Life Table Analysis for *Cactoblastis cactorum* Immatures and Female Adults under Five Constant Temperatures: Implications for Pest Management

JESUSA CRISOSTOMO LEGASPI[1] AND BENJAMIN C. LEGASPI, JR.[2]

USDA–ARS–CMAVE, Center for Biological Control, Florida A&M University, 6383 Mahan Drive, Tallahassee, FL 32308

ABSTRACT   The cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), was reported in Florida in 1989, and it is expanding its geographical range to threaten *Opuntia* cactus (Cactaceae) in the southwestern United States, into Mexico, where it is an important economic crop. Laboratory life history studies were conducted at 18, 22, 26, 30, and 34°C to understand cactus moth biology and to develop strategies for control. Duration of immature stages was generally longest at 18°C, declining significantly at 22°C, and shortest at 26, 30, and 34°C. Total immature developmental time from eggs to pupae was ≈180 d at 18°C, 116 at 22°C, and ranged from 65 to 72 d at 26–34°C. Developmental rate for egg-to-pupal stages was estimated using the logistic equation, $rate = 0.0165/(1 + (T/20.7093)^{-5.8823})$. Percentage survival of immatures was usually lowest at the temperature extremes tested (18 and 34°C), but they did not differ between the sexes. Estimated lower developmental threshold temperature was 13.3°C, resulting in estimated degree-days for development from ≈845 at 18°C to 1,387 at 34°C. In general, pupal weights declined with increasing temperature, and they were always lower in males than in females. Female adult survivorship was longest at 18°C, and shortest at 34°C, with the other treatments clustered between the temperature extremes. The highest reproductive values were found at 30°C, which indicates an approximate optimal temperature. Net reproductive rate (R_0), gross reproductive rate (*GRR*), generation time (*T*), intrinsic rate of increase (*r*), finite rate of increase (*λ*), and doubling time (*DT*) were 43.68 ♀/♀, 44.02 ♀/♀, 67.14 d, 0.0562 ♀/♀/d, 1.058 ♀/♀/d, and 12.33 d, respectively. An oviposition rate surface describing mean oviposition rate as a function of time and temperature was, $eggs = (-11.241 + 0.854T) \, d \exp (-0.020Td)$. Given the life history characteristics found in this study and other studies, cost-effective pest management strategies against *C. cactorum* are discussed.

KEY WORDS   cactus moth, life history, *Opuntia cacti*, development, fecundity

The cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), is widely cited as an example of successful classical biological control after its importation into Australia from Argentina in 1926 to control invasive species of *Opuntia* cacti (Cactaceae) (DeBach 1974). Its historic role as a biological control agent is well documented (Simmonds and Bennett 1966, Mahr 2001, van Driesche and Bellows 2001, Stiling 2002). Consequently, much of the biology, ecology, and control of the moth were summarized by Mahr (2001) (and articles in the same volume) and by Zimmermann et al. (2000, 2004). Ironically, this textbook example of successful biological control has recently been cited as a cautionary case of the risks caused by unintended consequences of introduced control agents (Zimmermann et al. 2000). In 1989, *C. cactorum* was reported in south Florida, its first documented occurrence in mainland North America (Mahr 2001). The method by which *C. cactorum* was introduced into Florida is unknown, but a compelling possibility was through commercial importations of *Opuntia* spp. from the Dominican Republic into Miami (Pemberton 1995). By 1999, *C. cactorum* had spread northward by natural dispersal, and it was found throughout the eastern Florida coastline and as far north as Tampa on the western coast (Hight et al. 2002). By 2002, the moth was reported as far west as Pensacola in Florida and as far north as Charleston, SC, along the eastern coast (Hight et al. 2002). Most recent published reports in July, 2004, show populations on Dauphin Island, AL ,and in Bull Island, SC, ≈80 km north of Charleston (Simonson et al. 2005). In Florida, *C. cactorum* attacks several species of endemic cacti, including rare species such as the Florida semaphore cactus, *Opuntia spinosissima* (Martyn) Mill (Cactaceae)

Table 1. Immature development of *C. cactorum*[a] (mean ± SE; days)

Life stage	Temp (°C)					Statistics
	18	22	26	30	34	
Egg	47.90 ± 0.28a	29.60 ± 0.22b	22.50 ± 0.22c	20.90 ± 0.23d	22.90 ± 0.35c	$F = 1788.44$; df = 4, 45; $P < 0.001$; $R^2 = 0.99$
Larva	78.39 ± 2.58a	61.36 ± 2.77b	33.52 ± 0.61c	29.89 ± 0.80c	30.08 ± 1.05c	$F = 147.74$; df = 4, 45; $P < 0.001$; $R^2 = 0.93$
Pupa	53.46 ± 1.52a	24.91 ± 0.14b	16.28 ± 0.51c	13.88 ± 0.66c	13.79 ± 0.67c	$F = 407.76$; df = 4, 45; $P < 0.001$; $R^2 = 0.98$
Complete	179.86 ± 2.92a	115.96 ± 2.84b	72.22 ± 0.79c	64.75 ± 0.88c	67.04 ± 1.65c	$F = 587.43$; df = 4, 45; $P < 0.001$; $R^2 = 0.98$
DD[b]	845.34	1,008.85	917.19	1,081.32	1,387.73	

[a] $n = 10$; within each row, means followed by different letters are significantly different (Tukey HSD; $P = 0.05$).
[b] Degree-days for development from eggs to pupae, assuming a lower temperature threshold for development of 13.3°C.

(Zimmermann et al. 2000); and the Spanish lady, *Opuntia triacantha* (Willd.) Sweet (Solis et al. 2004). The moth also was recorded on other *Opuntia* cacti, including *Opuntia stricta* (Haw.) Haw., *Opuntia pusilla* (Haw.) Nutt., *Opuntia humifusa* (Raf.) Raf., *Opuntia cochenillifera* (L.) Mill., and *Opuntia ficus-indica* (L.) Miller (Solis et al. 2004). The westward migration of the moth is estimated at 160 km/yr, and it projected to arrive at the Texas border in 2007 (Solis et al. 2004).

Despite its obvious threat to endemic *Opuntia* cacti, *C. cactorum* is perhaps not perceived as a serious problem to U.S. agriculture because the cacti are grown primarily as ornamental plants in Arizona, California, Nevada, New Mexico, and Texas. Nursery production is highest in Arizona (wholesale and retail values of $4.5 and $9.5 million, respectively), followed by southern California (Irish 2001). In contrast, *Opuntia* cacti are very important to the agriculture of Mexico and Central America (Soberón et al. 2001, Zimmermann et al. 2004). Because of the high protein content in the cladodes (modified stems) and high water content in the tissues, the cacti have a wide range of uses, including food, fodder, cosmetics, and adhesives. More than 250,000 ha is cultivated in Mexico, producing 2.5% of value of agricultural products and economic revenue of ≈$50 million annually (from 1990 to 1998) (Soberón et al. 2001, Stiling 2002).

Information on the basic reproductive biology of *C. cactorum* will be essential in developing control strategies in anticipation of its arrival into Texas and Mexico. Here, we report on detailed life history studies of *C. cactorum* immatures and female adults at five constant temperatures.

Materials and Methods

Temperature Treatments. Methods used for studies on the effects of selected temperatures on the development of *C. cactorum* were similar to those described previously (Legaspi 2004, Legaspi and Legaspi 2005). *C. cactorum* immatures and adult females were studied under five constant temperatures: 18, 22, 26, 30, and 34°C. Constant temperature conditions were maintained inside ThermoForma model 3740 growth chambers (ThermoForma, Marietta, OH) with a photoperiod of 14:10 (L:D) h and 50 ± 10% RH. Temperature and relative humidity inside each chamber were monitored by HOBO recorders (Onset Computer Corp., Bourne, MA). A small basin of water was placed in each chamber to maintain humidity.

***C. cactorum* Immatures.** For each temperature treatment, 10 newly laid cactus moth egg sticks (≈40–60 eggs per egg stick) were selected from the laboratory colony. The egg sticks were placed individually in clear 29.57 ml plastic cups (Bio-Serv, Frenchtown, NJ), together with a piece of *O. ficus-indica*, covered with paper lids, and maintained at the assigned temperature treatment. Egg hatch was recorded, and cohort neonates were transferred to plastic screened containers (25 by 14 by 7 cm) under the assigned temperatures. Fresh cactus pads served as the food source. Upon pupation, individual pupae were placed in clear plastic cups (29.57 ml) with paper lids and allowed to develop at the assigned temperature treatment. During immature development, body lengths and weights were recorded (Sartorius BP221S, Sartorius Corp., Edgewood, NY).

***C. cactorum* Adult Females.** After pupal emergence, weights, and sex of newly emerged adults were recorded. Ten newly emerged (1–2-d-old) females were placed individually into screened containers as described above. A newly emerged (1–2-d old) male was transferred into the container for mating. Adults were subjected to the same temperature regimes used for immature development. Fresh cactus pads were used for oviposition substrates. Eggs laid were counted daily, transferred to plastic cups, and placed in a growth chamber maintained at 30°C for hatching. Date of hatching and percentage of egg hatch were recorded. Eggs were collected until death of the female moth, which was recorded.

Life Table Calculations. Reproductive parameters calculated using methods described previously (Southwood and Henderson 2000, Legaspi 2004) included 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, in ♀/♀); generation time (T, mean period between birth of the parents and that of the offspring, in days); intrinsic rate of increase (r, in ♀/♀/d); finite rate of increase (λ, in ♀/♀/d); and doubling time (DT, time for population to double, in days). Number of female eggs laid was estimated by dividing total eggs by 2 because of the 1:1 sex ratio for *C. cactorum* (Robertson and Hoffmann 1989). The effect of temperature on immature developmental rate (1/duration of life stage) was analyzed using a logistic equation (Liu and Meng 2000) of the form, $rate = a/(1 + (T/X_0)^b)$ where T is temperature; and a, X_0, and b are estimated parameters. Developmental threshold temperature was

Table 2. Instar-specific duration times for *C. cactorum*[a] (mean ± SE; days)

Instar	Temp (°C)					Statistics
	18	22	26	30	34	
First	13.80 ± 1.20 (5)a	3.08 ± 0.08 (12)c	5.42 ± 0.15 (12)b	5.00 ± 0 (12)b	5.58 ± 0.19 (12)b	$F = 133.23$; df = 4, 48; $P < 0.001$; $R^2 = 0.92$
Second	15.20 ± 1.20 (5)a	11.18 ± 0.12 (11)b	6.00 ± 0 (10)c	5.00 ± 0 (12)c	6.00 ± 0 (8)c	$F = 185.40$; df = 4, 41; $P < 0.001$; $R^2 = 0.95$
Third	63.0 ± 0 (1)a	7.25 ± 0.41 (8)b	5.60 ± 0.16 (10)c	4.83 ± 0.11 (12)c	5.71 ± 0.18 (7)c	$F = 1772.59$; df = 4, 33; $P < 0.001$; $R^2 = 0.99$
Fourth	—[b]	6.00 ± 0.53 (7)b	5.00 ± 0.17 (9)c	7.18 ± 0.12 (11)a	5.00 ± 0 (7)c	$F = 19.89$; df = 3, 30; $P < 0.001$; $R^2 = 0.67$
Fifth	—	52.00 ± 4.44 (5)a	14.14 ± 0.55 (7)b	9.50 ± 0.69 (10)b	10.71 ± 0.52 (7)b	$F = 126.17$; df = 3, 25; $P < 0.001$; $R^2 = 0.94$

[a] Starting sample size = 12; numbers in parentheses indicate sample size available. Within each row, different letters following means indicate significant difference (Tukey HSD; $P = 0.05$).
[b] Complete mortality due to handling.

estimated as the intercept of the linear portion of the development data. Degree-days (*DD*) for development were calculated as $DD = (T - T_0) D$, where *T* is the constant temperature used in the treatment, *D* is mean developmental time at that temperature, and T_0 is lower temperature threshold (Greenberg et al. 2000).

An Enkegaard (1993) three-dimensional surface was estimated by nonlinear regression to describe the simultaneous effects of temperature and age on mean numbers of eggs laid daily. Mean numbers of eggs was fitted to the model, $eggs = (p + qT) d \exp(-wTd)$, where *T* is temperature (°C) and *d* is time (in days). The estimated parameters *p* and *q* describe how quickly maximal oviposition is reached as a function of temperature, and *w* described how quickly it returns to zero (Drost et al. 1988, Greenberg et al. 2000).

Statistical Analyses. The effect of temperature on life stage durations was analyzed at each life stage by using one-way analysis of variance (ANOVA). Means separation was tested by Tukey's honestly significant difference (HSD) test ($P = 0.05$). The effects of temperature and sex on pupal and adult body weights were analyzed using two-way ANOVA. Within instars, one-way ANOVA was performed to analyze the effects of temperature on life stage duration or body weight. Percentage of egg hatch was analyzed as a two-way ANOVA to test for the effects of temperature and time. Percentage data were converted using arcsine transformation, but values are presented as untransformed means (Sokal and Rohlf 1995). All statistical analyses were performed using Systat 11 (Systat Software, Inc., Point Richmond, CA).

Results

C. cactorum **Immatures.** Duration of immature stages was generally longest at 18°C, declining at 22°C, and shortest at 26, 30, and 34°C (Table 1). Total immature developmental time from eggs to pupae was ≈180 d at 18°C, 116 at 22°C, and ranged from 65 to 72 d
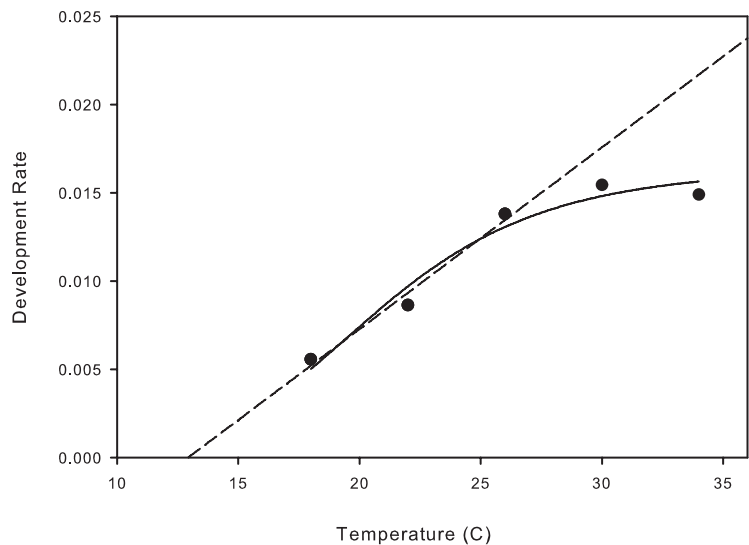

Fig. 1. Development rate for *C. cactorum* immatures (eggs to pupae). Developmental rate was fitted to the logistic equation $rate = 0.0165/(1 + (T/20.7093)^{-5.8823})$. The linear portion of the curve was used to estimate a lower development threshold temperature of 13.3°C.
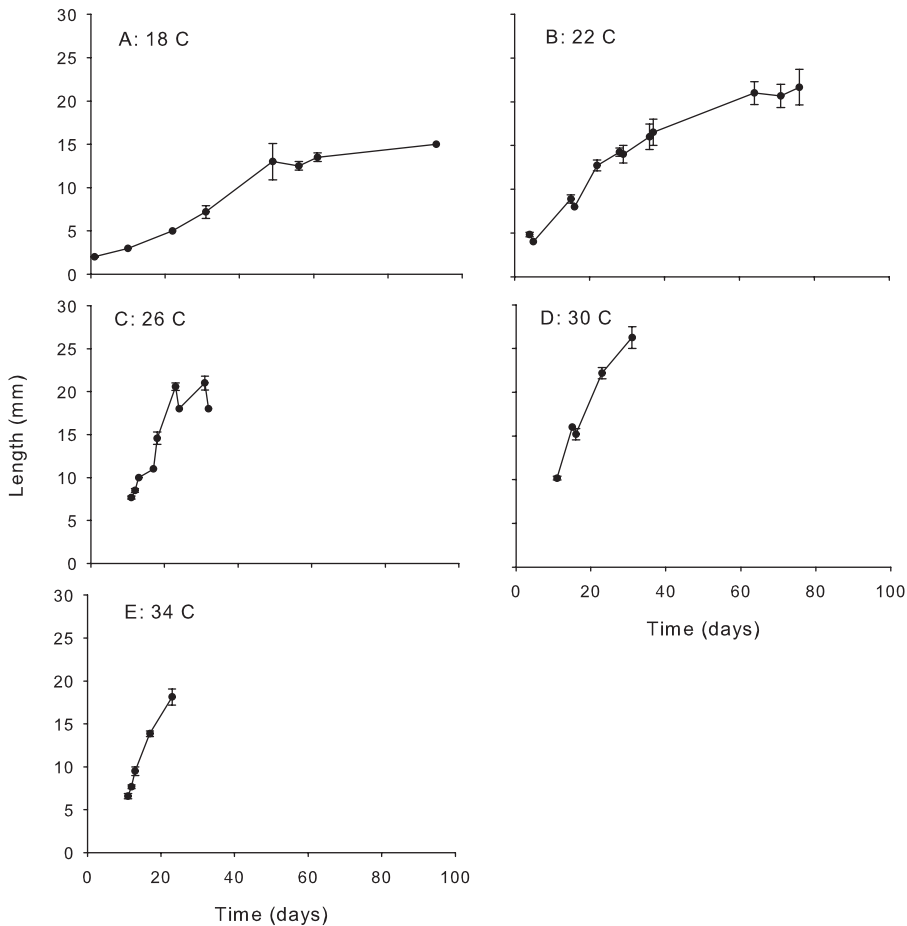
Fig. 2. Body length (millimeters) of *C. cactorum* immatures with time. Lower temperatures resulted in slower increases, but over longer periods.

at 26–34°C. Instar-specific developmental times were incomplete due to mortality caused by handling, especially in the 18°C treatment (Table 2). Generally, increasing temperatures resulted in declining durations, with exceptions in the first and fourth instars. Developmental rate for egg-to-pupal stages was estimated using the logistic equation, $rate = 0.0165/(1 + (T/20.7093)^{-5.8823})$ (SE = 0.0020, 1.2651, and 2.1466, respectively) ($F = 24.93$; df = 2, 4; $P < 0.05$; $R^2 = 0.92$). Regression of the linear portion of the curve resulted in an estimated lower developmental threshold temperature of 13.3°C (Fig. 1) ($rate = -0.0133 + 0.0010T$; SE = 0.0034, 0.0002, respectively; $F = 45.49$, $P = 0.09$; $R^2 = 0.96$). Based on this threshold, estimated degree-days for development were variable, from ≈845 at 18°C to 1387 at 34°C. Body lengths of immatures was significantly affected by temperature and time ($F = 79.58$; df = 38, 160; $P < 0.001$; $R^2 = 0.95$) (Fig. 2). Lower temperatures predictably showed slower growth rates reaching asymptotes of 15–20 mm. Higher temperatures showed shorter, but steeper increases with asymptotes of ≈25 and 20 mm at 30 and 34°C, respectively. Two-way ANOVA of percentage of

survival of immatures as affected by sex and temperature revealed that temperature was a significant factor ($F = 14.22$; df = 4, 90; $P < 0.001$; $R^2 = 0.41$), but sex was not ($F = 0.72$; df = 1, 90; $P = 0.39$; interaction: $F = 1.21$; df = 4, 90; $P = 0.316$) (Table 3).

C. cactorum **Adult Females.** In general, pupal weights declined with increasing temperature, and they were always lower in males than in females ($F = 31.71$; df = 9, 825; $P < 0.001$; $R^2 = 0.26$) (Table 4). For example, at 26°C, female pupae weighed ≈110 mg, whereas males weighed ≈70 mg. The same trends were found in adult insects: female adults weighed ≈74 mg and males ≈36 mg at 26°C. Female adult survivorship was longest at 18°C, and shortest at 34°C, with the other treatments clustered between the temperature extremes (Fig. 3A). Duration of the female adult stage was generally short. Adult female longevities declined with temperature, from 12.6 d at 18°C to 5.2 d at 34°C (Fig. 3B). Percentage of egg hatch declined with time and peaked at 26°C ($F = 4.811$; df = 35, 186; $P < 0.001$; $R^2 = 0.475$) (Fig. 4A and B).

Life Table Calculations. Life table parameters at each temperature are summarized in Table 5. Num-

Table 3. Effect of temperature on immature survival (mean ± SE; percent)

Life stage/sex[a]	Temp (°C)					Statistics
	18	22	26	30	34	
Egg	89.49 ± 3.27a	95.93 ± 1.76a	91.29 ± 2.74a	96.659 ± 1.29a	68.11 ± 6.02b	$F = 12.084$; df = 4, 45; $P < 0.001$; $R^2 = 0.518$
Larva	85.87 ± 3.65a	89.99 ± 1.49a	78.763 ± 8.71a	65.86 ± 9.19ab	47.02 ± 8.09b	$F = 5.904$; df = 4, 45; $P = 0.001$; $R^2 = 0.344$
Pupa	76.38 ± 5.39c	95.41 ± 1.35ab	93.20 ± 1.67ab	94.58 ± 2.02a	80.22 ± 5.47bc	$F = 5.937$; df = 4, 45; $P = 0.001$; $R^2 = 0.345$
Male	25.96 ± 2.33ab	40.93 ± 2.36a	33.93 ± 4.11a	30.06 ± 4.60a	14.89 ± 2.98b	$F = 6.438$; df = 4, 45; $P < 0.001$; $R^2 = 0.364$
Female	33.96 ± 4.64a	41.73 ± 2.87a	31.80 ± 4.27a	30.39 ± 5.16a	10.84 ± 1.99b	$F = 8.416$; df = 4, 45; $P < 0.001$; $R^2 = 0.428$

[a] Percentage of survival from eggs to pupae calculated based on numbers at end of given stage/numbers at start of stage; survival of sexes based on numbers of eggs surviving to adult emergence; numbers followed by common letters within a row are not significantly different (Tukey HSD; $P = 0.05$).

bers of female eggs laid were estimated by dividing eggs counted by 2, because of the 1:1 sex ratio found for *C. cactorum* (Table 3), also supporting the 1:1 sex ratio found by Robertson and Hoffmann (1989). The highest reproductive values were found at 26 and 30°C, which indicate optimal temperatures for this species. Within this range, *r*-values were above 0.05, compared with being >0.01 and 0.02 at 18 and 34°C, respectively (Table 5). The Enkegaard surface describing mean oviposition rate as a function of time and temperature was, $eggs = (-11.241 + 0.854T) \, d \exp (-0.020Td)$ (SE = 6.414, 0.330, and 0.003, respectively) ($F = 16.96$; df = 3, 54: $P < 0.001$; $R^2 = 0.35$), where T is temperature (°C) and d is time in days. The surface shows eggs laid early and at higher temperatures (Fig. 5).

Discussion

Detailed information on the life history and reproductive biology of *C. cactorum* will be essential in designing pest management strategies against this moth. Early descriptions of the biology of *C. cactorum* are found in Dodd (1940), Pettey (1948), and Mann (1969). Previous reports on adult longevity, immature developmental times, and average female fecundity are in general agreement with findings in this study. Adult lifespan is short, averaging 9 d (Zimmermann et al. 2004), compared with our findings of ≈5 d at 34°C, increasing to 12 d at 18°C (Fig. 3). The moth undergoes two or three generations per year, depending on climate. The life cycle is egg stage (50 d), larval stage (130–180 d), and pupal stage (40–70 d). Summer and winter generation times are 113–132 and 234–256 d,

respectively, in South Africa; 100–120 and 235–265 d, respectively, in Australia (Zimmermann et al. 2004). Reported average fecundity of winter generations range from 88 to 97 eggs per female in South Africa, and from 99 to 125 eggs per female in Australia. Summer generations were 161–188 d in South Africa and 75–120 d in Australia (Robertson 1989, Zimmermann et al. 2004). Lifetime fecundity was recorded at 172.3 d on *Opuntia ficus-indica* (L.) Miller, compared with 138.4 d on *Opuntia aurantiaca* Lindley for the summer generation (Robertson and Hoffmann 1989). Respective values for the winter generation were 177.0 and 159.4. Somewhat higher total fecundity of 200–300 eggs per female was reported by Zimmermann et al. (2000). In comparison, the pyralids *Diatraea saccharalis* (F.) and *Eoreuma loftini* (Dyar) have reported lifetime fecundities of 106 ± 10 and 370 ± 27, respectively, over oviposition periods averaging 9 d (Sétamou et al. 2002). A *C. cactorum* female lays most of her eggs early in the adult stage (Fig. 5). Similar findings are reported in other pyralids. For example, *Homoeosoma nebulellum* Denis & Schiffermuller females exhibit maximum fecundity during the first 2 d (total per female: 167.9 ± 72.2 [mean ± SD]; range 50–337) (Le Metayer et al. 1991).

In this study, we found total lifetime fecundity ranged from ≈12 eggs per female at 34°C to 100 eggs per female at 26°C (GRR values in Table 5, multiply by 2 to include male eggs). Life history parameters of *C. cactorum* indicate an insect with comparatively low reproductive potential compared with other species we have studied using similar methods. Here, we found highest *r*-values of ≈0.05, compared with 0.1632 at 30°C for the spined soldier bug, *Podisus maculiven-*

Table 4. Body weights for pupae and adult *C. cactorum*, divided by sex[a] (mean ± SE; milligrams)

Life stage	Temp (°C)					Statistics
	18	22	26	30	34	
Pupa ♂♂	85.42 ± 2.45 (51)b	111.66 ± 17.55 (59)a	70.46 ± 1.09 (103)bc	78.83 ± 1.37 (140)bc	59.59 ± 1.54 (79)c	$F = 9.632$; df = 4, 427; $P < 0.001$; $R^2 = 0.08$
Pupa ♀♀	132.68 ± 3.33 (54)a	126.93 ± 3.09 (58)ab	110.33 ± 1.86 (107)c	120.54 ± 1.99 (119)b	94.10 ± 2.41 (65)d	$F = 32.265$; df = 4, 398; $P < 0.001$; $R^2 = 0.25$
Adult ♂♂	42.55 ± 1.78 (47)ab	47.76 ± 6.60 (46)a	35.73 ± 1.03 (62)cd	38.63 ± 1.20 (85)abc	31.04 ± 0.98 (58)d	$F = 5.384$; df = 4, 293; $P < 0.001$; $R^2 = 0.07$
Adult ♀♀	84.27 ± 1.97 (49)abc	94.95 ± 10.83 (50)a	74.04 ± 2.37 (45)bc	86.50 ± 1.656 (71)ab	65.91 ± 2.59 (42)c	$F = 4.503$; df = 4, 252; $P = 0.002$; $R^2 = 0.07$

[a] Numbers in parentheses indicate sample size; within each row, different letters following means indicate significant difference (Tukey HSD; $P = 0.05$).
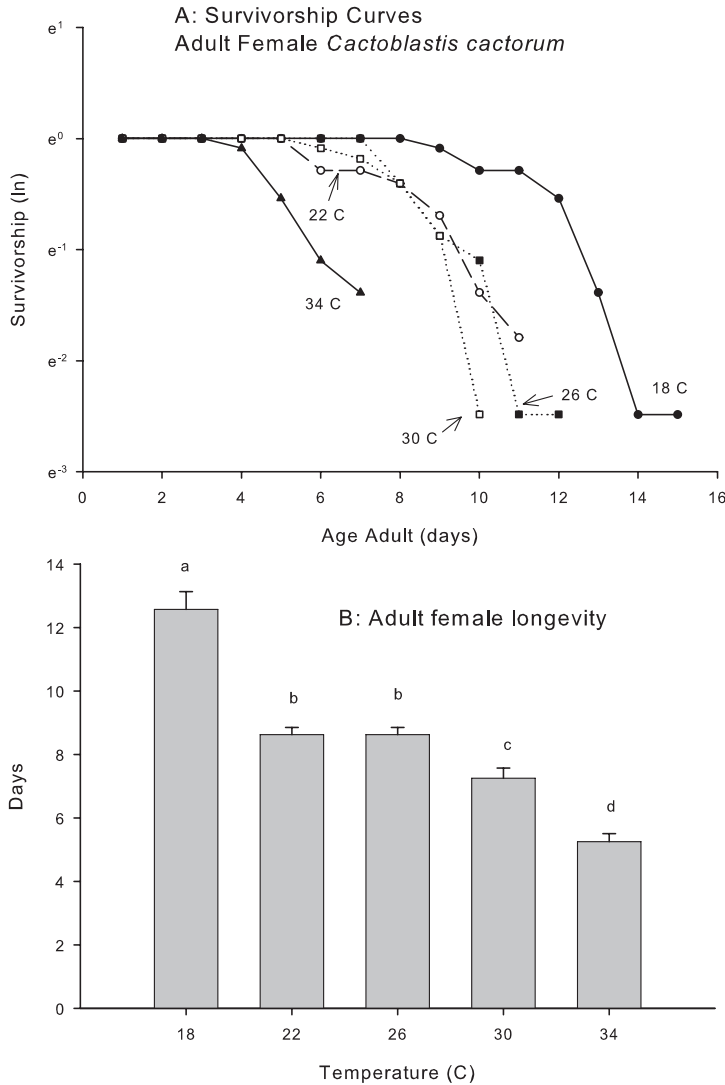
Fig. 3. (A) Survivorship curves for adult *C. cactorum* females (natural log scale). Survivorship was prolonged at 18°C, shortest at 34°C, and intermediate for the other temperature treatments. (B) Longevity of adult females is shown (mean ± SE; $n = 24$) (different letters indicate significant difference between means; Tukey HSD, $P = 0.05$).

tris (Say) (Heteroptera: Pentatomidae) (Legaspi and Legaspi 2005). However, *r*-values are comparable to those we found for *Delphastus catalinae* (Horn) (Coleoptera: Coccinellidae) of 0.082 at 30°C (J.C.L., unpublished data). The reproductive parameters we report for *C. cactorum* are also relatively low compared with those found in other pyralids. For example, r, λ, R_0, GRR, and T for *Ephestia kuehniella* Zeller at 28°C were 0.1375, 1.1473, 11.9, 54.9, and 18.2, respectively (Amir-Maafi and Chi 2006). In *D. saccharalis*, R_0, r, λ, T, DT, and total fecundity were 15.5, 0.066, 1.06, 41.6, 10.5, and 29.7, respectively. Corresponding values in *E. loftini* were 122, 0.096, 1.1, 50.2, 7.2, and 197, respectively (Sétamou et al. 2002). In *Diatraea grandiosella* Dyar, R_0 was reported to be 95 (Knutson and Gilstrap 1990), compared with maximal R_0 of 49 for *C. cactorum*

at 26°C (Table 5). Developmental time from first instar to pupation in *Dioryctria abietivorella* (Grote) at 25°C was 22.54 ± 0.56 d for males and 22.80 ± 0.80 d for females (Trudel et al. 1995). In comparison, larval developmental times in *C. cactorum* at 26°C was 33.5 ± 0.6 (Table 1).

To control *C. cactorum* infestations, Zimmermann et al. (2004) emphasize the importance of surveillance and early detection. One method reported was the use of different traps baited with virgin female moths (Bloem et al. 2005). In areas where the moth establishes as a pest, selection of control agent is determined by the value of the crop, the size of the affected area, and whether the moth is in use to control invasive cactus species (Zimmermann et al. 2004). Control methods may include management practices such as the collection and de-
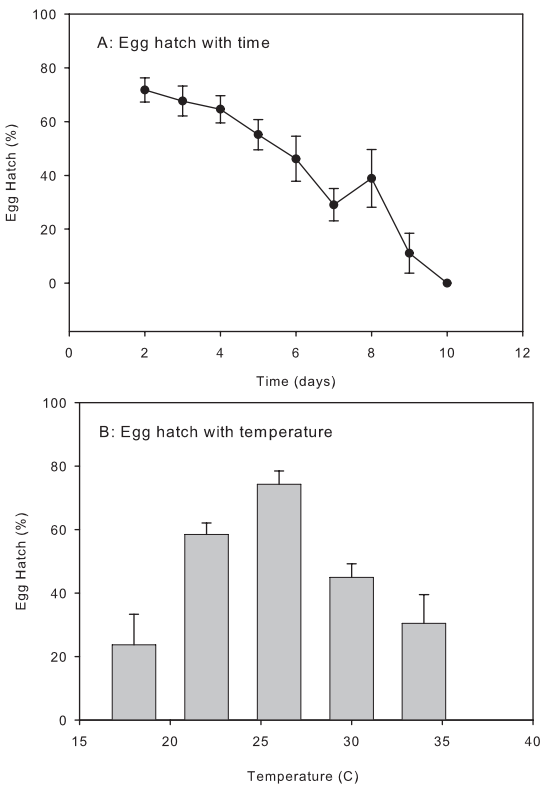
Fig. 4. Percentage of egg hatch ($\pm$ SE, nontransformed means) as functions of time (**A**) and temperature (**B**). Percentage of egg hatch declined with time, and peaked at 26°C ($F = 4.811$; df $= 35, 186$; $P < 0.001$; $R^2 = 0.475$).

Fig. 5. Enkegaard surface showing simultaneous effects of time and temperature on mean oviposition rate (female eggs). The estimated equation is: $eggs = (-11.241 + 0.854T)$ $d \exp(-0.020Td)$ ($F = 16.96$; df $= 3, 54$; $P < 0.001$; $R^2 = 0.35$).

struction of infested cladodes. Contact insecticides effective against Lepidoptera may be used against early instars, before they penetrate the cactus. Systemic insecticides have not proven effective against *C. cactorum* (Zimmermann et al. 2004). Chemical control options in Florida are restricted by the Environmental Protection Agency and the need for permits, the low value of *Opuntia* cactus, and possible detrimental effects on nontarget Lepidoptera (Stiling 2002).

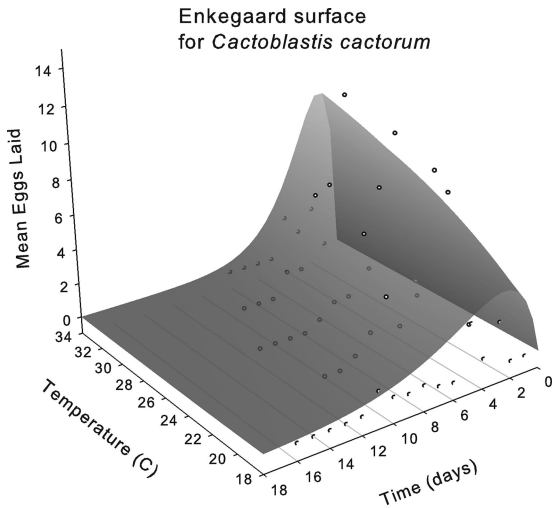Several potential biological control agents of *C. cactorum* have been mentioned in the literature, although none seem to be specific to the genus. The relatively low reproductive potential of the pest suggests that potential biological control agents need not possess extremely high reproductive rates. Instead, potential biological control agents might need to be either egg parasitoids or predators, or natural enemies specialized for searching and attacking the moth immatures within the cactus plant. Possible classical biological control agents from South America include one braconid larval parasitoid, five to six ichneumonid wasps, and a tachnid fly (Stiling 2002). *Apanteles alexanderi* Brethes (Hymenoptera: Braconidae) can cause parasitism levels >30% (Stiling 2002). Possible augmentative biological control agents in Florida include such endemic natural enemies as two pupal (Chalcidae) and one egg parasitoid (Trichogrammatidae) (Bennett and Habeck 1992) and a tachnid fly causing 10–50% parasitism (Stiling and Moon 2001). In South Africa and Australia, egg predation by ants is a significant regulatory factor in the dynamics of *C. cactorum* populations (Robertson 1985, Robertson and Hoff-

Table 5.   Life history parameters for *C. cactorum*

Parameter	Temp (°C)				
	18	22	26	30	34
Net reproductive rate $(R_0)^a$	8.550	46.24	49.20	43.68	5.95
Gross reproductive rate $(GRR)^b$	9.021	48.22	49.38	44.02	6.16
Generation time $(T)^c$	185.54	129.58	75.07	67.14	68.95
Intrinsic rate of increase $(r)^d$	0.0116	0.0296	0.0519	0.0562	0.0258
Finite rate of increase $(\lambda)^e$	1.0116	1.03	1.053	1.058	1.026
Doubling time $(DT)^f$	59.90	23.41	13.32	12.33	26.86

[a] $R_0 = \Sigma\ l_x m_x$ expressed in units of ♀ / ♀; egg numbers divided by 2 because of 1:1 sex ratio (see Table 3).
[b] $GRR = \Sigma\ m_x$ in ♀ / ♀.
[c] $T = (\Sigma\ x l_x m_x)/R_0$ in days.
[d] $r = \ln R_0/T$ in ♀ / ♀ /d.
[e] $\lambda = \exp(r)$ in ♀ / ♀ /d.
[f] $DT = \ln(2)/r$ in days.

mann 1989). Important ant predators include *Cremo-togaster liengmei* Forel, *Pheidole* sp., *Tetramorium erectum* Emery, *Tetramorium bacchus* Forel, *Tetramorium* sp., *Monomorium albopilosum* Emery, *Monomorium minutum* Mayr, and *Camponotus niveosetosus* Mayr. Estimates for egg mortality due primarily to ant predation range from 55 to 78% depending on season and cactus species (Robertson 1985). Minor predators recorded were an unidentified mite, *Nysius* sp. (Hemiptera: Lygaeidae), and *Trichogrammatoidea* sp. (Robertson and Hoffmann 1989). Robertson (1988) suspected other species of ants to be egg predators [*Technomyrmex albipes* Smith, *Monomorium delagoense* Forel, *Camponotus eugeniae* Forel, and *Camponotus rufoglaucus* (Jerdon)] and found spatial density-dependent predation in the winter, but not the summer.

Larval predators of *C. cactorum* included ants [*Pheidole* sp. and *Anoplolepis steingroeveri* (Forel)] and a tachinid (*Pseudoperichaeta* sp.). Pupal predation by the ant species *Dorylus helvolus* (L.) was an important mortality factor estimated at ≈13–34% predation. Pupal parasitism by chalcid parasites *Invreia* sp. and *Euchalcidia* sp. was estimated at ≈5% (Robertson and Hoffmann 1989).

No pathogenic fungi are known against *C. cactorum.* However, the protozoan *Nosema cactoblastis* has been reported from South Africa (Pemberton and Cordo 2001), but recorded infection levels are only 0–6% (Stiling 2002). Carpenter et al. (2001) advocated the use of the sterile insect technique (SIT) to study *C. cactorum* populations, and possibly for eradication in colonization sites or for controlling dispersal and movement into new areas. According to Stiling (2002), SIT is most likely to be successful in the Florida Keys where cacti are rare and *C. cactorum* populations are low, although control will be expensive.

Control measures against *C. cactorum* infestations in the United States will probably be limited in most regions, because *Opuntia* species are usually a low-value crop (Mahr 2001). Cost-effective control should include understanding and using endemic natural controls, especially parasites and predators (Zimmermann et al. 2004). Life history data such as those reported here indicate that the moth does not display particularly high reproduction, so its pest status is due largely to the protection from control agents once it has gained entry into the cactus tissue. The most vulnerable life stage seems to be the egg, both because it is exposed and because of the relatively long duration in this stage. Natural predation by ants may be encouraged, possibly by the adoption of management techniques favorable to ant populations. However, even after moth larvae have entered the plant, specialized natural enemies may be effective in seeking and attacking larvae inside the cactus plant. Similar behavior has been found in tachinids attacking stem-boring Pyralidae [e.g., *Lydella jalisco* Woodley (Diptera: Tachinidae) against *E. loftini;* Legaspi et al. 2000a, 2000b; Lauzière et al. 2001]. Effective integrated pest management of *C. cactorum* will need an understanding of all the management options available to develop comprehensive, yet cost-effective strategies under different geographical and socioeconomic scenarios.

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