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Developmental and Reproductive Biology of a Predatory *Franklinothrips* n. sp. (Thysanoptera: Aeolothripidae)

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The developmental and reproductive biology of a new species of predatory *Franklinothrips* was determined in the laboratory at three constant temperatures. At the intermediate experimental temperature (25°C), *Franklinothrips* n. sp. exhibited the greatest larval to adult survivorship, and mated females produced more progeny of which a greater proportion were female when compared to individuals reared at 20 and 30°C. Analysis of jackknife estimates of net reproduction (R_o), generation times (T_c), intrinsic rate of increase (r_m), and finite rate of increase (λ) were all significantly greater at 25°C than corresponding values at 20 and 30°C. Population doubling time (T_d) was significantly lower at 25°C, indicating that population growth is approximately 50% faster at this temperature than at 20 and 30°C. Unmated female *Franklinothrips* n. sp. produce only male offspring, confirming arrhenotoky in this species. At 30°C, 15% of larvae failed to produce silk pupation cocoons and propupal and pupal stages were observed for cocoonless individuals. This result indicates that *Franklinothrips* n. sp. has two pupal stages, contradicting earlier speculations about the pupal biology of this genus. Furthermore, at 30°C, 13% of mated females and 33% of unmated females failed to produce viable eggs when reared and maintained at this temperature.

***Key Words: Franklinothrips* n. sp.; bionomics; fecundity; longevity; reproductive demographics; jackknife; life tables.**

INTRODUCTION

The genus *Franklinothrips* (Thysanoptera: Aeolothripidae) has a pan-tropical distribution, with 10 described species known from Central and South America, the Caribbean, Africa, Asia, Australia, and the southern United States (Arakaki and Okajima, 1998; Mau *et al.*, 1989; Moulton, 1932; Mound and Marullo, 1996; Mound and Walker, 1987; Okajima, 1979; Stannard, 1952; Williams, 1918). Myrmecomorphy is a distinguishing feature of adult *Franklinothrips* and ant-like behavioral patterns reinforce their mimetic color patterns and morphology (Johansen, 1977, 1983). Female *Franklinothrips* spp. lay eggs directly into plant tissue. Developing larvae pass through two instars (second instars are distinguished from firsts by red hypodermal pigments), before pupating within protective silk cocoons which are spun from secretions produced from the anal region (Arakaki and Okajima, 1998; Reijne, 1920; Sureshkumar and Ananthakrishnan, 1987). Modified tarsi on forelegs may assist adult *Franklinothrips* spp. with emergence from cocoons, and the "hook and tooth" on the second foretarsal joint could also assist with prey capture and manipulation (Lewis, 1973; Reijne, 1920).

Franklinothrips spp. adults and larvae are generalist predators and attack a wide variety of arthropod pests. Known prey include greenhouse thrips [*Heliothrips haemorrhoidalis* (Bouché)], *Thrips palmi* Karny, redbanded thrips [*Selenothrips rubroccinctus* (Giard)], chili thrips (*Scirtothrips dorsalis* Hood), two spotted spider mite (*Tetranychus urticae* Koch), red spider mite (*Tetranychus yothersi* McGregor), silverleaf whitefly (*Bemisia argentifolii* Bellows and Perring) nymphs, avocado whitefly (*Trialeurodes floridensis* Quaintance) eggs, nymphs, and pupae, and serpentine leaf miner (*Liriomyza trifolii* Burgess) larvae (Arakaki and Okajima, 1998; Ebeling, 1959; Johansen and Mojica-Guzman, 1996; McCallan, 1943; Moznette, 1919; Okajima *et al.*, 1992; Stannard, 1952; Sureshkumar and Ananthakrishnan, 1987; Williams, 1918). The host plants on which *Franklinothrips* spp. are found in association with prey are varied and include such economically important crops as avocados (*Persea americana* Miller), beans (*Phaseolus vulgaris* Linnaeus), cacao (*Theobroma cacao* Linnaeus), chilies (*Capsicum frutescens* Linnaeus), citrus (*Citrus* spp.), coffee (*Coffea arabica* Linnaeus), eggplant (*Solanum melongena* Linnaeus), and melons (*Cucumis melo* Linnaeus) (Arakaki and Okajima, 1998; Ebeling, 1959; McCallan, 1943;

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Moznette, 1919; Okijima *et al.*, 1992; Strassen 1995; Williams, 1918).

Although *Franklinothrips* spp. are known to prey on a number of important agricultural pests, the impact these predators have on pest populations has not been quantified and predatory thrips are generally assumed to be unable to regulate pest populations because of their low reproductive rates (Lewis, 1973; McCallan, 1943; Williams, 1918). Consequently, the value of the genus *Franklinothrips* as a source of natural enemies for either classical or augmentative (inundative) biological control programs against phytophagous thrips has not been investigated. Surveys in southern California avocado orchards for natural enemies associated with a new avocado pest, *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae), have revealed that an undescribed species of *Franklinothrips* is the dominant predator where this pest has attained high densities (>10 *S. perseae* larvae per leaf) (Hoddle, unpublished).

S. perseae was first discovered damaging avocado foliage and fruit in southern California orchards in 1996 and at time of discovery was a species new to science (Nakahara, 1997). In 1998, crop loses due to down-graded fruit and increased production costs due to *S. perseae* feeding damage were estimated to have cost California growers (U.S.) $7–13 million (Hoddle *et al.*, 1999). Foreign exploration efforts to determine the native range of *S. perseae* indicate that this pest is of Central American origin (Hoddle and Morse, 1997) and associated natural enemies collected concurrently from avocados have included *Franklinothrips* spp. (Hoddle, unpublished). Examination of museum specimens held by the California Department of Food and Agriculture (Sacramento, CA) and the United States National Museum of Natural History (Washington, DC) indicates that *Franklinothrips* n. sp. has been collected from peaches (*Prunus persica* (Linnaeus) Batsch) and avocados in California and has been present in this state since at least 1938 but was consistently misidentified as *F. vespiformis* (S. Nakahara pers. comm., 1999).

The current study reported here investigated the developmental and reproductive biology of *Franklinothrips* n. sp. from California and is the first work we are aware of that has studied any species of *Franklinothrips* in this detail. The motivation for this research was to determine the optimal conditions under which mass rearing of *Franklinothrips* n. sp. should be conducted for possible augmentative releases against *S. perseae* in avocado orchards.

MATERIALS AND METHODS

Collecting Franklinothrips n. sp. for Laboratory Studies and Deposition of Voucher Specimens

Laboratory studies were initiated with field-collected adult male and female *Franklinothrips* n. sp. which were obtained by beating recently pruned avocado trees (cultivar Reed being regrafted to Hass) in Fallbrook, California. This inland site had a heavy infestation of *S. perseae* on young foliage (average of 12 *S. perseae* larvae per leaf when collections were made) and is within the plant–climate zone classified as "coastal valley," where the marine influence has a year-round

TABLE 1

Mean Duration in Days (±SE) of Each Lifestage of *Franklinothrips* n. sp. and Proportion of Offspring Reared from First Instar Larvae to Adulthood That Were Female

	Temperature (°C)								
	20			25			30		
Lifestage	Males	Females	Combined	Males	Females	Combined	Males	Females	Combined
Eggs			16.06 ± 0.08 (n = 517)			10.39 ± 0.07 (n = 487)			9.66 ± 0.05 (n = 246)
1st Instar	3.90 ± 0.09 (n = 52)	6.33 ± 1.20 (n = 3)	4.04 ± 0.12 (n = 55)	2.0 ± 0.00 (n = 34)	2.05 ± 0.04 (n = 38)	2.03 ± 0.02 (n = 72)	1.85 ± 0.08 (n = 40)	1.84 ± 0.07 (n = 31)	1.85 ± 0.05 (n = 71)
2nd Instar	3.90 ± 0.60	5.00 ± 0.58	3.96 ± 0.09	2.00 ± 0.04	2.16 ± 0.06	2.08 ± 0.04	1.15 ± 0.07	1.13 ± 0.06	1.14 ± 0.05
Pupal Cocoons	12.56 ± 0.10	11.33 ± 0.67	12.49 ± 0.11	7.50 ± 0.11	7.37 ± 0.09	7.43 ± 0.07	5.30 ± 0.14	5.35 ± 0.09	5.32 ± 0.09
Unmated Adults	25.85 ± 1.65a (n = 13)	22.11 ± 2.96a (n = 10)	24.32 ± 1.56 (n = 23)	16.60 ± 1.80a (n = 9)	16.33 ± 1.94a (n = 10)	16.47 ± 1.29 (n = 19)	10.60 ± 1.22a (n = 10)	8.07 ± 0.85a (n = 15)	9.08 ± 0.74 (n = 25)
Mated Adults	12.60 ± 2.10b (n = 10)	18.50 ± 2.94a (n = 10)	15.55 ± 1.89 (n = 20)	13.33 ± 1.87a (n = 10)	12.4 ± 2.54a (n = 10)	12.84 ± 1.57 (n = 20)	8.13 ± 0.97a (n = 16)	7.87 ± 0.82a (n = 15)	8.00 ± 0.63 (n = 31)
Prop. Females			0.41			0.53			0.44

Note. The total numbers (n) of first instar larvae hatched at each temperature and then reared through to adulthood are presented in parentheses as are the numbers of mated and unmated adults that were used to determine longevity. Mean adult longevity followed by the same letters within temperature regimens are not significantly different (P = 0.05).

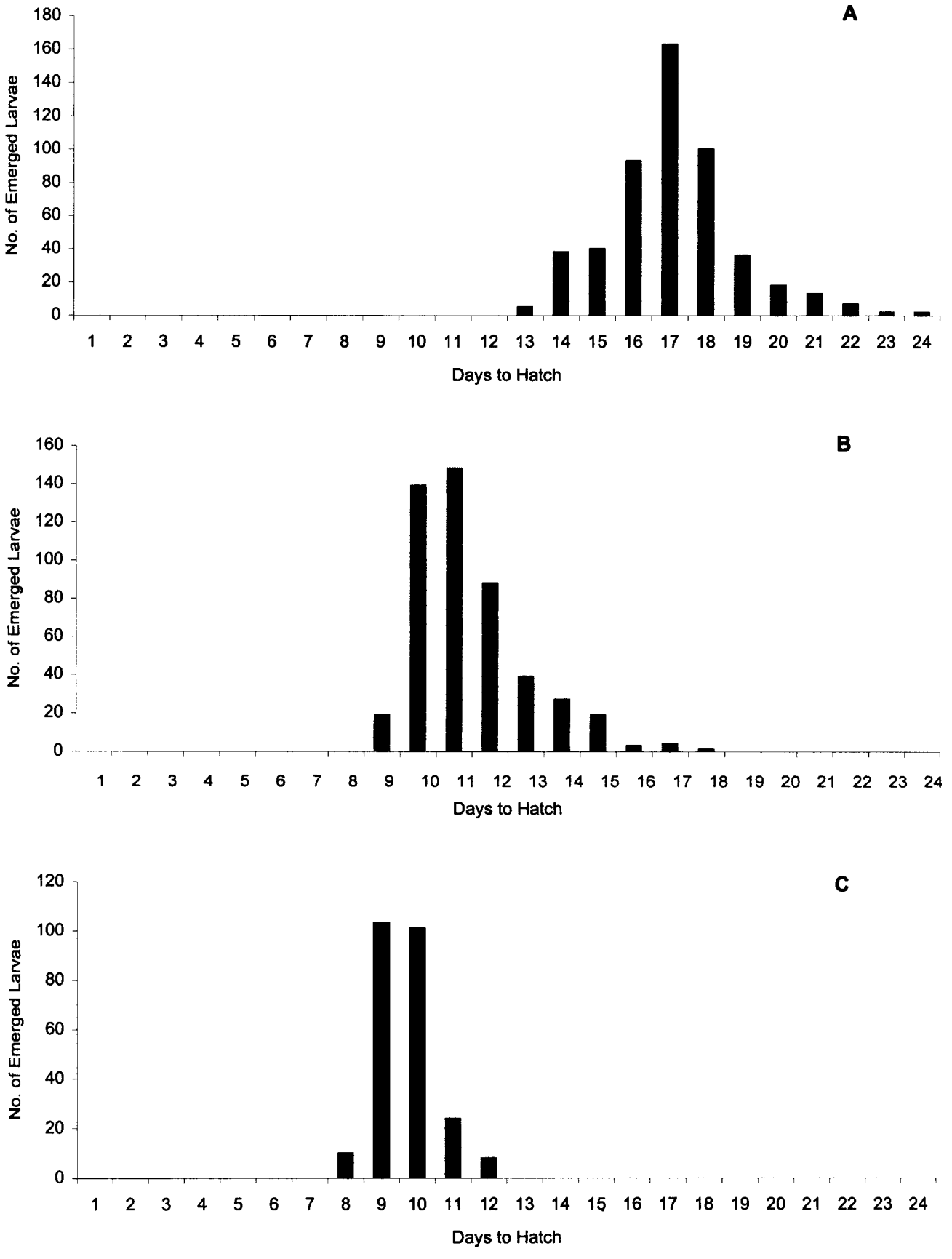

FIG. 1. Distribution of larval emergence from Hass avocado leaves over time for *Franklinothrips* n. sp. at 20°C (A), 25°C (B), and 30°C (C) following exposure to ovipositing females for 24 h.

moderating effect on temperatures (Kimball and Brooks, 1959). All adult specimens collected from the Fallbrook site and laboratory-reared progeny produced by field-collected *Franklinothrips* n. sp. were deposited with the Systematic Entomology Laboratory, USDA-ARS, Beltsville Maryland, and identified by Dr. S. Nakahara.

Calculating Egg Hatch Times

Undersides of mature Hass avocado leaves collected from the Biological Control Grove (this site does not have *S. perseae* nor has *Franklinothrips* n. sp. been collected there) at the University of California, Riverside, were presented to female *Franklinothrips* n. sp. for oviposition. Adult females were confined individually or with male *Franklinothrips* n. sp. when available within modified Munger cells (Munger, 1942; Morse *et al.*, 1986), fed irradiated *Ephestia kuehniella* (Zeller) (Lepidoptera: Phycitidae) eggs (supplied by Beneficial Insectaries, Oak Run CA), and left to oviposit in temperature cabinets which were set at 20, 25, or 30°C, under long days (L:D 14:10 h). Actual temperatures within cabinets were recorded every 15 min with Hobo dataloggers (Onset Computer Corp., Pocasset MA). Field-collected *Franklinothrips* n. sp. were moved to new leaves daily until death.

At the end of the 24-h oviposition period, the leaf area enclosed by the Munger cell which was exposed to ovipositing females was excised from the avocado leaf. Trimmed leaves were labeled, placed on water-saturated foam pads in stainless steel trays, and incubated at the temperature at which oviposition occurred. Leaves were examined daily for emerged *Franklinothrips* larvae and the mean number of days to egg hatch was calculated for each experimental temperature.

Preimaginal Development, Cocoon Construction, and Determination of Arrhenotoky

First instar larvae collected from the egg hatch study were placed individually in modified Munger cells with the underside of a mature Hass avocado leaf exposed as a foraging surface. Larvae were fed irradiated *E. kuehniella* eggs and reared at the temperature under which they hatched. Larvae were examined daily and their developmental stages, and numbers of cocoons constructed were recorded. Preimaginal developmental times for male and female *Franklinothrips* n. sp. and sex ratios of mature progeny were determined at 20, 25, and 30°C. To test for arrhenotoky, the sex ratios of 31 randomly selected larvae produced by 13 different unmated females were compared with those of 51 larvae from 13 mated *Franklinothrips* n. sp. females that were reared to adulthood at 20°C.

Determining Female Fecundity, Frequency of Oviposition Marks, and Adult Longevity

Adult *Franklinothrips* n. sp. reared from the preimaginal study (F_1 adults) were confined either individually in Munger cells or as male–female pairs (mating was assumed to have occurred under these conditions). Mated and unmated females were fed irradiated *E.*

TABLE 2

Preoviposition Period (±SE), Mean Lifetime and Daily (±SE) Progeny Production as Estimated from Emerged Larvae and Mean Lifetime and Daily Number of Oviposition Wounds Recorded on Avocado Leaves by Mated and Unmated *Franklinothrips* n. sp. Females at Three Different Temperatures

	Temperature (°C)		
Biological parameter	20	25	30
Unmated females			
Number of females used	10	10	15
Preoviposition period (days)	1.56 ± 0.24	0.90 ± 0.23	2.44 ± 1.00
Mean total progeny	67.89 ± 21.40 (a, 1)	71.2 ± 12.92 (a, 1)	8.53 ± 3.81 (a, 2)
Mean daily progeny	2.33 ± 0.18	4.12 ± 0.30	1.05 ± 0.17
Mean lifetime oviposition wounds	154 ± 22.37 (x, 1)	314 ± 44.14 (x, 2)	105 ± 17.94 (x, 1)
Mean daily oviposition wounds	7.07 ± 0.43	18.13 ± 13.58	12.98 ± 1.31
Mated females			
Number of females used	10	10	14
Preoviposition period (days)	1.50 ± 0.24	0.90 ± 0.10	0.77 ± 0.26
Mean total progeny	35.20 ± 6.64 (a, 1)	44.44 ± 11.77 (a, 1)	8.43 ± 2.78 (a, 2)
Mean daily progeny	1.81 ± 0.14	3.17 ± 0.22	0.96 ± 0.21
Mean lifetime oviposition wounds	128.10 ± 25.54 (x, 1, 2)	220 ± 47.85 (x, 1)	101 ± 14.74 (x, 2)
Mean daily oviposition wounds	6.50 ± 0.50	15.86 ± 1.09	12.84 ± 1.13

Note. Means followed by the same letters (a and b are used for comparison of mean total progeny between mated and unmated females within temperature regimens; x and y are used to compare mean lifetime oviposition wounds between mated and unmated females within temperature regimens) within a column and numbers within rows are not different from each other at the 0.05 level of significance.

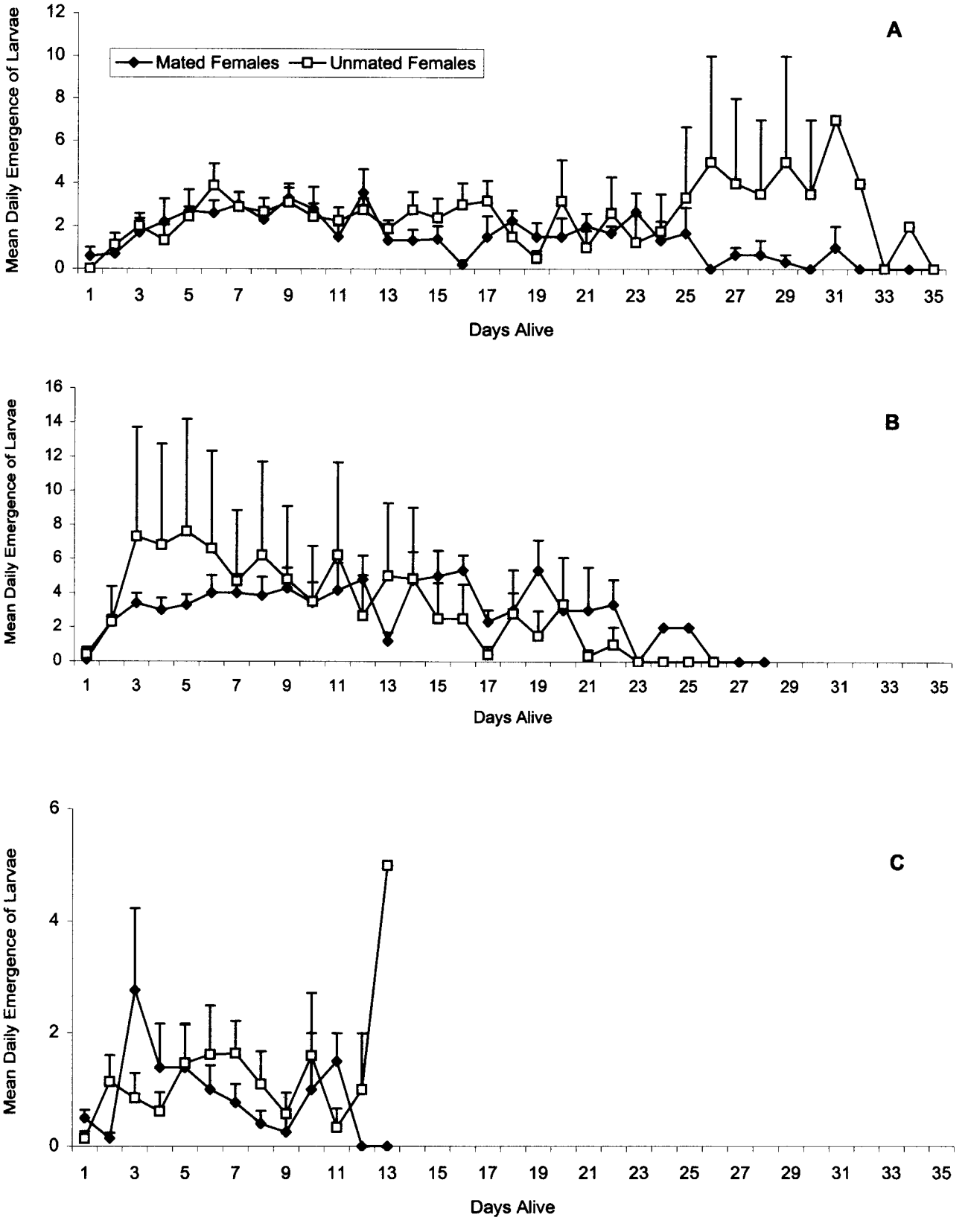

FIG. 2. Mean number of first instar *Franklinothrips* n. sp. emerging daily from Hass avocado leaves following exposure to either mated or unmated females for 24 h at 20°C (A), 25°C (B), or 30°C (C).

TABLE 3

Demographic ($l_x m_x$) Life Tables for Cohorts of Adult Female *Franklinothrips* n. sp. Prepared from Daily Fecundity, Larval Development, and Sex Ratio Experiments at Three Different Temperatures

	20°C		25°C		30°C	
Age (days)	Proportion alive (l_x)	Offspring (m_x)[a]	Proportion alive (l_x)	Offspring (m_x)[a]	Proportion alive (l_x)	Offspring (m_x)[a]
0	1.00	Preimaginal	1.00	Preimaginal	1.00	Preimaginal
1	1.00	development	1.00	development	1.00	development
↓	1.00	↓	1.00	↓	1.00	↓
	1.00		1.00		1.00	
10	1.00	0.00	1.00	0.00	1.00	0.00
11	1.00	0.00	1.00	0.00	0.96	0.00
12	1.00	0.00	0.95	0.00	0.92	0.00
13	1.00	0.00	0.95	0.00	0.92	0.00
14	1.00	0.00	0.95	0.00	0.92	0.00
15	1.00	0.00	0.95	0.00	0.92	0.00
16	0.96	0.00	0.95	0.00	0.88	0.00
17	0.91	0.00	0.95	0.00	0.88	0.00
18	0.91	0.00	0.95	0.00	0.83	0.00
19	0.91	0.00	0.95	0.64	0.83	0.20
20	0.91	0.00	0.95	1.30	0.83	0.13
21	0.87	0.00	0.95	1.59	0.83	1.08
22	0.87	0.00	0.95	2.69	0.79	0.53
23	0.87	0.00	0.90	2.15	0.79	0.60
24	0.87	0.00	0.90	2.62	0.79	0.72
25	0.87	0.00	0.90	2.54	0.79	0.69
26	0.87	0.00	0.90	2.48	0.67	0.69
27	0.87	0.00	0.81	2.62	0.58	0.47
28	0.87	0.00	0.81	2.49	0.50	0.48
29	0.87	0.00	0.81	2.31	0.29	0.38
30	0.87	0.00	0.76	2.42	0.21	0.53
31	0.87	0.00	0.76	2.12	0.13	0.15
32	0.87	0.00	0.76	1.86	0.04	0.88
33	0.87	0.00	0.71	1.59	0.04	2.20
34	0.87	0.00	0.43	1.35	0.00	0.00
35	0.87	0.21	0.43	1.47		
36	0.87	0.82	0.43	1.59		
37	0.87	0.12	0.38	1.52		
38	0.87	0.46	0.29	2.21		
39	0.87	0.41	0.29	0.97		
40	0.87	0.39	0.24	1.91		
41	0.87	0.73	0.24	1.27		
42	0.87	0.88	0.24	0.95		
43	0.87	0.86	0.24	1.06		
44	0.83	1.21	0.19	1.19		
45	0.83	1.25	0.14	0.00		
46	0.83	1.01	0.10	0.53		
47	0.78	1.01	0.10	0.53		
48	0.78	0.97	0.05	0.00		
49	0.74	1.09	0.05	0.00		
50	0.70	1.13	0.05	0.00		
51	0.61	1.29	0.00	0.00		
52	0.61	0.79				
53	0.57	0.57				
54	0.52	0.79				
55	0.52	0.79				
56	0.52	0.51				
57	0.52	0.68				
58	0.48	0.45				
59	0.39	0.87				
60	0.35	0.36				
61	0.30	1.05				
62	0.30	0.76				
63	0.30	0.59				

TABLE 3—*Continued*

Age (days)	20°C		25°C		30°C	
	Proportion alive (l_x)	Offspring (m_x)[a]	Proportion alive (l_x)	Offspring (m_x)[a]	Proportion alive (l_x)	Offspring (m_x)[a]
64	0.30	0.82				
65	0.22	0.90				
66	0.22	0.74				
67	0.22	0.82				
68	0.22	0.82				
69	0.13	1.23				
70	0.13	0.96				
71	0.13	0.55				
72	0.13	0.00				
73	0.09	0.41				
74	0.04	0.00				
75	0.00	0.00				

[a] Daily progeny production adjusted for female sex ratio observed at each experimental temperature.

kuehniella eggs and moved to new mature Hass avocado leaves every 24 h until death. After this oviposition period, the area of leaf exposed to females was excised from the leaf and the number of visible oviposition marks was recorded using a dissecting microscope. The mean daily and lifetime numbers of oviposition marks produced by mated and unmated female *Franklinothrips* n. sp. were calculated.

Leaves exposed to females for each 24 h oviposition period were maintained on water-saturated foam pads in temperature cabinets at the same temperature at which oviposition occurred and examined daily for emergence of offspring. Mean daily and lifetime fecundities for mated and unmated female *Franklinothrips* n. sp. were calculated using numbers of larvae that emerged from each leaf after 24 h exposure to individual females. Mean numbers of progeny produced by mated and unmated females were compared within temperature regimens using Student's *t* test ($P = 0.05$).

Survivorship of all adult *Franklinothrips* n. sp. was recorded daily and mean and daily longevities of mated and unmated males and females were calculated for each experimental temperature.

Constructing l_xm_x Life Tables and Calculating Demographic Growth Parameters

Larval to adult survivorship data, daily fecundity of F_1 females, and sex ratio of progeny reared from F_1 females at their respective temperatures were used to construct l_xm_x life tables from which demographic growth parameters were calculated. Survivorship of oviposited eggs as estimated from daily fecundity for F_1 females was assumed to be unity and was recorded as such in the l_xm_x life tables for each temperature.

No significant differences were observed in the total numbers of progeny produced by mated and unmated females within their respective temperature regimens (see Results section) for 20, 25, and 30°C. Consequently, development and survivorship data and daily progeny production were combined for mated and unmated *Franklinothrips* n. sp. females to produce a birth cohort of females ($n = 20$) for each temperature. The sex ratio [i.e., No. females/(males + females)] of progeny reared from mated females at each experimental temperature was used. The following demographic parameters were calculated from l_xm_x life tables: (1) Net reproductive rates [$R_o = \Sigma l_x m_x$ (where l_xm_x is the net female maternity, where l_x is the fraction of females alive at age x, and m_x is the number of daughters born to surviving females at age x)] express the per generation growth rate of the population as the number of daughters produced by females (if $R_o > 1.0$ the population increases in size, if $R_o = 1.0$ no increase in population size, and if $R_o < 1.0$ population growth is declining) (Carey, 1993). (2) Mean generation time ($T_c = \Sigma x l_x m_x/R_o$) is the average interval separating births of one generation from the next (Carey, 1993). (3) The intrinsic rate of natural increase, r_m [found as the solution to $1 = \Sigma l_x m_x \exp(-r_m x)$ (this equation was iterated for r_m until a value of 1 was obtained)], is the maximum exponential rate of increase by a population growing within defined physical conditions (Birch, 1948). (4) Finite rate of increase [$\lambda = \exp(r_m)$] is the factor by which a population multiplies between each time step (Birch, 1948). (5) Doubling time ($T_d = \ln(2)/r_m$) is the time required by a population growing exponentially without limit to double in size when increasing at a given r_m (Carey, 1993).

Mean demographic parameter estimates with standard errors (SE) were generated by jackknife analysis of $l_x m_x$ life table data. The jackknife method removes one observation at a time from the original data set and recalculates the statistic of interest from the truncated data set. These new estimates, or pseudo-values, form a set of numbers from which mean values and variances can be calculated and compared statistically (Miller, 1974; Efron, 1981; Meyer *et al.*, 1986; Shao and Tu, 1995). The jackknife method of resampling is well suited for estimating variance for population growth statistics (Meyer *et al.*, 1986). Mean jackknife estimates of demographic parameters were compared across temperatures using ANOVA and Tukey's studentized range test ($P = 0.05$) to determine if temperature had significant effects on *Franklinothrips* n. sp. population growth statistics.

RESULTS

Egg Hatch Times, Preimaginal Development, Cocoon Construction, and Arrhenotoky

Mean egg hatch times decreased with increasing temperature (Table 1) and the time period over which larval emergence from avocado leaves was observed was also reduced (Fig. 1). Increased temperatures reduced developmental times for all preimaginal stages of *Franklinothrips* n. sp., and the proportion of females reared to adulthood was greatest at 25°C and lowest at 20°C (Table 1). Larval to adulthood survivorship was 88, 95, and 82% at 20, 25, and 30°C, respectively.

At 20 and 25°C, 100% of larvae produced single pupation cocoons when they were second instar larvae. At 30°C, 15% of reared larvae failed to produce cocoons within which to pupate. Cocoonless *Franklinothrips* n. sp. were observed to pass through a propupal stage (mean duration = 1.33 days ± 0.33) and a pupal stage (mean duration = 3.33 days ± 0.67), thereby confirming by observation of molting that this predator has two quiescent pupal stages prior to eclosion as an adult at 30°C.

Franklinothrips n. sp. exhibited arrhenotoky at 20°C. Of the 51 larvae reared to adulthood from 13 different mated females, 41% were female. In comparison, the 31 larvae reared from 13 different unmated females all matured into males.

Fecundity, Oviposition Marks, and Adult Longevity

Comparison of mean lifetime fecundities between mated and unmated females at 20°C ($t = 1.53$, $df = 18$, $P = 0.07$), 25°C ($t = 1.53$, $df = 18$, $P = 0.07$), 30°C ($t = 0.02$, $df = 27$, $P = 0.49$) were not significant (Table 2). Significant differences in mean lifetime fecundities among mated ($F = 7.41$, $df = 2, 33$, $P = 0.002$) and unmated ($F = 9.52$, $df = 2, 34$, $P = 0.0006$) females when compared across temperatures existed, with higher average lifetime fecundities being observed at 20 and 25°C (Table 2). The average daily distributions of emerged progeny for each day females were alive were similar for mated and unmated females (Fig. 2). At 20°C, progeny were reared from mated and unmated females up to days 31 and 34, respectively, and females died within 1–4 days of their last oviposition event at this temperature (Fig. 2A). Progeny production at 25°C occurred up to days 25 and 22 for mated and unmated females, respectively. After the last oviposition females lived for an additional 3–4 days before dying. At 30°C, the period over which progeny were produced was substantially shorter than that for 20 and 25°C. Mated females produced progeny up to day 11, while unmated females laid eggs on day 13 before dying on that same day (Fig. 2C). All mated and unmated females produced progeny at 20 and 25°C. At 30°C, 13% of mated and 33% of unmated females appeared to be sterile because they did not produce any viable eggs that hatched over their entire lifetimes (Table 3).

Franklinothrips n. sp. females oviposited preferentially along the avocado leaf mid-rib and lateral leaf veins. Slits in leaf tissue made by the ovipositor turned a characteristic brown color. Occasionally, ovipositing females would cap oviposition wounds with a yellow–orange-colored substance. The source of this capping secretion was not identified for *Franklinothrips* n. sp., and capping has also been observed with *F. vespiformis* (Arakaki and Okajima, 1998). Mean lifetime production of oviposition wounds was not significantly different between mated and unmated females at 20°C ($t = 0.78$, $df = 18$, $P = 0.23$), 25°C ($t = 1.43$, $df = 18$, $P = 0.08$), and 30°C ($t = 0.15$, $df = 27$, $P = 0.44$) (Table 2; Fig. 3).

Significant differences in mean lifetime oviposition wound production was detected across temperatures for mated ($F = 4.06$, $df = 2, 33$, $P = 0.03$) and unmated ($F = 14.98$, $df = 2, 34$, $P < 0.0005$) females. Mated females produced significantly more oviposition punctures at 25°C than at 20 and 30°C. A similar number of wounds were produced at 20 and 30°C (Table 2). Unmated females also produced significantly more oviposition wounds at 25°C than at 20 or 30°C where lifetime wound production was similar at 20 or 30°C (Table 2).

There were no significant differences in mean longevity between mated and unmated females at each temperature at 20°C ($t = 0.86$, $df = 17$, $P = 0.20$), 25°C ($t = 1.21$, $df = 17$, $P = 0.12$), and 30°C ($t = 0.17$, $df = 28$, $P = 0.43$) (Table 1; Fig. 4). Unmated males lived significantly longer at 20°C in comparison to mated males at this temperature ($t = 5.04$, $df = 21$, $P < 0.0005$) (Table 1; Fig. 4A). No significant differences in mean longevity were observed between mated and unmated males at 25°C ($t = 1.26$, $df = 17$, $P = 0.11$)

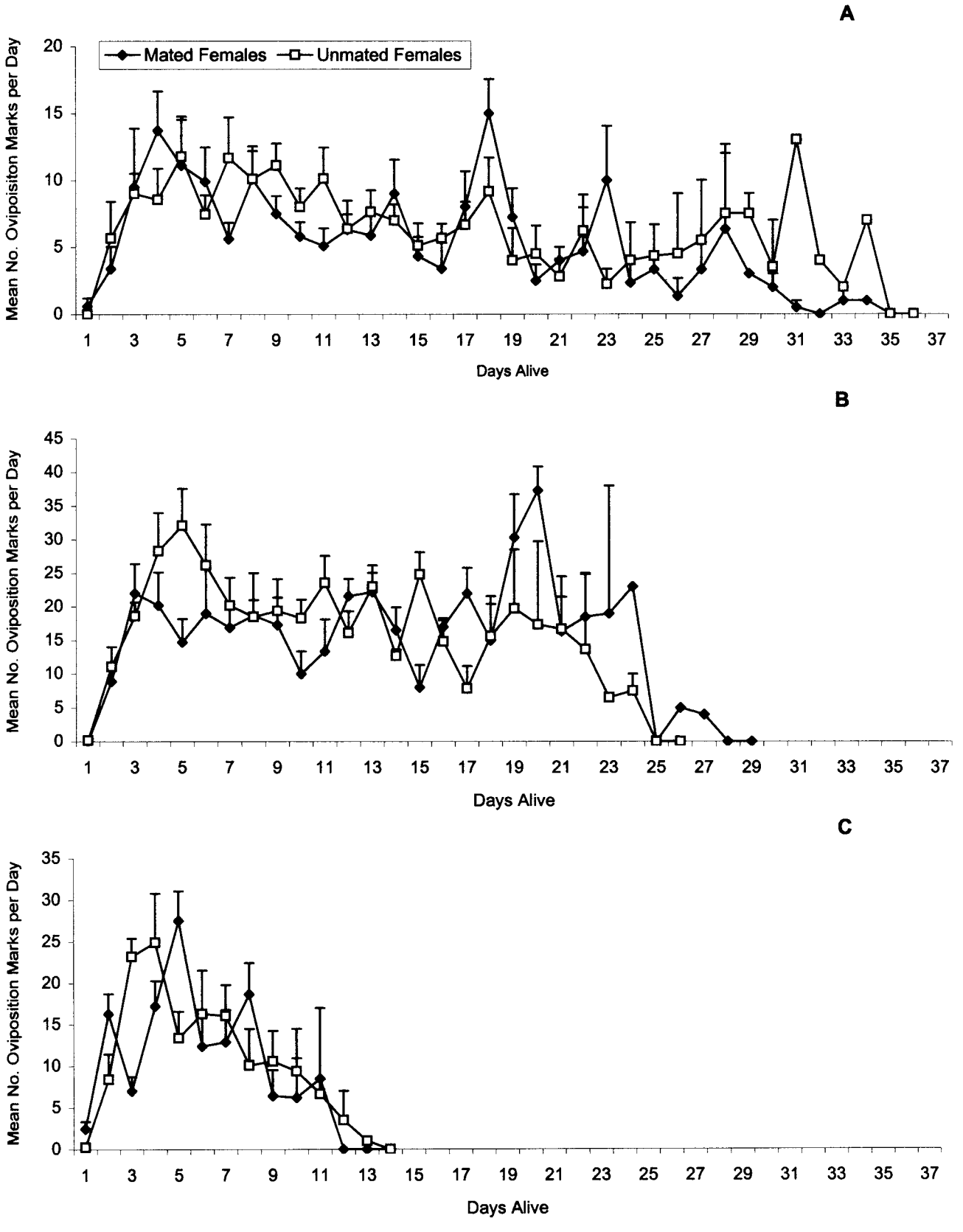

FIG. 3. Mean number of oviposition wounds counted on Hass avocado leaves following exposure to either mated or unmated *Franklinothrips* n. sp. for 24 h at 20°C (A), 25°C (B), or 30°C (C).

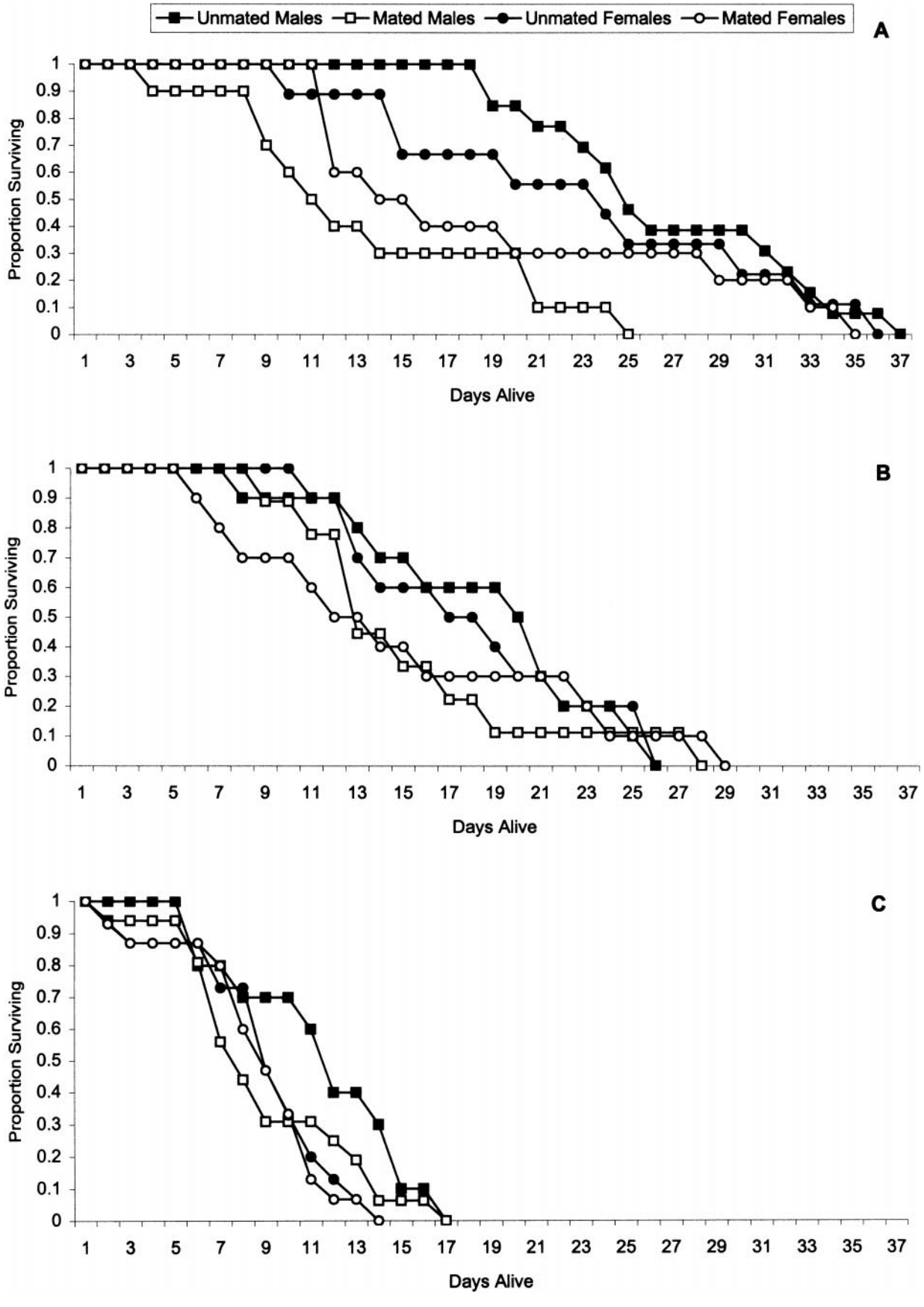

FIG. 4. Daily survivorship of mated and unmated adult male and female *Franklinothrips* n. sp. at 20°C (A), 25°C (B), and 30°C (C).

or 30°C ($t = 1.59$, $df = 24$, $P = 0.06$) (Table 1; Figs. 4B and 4C).

Demographic Growth Parameters

Significant differences existed among the five demographic growth parameters as estimated by jackknife analysis and compared across temperatures using ANOVA (Table 4). At 25°C, *Franklinothrips* n. sp. had a significantly higher net reproductive rate (R_o) ($F = 5556$, $df = 2, 57$, $P < 0.0005$), intrinsic rate of increase (r_m) ($F = 9036$, $df = 2, 57$, $P < 0.0005$), and finite rate of increase (λ) ($F = 9490$, $df = 2, 57$, $P < 0.0005$). Generation time (T_c) was significantly shorter at 30°C ($F = 3612$, $df = 2, 57$, $P < 0.0005$) and population doubling time (T_d) was 53% faster at 25°C when compared to 20°C and 30°C ($F = 2107$, $df = 2, 57$, $P < 0.005$) (Table 4).

DISCUSSION

Franklinothrips n. sp. development and reproduction was significantly affected by temperature. At 25°C, the demographic growth parameters R_o (net reproductive rate), r_m (intrinsic rate of increase), and λ (finite rate of increase) were significantly greater than the same parameters calculated for *Franklinothrips* n. sp. at 20 and 30°C. The sex ratio for *Franklinothrips* n. sp. was female biased at 25°C (at 20 and 30°C sex ratio estimates were male biased) and population doubling time was 53% faster because of greater daily daughter production at this temperature. Together, these data indicate greater potential for population increase by this predator at 25°C in an environment with unlimiting resources.

Temperature had a significant influence on cocoon building by *Franklinothrips* n. sp. We observed that 15% of *Franklinothrips* n. sp. larvae failed to pupate within silk cocoons when reared at 30°C. However, exposed larvae did pass through both propupal and pupal stages, contrary to previous statements that members of this genus have just one pupal stage (Reijne, 1920; Stannard, 1952). Reijne's (1920) observations of *Franklinothrips tenuicornis* Hood noted that 20% of larvae failed to pupate within cocoons. The temperature at which Reijne (1920) made observations was not reported. In contrast, all *Franklinothrips* n. sp. larvae produced one cocoon as second instar larvae when reared at 20 and 25°C in this study. However, if *Franklinothrips* n. sp. larvae were incubated and hatched at 25°C and then reared at 20°C, 31% of larvae produced two to three cocoons before entering the pupal stage and cocoon construction was initiated by first instar larvae (Hoddle, unpublished data). Cocoon production appears to be influenced by environmental stress. Work on the cocooning behavior of *Franklinothrips* n. sp. is continuing.

S. perseae builds to damaging levels in California avocado orchards in the winter and spring, when temperatures are relatively cool and trees are producing abundant young leaves and fruit which are suitable for pest feeding and oviposition. *S. perseae* is the only species in this genus that is known to outbreak in cool weather and populations can decline rapidly when summer temperatures are high (>32°C) even if abundant food is available (Hoddle and Morse, 1997). Laboratory studies on the reproductive and developmental biology of *S. perseae* indicate that the optimal temperature for population growth is 20°C (R_o is 15 at 20°C and declines to 5 at 25°C) (Hoddle and Morse, 1997).

Consequently, an efficacious natural enemy would have to respond to rapidly increasing *S. perseae* populations when temperatures are relatively cool and then survive hot summers, when *S. perseae* densities are extremely low. Under these environmental conditions our laboratory results suggest that endemic populations of *Franklinothrips* n. sp. will not increase in number quickly at low temperatures because of low fecundity and male-biased sex ratios. Similarly, predator numbers would be expected to decline over summer, when temperatures are hot, because *S. perseae* populations decline and *Franklinothrips* n. sp. demographic growth parameters indicate a propensity for slow population growth. It is therefore possible that repeated early seasonal releases of insectary-reared *Frankli-*

TABLE 4

Mean Demographic Growth Parameters (±SE) Generated by Jackknife $l_x m_x$ Data in Table 3 for *Franklinothrips* n. sp. ($n = 20$ Females in a Cohort). Means Followed by Different Letters across Temperatures (within a Column) Are Significantly Different at the 0.05 Level (ANOVA)

Temperature (°C)	R_o	T_c	r_m	λ	T_d
20	18.49 ± 0.18a	49.09 ± 0.12a	0.06 ± 0.0002a	1.06 ± 0.0002a	11.12 ± 0.03a
25	33.32 ± 0.28b	27.92 ± 0.05b	0.13 ± 0.0003b	1.14 ± 0.0004b	5.16 ± 0.01b
30	4.47 ± 0.07c	24.16 ± 0.06c	0.06 ± 0.0007a	1.07 ± 0.0007c	11.05 ± 0.12a

Note. R_o, net reproductive rate; T_c, generation time; r_m, intrinsic rate of increase; λ, finite rate of increase; T_d, doubling time in days. For more information on demographic growth parameters see Birch, (1948), Southwood (1978), and Carey (1993).

nothrips n. sp. into avocado orchards in spring and early summer when temperatures tend to become moderate may be necessary to more quickly increase numbers of this naturally occurring predator for *S. perseae* control. Field trials with *Franklinothrips* n. sp. alone and in combination with natural enemy compatible insecticides [e.g., sabadilla (Veratran-D, Dunhill Chemical Company, Azusa, California) (Bellows *et al.*, 1985)] for *S. perseae* control are currently underway to determine the efficacy of augmentative releases of *Franklinothrips* n. sp.

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