Development and Life History of *Anthonomus eugenii* (Coleoptera: Curculionidae) at Constant Temperatures

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ABSTRACT Pepper weevil, *Anthonomus eugenii* Cano, is the major arthropod pest of peppers, *Capsicum* spp. L., in tropical and subtropical America. Adult weevils feed and oviposit in buds, flowers, and, especially, fruit. Larvae develop and feed inside those plant structures, thus reducing crop yields. Management is difficult and requires precise knowledge of developmental times and thresholds for maximum efficiency. Therefore, the developmental biology and life history parameters of *A. eugenii* were characterized in the laboratory on *Capsicum annuum* 'Jalapeño' fruits at seven constant temperatures ranging from 15 to 33°C. *A. eugenii* developed through three instars at all temperatures. Linear regression analysis estimated a lower developmental threshold of 9.6°C and a degree-day requirement of 256.4 for development from egg to adult. Fecundity increased with increasing temperatures to a maximum at 30°C but declined at 33°C. Net reproductive rate (R_o), intrinsic rate of increase (r_m), and finite rate of increase (λ) were greatest at 30°C, whereas development time and mortality were least at this temperature regimen. Thus, 30°C proved to be the optimal temperature for population increase because a maximum fecundity of 3.1 eggs/female/d, the shortest development time of 12.9 d, minimal mortality, and the highest life history parameters were obtained. This information should prove useful for predicting infestations, timing insecticide applications, and using other control strategies.

KEY WORDS *Anthonomus eugenii*, degree-days, life table analysis, pepper weevil, reproduction

PEPPER WEEVIL, *Anthonomus eugenii* Cano, is the major insect pest of all species of pepper (*Capsicum* spp.) in the southern United States (Elmore et al. 1934, Goff and Wilson 1937), Mexico (Quiñonez 1986), Central America (Andrews et al. 1986), and the Caribbean (Abreu and Cruz 1985). A recent review of the biology and management of *A. eugenii* revealed a lack of detailed knowledge on the biology and ecology of this widely distributed species (Riley and King 1994). Studies on its biology in the laboratory include only those by Elmore et al. (1934) and Gordon and Armstrong (1990). Unfortunately, these reports failed to give details on rearing conditions, particularly temperature, and present insufficient data for constructing life tables and degree-day models.

Temperature is probably the most important environmental factor affecting development in poikilothermic organisms and has been used to describe developmental rates (Sharpe and DeMichele 1977). The most widely used approach is thermal summation or the degree-day model. This method is commonly used for predicting insect biological processes controlled by heat accumulation and uses the linear portion of the rate versus temperature development curve (Pruess 1983, Higley et al. 1986). Comprehensive studies on the development for *A. eugenii* over a wide range of temperatures that would be necessary to allow for calculation of species-specific developmental rates (Wagner et al. 1984) are lacking.

Construction of life–fertility tables would help enhance pest management. Calculation of vital statistics such as intrinsic rate of increase, net reproductive rate, generation time, finite rate of increase, and doubling time help explain oscillations in population density and provide a better understanding of the population dynamics of a species (Southwood and Henderson 2000, Carey 2001).

Insecticides are commonly used to effectively suppress weevil populations, thereby avoiding yield losses; however, chemical control should be combined with other control tactics for an adequate long-term solution (Schuster et al. 1999). A sound pest management program for the pepper weevil should incorporate chemical, cultural, and biological control as well, which could require a more detailed understanding of pest biology. The objective of this study was to determine the effect of constant temperatures on development, survivorship, and reproduction of *A. eugenii*

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and to provide quantitative parameters for describing the population dynamics of the species.

Materials and Methods

Laboratory Pepper Weevil Colony. A laboratory colony of *A. eugenii* was established in Gainesville, FL, from adult weevils collected in Manatee and Collier counties, FL, in 1999, following procedures described by Toapanta (2001). The colony was initiated by confining 300–350 field-collected male and female adults in oviposition cages made of Plexiglas (50 by 40 by 40 cm) kept in a laboratory at the Division of Plant Industry, Department of Agriculture and Consumer Services, Gainesville, FL, at 20–24°C, 50–60% RH, and 14:10 (L:D)-h photoperiod. Forty to 50 'Jalapeño' and 'Serrano' pepper fruit were placed in the cages for weevil oviposition for 48–72 h. The fruit for weevil oviposition were tied in groups of 10 with wire and hung from hooks glued to each side of the cage walls to simulate the normal position in the plant. After oviposition, peppers were transferred to clear plastic boxes and maintained, under the same environmental conditions as described above, until emergence of adults occurred. Two 2.5-cm diameter holes were bored on each side of the boxes for air circulation and were sealed with silkscreen (Hunt Manufacturing, Statesville, NC). To absorb condensation, layers of paper towels were placed inside the box at the bottom and at the top with the lid. Emergence boxes were observed daily, and adult weevils emerging in the same week were aspirated with an electrical vacuum pump and confined to an oviposition cage as described above. A new cage was prepared every week, and four oviposition cages were maintained at the same time. One-month-old weevils were discarded, and at that time, a new oviposition cage was initiated. The colony was maintained primarily on the variety 'Serrano' obtained from a grower in Collier County, south Florida.

Development and Survival of Immatures. Development, survivorship, and reproduction were studied in Florida Reach-In incubation chambers (Walker et al. 1993) at seven constant temperatures (15, 18, 21, 24, 27, 30, and 33 ± 0.5°C), 60% RH, and 14:10 (L: D)-h photoperiod. This temperature range was chosen to include the linear portion of the developmental rate curve (Campbell et al. 1974) and was based on temperatures that normally occur during the summer and fall in Manatee County (Florida Automated Weather Network 2001). Every 5 s, a computer equipped with an analog-to-digital board and sensors monitored temperature and humidity in each chamber and compared the values with the setpoints (Walker et al. 1993). A mercury thermometer was also used daily to check the temperature in each chamber.

Development studies were initiated with weevil eggs obtained from a sample of 50 1-wk-old male and female weevils from the laboratory colony. The weevils were confined in a small Plexiglas cage (20 by 20 by 30 cm) from 0900 to 1100 hours with 10–15 immature 'Jalapeño' or 'Serrano' peppers. Pepper fruits were examined under a Nikon SMZ-1B dissecting microscope (Southern Micro Instruments, Atlanta, GA) to locate the weevil eggs. The oviposition plug covering the oviposition hole was detached using a no. 5 forceps with superfine tips (BioQuip, Gardena, CA), and the pericarp surrounding the egg was carefully removed. Twenty newly oviposited eggs (<6 h old) per temperature were transferred to mature 'Jalapeño' peppers using the tip of a no. 5 superfine forceps. The side of each pepper fruit had a 3 by 2-cm flap cut through the fruit wall with a scalpel. Two small punctures were made in the placenta of each fruit with the tip of the forceps, and an egg was deposited in each. The flaps were closed and sealed with one layer of stretched parafilm (American National Can, Greenwich, CT). Instruments were cleaned with 70% alcohol during the infestation process to avoid contamination. The artificially infested fruit were placed in the Florida Reach-In incubation chambers at the appropriate temperature. Because all immature stages are completed inside a fruiting structure (Elmore et al. 1934), immature weevils were transferred to new fruit whenever pepper fruit deterioration became apparent.

To determine the width, length, color, and surface morphology of eggs, weevil eggs ($n = 50$) <12 h old were obtained at a constant temperature of 27°C as explained above. Measurements were transformed and verified using a mini-scale tool (BioQuip), with a range of 5 mm and divisions of 0.1 mm.

To determine the number of weevil instars, 1- to 2-h-old weevil eggs ($n = 71$) were collected and artificially implanted into mature 'Jalapeño' peppers as described above at a constant temperature of 27°C. Weevil larvae were located by removing the parafilm from the pepper and carefully lifting the flap. After egg hatch, the width of the larval head capsule was recorded daily until pupation using a graticule installed in one of the eyepieces of the microscope and verified with the mini-scale.

To determine the development and survival of weevils at seven temperatures, larval head capsule measurements were recorded daily as described above until adult emergence. Cast head capsules were removed when detected, and on adult emergence, weevil sex was determined by characters described by Clark and Burke (1996).

The relationship between temperature and developmental rate (1/development time in days) of all stages was estimated with linear regression analyses (Campbell et al. 1974). Individual development times obtained from temperatures at 15, 18, 21, 24, 27, and 30°C were used to fit the linear regression models. The lower developmental threshold (t) was estimated by the "x-intercept" method (Arnold 1959). Values of t were obtained using the equation $t = -a/b$, where a is the y intercept and b is the slope of the line derived from the regression model. The degree-days required for development were calculated using the equation degree-days $= y(T - t)$, where y is the development time in days, T is the temperature (°C) during development, and t is the lower developmental threshold (°C) derived from the regression model (Sharpe and

DeMichele 1977). Degree-days were determined for each individual at each temperature.

Reproduction. Newly emerged adult weevils from the development study and from the laboratory colony were used to estimate fecundity, fertility, and adult longevity at the respective temperatures. On emergence, one male and one female were confined in a cylindrical transparent plastic container (11 cm length and 5 cm diameter; Thorton Plastics, Salt Lake City, UT), and the bottom was replaced with fine mesh for ventilation. A freshly excised 'Serrano' pepper fruit was placed into each container and replaced daily until the female had died. Containers were laid horizontally inside the environmental chamber to improve aeration and light exposure. The number of eggs and feeding punctures was recorded at the base, middle, and apex of each pepper fruit and egg hatch was monitored daily.

Life–Fertility Tables and Population Parameters. Summarized mortality and fertility data were used to form age-specific life–fertility tables for all cohorts at the seven temperatures (Southwood and Henderson 2000). Values included in the life–fertility tables were x_i, the pivotal age (d at the beginning of each age class); lx_i, the number surviving at the beginning of age class x_i; dx_i, the number dying in age interval x_i; qx_i, the proportion of mortality during age class x_i ($qx_i = dx_i/lx_i$); rx_i, the proportion of generation mortality at age interval x_i ($rx_i = dx_i/lx_1$), where lx_1, is the number in the initial cohort; Lx_i, the survivorship of age class x_i ($Lx_i = lx_i/lx_1$); and mx_i, the average number of female offspring produced per female per day [mx_i = (number of eggs laid on x_i) × (proportion of females produced in a cohort)/number of females laying eggs on x_i]. Other values such as number of eggs laid by a female, ratio of females within each cohort, and percent of offspring females alive until adulthood were calculated for each temperature using formulas given by Maia et al. (2000).

Values calculated from the life–fertility tables were used to estimate parameters related to the population growth potential at each temperature. These parameters included the net reproductive rate (R_o), the cohort generation time (T), the intrinsic rate of increase (r_m), the doubling time (Dt), and the finite rate of increase (λ) (Maia et al. 2000, Southwood and Henderson 2000).

Data Analyses. Mean egg width and length and width of head capsules (in mm) were recorded and calculated with PROC MEANS using all samples (SAS Institute 1994). Head capsule widths were subjected to a frequency distribution analysis and a test of independence between the head capsule measurements and instars using PROC FREQ (Sokal and Rohlf 1981, SAS Institute 1994). The formula of Gaines and Campbell (1935) and the constant of Dyar (1890) were used to define head capsule growth. A regression of the relationship between the natural logarithm of the width of the head capsule and the presumed instar number (independent variable) was performed to confirm that no instars were missed (Daly 1985). Measurements of the head capsule widths obtained from the 71 larvae at 27°C were compared using a general linear model (PROC GLM, SAS Institute 1994), and means between instars were separated using the least significant difference (LSD) test after a significant F test at $P \leq 0.05$ (SAS Institute 1994). Temperature effects on development times, fecundity, fertility, and oviposition period obtained at each temperature were evaluated using a general linear model (PROC GLM, SAS Institute 1994). Means were compared using the LSD after a significant F test with $\alpha < 0.05$ (SAS Institute 1994).

The Monte Carlo methods including jacknife and bootstrap tests (Manly 1991) were used to estimate the variance of the r_m estimate and extended to the other life table parameters as proposed by Meyer et al. (1986) and Maia et al. (2000). Briefly, those tests are based on recombining the original data, calculating pseudovalues of the parameter of interest for each recombination of the original data, and estimating the mean value and SE of the parameter of interest from the resulting frequency distribution of pseudovalues (Efron 1983). Confidence intervals for each estimated parameter were calculated using algorithms in a SAS program, which integrates an iterative method of calculation (Maia et al. 2000).

Results

Development. Weevil eggs were whitish-cream when newly oviposited, but turned yellow and then brown as they matured. They were ovoid, usually with a smooth surface, and rather soft, without surface ornamentation. Eggs were laid singly in oviposition holes made by adult females. All oviposition holes examined on pepper fruit contained a single egg and were sealed by the females with anal secretions. Before egg hatch, two eye spots and the tips of the darkly pigmented mandibles of the developing embryo were visible through the chorion. Mean width was 0.356 ± 0.002 mm and mean length was 0.493 ± 0.004 mm (n = 50 eggs). The mean incubation period for the eggs at 27°C was 2.0 ± 0.1 d.

The data indicated that *A. eugenii* had three instars. The frequency distribution analysis of the measurements of the head capsule widths of 71 individuals reared at 27°C indicated three discrete unimodal peaks, which did not overlap (Fig. 1), and three exuviae were collected from each larva reared from egg to pupa. A test of independence showed a highly significant association between the head capsule measurements and the number of instars established (χ^2 = 1160; df = 36; $P < 0.001$). Highly significant differences were detected among the means of the head capsule widths of the proposed three instars (F = 40792; df = 2,577; $P < 0.0001$), and the range of the head capsule widths for each instar did not overlap. The growth ratio or Dyar's constant of the head capsule of *A. eugenii* larvae was 1.5 between first and second instars and between the second and third instars (Table 1). The logarithm of the head capsule widths was plotted against the number of instars and resulted in a straight line, indicating no instars had

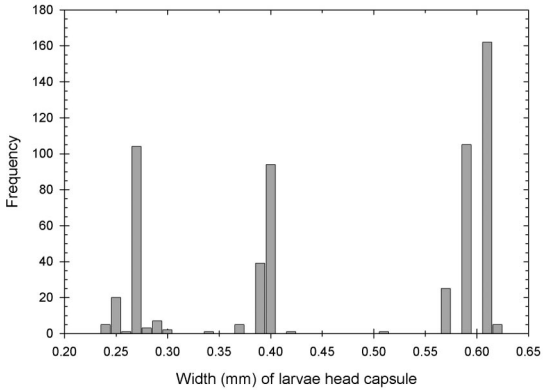

Fig. 1. Frequency distribution of head capsule measurements of *A. eugenii* maintained at 27°C, 60% RH, and 14:10 (L:D)-h photoperiod ($n = 71$).

been omitted. The regression equation obtained from these data was Ln Y = −1.73 + 0.40x and was highly significant ($P < 0.0001$, $r^2 = 0.99$; $n = 67$).

The mean development times for the first and second instars were not significantly different, but both were significantly less than that of the third instar ($F = 197.76$; df = 2,195; $P < 0.0001$; Table 1). The first molt occurred between 48 and 60 h, and the second molt occurred between 96 and 108 h after egg hatch. All larvae had pupated 10.5 d after eggs were implanted in the placenta of the peppers. Before pupation, the third-instar larva formed a pupal cell in the placenta of the pepper by lining it with excrement. The larva rested inside the cavity and very little activity followed. The pupal stage averaged 2.4 ± 0.1 d, and mean development time from egg to adult was 12.9 ± 0.2 d. Survivorship to pupation was 94%.

A significant decrease in development time was observed for each life stage of *A. eugenii* with each successive increase in temperature up to but not including 33°C, the highest temperature tested (Table 2). Total development time from egg to adult (mean ± SEM) decreased from 41.8 ± 0.6 d at 15°C to 12.9 ± 0.2 d at 30°C, but increased to 15.8 ± 0.6 d at 33°C. Although the duration of stages varied with temperature, the proportion of total development time spent in each stage was relatively consistent regardless of temperature. The eggs required between 17 and 21% of total development time, the larvae between 53 and 65%, and the pupae between 16 and 26%. The proportion of total larval development time for each instar of *A. eugenii* was also consistent regardless of temperature (Table 2).

Linear regression parameters describing the relationship between development rate (y) and temperature (x) of *A. eugenii* estimated 9.6°C for the lower development threshold (t) and a total of 256.4 DD for egg to adult development (Table 3). The estimated lower developmental threshold (t) ranged from 7.9 (first instar) to 12.4°C (second instar). The coefficient of determination value for the regression of total development from egg to adult estimated that 92% of the total variation in developmental rate was explained by temperature. The data from the highest temperature tested (33°C) were not included in the regression model because the values were considered beyond the linear portion of growth responsive to temperature (Sharpe and DeMichele 1977) and because the upper developmental threshold was apparently reached (Campbell et al. 1974).

Reproduction. Temperature affected the reproductive life parameters of *A. eugenii* females (Table 4). Total fecundity tended to increase with increasing temperature, except at 27 and 33°C, and it differed significantly ($F = 82.9$; df = 6,3462; $P < 0.0001$). Fecundity was highest at 30°C and lowest at 18°C. Although temperature significantly affected fertility ($F = 4.85$; df = 6,2080; $P < 0.0001$), there was no trend over the entire temperature range, with the highest fertility obtained between 24 and 30°C. The oviposition period differed significantly among all temperatures tested ($F = 2.7$; df = 6,42; $P < 0.02$), with the period tending to be longer at temperatures below 27°C (Table 4).

Regardless of temperature, female weevils deposited significantly more eggs at the base of the fruit (stem end of the fruit, through or near the calyx of the fruit) than at the middle and apex of the fruit ($F = 1178$; df = 2,10421; $P < 0.0001$). Of the total number of eggs oviposited in the pepper fruit, 63–78% were found at the base, 14–25% at the middle, and 4–18% at the apex. Fecundity significantly differed among temperatures at the base ($F = 81.2$; df = 6,3475; $P < 0.0001$), middle ($F = 15.1$; df = 6,3475; $P < 0.0001$), and apex ($F = 6.9$; df = 6,3475; $P < 0.0001$) of the fruit. Fertility of eggs was significantly different among temperatures at the base ($F = 3.5$; df = 6,1894; $P < 0.001$), middle ($F = 8.3$; df = 6,622; $P < 0.0001$), and apex ($F = 4.1$; df = 6,342; $P < 0.0005$) of the fruit (Table 4).

The total number of feeding punctures on a pepper fruit was significantly different among temperatures ($F = 62.7$; df = 6,3462; $P < 0.0001$), with the highest

Table 1. Head capsule widths, inter-instar ratios, and development time of larvae of *A. eugenii* maintained at 27°C, 60% RH, and 14:10 (L:D)-h photoperiod

Instar	*N*	Head capsule width (mm)		Dyar's constant	Development time (d) (mean ± SEM)
		Mean ± SEM	Range		
First	71	0.264 ± 0.001	0.233–0.300	—	2.0 ± 0.07
Second	69	0.394 ± 0.001	0.333–0.500	1.50	2.0 ± 0.11
Third	67	0.591 ± 0.001	0.566–0.616	1.50	4.4 ± 0.12
LSD $P \leq 0.05$		0.002			0.3

Table 2. Effect of temperature on development time of immature life stages of *A. eugenii* reared on 'Jalapeño' peppers at 60% RH and 14:10 (L:D)-h photoperiod in the laboratory

Temperature (°C)	*n*	Egg	*n*	First instar	*n*	Second instar	*n*	Third instar	*n*	Total for instars	*n*	Pupa	*n*	Egg to adult
15	20	7.8 ± 0.3 (18.2)	19	5.3 ± 0.3 (12.4)	16	6.0 ± 0.3 (14.2)	15	16.4 ± 0.4 (38.9)	15	27.4 ± 0.5 (65.5)	14	6.8 ± 0.5 (16.3)	14	41.8 ± 0.6
18	20	7.1 ± 0.5 (18.4)	19	4.6 ± 0.3 (12.4)	19	4.6 ± 0.3 (12.3)	19	12.5 ± 0.9 (34.3)	19	21.5 ± 1.1 (58.9)	17	7.8 ± 0.5 (22.6)	15	35.9 ± 1.4
21	20	4.3 ± 0.2 (18.0)	19	2.2 ± 0.2 (9.4)	18	2.9 ± 0.2 (12.8)	18	7.9 ± 0.4 (35.0)	18	12.9 ± 0.5 (57.1)	18	5.7 ± 0.3 (25.5)	18	22.7 ± 0.6
24	20	3.5 ± 0.1 (19.5)	20	2.0 ± 0.2 (12.1)	20	2.7 ± 0.2 (14.9)	18	5.7 ± 0.5 (32.2)	18	10.4 ± 0.5 (59.1)	18	3.7 ± 0.2 (21.3)	18	17.5 ± 0.4
27	20	2.9 ± 0.1 (20.9)	20	1.7 ± 0.1 (11.9)	20	1.7 ± 0.1 (12.3)	20	4.1 ± 0.2 (29.2)	19	7.5 ± 0.3 (53.4)	19	3.6 ± 0.1 (25.7)	18	13.9 ± 0.3
30	20	2.1 ± 0.2 (16.6)	20	1.8 ± 0.1 (13.6)	20	1.4 ± 0.1 (10.9)	20	4.7 ± 0.2 (36.7)	20	7.9 ± 0.3 (61.2)	19	2.8 ± 0.2 (22.9)	19	12.9 ± 0.2
33	20	2.8 ± 0.3 (17.3)	18	1.9 ± 0.2 (10.6)	17	1.8 ± 0.3 (11.3)	17	6.4 ± 0.4 (38.9)	17	10.1 ± 0.4 (60.9)	13	3.5 ± 0.3 (21.8)	13	15.8 ± 0.6
LSD $P \leq 0.05$		0.7		0.6		0.6		1.3		1.7		0.9		1.8

Numbers in parentheses are the percentage of development time for each life stage.
Mean days ± SEM required to complete development at given stage.

number of punctures observed at 27°C and the lowest at 15°C (Table 5). As found for fecundity, regardless of temperature, the weevils produced a significantly higher number of feeding punctures at the base of the fruit compared with the middle and apex of the fruit ($F = 1052$; df = 2,10421; $P < 0.0001$).

Life–Fertility Tables and Population Parameters. Life–fertility tables were constructed for all cohorts at each temperature (data not shown). Survivorship curves derived from Lx_i of all cohorts are shown in Fig. 2. Degree-days rather than days of development were used so that the curves of cohorts reared at different temperatures could be compared on a standardized x-axis. Temperatures most favorable for *A. eugenii* survival were 21, 27, and 30°C. Mortality at 15 and 33°C was greater at the third-instar and pupal stages compared with the other temperatures (Fig. 2).

Population reproductive statistics and their respective 95% confidence limits were calculated for *A. eugenii* from the life–fertility tables (Table 6). Nonoverlapping 95% limits corresponds to the rejection of the hypothesis of no temperature effect ($\alpha = 0.05$) based on one- or two-tailed tests. Each life table parameter calculated was significantly affected by temperature (Table 6). Net reproductive rate, intrinsic rate of increase, and finite rate of increase were greatest at 30°C, and conversely, doubling time and generation time were the lowest. The net reproductive rate increased from nine females per female at 18°C to 27 females per female at 24°C, decreased at 27°C, and significantly increased to reach the highest value at 30°C. Intrinsic rate of increase and finite rate of increase significantly increased between 18 and 27°C and reached its highest value at 30°C. Maximum reproduction for *A. eugenii* occurred at 30°C, where the net reproductive rate, the intrinsic rate of increase, and the finite rate of increase were the greatest, doubling time the lowest, and generation mortality was the least (5%; Table 6; Fig. 2). These results indicate that the optimal temperature for population increase of *A. eugenii* was around 30°C.

Discussion

In this study, pepper fruit were suitable hosts for rearing *A. eugenii* and for weevil oviposition, development, and survival. Previously, nightshade fruit have been shown capable of supporting immature weevil development as well (Patrock and Schuster 1992), without major effects on the development time and survival of the weevils.

The dimensions of the pepper weevil egg recorded here were ≈9% less than the average length and width recorded previously by Elmore et al. (1934), but as much as 47% less than the egg measurements recorded in Puerto Rico (Gordon and Armstrong 1990). The eggs checked in this study were deposited by 3- to 5-d-old weevils reared in a laboratory colony as explained above; however, previous reports did not mention the age of the females used or their origin (Elmore et al. 1934, Gordon and Armstrong 1990). Thus, the

Table 3. Parameters of linear regression models using developmental rate as the dependent variable and temperature as the independent variable and the lower developmental thresholds (t) and degree-days for immature life stages of *A. eugenii* at temperatures from 15 to 30°C, 60% RH, and 14:10 (L:D)-h photoperiod

Stage	Intercept ± SEM	Slope ± SEM	R^2	P	t (°C)	Degree-days ± SEM
Egg	−0.288 ± 0.047	0.025 ± 0.002	0.612	<0.01	11.22	41.29 ± 1.09
First instar	−0.259 ± 0.090	0.032 ± 0.003	0.409	<0.01	7.88	35.67 ± 1.18
Second instar	−0.550 ± 0.077	0.044 ± 0.003	0.641	<0.01	12.44	24.54 ± 0.84
Third instar	−0.134 ± 0.026	0.013 ± 0.001	0.576	<0.01	10.24	83.28 ± 2.18
Total larva	−0.072 ± 0.008	0.007 ± 0.000	0.779	<0.01	10.14	145.49 ± 2.87
Pupa	−0.160 ± 0.050	0.017 ± 0.002	0.435	<0.01	8.94	60.93 ± 1.72
Egg to adult	−0.038 ± 0.002	0.003 ± 0.000	0.921	<0.01	9.64	256.41 ± 3.41

differences in the egg dimensions found here might be caused by nutritional and/or physiological factors.

Similarly, comparisons of development times of *A. eugenii* with previous reports are difficult to make, because temperature, humidity, and habitat were not established and/or were not mentioned in the few reports available on the biology of the pepper weevil. The mean egg incubation period of 2.9 d recorded here at 27°C was similar to that reported by Goff and Wilson (1937) during the month of June under Florida conditions, but was lower than the 4.3 d reported by Elmore et al. (1934) in California. The latter researchers did not mention the temperature regimen used to rear the eggs, which significantly impacted incubation time in this study. In Puerto Rico, Gordon and Armstrong (1990) used a temperature that varied from 22 to 28°C and reported an incubation period of 3.6 d, which agreed with the value obtained here at 24°C.

The head capsule widths of larvae of *A. eugenii* and the frequency analysis indicated three, well-defined instars (Table 1), which agrees with previous reports for other Anthonomine weevils (Amhad and Burke 1972). The close fit of the regression line, along with the calculation of the constant of Dyar (1890), indicates that no instar was overlooked. Measurements of the head capsule width of the boll weevil, *A. grandis*, also showed three well-defined instars (Parrott et al. 1970). Based on previous data for the boll weevil head capsules, the growth ratio between the first and second instars was 1.5 and between second and third instars was 1.6 (Parrott et al. 1970), which were the same or nearly the same as those for *A. eugenii* (Table 1). The constancy of the growth ratios across species may be related to their similar mode of feeding inside flower and fruit structures (Burke 1976). There are no previous reports on the determination of instars for *A. eugenii* larvae using the width of the head capsule; thus, these data represent the first report on the determination of the instars of *A. eugenii.*

The development of *A. eugenii* was characteristic of poikilothermic organisms. Development rates were nonlinear at both high and low temperatures but were linear at intermediate temperatures (Sharpe and DeMichele 1977) (Table 2). *A. eugenii* survived and developed on 'Jalapeño' peppers better over the temperature range of 21–30°C than at the extremes of 15 or 33°C.

More than 50% of total larval development time of *A. eugenii* occurred in the third instar. The same pattern of development was found previously for *A. eugenii* (Elmore et al. 1934), as well as for *A. grandis* when reared at 29.4°C and 50% RH (Parrott et al. 1970). The mean larval development time of 9.5 d obtained by Gordon and Armstrong (1990) fell between the values obtained here at 24 and 27°C. The mean development time for each instar recorded here is the first report for development of *A. eugenii* by instar under controlled temperature and humidity conditions. The egg to adult developmental values for *A. eugenii* under "laboratory conditions" reported by Elmore et al. (1934) (host not given) and by Gordon and Armstrong (1990) on pepper fruit fell between the values of 21 and 24°C obtained in this study. Total development time from egg to adult reported by El-

Table 4. Reproductive parameters for *A. eugenii* according to position of eggs in pepper fruit at constant temperatures, 60% RH, and 14:10 (L:D)-h photoperiod (n = 8 females per temperature)

Temperature (°C)	Total		Base		Middle		Apex		LSD[a] value $P \leq 0.05$		Oviposition period (d)
	Fecundity (eggs/female)	Fertility (% hatch)	Fecundity	Fertility	Fecundity	Fertility	Fecundity	Fertility	Fecundity	Fertility	
15	0.9 ± 0.1	86.2 ± 1.5	0.7 ± 0.0	90.2 ± 1.6	0.2 ± 0.0	69.7 ± 4.9	0.1 ± 0.0	72.9 ± 5.5	0.07	9.8	71.5 ± 15.8
18	0.8 ± 0.0	90.4 ± 2.1	0.6 ± 0.0	89.2 ± 1.9	0.1 ± 0.0	88.6 ± 3.7	0.1 ± 0.0	73.3 ± 11.8	0.06	14.2	74.0 ± 16.0
21	1.9 ± 0.1	85.7 ± 1.7	1.4 ± 0.1	85.6 ± 1.7	0.3 ± 0.0	91.2 ± 3.0	0.1 ± 0.0	86.9 ± 4.5	0.12	NS	76.1 ± 14.6
24	2.1 ± 0.1	91.9 ± 1.2	1.6 ± 0.1	92.1 ± 1.2	0.3 ± 0.0	94.9 ± 2.0	0.2 ± 0.0	91.8 ± 3.0	0.13	NS	75.9 ± 13.9
27	1.7 ± 0.1	93.3 ± 1.2	1.2 ± 0.1	93.3 ± 1.4	0.3 ± 0.0	91.6 ± 2.9	0.2 ± 0.0	91.7 ± 3.7	0.12	NS	52.0 ± 9.4
30	3.1 ± 0.1	90.2 ± 1.3	2.3 ± 0.1	90.1 ± 1.5	0.6 ± 0.1	95.1 ± 1.6	0.2 ± 0.0	93.8 ± 3.0	0.19	NS	50.6 ± 8.2
33	1.5 ± 0.1	82.3 ± 2.9	1.0 ± 0.1	83.3 ± 3.2	0.4 ± 0.1	88.8 ± 3.4	0.2 ± 0.1	80.0 ± 7.4	0.20	NS	34.4 ± 5.4
LSD $P \leq 0.05$	0.2	4.8	0.2	5.0	0.1	8.7	0.1	14.4			28.8

Values are mean ± SEM.

[a] LSD values to test for differences among the base, middle, and apex of the pepper fruit at each temperature.

NS, not significant at $P \leq 0.05$ according to the LSD test.

Table 5. Mean no. of feeding punctures made by adults of *A. eugenii* according to position within a pepper fruit at seven constant temperatures, 60% RH, and 14:10 (L:D)-h photoperiod (n = 8 female and male weevils per temperature)

Temperature (°C)	Total	Base	Middle	Apex	LSD $P \leq 0.05$
15	2.06 ± 0.09	1.45 ± 0.06	0.25 ± 0.03	0.36 ± 0.04	0.13
18	2.40 ± 0.14	1.54 ± 0.07	0.43 ± 0.05	0.43 ± 0.06	0.16
21	2.74 ± 0.13	2.11 ± 0.08	0.31 ± 0.04	0.33 ± 0.05	0.16
24	3.79 ± 0.17	2.50 ± 0.10	0.61 ± 0.06	0.69 ± 0.07	0.21
27	6.11 ± 0.34	3.65 ± 0.17	1.42 ± 0.16	1.04 ± 0.10	0.39
30	5.37 ± 0.28	3.57 ± 0.14	0.90 ± 0.09	0.91 ± 0.11	0.32
33	5.01 ± 0.27	3.34 ± 0.16	0.79 ± 0.12	0.87 ± 0.11	0.36
LSD $P \leq 0.05$	0.49	0.28	0.20	0.18	

Values are mean ± SEM feeding punctures per pepper fruit.

more et al. (1934) during the summer in California is almost 2 d shorter (20 d) than here at 21°C (22.7 d); and the 16.4 d obtained by Gordon and Armstrong (1990) is 1 d shorter than that obtained at 24°C (17.5 d). In another study, using a temperature range of 25.7–27.7°C, total development times were 14.1 and 13.8 d on pepper and nightshade fruits, respectively (Wilson 1986). These observations agree with those obtained in this study at 27°C (13.9 d; Table 1). Interestingly, when pepper weevils were reared on an artificial diet at a temperature of 26.5°C (Toba et al. 1969), the total development time was 17.5 d, which was the same as that obtained in this study, but at the lower temperature of 24°C. Thus, artificial diet seemed to have a negative effect on development rate. Genung and Ozaki (1972) in Florida obtained a similar development time of 17.5 d at 23.9–26.7°C, which agreed with the value obtained here at 24°C.

Degree-days for total development from egg to adult calculated for *A. eugenii* using the lower developmental threshold t of 9.6°C were 256.4 on 'Jalapeño' pepper (Table 3). This is the first report of the determination of lower developmental threshold and number of degree-days required for the weevil to complete development. Although t ranged from 7.9 (first instar) to 12.4°C (second instar), there was no statistical evidence to conclude that t estimates were different among life stages. Differences in t among insect life stages have been observed for the carrot weevil, *Listronotus texanus* (Stockton) (Woodson and Edelson 1988), and the borer *Diatraea lineolata* (Walker) (Rodríguez del Bosque et al. 1989). The thresholds reported here for *A. eugenii* are in accordance with recommendations on standardized development thresholds reported earlier (Pruess 1983).

The oviposition behavior of weevils observed in the laboratory colony was similar to descriptions made on the oviposition behavior of pepper weevils recorded earlier from California (Elmore et al. 1934) and from Florida (Goff and Wilson 1937). This type of oviposition, in which a single egg is placed in a hole prepared with the rostrum of the adult weevil in fruit or seedpod, is known in other species of weevils. It has been recorded in *Curculio niveopictus* (Lea) (Coleoptera: Curculionidae), in *Apion ulicis* Forster (Coleoptera: Apionidae), and in *Merynchites bicolor* (Fabricius) (Coleoptera: Attelabidae) by Howden (1995), who called it category 8, among various oviposition behaviors. She noted that, in this category, females drill the oviposition hole into the fruit using the rostrum, inserting it up to the eyes. However, it is known that *A. eugenii* females also oviposit in flower buds (Elmore et al. 1934, Patrock and Schuster 1992) in a hole prepared with the rostrum, which Howden (1995) called category 7. Thus, these data suggest that *A. eugenii* females fall under both categories. A similar type of oviposition behavior also was observed and described for the boll weevil, *A. grandis*, when ovipositing in cotton squares (Hunter and Pierce 1912) and in flower buds of the tree, *Hampea nutricia* Fryxell, in Mexico (Stansly and Cate 1984). Ovipositional sites on the plants vary considerably among species of the subfamily Anthonominae as well as within some species (Burke 1976). In this study, a single egg was found in each oviposition hole. A single egg per hole was also observed in most species of Anthonomine weevils (Burke 1976), as well as in *C. niveopictus* and *M. bicolor* (Howden 1995).

Oviposition of female *A. eugenii* weevils on a pepper fruit peaked at 30°C (3.1 eggs/female/d) with a mean oviposition period of 51 d (Table 4). Previous reports on pepper weevil oviposition rates were higher than the value recorded here. For example, the present maximum value of 3.1 eggs/female/d was less than one-half of the estimates of 7.1 and 8 reported by Wilson (1986) and Gordon and Armstrong (1990), respectively. Recently, Seal et al. (2000) reported an oviposition rate of 5.3 eggs/female on pepper leaves, held with parafilm around glass marbles, hanging from cage walls. Elmore et al. (1934) and Goff and Wilson (1937) reported daily oviposition rates of 4.7 and 6.6 eggs per female with an oviposition period of 72 and 30 d, respectively, although the substrate was not identified.

In this study, pepper weevils were able to oviposit at all temperatures tested, with the fertility being the highest between 24 and 27°C and the lowest at 15 and 33°C (Table 4); however, the longest oviposition period occurred at the lowest temperature. Information has been lacking on fertility and on the oviposition period for the pepper weevil. Previous reports failed to record fertility for this pest, and this variable was not mentioned in a review on the biology of the pepper weevil (Riley and King 1994). Low fecundity and fertility were also reported for *A. grandis* at temperatures <18 and >32°C (Hunter and Pierce 1912, Cole

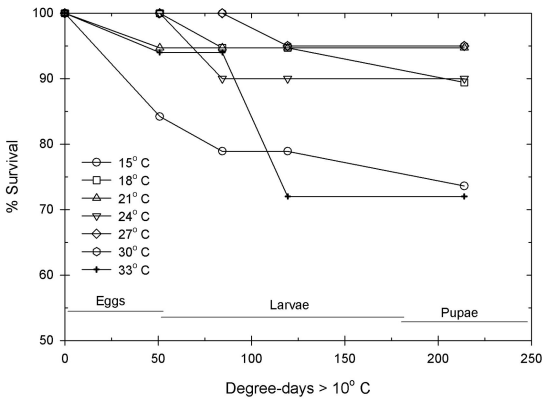

Fig. 2. Survival of immatures of *A. eugenii* on pepper fruit at seven constant temperatures, 60% RH, and 14:10 (L:D)-h photoperiod.

and Adkisson 1981, 1982,) and for *L. texanus* at 10°C (Woodson and Edelson 1988).

Weevils preferred the base of the pepper to oviposit and feed compared with the middle and apex of the fruit, regardless of temperature (Tables 4 and 5). This is the first report on the position of the eggs and feeding punctures by the pepper weevil within the pepper fruit. Hunter and Pierce (1912) found that the majority of egg punctures by *A. grandis* were made on a line about halfway between the base and the apex of the flower bud and only rarely appeared below this line. They also observed that almost invariably egg punctures were started through the calyx in preference to the tenderer portion of the square. The majority of oviposition and feeding of pepper weevils also occurred near or through the calyx on young fruit. It might be easier for the weevil to drill the oviposition hole or feed from the calyx. Another advantage for pepper weevils ovipositing through the calyx could be because of the wound healing capabilities of the calyx tissue, which may help seal the oviposition hole more thoroughly. In contrast, oviposition holes made in the middle and apex of the fruit are covered only by the slight filling of mucilaginous anal secretion deposited by the weevil, similar to the one reported for *A. grandis* (Hunter and Pierce 1912).

Survivorship of the cohorts reared at 15 and 33°C followed a type IV curve, where mortality is greater at early life stages (Southwood and Henderson 2000). Survivorship of cohorts at other temperatures exhibited characteristics of both types IV and I, where mortality occurs at early as well as late life stages. Extreme temperatures such as 15, 18, and 33°C were expected to have negative effects on population development parameters. Therefore, it was not surprising that the values for R_o, r_m, and λ at these temperatures were lower than the respective values for the intermediate temperatures of 21–30°C. The values for T and Dt were higher at the extreme temperatures, also as expected.

Population reproductive statistics for *A. eugenii* on pepper fruit or other hosts are not available for comparison. Seal et al. (2000) reported the highest r_m of 0.129 and the lowest *T* of 17.7 d at 25°C, which differed with results of this study; however, these authors did not give details on the rearing conditions nor did they detail procedures used to obtain the estimated parameters. No other studies have reported population parameters for *A. eugenii.* Interestingly, the values of r_m, λ, and T estimated for *A. grandis* reared in the laboratory (Stansly 1985) agreed well with estimates obtained here at 30°C; however, the R_o estimate calculated for the boll weevil was much higher than that calculated for the pepper weevil.

In conclusion, *A. eugenii* development, reproduction, fecundity, and fertility were temperature-dependent. Weevils preferred the base of the pepper to oviposit and feed compared with the middle and apex of the fruit. The number of instars for the pepper weevil (three) was identical at all temperatures tested. Mortality was minimal and fecundity was maximal at 30°C. Reproduction parameters were different

Table 6. Life table parameters and ±95% confidence limits for *A. eugenii* at seven constant temperatures, 60% RH, and 14:10 (L:D)-h photoperiod

Temperature (°C)	Net reproductive rate (R_o)[a]	Intrinsic rate of increase (r_m)[b]	Generation time (T)[c]	Doubling time (Dt)[c]	Finite rate of increase (λ)[b]
15	15.38	0.0360	76.42	19.18	1.036
	8.02–22.76	0.0306–0.0413	63.80–89.03	16.37–21.99	1.031–1.042
18	8.81	0.0330	67.25	20.59	1.033
	2.33–15.30	0.0232–0.0429	54.55–79.95	14.06–27.13	1.023–1.043
21	25.15	0.0610	52.51	11.21	1.062
	12.00–38.30	0.0439–0.0780	36.12–68.90	8.30–14.12	1.044–1.081
24	27.19	0.0539	61.40	12.79	1.055
	11.23–43.16	0.0458–0.0620	44.60–78.20	10.95–14.63	1.046–1.063
27	11.76	0.0691	35.79	9.97	1.071
	6.26–17.27	0.0585–0.0798	28.06–43.52	8.47–11.48	1.060–1.083
30	33.57	0.1088	32.39	6.35	1.115
	19.04–48.11	0.0989–0.1187	27.83–36.96	5.78–6.93	1.103–1.126
33	4.99	0.0547	30.10	12.42	1.056
	1.69–8.29	0.0372–0.0722	20.54–39.65	8.12–16.71	1.037–1.074

[a] Female/female.
[b] Female/female/d.
[c] Day.

across the range of temperatures tested. Population growth seems optimal at 30°C, because *A. eugenii* has a greater reproductive capacity at this temperature.

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