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Evaluation of diets for the development and reproduction of *Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae)

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Abstract

The suitability of ten diets for the development and reproduction of *Franklinothrips orizabensis* Johansen, the key natural enemy of *Scirtothrips perseae* Nakahara, a pest of California grown avocados, was determined in the laboratory. The experimental diets evaluated were: (i) irradiated *Ephestia kuehniella* Zeller eggs; (ii) irradiated *E. kuehniella* eggs and avocado pollen; (iii) *Tetranychus pacificus* McGregor eggs; (iv) *T. pacificus* eggs and avocado pollen; (v) irradiated *E. kuehniella* eggs and *T. pacificus* eggs; (vi) irradiated *E. kuehniella* eggs, *T. pacificus* eggs and avocado pollen; (vii) *Scirtothrips perseae*; (viii) *Heliothrips haemorrhoidalis* (Bouchè); (ix) avocado pollen; and (x) a young avocado leaf. *Franklinothrips orizabensis* larvae were unable to develop to adulthood on diets 9 and 10. The remaining eight diets supported complete development of *F. orizabensis*, but only diets 1, 2, 5, 6, 7 and 8 produced fecund females. On diet 5, *F. orizabensis* exhibited high larval to adult survivorship (90%), mated females exhibited highest daily and lifetime fecundity, and the progeny of mated females were female biased (53%). Analysis of jackknife estimates of net reproduction (R_o), intrinsic rate of increase (r_m), and finite rate of increase (λ) were all significantly greater for *F. orizabensis* reared on irradiated *E. kuehniella* eggs and *T. pacificus* eggs (i.e. diet 5) than corresponding values for other diets on which female *F. orizabensis* were able to complete development and reproduce. Incorporation of avocado pollen into diets had an adverse effect on demographic statistics for *F. orizabensis*, and low quality diets resulted in male biased sex ratios for this predator.

Introduction

The genus *Franklinothrips* (Thysanoptera: Aeolothripidae) currently comprises ten known species, and the geographic distribution of this genus is restricted to tropical and subtropical areas (Moulton, 1932; Stannard, 1952; Mound & Walker, 1987; Mound & Marullo, 1996). *Franklinothrips* spp. adults and larvae are generalist predators and have been observed in association with or feeding on a wide variety of pest species, which include thrips (Thysanoptera) and spider mites (Acari) (Ebeling, 1959; Sureshkumar & Ananthakrishnan, 1987; Johansen & Mojica-Guzman, 1996; Arakaki & Okajima, 1998; Hoddle *et al.*, 2000).

Female *Franklinothrips* spp. lay eggs directly into plant tissue. Larvae pass through two larval instars before entering propupal and pupal stages within protective silk cocoons. *Franklinothrips* spp. are haplo-diploid and aspects of the basic developmental and reproductive biology of this genus have been studied in the laboratory (Reijne, 1920; Sureshkumar & Ananthakrishnan, 1987; Arakaki & Okajima, 1998; Hoddle *et al.*, 2000).

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Scirtothrips perseae Nakahara (Thysanoptera: Thripidae), a new pest of avocado, *Persea americana* Miller (Lauraceae), was discovered attacking fruit and foliage in southern California in 1996 (Nakahara, 1997). Crop loses in 1998 due to *S. perseae* feeding damage to fruit were estimated at US$7–13 million (Hoddle & Morse, 1997; Hoddle *et al.*, 1999a). Phenology studies on *S. perseae* in avocado orchards have revealed that *Franklinothrips orizabensis* Johansen is the dominant natural enemy when this pest has attained high densities (> 10 *S. perseae* larvae per leaf) (M.S. Hoddle, unpublished). The potential of using mass-reared *F. orizabensis* for use in early season augmentative biological control programmes against *S. perseae* in avocado orchards has been suggested, and the optimal temperature regimen for mass rearing this natural enemy has been determined (Hoddle *et al.*, 2000).

Before mass rearing can be conducted efficiently, the best diet that would support *F. orizabensis* development and reproduction needs to be determined. The purpose of this work was to identify optimal diets for rearing *F. orizabensis* from readily available food items. To evaluate the suitability of different food types and combinations of foods, demographic growth parameters were calculated and compared for *F. orizabensis* when reared on ten diets.

Materials and methods

Experimental diets

Ten diets were evaluated for their ability to support larval development of *F. orizabensis* and for their continued suitability as a food source for adults once larval development on an experimental diet was completed. Evaluated diets were: (i) irradiated eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) supplied by Beneficial Insectaries (Oak Run, California, USA); (ii) irradiated *E. kuehniella* eggs and avocado pollen; (iii) eggs of *Tetranychus pacificus* McGregor (Acari: Tetranychidae) obtained from Biotactics (Riverside, California, USA); (iv) *Tetranychus pacificus* eggs and avocado pollen; (v) irradiated *E. kuehniella* eggs and *T. pacificus* eggs; (vi) irradiated *E. kuehniella* eggs, *T. pacificus* eggs, and avocado pollen; (vii) *Scirtothrips perseae* larvae and adults which were collected every 2–5 days from a heavily infested avocado orchard in Fallbrook, California, USA; (viii) late second instar larvae, propupal, and pupal *Heliothrips haemorrhoidalis* (Bouché) (Thysanoptera: Thripidae), lacking protective faecal droplets, which were harvested from a colony maintained at the University of California at Riverside on green lemons; (ix) fresh avocado pollen collected from an avocado orchard in Fallbrook California, USA and stored in a refrigerator; and (x) immature three quarters expanded avocado leaves. From here on, each diet will be referred to by its respective number.

Source of Franklinothrips orizabensis *for diet studies*

Evaluation of experimental diets were initiated with colony reared adult male and female *F. orizabensis* which were maintained in cages in a temperature controlled room (25°C, 60% rh, L:D 14:10) with lima beans (*Phaseolus lunatus* Linnaeus cv 'Baby Fordhook') as an oviposition and foraging substrate. Colony-reared *F. orizabensis* were fed irradiated *E. kuehniella* eggs which were liberally deposited on upper surfaces of horizontal bean leaves to prevent deposited eggs from falling to the cage floor. This colony was initiated with adult *F. orizabensis* collected from an avocado orchard infested with *S. perseae* in Fallbrook, California, USA. Adult progeny produced by field collected *F. orizabensis* used to initiate the colony were deposited with the Systematic Entomology Laboratory, USDA-ARS, Beltsville, Maryland, USA.

Source of larvae for diet studies

Mature avocado leaves, cv 'Hass', were collected from the Biological Control Grove at the University of California, Riverside. *Franklinothrips orizabensis* and *S. perseae* have never been collected in this orchard. Harvested leaves were presented to colony-reared female *F. orizabensis* for oviposition. Adult male and female *F. orizabensis* were confined within modified Munger cells (Munger, 1942; Morse *et al.*, 1986), fed irradiated *E. kuehniella* eggs, and left to oviposit under controlled conditions (25°C, L:D 14:10 h). Male–female pairs were moved to new leaves daily until death.

At the end of each 24 h oviposition period, the leaf area enclosed by the Munger cell which was exposed to ovipositing females was excised from the avocado leaf. Leaf discs were labelled, placed on water-saturated foam pads in stainless steel trays, and incubated in temperature-controlled cabinets at 25°C. Leaves were examined daily for emerged *F. orizabensis* larvae which were then reared on one of the ten experimental diets.

Preimaginal development on experimental diets

Young (< 24 h old) first instar *F. orizabensis* larvae that emerged from avocado leaves exposed to ovipositing females were placed individually in modified Munger cells with the underside of a mature avocado leaf, cv 'Hass', exposed as a foraging surface. Larvae were randomly assigned to one of the ten experimental diets and maintained in temperature controlled cabinets at 25°C. Larvae were examined daily and developmental stages were recorded. Preimaginal developmental times and survivorship rates for *F. orizabensis* larvae reared on each diet were calculated. Preimaginal developmental time data were transformed (ln x + 1) and compared using ANOVA and Tukey's Studentized Range test for means separation ($P = 0.05$) to detect effects of diet and sex on developmental times.

Female fecundity, egg hatch times and adult longevity

Adult *F. orizabensis* reared from larvae on an assigned diet (designated here as F_1 adults) were confined as male–female pairs (mating was assumed to have occurred under these conditions) in modified Munger cells. Adults were maintained on the same diet on which they had been reared as larvae and moved to new mature (Hass) avocado leaves every 24 h until death. After each 24 h oviposition period, the leaf area exposed to females within modified Munger cells was excised, labelled, and maintained on water-saturated foam pads in temperature cabinets at 25°C. Leaves were examined daily for emergence of offspring. Mean daily and lifetime fecundities for females were calculated for each diet using numbers of larvae that emerged from each leaf after 24 h exposure to individual females. Mean daily and total progeny produced by females were compared across diets using ANOVA and Tukey's Studentized Range Test ($P = 0.05$). Mean number of days for eggs to hatch on each experimental diet that supported larval development through to adulthood and subsequent oviposition by female *F. orizabensis* was compared across diets with ANOVA and Tukey's Studentized Range Test ($P = 0.05$). Survivorship of adult *F. orizabensis* was recorded daily and mean daily longevity of mated males and females was calculated. Analysis of survivorship was performed on logit transformed data (ln live/dead) with weighing for sample size. Mean adult longevity for diet and sex were tested for significance using Chi-square and pair-wise T-test comparisons ($P = 0.025$ level of significance to maintain the experimentwise level of significance at 0.05).

Life tables and demographic growth parameters

Larval to adult survivorship data and daily fecundity of individual F_1 females, and sex ratio of progeny reared from F_1 females on their respective diets 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 *F. orizabensis* females were used to produce a birth cohort of females for each diet that produced fecund females. The proportion of larvae produced by F_1 females reared and maintained on experimental diets 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 ($R_o = \sum l_x m_x$ (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 ($R_o > 1.0$ the population increases in size, $R_o = 1.0$ no increase in population size, $R_o < 1.0$ population growth is declining) (Carey, 1993).

2. Mean generation time ($T_c = \sum x l_x m_x / Ro$) 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 diets using ANOVA and Tukey's Studentized Range Test ($P = 0.05$) to determine if diet had significant effects on *F. orizabensis* population growth statistics.

Size of females reared on experimental diets

The size of female *F. orizabensis* successfully reared to adulthood on experimental diets was determined by slide mounting females in Hoyer's solution and measuring the length of the right tibia of the metathoracic leg. Mean tibia length measurements (mm) for slide mounted females were compared across diets and to female *F. orizabensis* that were field collected from an avocado orchard heavily infested with *S. perseae* in Fallbrook, California, USA using ANOVA and Tukey's Studentized Range Test ($P = 0.05$).

Results

Preimaginal survivorship and development

Eight of the ten diets tested were able to support *F. orizabensis* larval development through to adulthood (table 1). The highest quality diets in terms of larval to adult survivorship rates (90–93%) were diets 1, 5 and 7. Diets of intermediate quality (83–88% larval to adult survivorship) were 2, 6 and 8. Low quality diets (37–40% larval to adult survivorship) were 3 and 4. Diets that were unsuitable for development of larval *F. orizabensis* (0% larval to adult survivorship) were 9 and 10 (table 1).

Low quality diets resulted in highest *F. orizabensis* mortality in the cocoon stage where adults failed to emerge (table 1). *Franklinothrips orizabensis* second instar larvae, and stages in cocoons exhibited highest mortality when reared on diet 9 (table 1). High and intermediate quality diets resulted in consistently low levels of mortality across all preimaginal stages (table 1).

Significant differences in *F. orizabensis* developmental times for first instars ($F = 35.3$, df = 7, 170, $P < 0.0005$), second instars ($F = 42.4$, df = 7, 170, $P < 0.0005$), and pupal stages ($F = 17.5$, df = 7, 170, $P < 0.0005$) were detected across diets, irrespective of the sex of developing larvae (table 2). No significant differences were detected in developmental times for male and female first instar larvae, ($F = 0.01$, df = 1, 170, $P = 0.93$), and pupal stages ($F = 5.71$, df = 1, 170, $P = 0.02$). Significant differences in developmental times of second instar larvae were detected ($F = 4.80$, df = 1, 170, $P = 0.03$) with male second instars, on average, developing 0.3 days faster than females. No significant diet by sex differences were found for experimental diets ($\chi^2 > 1.92$, df = 7, P = 0.1 (for all stages)). First instar *F. orizabensis* larvae survived for approximately two days on young avocado leaves. One larva developed through to the second instar but consumption of conspecifics emerging from leaves prior to isolation in a modified Munger cell may have been responsible for this development (table 2).

Preoviposition, egg hatch times, fecundity and adult longevity

Of the eight diets that supported larval to adult development of *F. orizabensis*, six diets (1, 2, 5, 6, 7 and 8)

Table 1. Partial life-table for *Franklinothrips orizabensis* reared on experimental diets.

	Developmental stage										
	First instar			Second instar			Pupal cocoon				
Diet number and type	l_x	d_x	q_x	l_x	d_x	q_x	l_x	d_x	q_x	Adults	% first instar to adult survivorship
1. Irradiated *Ephestia* eggs	30	0	0	30	1	0.03	29	1	0.03	28	93
2. Irradiated *Ephestia* eggs and avocado pollen	30	0	0	30	1	0.03	29	4	0.14	25	83
3. *Tetranychus* eggs	30	0	0	30	0	0.00	30	19	0.63	11	37
4. *Tetranychus* eggs and avocado pollen	30	0	0	30	0	0.00	30	18	0.60	12	40
5. Irradiated *Ephestia* eggs and *Tetranychus* eggs	30	0	0	30	1	0.03	29	2	0.07	27	90
6. Irradiated *Ephestia* eggs, *Tetranychus* eggs and avocado pollen	30	0	0	30	2	0.07	28	3	0.11	25	83
7. *Scirtothrips perseae*	32	0	0	32	0	0.00	32	3	0.09	29	91
8. *Heliothrips haemorrhoidalis*	34	1	0.33	33	0	0.00	33	3	0.09	30	88
9. Avocado pollen	30	0	0	30	7	0.23	23	23	1.00	0	0
10. Immature avocado leaf	30	29	0.97	1	1	1.00	0			0	0

l_x = number entering stage; d_x = number dying in stage; q_x = proportion dying in stage. For more information on parts of life-tables see Southwood (1978) and Carey (1993).

were able to sustain the reproductive activity of females that developed to maturity on these diets.

Significant differences in mean preoviposition periods across diets were detected (F = 26.2, df = 5, 63 $P < 0.0005$) and preoviposition was longest for females reared and maintained on diet 7 (table 3). Significant differences in egg hatch times existed between diets (F = 424, df = 5, 4002 $P < 0.0005$). Egg hatch times were shortest for females reared and maintained on diets 7 and 8 with the majority of larvae emerging approximately eight days post oviposition (table 3). Egg hatch times were longest for females reared and maintained on diet 6 (table 3).

Mean daily progeny production differed significantly across diets (F = 52.0, df = 5, 941 $P < 0.0005$). Females produced significantly more offspring each day when reared and maintained on diet 5 (table 3). Daily progeny production was lowest for females reared and maintained on diet 7 (table 3). Estimates of mean total lifetime fecundity as measured by numbers of emerged larvae differed significantly across diets for female *F. orizabensis* (F = 7.37, df = 5, 63 $P < 0.0005$). Lifetime fecundity was highest when females were reared and maintained on diet 5 and lowest on diet 7 (table 3). The proportion of offspring that were female was highest when females were reared and maintained on diet 8 and lowest on diet 2 (table 3).

Mated adult *F. orizabensis* exhibited significant differences in longevity when reared and maintained on different diets ($\chi^2 = 84.9$, df = 7, $P < 0.0005$) (table 2). For all diets, females tended to live longer than males ($\chi^2 = 74.5$, df = 1, $P < 0.0005$) and this difference in longevity was significantly affected by diet ($\chi^2 = 156$, df = 6, $P < 0.0005$) (table 2). Adult longevity was less than one day for males and females on diet 3. Adult longevity was increased if avocado pollen was supplied with *T. pacificus* eggs (diet 4) but females failed to produce viable eggs even though they lived longer (table 2). On high quality diets (diets 1, 5 and 7) females tended to outlive males, and mean female longevity on these diets was generally greater than ten days (table 2).

Demographic growth parameters

Survivorship of oviposited eggs as estimated from daily fecundity for F_1 females was assumed to be unity (eggs were laid into leaves and could not be observed directly for survivorship) and was recorded as such in the $l_x m_x$ life tables for each of the six diets that produced and maintained fecund females. Significant differences existed amongst the five demographic parameters as estimated by jackknife analysis of $l_x m_x$ life table data when compared across diets (table 4). Mean net reproductive rate (R_o) (F = 1172, df = 5, 69 $P < 0.005$), intrinsic rate of increase (r_m) (F = 5521, df = 5, 69 $P < 0.005$) and finite rate of increase (λ) (F = 4779, df = 5, 69 $P < 0.005$) were all significantly higher for *F. orizabensis* reared and maintained on diet 5 (table 4). Mean generation times (T_c) were significantly shorter (F = 602, df = 5, 69 $P < 0.005$) when *F. orizabensis* was reared on diets 7 and 8 (table 4). Mean estimates for population doubling times (T_d) were significantly lower (F = 3223, df = 5, 69 $P < 0.005$) for diets 5 and 8, and mean T_d estimates were longest for *F. orizabensis* reared on diet 7 (table 4).

Size of females

The size of females as estimated from measurements of the right metathoracic tibia differed significantly across diets and in comparison to the size of field collected females (F = 6.65, df = 8, 133, $P < 0.0005$). Large females resulted when larvae were reared on diets 1 and 5, or were field collected. Females of intermediate size were reared from larvae maintained on diets 2, 5, 7 and 8. Small females resulted from rearing on diets 3 and 4 (table 5).

Discussion

Development, reproduction, and survivorship of *F. orizabensis* were significantly affected by diet and irradiated *E. kuehniella* eggs combined with *T. pacificus* eggs produced

Table 2. Mean duration in days (± SE) of each life stage of *Franklinothrips orizabensis* on experimental diets.

	Diet number and type														
	(1) Irradiated *Ephestia* eggs			(2) Irrdiated *Ephestia* eggs and avocado pollen			(3) *Tetranychus* eggs			(4) *Tetranychus* eggs and avocado pollen			(5) Irradiated *Ephestia* eggs and *Tetranychus* eggs		
Lifestage	Males	Females	Combined	Males	Females	Combined	Males	Females	Combined	Males	Females	Combined	Males	Females	Combined
First instar	2.38 ± 0.18 (n = 21)	2.71 ± 0.29 (n = 7)	2.50 ± 0.15de (n = 30)	2.35 ± 0.15 (n = 17)	2.13 ± 0.13 (n = 8)	2.27 ± 0.10cd (n = 30)	1.13 ± 0.13 (n = 8)	1.00 ± 0.00 (n = 3)	1.03 ± 0.06ab (n = 30)	0.78 ± 0.22 (n = 9)	0.67 ± 0.33 (n = 3)	1.03 ± 0.22a (n = 30)	2.53 ± 0.19 (n = 15)	2.00 ± 0.20 (n = 13)	2.33 ± 0.14cd (n = 30)
Second instar	2.86 ± 0.23 (n = 21)	2.71 ± 0.18 (n = 7)	2.76 ± 0.18d (n = 29)	1.94 ± 0.10 (n = 17)	2.63 ± 0.18 (n = 8)	2.34 ± 0.17cd (n = 29)	6.00 ± 0.38 (n = 8)	7.00 ± 1.00 (n = 3)	6.18 ± 0.26g (n = 30)	5.56 ± 0.44 (n = 9)	7.00 ± 0.33 (n = 3)	5.53 ± 0.31f (n = 30)	1.73 ± 0.25 (n = 15)	2.00 ± 0.30 (n = 13)	2.00 ± 0.25abc (n = 30)
Pupal cocoon	8.86 ± 0.26 (n = 21)	9.0 ± 0.22 (n = 7)	8.89 ± 0.20d (n = 28)	7.94 ± 0.23 (n = 17)	7.38 ± 0.32 (n = 8)	7.76 ± 0.19c (n = 25)	6.25 ± 0.31 (n = 8)	6.00 ± 0.58 (n = 3)	6.18 ± 0.26a (n = 11)	6.44 ± 0.18 (n = 9)	6.67 ± 0.67 (n = 3)	6.50 ± 0.19ab (n = 12)	6.80 ± 0.22 (n = 15)	6.92 ± 0.18 (n = 13)	6.86 ± 0.14ab (n = 28)
Mated adults	10.31 ± 1.25b (n = 21)	13.58 ± 1.67a (n = 7)	11.88 ± 1.06 (n = 28)	12.07 ± 1.24a (n = 17)	9.92 ± 1.51b (n = 8)	11.11 ± 0.96 (n = 25)	< 1 day d (n = 8)	< 1 day d (n = 3)		9 (n = 1)	5.67 ± 1.67c (n = 3)	6.50 ± 1.44 (n = 4)	7.30 ± 1.64abc (n = 15)	12.27 ± 2.12a (n = 13)	9.90 ± 1.44 (n = 28)

	Diet number and type														
	(6) Irradiated *Ephestia* eggs, *Tetranychus* eggs and avocado pollen			(7) *Scirtothrips perseae*			(8) *Heliothrips haemorrhoidalis*			(9) Avocado pollen			(10) Avocado leaf		
Lifestage	Males	Females	Combined	Males	Females	Combined	Males	Females	Combined	Males	Females	Combined	Males	Females	Combined
First instar	3.36 ± 0.24 (n = 11)	3.07 ± 0.07 (n = 14)	3.13 ± 0.10e (n = 30)	2.55 ± 0.16 (n = 11)	2.61 ± 0.12 (n = 18)	2.63 ± 0.10de (n = 32)	1.00 ± 0.00 (n = 17)	1.50 ± 0.19 (n = 12)	1.21 ± 0.09b (n = 29)			4.83 ± 0.36f (n = 30)			1.8 ± 0.18c (n = 30)
Second instar	1.45 ± 0.25 (n = 11)	1.57 ± 0.17 (n = 14)	1.64 ± 0.18ab (n = 28)	1.09 ± 0.21 (n = 11)	1.39 ± 0.12 (n = 18)	1.34 ± 0.12a (n = 32)	2.12 ± 0.12 (n = 17)	2.00 ± 0.21 (n = 12)	2.07 ± 0.11bcd (n = 29)			4.04 ± 0.33e (n = 23)			5 (n = 1)
Pupal cocoon	7.18 ± 0.48 (n = 11)	6.93 ± 0.13 (n = 14)	7.04 ± 0.22b (n = 25)	7.36 ± 0.15 (n = 11)	6.67 ± 0.11 (n = 18)	6.93 ± 0.11b (n = 29)	6.88 ± 0.12 (n = 17)	6.17 ± 0.21 (n = 12)	6.59 ± 0.13ab (n = 29)			0			0
Mated adults	6.83 ± 1.49bc (n = 11)	11.45 ± 1.11ab (n = 14)	9.82 ± 1.02 (n = 25)	1.38 ± 0.50d (n = 8)	9.67 ± 2.12b (n = 12)	6.35 ± 1.57 (n = 20)	6.60 ± 2.57b (n = 7)	13.70 ± 2.04a (n = 10)	11.65 ± 1.65 (n = 17)			0			0

Means followed by the same letters are not significantly different within developmental stages (i.e. within rows) across diets at the 0.05 level of significance (ANOVA).
Note: in some instances data was used for calculation of developmental times for immature stages that died before sex was determined.

Table 3. Preoviposition period (± SE), mean number (± SE) of days for eggs to hatch, mean daily (± SE) and lifetime progeny production as estimated from emerged larvae, and the proportion of larvae reared from fecundity studies that were female for each experimental diet that produced fecund female *Franklinothrips orizabensis*.

Diet number and type	Preoviposition period (days)	Egg hatch (days)	Daily progeny	Total progeny	Proportion female progeny
1. Irradiated *Ephestia* eggs	0.93 ± 0.13a	9.90 ± 0.04a	4.40 ± 0.29a	68.6 ± 12.0ab	0.45
2. Irradiated *Ephestia* eggs and avocado pollen	1.25 ± 0.18a	9.90 ± 0.04a	4.90 ± 0.39a	58.4 ± 13.7bc	0.26
5. Irradiated *Ephestia* eggs and *Tetranychus* eggs	0.73 ± 0.14a	9.63 ± 0.03b	7.81 ± 0.41b	114.4 ± 21.5a	0.53
6. Irradiated *Ephestia* eggs, *Tetranychus* eggs and avocado pollen	0.91 ± 0.16a	11.4 ± 0.06c	4.26 ± 0.32a	57.3 ± 10.0bc	0.52
7. *Scirtothrips perseae*	3.56 ± 0.38b	8.78 ± 0.11d	0.66 ± 0.09c	7.83 ± 2.04c	0.32
8. *Heliothrips haemorrhoidalis*	1.42 ± 0.72a	8.35 ± 0.06e	3.79 ± 0.26a	56.8 ± 8.06bc	0.67

Means followed by different letters within colums are significantly different at the 0.05 level (ANOVA).

Table 4. Mean demographic growth parameters (± SE) generated from jackknifed $l_x m_x$ data for *Franklinothrips orizabensis*.

Diet number and type	R_o	T_c	r_m	λ	T_d
1. Irradiated *Ephestia* eggs	29.9 ± 0.46c	31.1 ± 0.06a	0.11 ± 0.0005a	1.12 ± 0.0005a	6.08 ± 0.03a
2. Irradiated *Ephestia* eggs and avocado pollen	13.2 ± 0.26d	33.8 ± 0.06b	0.08 ± 0.0005b	1.08 ± 0.0006b	8.97 ± 0.06b
5. Irradiated *Ephestia* eggs and *Tetranychus* eggs	60.8 ± 1.16a	32.7 ± 0.13c	0.13 ± 0.0005c	1.14 ± 0.002c	5.23 ± 0.02c
6. Irradiated *Ephestia* eggs, *Tetranychus* eggs and avocado pollen	27.9 ± 0.53c	32.1 ± 0.07d	0.11 ± 0.0007d	1.11 ± 0.0008d	6.50 ± 0.04a
7. *Scirtothrips perseae*	2.42 ± 0.02e	28.1 ± 0.06e	0.03 ± 0.0004e	1.03 ± 0.0004e	21.4 ± 0.26d
8. *Heliothrips haemorrhoidalis*	35.3 ± 0.54b	30.2 ± 0.11f	0.12 ± 0.0005f	1.13 ± 0.0005f	5.56 ± 0.02c

Means followed by different letters within colums are significantly different at the 0.05 level (ANOVA).
R_o = net reproductive, T_c = mean generation time, r_m = intrinsic rate of natural increase, λ = finite rate of increase, T_d = doubling time.
For more information of demographic statistics see Southwood (1978) and Carey (1993).

Table 5. Mean length (± SE) of right metathoracic tibia of female *Franklinothrips orizabensis* reared to adulthood on experimental diets and compared to field collected females.

Diet number and type	Mean tibia length (mm)	n
1. Irradiated *Ephestia* eggs	0.551 ± 0.005a	20
2 Irradiated *Ephestia* eggs and avocado pollen	0.523 ± 0.006ab	20
3. *Tetranychus* eggs	0.498 ± 0.008bc	2
4. *Tetranychus* eggs and avocado pollen	0.467 ± 0.035c	4
5. Irradiated *Ephestia* eggs and *Tetranychus* eggs	0.532 ± 0.005ab	20
6. Irradiated *Ephestia* eggs, *Tetranychus* eggs and avocado pollen	0.541 ± 0.005a	20
7. *Scirtothrips perseae*	0.528 ± 0.006ab	16
8. *Heliothrips haemorrhoidalis*	0.532 ± 0.006ab	20
Field collected *Franklinothrips orizabensis*	0.536 ± 0.006a	20

Means followed by different letters are significantly different from each other at the 0.05 level (ANOVA).

highest estimates for demographic statistics affecting population growth. Larval *F. orizabensis* were unable to complete development on a diet consisting only of avocado pollen, and incorporation of avocado pollen with irradiated *E. kuehniella* eggs significantly reduced larval to adult survivorship rates, total progeny production, and adversely affected demographic growth statistics in comparison to females reared on irradiated *E. kuehniella* eggs only. All adult females reared on diets with avocado pollen as a component were small to intermediate in size.

Predators that consume plant material may potentially ingest harmful allelochemicals that adversely affect their survival, behaviour, development, and fecundity (Barbosa & Wratten, 1998). Avocado leaves, seeds, roots and fruit contain idioblast oil cells. Oil from these cells contains avocadofurans, which inhibits growth of generalist insect herbivores (Rodriguez-Soana *et al*., 1998; Rodriguez-Soana & Trumble, 1999). It is unknown whether avocado pollen contains avocadofurans or related compounds that could negatively affect *F. orizabensis* larval development and adult longevity following ingestion. However, it is possible that secondary plant compounds may be responsible for impaired growth and reproduction in *F. orizabensis* when avocado pollen is part of this predator's diet.

The least nutritious diet tested that supported larval development of *F. orizabensis* and enabled females to produce fertile eggs was *S. perseae*. This prey resulted in the lowest estimates of R_o and r_m and lifetime progeny production. Females reared on *S. perseae* were of intermediate size as determined by tibia lengths. *Scirtothrips perseae* is not an unsuitable food source for *F. orizabensis*. This predator readily responds to increasing *S. perseae* densities in avocado orchards (M.S. Hoddle, unpublished) and field collected females from avocado orchards heavily infested with *S. perseae* (the only substantial food source observed) were classified as large when tibia lengths were measured. Consequently, the reproductive potential of *F. orizabensis* was probably underestimated in the laboratory because of an inability to supply enough field collected *S. perseae* to larval and adult predators on a daily basis.

Diets consisting of *T. pacificus* eggs enabled *F. orizabensis* to complete development through to adulthood. However, adult male and female *F. orizabensis* died within 24 h of emerging from cocoons when reared on a diet consisting solely of *T. pacificus* eggs. Supplying avocado pollen with *T. pacificus* eggs increased adult longevity but females failed to produce progeny on this diet. The inability of *F. orizabensis* to develop solely on a diet of tetranychid prey may explain why this predator has not been frequently observed in California (USA) avocado orchards infested with *Oligonychus perseae* Tuttle Baker & Abbatiello and *Oligonychus punicae* (Hirst) (both Acari: Tetranychidae). These two tetranychid species are serious foliar pests that regularly induce defoliation of avocados when densities are high (Hoddle *et al.*, 1999b).

The results of the work presented here indicate that *F. orizabensis* is polyphagous and can develop and sustain itself to varying degrees on lepidopteran, thysanopteran, and tetranychid prey, and to a very limited extent, avocado pollen. Diet quality not only influences daily and lifetime fecundity of *F. orizabensis*, but it appears to affect progeny sex ratio with high quality diets resulting in female biased sex ratios and low quality diets resulting in more male offspring. Resource quality and subsequent sex allocation of offspring has been observed for other haplo-diploid natural enemies, in particular, parasitic Hymenoptera (Godfray, 1994). Factors such as food quality that potentially affects progeny sex allocation in predatory haplo-diploid Thysanoptera would benefit from additional investigation.

Although naturally occurring *Franklinothrips* spp. have been recorded in association with a large variety of prey species (e.g. whiteflies (Hemiptera: Aleyrodidae) and leaf miners (Diptera: Agromyzidae)) (Arakaki & Okajima, 1998) on economically important crops, there are no published field data to indicate that members of this genus can effectively regulate pest arthropod populations (McCallan, 1943; Lewis, 1973; Sabelis & van Rijn, 1997). Lack of density dependent population growth by *Franklinothrips* spp. in response to increasing pest densities in field situations may in part be due to the unsuitability of prey for predator growth and reproduction, even though pest consumption is observed in the field.

Furthermore, augmentative releases of mass-reared *F. orizabensis* onto avocado trees to bolster indigenous populations have failed to significantly suppress *S. perseae* populations in California. This failure may have been due more to the poor quality of *F. orizabensis* after shipping from an insectary in Europe (> 50% transit mortality) rather than the inherent ineffectiveness of this predator (Silvers, 2000). A novel technique for collecting *F. orizabensis* pupae has been developed, and long distance shipping of pupae significantly reduced predator mortality rates in comparison to aspirated and shipped adult *F. orizabensis* (Hoddle *et al.*, 2001). Diets utilizing irradiated *E. kuehniella* eggs with *T. pacificus* eggs are recommended for commercial mass rearing of *F. orizabensis*. Both of these food types are available commercially as they are used for mass rearing either trichogrammatids (irradiated *E. kuehniella* eggs) or phytoseiids (*T. pacificus* eggs).

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