

# Developmental and reproductive biology of *Scirtothrips perseae* (Thysanoptera: Thripidae): a new avocado pest in California

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## Abstract

The developmental and reproductive biology of a new avocado pest, *Scirtothrips perseae* Nakahara, was determined in the laboratory at five constant temperatures, 15, 20, 25, 27.5 and 30°C. At 20°C, *S. perseae* exhibited greatest larval to adult survivorship (41%), and mated females produced a greater proportion of female offspring at this temperature when compared to 15, 25, 27.5 and 30°C. Average lifetime fecundity and preoviposition period was greatest at 15°C at 39.6 eggs per female and 17.6 days, respectively. Jackknifed estimates of net reproduction ( $R_0$ ), capacity for increase ( $r_c$ ), intrinsic rate of increase ( $r_m$ ), and finite rate of increase ( $\lambda$ ) were all significantly greater at 20°C than corresponding values at 15, 25 and 27.5°C. Population doubling time ( $T_d$ ) was significantly lower at 20°C, indicating *S. perseae* populations can double 33–71% faster at this temperature in comparison to 15, 25 and 27.5°C. Mean adult longevity decreased with increasing temperature, from a maximum of 52.4 days at 15°C to a minimum of 2.4 days at 30°C. Developmental rates increased linearly with increasing temperatures for eggs and rates were non-linear for development of first and second instar larvae, propupae, pupae, and for egg to adult development. Linear regression and fitting of the modified Logan model to developmental rate data for egg to adult development estimated that 344.8 day degrees were required above a minimum threshold of 6.9°C to complete development. An upper developmental threshold was estimated at 37.6°C with an optimal temperature of 30.5°C for egg to adult development. Unmated females produced only male offspring confirming arrhenotoky in *S. perseae*.

## Introduction

In June 1996, an unknown species of thrips was discovered damaging foliage and fruit of Hass avocado, *Persea americana* var. *drymifolia* Blake (Lauraceae) in Ventura County, California USA. By July 1997, the thrips had spread to all coastal avocado growing areas of California (Hoddle & Morse, 1997; 1998). This pest has subsequently been described and named *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) (Nakahara, 1997), and foreign

exploration efforts indicate that this pest is probably of Central American origin (Hoddle *et al.*, 2002a).

Feeding damage by adult and larval *S. perseae* to young leaves causes distortion, and brown scarring along the midrib and veins on the leaf underside becomes increasingly visible as leaves mature. Thrips larvae and adults also feed on developing fruit. Feeding can scar the entire fruit surface, while localized feeding produces discrete brown scars that elongate as fruit matures. Avocados are an economically important crop in California and the harvest in 1999–2000 was worth \$339 million (US) (California Avocado Commission, 1999–2000). Economic losses are incurred when fruit is disfigured by thrips

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feeding as it is either culled or down-graded in packing-houses after harvest.

Biological control has succeeded in California avocado orchards because of minimal pesticide use (McMurtry, 1992). Avocado pests like greenhouse thrips (*Heliothrips haemorrhoidalis* (Bouché) (Thysanoptera: Thripidae) (McMurtry *et al.*, 1991), avocado brown mite *Oligonychus punicae* (Hirst) (Acari: Tetranychidae) and sixspotted mite *Eotetranychus sexmaculatus* (Riley) (Acari: Tetranychidae) have been kept below economically injurious levels by natural enemies in California (Fleschner, 1953; Fleschner *et al.*, 1955). However, biological control of this pest complex is now threatened by *S. perseae* as growers have resorted to regular pesticide applications to reduce fruit damage caused by this pest. Efforts to register new pesticides for *S. perseae* control on avocados are underway (Hoddle & Morse, 1998).

The research presented here provides information on the developmental and reproductive biology of *S. perseae*. These data are necessary for several reasons. First, they will assist with *S. perseae* laboratory production and colony management on which natural enemies from Central America will be reared. Second, knowledge of the pest's life cycle will assist with timings of natural enemy releases or application of selective pesticides in orchards. Third, the effect of temperature on *S. perseae* development and survivorship will assist our understanding of the constrained coastal distribution of this pest in California, and will guide foreign exploration efforts for this pest and its natural enemies in Central America.

### Materials and methods

#### *Collecting experimental Scirtothrips perseae, calculating egg hatch times and deposition of voucher specimens*

Adult *S. perseae* were field collected by beat sampling heavily infested trees in a commercial avocado orchard in Fallbrook California, USA. Groups of 5–20 adult thrips (males and females combined) were caged in glass cells, one glass cell (height = 15 mm; diameter = 28 mm) was attached to the underside of selected avocado leaves with a ring of Duco Stik-Tak® (Devcon Consumer Products, Des Plaines Illinois). The upper side of the glass cell was covered with polyester mesh screening with a 95 µm opening size. Young avocado leaves used for experiments were collected from Hass avocados at the University of California, Riverside, USA. *Scirtothrips perseae* has never been collected from this orchard. Adult thrips were aspirated, moved daily until death and enclosed within glass cells on the undersides of immature avocado leaves. Leaves exposed to ovipositing females for 24 h were placed on water-saturated foam pads in stainless steel pans and incubated in temperature cabinets set at 15, 20, 25, 27.5 and 30°C, under long days (L:D 14:10). Actual temperatures within cabinets were recorded every 15 min with Hobo® dataloggers (Onset Computer Corporation, Pocasset Massachusetts, USA). Leaves were examined daily for emerged thrips larvae and the mean number of days to egg hatch was calculated from daily larval emergence rates for each temperature. Voucher specimens of *S. perseae* infesting avocados in California have been deposited with Systematic Entomology Laboratory, USDA-ARS, Beltsville Maryland, USA and identified as *S. perseae* by Dr S. Nakahara.

#### *Preimaginal development at constant temperatures and partial life table construction*

First instar larvae collected from the egg hatch study were placed individually in modified Munger cells (Munger, 1942a; Morse *et al.*, 1986) with the underside of a young 'Hass' avocado leaf exposed as a food source and larvae were reared at the temperature from which they were hatched. Larvae were examined daily, and survival and developmental stages were recorded. Preimaginal developmental times in days for each life stage for male and female *S. perseae* were calculated for 15, 20, 25, 27.5 and 30°C. Survivorship statistics for each life stage at each temperature were used to generate a partial life table for *S. perseae* reared in modified Munger cells in temperature cabinets.

#### *Adult longevity, female fecundity, and offspring sex ratio*

Adult male and female *S. perseae* reared from the preimaginal study were confined either individually in modified Munger cells or as male–female pairs (mating was assumed to have occurred under these conditions). Every 24 h, mated and unmated females and males were anaesthetized with carbon dioxide and moved to fresh avocado leaves until death. The leaf areas exposed to females for the 24 h oviposition period were excised from leaves, labelled, and were maintained on water-saturated foam pads at the same temperature under which oviposition had occurred. Leaves were examined daily for emergence of offspring and larval emergence data were used to determine mean pre-oviposition period in days, and mean daily and lifetime fecundity for mated and unmated females at each experimental temperature. Mean pre-oviposition periods, and daily and lifetime fecundity estimates for mated and unmated females were compared across temperatures using ANOVA and Tukey's Studentized Range Test ( $P = 0.05$ ) to determine if temperature had significant effects on *S. perseae* fecundity parameters.

A minimum of 60 randomly selected progeny hatched at 15, 20, 25 and 27.5°C were reared to adulthood in modified Munger cells to determine sex ratio of offspring produced by mated females. Females failed to produce progeny at 30°C for fecundity studies (see Results). Progeny (27) from unmated females reared at 20°C were reared to adulthood to determine if *S. perseae* exhibits arrhenotoky.

#### *Demographic growth parameters*

Larval to adult survivorship data and daily fecundity of individual females, and sex ratio of progeny reared from females at each experimental temperature were used to construct  $l_x m_x$  life tables from which demographic growth parameters were calculated. Daily development and survivorship data, and daily progeny production for mated *S. perseae* females were used to produce a birth cohort of females for each temperature regimen that produced fecund females. The proportion of larvae produced by females reared and maintained at experimental temperatures that were female (i.e. no. females/[males + females]) was used to adjust daily progeny production in the  $m_x$  column to estimate the number of daughters produced daily by surviving females. The following demographic parameters were calculated from  $l_x m_x$  life tables:

1. Net reproductive rates ( $R_0 = \sum l_x m_x$  [where  $l_x m_x$  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 ( $R_0 > 1.0$  the population increases in size,  $R_0 = 1.0$  no increase in population size,  $R_0 < 1.0$  population growth is declining) (Carey, 1993).
2. Mean generation time ( $T_c = \sum x l_x m_x / R_0$ ) 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:  $1 = \sum l_x m_x \exp(-r_m x)$  [this equation was iterated for  $r_m$  until a value of one 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 & 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 *S. perseae* population growth statistics.

#### Temperature thresholds and degree day calculations

The modification by Lactin *et al.* (1995) to the Logan model (Logan *et al.*, 1976) was used to regress developmental rate (1/days) with temperature for data from individually reared thrips,

$$R(T) = e^{\rho T} - e^{(\rho TM - [TM - T]/\Delta)} + \lambda$$

where  $T$  is temperature ( $^{\circ}\text{C}$ ), and  $\rho$ ,  $TM$ ,  $\Delta$ , and  $\lambda$  are fitted coefficients. This model was used to estimate minimum, maximum and optimal temperatures for life stage development. Curves were fitted by iterative non-linear regression (PROC NLIN, SAS Institute, 1989). The model was fitted to individual data for each life stage, except eggs, which exhibited a strict linear relationship between developmental rate and temperature. For estimation of the lower temperature threshold for eggs and for first instar larvae and egg to adult (the modified Logan model could not converge on a minimum temperature threshold for first instars and egg to adult development) a simple regression over the linear range of the of the relationship between developmental rate and temperature was used (Campbell *et al.*, 1974). Development at temperatures  $> 27.5^{\circ}\text{C}$  was outside the linear segment of the growth curve and excluded in the linear regression. Linear regression coefficients were used to estimate day degree requirements for development of each life stage (Campbell *et al.*, 1974).

## Results

### Partial life tables, preimaginal development and degree day requirements

First instar to adult survivorship of *S. perseae* was greatest at  $20^{\circ}\text{C}$  (41.4%), lowest at  $30^{\circ}\text{C}$  (15.2%) and intermediate at 15, 25 and  $27.5^{\circ}\text{C}$  (26.1–37.3%) (table 1). Real mortality of first instar larvae was highest at  $15^{\circ}\text{C}$  (53%) and lowest at  $25^{\circ}\text{C}$  (11%). Second instars exhibited highest real mortality at  $30^{\circ}\text{C}$  (55%). Real mortality was lower than 8% for propupal and pupal stages at all temperatures (table 1).

Development periods of pre-imaginal stages were longest at  $15^{\circ}\text{C}$  and shortest at temperatures above  $27.5^{\circ}\text{C}$ . No significant differences in developmental times for male and female *S. perseae* within temperature regimes were found (table 2). Significant relationships between developmental rates and temperature for all developmental stages of *S. perseae* were detected. Egg development was highly linear over the experimental temperature range ( $F = 1294$ ,  $df = 1$ ,  $2938$ ,  $P < 0.0005$ ). Fit of the modified Logan model to non-linear developmental data for individual thrips was highly significant for first instar larvae ( $F = 232$ ,  $df = 1$ ,  $518$ ,  $P < 0.005$ ), second instar larvae ( $F = 257$ ,  $df = 1$ ,  $338$ ,  $P < 0.005$ ), propupae ( $F = 218$ ,  $df = 1$ ,  $331$ ,  $P < 0.005$ ), pupae ( $F = 216$ ,  $df = 1$ ,  $313$ ,  $P < 0.005$ ), and egg to adult development ( $F = 1398$ ,  $df = 1$ ,  $331$ ,  $P < 0.005$ ) (fig. 1). The modified Logan model failed to converge on a lower developmental threshold for first instar larvae and egg to adult development, and minimum temperature thresholds were determined by linear regression. For egg to adult development, the lower temperature threshold for development was estimated at  $6.9^{\circ}\text{C}$ , the upper developmental threshold estimate was  $37.6^{\circ}\text{C}$  and fastest rate of development was estimated at  $30.5^{\circ}\text{C}$ . A total of 344.8 degree days above the minimum temperature threshold were needed for complete development from egg to adult (table 3).

### Fecundity, sex ratio and arrhenotoky

No progeny were produced by mated *S. perseae* females at  $30^{\circ}\text{C}$ . The preoviposition period was significantly longer at  $15^{\circ}\text{C}$  than any other experimental temperature ( $F = 211$ ,  $df = 3$ ,  $62$ ,  $P < 0.005$ ) (table 4). Lifetime fecundity of mated females was significantly higher at  $15^{\circ}\text{C}$  ( $F = 3.46$ ,  $df = 3$ ,  $43$ ,  $P = 0.02$ ), but daily egg production by mated females at this temperature was significantly lower than the other three experimental temperatures ( $F = 13$ ,  $df = 3$ ,  $707$ ,  $P < 0.005$ ). No significant differences in lifetime ( $F = 1.21$ ,  $df = 2$ ,  $24$ ,  $P = 0.32$ ) and daily fecundity ( $F = 0.08$ ,  $df = 2$ ,  $282$ ,  $P = 0.93$ ) existed (table 4). Mated females produced the most daughters at  $20^{\circ}\text{C}$ , (69% of progeny were female), and offspring sex ratio was strongly male biased at  $27.5^{\circ}\text{C}$  with just 15% of reared progeny being female (table 4). All offspring reared from unmated females at  $20^{\circ}\text{C}$  were male, confirming arrhenotoky for *S. perseae*.

### Demographic growth parameters

Survivorship of oviposited eggs as estimated from daily fecundity data for females at 15, 20, 25 and  $27.5^{\circ}\text{C}$  was assumed to be unity (eggs were laid directly into leaves and could not be directly observed for survivorship) and was recorded as such in  $l_x m_x$  life tables for each temperature. Significant differences existed amongst the five demographic

Table 1. Partial life table for *Scirtothrips perseae* reared in Munger cells at five constant temperatures.

Life stage	$l_x^1$					$d_x^2$					$q_x^3$					$M_r^4$				
	15°C	20°C	25°C	27.5°C	30°C	15°C	20°C	25°C	27.5°C	30°C	15°C	20°C	25°C	27.5°C	30°C	15°C	20°C	25°C	27.5°C	30°C
First instar	215	222	185	168	164	114	44	20	73	31	0.53	0.20	0.11	0.43	0.19	0.53	0.20	0.11	0.43	0.19
Second instar	101	178	165	95	133	41	62	80	21	90	0.41	0.35	0.48	0.22	0.68	0.19	0.28	0.43	0.13	0.55
Propupa	60	116	85	74	43	4	9	4	6	6	0.07	0.08	0.05	0.08	0.14	0.02	0.04	0.02	0.04	0.04
Pupa	56	107	81	68	37	0	15	12	7	12	0.00	0.14	0.15	0.10	0.32	0.00	0.07	0.06	0.04	0.07
Adult	56	92	69	61	25															
% Reared to adult	26.0	41.4	37.3	36.3	15.2															

<sup>1</sup>  $l_x$  = number entering stage; <sup>2</sup>  $d_x$  = number dying or disappearing in stage; <sup>3</sup>  $q_x$  = apparent mortality (proportion dying in stage); <sup>4</sup>  $M_r$  = real mortality (proportion dying in stage as a function of initial cohort size). For more information on parts of life tables see Southwood (1978) and Carey (1993).

Table 2. Mean duration in days ( $\pm$ SE) of each life stage, and longevity of mated and unmated adult *Scirtothrips perseae*.

Stage	Temperature									
	15°C		20°C		25°C		27.5°C		30°C	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Eggs	21.3 $\pm$ 0.08 n = 1121		14.3 $\pm$ 0.14 n = 573		10.9 $\pm$ 0.07 n = 824		9.9 $\pm$ 0.09 n = 268		8.8 $\pm$ 0.10 n = 153	
First instar	3.9 $\pm$ 0.25 (n = 18)	3.9 $\pm$ 0.17 (n = 36)	3.1 $\pm$ 0.18 (n = 28)	2.8 $\pm$ 0.12 (n = 61)	1.9 $\pm$ 0.13 (n = 23)	2.1 $\pm$ 0.09 (n = 37)	1.2 $\pm$ 0.07 (n = 25)	1.4 $\pm$ 0.08 (n = 35)	1.7 $\pm$ 0.24 (n = 10)	1.8 $\pm$ 0.12 (n = 13)
Second instar	7.4 $\pm$ 0.35	7.8 $\pm$ 0.21	4.1 $\pm$ 0.19	3.9 $\pm$ 0.11	3.4 $\pm$ 0.17	3.3 $\pm$ 0.18	2.1 $\pm$ 0.15	2.2 $\pm$ 0.09	1.9 $\pm$ 0.22	1.9 $\pm$ 0.14
Propupae	2.9 $\pm$ 0.25	3.0 $\pm$ 0.20	1.7 $\pm$ 0.09	1.7 $\pm$ 0.09	1.2 $\pm$ 0.08	1.3 $\pm$ 0.06	1.2 $\pm$ 0.08	1.1 $\pm$ 0.06	1.4 $\pm$ 0.15	1.4 $\pm$ 0.18
Pupae	8.1 $\pm$ 0.32	7.1 $\pm$ 0.23	3.9 $\pm$ 0.11	3.8 $\pm$ 0.10	2.5 $\pm$ 0.10	2.5 $\pm$ 0.10	2.4 $\pm$ 0.14	2.4 $\pm$ 0.11	2.5 $\pm$ 0.21	2.5 $\pm$ 0.14
Mated adults	– (n = 7)	40.4 $\pm$ 3.39 (n = 7)	15.1 $\pm$ 4.33 (n = 7)	13.5 $\pm$ 2.24 (n = 7)	8.6 $\pm$ 0.90 (n = 11)	8.4 $\pm$ 0.92 (n = 21)	4.5 $\pm$ 0.73 (n = 22)	9.8 $\pm$ 1.17 (n = 5)	2.4 $\pm$ 0.68 (n = 11)	3.9 $\pm$ 0.39
Unmated adults	30.5 $\pm$ 3.7 (n = 6)	52.4 $\pm$ 6 (n = 5)	15.46 $\pm$ 2.1 (n = 13)	14.07 $\pm$ 1.5 (n = 14)	10 $\pm$ 1 (n = 9)	9.7 $\pm$ 0.8 (n = 20)	– (n = 6)	6.2 $\pm$ 3.4 (n = 6)	–	–

parameters as estimated by jackknife analysis of  $l_x m_x$  life table data when compared across temperatures (table 5). Mean net reproductive rate ( $R_0$ ) ( $F = 16555$ ,  $df = 3, 174$ ,  $P < 0.005$ ), intrinsic rate of increase ( $r_m$ ) ( $F = 29999$ ,  $df = 3, 174$ ,  $P < 0.005$ ) and finite rate of increase ( $\lambda$ ) ( $F = 29864$ ,  $df = 3, 174$ ,  $P < 0.005$ ) were all significantly higher for *S. perseae* reared and maintained at 20°C (table 5). Mean generation times ( $T_G$ ) were significantly shorter ( $F = 26703$ ,  $df = 3, 174$ ,  $P < 0.005$ ) when *S. perseae* was reared at 27.5°C (table 5). Mean estimates for population doubling times ( $T_d$ ) were significantly lower ( $F = 5783$ ,  $df = 3, 174$ ,  $P < 0.005$ ) for *S. perseae* reared at 20°C (table 5).

## Discussion

Ten species of *Scirtothrips* are formally recognized as economic pests (Mound & Palmer, 1981). Of these, *S. citri* (Moulton), a pest of citrus and mango in California, *S. aurentii* Faure, a pest of citrus and mango in South Africa, and *S. dorsalis* Hood, a pest of tea and chillies in India and grapes in Japan are the best studied (Mound & Teulon, 1995; Mound, 1997). These three pestiferous species are native to the countries in which they are problematic, and utilize exotic crops in addition to native host plants as food sources. In contrast, *S. perseae* is an exotic species in California attacking a host plant (avocado) exotic to California, and to date it has not been recorded from any other host plants in the USA suggesting that it may have a restricted host range and close evolutionary history with avocados in Central America (Hoddle *et al.*, 2002a).

Laboratory data indicate that *S. perseae* survivorship and reproduction is favoured at low temperatures. At 20°C, a greater percentage of larvae survived to adulthood in modified Munger cells, the sex ratio of reared progeny was female biased, significantly more progeny were produced by mated females, net reproductive rates ( $R_0$ ) were 2.3–8.2 times higher, and the population doubling time was 33–71% faster in comparison to the three (i.e. 15, 25 and 27.5°C) other experimental temperatures at which females successfully produced offspring. Optimal temperatures for pre-imaginal development were estimated with the modified Logan model to lie between 28°C and 34°C with upper lethal developmental temperatures being approximately 34–38°C depending on the life stage. Under these elevated temperature regimens in avocado orchards, *S. perseae* populations would rapidly decline because optimal larval development would occur at temperatures that reduce the fecundity of mated females, and promote low larval to adult survivorship rates and strongly male-biased progeny sex ratios.

*Scirtothrips perseae* is most problematic in California avocado orchards in plant-climate zones which are classified as direct ocean and coastal (Kimball & Brooks, 1959) or in orchards which are inland in coastal valley zones where the marine influence has a year round moderating effect on temperature (Kimball & Brooks, 1959). Collection records in Mexico and Guatemala further support the cool temperature preference of *S. perseae* as this insect has only been found on avocados growing at elevations exceeding 1500 m (Hoddle *et al.*, 2002a). The marine influence in coastal California

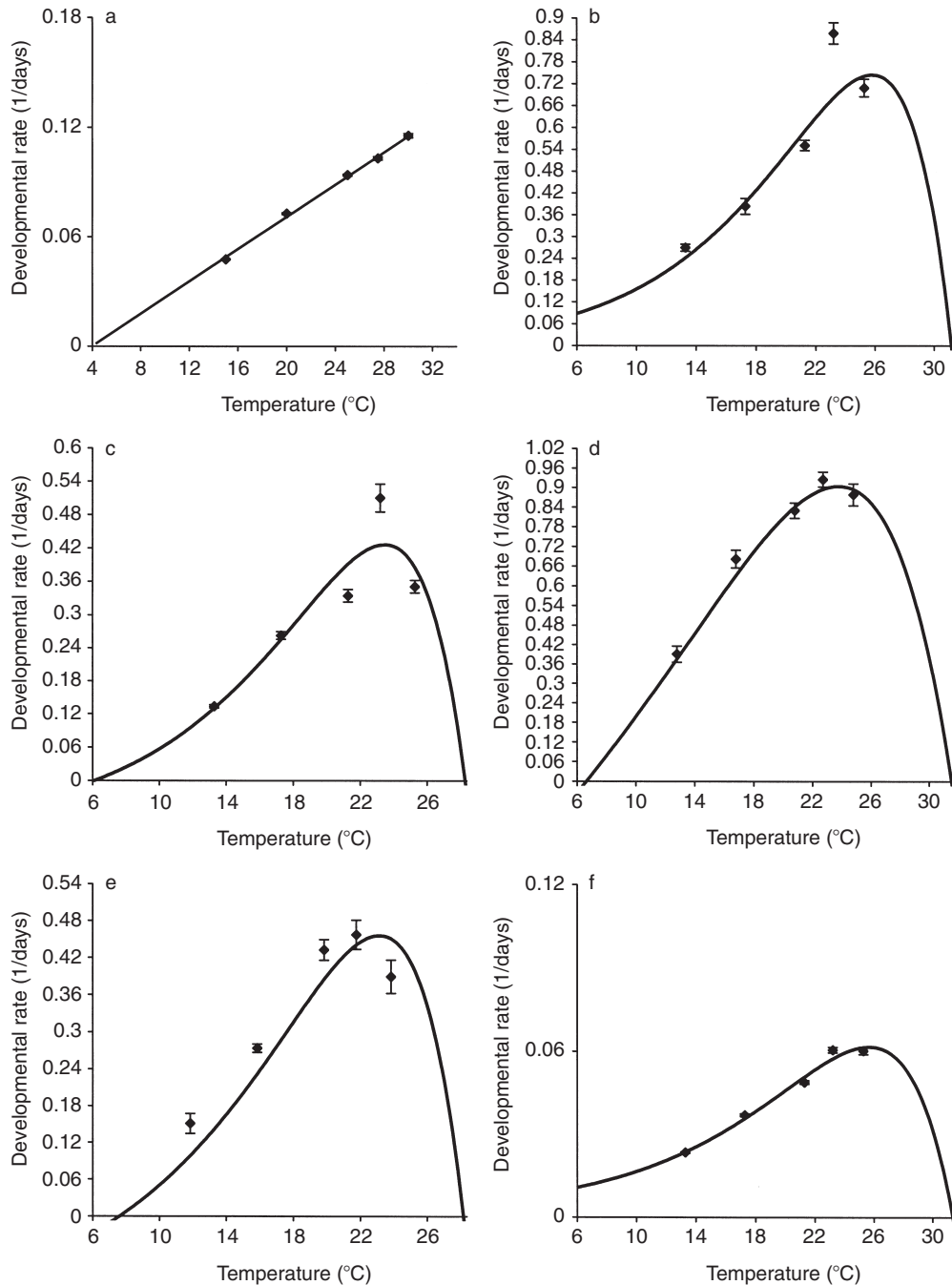


Fig. 1. Developmental rate of *Scirtothrips perseae* eggs (a) expressed as linear function of temperature, and the relationship of developmental rates for first (b), and second instar larvae (c), propupae (d), pupae (e), and egg to adult development (f) with temperature as described by the modified Logan model after Lactin *et al.* (1995).

avocado orchards may produce yearly temperature regimens similar to those under which *S. perseae* evolved at high altitudes in Mexico and Guatemala thereby facilitating the establishment of this pre-adapted pest in California.

Consequently, *S. perseae* populations build to their highest levels on young avocado foliage in the winter and spring when temperatures are low in California, and economic damage to young fruit by immature and adult thrips occurs in the spring. Low temperature preferences

probably help synchronize *S. perseae* population growth with production of young avocado foliage and fruit, which is used for feeding and oviposition. Populations decline rapidly to undetectable levels when mean weekly maximum temperatures consistently exceed 35°C over several consecutive days in summer even when there is sufficient young foliage to sustain high *S. perseae* densities in avocado orchards (M. Hoddle, unpublished data).

This affinity for low temperatures by *S. perseae* is in direct

Table 3. Lower and upper thresholds, and optimal temperatures of development, and thermal constants for *Scirtothrips perseae*.

Stage	Lower threshold (°C)	Upper threshold (°C) <sup>b</sup>	Optimum temp. (°C) <sup>b</sup>	n	r <sup>2</sup>	Thermal constant (K) (degree-days) <sup>a</sup>
Eggs	4.1 <sup>a</sup>	–	–	2939	0.99 <sup>a</sup>	227.3
First instar	9.9 <sup>a</sup>	37.4	30.7	554	0.31 <sup>b</sup>	23.1
Second instar	6.0 <sup>b</sup>	33.8	27.5	338	0.43 <sup>b</sup>	36.9
Propupa	6.7 <sup>b</sup>	37.8	28.1	333	0.40 <sup>b</sup>	24.1
Pupa	7.9 <sup>b</sup>	37.3	33.6	315	0.41 <sup>b</sup>	38.9
Egg–adult	6.9 <sup>a</sup>	37.6	30.5	315	0.82 <sup>b</sup>	344.8

<sup>a</sup> Determined by linear regression; <sup>b</sup> determined with modified Logan model (Lactin *et al.*, 1995)

Table 4. Mean preoviposition period ( $\pm$  SE) and mean daily and lifetime fecundity ( $\pm$  SE) of mated and unmated female *Scirtothrips perseae* estimated from numbers of emerged larvae and proportion of reared larvae from mated females that were female (sex ratio).

	Temperature			
	15°C	20°C	25°C	27.5°C
Preoviposition period (days)	17.6 $\pm$ 1.7a	1 $\pm$ 0.18b	0.97 $\pm$ 0.15b	1.6 $\pm$ 0.22b
Total progeny from mated females	39.6 $\pm$ 7.6a	31 $\pm$ 6.1ab	19.8 $\pm$ 1.52b	20.6 $\pm$ 3.68ab
Mean daily progeny from mated females	0.97 $\pm$ 0.13a	2.3 $\pm$ 0.36b	2.3 $\pm$ 0.24b	1.9 $\pm$ 0.12b
Total progeny from unmated females	–	27.1 $\pm$ 3.19a	21.4 $\pm$ 0.63a	15.7 $\pm$ 10.55a
Mean daily progeny from unmated females	–	2.1 $\pm$ 0.18a	2.2 $\pm$ 0.21a	2.3 $\pm$ 0.31a
Sex ratio	0.63	0.69	0.62	0.15

Means followed by the same letters within rows are not significantly different at the 0.05 level of significance.

Table 5. Mean demographic growth parameters ( $\pm$ SE) generated from jackknifed  $l_{x,m_x}$  data for *Scirtothrips perseae*.

Temperature (°C)	R <sub>0</sub>	T <sub>c</sub>	r <sub>m</sub>	$\lambda$	T <sub>d</sub>
15	6.5 $\pm$ 0.09a	65.9 $\pm$ 0.09a	0.03 $\pm$ 0.0002a	1.03 $\pm$ 0.0003a	23.7 $\pm$ 0.22a
20	15.1 $\pm$ 0.06b	28.4 $\pm$ 0.02b	0.10 $\pm$ 0.0002b	1.11 $\pm$ 0.0003b	6.88 $\pm$ 0.02b
25	5.3 $\pm$ 0.04c	25.1 $\pm$ 0.02c	0.07 $\pm$ 0.0003c	1.07 $\pm$ 0.001c	10.3 $\pm$ 0.04c
27.5	1.8 $\pm$ 0.008d	20.8 $\pm$ 0.02d	0.02 $\pm$ 0.0002d	1.02 $\pm$ 0.0002d	23 $\pm$ 0.16d

Means followed by letters within columns are significantly different at the 0.05 level (ANOVA). R<sub>0</sub> = net reproductive rate; T<sub>c</sub> = generation time; r<sub>m</sub> = intrinsic rate of increase;  $\lambda$  = finite rate of increase; T<sub>d</sub> = doubling time in days. For more information on demographic growth parameters see Southwood (1978) and Carey (1993).

contrast to other pest *Scirtothrips* species. *Scirtothrips citri*, *S. aurantii* and *S. dorsalis* all inflict economic damage to crops over summer when temperatures are high (Horton, 1918; Faure, 1929; Bedford, 1943; Shibao *et al.*, 1993; Shibao, 1996), and *S. citri* is typically most damaging to citrus grown in arid interior valleys of California (Tanigoshi, 1981). The thermophilic nature of *S. citri* is supported by phenological models, which predict that minimum threshold temperatures for development are high, and lie between 14.6°C and 18.3°C (Tanigoshi *et al.*, 1980; Rhodes *et al.*, 1989). In contrast, *S. perseae* minimum temperature thresholds were estimated in this study to lie between 4°C and 10°C. Furthermore, the recommended rearing temperature for laboratory colonies of *S. citri* is 31°C (Munger, 1942a) and 95.5% of hatched larvae reach the pupal stage at this temperature (Munger, 1942b). To maintain laboratory colonies of *S. perseae* on avocado seedlings, temperatures need to be maintained below 25°C. At temperatures that regularly exceed 25°C abrupt population crashes occur that ultimately lead to colony extinction (M. Hoddle, unpublished data).

Climatic matching may be of great importance for locating effective natural enemies in Central America for establishment against *S. perseae* in California in a classical biological control programme targeting this pest. To be efficacious, imported predators or parasitoids will 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 in avocado orchards. It is possible that under these conditions seasonal inoculative releases of insectary reared natural enemies into avocado orchards may be necessary (Hoddle *et al.*, 2001b).

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# The Biology of Wetas, King Crickets and their Allies

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