Life History of *Trichogrammatoidea bactrae* (Hymenoptera: Trichogrammatidae), an Egg Parasitoid of Pink Bollworm (Lepidoptera: Gelechiidae), with Emphasis on Performance at High Temperatures

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ABSTRACT Selected life history characteristics of *Trichogrammatoidea bactrae* Nagaraja, a newly imported egg parasitoid of pink bollworm, *Pectinophora gossypiella* (Saunders), were studied at constant and fluctuating temperatures, with emphasis on high temperatures typical of desert cotton production areas in Arizona and southern California. Developmental times from egg to adult ranged from 11 to just over 7 d at mean temperatures of 22.5 and 29.5°C, respectively. Development was delayed under fluctuating temperatures with maximums ≥33.5°C. Survivorship was >90% under all but a fluctuating 25/40°C regime. Similar results were found for *Trichogramma pretiosum* Riley, an established species in the southwestern United States. Mean female longevity of *T. bactrae* adults ranged from 138 h at a constant 15°C to 1.5 h at 40°C. Mean fecundity peaked at 25°C (55 progeny per female), but modest fecundity (14–23 progeny per female) was maintained at temperatures from 30–35°C. The majority of eggs oviposited by newly emerged adults within the first 24 h of exposure to hosts were laid in the first 3 h and >90% were laid within 12 h. The 24-h rate of oviposition was a nonlinear function of female age and temperature that was maximal for 10-h-old females at ≈25°C. The time of day that females of equal age were initially exposed to hosts did not significantly affect 24-h oviposition rates. *T. bactrae* appears well adapted to high temperatures; this environmental factor should not significantly hinder the efficacy of this biological control agent in the field.

KEY WORDS *Pectinophora gossypiella, Trichogrammatoidea bactrae,* life history

EVER SINCE THE pink bollworm, *Pectinophora gossypiella* (Saunders), was first discovered in southern California in the mid-1960s there have been numerous attempts to establish exotic parasitoids for biological control in the cotton-growing regions of Arizona and California (Bryan et al. 1973a, b; 1976; Legner & Medved 1979; Gordh & Medved 1986). Most of these parasitoids failed to establish, and only a few species displayed any potential for biological control of pink bollworm. In general, the basic biology of many of these parasitoids was poorly understood before they were released. Among the factors cited for the lack of success were low release numbers, limited genetic heterogeneity of founder populations, host dispersal into release areas from surrounding fields, dispersal of parasitoids out of release areas, lack of host/parasitoid synchrony between seasons, and the widespread use of insecticides (Bryan et al. 1973a, b; Legner & Medved 1979).

In recent years there has been renewed interest in expanding the use of biological control for cotton pest suppression in the southwestern United States. *Trichogrammatoidea bactrae* Nagaraja, an egg parasitoid recovered from *P. scutigera* (Holdaway) in Queensland, Australia, was imported into California in 1985 by Gordon Gordh (Division of Biological Control, Department of Entomology, University of California, Riverside) for the biological control of pink bollworm. Unlike the better known species of the genus *Trichogramma*, the biology of species of *Trichogrammatoidea* is not well known, although several species are considered to be important in the biological control of agricultural pests in other parts of the world (Nagaraja 1978). *T. bactrae* is currently being evaluated as an augmentative biological control agent against pink bollworm in cotton. Hutchison et al. (1990) studied the biology and morphology of this parasitoid at constant temperatures in the laboratory and small-scale releases have been underway since 1986 (Hutchison et al. 1990; Naranjo et al. 1992).

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The pink bollworm remains one of most serious pests of cotton in the southwestern United States. Estimates from Arizona in 1990 indicate that >90% of the cotton acreage was infested with pink bollworm and losses were estimated at >47,000 bales, even with an average of seven insecticide applications (Head 1991). To date, biological control has not played a significant role in overall pink bollworm management in the southwestern deserts, but there is interest in viable, cost-effective alternatives to the near sole reliance on chemical pesticides. A thorough understanding of the biology of potential natural enemies may allow us to use their activity better for biological control of pink bollworm.

Weather is one of the most important factors influencing the performance of introduced biological control agents (Messenger 1970). Temperature is perhaps the most severe constraint in the southwestern desert. Ambient air temperatures in desert cotton-growing areas of California and Arizona frequently exceed 40°C over extended periods of a day throughout much of the season, and it is not unusual for temperatures to exceed 45°C for brief periods of a day. Although these temperature extremes are lower within the cotton canopy (unpublished data), the performance of a released natural enemy will depend, in part, on its ability to cope with these severe environmental conditions.

This study was undertaken to augment our existing knowledge of the biology of *T. bactrae* with emphasis on the effect of high temperatures on life history characteristics. Immature development and survival, adult reproduction, longevity, and ovipositional activity patterns were examined in *T. bactrae* under a broad range of constant and fluctuating temperature regimes typical of desert cotton-growing conditions in Arizona and southern California. Comparative developmental studies were also conducted with *Trichogramma pretiosum* Riley, a species well established in the southwestern United States.

Materials and Methods

General Protocols. All studies were carried out in environmental chambers (Verling, Los Angeles, CA) maintained at constant (±0.5°C) or fluctuating temperatures. Temperatures in the fluctuating regimes varied according to smooth, asymmetrical sine wave patterns (Partlow, New Hartford, CN) over a 24-h period with a ±7.5°C amplitude, and minimum and maximum temperatures occurring at 0500 and 1400 hours (MST), respectively. Unless otherwise noted, photoperiods were maintained at 14:10 (L:D) h with the photophase beginning at 0600 hours. Within environmental chambers, parasitoids were maintained inside plastic boxes (26 by 36 by 16.5 cm) containing beakers of saturated NaCl which maintained the relative humidity at ≈75% at all experimental temperatures (Winston & Bates 1960).

Both parasitoid species, originally from the University of California, Riverside, were obtained from colonies maintained on pink bollworm eggs at 27°C and 50–75% RH with a 14:10 (L:D) h photoperiod. *T. bactrae* were identified by H. Nagaraja and *T. pretiosum* by J. Pinto. Voucher specimens for both species have been deposited in the University of California, Riverside, insect museum.

Development and Survival. Small sections of pink bollworm egg sheets (<1 d old) obtained from the colony maintained at the Western Cotton Research Laboratory were exposed at ≈25°C to equal numbers of male and female *T. bactrae* for 3 h in petri dishes at a rate of one female per 25 host eggs. After exposure, egg sheets were subdivided into sections containing 25–75 eggs and these sections were placed in 32 separate petri dishes (50 by 9 mm). The subdivision of the egg sheets facilitated counting of emerged parasites. Four dishes of parasitized eggs were randomly chosen and exposed to each of four constant temperatures (22.5, 26, 29.5, and 32.5°C) and to each of four fluctuating temperature regimes with the same respective means (see above). These fluctuating regimes (15–30, 18.5–33.5, 22–37, and 25–40°C) were selected to mimic those that occur in the field over the course of a cotton-growing season. Host eggs were monitored every 12 h for parasitoid emergence. The same experiment was run concurrently with *T. pretiosum*. Cohorts of *T. bactrae*-parasitized host eggs were also exposed to constant temperatures of 35 and 37.5°C regimes to estimate developmental times and survival for estimating demographic parameters.

Reproduction and Longevity. Newly emerged, mated females were provided with a 10% honey solution and an excess of pink bollworm eggs <1 d old. Females (n = 20 per temperature regime) were confined individually in dishes 50 by 9 mm and were exposed to constant temperatures of 15, 20, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C. Host eggs were replaced after the first 3 h of exposure, then at 24 h intervals until parasitoids died.

Ovipositional Patterns. Results of reproduction studies above indicated that females lay most of their eggs early in life. Three studies were conducted to examine ovipositional activity further within the first 24 h of exposure to host eggs under conditions representative of the desert environment during the cotton-growing season. In the first study, fresh pink bollworm eggs (<1 d old) were provided to mated females (emerged 0600–0700 hours) at 3-h intervals over a 24-h period beginning at ≈0900 hours. Twenty females were individually confined as described in the previous section and exposed to one of the four fluctuating temperature regimes described

above. The remaining two studies were designed to examine age and time-of-day influences on oviposition. In first of these two studies, females that emerged between 0600 and 0700 hours were individually confined and exposed to host eggs for a single 3-h period beginning at 0700, 0900, 1200, 1500, 1800, 2100, or 2400 hours at a constant 27°C. While parasitoids awaited later exposure intervals (0900 hours and later), they were provided with 10% honey but no host eggs, and were maintained at either 15°C or at the normal colony rearing temperature of 27°C. These two holding conditions were used to compare the effects of storage temperature on subsequent female performance. Ten females were tested per interval for each holding temperature. In the final study, females that emerged between 0600 and 0700 hours were individually confined and first exposed to host eggs for 24-h periods beginning at 0800, 0930, 1100, 1700, 1830, and 2000 hours at each of the four fluctuating temperature regimes. Ten females were tested at each temperature and exposure time. Results of the second study indicated that mortality was lower when females were stored at 15 rather than at 27°C, but there was no difference in ovipositional rates. Thus, females to be exposed to host after 0800 hours were maintained at 15°C and provided with a 10% honey solution. This final study was repeated with some modification. A reverse photoperiod colony was developed and maintained for two generations. This colony was maintained at 27°C with a 14:10 (L:D) h cycle but with the photophase beginning at 1500 hours. Because most adult emergence occurs within the first several hours of the photophase (Hutchison et al. 1990), this provided newly emerged females from 1500 to 1600 hours. Ten of these females were individually confined and exposed to host eggs for 24 h beginning at 1700, 1830, or 2000 hours at each of the fluctuating temperatures and at a constant 27°C. The original study was repeated at the four fluctuating temperatures and at a constant 27°C using normal light cycle females.

In all reproduction and oviposition studies, parasitized eggs were held at 27°C until adult eclosion; emerging adults were separated by sex. Oviposition per se was not measured directly but was inferred from the number of progeny emerging from parasitized host eggs. Thus, throughout this article the term oviposition and progeny produced represent the same parameter.

Data Analysis. Differences in developmental times between constant and fluctuating regimes for each species were subjected to *t* tests. Survival to adulthood was estimated as the quotient of emerged parasites and the number of parasitized eggs. This measure overestimates survival if females lay more than one egg per host. However, given an abundance of host, *T. bactrae* rarely lays more than one egg in an individual host egg (Hutchison et al. 1990). Adult female longevity was calculated assuming that individuals found dead at the beginning of an observation interval died midway through the preceding interval. To compare reproductive output under ideal conditions in the laboratory, net reproductive rates, R_o, and intrinsic rates of increase, r_m, were calculated from constant-temperature studies according to the methods of Birch (1948) and using mean immature developmental times from Hutchison et al. (1990) and this study. R_o was estimated by $\Sigma l_x m_x$, where l_x is the proportion of females surviving to day x and m_x is the mean number of female progeny produced during day x. r_m was estimated by selecting values of r that satisfies the expression $\Sigma e^{-rx} l_x m_x \approx 1$. Survivorship varied little at mean temperatures between 22.5 and 29.5°C, so an average value of 96% immature survival was used at temperatures between 15 and 30°C (see Table 1). For temperatures above 30°C, estimated survival values were used. Data from ovipositional activity studies were subjected to linear and quadratic regression analyses (SAS Institute 1985) to test for temperature- and age (time)-related differences. Analysis of variance (ANOVA) and preplanned single-degree-of-freedom contrasts were used to compare 24-h oviposition rates in relation to female age and time of day of exposure to hosts.

Results

Development and Survival. Mean female and male developmental times differed by <0.2 d for any temperature regime, so the sexes were pooled for further comparisons. *T. bactrae* developmental times declined from 11.1 d at a constant 22.5°C to 7.3 d at 29.5°C (Table 1). Under fluctuating temperatures, development began to decelerate when the maximum temperature reached 33.5°C. Development took 11 d at a mean temperature of 22.5°C, but was ≈ 1 and 2 d longer at mean temperatures of 26 (18.5–33.5) and 29.5 (22–37°C), respectively, compared with that of counterparts developing at constant temperatures (Table 1). Parasitoids did not survive to adulthood in the hottest regime (25–40°C) or at constant temperatures of 35 and 37.5°C, even though some development was indicated by the presence of darkened host chorions. Subsequent dissection of many of these darkened host eggs revealed desiccated parasitoid pupae. Similar patterns were evident for *T. pretiosum* where developmental times did not differ from those of *T. bactrae* held at the same temperatures.

Survivorship of both species was >0.90 in both constant and fluctuating regimes with mean temperatures ≤29.5°C but dropped to 0.62 and 0.74 at a constant 32.5°C for *T. bactrae* and *T. pretiosum*, respectively (Table 1). Sex ratios were female-biased (range 61–69% female for *T. bactrae*; 54–61% female for *T. pretiosum*), but did

Table 1. Development and survival of *T. bactrae* and *T. pretiosum* reared at constant and fluctuating temperatures

Mean temperature,°C	Constant temp				Fluctuating temp[a]			
	Developmental time[b]		No. progency per host[d]	Proportion ♀	Developmental time[b]		No. progeny per host	Proportion ♀
	Mean (SEM)[c]	*n*			Mean (SEM)	*n*		
			Trichogrammatoidea bactrae					
22.5	11.1 (0.02)	191	0.95	0.63	11.0 (0.02)	257	0.97	0.63
26.0	8.2 (0.03)**	224	0.97	0.62	9.1 (0.02)	250	0.95	0.61
29.5	7.3 (0.04)**	203	0.96	0.63	9.6 (0.04)	249	0.94	0.69
32.5	7.6 (0.06)	116	0.62	0.66	—	—	—	—
			Trichogramma pretiosum					
22.5	11.2 (0.03)	149	0.93	0.66	11.1 (0.02)	292	0.95	0.56
26.0	8.3 (0.03)**	279	0.95	0.56	9.2 (0.03)	224	0.89	0.61
29.5	7.7 (0.03)**	214	0.95	0.59	9.5 (0.04)	151	0.97	0.54
32.5	7.6 (0.05)	150	0.74	0.60	—	—	—	—

[a] Mean temperature, ± 7.5°C.
[b] Oviposition to adult in days.
[c] Asterisks indicate developmental times were significantly different between constant and fluctuating regimes (*t* tests, $P < 0.01$).
[d] Total parasitoids emerged divided by total parasitized host eggs.

not change appreciably in relation to temperature, indicating no differential mortality of the sexes.

Reproduction and Longevity. Longevity of female parasitoids declined with increasing temperature (Table 2). Females lived longest at a constant 15°C, averaging 138 h (5.8 d), but lived <3 h at a constant 40°C. Examination of survivorship curves for adult females (Fig. 1) at temperatures between 15 and 27.5°C suggested a pattern somewhere between type II and type III survivorship. This indicates a pattern between constant rates of mortality with age and higher rates of mortality for younger females. Observation intervals were not frequent enough at temperatures ≥30°C to discern any patterns in survivorship.

Oviposition was not observed at fine enough intervals to determine if *T. bactrae* had a preovipositional period. However, in only rare cases did individual females fail to parasitize host eggs during a 3-h interval, 2–3 h following adult eclosion. Mean lifetime fecundities rose from 36 progeny per female at 15°C to a maximum of 55 at 25°C, then declined to 7 at a constant 40°C (Table 2). At 20°C, one female lived 22 d and produced 151 progeny. Rates of oviposition were highest the first day and declined rapidly thereafter at all temperatures (Fig. 1). Oviposition activity was further skewed within the first day. The average

Table 2. Reproduction and longevity of *T. bactrae* at different constant temperatures

Temp, °C[a]	Mean (SEM) [range]				R_o[b]	r_m[b]
	Longevity, h	No. progeny per ♀	% Progeny in hours 1–3	% Female		
15	138.2 (29.1) [13.5–444]	35.5 (6.2) [8–103]	37.7 (7.8) [0.0–100.0]	61.9 (3.3) [28.4–75.0]	15.91	0.0913
20	100.9 (24.7) [13.5–516]	49.7 (7.1) [13–151]	28.2 (5.9) [0.0–100.00]	63.1 (4.0) [12.5–82.9]	27.86	0.2387
25	87.8 (17.9) [13.5–300]	54.8 (7.7) [6–116]	30.9 (6.2) [0.0–100.0]	68.8 (2.5) [48.9–93.8]	26.93	0.3269
27.5	34.7 (5.4) [1.5–84]	34.7 (4.8) [7–78]	38.2 (5.9) [0.0–87.5]	72.3 (3.2) [43.2–91.7]	16.23	0.3179
30	19.1 (2.2) [13.5–36]	22.9 (2.5) [5–46]	60.7 (4.9) [31.4–100.0]	70.9 (2.3) [53.3–93.8]	10.88	0.3250
32.5	17.0 (2.9) [13.5–60]	19.8 (2.0) [8–36]	62.4 (7.0) [0.0–100.0]	73.9 (2.3) [47.6–88.9]	5.76	0.2405
35	14.6 (1.8) [1.5–36]	14.4 (1.1) [6–22]	90.5 (5.0) [0.0–100.0]	76.2 (2.4) [50.0–94.4]	—	—
37.5	11.7 (0.9) [1.5–13.5]	12.4 (0.7) [7–19]	100.0 (0.0)	76.8 (2.8) [54.6–100.0]	—	—
40	1.5 (0.0)	7.2 (0.9) [1–13]	100.0 (0.0)	79.3 (1.7) [66.7–87.5]	—	—

[a] Twenty females were tested at each temperature.
[b] —, no immature development was completed at constant temperatures of ≥35°C.

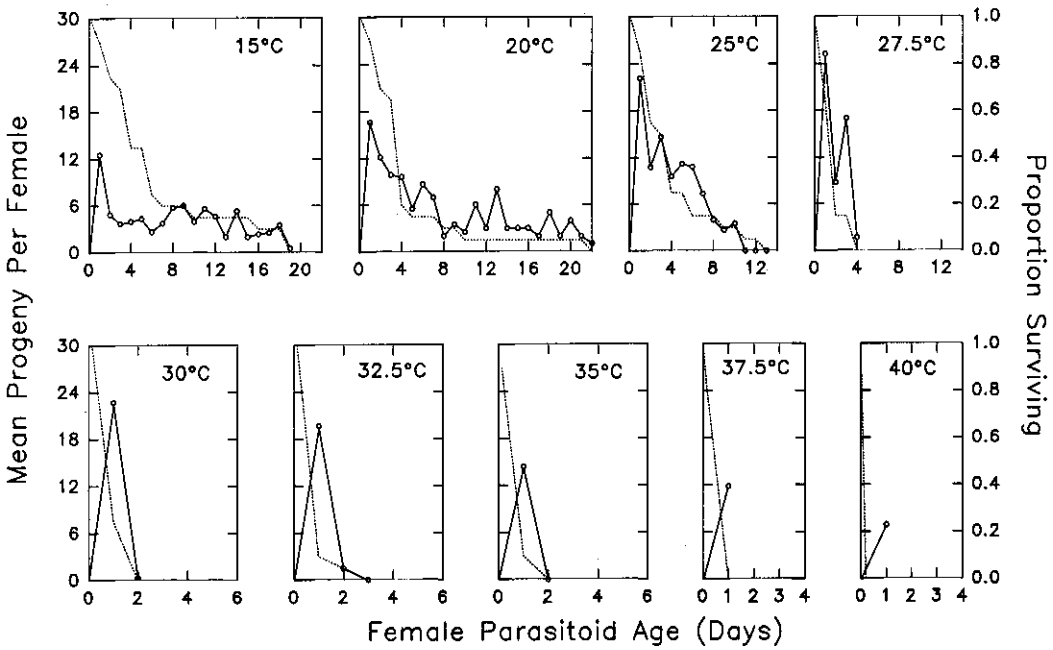

Fig. 1. Age-specific oviposition (circles and solid lines) and survivorship (dotted lines) of *T. bactrae* at various constant temperatures. Rates of oviposition are based on surviving females.

female laid from 28 to 38% of all her eggs within the first 3 h of exposure to hosts at temperatures between 15 and 27.5°C and oviposition was >50% complete in the first 3 h at temperatures ≥30°C (Table 2). Progeny sex ratios were female-biased (62–79% female) and the bias increased with temperature. This resulted primarily because sex ratios were more female-biased early in adult life (data not shown) and female longevity was short at higher temperatures.

Net reproductive rates (R_o) were highest at 20–25°C and declined rapidly with increasing temperature (Table 2). Daily intrinsic rates of increase (r_m) varied in relation to temperature, with maximal rates at temperatures between 25 and 30°C and the lowest rate at 32.5°C. Rates could not be calculated at temperatures >32.5°C because there was no survival to adulthood.

Ovipositional Patterns. When fresh host eggs were provided to females every 3 h, >50% of the 24-h total progeny were produced in the first 3 h, and >90% were produced in the first 9–12 h regardless of temperature (Fig. 2). Very little oviposition occurred after 12 h, which coincided with the scotophase of the light cycle. In the hottest regime (25–40°C) females did not survive beyond the first 6 h (maximum temperature occurred at 1400 hours), but 24-h survival was 80–100% in the three cooler regimes. Oviposition was highly variable among females, but regression analysis indicated that temperature had a significant influence only within the first 9 h of exposure to host eggs (Fig. 2 B–D). Rates of oviposition were not influenced by temperature during subsequent 3-h intervals ($F < 2.33$; df = 1,48; $P > 0.13$), nor over 24 h as a whole ($F = 0.94$; df = 1,77; $P = 0.34$). Mean (± SEM) 24 h rates of oviposition were 19.8 ± 2.1, 22.8 ± 1.6, 19.9 ± 2.2 and 17.9 ± 1.6 for 15–30, 18.5–33.5, 22–37, and 25–40°C regimes, respectively.

In the second study, there were no significant differences in 3-h oviposition rates between females stored at 15 or 27°C while awaiting host exposure ($t < 1.88$, df = 18, $P > 0.08$). Thus, these treatment groups were pooled for further analyses. There was a concave downward relationship between oviposition and female age (or time of day, or both) (Fig. 3). The low rate of oviposition during the first interval (0700–1000 hours) resulted because only 4 of the 10 females tested laid eggs. It was also noteworthy that females exposed to hosts in the last two intervals (2100–2400 and 0000–0300 hours) parasitized hosts during the scotophase of the light cycle.

The third study expanded on the second by exposing females to hosts for 24-h periods beginning at six different times (0800, 0930, 1100, 1700, 1830, and 2000 hours) during the day and by using a reverse photoperiod colony that provided newly emerged adults at 1500 hours instead of the usual 0600 hours. Results from treatments that used females reared on the normal 14:10 (L:D) h cycle did not differ between the two trials of this study ($t < 2.01$; df = 18; $P > 0.06$), so data were pooled for further analyses. As in the second study, females first exposed to host eggs later in the day produced more progeny. However, this pattern is attributable primar-

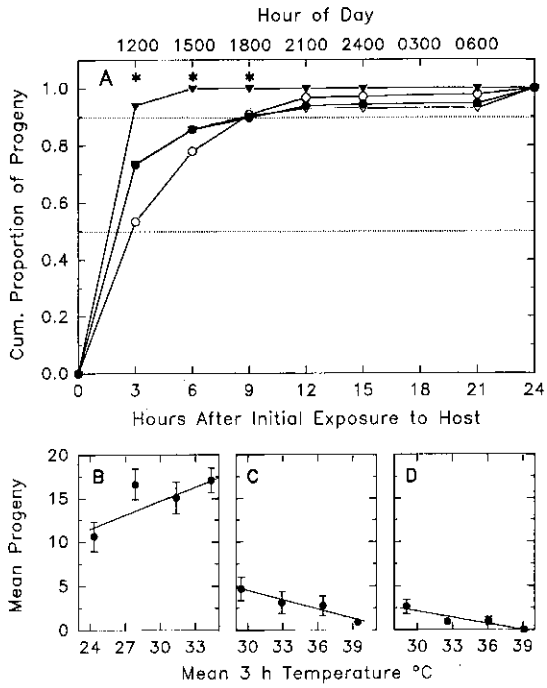

Fig. 2. (A) Twenty-four hour oviposition activity by 20 newly emerged *T. bactrae* under each of four fluctuating temperature regimes. Horizontal dotted lines indicate the 50th and 90th percentiles of total oviposition within the first 24 h of exposure to host. Open circles, 15–30°C; solid circles, 18.5–33.5°C; open triangles, 22–37°C; solid triangles, 25–40°C regime. Asterisks denote 3-h intervals during which temperature significantly ($P < 0.05$) influenced rates of oviposition. These intervals are detailed in B–D. (B) Mean progeny produced within first 3 h of exposure to host. Oviposition increased significantly with mean temperature ($F = 5.82$; df = 1,77; $P = 0.02$). (C) Mean progeny produced between 3 and 6 h of first exposure to host. Oviposition declined significantly with increasing mean temperature ($F = 5.93$; df = 1,74; $P = 0.02$). (D) Mean progeny produced between 6 and 9 h of first exposure to host. Oviposition declined significantly with increasing mean temperature ($F = 6.59$; df = 1,58; $P = 0.01$). In B–D, regression analyses were conducted based on individual data points, but for clarity only means and SEM bars are presented.

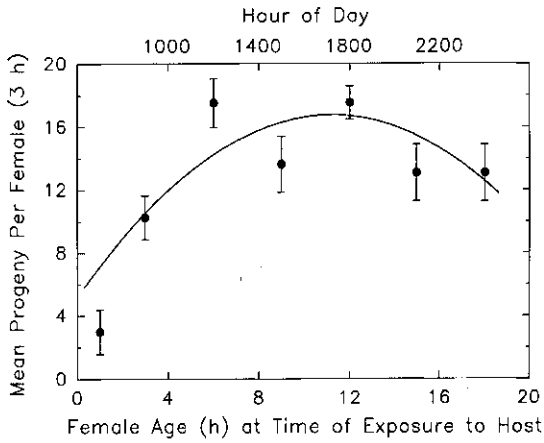

Fig. 3. Oviposition of *T. bactrae* exposed to host eggs for 3 h beginning at different times throughout the day at a constant 27°C. All parasitoids emerged at or before 0600 hours on day of testing. Progeny production was significantly influenced by female age at the time of exposure ($F = 13.14$; df = 2,127; $P = 0.0001$). Regression analysis was performed on individual data points, but for clarity only means and SEM bars are presented. Twenty females were tested per time interval.

ily to female age (or host deprivation) and not time of day (Table 3). The number of progeny produced during a 24-h period was the same for females of the same age and exposed to hosts at equivalent times after eclosion (i.e., normal photoperiod females exposed in the morning and reverse photoperiod females exposed in the evening) but was different for females of different ages (i.e., females exposed in the morning [younger] produced fewer progeny than those exposed in the evening [older]). This pattern did not hold in the 25–40°C regime because females did not survive the 40°C exposure which occurred at ≈1400 hours. Thus, those exposed to host in the morning lived only 3–6 h whereas those exposed in the evening survived for 18–21 h and produced more progeny.

Multiple regression analysis was performed to quantify the influence of temperature, female age, and time of day on 24-h oviposition rates. A stepwise procedure was used to estimate the best model using linear and quadratic terms of three independent variables: female age (a), time of day (t), and weighted temperature (T). Because females oviposit at greater rates during the first few hours of exposure to host, temperatures during these first few hours carried greater weight. Consistent with results in Table 3 (morning/reverse), time of day did not contribute significantly to the model (Fig. 4). Both the linear and quadratic terms of female age and temperature were significant and explained 30% of the variation in 24-h oviposition rates [$O(T,a)$]. The best regression model is given by:

$$O(T,a) = -31.063 + 3.301T - 0.066T^2 + 3.182a - 0.156a^2$$

Analysis of the surface response indicated that oviposition was maximal at about 25°C for females 10.4 h of age.

Discussion

Based on an experimental resolution of 0.5 d, developmental times for *T. bactrae* were about the same as reported by Hutchison et al. (1990)

Table 3. Mean number of progeny produced in 24 h in relation to female age and time of day that *T. bactrae* were initially exposed to host eggs under different temperature regimes

Time of exposure[a]	Temp regime, °C[b]				
	15–30	18.5–33.5	22–37	25–40	27
Morning hours	18.5[a] (0.9)	16.9 (1.0)	16.9 (0.7)	9.6 (0.6)	22.2 (1.7)
Evening hours	25.2 (1.0)	25.9 (1.1)	23.5 (0.9)	17.7 (0.9)	28.2 (1.5)
Reverse photoperiod	18.0 (1.0)	17.3 (1.4)	18.5 (1.1)	14.7 (1.3)	17.9 (1.9)
Contrasts (*F* value)[c]					
Morning–evening	28.65**	39.15**	37.33**	57.15**	6.55*
Evening–reverse	22.59**	23.83**	14.19**	5.15*	19.09**
Morning–reverse	0.15	0.07	1.49	15.23**	3.28

[a] Morning hours, 0800–1100; evening and reverse photoperiod hours, 1700–2000; morning and evening L:(0600–2000); reverse photophase L:(1500–0500).
[b] Mean (SE) progeny in 24 h; morning and evening, $n = 60$; reverse, $n = 30$; 27°C all times, $n = 30$
[c] Asterisks indicate statistical significance: **, $P < 0.01$; *, $P < 0.05$.

for this species and by Lim (1986) for *T. bactrae fumata* Nagaraja parasitizing *Corcyra cephalonica* Stainton at similar temperatures and relative humidities. Developmental times of *T. bactrae* and *T. pretiosum* were essentially identical, which deviated from other studies on the latter species by as much as 1–2 d depending on temperature and host species (Butler & Lopez 1980; Calvin et al. 1984; Harrison et al. 1985). Under fluctuating temperatures there was a progressive deceleration of development rate with increasing maximal temperatures ≥33.5°C in both species. This pattern agrees with other fluctuating temperature studies with *T. pretiosum* (Butler & Lopez 1980; Calvin et al. 1984) and supports an optimal developmental temperature near 31°C calculated for *T. bactrae* (Hutchison et al. 1990).

Although high temperatures reduced developmental speed, survival to adulthood remained >90% for both species when maximal temperatures reached 37°C, and some parasitoids developed to the pupal stage even at maximal temperatures of 40°C. Butler & Lopez (1980) reported no survival of *T. pretiosum* to adulthood under a fluctuating regime with a maximal temperature of 40.6°C, but they did not note if any development had occurred. Egg-to-adult survivorship of *T. bactrae* was similar to that reported by Lim (1986) at ≈26°C, but Hutchison et al. (1990) reported survival rates from 72% at 25°C to 27% at 32.5°C. The disparity between this study and that of Hutchison et al. (1990) is somewhat perplexing. Both studies maintained relative humidity at ≈75%, used the same host species obtained from the same rearing facility, and used parasitoids from the same colony. One factor that did differ was the density of parasitoids used during the initial parasitization of host eggs. This study used a ratio of one female to 25 host eggs, whereas Hutchison et al. used a ratio of ≈1:10. In preliminary trials, it was found that under conditions of severe crowding (approximately one female per host egg), superparasitism was frequent and overall emergence averaged from 1.3 to 1.4 adults per host egg (unpublished data). Under these circumstances, the mean developmental times of *T. bactrae* and *T. pretiosum* increased 1–2 d, the period of adult emergence was extended by 2–3 d, and many of the resulting adults were very small. Slightly greater crowding in the Hutchison et al. study may have contributed to lower survival. Differences in our studies may also be reflective of changes in the vigor of the parasitoid colony.

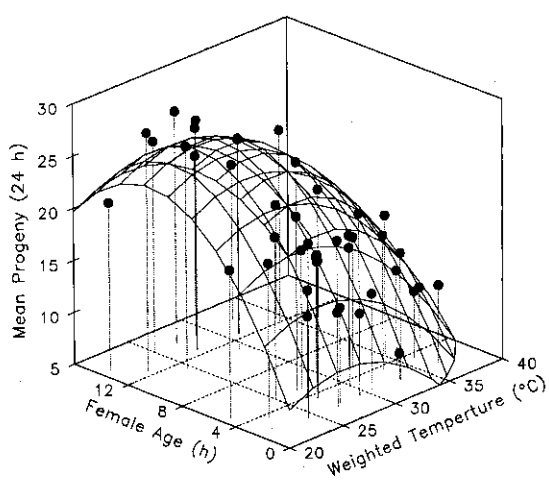

Fig. 4. Surface response depicting relationship between temperature, *T. bactrae* female age, and the number of progeny produced within the first 24 h of exposure to host eggs ($F = 71.11$; df = 4,683; $P = 0.0001$). Regression was performed on individual data but for clarity only means are presented. Equation for the surface response is given in the text.

Trichogrammatoidea bactrae given a 10% honey solution averaged up to 55 progeny at 25°C and survived an average of up to 6 d at 15°C. The same species fed a 5% sucrose solution survived an average of 1.2 d and produced a mean of from 26 to 16 progeny at temperatures between 22.5 and 30°C (Hutchison et al. 1990), and honey-fed *T. bactrae fumata* averaged 67 progeny and lived almost 9 d at 26.2°C (Lim 1986). Honey has been shown to be a highly suitable food source for adult *Trichogramma*, equal in nutritive value

to cotton nectar (Ashley & Gonzales 1974). Sucrose is less representative of a natural diet and may have contributed to the lower fecundity and longevity observed by Hutchison et al. (1990). Also, in this study a conscious effort was made to select relatively large females; this may have further contributed to the disparity in our respective studies. It is known for several *Trichogramma* species that larger females are more fecund and live longer than smaller females (Waage & Ng 1984; Hohmann et al. 1988; Bai et al. 1992). Although Lim (1986) reported a 1:1 sex ratio for *T. bactrae fumata*, this study and others (e.g. Lim & Pan 1974 cited in Lim 1986; Calvin et al. 1984; Hohmann et al. 1988) have shown that female-biased sex ratios are more typical of *Trichogramma* and *Trichogrammatoidea* species.

Three-hour observations of *T. bactrae* oviposition demonstrated that females display high rates of oviposition very early in adult life. Because of this behavior, females exposed to lethal temperature cycles (25–40°C) produced a statistically equivalent number of progeny within 24 h when compared with females exposed to more moderate conditions. This resulted primarily from higher rates of oviposition within the first 3 h at higher temperatures (Fig. 1B). In comparison, temperature appeared to play a larger role in determining 24-h rates of oviposition in the third study (Table 3; Fig. 4). This inconsistency may be related to female age because closer scrutiny of the surface response (Fig. 4) suggests that temperature had a greater effect on older females in comparison with younger females.

The propensity for females to lay a significant amount of their egg complement soon after emergence has been observed for other trichogrammatids. In greenhouse tests with *T. minutum* Riley, Fye & Larsen (1969) reported that females completed nearly half of their oviposition within the first 24 h of emergence and 90% within 4 d of emergence. Pak & Oatman (1982) noted that *T. brevicapillum* Pinto & Platner laid >3 times as many eggs within the first 6 h after emergence as within 6–12 h after emergence and also reported that hourly rates of oviposition were maximal during the 3rd and 4th h after emergence.

This pattern of early oviposition for *T. bactrae* contributed significantly to the high net reproductive rates and the high intrinsic rates of increase estimated here. Furthermore, net reproductive rates of >1.0 and positive intrinsic rates of increase at constant temperatures up to 32.5°C suggest that populations of this parasitoid have growth potential at relatively high temperatures. It is unlikely that such high rates of increase would be realized under field conditions, but the potential for relatively high rates of oviposition soon after release may be a significant feature underlying the biological control potential of this parasitoid and other trichogrammatid species.

Results from these laboratory studies have implications for the utility of *T. bactrae* as a biological control agent in the southwestern deserts. First, this parasitoid appears to share some of the attributes of a well-established species, *T. pretiosum*, in terms of rapid development and high survival at high temperatures. Second, adult female *T. bactrae* are comparatively long-lived at low to moderate temperatures and can survive ≈1 d at constant temperatures of 30–35°C. Survival may be even higher under more realistic fluctuating temperatures with high maxima. Field observations indicate that adults may live up to 4 d under typical summer conditions (unpublished data). Third, even when ambient air temperatures exceed 42°C during the early afternoon, the temperature on the surface of cotton leaves exposed to full sun rarely exceeds 36°C (unpublished data). Thus, *T. bactrae* would probably not be subject to as severe conditions as might be expected from measurements of ambient temperature. Humidity effects were not examined here but may be worthy of consideration. For example, Calvin et al. (1984) found that *T. pretiosum* development was prolonged and adult fecundity was reduced at relative humidities as low as 20%. The relative humidity within a crop canopy or on the surface of a plant is a complex function of many variables, including wind turbulence, leaf and canopy architecture, and ambient conditions (Cloudsley-Thompson 1962; Wilmer 1986). The relative humidity experienced by *T. bactrae* on the surface of a cotton plant would be expected to change significantly throughout the season depending on irrigation practices and weather patterns. The value of 75% RH used in this study may be realistic during only limited periods of the day or season. Further study of humidity-related effects on *T. bactrae* biology and measurement of relative humidity on the plant surface may be warranted.

Finally, in developing augmentative release strategies, results suggest that holding females without hosts for up to 14 h may enhance 24-h rates of oviposition and induce females to oviposit during the scotophase. Temporarily storing *T. bactrae* that have emerged in early morning for later release in the evening might be beneficial from this aspect, and the fact that parasitoids would be exposed to more moderate temperatures that may extend their longevity and reproductive capacity. Pak & Oatman (1982) observed that *T. brevicapillum* laid very few eggs during the scotophase, but Orphanides & Gonzales (1970) reported higher rates of longevity and fecundity for *T. pretiosum* under almost continuous dark conditions compared with those reared under continuous light. Whether *T. bactrae* would search for and sting hosts in the field during the scotophase is unknown; however, even if ovipositional activity was minimal during the night, females would have the opportunity to

acclimate to the environment and begin searching for host in the early morning during more optimal temperatures. The demands of host searching in the field would no doubt modify the daily ovipositional patterns and reduce the reproductive rates demonstrated in this study. Thus, assessing the actual benefits of manipulating release times must await careful field studies.

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