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The Influence of Temperature Variation on Life History Parameters and Thermal Performance Curves of *Tamarixia radiata* (Hymenoptera: Eulophidae), a Parasitoid of the Asian Citrus Psyllid (Hemiptera: Liviidae)

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Abstract

This study examined the effects of seven constant and fluctuating temperature profiles with corresponding averages of 12 to 38°C on the life history of the Punjab, Pakistan-sourced *Tamarixia radiata* (Waterston) released in California for biological control of *Diaphorina citri* Kuwayama. One linear and seven nonlinear regression functions were fit to egg-to-adult development rate data to characterize thermal performance curves. Temperature fluctuations significantly affected both development and longevity of *T. radiata*. Estimates of degree-days predicted by the linear model were 30% higher for the fluctuating regime than the constant regime. Nonlinear model estimations of theoretical minimum and maximum developmental thresholds were lower for the fluctuating regime when compared to the constant regime. These predictions align with experimental observations. Parasitoids reared under fluctuating profiles at low average temperatures developed faster (15°C) and survived longer (15–20°C) when compared to those reared under constant regimes with corresponding means. In contrast, high average fluctuating temperatures produced parasitoids with an extended developmental period (35°C) and reduced longevity (30–35°C). A meta-analysis of published *T. radiata* development datasets, together with the results of this study, indicated convergence in degree-days and theoretical minimum developmental thresholds among geographically distinct parasitoid populations. These findings demonstrate the significant effects of temperature on *T. radiata* life history and have important implications for optimization of mass-rearing and release efforts, improvement of predictions from climate modeling, and comparison of *T. radiata* population performance across climatic gradients and geographic regions.

Key words: biological control, *Diaphorina citri*, temperature-dependent development rate, longevity, nonlinear regression models

Climate is the primary driver of many important biological and ecological processes in insects (Atkinson 1994, Damos and Savopoulou-Soultani 2012). Among abiotic factors, temperature exerts the strongest effects (Taylor 1981, Hallman and Denlinger 1998), influencing biochemical reactions, physiology, behavior (Denlinger and Yocum 1998, Colinet et al. 2015), phenology and population dynamics (Porter et al. 1991, Kang et al. 2009, Nelson et al. 2013), and the structure and functioning of communities and ecosystems (Nooten et al. 2014, Bjorkman and Niemela 2015). Many of these temperature-influenced phenomena, such as life history and phenology, play a fundamental role in the management of insect pests by informing the timing and implementation of control actions (Horn 1998, Roy et al. 2002, Terblanche et al. 2015).

The majority of empirical mathematical functions used to model insect development rates are temperature-driven (Damos and Savopoulou-Soultani 2012, Shi et al. 2015, Mirhosseini et al. 2017, Quinn 2017). The most widely utilized models are linear (Quinn 2017), which provide estimates of degree-days (i.e., accumulation of thermal energy necessary for completion of development in a specific life stage) and, through extrapolation of the regression line, the theoretical minimum temperature threshold below which development cannot occur (Campbell et al. 1974, Damos and Savopoulou-Soultani

2012). However, these simple linear models cannot fit the curvilinear portion of responses typically observed at the higher end of thermal clines (Davidson 1944, Colinet et al. 2015, Mirhosseini et al. 2017). Nonlinear models more accurately describe development rate across broader thermal gradients, allow estimation of the optimum developmental temperature and theoretical minimum and maximum developmental thresholds, and often incorporate biologically meaningful parameters (Shi et al. 2015, Mirhosseini et al. 2017, Ratkowsky and Reddy 2017). In conjunction with other life history data, thermal performance curves are highly relevant for pest management as they are used to calibrate climate-based software (e.g., CLIMEX) which forecast the growth, geographic distribution, spread, synchrony, and stability of pest and natural enemy populations across varying spatiotemporal scales (Roitberg et al. 2001, Régnière et al. 2012). These predictions may help improve biological control programs by facilitating the selection and utilization of climatically adapted biocontrol agents, optimizing release strategies (e.g., timing releases when targets are concentrated in vulnerable life stages), and promoting synergy among natural enemies (such as through geographic partitioning) (Horn 1998, Hart et al. 2002, Roy et al. 2002, Damos and Savopoulou-Soultani 2012, Terblanche et al. 2015). Further, temperature-driven developmental biology data can assist with the development of protocols for optimized mass-rearing, storage, release, and monitoring of biocontrol agents, potentially reducing costs and improving product quality (Leopold 1998, Mirhosseini et al. 2017).

Biological control has played an important role in management programs for the Asian citrus psyllid, *Diaphorina citri* Kuwayama, vector of the phloem-limited bacterium *Candidatus* Liberibacter asiaticus (CLas) which causes the lethal citrus disease huanglongbing (HLB; Bové 2006, Gottwald 2010, Grafton-Cardwell et al. 2013). Most major citrus-growing regions have been invaded by the *D. citri*-CLas pest complex, resulting in greatly increased pest management costs, yield quantity and quality reductions, and loss of productive acreage (Halbert and Manjunath 2004, Yang et al. 2006, Bassanezi et al. 2011, Durborow 2012, Grafton-Cardwell et al. 2013, Hall et al. 2013, Khan et al. 2014, Spreen et al. 2014).

California's citrus industry is valued at $7.1 billion annually, generating $3.4 billion in sales of fresh fruit and an additional $3.7 billion through dependent industries and induced economic activities (i.e., income spent by households supported by the citrus industry) (Babcock 2018). As the leading producer of fresh-market citrus in the USA (Babcock 2018, USDA 2018), the profitability of California's citrus industry is particularly susceptible to CLas-associated economic losses. Although *D. citri* is widely established in southern California, *D. citri*-CLas is currently restricted to residential areas (Hoddle and Pandey 2014, Milosavljević et al. 2018, Milosavljević and Hoddle 2019). Spillover of CLas-infected *D. citri* from urban infestation foci into major growing regions could expedite establishment of CLas and HLB expression in commercial production areas (Bayles et al. 2017).

Because sustained chemical management of *D. citri* infestations in California's vast urban citrus landscape is cost-prohibitive, biological control is the primary means of suppressing *D. citri* populations and delaying CLas spread to adjacent production zones (Hoddle and Pandey 2014, Milosavljević et al. 2017). The classical biocontrol program for *D. citri* has centered on establishment of *Tamarixia radiata* (Waterston) sourced from Punjab, Pakistan (Hoddle and Pandey 2014). *Tamarixia radiata* is a host-specific, idiobiont ectoparasitoid capable of inflicting substantial *D. citri* mortality through parasitism of nymphs (third through fifth instar) and host feeding (Chien et al. 1991, Chen and Stansly 2014, Hoddle and Pandey 2014, Kistner et al. 2016, Milosavljević et al. 2017). The California Department of Food and Agriculture (CDFA) has released over twelve million *T. radiata* at more than 1,000 sites covering 4,000 square miles of urban southern California (David Morgan CDFA, personal communication 19 November 2018), resulting in widespread establishment (Hoddle et al. 2016) and significant impacts on *D. citri* populations (Kistner et al. 2016). The observed seasonal and regional variation in efficacy of *T. radiata* in California may be partially mediated by temperature, as it is known to strongly affect host and parasitoid development, longevity, and fecundity (McFarland and Hoy 2001, Chen and Stansly 2014, Kistner et al. 2016).

Temperature-driven development rate models for *T. radiata* have previously been constructed from data collected under constant temperatures (Quilici and Fauvergue 1990; Chien et al. 1993; Gómez-Torres et al. 2012, 2014; Li et al. 2018). However, under natural field conditions, ambient temperatures follow a thermal cycle that exposes insects to temperatures above and below daily temperature means. The asymmetric nature of thermal performance curves means the warming phase of a cycle has a stronger influence on the physiological and biochemical responses of insects (e.g., metabolism) than the cooling phase (Jensen 1906, Colinet et al. 2015). Because constant temperature profiles fail to account for such thermal complexities independent of average conditions, they may produce unrealistic estimates of biological performance (Ruel and Ayres 1999, Lyons et al. 2013, Warren and Anderson 2013, Spanoudis et al. 2015, Wu et al. 2015). Thus, laboratory studies examining the development rate of *T. radiata* across a range of temperatures should account for the effects of thermal variance to more accurately model conditions experienced in the field (Colinet et al. 2015).

Understanding the effects of temperature on *T. radiata* life history could facilitate improvements in mass-rearing methods, inform the timing of inoculative and augmentative parasitoid releases, assist prediction of parasitoid establishment, spread, and efficacy across climatic gradients in citrus-growing regions, and enable comparisons among parasitoid populations sourced from different geographic areas for biological control programs (e.g., Pakistan vs. China). Thus, this study investigated the effects of constant and fluctuating temperatures (12 to 38°C) on the developmental biology (as modeled by eight thermal performance functions) and host-killing capacity of *T. radiata* sourced from Punjab, Pakistan. In addition, a meta-analysis of published work (10 studies) examining the effects of constant temperature on geographically distinct *T. radiata* populations was conducted.

Materials and Methods

Source of Experimental Insects

Tamarixia radiata adults used in experimental trials were obtained from 17 Punjab, Pakistan-sourced bi-parental isocage lines maintained at the University of California Riverside Insectary and Quarantine Facility (UCR IQF) (Hoddle and Hoddle 2013, Hoddle and Pandey 2014). *Diaphorina citri* offered to *T. radiata* for colony propagation and experimental trials were obtained from southern California-collected, CLas-free colonies maintained at UCR IQF (Hoddle and Pandey 2014, Bistline-East et al. 2015, Bistline-East and Hoddle 2015).

Stock Colony Production

Diaphorina citri colonies were maintained on 1- to 2-yr-old *Citrus volkameriana* Tenore and Pasquale (Sapindales: Rutaceae) that were pruned to produce the new foliar growth (i.e., flush) required for oviposition. Flushing plants were transferred from greenhouses maintained at 27 ± 1°C, 50 ± 20% RH, and a 14:10 (L:D) h photoperiod at UCR Agricultural Operations (UCR AgOps) to a climate-controlled rearing room in UCR IQF held at 27 ± 1°C, 40 ± 20% RH, and a 14:10 (L:D) h photoperiod. Individual plants in 0.5 l pots were placed in rectangular clear acrylic and fine mesh cages (15 × 15 × 30 cm WxDxH) (methods in Bistline-East et al. 2015). Caged *C. volkameriana* were inoculated with adult *D. citri*, and the resultant nymphs were allowed to develop to fourth and fifth instar (10–14 d post oviposition), stages preferred by *T. radiata* for parasitization (Hall et al. 2008). *Tamarixia radiata* that emerged from parasitized *D. citri* were transferred as male-female pairs to honey-provisioned 2-ml O-ring microcentrifuge vials (Micrewtube brand, Simport Scientific Inc., Vancouver, Canada) to ensure mating and held in cold storage cabinets maintained at 16 ± 1°C, 40 ± 20% RH, and a photoperiod of 14:10 (L:D) h until use in experimental trials.

Experimental Plant Preparation

Diaphorina citri nymphs exposed to female *T. radiata* for parasitization in experimental trials were hand-transferred from stock colonies to 6- to 12-mo-old *C. volkameriana* seedlings with suitable foliar growth for feeding. Seedlings were planted in 114-ml plastic growing cones (Ray Leach cone-tainers, SC7 Stubby, Stuewe and Sons Inc., Portland, OR) and maintained in UCR AgOps greenhouses with *D. citri* stock colony plants.

Experimental Procedure

In a UCR IQF preparation laboratory maintained at 25 ± 1°C, 40 ± 20% RH, and a photoperiod of 14:10 (L:D) h, 20 *C. volkameriana* seedlings in cone-tainers each inoculated with 10 fifth instar *D. citri* were contained within clear, ventilated 148-ml vial ‘arenas’ (Thornton Plastic Co., Salt Lake City, UT) (methods in Bistline-East et al. 2015). Enclosed cone-tainers were secured in plastic holding bins (4.92 liters; Greenbrier International Inc., Chesapeake, VA) and *D. citri* nymphs were allowed to settle on plants (4–6 h) prior to introduction of *T. radiata* into experimental arenas.

One mated female *T. radiata* was released from a honey-provisioned 2-ml O-ring microcentrifuge vial into each of the 10 arenas containing *D. citri*. Cone-tainers were then promptly transferred into environmental chambers (model I-30BLL; Percival Scientific Inc., Perry, IN) running one of fourteen constant or fluctuating experimental temperature profiles (see ‘Temperature Regimes’ for further detail). *Tamarixia radiata* were allowed to oviposit for 6 h before removal. This procedure was repeated at least once for each temperature regime to provide sufficient *T. radiata* development data for model fitting and statistical analyses.

Across all temperature regimes, cone-tainers were inspected daily for *T. radiata* emergence to measure development rate. *Tamarixia radiata* were collected upon emergence, sexed, and transferred individually into labeled 2-ml microcentrifuge vials provisioned with honey. Adult *T. radiata* were maintained under their respective experimental temperature regimes and monitored daily for mortality to determine parasitoid longevity.

For fluctuating temperature regimes only, an additional 10 cone-tainers with *D. citri* only were paired with the 10 *T. radiata*-exposed cone-tainers. These control replicates measured baseline mortality rates for *D. citri* in the absence of *T. radiata* across all fluctuating temperature regimes. Daily monitoring of parasitoid-exposed and control cone-tainers included an assessment of *D. citri* nymph mortality, parasitism status, and emergence of adult *T. radiata* and *D. citri*. Daily monitoring of cone-tainers ceased following eclosion or death of all *D. citri*.

Temperature Regimes

Tamarixia radiata life history parameters were examined across seven average temperatures, 12, 15, 20, 25, 30, 35, and 38 ± 0.5°C, 50 ± 20% RH, and a photoperiod of 14:10 (L:D) h that were held constant or fluctuated over time (Table 1). To produce fluctuating regimes, climate-controlled cabinets were programmed with ramping temperature increments oscillating over a 24-h cycle with a mean temperature equivalent to the constant counterpart. Incremental steps were based on the hourly temperature profiles of days with target average temperatures from 2 yr of field-recorded data (January 2013 to December 2015; Indio, CA #2 weather station [CIMIS 2018]). Detailed methods for fluctuating temperature profile selection can be found in Milosavljević et al. (2019). Target environmental conditions were verified by HOBO Pro V2 Temperature/RH loggers programmed to record at 15-min intervals (Onset Computer Corp., Bourne, MA).

Statistical Methods

Following initial descriptive analyses, means comparisons were carried out using the statistical software package R (version 3.4.4, R Development Core Team [2018]). Generalized linear models (GLMs) were used to examine the main effect of average temperature, thermal variation (i.e., constant or fluctuating regime), gender, and their interactions on *T. radiata* development time (i.e., total number of days required to develop from egg to adult; Poisson distribution) and adult longevity (i.e., total number of days survived as adults; negative binomial distribution [‘*glm.nb*’ function in MASS package, R]). Because temperature held a nonlinear relationship with both development time and longevity, it was treated as a categorical rather than continuous variable. Although it is recognized that dichotomizing a continuous variable generally results in information loss, dividing a continuous variable up into ordered categories can be justified when the variable is highly nonnormally distributed or when its relationship to a response variable is highly nonlinear (Streiner 2002, Pasta 2009). The estimated marginal means function (‘*emmeans*’ in emmeans package, R) was used to compare development time and longevity between constant and fluctuating regimes across various temperatures (Table 2). All comparisons were made at the 0.05 level of significance.

For all fluctuating regime cohorts, mean total mortality of *D. citri* nymphs and mortality excluding parasitism were compared between treatments (i.e., *T. radiata*-exposed and control) and across temperatures using GLMs with a Poisson distribution. *Diaphorina citri* mortality estimates (in the *T. radiata*-exposure treatment) were additionally corrected for baseline *D. citri* mortality (control treatment) using the Schneider-Orelli formula (Schneider-Orelli 1947) following analysis. For fluctuating regime cohorts exposed to *T. radiata*, the effect of temperature on rate of *D. citri* parasitism and developmental mortality of parasitoids (i.e., death prior to emergence) were modeled using GLMs with a negative binomial distribution. All GLMs were followed by multiple comparison tests with emmeans at the 0.05 level of significance.

Mathematical Models and Evaluation

The performance of eight regression functions (i.e., ordinary linear, Lactin-2, Weibull, Brière-2, Beta, LRF, Ratkowsky, and Performance-2) for predicting development rate (D_r=1/D_t, where D_t is mean duration of egg-to-adult development in days) of *T. radiata* reared under constant and fluctuating thermal profiles (15 to 35°C; Table 3) was assessed. Models were evaluated on the basis of multiple criteria: model goodness-of-fit, deviation of predicted values from estimated values, estimates of theoretical developmental

Table 1. Fluctuating temperature profiles utilized for rearing *Tamarixia radiata*

	Mean temperature (°C)							
Hour	12	15	20	25	30	35	38	Photoperiod
0100	10	11	16	21	26	30	33	Dark
0200	9	11	16	20	26	30	32	
0300	9	11	17	20	26	30	33	
0400	8	10	17	20	26	30	33	
0500	8	10	16	20	25	30	32	
0600	7	9	15	19	25	30	32	Light
0700	8	9	15	20	26	31	34	
0800	9	10	17	23	28	33	36	
0900	12	14	20	25	29	35	38	
1000	15	18	22	27	32	36	40	
1100	17	20	24	29	33	38	42	
1200	18	22	25	30	34	40	43	
1300	19	23	26	31	35	40	44	
1400	19	23	27	32	35	40	45	
1500	19	23	27	32	36	41	45	
1600	18	23	27	32	36	41	45	
1700	16	20	25	31	35	41	45	
1800	13	16	22	30	34	40	44	
1900	11	14	20	27	32	37	41	
2000	10	13	18	24	30	36	38	Dark
2100	9	13	18	23	30	35	37	
2200	9	13	17	22	28	33	35	
2300	7	11	16	21	26	31	32	
2400	7	11	16	21	26	31	32	
Total steps	18	13	16	17	15	14	18	

Table 2. Mean development times and adult longevity (days ± SE) of *Tamarixia radiata* under constant and fluctuating temperature regimes

	Development time (mean days ± SE)					
	12°C	15°C	20°C	25°C	30°C	35°C
Constant	No emergence	33.87 ± 0.31a (96)	16.64 ± 0.11a (80)	10.45 ± 0.06a (80)	8.49 ± 0.04a (80)	8.14 ± 0.06a (53)
Fluctuating	48.50 ± 0.81 (6)	23.57 ± 0.34b (28)	17.02 ± 0.18a (53)	10.98 ± 0.09a (58)	9.28 ± 0.23a (40)	12.14 ± 0.34b (7)
P	N/A	<0.001	1.000	1.000	0.983	0.043
	Adult longevity (mean days ± SE)					
Constant	No emergence	18.41 ± 1.57a (95)	32.45 ± 1.74a (80)	29.34 ± 1.07a (80)	23.14 ± 1.02a (80)	6.99 ± 0.46a (53)
Fluctuating	70.50 ± 10.50 (6)	79.36 ± 3.35b (25)	62.63 ± 2.06b (51)	31.14 ± 1.32a (50)	17.33 ± 1.25b (40)	1.17 ± 0.17b (6)
P	N/A	<0.001	<0.001	0.999	0.038	0.001

For development time and longevity, means followed by the same letter within the same temperature are not significantly different α = 0.05 (estimated marginal means). (*n*) denotes the number of individuals.

thresholds, and inclusion of biologically interpretable parameters. To facilitate direct comparison of models, temperatures at which development did not occur in one or both regimes (i.e., 12 and 38°C) were excluded from analyses.

Linear regression was used to calculate the theoretical minimum developmental threshold ($T_{min} = -a/b$, where a is the development rate when T = 0°C and b is the slope), thermal constant or degree-days necessary for completion of development ($K = 1/b$), and coefficient of determination, a measure of model goodness-of-fit ($R^2 = 1 - \frac{RSS}{TSS}$; where RSS and TSS are the residual and total sum of squares, respectively) (Table 4). To ensure accurate calculation of these measures, data were plotted in the statistical software SAS (version 9.4, SAS Institute Inc., Cary, NC) using PROC SGPLOT and fit with a linear regression using PROC REG. Temperatures at which development rate deviated from rectilinearity were omitted from analysis (Damos and Savopoulou-Soultani 2012, Milosavljević et al. 2019). Observations were considered outliers if the absolute value of their externally studentized residual (provided by the output term '*rstudent*') was greater than three.

Nonlinear regression models were computed using the PROC NLIN procedure in SAS for temperatures 15–35°C and graphed in Excel. Unless given explicitly as model parameters, theoretical thermal tolerance limits were estimated mathematically using graphic software (i.e., Excel and SAS) (Zahiri et al. 2010, Milosavljević et al. 2019). The optimum development point (T_{opt}) was estimated from the development curve peak (where D_r = max), while the theoretical minimum and maximum developmental thresholds (T_{min} and T_{max}) were measured at the sites of intersection between the curve and temperature axis (where D_r = 0) (Table 5).

All nonlinear models examined had four parameters and, therefore, the same df (Table 3). This eliminated the need for multiple, complex comparison criteria (e.g., AIC, AIC_c, BIC, etc.

Table 3. Mathematical equations and parameter estimates for eight performance functions describing the relationship between development rate (D_r) and temperature for *Tamarixia radiata* reared under constant and fluctuating temperature regimes

Model	Model equation	Parameter	Parameter estimate		Reference
			Constant	Fluctuating	
Ordinary linear	$D_r = a + bT$	a	-0.0592	-0.0290	Campbell et al. (1974)
		b	0.0060	0.0047	
Lactin-2 (Logan-Lactin)	$D_r = \lambda + e^{\rho T} - e^{(\rho T_u - (T_u - T)/\delta)}$	λ	-1.0689	-1.0286	Logan et al. (1976) Lactin et al. (1995)
		ρ	0.0063	0.0044	
		T_u	51.1326	40.7663	
		δ	4.9804	1.8892	
Weibull	$D_r = a\left(\frac{d-1}{d}\right)^{\frac{1-d}{d}}\left[\frac{T-b}{c}+\left(\frac{d-1}{d}\right)^{\frac{1}{d}}\right]^{d-1} e^{\left[-\left(\frac{T-b}{c}+\left(\frac{d-1}{d}\right)^{\frac{1}{d}}\right)^{d}+\frac{d-1}{d}\right]}$	a	0.0763	0.0544	Angilletta (2006)
		b	40.2620	36.1118	
		c	32.9344	30.5081	
		d	7.8314	17.7261	
Brière-2	$D_r = aT\,(T - T_{min})\,(T_{max} - T)^{1/b}$	$T_{\min}$	0.0000	0.0001	Brière et al. (1999)
		$T_{\max}$	8.8934	-6.1967	
		a	43.3516	35.1672	
		b	1.4193	6.0321	
Beta	$D_r = r_m\,\left(\frac{T_2-T}{T_2-T_m}\right)\left(\frac{T-T_1}{T_m T_1}\right)^{\frac{T_m-T_1}{T_2-T_m}}$	T_1	5.2869	-273	Yin et al. (2003) Auzanneau et al. 2011 Shi et al. (2015)
		T_2	46.1509	38.2160	
		T_m	33.3844	30.6802	
		r_m	0.1245	0.1098	
Lobry-Rosso-Flandrois	$D_r = \mu_{opt}\frac{(T-T_{max})(T-T_{min})^2}{(T_{opt}-T_{min})\left[(T_{opt}-T_{min})(T-T_{opt})-(T_{opt}-T_{max})(T_{opt}+T_{min}-2T)\right]}$	$T_{\min}$	6.1237	-3.8214	Lobry et al. (1991) Rosso et al. (1993)
		$T_{\max}$	46.0568	36.5141	
		T_{opt}	33.4138	31.5669	
		μ_{opt}	0.1245	0.1123	
Ratkowsky	$D_r = \left(b\,(T - T_{min})\,\left(1 - e^{c(T-T_{max})}\right)\right)^2$	$T_{\min}$	5.8497	-5.0733	Ratkowsky (1983)
		$T_{\max}$	51.6464	38.9538	
		b	0.0236	0.0100	
		c	0.0428	0.3175	
Performance-2	$D_r = b\,(T - T_{min})\,\left(1 - e^{c(T-T_{max})}\right)$	$T_{\min}$	10.7657	6.7013	Shi et al. (2011) Wang et al. (2013)
		$T_{\max}$	42.128	36.731	
		b	0.00344	0.00484	
		c	0.1885	0.5356	

See corresponding references for full description of models and parameters.

Table 4. Comparison of development times, degree-days, theoretical minimum developmental thresholds, and R^2 values for *Tamarixia radiata* populations from China, Brazil, Réunion Island, Taiwan, and California

Development time (mean days)														Calculations			Source of *Tamarixia radiata* used in experiments			
12°C	15°C	18°C	20°C	22°C	25°C	26°C	27°C	28°C	30°C	32°C	34°C	35°C	38°C	K (degree-days)	T_{min}	R^2	Country of study	Reference	Country of origin	Reference
-	-	-	-	-	12.6	-	-	-	-	-	-	-	-	-	-	-	Southeast China (Fujian)	Xu and Tang 1993	China	Tang 1989, 1990
-	-	19.6	-	$14.5^{a,d}$	-	13.4	-	-	11.3^{d}	-	10.2	-	-	333.3	0.8	0.9980	South China (Guangdong)	Li et al. 2018	China	Li et al. 2018
-	20.3^{b}	-	18.8^{b}	-	15.5^{b}	-	-	-	11.8^{b}	-	-	10.4^{b}	-	-	-	-	Brazil	Gomez-Torres et al. 2012	Unknown	Torres et al. 2006
-	-	-	-	-	-	-	-	10.4	-	-	-	-	-	-	-	-	Brazil	Baños et al. 2013	Unknown	Torres et al. 2006
-	-	17.3	14.2	12.4	10.3	-	-	10.1^{a}	7.6	7.6	-	-	-	178.6	7.6	0.9951	Brazil	Gomez-Torres et al. 2014	Unknown	Torres et al. 2006
-	-	-	-	-	10.0	-	-	-	-	-	-	-	-	-	-	-	Brazil	Beloti et al. 2015	Unknown	Torres et al. 2006
-	-	-	-	-	11.6^{c}	-	-	-	-	-	-	-	-	-	-	-	Brazil	Alves et al. 2016[c]	Unknown	Torres et al. 2006
-	-	-	16.8	-	10.1	-	9.1	-	8.5^{a}	-	-	-	-	137.0	11.8	0.9945	Réunion	Quilici and Fauvergue 1990	Pakistan	Etienne and Aubert 1980
-	-	-	-	-	11.4	-	-	-	-	-	-	-	-	-	-	-	Taiwan	Chien et al. 1991	Réunion (Pakistan)	Chiu et al. 1988
-	36.6	-	20.3^{a}	-	11.6	-	-	-	8.7	7.8	-	No emerg.	-	169.5	10.4	0.9998	Taiwan	Chien et al. 1993	Réunion (Pakistan)	Chiu et al. 1988
No emerg.	33.87	-	16.6	-	10.5	-	-	-	8.5	-	-	8.1^{a}	No emerg.	166.7	9.9	0.9923	California	This study (constant)	Pakistan	Hoddle et al. 2014
48.5^{a}	23.6	-	17.0	-	11.0	-	-	-	9.3	-	-	12.1^{a}	-	217.4	6.0	0.9813	California	This study (fluctuating)	Pakistan	Hoddle et al. 2014

[a] Outliers excluded from K, T_{min}, and R^2 calculations.

[b] Development times provided for female *T. radiata* only.

[c] Values averaged across all citrus varieties investigated in the study.

[d] Values estimated from figures.

[Akaike 1974, Schwarz 1978, Hurvich and Tsai 1989]) and selection-associated bias (Ratkowsky and Reddy 2017, Milosavljević et al. 2019). Though R^2 and its adjusted derivative (R^2_{adj}) are commonly used to describe the fit of nonlinear models to developmental data, this usage is inappropriate. Important mathematical assumptions of the linear model-based R^2 equation are violated by nonlinear models, producing erroneous estimations (see further explanation in Spiess and Neumeyer 2010, who conclude that R^2 usage for nonlinear models is inappropriate and recommend its removal from scientific literature for this purpose). Thus, nonlinear model goodness-of-fit was assessed solely with *RSS* (Shi et al. 2015, Ratkowsky and Reddy 2017, Milosavljević et al. 2019) (Table 5):

$$RSS = \sum_{i=1}^{n} (y_i - \hat{y}_i)^2$$

here, n denotes the sample size and y_i and $\hat{y}_i$ denote the observed and expected development rate at the i-th temperature, respectively. A lower value of *RSS* indicates superior model fit.

The relative accuracy of model-predicted development rates was assessed using the percent deviation formula (Liu et al. 1995, Quinn 2017, Sánchez-Ramos et al. 2018) (Table 5):

$$d = \left(\frac{PDT}{RDT} - 1\right) \times 100$$

here, *PDT* and *RDT* are the sum of predicted and recorded development rates, respectively. The percentage of their deviation is represented as d, with overestimations expressed as positive values and underestimations as negative values. It is important to note that this calculation provides an assessment of model precision solely at experimentally measured temperatures.

Meta-analysis of *Tamarixia radiata* Development

A literature search was conducted to locate published studies examining the temperature-dependent development of *T. radiata* to compare with results presented in this study. Relevant papers were retrieved manually using keyword searches (i.e., combinations of '*Tamarixia radiata*' or '*Tetrastichus radiatus*' with 'development rate', 'growth', 'performance curve', or 'life history', and 'temperature' or 'thermal cline') in Google Scholar, Web of Science, and the University of Florida Huanglongbing Bibliographical Database (Vanaclocha and Stansly 2009). In addition to the present study, ten papers containing constant temperature regime-derived and combined gender development data for *T. radiata* sourced from China, Brazil, Réunion Island, and Taiwan were compiled (Table 4). For the subset of four papers (Quilici and Fauvergue 1990, Chien et al. 1993, Gómez-Torres et al. 2014, Li et al. 2018) that provided development time across multiple temperatures, the reciprocal (i.e., D_r=1/D_t, development rate) was taken. These data were plotted in SAS with PROC SGPLOT and fit to a linear regression with PROC REG. Following identification and removal of outliers (i.e., observations with externally studentized residuals larger than |3|, as indicated by rstudent), T_{min}, degree-days, and R^2 were estimated (for methods, see previous section 'Mathematical Models and Evaluation') and compared across published datasets. Gómez-Torres et al. (2012) was not included in this analysis, as development time was presented separately by gender. Furthermore, this study was superseded by Gómez-Torres et al. (2014) (included in the analysis) which examined the same source population of *T. radiata* (São Paulo, Brazil) across a broader range of temperatures.

Results

Effect of Temperature and Regime Type on *T. radiata* Development Time

Tamarixia radiata completed egg-to-adult development under experimental temperature profiles from 15 to 35°C in the constant regime and 12 to 35°C in the fluctuating regime. Average temperature ($\chi^2 = 1410.10; \mathrm{df} = 4; P < 0.001$), regime type (i.e., constant or fluctuating) ($\chi^2 = 63.15; df = 1; P < 0.001$), and their interaction ($\chi^2 = 73.00; \mathrm{df} = 4; P < 0.001$) significantly affected mean development time. Gender was also a significant model factor ($\chi^2 = 4.88; \mathrm{df} = 1; P = 0.027$) but its interaction with temperature ($\chi^2 = 0.76; \mathrm{df} = 4; P = 0.943$) and regime were not ($\chi^2 = 0.30; \mathrm{df} = 1; P = 0.586$). Egg-to-adult development time decreased with increasing temperature to a minimum of 8.14 ± 0.06 d at 35°C constant and 9.28 ± 0.23 d at 30°C fluctuating (Table 2). *Tamarixia radiata* reared under the fluctuating regime developed significantly faster at 15°C ($Z = 8.39; P < 0.001$) and slower at 35°C ($Z = -3.21; P = 0.043$) than at the corresponding constant temperatures. No significant differences in development time between constant and fluctuating regimes were detected at 20°C ($Z = -0.3; P = 1.000$), 25°C ($Z = -0.54; P = 1.000$), and 30°C ($Z = -1.12; P = 0.983$).

Development Rate Model Comparison

The linear model provided a good fit for *T. radiata* development rate in both constant and fluctuating regimes, with an R^2 of 0.99 and 0.98, respectively (Table 4). The regression line predicted a T_{min} of 9.9°C for the constant regime and 6.0°C for the fluctuating regime. Estimates of the thermal requirement for development completion were lower for the constant regime than the fluctuating counterpart, with 166.7 and 217.4 degree-days, respectively.

Table 5 summarizes nonlinear model (i.e., Lactin-2, Weibull, Brière-2, Performance-2, Beta, LRF, and Ratkowsky) goodness-of-fit and theoretical developmental thresholds and Fig. 1 displays thermal performance curves. In general, all models fit the observed data well, producing low values of *RSS* and percent deviation. Mathematically, the best fitting models were Ratkowsky, Beta, and LRF while Weibull, Lactin-2, and Performance-2 provided poorer fits. Estimations of T_{opt} were similar among models, ranging from 33.3 to 33.4°C for constant regimes and 29.4 to 31.8°C for fluctuating regimes. Considerable divergence in model predictions were observed for values of T_{min}, which ranged from 5.3 to 11.5°C (constant) and –273 to 7.3°C (fluctuating), and T_{max}, which ranged from 42.1 to 52.5°C (constant) and 35.2 to 40.5°C (fluctuating) (Table 5).

Meta-analysis of *T. radiata* Development

Among the ten papers evaluated, *T. radiata* development was reported to occur at temperatures between 15 and 35°C. The temperatures most frequently examined were 20, 25, and 30°C, with average development times of 16.98 ± 1.26, 11.01 ± 0.27, and 9.06 ± 0.76 d, respectively. *Tamarixia radiata* from Brazil (unknown origin), Réunion (Pakistan), Taiwan (parasitoids sourced from populations established on Réunion that were originally collected from Pakistan), and California (Pakistan) were estimated to have similar developmental parameters, with a T_{min} ranging from 7.6 to 11.8°C and requiring 137.0 to 178.6 degree-days to complete development (Table 4). These values diverged considerably from the T_{min} of 0.8 and 333.3 degree-days calculated for the China-sourced *T. radiata*.

Table 5. Comparison of goodness-of-fit, percent deviation, and theoretical developmental thresholds among 7 thermal performance functions fit to the development rate of *Tamarixia radiata* under constant and fluctuating temperature regimes

	Residual sum of squares (*RSS*)		Percent deviation (%)		Theoretical minimum developmental threshold (T_{min})		Optimum developmental temperature (T_{opt})		Theoretical maximum developmental threshold (T_{max})	
Model	Constant	Fluctuating	Constant	Fluctuating	Constant	Fluctuating	Constant	Fluctuating	Constant	Fluctuating
Lactin-2	9.2×10^{-6}	4.1×10^{-5}	0.0023	−0.0182	10.66	6.35	33.32	31.65	42.35	36.83
Weibull	1.3×10^{-5}	4.5×10^{-5}	0.0117	0.0052	11.54	7.33	33.28	31.65	52.54	40.52
Brière-2	5.0×10^{-6}	3.4×10^{-5}	−0.0047	−0.0415	8.89	−6.20	33.39	29.43	43.35	35.17
Beta	3.8×10^{-6}	2.2×10^{-5}	−0.0047	−0.1064	5.29	−273[a]	33.38	30.68	46.15	38.22
LRF	4.0×10^{-6}	3.0×10^{-5}	−0.0117	−0.0337	6.12	−3.82	33.41	31.57	46.06	36.51
Ratkowsky	3.6×10^{-6}	2.6×10^{-5}	0.0000	−0.0337	5.85	−5.07	33.44	31.01	51.64	38.95
Performance-2	9.8×10^{-6}	4.3×10^{-5}	0.0000	−0.0052	10.77	6.70	33.33	31.76	42.13	36.73

[a] Beta model achieved convergence at absolute zero.

Effect of Temperature and Regime Type on *T. radiata* Adult Longevity

Mean longevity of adult *T. radiata* was significantly affected by average temperature ($\chi^2 = 253.93; df = 4; P < 0.001$), thermal variation ($\chi^2 = 223.03; df = 1; P < 0.001$), and their interaction ($\chi^2 = 281.44; df = 4;\ P < 0.001$). The main effect of gender was not significant ($\chi^2 = 1.47; df = 1;\ P = 0.226$) but significant interactions with temperature ($\chi^2 = 16.8; df = 4;\ P = 0.002$) and regime ($\chi^2 = 4.32; df = 1;\ P = 0.038$) were detected. Maximum longevity of 79.36 ± 3.35 d was observed at 15°C fluctuating and 32.45 ± 1.74 d at 20°C constant (Table 2). Above these temperatures, longevity steadily decreased with rising temperature, reaching minimums of 1.17 ± 0.17 (fluctuating) and 6.99 ± 0.46 d (constant) at 35°C. Despite the similarity in overall trend (Fig. 2), average lifespan duration was significantly different between regimes across all temperatures (15°C: $Z = -15.88; P < 0.001$; 20°C: $Z = -9.25; P < 0.001$; 30°C: $Z = 3.26; P = 0.038$; 35°C: $Z = 4.14; P = 0.001$) except 25°C ($Z = -0.78; P = 0.999$) (Table 2). The magnitude of this effect was greatest at temperature cline margins. In comparison with constant regimes, fluctuating regimes produced *T. radiata* with a lifespan approximately four times longer at 15°C, two times longer at 20°C, and six times shorter at 35°C.

Effect of Fluctuating Temperature Regimes on *D. citri* Parasitism Rates

Parasitism of *D. citri* by *T. radiata* occurred under all fluctuating experimental temperatures except 38°C. Temperature significantly affected parasitism rate ($\chi^2 = 83.63; df = 5; P < 0.001$). Parasitism was significantly higher at intermediate temperatures 20°C (58.0 ± 5.93%), 25°C (70.0 ± 6.15%), and 30°C (51.0 ± 6.40%) than at cline margins 12°C (20°C: $Z = -5.2; P < 0.001$; 25°C: $Z = -5.79; P < 0.001$; 30°C: $Z = -4.8; P < 0.001$) and 35°C (20°C: $Z = 4.53; P < 0.001$; 25°C: $Z = 5.23; P < 0.001$; 30°C: $Z = 4.06; P < 0.001$), where parasitism was 9.0 ± 4.82% and 14.44 ± 6.26%, respectively (Fig. 3).

Developmental Mortality of *T. radiata* in Fluctuating Temperature Regimes

Temperature significantly affected the mean developmental mortality rate of developing *T. radiata* reared under fluctuating regimes ($\chi^2 = 90.48; df = 5; P < 0.001$). Mortality was similar among intermediate temperatures (less than 25% from 15 to 30°C) but significantly higher at 12°C (15°C: $Z = -3.42; P = 0.008$; 20°C: $Z = -5.11; P < 0.001$; 25°C: $Z = -5.29; P < 0.001$; 30°C: $Z = -4.33; P < 0.001$) and 35°C (15°C: $Z = 3.19; P = 0.018$; 20°C: $Z = 4.86; P < 0.001$; 25°C: $Z = 5.04; P < 0.001$; 30°C: $Z = 4.09; P < 0.001$), where 30.56 ± 19.44% and 73.0 ± 16.70% of *T. radiata* failed to emerge from *D. citri* hosts, respectively (Fig. 4).

Effect of Fluctuating Temperature Regimes and *T. radiata* Exposure on Mortality of *D. citri* Nymphs

Tamarixia radiata-exposure treatment ($\chi^2 = 298.48; df = 1; P < 0.001$), average temperature ($\chi^2 = 79.5; df = 5; P < 0.001$), and the interaction between treatment and temperature ($\chi^2 = 113.58; df = 5; P < 0.001$) were significant factors affecting mean total developmental mortality of *D. citri*. Across all temperatures, total mortality rate was significantly higher in *T. radiata*-exposed cohorts than in controls lacking parasitoid exposure (12°C: $Z = -15.21; P < 0.001$; 15°C: $Z = -17.12; P < 0.001$; 20°C: $Z = -21.08; P < 0.001$; 30°C: $Z = -20.21;\ P < 0.001$; 35°C: $Z = -15.31;\ P < 0.001$; Fig. 5). Control cohort total mortality was 7–10% from 15 to 30°C, increasing slightly at temperature cline margins of 12°C (13.0 ± 3.67%) and 35°C (19.0 ± 5.67%). By contrast, corrected total mortality of *T. radiata*-exposed cohorts was over 55% across all temperatures, reaching 92.0 ± 3.27%, 91.0 ± 4.58%, and 85.0 ± 6.87% at 20, 25, and 30°C, respectively.

As with mean total *D. citri* nymph mortality, mortality excluding parasitism was significantly influenced by *T. radiata*-exposure treatment ($\chi^2 = 213.61; df = 1; P < 0.001$), temperature ($\chi^2 = 79.5; df = 5; P < 0.001$), and the interaction between treatment and temperature ($\chi^2 = 32.07; df = 5; P < 0.001$; Fig. 5). Non-parasitism related *D. citri* mortality was significantly higher in the *T. radiata*-exposure treatment than the control treatment across all experimental temperatures (12°C: $Z = -13.21; P < 0.001$; 15°C: $Z = -11.87; P < 0.001$; 20°C: $Z = -10.76; P < 0.001$; 25°C: $Z = -5.65; P < 0.001$; 30°C: $Z = -11.64;\ P < 0.001$; 35°C: $Z = -12.04;\ P < 0.001$). At 25°C, *T. radiata*-exposed cohorts had the lowest rate of non-parasitism related mortality (21.0 ± 4.58%) but the highest rate of parasitism (70.0 ± 6.15%) (Fig. 3). Non-parasitism related mortality peaked at temperature cline margins of 12 and 35°C (48.0 ± 6.63% and 53.33 ± 7.99%, respectively), where parasitism rate was observed to be the lowest (9.0 ± 4.82% and 14.44 ± 6.26%, respectively).

Discussion

Establishment of the *D. citri*-CLas pest complex in major citrus-growing regions could threaten the sustained profitability of

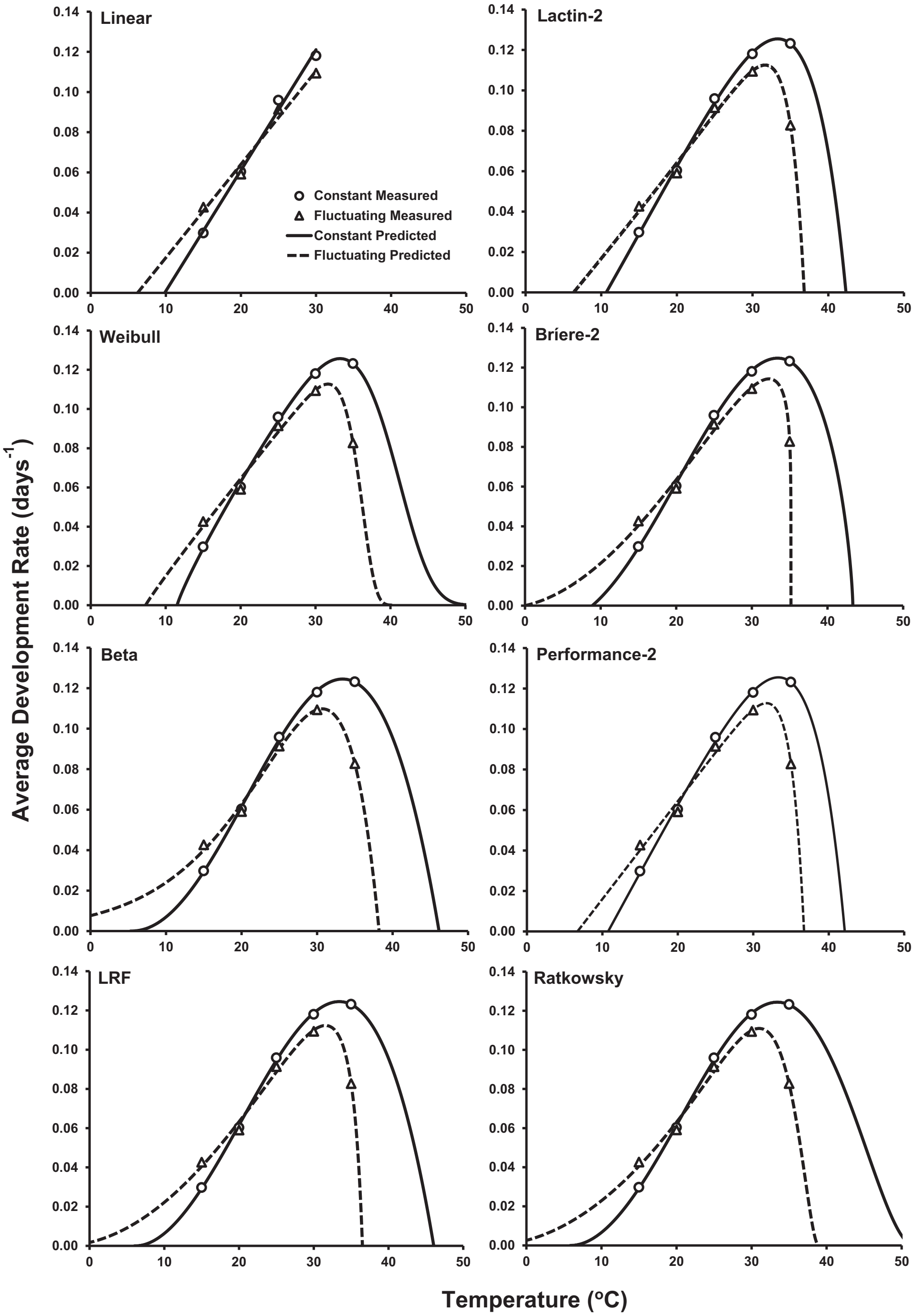

Fig. 1. Relationship between temperature (°C; *x*-axis) and development rate (days^{-1}; *y*-axis) of *Tamarixia radiata* as described by eight thermal performance functions. Solid lines represent model predictions for constant temperatures and dashed lines for fluctuating temperatures. Experimentally measured values are represented by circles (constant) and triangles (fluctuating). The 35°C data point in both the constant and fluctuating dataset has been omitted from the linear model due to outlier status. The 12°C data point (fluctuating) has been omitted from both the linear and nonlinear models to facilitate direct comparison between constant and fluctuating datasets.

California's multi-billion-dollar citrus industry (Babcock 2018). southern California's extensive residential landscape is a liability for CLas spread, as there are millions of backyard citrus trees that could harbor infected *D. citri* (Gottwald 2010, Hoddle and Pandey 2014). In these high-risk urban areas where pesticide use is minimal, *T. radiata* is critical for suppressing vector populations and limiting dispersal into commercial production zones (Milosavljević et al. 2017).

Consequently, a thorough understanding of the effects of temperature on the developmental biology of *T. radiata* sourced from Pakistan and used for biocontrol in California is necessary for interpreting parasitoid impacts in different citrus producing regions with varying climates (e.g., hot desert interior regions and cool coastal zones) and for the optimization of mass-production programs. Thus, this study aimed to provide a comprehensive overview of the effects of constant and fluctuating temperatures on life history parameters of *T. radiata*.

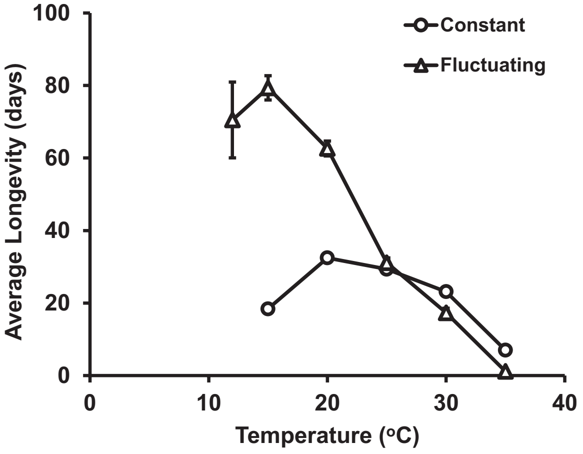

Fig. 2. Average longevity (days) of adult *Tamarixia radiata* maintained under various constant (circle) and fluctuating (triangle) average daily temperatures (°C).

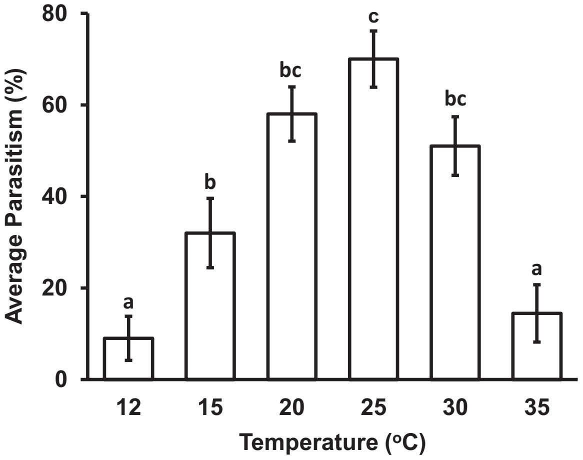

Fig. 3. Comparison of parasitism rates of *Diaphorina citri* by *Tamarixia radiata* in fluctuating regime cohorts across average daily temperatures (°C). Means followed by the same letter are not significantly different at α = 0.05.

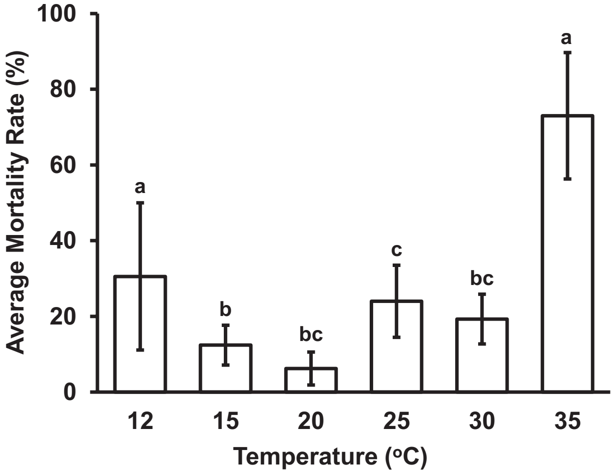

Fig. 4. Developmental mortality of *Tamarixia radiata* in fluctuating regime cohorts compared across average daily temperatures (°C). Means followed by the same letter are not significantly different at α = 0.05.

Average daily temperature and regime type significantly affected *T. radiata* development time and longevity, with the greatest mean differences between control and fluctuating profiles observed near the lower and upper extremes of experimental temperature clines. At cooler temperatures, parasitoids reared under fluctuating profiles developed more rapidly (15°C) and survived longer (15 and 20°C) than those reared under constant temperatures with equivalent means (Table 2). The reverse was true at high temperatures, with fluctuating profiles producing parasitoids with a longer development period (35°C) and shorter lifespan (30 and 35°C) than constant temperature counterparts. The observed response for *T. radiata* reflects that of other arthropods reared under variable temperature regimes (Williams et al. 2012, Colinet et al. 2015, Sánchez-Ramos et al. 2018). This pattern is likely a consequence of the asymmetrical structure of nonlinear functions as described by Jensen's inequality (Jensen 1906, Ruel and Ayres 1999). For thermal performance curves, the rate of physiological output accelerates with increasing temperature. As a result, insects are more sensitive to small temperature changes at the high end of the thermal gradient in comparison to the low end (Colinet et al. 2015). This effect is compounded by thermal oscillation in fluctuating regimes, where the metabolic 'cost' of the heating period (i.e., time spent above the daily mean) exceeds the 'savings' of the cooling period (i.e., time spent below the daily mean) (Martin and Huey 2008, Williams et al. 2012, Colinet et al. 2015). Consequently, fluctuating regimes are more energy-demanding environments than constant regimes held at equivalent mean temperatures and tend to produce divergent responses. The beneficial or deleterious impact of this imbalance is dependent on insect sensitivity, amplitude of incremental temperature ramping, and mean temperature (Colinet et al. 2015).

At high temperatures, insects have a narrow range of thermotolerance. Because fluctuating regimes expose insects to temperatures above the mean, there is greater risk of crossing critical thermal limits at which severe or catastrophic injury is sustained (e.g., systemic cell death induced by reduced respiration) (Colinet et al. 2015). Even if subsequently returned to permissible thermal conditions, insects may not survive damage sustained from previously experienced temperature shocks (Neven 2000). Recovery from acute thermal exposure (e.g., reestablishment of ion balance, upregulation of heat shock proteins, and DNA repair) is an energetically costly process that may further limit insect performance (Yocum 1992, Colinet et al. 2015). In the present study, this trade-off may have been expressed as increased development time and reduced longevity of *T. radiata* reared under fluctuating temperatures in comparison with those reared under equivalent constant regimes at high average temperatures (≥30°C) (Table 2).

In contrast to the adverse effects insects experience under high fluctuating temperatures, thermal variation at low average temperatures can produce favorable conditions for insect performance (Colinet et al. 2015). Warming intervals that interrupt periods of prolonged cold exposure activate biochemical pathways involved in damage repair and allow essential behaviors such as feeding to occur, thereby protecting against future injury (Denlinger et al. 1992, Yocum and Denlinger 1992, Neven 2000, Colinet et al. 2015). Consequently, fluctuating regimes may allow insect development to occur at temperatures outside the limits defined by constant regimes (Colinet et al. 2015). In this study, thermal variation reduced egg-to-adult development time for *T. radiata* reared under low temperatures and expanded its minimum developmental range (i.e., 12–35°C fluctuating vs. 15–35°C constant). This observation could be critical for accurately predicting the potential distribution range for *T. radiata*. Additionally, *T. radiata* reared under low fluctuating temperatures had greatly increased longevity in comparison with parasitoids reared under constant temperature

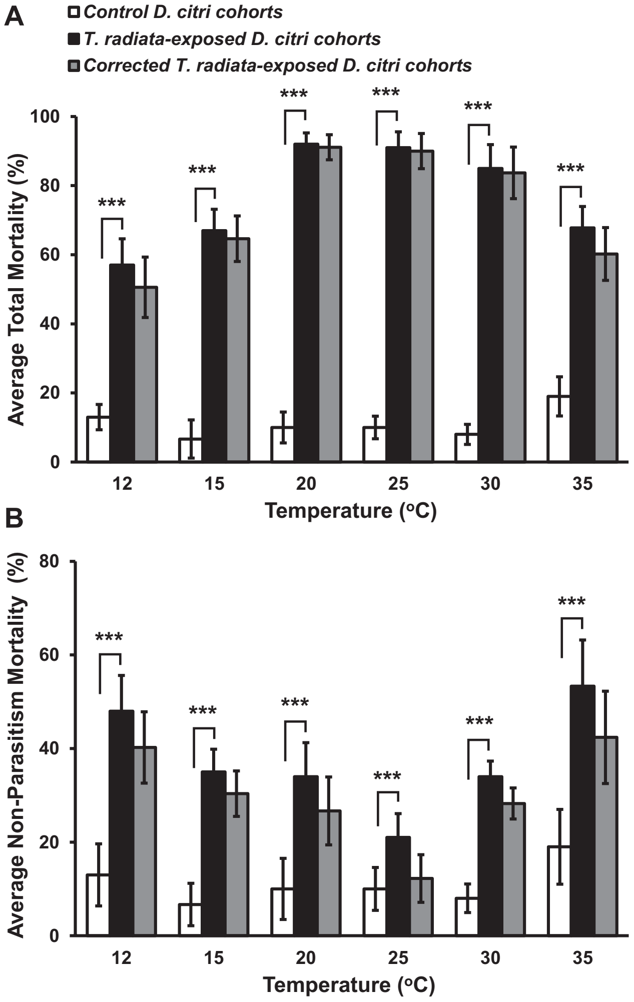

Fig. 5. Average total mortality rate (A) and average mortality rate excluding parasitism (B) of *Diaphorina citri* nymphs reared under fluctuating temperature regimes for control cohorts (white) and *Tamarixia radiata*-exposed cohorts (black). Grey bars represent total mortality in *T. radiata*-exposed cohorts corrected for baseline mortality with the Schneider-Orelli formula. Asterisks indicate a significant difference in *D. citri* mortality between control and parasitoid-exposed cohorts at α = 0.05.

counterparts (Table 2). Under the 15°C fluctuating profile, the maximum lifespan of *T. radiata* was 79 d, a value over four times greater than the 18 d recorded at 15°C constant and more than double the 32 d maximum recorded at 20°C constant. These findings have important implications for commercial production of *T. radiata*, as an extended shelf-life could facilitate releases of better-performing parasitoids or allow for greater flexibility in timing of deployments. Moreover, inclusion of a warming period during cold storage of mass-reared *T. radiata* would be an inexpensive, easily implementable management practice that would increase parasitoid longevity.

A significant number of mathematical functions have been developed to characterize insect development rates across thermal clines. While certain models consistently perform better within a specific context, there is no consensus on which are generally 'best' across a wide range of applications. Model selection is generally left to author discretion and strongly subject to field-associated biases. Studies investigating arthropod temperature-dependent development typically examine the fit of a single or few models drawn from a limited pool standard for that particular taxonomic group, often without justification (Quinn 2017). Alternative models with potentially superior predictive power or other beneficial qualities (e.g., low complexity, inclusion of parameters with biological relevance, and consistency between observed and predicted values) may be overlooked. Consequently, the vast majority of insect developmental datasets are not fit with optimal functions, limiting the reliability of critical inferences and predictions drawn from these data (Quinn 2017). These criteria were considered in initial selection of nonlinear models fit to *T. radiata* developmental datasets and in the subsequent review of their performance. Functions evaluated included those with widespread usage in the entomological field (i.e., Lactin-2, Weibull, and Brière-2) and those not commonly used but with desirable properties (i.e., Beta, LRF, Ratkowsky, and Performance-2) (Shi et al. 2015).

All nonlinear models provided a relatively good fit to both constant and fluctuating datasets, a finding which could be partially attributed to the limited number of temperatures evaluated. However, differences in model performance were still apparent. The Ratkowsky, Beta, LRF, and Brière-2 consistently produced the lowest values of *RSS* while the Weibull, Lactin-2, and Performance-2 produced the highest (Table 5). While goodness-of-fit is an important measure of performance, it has been overly relied upon as an indicator of superior model function (Damos and Savopoulou-Soultani 2012, Régnière et al. 2012, Ratkowsky and Reddy 2017). For any given dataset, there are generally several models that will provide a good mathematical fit. High conformity between experimental and model-estimated values does not guarantee reliability of predicted thermal performance curves across the entire temperature cline range (Schwarz 1978, Damos and Savopoulou-Soultani 2012, Régnière et al. 2012, Mirhosseini et al. 2017). To ensure evaluation accurately represented overall model performance, other criteria such as inclusion of biologically interpretable model parameters and theoretical threshold estimates were examined in addition to goodness-of-fit.

In evaluating model predictions of T_{min} and T_{max}, it is important to emphasize that these measures are fixed, mathematical model extrapolations which represent the absolute minimum and maximum temperatures at which development is not theoretically observable. While empirical models cannot directly provide the actual developmental limits (i.e., *MINt* and *MAXt*), these 'true' threshold values generally lie within the conceptual bounds delimited by T_{min} and T_{max} (McMeekin et al. 2013, Ratkowsky and Reddy 2017, Milosavljević et al. 2019). Although T_{min} and T_{max} are not equivalent to *MINt* and *MAXt*, they may provide approximations of these points depending on the model structure, taxa examined, and sample size of the dataset (Shi et al. 2015). To minimize model extrapolation and improve accuracy in estimation of thermal bounds, experiments should be designed to examine a wide range of temperatures, especially those near T_{min} and T_{max} (Régnière et al. 2012, Quinn 2017, Rebaudo and Rabhi 2018). Regardless, theoretical thresholds should always be viewed as hypotheses which require experimental confirmation in the laboratory and field (Shi et al. 2015, Ratkowsky and Reddy 2017, Milosavljević et al. 2019). This step is particularly important, as pest management inferences made from erroneous estimates of development rates and thresholds can have economically significant consequences (Horn 1998, Roitberg et al. 2001, Hart et al. 2002, Régnière et al. 2012). Comparison of theoretical thermal limits across multiple models can facilitate delineation of the true tolerable thermal range for a species by producing a range of overlapping threshold values that may serve as a starting point for further experimental evaluation.

Estimates of the optimum development point for *T. radiata* were relatively consistent across models and regimes, ranging from 33.3 to 33.4°C for constant temperatures and 29.4 to 31.8°C for fluctuating temperatures (Table 5). Model-predicted values of T_{min} were generally higher for the constant regime (5.3–11.5°C) than the fluctuating regime (−6.2 to 7.3°C excluding the Beta model estimate). These model predictions are supported by experimental observations, as *T. radiata* was recorded to develop under the 12°C fluctuating profile but not under the 12°C constant counterpart. Regardless of regime, Lactin-2, Weibull, and Performance-2 produced higher estimates of T_{min} than Ratkowsky, Beta, LRF, and Brière-2. The sub-zero T_{min} values produced by the latter four models for the fluctuating dataset may not directly facilitate estimation of a range for *MINt*, as insect development is seldom reported to occur below 6°C (Damos and Savopoulou-Soultani 2012, Quinn 2017). This is particularly the case for the Beta model, which, despite providing the best mathematical fit to the fluctuating dataset, produced a T_{min} well outside the range of biological relevance (absolute zero; −273°C). As with T_{min}, predicted values of T_{max} were higher for the constant regime (42.1–52.5°C) than the fluctuating regime (35.2–40.5°C). Although the Weibull and Ratkowsky models consistently produced the highest estimates of T_{max}, for the constant regime dataset, all models predicted values of T_{max} that were well above the experimentally measured maximum developmental bound of 38°C. This example further illustrates the importance of treating theoretical thresholds as hypotheses which require empirical validation, particularly if estimations are based upon a limited number of temperature observations.

Percent deviation between measured and predicted development rates was relatively small for all models examined. The Ratkowsky and Performance-2 models produced values of zero for the constant dataset, and the Performance-2 and Weibull models produced values nearest zero for the fluctuating dataset. In addition to having biologically meaningful parameters, the Ratkowsky, Beta, and LRF models provided excellent fits to both the constant and fluctuating datasets and produced biologically realistic estimates for T_{opt}. The Beta model, however, was found to be unreliable with its T_{min} prediction of absolute zero and accompanying percent deviation of −0.11%, the largest recorded among models. The Brière-2 model was middling both in fit and estimation of theoretical developmental thresholds. The Performance-2 and Lactin-2 models provided poorer fits than the aforementioned models but gave higher estimates of T_{min} that could be potentially valuable in approximating *MINt* (Shi et al. 2015). Additionally, the Performance-2 model includes parameters of direct biological relevance. The Weibull function was the worst performing of the group, consistently providing the poorest fit to datasets and lacking any parameters with biological meaning.

Of the seven functions evaluated, the Ratkowsky and LRF models were found to be consistently best for predictions associated with interpolation (i.e., estimation of T_{opt} or other development rates within the measured temperature range) as they produced small percent deviations and the best overall fit to the datasets. While the Performance-2 model (a simple modification of the Ratkowsky model [see Table 3 for comparison]) provided a somewhat poorer fit to datasets, it produced the lowest percent deviation for both constant and fluctuating regimes and predicted theoretical thresholds within a potentially biologically realistic range. However, estimates derived from such extrapolative methods have limited reliability. Future studies which examine the temperature-dependent development of insects should consider inclusion of the Ratkowsky, LRF, and Performance-2 functions for modeling thermal performance curves.

The meta-analysis presented in Table 4 represents a literature review pertaining to development of geographically disparate populations of *T. radiata* reared under constant temperatures. In general, estimates of development time were similar across different source populations of *T. radiata*. *Tamarixia radiata* was reported to always complete development between 15 and 35°C when these temperatures were evaluated. A notable exception is the Taiwan-sourced *T. radiata* which failed to complete development at 35°C (Chien et al. 1993). In comparison to other published studies, the experimental work reported here covered a wider range of temperatures that better defined developmental bounds at thermal cline peripheries (12 and 38°C). Inclusion of additional lower and upper temperatures in future studies investigating *T. radiata* development could better facilitate comparison of thermal limits among populations from different geographic regions. Such studies would further our understanding of the importance of climate matching in the development of foreign exploration programs for biocontrol agents.

Although average development time varied among source populations of *T. radiata*, values reported for California and Réunion were nearly identical. Linear regression provided similar estimates of degree-days (137–179) and T_{min} (7.6–11.8°C) for *T. radiata* from all regions except China (333 degree-days and T_{min} of 0.8°C). Interestingly, *T. radiata* with similar parameter estimates (i.e., California, Réunion, and Taiwan) were originally introduced from Punjab, Pakistan. While the source of introduction for the Brazilian *T. radiata* is unknown (Torres et al. 2006), degree-day and theoretical minimum threshold estimates are strongly divergent from China-sourced parasitoids and similar to that of Pakistan-sourced parasitoids. Molecular studies could help resolve the initial area of origin for *T. radiata* found in Brazil by investigating its genetic relatedness to Pakistan-sourced populations.

A comparison of *T. radiata* populations sharing a Punjab, Pakistan origin could provide valuable insight into the impacts of genetic diversity on *T. radiata* performance. The population of *T. radiata* established in southern California is genetically diverse, as it was seeded by thousands of Pakistan-collected individuals accumulated over multiple collecting trips and maintained in 17 isocage lines to limit the effects of genetic drift in mass-production (Hopper et al. 1993, Roush and Hopper 1995, Hoddle and Hoddle 2013, Hoddle et al. 2014). By comparison, *T. radiata* populations currently present in Taiwan underwent two extreme genetic bottlenecks, first from the eight individuals released to establish the population on Réunion Island (Etienne and Aubert 1980) and again from the 62 individuals shipped from Réunion Island to propagate colonies released in Taiwan (Chiu et al. 1988, Chien and Chu 1996). Examination of developmental biology for all three *T. radiata* populations was conducted around the time of collection and introduction. These populations could be re-evaluated to compare performance among genetically poor (Réunion and Taiwan) and rich (California) populations and check for evidence of local and regional adaptation. An investigation of the effects of varying temperatures on the developmental biology of *T. radiata* established in major citrus producing regions within the continental United States (e.g., Texas and Florida) and Mexico could provide further insight into evolution of regional thermal tolerance variation among established parasitoid populations.

In addition to development rates and longevity, this study examined the biocontrol performance of *T. radiata* under fluctuating temperature regimes. Across all experimental temperatures, estimates of *D. citri* total mortality and mortality unrelated to visually identifiable parasitism in *T. radiata*-exposed *D. citri* cohorts (e.g., host feeding, failed oviposition attempts, etc.) were significantly higher than mortality rates for control *D. citri* cohorts (Fig. 5). In relation to temperature, parasitism of *D. citri* by *T. radiata* (Fig. 3) followed a dome-shaped pattern and non-parasitism related *D. citri* mortality followed a 'U'-shaped pattern. Despite low parasitism rates at 12 and 35°C (<15%), total *D. citri* mortality was relatively high (57 and 68%, respectively) as a consequence of increased non-parasitism mortality (48 and 53%, respectively). Non-parasitism mortality was lower (21–34%) at temperatures optimal for parasitism (20, 25, and 30°C; 51–70%), but combined factor contributions increased total mortality to generally high levels (85–92%). Thus, the effects of non-parasitism mortality were important across all temperatures, contributing the highest proportion of total mortality near temperature cline ends (84 and 79% at 12 and 35°C, respectively) and the lowest at intermediate temperatures (23% at 25°C). These results suggest *T. radiata* inflicts substantial *D. citri* mortality through mechanisms other than successful parasitism (e.g., host feeding), the effects of which are pronounced near lower and upper temperature bounds.

In many regions where *T. radiata* has been introduced for *D. citri* biological control, considerable suppression of *D. citri* populations has been reported following parasitoid releases (Étienne and Aubert 1980, Chien and Chu 1996, Étienne et al. 2001, Pluke et al. 2008, Kistner et al. 2016, Flores and Ciomperlik 2017). However, the efficacy of this parasitoid has been questioned because *T. radiata* parasitism is spatiotemporally variable in the field (Hall et al. 2013, Grafton-Cardwell et al. 2013, Kistner et al. 2016, Milosavljević et al. 2018, Milosavljević and Hoddle 2019). This inconsistency, along with the results presented here, suggests that other sources of mortality inflicted by *T. radiata* (i.e., host feeding) may contribute significantly to total *D. citri* mortality. Thus, the parasitism estimates currently relied upon for verification of *T. radiata* effectiveness may underestimate its impact in the field, with prevailing temperature as an important but overlooked co-factor affecting parasitoid inflicted mortality on *D. citri* nymphs.

In summary, this study complements a growing body of literature demonstrating the important role of temperature variation in predicting insect life history responses that are transposable to field conditions (Colinet et al. 2015, Rebaudo and Rabhi 2018). The fluctuating regimes under which *T. radiata* performance was measured accurately represent the thermal conditions experienced by this parasitoid in inland southern California, improving our general understanding of this parasitoid's developmental biology. Incorporation of these results into biological control programs for *D. citri* may streamline mass-rearing, enhance release efforts, improve accuracy of predictions pertaining to parasitoid-host establishment and spread produced by climate forecasting models, and enable performance comparisons between Pakistan-sourced *T. radiata* and other geographically distinct populations.

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