). R^2 values ranged from 0.786 for female eggs to 0.955 for all immature male stages. Undoubtedly, the data could have been fitted to many different equations, including a simple linear one. We chose a log-
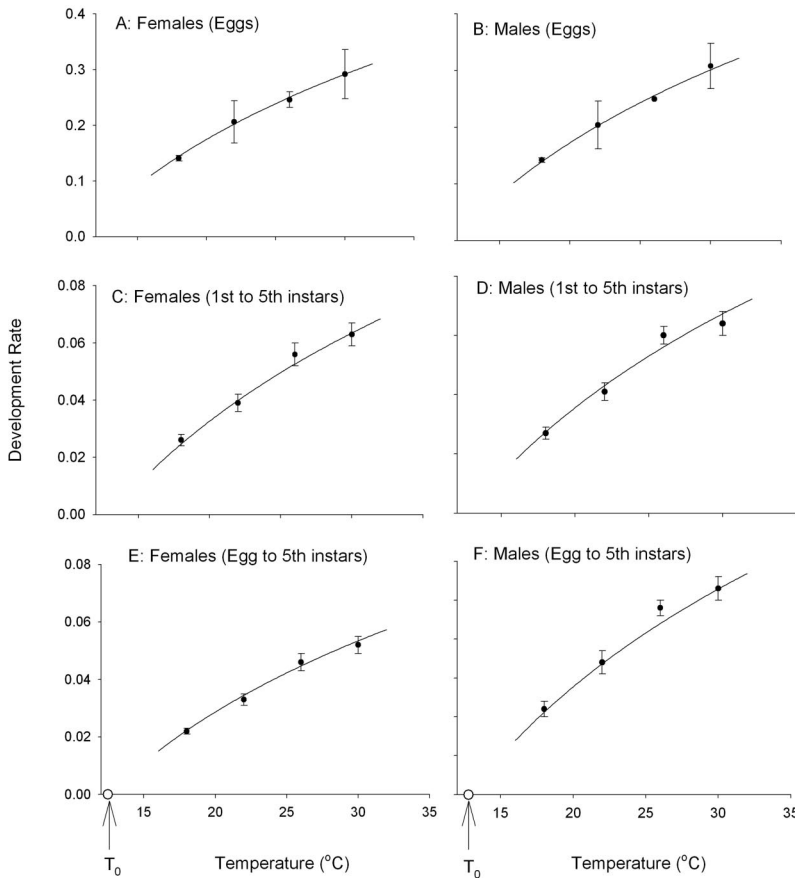
Fig. 1. Development rate (1/development time) as a function of temperature. Development rate (Y) was fitted to the equation Y = a + bT, where T is temperature (°C), and a and b are constants. Development threshold was estimated as $T_0 = \exp(-a/b)$. Theoretical development thresholds are indicated by arrows.

Table 2.　Effect of temperature and sex on immature lifestages of *P. maculiventris*

T (°C)	Sex (n)	Life stage						Degree-days (DD)[a]
		Eggs	First	Second	Third	Fourth	Fifth	
18	♂♂ (16)	7.062	4.125	7.375	6.625	8.063	11.563	233.92
		(0.250)	(0.719)	(0.885)	(0.806)	(1.769)	(1.031)	
	♀♀ (13)	7.077	4.231	7.538	7.154	7.923	11.923	253.07
22		(0.277)	(0.599)	(0.967)	(1.281)	(1.188)	(1.115)	
	♂♂ (12)	5.083	3.750	4.583	4.667	4.583	6.833	271.98
		(0.996)	(0.754)	(0.996)	(1.371)	(0.669)	(0.718)	
	♀♀ (13)	5.000	3.769	5.308	4.462	5.077	7.077	292.20
		(0.913)	(0.927)	(0.855)	(1.050)	(0.277)	(0.494)	
26	♂♂ (12)	4.000	2.250	3.417	2.833	3.250	5.000	274.32
		(0.000)	(0.452)	(0.900)	(0.835)	(1.055)	(0.426)	
	♀♀ (13)	4.077	2.154	3.769	3.077	3.538	5.308	296.40
		(0.277)	(0.376)	(0.725)	(0.494)	(0.877)	(0.630)	
30	♂♂ (13)	3.308	2.154	2.846	3.308	2.769	4.538	325.85
		(0.480)	(0.376)	(0.555)	(0.855)	(0.599)	(0.519)	
	♀♀ (12)	3.500	2.417	2.917	3.083	2.667	4.750	338.73
		(0.522)	(0.515)	(0.793)	(0.793)	(0.492)	(0.622)	

Means (days) are shown with SD in parentheses below. Lifestage durations were shorter at higher temperatures ($F = 809.044$; df = 3,96; $P < 0.01$), and females had longer duration times ($F = 4.919$; df = 1,96; $P = 0.029$; sex × temperature: $F = 0.178$; df = 3,96; $P = 0.911$; $R^2 = 0.962$; two-way ANOVA).

[a] DD = (treatment temperature − theoretical development threshold) × duration time.

arithmic equation based on its simplicity, as well as the decline in slope evident at the higher temperatures. The high temperature range selected in this experiment did not result in a decline in development rate, as has been observed in other insects. Therefore, we did not have to use a more complex model, such as those of Sharpe and DeMichele (1977) or Stinner et al. (1974).

Duration of Immature Lifestage. As expected, lifestage durations were shorter at higher temperatures ($F = 809.044$; df = 3,96; $P < 0.01$; Table 2). Not expected was the statistically significant difference between the sexes, with females having longer duration times ($F = 4.919$; df = 1,96; $P = 0.029$; sex × temperature: $F = 0.178$; df = 3,96; $P = 0.911$; $R^2 = 0.962$). Degree-days for development ranged from 233.92 in males at 18°C to 338.73 in females at 30°C. In comparison, O'Neil et al. (1996) used values ranging from 385 to 584 in modeling *P. maculiventris* feeding on the Mexican bean beetle, *Epilachna varivestis* (Mulsant) (Coleoptera: Coccinellidae). Our use of a nonlinear development curve may have resulted in a higher temperature development threshold than would have been calculated using linear regression, thereby decreasing our estimate of the degree-day requirements. Theoretical development threshold (T_0) was 12.48°C for females and 12.78°C for males. Calculated degree-days for immature development by sex showed variation at each temperature tested. Although in theory these estimates should be approximately equal, this method also yielded variation in degree-days calculated for the development of *Bemisia argentifolii* Bellows and Perring and *Trialeurodes vaporariorum* (Westwood) (both Homoptera: Aleyrodidae) (Greenberg et al. 2000).

Prey Consumption. The number of prey consumed by *P. maculiventris* immatures was not affected by temperature ($F = 0.919$; df = 3,96; $P = 0.435$; $R^2 = $

0.031). Similarly, prey consumption did not differ between the two sexes ($F = 0.351$; df = 1,96; $P = 0.555$; temperature × sex: $F = 0.016$; df = 3,96; $P = 0.997$). In all treatments, *P. maculiventris* immatures consumed a mean of approximately eight prey items (Table 3).

Immature Weights. Mean body weights of the different instars are shown by sex and temperature (Fig. 2). In third instars, temperature significantly affected body weights ($F = 38.477$; df = 3,96; $P < 0.01$; $R^2 = 0.548$), whereas sex had no effect ($F = 0.273$; df = 1,96; $P = 0.603$; temperature × sex: $F = 0.043$; df = 3,96; $P = 0.988$). The same effects were found in fourth instars (temperature: $F = 4.797$; df = 3,96; $P < 0.01$; $R^2 = 0.144$; sex: $F = 0.425$; df = 1,96; $P = 0.516$; temperature × sex: $F = 0.567$; df = 3,96; $P = 0.638$). However, in fifth instars, both temperature and sex had significant effects on weights (temperature: $F = 8.766$; df = 3,94; $P < 0.01$; $R^2 = 0.359$; sex: $F = 25.861$; df = 1,94; $P < 0.01$; temperature × sex: $F = 0.01$; df = 3,94; $P = 0.999$). In *P. maculiventris,* female adults are

Table 3.　Effect of temperature and sex on no. prey consumed by *P. maculiventris* immature stages

T (°C)	Sex (n)	Number prey consumed		
		n	Mean	SD
18	♂♂	16	8.688	2.213
	♀♀	13	8.615	1.325
22	♂♂	12	8.750	1.138
	♀♀	13	8.538	1.330
26	♂♂	12	8.500	2.153
	♀♀	13	8.308	1.316
30	♂♂	13	8.154	1.144
	♀♀	12	7.917	0.793

Prey consumption was not affected by temperature ($F = 0.919$; df = 3,96; $P = 0.435$; $R^2 = 0.031$) or sex ($F = 0.351$; df = 1,96; $P = 0.555$; temperature × sex: $F = 0.016$; $P = 0.997$).
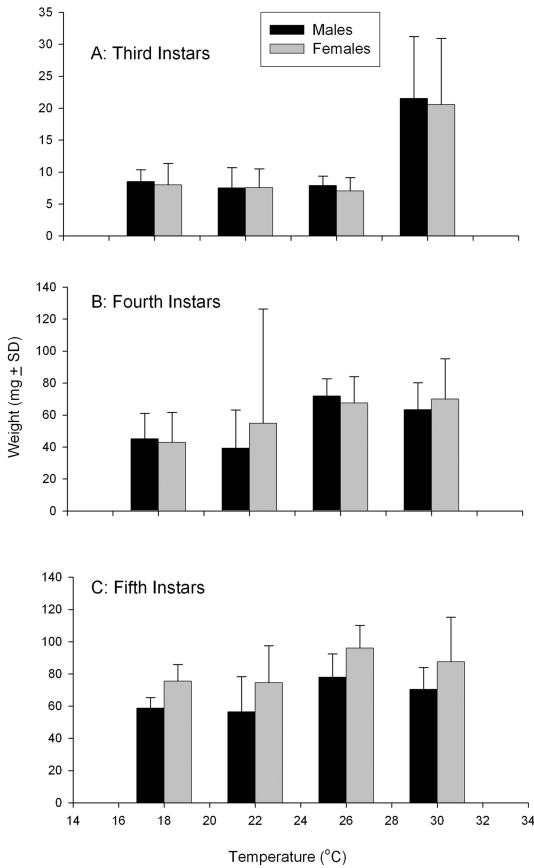
Fig. 2. Weights of *P. maculiventris* nymphs (mg ± SD). In all instars, temperature significantly affected immature body weight (two-way ANOVA, $P < 0.05$). Only in the fifth instar (C) are females significantly heavier than males.

known to be heavier than males (Legaspi et al. 2004). Females from the laboratory colony (85.0 mg) were significantly heavier than males (57.0 mg). Average body weight of a field-collected female (56.0 mg) was

also heavier than that of the male (43.0 mg). This study shows that the weight difference occurs in the fifth-instar stage.
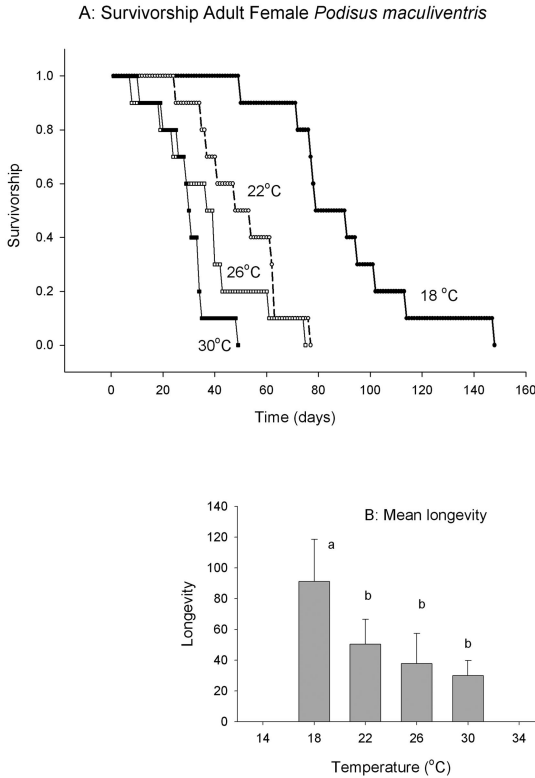
Podisus maculiventris Adults

Oviposition Measurements. Temperature was not a statistically significant factor affecting total number of eggs laid ($P = 0.054$), number of egg clutches ($P = 0.056$), number of eggs per clutch ($P = 0.151$), or number of eggs in the first clutch ($P = 0.478$; Table 4). However, increasing temperature resulted in shorter preoviposition periods ($P < 0.01$). The highest number of eggs laid per female occurred at 26°C (755.4), which corresponds to unmated females feeding on *E. varivestis* ad libitum (Legaspi and O'Neil 1993). The number of egg clutches laid ranged from 18 to 29.8 per female, which is more than the 5.8–9.4 found in Legaspi (2004). Numbers of eggs per clutch ranged from 0.24 to 0.28, which is also more than the 13–14 found previously. Age at first oviposition ranged from 2.7 to 13.4 d at 30 and 18°C, respectively, which are earlier than previous findings (4.9 d at 30°C and 20.3 d at 16°C). Greater differences were reported by Legaspi and O'Neil (1993), who found age at first oviposition to range from 19 d in unmated *P. maculiventris* females fed one prey of *E. varivestis* daily to 56.6 d in females fed every 17 d. Earliest oviposition was found in 10-d-old females fed one yellow mealworm, *Tenebrio molitor* L. (Coleoptera: Tenebrionidae), daily to >30 d in predators fed every 16 d (Wiedenmann et al. 1996). Numbers of eggs in the first clutch ranged from 0.20 to 0.28 compared with 0.9–0.10 found earlier. Percentage of egg hatch was lowest at 18°C (11%) and highest at 30°C (36.4%). Percentages of egg hatch reported earlier were higher (37.9–45.8%). The significant effects on egg hatch indicate that simply counting the numbers of eggs laid might be insufficient in measuring the effects of temperature or other external factors on the reproductive success of *P. maculiventris* or other test insects.

Table 4. Effects of temperature on various oviposition parameters in *P. maculiventris* (numbers in parentheses beneath means are SD)

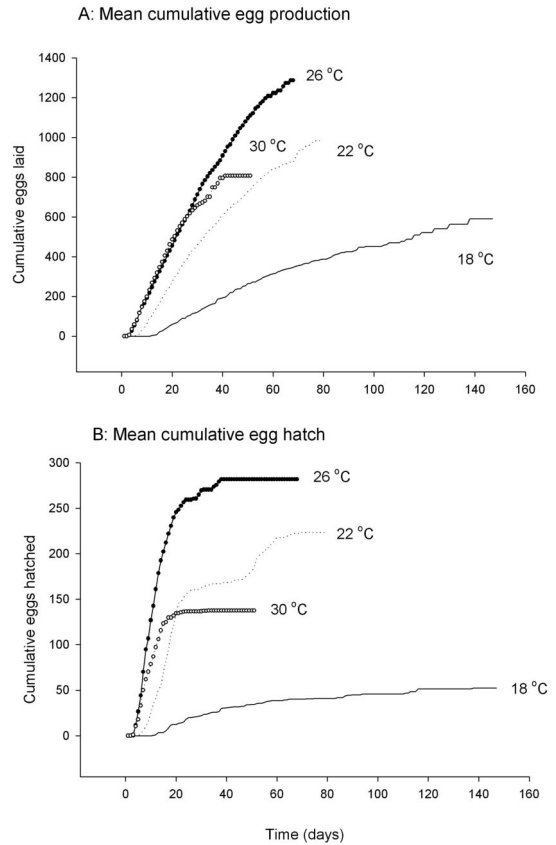| Factor	Temperature (°C)				Statistics
	18	22	26	30	
Total no. eggs laid	429.4	726	755.4	615.9	$F = 2.800$; df = 3,36
	(155.07)	(269.58)	(407.98)	(219.25)	$P = 0.054$; $R^2 = 0.189$
No. egg clutches	18	29.8	28.6	22.1	$F = 2.767$; df = 3,36
	(5.98)	(10.43)	(15.89)	(7.09)	$P = 0.056$; $R^2 = 0.187$
No. eggs per clutch	24.124	24.275	27.535	28.109	$F = 1.875$; df = 3,36
	(4.74)	(3.11)	(6.35)	(4.71)	$P = 0.151$; $R^2 = 0.135$
Age at first oviposition (d)	13.4a	5.4b	3.8bc	2.7c	$F = 110.475$; df = 3,36
	(2.63)	(0.52)	(0.63)	(0.95)	$P < 0.01$; $R^2 = 0.902$
No. eggs in first clutch	27.9	23.7	19.6	27.5	$F = 0.846$; df = 3,36
	(15.26)	(14.09)	(8.60)	(14.32)	$P = 0.478$; $R^2 = 0.066$
No. eggs hatched	44.2b	161.4ab	243.6a	145.9ab	$F = 5.322$; df = 3,36
	(25.22)	(89.55)	(171.20)	(111.28)	$P < 0.01$; $R^2 = 0.307$
Percentage of egg hatch	11.04b	22.38ab	36.37a	25.02ab	$F = 3.882$; df = 3,36
	(6.70)	(9.39)	(20.418)	(20.89)	$P = 0.017$; $R^2 = 0.244$

Where statistical analysis was significant, Tukey's HSD was performed. Different letters in a row indicate significant differences between means ($P = 0.05$).

A: Survivorship Adult Female *Podisus maculiventris*

B: Mean longevity

Fig. 3. Survivorship and mean longevity of *P. maculiventris* adult females (*n* = 10). Means (B) with different letters are significantly different (Tukey's HSD, *P* < 0.05).

A: Mean cumulative egg production

B: Mean cumulative egg hatch

Fig. 4. Mean cumulative eggs laid (A) and mean cumulative eggs hatched (B). Cumulative eggs laid was calculated by accumulating means of eggs laid at each day. In calculating cumulative eggs hatched, only those eggs that hatched were added.

Survivorship Curves of Adult Females. Higher temperatures predictably resulted in faster development and more rapid death (Fig. 3A). As a consequence, mean adult longevity declined with increasing temperature, being longest at 18°C ($F = 20.038$; df = 3,26; $P < 0.01$; $R^2 = 0.625$). The linear decline with time was also found in *P. maculiventris* fed *E. varivestis* at different intervals (Legaspi and O'Neil 1993) and in *P. nigrispinus* (Medeiros et al. 2000).

Cumulative Eggs Laid and Cumulative Egg Hatch. Different temperatures produced different patterns of cumulative eggs laid (Fig. 4A). Higher temperatures of 26 and 30°C had the steepest slopes, indicating highest oviposition rates. However, the 30°C curve tapers off when the individuals die. The 18°C curve shows the most gradual slope, indicating a lower oviposition rate. However, these individuals also live longest and egg production is longer and more sustained. Females at 22°C produced a curve intermediate to those of the temperature extremes, both in terms of slope and duration. The sustained oviposition at the lower temperatures apparently compensated for the higher oviposition rates at the higher temperatures, resulting in insignificant differences in total numbers of eggs laid at the different temperatures (Table 4).

Cumulative egg hatch revealed interesting differences compared with cumulative egg numbers (Fig. 4B). The higher temperatures again had the steeper slopes. However, cumulative eggs hatched reached an asymptote because eggs laid no longer hatched. In the 26°C treatment, this occurred on day 38. At 30°C, eggs laid no longer hatched after day 20. Eggs laid at the lower temperature treatments continued to hatch late into the life of the females. In contrast to total numbers of eggs laid, total numbers of eggs that actually hatched were highest at 26°C. Therefore, for purposes of mass rearing or maintaining a colony, older females do not seem to contribute to production of viable eggs and should be discarded.

Mean egg numbers are shown as a function of female age and temperature; the surface map shows the equation of Enkegaard (1993): eggs = $(-6.658 + 0.432T) d \exp(-0.002Td)$ (SE values: 0.654, 0.034, and <0.01 for p, q, and w, respectively; d and T are age in days and temperature in °C, respectively; $R^2 = 0.586$; Fig. 5). The smoothing surface shows a slow increase and decline in egg numbers at lower temperatures and
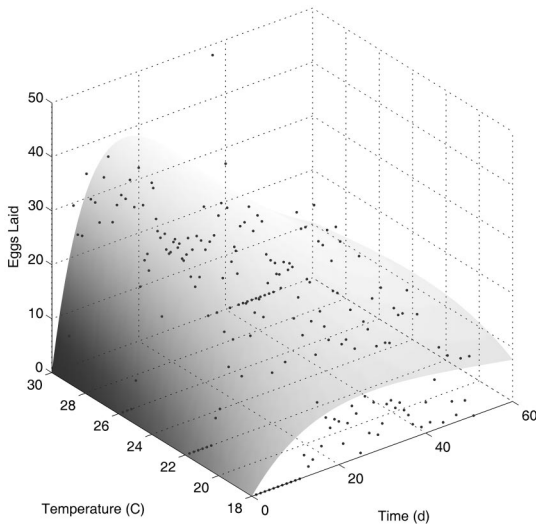
Fig. 5. Enkegaard (1993) surface equation overlaid on mean numbers of eggs laid as a function of age and temperature. The equation fitted was eggs = $(-6.658 + 0.432T)$ d exp $(-0.002Td)$, where eggs is mean eggs laid, T is temperature (°C), and d is age in days.

more pronounced rates at higher temperatures. The figure also shows longer preovipositional periods at lower temperatures as described earlier (Table 4). The Enkegaard equation was developed to model fecundity as a function of age and temperature (Drost et al. 1998) and was applied to the cotton whitefly (*Bemisia tabaci* Gennadius [Homoptera: Aleyrodidae]). The equation was applied to two other whiteflies: *B. argentifolii* and *T. vaporariorum* (Greenberg et al. 2000). Modified forms of the equation were used to model spatial dynamics of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (Wang and Shipp 2001) and the effects of age and host density in *Allorhogas pyralophagus* (Harbison et al. 2001).

Body Weight. Adult female body weight followed a similar pattern in all temperatures: increase early in adult life, followed by a sustained period of nearly constant weight, and possibly a slight decline late in life, accompanied by fluctuating measurements caused by smaller sample sizes (Figs. 6A–D). Temperatures significantly affect female body weight of *P. maculiventris* ($F = 6.422$, df = 3,55; $P < 0.01$; $R^2 = 0.259$; Fig. 6E), being highest at 26°C and lowest at 18°C. Body weights were usually >100 mg, which at the higher range of weights reported in the literature (e.g., Wiedenmann et al. 1996, Coudron et al. 2002), also suggesting that these females were well fed (Legaspi et al. 1996).

Life Table Calculations. The present life table calculations (Table 5) are compared with those reported earlier (Legaspi 2004). Net and gross reproductive rates were highest at 26°C (379.126 and 491.273 ♀/♀, respectively) and lowest at 18°C (207.873 and 294.972,

respectively). The previous study also showed highest net reproductive rate at 26°C, although calculated values ware only 47.8 and 156.0, respectively. Generation and doubling times were shortest at 30°C (35.021 and 4.270 d, respectively), in part because of shorter developmental times at that temperature. Previously, generation and doubling times also were shortest at 30°C (42.2 and 7.7 d, respectively). The intrinsic and finite rates of increase were also highest at 30°C (0.1623 and 1.1763, respectively). Calculated values for r and λ are highest at 30°C, although values were lower in the previous study (0.09 and 1.09 ♀/♀/d, respectively). Therefore, both studies found the same general results, but reproductive rates are higher here.

When reproductive parameters are calculated using numbers of eggs that actually hatch, the values are predictably lower, but the data trends are maintained (Table 5). For example, maximal r at 30°C declined from 0.1623 to 0.1398. It is likely that differential hatching percentages at different temperatures will have significant effects in the population dynamics of *P. maculiventris*.

The lower life table parameter values reported previously can be traced to lower numbers of eggs laid compared with this study. At 16°C, mean total number of eggs laid by *P. maculiventris* was 84.8 ± 23.4 (SE; $n = 10$); at 26°C, the number was 158.9 ± 53.9; and at 30°C, the number was 112.4 ± 38.7. Females in the 36°C treatment did not lay eggs. In comparison, mean numbers of eggs laid in this study were 755.4 ± 407.98 at 26°C (SD; $n = 10$) and 615.9 ± 219.25 at 30°C. The higher numbers of eggs laid in this study is caused in part by longer adult duration times. Legaspi (2004) reported mean adult durations of 47.2 ± 8.1 (SE; $n = 10$) at 16°C; 14.3 ± 3.1 at 26°C; 12.0 ± 2.1 at 30°C; and 4.9 ± 1.5 at 36°C. In contrast, we found the shortest adult duration of 29.9 ± 9.9 (SD; $n = 10$) at 30°C (Fig. 3). However, percentages of egg hatch in this study were slightly lower (11–36%) than that reported previously (≈40%) in all temperature treatments. Reasons for differences in fecundity between the present and previous studies are unclear because similar protocols were used, including prey species. Possible explanations may include natural variation in *P. maculiventris* and the use of an especially fecund cohort of test insects.

The key findings in this study hold important implications for mass rearing insects such as *P. maculiventris* for use in biological control programs. When defining optimal temperature for mass rearing, it is insufficient to rely on published literature on lifetime fecundities. This study and others have shown that insects reared at lower temperatures can compensate for lower oviposition rates by laying eggs over a longer duration relative to counterparts that complete their life cycles at higher temperatures. Reproductive parameters such as r and λ are more helpful in that insect lifetime and survivorship are included in calculating reproductive rates. However, these calculations may be misleading if eggs laid later in the insect adult life are not viable. In the case of *P. maculiventris*, our
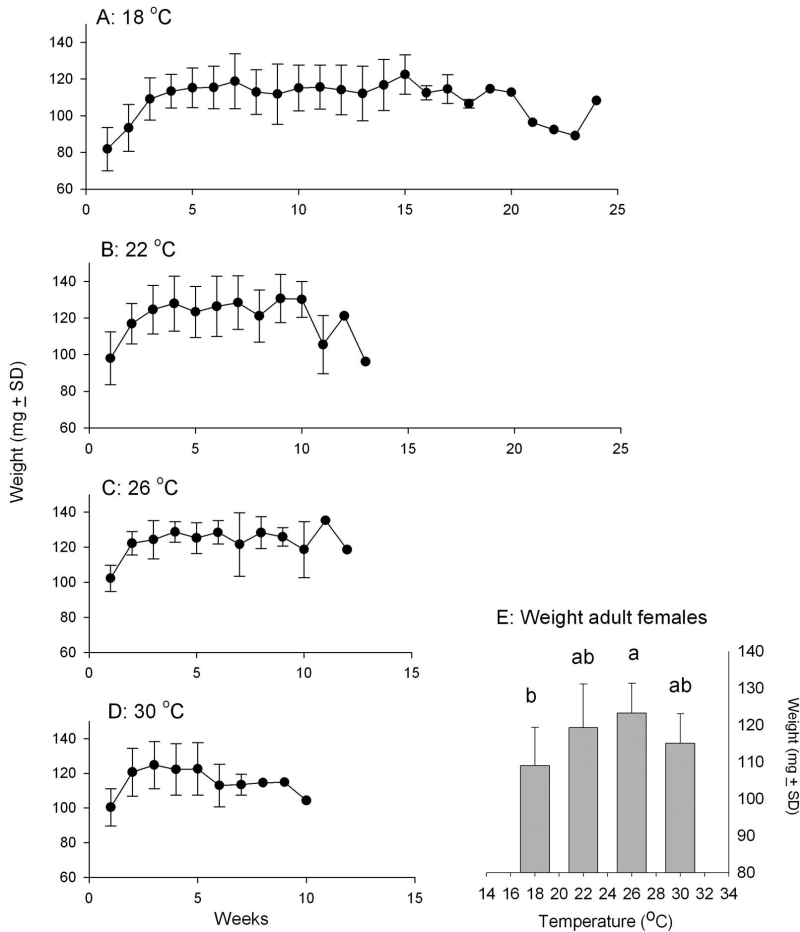
Fig. 6. Mean weights adult female *P. maculiventris*. Means (E) with different letters are significantly different (Tukey's HSD, $P < 0.05$).

findings suggest that 26°C is the optimal rearing condition but that female predators older than 21 d should not be used for rearing because they are no longer capable of laying viable eggs.

Table 5. Life table parameters for adult *P. maculiventris*

Parameter	Temperature (°C)			
	18	22	26	30
R_0	207.873	345.426	379.126	295.123
	(21.758)	(94.796)	(123.075)	(64.799)
GRR	294.972	491.273	643.640	403.394
	(26.252)	(111.687)	(140.855)	(68.824)
T	93.267	59.184	44.393	35.021
	(82.136)	(53.008)	(35.225)	(29.824)
r	0.0572	0.0988	0.1338	0.1623
	(0.0375)	(0.0859)	(0.1366)	(0.1398)
λ	1.0589	1.104	1.1431	1.1763
	(1.0376)	(1.0897)	(1.1464)	(1.15)
DT	12.118	7.015	5.1804	4.270
	(18.484)	(8.069)	(5.074)	(4.958)

Numbers in parentheses are calculations based on no. eggs that hatched.

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