Journal of Economic Entomology, 112(3), 2019, 1062–1072
doi: 10.1093/jee/toy429
Advance Access Publication Date: 3 May 2019
Research

Biological and Microbial Control

Effects of Constant and Fluctuating Temperatures on Development Rates and Longevity of *Diaphorencyrtus aligarhensis* (Hymenoptera: Encyrtidae)

Ivan Milosavljević,[1,4] Kelsey A. McCalla,[1] David A. Ratkowsky,[2] and Mark S. Hoddle[1,3]

[1]Department of Entomology, University of California, 900 University Avenue, Riverside, CA 92521, [2]Tasmanian Institute of Agriculture, Private Bag 98, Hobart, Tasmania 7001, Australia, [3]Center for Invasive Species Research, University of California, Riverside, CA 92521, [4]Corresponding author, e-mail: ivanm@ucr.edu

Received 16 October 2018; Editorial decision 19 December 2018

Subject Editor: Julio Bernal

Abstract

The effects of fluctuating and constant temperatures on the development and longevity of *Diaphorencyrtus aligarhensis* (Shafee, Alam, and Argarwal) (Hymenoptera: Encyrtidae), a parasitoid sourced from Pakistan and released in California for the classical biological control of *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), were examined. The influence of six fluctuating temperatures that averaged 15, 20, 25, 30, 32, and 35°C, over 24 h on the development times and longevity of male and female *D. aligarhensis* were quantified and compared to six constant temperatures set at the same average temperatures. The development rates of immature stages of *D. aligarhensis* as a function of temperature were modeled using one linear and four nonlinear models. Fluctuating temperatures had significant effects on parasitoid development times and longevity which differed across experimental temperatures. Degree-days required for completion of cumulative development of *D. aligarhensis* were significantly different being 21% lower under fluctuating temperature regimens when compared with constant temperatures. The lower temperature threshold estimates above which development occurred were estimated to be lower under constant than fluctuating temperatures. The estimated values of upper and optimum temperature limits were similar for individuals reared under constant and fluctuating temperatures. *Diaphorencyrtus aligarhensis* lived longer at constant intermediate temperatures and for shorter times at constant lower temperature extremes when compared with their fluctuating temperature counterparts. Daily thermal fluctuations significantly influenced life history parameters of *D. aligarhensis* and should be considered when assessing likelihoods of establishment and impacts of this parasitoid on *D. citri* across diverse citrus-growing climates.

Key words: biological control, degree-days, development rates, *Diaphorina citri*, nonlinear regression models

Temperature has significant effects on development rates and behavior of insects (Gilbert and Raworth 1996, Koda and Nakamura 2010, Marchioro and Foerster 2011), population performance and distribution (Milosavljević et al. 2016, 2017a; 2018a,b; Damos and Kouloussis 2018), community structure (Nooten et al. 2014), and ecosystem functioning (Schowalter 2016). From a biological control perspective, ambient temperature mediates population dynamics and reproduction rates of pest arthropods and associated natural enemies (Broatch et al. 2006, Logan et al. 2006). Characterizing responses such as survivorship and development rates across temperature clines can provide insight on potential performance of natural enemies under consideration for release into new areas for pest population suppression (Obrycki and Kring 1998).

Linear, simple curvilinear, and complex nonlinear functional equations have been used to model development rates and estimate thermal thresholds (e.g., minimum and maximum threshold temperatures for growth) for insect development (Shi et al. 2017, Quinn 2017). For biological control programs, temperature-dependent development and survivorship rate data are used to predict geographic ranges for natural enemies and optimize mass rearing, storage, and release strategies (Roy et al. 2002; Kontodimas et al. 2004, 2007; Pilkington and Hoddle 2006a, 2007a; Pilkington et al. 2014). For example, linear models have been used to calculate thermal constants (i.e., degree days needed to complete development) and lower temperature thresholds above which development occurs (Zamani et al. 2007, Eliopoulos et al. 2010). Nonlinear models are superior to linear models for modeling insect development as they incorporate readily interpretable parameters of biological relevance, can be fit to development data derived over broad temperature ranges, and can provide estimates of optimum and upper temperature developmental thresholds (Shi and Ge 2010, Ratkowsky and Reddy 2017). Generally, temperature-driven development rate models for pest and associated natural enemy species have been constructed from studies performed at constant temperatures (Pilkington and Hoddle 2006b, 2007b). In the field, however, ambient temperatures fluctuate over time. Exposure to thermal variation during development can significantly affect development times and subsequent adult fitness (Lyons et al. 2013, Warren and Anderson 2013, Wu et al. 2015). Failing to consider the effect of these temperature fluctuations on insect development and longevity could result in inaccurate predictions generated by models using (less realistic) constant temperature data (Colinet et al. 2015). Consequently, the parameter estimates (e.g., rates of development, upper and lower thresholds) and the goodness of fit of the models (i.e., how accurately they predict development times over a range of temperatures) could differ appreciably between models fit to constant versus fluctuating temperature datasets.

Citrus production in California is worth over $3 billion annually and 80% of California's citrus is packed for the fresh market (USDA NASS 2017, Babcock 2018). Citrus in California is threatened by an invasive pest, the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae) (Milosavljević et al. 2017b, 2018a, Milosavljević and Hoddle 2019). *Diaphorina citri* vectors a phloem-dwelling bacterium, *Candidatus* Liberibacter asiaticus (CLas), the putative agent of a lethal and incurable citrus disease, huanglongbing (Gottwald 2010, Grafton-Cardwell et al 2013), that eventually renders citrus production unprofitable (Durborow 2012, Spreen 2014). Southern California's dense urban environment is largely characterized by unmanaged backyard citrus. These urban trees are reservoirs of *D. citri*-CLas from which dispersal into neighboring commercial citrus groves may occur (Bayles et al. 2017). Because residential zones are rarely under chemical management, biological control is the primary means of suppressing *D. citri* populations and, consequently, delaying CLas dissemination from these areas into commercial citrus (Hoddle and Pandey 2014).

The *D. citri* biocontrol program in California has, in part, focussed on the mass production, release, and establishment of a bi-parental endoparasitoid, *Diaphorencyrtus aligarhensis* (Shafee, Alam, and Argarwal) (Hymenoptera: Encyrtidae), sourced from Punjab, Pakistan (Bistline-East et al. 2015). *Diaphorina aligarhensis* parasitizes second through fourth instar nymphs and provides additional mortality through host feeding (Rohrig 2010, Rohrig et al., 2011, Hoddle et al. 2014, Bistline-East et al. 2015, Vankosky and Hoddle 2017a,b). Understanding the effects various temperature regimens have on the developmental biology of *D. aligarhensis* could improve the efficacy of inoculative and augmentative releases of mass-reared parasitoids and predict performance in different geographical areas, as urban and commercial citrus are grown across diverse climatic zones (e.g., hot desert interior regions [Coachella Valley] and cooler coastal areas [Ventura]) in California.

The rationale for attempting to establish *D. aligarhensis* in California was to complement parasitism by *Tamarixia radiata* (Waterston) (Hymenoptera: Eulophidae) (sourced from Punjab Pakistan and established in California for *D. citri* biological in 2012; Hoddle et al. 2016), as the two natural enemies successfully coexist in citrus orchards in the native range of *D. citri* (i.e., Punjab, Pakistan), and both contribute to *D. citri* control (Khan et al. 2014). It has been speculated that temperature tolerances for *D. aligarhensis* and *T. radiata* may be different, and if so, heterogeneous climates across major citrus production areas may favor establishment of *D. aligarhensis* in parts of southern California that could be unfavorable for *T. radiata* (or vice versa) (Milosavljević et al. 2017b). If this is the case, both parasitoids may have potential to simultaneously contribute to *D. citri* control in California through geographical partitioning.

The effects of varying temperatures and thermal dynamics on the development and longevity of *D. aligarhensis* are unknown. To investigate the effects of temperature on *D. aligarhensis*, we compared development rates and longevity of male and female parasitoids reared under six average daily temperatures (15, 20, 25, 30, 32, and 35°C) that were either constant or fluctuated over 24 h. The developmental thresholds for *D. aligarhensis* were estimated using one linear and four nonlinear (Brière-2, Lactin-2, Ratkowsky, and Lobry-Rosso-Flandrois [LRF]) temperature-driven models. Models were evaluated based on their goodness-of-fit to constant and fluctuating temperature datasets and biological values of the fitted coefficients. The method of least squares polynomial fitting was used to characterize the relationship between temperature and longevity of adult parasitoids. Our goal was to examine whether models fit to constant (more often examined in the literature) versus fluctuating (more realistic) temperature data produce appreciably different results with regards to natural enemy development rate and thermal tolerance, which could have important implications for predicting agent establishment and efficacy in different regions of proposed areas of introduction.

Materials and Methods

Material Sources

Diaphorencyrtus citri nymphs exposed to *D. aligarhensis* for parasitization were sourced from CLas-free colonies maintained at the University of California Riverside Insectary and Quarantine Facility (UCR-IQF) (Hoddle and Pandey 2014, Bistline-East and Hoddle 2015, Bistline-East et al. 2015). *Diaphorencyrtuscitri* were reared on ~1.5-yr-old *Citrus volkameriana* V. Tenore & Pasquale (Sapindales: Rutaceae) in 0.5-liter pots with UCR Type III potting soil mix. Plants were maintained under natural sunlight in greenhouses (27 ± 2°C, 50 ± 6% relative humidity [RH]) at UCR Agricultural Operations (Ag. Ops.), with daily watering and Osmocote Pro 19:6:12 granular fertilizer (The Scotts Company LLC, Marysville, OH) applied every 3 mo. (see Bistline-East et al. 2015 for details on plant preparation and maintenance). Plants were pruned regularly to promote flush, a growth stage of young leaves, required for oviposition by female *D. citri* and the subsequent development of *D. citri* nymphs (Milosavljević et al. 2018a).

Flushing *C. volkameriana* plants were transferred from greenhouses at Ag. Ops. to UCR-IQF for *D. citri* inoculation and held in a climate-controlled rearing room in UCR-IQF at 27°C, 40% RH, and a photoperiod of 14:10 (L:D) h. Individual flushing citrus plants were isolated in 150 × 150 × 300-mm cages that consisted of two 'U'-shaped clear acrylic risers (S&W Plastics F2191, Riverside, CA) with the open back covered with no-see-um ultrafine netting (Skeeta Inc., Bradenton, FL). The front was covered with a 30-cm long no-see-um fabric sleeve to allow access into cages (Bistline-East et al. 2015). Each caged citrus plant was inoculated with 20 adult *D. citri* psyllids and females were allowed approximately 8–10 d to lay eggs until they were removed from plants using an aspirator. *Diaphorencyrtus citri* nymphs were left to develop to second through fourth instars, which required approximately 7–10 d.

Diaphorencyrtus aligarhensis adults were obtained from colonies maintained in UCR-IQF, which were established from bi-parental individuals reared from parasitized *D. citri* nymphs collected in Punjab, Pakistan (Bistline-East et al. 2015). *Diaphorencyrtus aligarhensis* colonies were maintained on second through fourth-instar *D. citri* nymphs following the procedures described above. Newly emerged parasitoids were collected daily, labeled, and held in individual 200-µl O-ring centrifuge tubes (Micrewtube brand, Simport Scientific Inc., Vancouver, Canada) provisioned with honey droplets and maintained at 16°C and 14:10 (L:D) h until used for experiments. Single female *D. aligarhensis* were confined with two males for 24 h within each vial to ensure they were mated before being introduced to caged *D. citri* nymphs in stages suitable for parasitization.

Experimental Treatments and Observations

After 8–10 d, individual citrus plants infested with second- through fourth-instar *D. citri* nymphs were transferred to acrylic riser cages at UCR-IQF (27°C, 40% RH, 14:10 [L:D] h). Ten male and five female *D. aligarhensis* were released into each riser cage and females were allowed to oviposit for 6 h before removal. Immediately after removing parasitoids, riser cages with plants and parasitized *D. citri* nymphs were placed into Percival environmental chambers (model I-30BLL; Percival Scientific, Perry, IN) set to 1 of 12 designated temperature regimens (see 'Temperature regimens' for temperature calculations and growth chamber settings; Table 1). Four riser cages were assigned to each of 12 temperature regimens to provide sufficient development data for a minimum combined total of 20 emerged adult male and female *D. aligarhensis*. For all temperature treatments, a complete set of replicates was run simultaneously. To minimize the influence of potential thermal gradients within incubators, the four riser cages were rotated daily (Packard and Packard 1993, Ashmore and Janzen 2003).

Within each temperature regimen, riser cages were inspected for adult *D. aligarhensis* that emerged from the initial *D. citri* cohort, beginning 7 d after experimental treatments were initiated. Emerged parasitoids were collected daily into individual 200-µl O-ring centrifuge tubes (Micrewtube brand, Simport Scientific Inc.), sexed, labeled, and maintained in their respective incubators. Collections continued until parasitoid emergence ceased for 14 consecutive days. A carbohydrate-rich food, supplied as honey droplets, was provided on alternating days to each individual adult parasitoid for the duration of the experiment. Emerged male and female parasitoids were monitored daily until death to determine adult longevity under each temperature regimen.

Temperature Regimens

Experiments were conducted at an average of 15, 20, 25, 30, 32, and 35°C for both constant and fluctuating temperature regimens (Table 1). For constant temperature regimens, growth chambers held the target temperature constant (±0.25°C) for the entirety of the study. For fluctuating temperature regimens, growth chambers were programed with nine temperature steps to incrementally increase and decrease temperatures around target mean temperatures. Averaged fluctuating temperatures were equivalent to the corresponding constant temperatures (±0.25°C) over a 24-h period. Each fluctuating temperature profile was modeled after field recorded temperatures that had the desired average target temperature (Table 1; CIMIS 2018).

To achieve the target average temperature, incremental temperature increase and decrease steps for fluctuating temperature regimens were modeled upon 3 yr (January 2013 – December 2015) of daily temperature data from a weather station located at the Riverside Citrus Experiment Station, Riverside, CA (CIMIS 2018). Each year, respective time periods and dates that provided corresponding daily temperature averages within 0.25°C of each of the target constant temperatures were determined. Hourly air temperatures (compiled

Table 1. Stepwise settings used in temperature cabinets for fluctuating temperature regimens

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

from CIMIS 2018) for each selected day were averaged per hour for every target mean temperature. These data were used to program temperature changes within incubators (i.e., temperature fluctuations) over a 24-h period that when averaged were equivalent to the target mean temperature (Table 1). All growth chambers were maintained at 14:10 (L:D) h period at a light intensity of 100 µE/m^2/s, and 50% RH (an observed average RH for selected time periods in Riverside, CA; CIMIS 2018) regardless of the experimental temperature regimen. Target temperature conditions were confirmed using HOBO Pro V2 Temperature/RH loggers (Onset Computer, Pocasset, MA) placed within temperature cabinets, which automatically measured temperature and humidity at 15 min intervals for the duration of experiments (see Data Collection for more details). No differences in relative humidity among temperature treatments were characterized.

Statistical Analyses

To assess the effects of temperature profile and temperature regimen on development rate and longevity of *D. aligarhensis* males and females, each temperature profile (i.e., 15, 20, 25, 30, 32, or 35°C) was considered separately. A one-way analysis of variance was conducted for each temperature profile using the four treatment combinations (i.e., males constant, males fluctuating, females constant, and females fluctuating). Prior to analysis of variance, all datasets were log-transformed to stabilize the variance and meet the normality assumptions of regression analysis. Analyses were conducted using the PROC GLM procedure in SAS (version 9.4; SAS Institute Inc., Cary, NC). If the analysis of variance was significant at the 0.01 level, individual pairwise comparisons were made, for regimen within gender (i.e., comparing constant vs. fluctuating for males and females separately) as well as gender within regimens (i.e., comparing males vs. females for constant and fluctuating regimes separately), a total of four comparisons were made, between treatment means using the LSMEANS and DIFF statements of the GLM procedure. For all experimental temperatures, there were no significant differences between the developmental rates and longevity of male and female *D. aligarhensis*, and the values were pooled for subsequent model fitting (see Results, Table 2).

Mathematical Models

To evaluate the relationship between temperature and development rate ($r = 1/d$, where d is mean development time in days) of *D. aligarhensis* (pooled male and female data) under constant and fluctuating temperature regimens, the performance of four nonlinear (i.e., Lactin-2, Brière-2, LRF, and Ratkowsky) development rate models were compared (Tables 3 and 4). In addition, a linear regression model was used to calculate thermal constants (i.e., degree days needed to complete development in a specific life stage [K]; $K = 1/b$, where b is the slope of the regression line) and lower development thresholds ([$T_{\min}$]; $T_{\min} = -a/b$, where a is the development rate at $T = 0$°C), respectively (Table 5; Campbell et al. 1974). The linear relationship between development rate of *D. aligarhensis* and temperature was assessed using the PROC REG procedure in SAS (version 9.4; SAS Institute Inc., Cary, NC). Outliers exhibiting large residuals and leverage were identified and, if necessary, removed using the Cook's D metric (observations were considered outliers if they had a Cook's D-value $>4/n$, where n represents the number of observations; [Bollen and Jackman 1990]). For the linear model, temperatures higher than 32°C were excluded from analyses because they did not align with the linear portion of the dataset which would affect estimation of the lower development threshold (Ikemoto and Takai 2000, Ganjisaffar and Perring 2015). Therefore, the linear model with five data points could not be statistically compared to the four nonlinear models, which were fitted to six temperatures (Table 5).

Development rate data of *D. aligarhensis* were used to parameterize nonlinear models. Accuracy of nonlinear models was evaluated based on the goodness-of-fit to observed development rates for constant and fluctuating temperatures, the values of fitted coefficients, and lower and upper threshold estimations. All nonlinear models tested have four parameters (and thus, the same degrees of freedom [df], which eliminates bias stemming from model selection criteria), and two comparable 'notional' development thresholds (i.e., lower and upper thresholds), at which development rates equal zero (Mirhosseini et al. 2017, Ratkowsky and Reddy 2017). These 'conceptual' development thresholds are not necessarily the observed minimum or maximum temperatures for growth, as these are points on the graphs at which the model-derived curves intersect the temperature axis (Shi et al. 2017). Of the four nonlinear models, the Lactin-2 model lacks 'conceptual' lower and upper development thresholds that are interpretable in this manner. However, this model still produces a curve that has two intersections with the temperature axis. These are equivalent to 'conceptual' temperatures (i.e., $T_{\min}$ and $T_{\max}$) and can be estimated by the model's fit to development rate data.

Residual sum of squares (RSS) values alone, rather than in combination with the coefficient of determination (R^2) and its adjusted value (R^2_{adj}) (these two measures do not describe accurately the validity of a nonlinear fit; see Spiess and Neumeyer 2010, for further explanation), were used to assess goodness of fit for nonlinear models:

$$RSS = \sum_{i=1}^{n} \left(r_i - \widehat{r}_i\right)^2 \tag{1}$$

where n is the number of observations, and r_i and $\widehat{r}_i$ represents the ith observation of development rate and predicted development rate,

Table 2. Mean development time in days (± SE) for female and male *D. aligarhensis* reared under constant and fluctuating temperatures

	Development time (mean days ± SE)					
	15°C	20°C	25°C	30°C	32°C	35°C
Female						
Constant	56.07 ± 0.85^{b} (14)	31.83 ± 1.17^{b} (18)	18.91 ± 0.53^{ab} (11)	15.56 ± 0.50^{a} (9)	14.80 ± 0.38^{a} (56)	22.29 ± 0.51^{a}(14)
Fluctuating	64.19 ± 0.79^{a} (16)	31.86 ± 1.33^{b} (14)	18.93 ± 0.47^{ab} (14)	13.06 ± 0.37^{b} (16)	13.54 ± 0.58^{a} (24)	18.91 ± 0.57^{b}(11)
Male						
Constant	55.75 ± 0.79^{b} (16)	32.09 ± 0.86^{b} (33)	20.00 ± 0.37^{a} (22)	15.88 ± 0.37^{a} (16)	14.87 ± 0.35^{a} (68)	21.97 ± 0.35^{a} (30)
Fluctuating	64.57 ± 0.66^{a} (23)	40.82 ± 1.20^{a} (17)	17.92 ± 0.51^{b} (12)	12.53 ± 0.36^{b} (17)	14.96 ± 0.54^{a} (28)	20.00 ± 0.63^{b} (9)

Means followed by the same letter within the same temperature are not significantly different at α = 0.05; n denotes number of individuals. SEs are based upon the pooled variance and the individual sample sizes.

Table 3. Estimated parameters of the four nonlinear models with values of their evaluation criteria for describing the relationship between development rate and temperature for *D. aligarhensis* (male and female data combined) under constant and fluctuating temperature regimens

Model	Model equation	Parameter	Parameter estimate		Reference
			Constant	Fluctuating	
Lactin-2 (Logan-Lactin)	$D_r = \lambda + e^{\rho T} - e^{(\rho T_u - (T_u - T)/\delta T)}$	λ	–1.029	–1.0494	Logan et al. (1976)
		ρ	0.003	0.004	Lactin et al. (1995)
		δ	1.321	1.892	
		T_u	39.516	41.025	
		RSS	0.000009	0.000065	
Brière-2	$D_r = aT\,(T - T_{min})\,(T_{max} - T)^{1/b}$	a	0.000062	0.000081	Brière et al. (1999)
		b	5.343	3.814	
		T_{min}	4.298	10.188	
		T_{max}	35.128	35.317	
		RSS	0.000016	0.000052	
LRF	$D_r = \mu_{opt}\frac{(T-T_{max})(T-T_{min})^2}{(T_{opt}-T_{min})\left[\left(T_{opt}-T_{min}\right)\left(T-T_{opt}\right)-(T_{opt}-T_{max})(T_{opt}+T_{min}-2T)\right]}$	μ_{opt}	0.068	0.0773	Rosso et al. (1993)
		T_{min}	1.099	6.681	
		T_{max}	36.060	36.591	
		T_{opt}	31.847	31.380	
		RSS	0.000008	0.000035	
Ratkowsky	$\sqrt{D_r} = b\,(T - T_{min})\,(1 - e^{c(T-T_{max})})$; $D_r = \left[b\,(T - T_{min})\left(1 - e^{c(T-T_{max})}\right)\right]^2$	b	0.009	0.0124	Ratkowsky et al. (1983)
		c	0.426	0.3021	
		T_{min}	–0.236	5.645	
		T_{max}	37.725	38.263	
		RSS	0.000012	0.000024	

In all models, T is temperature in degrees Celsius, D_r is the development rate at temperature T; In the Brière-2, LRF, and Ratkowsky models, T_{min} and T_{max} represent 'notional' lower and upper development thresholds, respectively, at which development rates equal zero. In the Lactin-2 (i.e., Logan-Lactin) model, e denotes the base of natural logarithms; λ, ρ, δ, and T_u are constants. T_u represents the 'upper lethal temperature'. This model produces a curve that has two intersections with the temperature axis and are the functional equivalent of the lower and upper 'conceptual' temperatures for development, which can be evaluated numerically. In the Brière-2, a and b are model parameters; In the LRF model, μ_{opt} and T_{opt} are model parameters; T_{opt} is a value of T at which insect growth is optimal and μ_{opt} is the growth rate at optimum conditions. In the Ratkowsky model, b and c are regression constants; b determines the slope of the regression (per °C/h$^{0.5}$), and c enables the model to fit the data for temperatures above optimal temperature (per °C). All four models were fitted with development rate as the response variable; for the Ratkowsky (square-root) model, it is necessary to square both sides of the expression, so that the left-hand side of the equation is the development rate rather than square root of the rate.

Table 4. Lower (*Tmin*), optimal (*Topt*), and upper (*Tmax*) temperatures estimated by four nonlinear models for the development of *D. aligarhensis* reared under constant and fluctuating temperatures

Regime	Minimum development threshold (T_{min})				Optimal development threshold (T_{opt})				Maximum development threshold (T_{max})			
	Lactin-2	Brière-2	LRF	Ratkowsky	Lactin-2	Brière-2	LRF	Ratkowsky	Lactin-2	Brière-2	LRF	Ratkowsky
Constant	9.50	4.30	1.10	-0.24	32.19	32.32	31.85	31.45	36.12	35.13	36.06	37.72
Fluctuating	12.07	10.19	6.68	5.65	31.72	31.93	31.38	31.11	36.50	35.32	36.59	38.26

respectively. The model with the lowest values of *RSS* has the superior fit to the data. For all datasets, the variability of the response variable (i.e., development rate) was homogeneous throughout the entire temperature range. The four nonlinear models were thus fitted with development rate as the response variable, in its untransformed form (Table 3). No further transformation was therefore necessary for the Lactin-2, Brière-2, and LRF models and the least squares procedure was applied to each model as it stands (see Ratkowsky 2004 for more details). For the square-root (Ratkowsky) model, it was necessary to square both sides of the expression, so that the left-hand side of the equation is the development rate rather than the square root of the rate (Table 3; Shi and Ge 2010). All temperature-based development models were fit for each response variable using the PROC NLIN procedure in SAS (version 9.4; SAS Institute Inc., Cary, NC; Fig. 1).

In addition to development rate models, the least squares fitting technique was used to model the relationships between temperature and longevity (days) of *D. aligarhensis* (pooled for males and females) under constant and fluctuating temperature regimens (PROC GLM in SAS, version 9.4; SAS Institute, Cary, NC). The insignificance of the quadratic term (*F*-tests on the quadratic terms; Colinet et al. 2005) in the model was used as an indicator of the nearly linear fit to the dataset (Colinet et al. 2007). All models were fit with normal distributions based on the variance of the response variables.

Results

Effects of Temperature and Regimen on Parasitoid Development

Male and female *D. aligarhensis* completed development across all experimental temperature regimens (Table 2). Constant and fluctuating temperatures significantly affected mean development time of *D. aligarhensis* females and males (regimen effect: $P < 0.001$ for all temperature profiles). However, female and male parasitoids

Table 5. Estimated parameters of the linear model with values of its evaluation criteria for describing the relationship between development rate and temperature for *D. aligarhensis* (male and female data combined) under constant and fluctuating temperature regimens

Model	Model equation	Parameter	Parameter estimate		Reference
			Constant	Fluctuating	
Ordinary linear	$D_r = a + bT$	a	−0.0284	−0.0444	Campbell et al. (1974)
		b	0.0031	0.0039	
		Adjusted R^2	0.991	0.954	
		RSS	0.000012	0.000108	
		K (degree-days)	322.58	256.41	
		T_{min}	9.16	11.38	

In the linear model, T is temperature in degrees Celsius, D_r is the development rate at temperature T; a is the development rate at T = 0°C and b is the slope of the regression line.

responded equivalently to the temperature treatments (gender effect: $P > 0.25$ for all temperature profiles; Table 2). *Diaphorencyrtus aligarhensis* females completed development faster at constant 15°C and slower at constant 30 and 35°C when compared with their fluctuating temperature counterparts (Table 2). Development time for *D. aligarhensis* females was not significantly different between constant and fluctuating regimes at 20, 25, and 32°C (Table 2). Similarly, the development time for *D. aligarhensis* males was shorter at constant 15 and 20°C when compared with their fluctuating temperature counterparts (Table 2). The development times for male parasitoids were longer at constant 25 and 30°C, and shorter at 35°C when compared with the corresponding fluctuating temperatures. Male development times did not vary between constant and fluctuating temperature regimens at 32°C (Table 2).

Parameter estimates for the linear and four nonlinear models fitted to development rate data for *D. aligarhensis* and goodness-of-fit values (i.e., *RSS*) for model coefficients are presented in Tables 3–5. All four nonlinear models had small values of *RSS* (<0.0001) for both constant and fluctuating temperature regimens (Table 3). Compared with the LRF and Ratkowsky nonlinear equations, the Lactin-2 and Brière-2 models yielded a higher *RSS* values for fluctuating regimens (Table 3), indicating a slightly poorer fit. The linear model had *RSS* values < 0.0001 for both males and females across all temperatures (Table 5).

Linear regression estimates indicated the total development time from oviposition to adult emergence (i.e., thermal constants or degree-days) of *D. aligarhensis* was significantly lower (i.e., 21% lower) under fluctuating temperature regimens than corresponding constant regimens (Table 5, Fig. 1). All four nonlinear models estimated similar thermal values for the optimum development temperature (T_{opt}) for *D. aligarhensis*, irrespective of gender or temperature regimen (Table 4, Fig. 1). The lower and upper development thresholds, however, were not estimated equally by all models. The critical lower temperatures (T_{min}) above which development of female and male parasitoids occurs as estimated by the linear and Lactin-2 equations were consistently higher than those estimated by the three other nonlinear models across constant and fluctuating temperature regimens (Tables 3 and 4). The Ratkowsky model consistently provided higher estimates of T_{max} for *D. aligarhensis* parasitoids compared with Lactin-2, Brière-2, and LRF nonlinear equations, regardless of temperature regimen (Table 4, Fig. 1).

Effects of Temperature and Regimen on Parasitoid Longevity

Constant and fluctuating temperatures significantly affected mean adult longevity of *D. aligarhensis* females and males (regimen effect: $P < 0.001$ for all temperature profiles). *Diaphorencyrtus aligarhensis* males and females responded equivalently to temperature treatments (gender effect: $P > 0.18$ for all temperature profiles). Parasitoids lived longer at 15°C constant and for shorter times at constant 20, 25, and 30°C than the corresponding fluctuating temperatures (Table 6). Longevity for males and females was shortest at 32 and 35°C (Table 6).

The longevity of *D. aligarhensis* reared at constant temperatures decreased linearly with increasing temperatures (R^2 = 0.91; F = 13.71; df = 1, 9; P = 0.005; Fig. 2). The addition of a quadratic term did not improve the adjustment of the data (F = 1.27; df = 1, 9; P = 0.26). For the longevity of *D. aligarhensis* parasitoids reared at fluctuating temperatures, the best fit was obtained with a quadratic model (F = 25.67; df = 1, 9; P = 0.001). The longest duration of adult lifespan for *D. aligarhensis* males and females was observed between 20 and 25°C fluctuating (Fig. 2).

Discussion

This study is the first to evaluate and demonstrate the significant effects of different temperature exposure regimens on development and longevity of *D. aligarhensis*. Development rate of female and male *D. aligarhensis* were positively correlated with temperature from 15 to 32°C, before decreasing slightly at 35°C, the highest experimental temperature evaluated. Results indicate successful development of *D. aligarhensis* at 35°C is possible under both constant and fluctuating temperature regimens. In addition to development rates, fluctuating temperatures had a significant effect on the duration of adult lifespan of *D. aligarhensis* with increasing average temperatures generally lowering mean longevity, an effect that was somewhat less pronounced when temperatures fluctuated.

The experimental temperature means used in this study were based on a range of prevailing temperatures experienced in citrus producing regions of California. These temperatures are biologically relevant and with respect to fluctuating temperature regimens, they represent realistic temperature exposure scenarios. The lowest temperature examined experimentally averaged 15°C, and for fluctuating temperatures, this exposed parasitoids to 3 h at 9°C (lowest temperature exposure) and 4 h at 21°C (highest temperature exposure). This is particularly important, as temperatures below 15°C may potentially stop or significantly slow development of *D. aligarhensis*, whereas higher temperatures (e.g., 21°C) allow these physiological processes to take place more readily (Gilbert and Raworth 1996, Kontodimas et al. 2004). Indeed, it was found that *D. aligarhensis* reared at 15°C (and males at 20°C) fluctuating temperatures experienced a delay in development when compared with constant

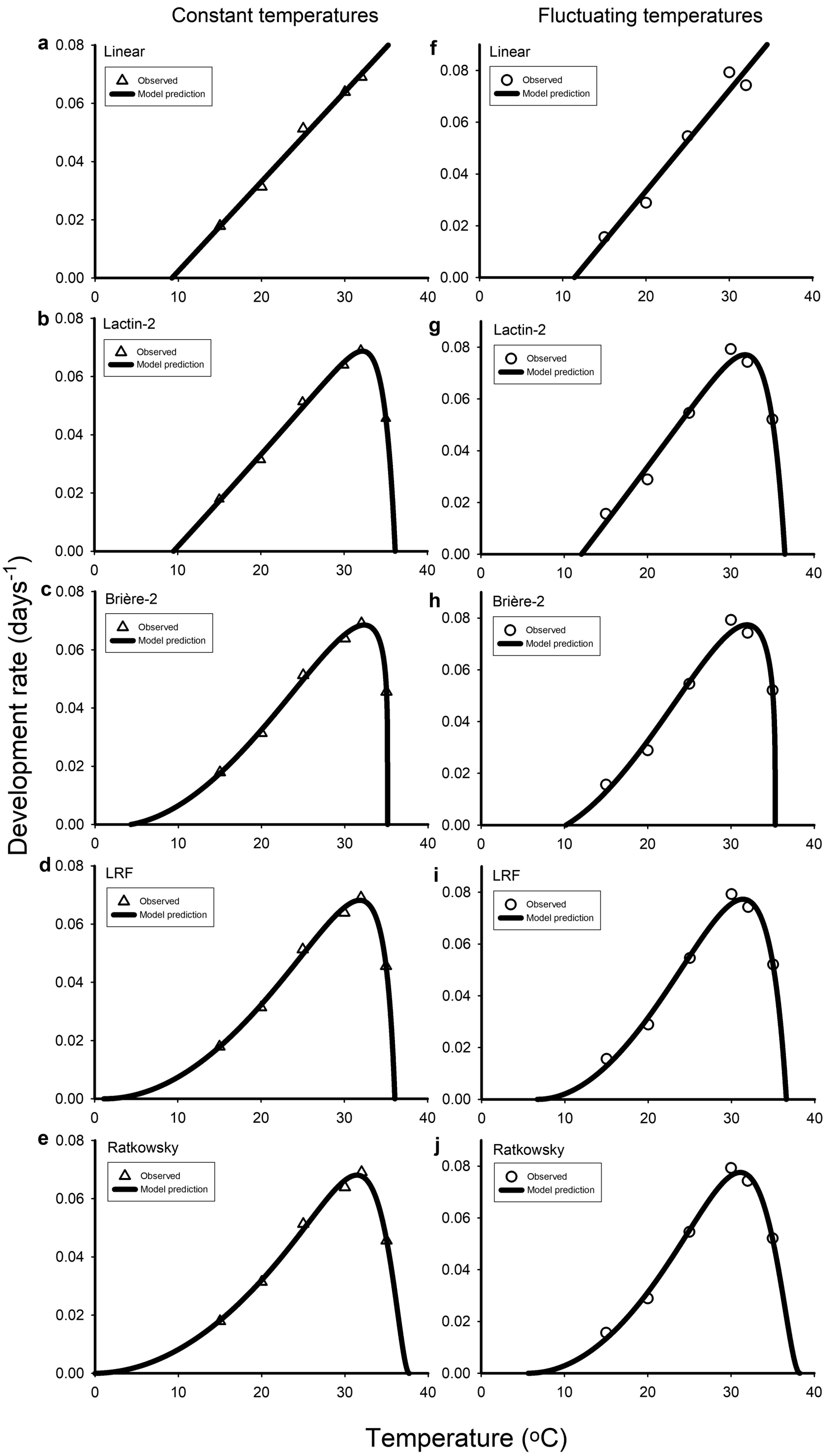

Fig. 1. Predicted rate of total development as a function of temperature for *D. aligarhensis* (pooled males and females) at different constant (a–e) and fluctuating (f–j) temperatures using linear (a and f), Lactin-2 (b and g), Brière-2 (c and h), LRF (d and i), and Ratkowsky (e and j) models. In all charts, the ordinate is the rate of development (1/*D*, per day), and the abscissa is the temperature (°C). *Symbols* represent mean observed data. In the linear regression, data values for 35°C were omitted because of significant deviation from a straight line.

temperature counterparts. The reason for this may pertain to cumulative cold stress that parasitoids experienced under fluctuating temperature regimens (Hall et al. 2011, Colinet et al. 2015). As a result of this cumulative sublethal cold stress, adult parasitoids that developed successfully at 15°C fluctuating had reduced lifespan (Table 6). Further studies could be developed to determine whether exposure to temperatures lower than those used here and which are typical of citrus-producing areas in southern and central California have deleterious effects on development, longevity, and reproductive output of *D. aligarhensis*.

Studies on the effects of temperature on insect development have been criticized because analyses commonly use models that are

Table 6. Mean longevity in days (±SE) for female and male *D. aligarhensis* maintained under the constant and fluctuating temperatures at which they were reared

	Longevity (mean days ± SE)					
	15°C	20°C	25°C	30°C	32°C	35°C
Female						
Constant	64.57 ± 1.06^{a} (14)	33.67 ± 0.69^{b} (18)	25.91 ± 0.52^{c} (11)	16.56 ± 0.63^{b} (9)	1.98 ± 0.24^{a} (56)	2.79 ± 0.47^{a} (14)
Fluctuating	19.63 ± 0.99^{b} (16)	43.71 ± 0.78^{a} (14)	36.43 ± 0.46^{ab} (14)	23.60 ± 0.48^{a} (15)	1.91 ± 0.38^{a} (22)	1.82 ± 0.53^{ab} (11)
Male						
Constant	66.38 ± 0.99^{a} (16)	31.21 ± 0.51^{b} (33)	25.59 ± 0.37^{c} (22)	17.06 ± 0.47^{b} (16)	2.20 ± 0.22^{a} (65)	1.74 ± 0.34^{ab} (27)
Fluctuating	17.00 ± 0.83^{b} (23)	44.00 ± 0.76^{a} (15)	34.00 ± 0.50^{b} (12)	23.43 ± 0.50^{a} (14)	1.83 ± 0.37^{a} (24)	1.11 ± 0.58^{b} (9)

Means followed by the same letter within the same temperature are not significantly different $\alpha = 0.05$; *n* denotes number of individuals. SEs are based upon the pooled variance and individual sample sizes.

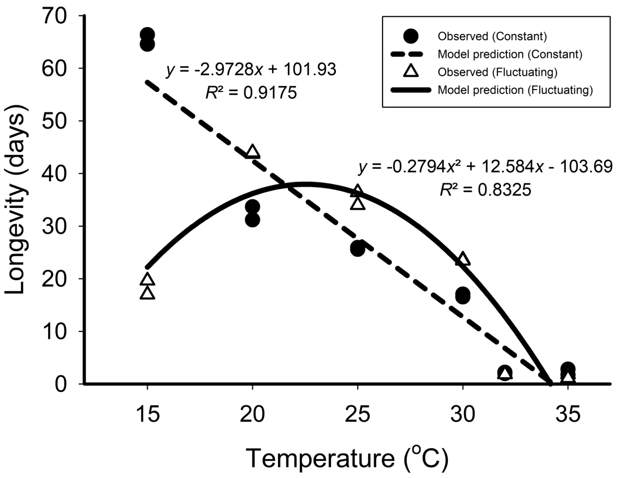

Fig. 2. Change in longevity of adult *D. aligarhensis* (pooled males and females) in relation to average experimental temperatures for constant and fluctuating temperature regimes. For longevity, the ordinate is the time from adult emergence to death (days), and the abscissa is temperature (°C). The dashed line is the least-squares linear regression showing a reduction in adult longevity with increasing constant temperatures. The solid line represents the curvilinear function which best fits the fluctuating datasets, with peak longevity occurring between 20 and 25°C. Symbols represent the observed mean values for each rearing temperature. See top of the fitted lines for associated regression equations R^2 estimates.

considered standard to the field of investigation or are preferred for a particular taxonomic group (Mirhosseini et al. 2017, Ratkowsky and Reddy 2017, Shi et al. 2017). As a result, alternative models that could provide superior fits to experimental datasets may be overlooked (Quinn 2017). Other important criteria that should be considered for fitting nonlinear models to temperature-driven development rate data for insects include use of parameters that have biological relevance are close-to-linear, which means that the least squares estimators are close to being normally distributed and are unbiased, minimum variance estimators. In these situations, good initial parameter estimates can be obtained which promotes successful model convergence (see Ratkowsky and Reddy 2017 for further explanation). In our analyses, model selection took into consideration these criteria. Additionally, nonlinear models evaluated here have the same number of parameters and therefore the same degrees of freedom when assessed statistically. This ensures the same predictive power which eliminates bias in regard to model selection criteria (see Development Rate Models).

The goodness of fit of linear and nonlinear models fitted to experimental data for both constant and fluctuating temperatures regimens was similar, as indicated by the low *RSS* values (Table 3). The use of development data obtained from fluctuating temperature studies would, thus, not reduce the predictive accuracy of phenological models used for pest management programs targeting *D. citri* (Milosavljević et al. 2018a). The overall best fitting models fitted to the fluctuating datasets used in this study were LRF and Ratkowsky (Table 3). There was little difference between the *RSS* values for these two models when fitted to constant and fluctuating datasets. The Lactin-2 model fitted the datasets well. However, many of its parameters (i.e., λ, ρ, and δ) have no biological relevance and are of no practical use (e.g., T_u) (Ratkowsky and Reddy 2017). Furthermore, the Lactin-2 and Brière-2 models yielded higher *RSS* values for fluctuating regimens, when compared with the LRF and Ratkowsky models, indicating a slightly poorer fit (Table 2). The LRF and Ratkowsky models, thus, emerge as the most suitable models of the four models studied to be used for modeling the development of *D. aligarhensis*.

There were differences, however, in estimated values of thermal constants (and lower development thresholds [see below]) for *D. aligarhensis* females and males between the models and experimental temperature regimens. In general, it was found that fewer degree days were required for completion of development under fluctuating temperature regimens when compared with constant temperatures, a finding that aligns with the results of previous studies examining insect development under fluctuating temperatures (Fischer et al. 2011, Lyons et al. 2013, Warren and Anderson 2013, Wu et al. 2015). These findings suggest that field populations of *D. aligarhensis* experiencing fluctuating ambient temperatures have higher population growth potential and faster growth rates than populations developing at equivalent temperatures that are constant. This further implies that the phenology predictions using models fit to constant temperature data (often used in the literature) would erroneously predict longer-than-actual generation times for *D. aligarhensis* during the growing season.

In addition to thermal constants, the lower development threshold is crucial for characterizing degree-day accumulations, adult emergence, overwintering capabilities, and range expansion of pest and natural enemy species (Jalali et al. 2009, Luhring and DeLong 2016, Mirhosseini et al. 2017, Ratkowsky and Reddy 2017, Shi et al. 2017). In our study, the critical lower temperatures (T_{min}) for the development of *D. aligarhensis* estimated by the linear and nonlinear equations were consistently higher under fluctuating temperatures than those estimated under constant temperature regimen counterparts (Tables 4 and 5). The use of constant temperature data could underestimate the ability of this species to survive in cooler regions of California (e.g., coastal areas) that may be unfavorable for *T. radiata*

(Hoddle et al. 2016). Previous research on temperature-driven development of *D. citri* and associated natural enemy species has been conducted under constant temperature regimens only (Chien et al. 1993, Liu and Tsai 2000, Skelley and Hoy 2004, Gómez-Torres et al. 2012, Li et al. 2018). These studies did not account for the effects of daily temperature fluctuations on development rates. Future studies that examine the life history or attempt to forecast performance of natural enemies under consideration for release into new areas for pest population suppression should assess the potential effects of both average daily temperature and exposure regime type (i.e., fluctuating daily temperatures) to improve reliability of predictions.

Parameters such as T_{min} and T_{max} are parameter estimates that do not necessarily predict the exact threshold temperatures for development. Consequently, consideration of parameter values estimated from fitted models should be viewed cautiously, as 'true' development threshold values for *D. aligarhensis* may lie within the entire range of estimated parameter values produced by multiple fitted models. For example, fitted models produced a range of T_{min} values (~6 [Ratkowsky] to ~12°C [linear and Lactin-2] fluctuating [see Tables 4 and 5]) for *D. aligarhensis*. These T_{min} estimates should be considered hypotheses that need testing experimentally to better determine where within this predicted range (i.e., ~6 to 12°C) the 'true' value of the minimum temperature for development lies. This is important as lower (and upper) temperature thresholds could limit the potential geographical range for establishment of *D. aligarhensis* across different climatic zones where citrus is grown.

The Lactin-2, the Brière-2, the LRF, and the Ratkowsky models gave relatively comparable predictions of the upper temperature thresholds (T_{max}) for *D. aligarhensis*, regardless of the temperature regimen (Table 3). The four models also produced similar estimates for the optimum development temperature (T_{opt}) of *D. aligarhensis* with the maximum development rate being observed between 30 and 32°C. Indeed, the greatest numbers of female and male parasitoids developed at 32°C under both constant and fluctuating experimental regimens (Table 2). As with low temperatures, our findings tentatively suggest that *D. aligarhensis* may be able to tolerate high summer temperatures (i.e., > 35°C for >11 h) that may occur in some citrus-growing regions in southern California (e.g., Coachella Valley). Adult *D. aligarhensis*, however, lived longer at intermediate temperatures than at extreme upper and lower temperatures under fluctuating temperature scenarios as indicated by the quadratic equation fitted to fluctuating datasets. Parasitoid storage under fluctuating temperature cycles that average between 20 and 30°C holds practical applications for managing mass reared *D. aligarhensis* as it maximizes longevity prior to release into areas where the target pest is present.

Daily temperature fluctuations significantly affected development times and longevity of *D. aligarhensis*, resulting in marked deviations when compared constant temperature regimen counterparts (Table 7). Based on the results of this work, it is proposed that evaluating and modeling the effects of realistic fluctuating temperatures scenarios on natural enemy developmental and reproductive biology may improve the predictions of establishment, spread, and impact of not only *D. aligarhensis*, but other biological control agents, such as *Tamarixia radiata*, that are being released for suppression of *D. citri* across different citrus producing regions of California.

Table 7. General differences in important thermal parameters for *D. aligarhensis* between constant and fluctuating temperature regimens

	Results	Future implications
Development rate models	• The goodness of fit of models fitted to constant versus fluctuating temperatures was generally similar.	• The use of fluctuating temperature data would not be expected to reduce the predictive accuracy of models when used for phenological predictions as part of pest management programs for *D. citri*.
Thermal constant (*K*)	• Fewer degree days were required for completion of development under fluctuating regimens than at constant temperatures.	• Phenology predictions using models fit to constant temperature data could erroneously predict longer-than-actual generation times for *D. aligarhensis* during the season.
Lower development threshold (T_{min})	• The estimated values of lower development temperature threshold (T_{min}: 6–12°C) was generally estimated to be higher under fluctuating regimens than at constant temperatures.	• The use of constant temperature data may underestimate the ability of this species to survive in cooler regions. • Consideration of T_{min} values estimated from fitted models should be viewed cautiously, as 'true' development threshold values for *D. aligarhensis* may lie within the entire range of estimated values produced by multiple fitted models.
Optimal temperature for development (T_{opt}) and Upper development threshold (T_{max})	• The estimated values of upper (T_{max}: 35–38°C) and optimum (T_{opt}: 30–32°C) temperature limits were similar for individuals reared under constant and fluctuating temperatures. • The greatest numbers of females and males developed at 32°C under constant and fluctuating temperatures.	• *Diaphorencyrtus aligarhensis* should be able to tolerate high summer temperatures typical of citrus-growing regions in southern and central California.
Adult longevity	• Parasitoids lived longer at 15°C constant and for shorter times at 20, 25, and 30°C constant than at fluctuating temperatures. • Parasitoids lived longer at intermediate temperatures than at upper and lower extreme temperatures under fluctuating temperature scenarios, as indicated by the quadratic equation fitted to fluctuating datasets.	• Parasitoid storage under fluctuating temperature cycles that average between 20 and 30°C holds practical applications for managing mass reared *D. aligarhensis* as it maximizes longevity prior to release into areas where the target pest is present.

Acknowledgments

This work was supported, in part, from funds provided by the Citrus Research Board (award number 5500-191) and USDA-MAC Agreement Number #15-8130-0336-CA.

References Cited

Ashmore, G. M., and F. J. Janzen. 2003. Phenotypic variation in smooth softshell turtles (*Apalone mutica*) from eggs incubated in constant versus fluctuating temperatures. Oecologia. 134: 182–188.

Babcock, B. 2018. Economic impact of California's citrus industry. Citrograph. 9: 36–39.

Bayles, B. R., S. M. Thomas, G. S. Simmons, E. E. Grafton-Cardwell, and M. P. Daugherty. 2017. Spatiotemporal dynamics of the Southern California Asian citrus psyllid (*Diaphorina citri*) invasion. Plos One. 12: e0173226.

Bistline-East, A., and M. S. Hoddle. 2015. Biology of *Psyllaphycus diaphorinae* (Hymenoptera: Encyrtidae), a hyperparasitoid of *Diaphorencyrtus aligarhensis* (Hymenoptera: Encyrtidae) and *Tamarixia radiata* (Hymenoptera: Eulophidae). Ann. Entomol. Soc. Am. 109: 22–28.

Bistline-East, A., R. Pandey, M. Kececi, and M. S. Hoddle. 2015. Host range testing of *Diaphorencyrtus aligarhensis* (Hymenoptera: Encyrtidae) for use in classical biological control of *Diaphorina citri* (Hemiptera: Liviidae) in California. J. Econ. Entomol. 108: 940–950.

Bollen, K. A., and R. W. Jackman. 1990. Regression diagnostics: An expository treatment of outliers and influential cases. Mod. Methods Data Anal. 13: 257–291.

Brière, J. F., P. Pracross, A. Y. Rioux, and J. S. Pierre. 1999. A novel rate model of temperature dependent development for arthropods. Environ. Entomol. 28: 22–29.

Broatch, J. S., L. M. Dosdall, G. W. Clayton, K. N. Harker, and R. C. Yang. 2006. Using degree-day and logistic models to predict emergence patterns and seasonal flights of the cabbage maggot and seed corn maggot (Diptera: Anthomyiidae) in canola. Environ. Entomol. 35: 1166–1177.

Campbell, A., B. D. Frazer, N. Gilbert, A. P. Gutierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431–438.

Chien, C. C., Y. I. Chu, and S. C. Ku. 1993. Influence of temperature on the population increase, host-killing capability and storage of *Tamarixia radiata*. Chin. J. Entomol. 13: 111–123.

[CIMIS] California Irrigation Management Information System. 2018. California Department of Water Resources' California Irrigation Management Information System. State of California, Sacramento, CA. http://www.cimis.water.ca.gov. (accessed 10 September 2018).

Colinet, H., C. Salin, G. Boivin, and T. H. Hance. 2005. Host age and fitness-related traits in a koinobiont aphid parasitoid. Ecol. Entomol. 30: 473–479.

Colinet, H., G. Boivin, and T. Hance. 2007. Manipulation of parasitoid size using the temperature-size rule: fitness consequences. Oecologia. 152: 425–433.

Colinet, H., B. J. Sinclair, P. Vernon, and D. Renault. 2015. Insects in fluctuating thermal environments. Annu. Rev. Entomol. 60: 123–140.

Damos, P. T., N. A. Kouloussis, and D. S. Koveos. 2018. A degree-day phenological model for *Cydia pomonella* and its validation in a Mediterranean climate. Bull. Insectol. 71: 131–142.

Durborow, S. 2012. An analysis of the potential economic impact of Huanglongbing on the California citrus industry. Master thesis, Texas A&M University, Commerce, TX.

Eliopoulos, P. A., D. C. Kontodimas, and G. J. Stathas. 2010. Temperature-dependent development of *Chilocorus bipustulatus* (Coleoptera: Coccinellidae). Environ. Entomol. 39: 1352–1358.

Fischer, K., N. Kölzow, H. Höltje, and I. Karl. 2011. Assay conditions in laboratory experiments: is the use of constant rather than fluctuating temperatures justified when investigating temperature-induced plasticity? Oecologia. 166: 23–33.

Ganjisaffar, F., and T. M. Perring. 2015. Relationship between temperature and development of *Galendromus flumenis* (Acari: Phytoseiidae), a predator of Banks grass mite (Acari: Tetranychidae). Exp. Appl. Acarol. 67: 535–546.

Gilbert, N., and D. A. Raworth 1996. Insects and temperature-a general theory. Can. Entomol. 128: 1–13.

Gómez-Torres, M. L., D. E. Nava, and J. R. Parra. 2012. Life table of *Tamarixia radiata* (Hymenoptera: Eulophidae) on *Diaphorina citri* (Hemiptera: Psyllidae) at different temperatures. J. Econ. Entomol. 105: 338–343.

Gottwald, T. R. 2010. Current epidemiological understanding of citrus Huanglongbing. Annu. Rev. Phytopathol. 48: 119–139.

Grafton-Cardwell, E. E., L. L. Stelinski, and P. A. Stansly. 2013. Biology and management of Asian citrus psyllid, vector of the huanglongbing pathogens. Annu. Rev. Entomol. 58: 413–432.

Hall, D. G., E. J. Wenninger, and M. G. Hentz. 2011. Temperature studies with the Asian citrus psyllid, *Diaphorina citri*: cold hardiness and temperature thresholds for oviposition. J. Insect Sci. 11: 1–15.

Hoddle, M. S., and R. Pandey. 2014. Host range testing of *Tamarixia radiata* (Hymenoptera: Eulophidae) sourced from the Punjab of Pakistan for classical biological control of *Diaphorina citri* (Hemiptera: Liviidae: Euphyllurinae: Diaphorinini) in California. J. Econ. Entomol. 107: 125–136.

Hoddle, M. S., C. D. Hoddle, S. V. Triapitsyn, S. Z. Khan, and M. J. Arif. 2014. How many primary parasitoid species attack nymphs of *Diaphorina citri* (Hemiptera: Liviidae) in Punjab, Pakistan? Fla. Entomol., 97: 1825–1828.

Hoddle, M. S., R. Amrich, C. D. Hoddle, and E. J. Kistner. 2016. Where's *Tamarixia*. Citrograph. 7: 64–66.

Ikemoto, T., and K. Takai. 2000. A new linearized formula for the law of total effective temperature and the evaluation of line-fitting methods with both variables subject to error. Environ. Entomol. 29: 671–682.

Institute SAS. 2009. SAS/STAT, version 9.2 user's guide, 2nd ed. SAS Institute, Cary, NC.

Jalali, M. A., L. Tirry, and P. De Clercq. 2009. Effects of food and temperature on development, fecundity and life-table parameters of *Adalia bipunctata* (Coleoptera: Coccinellidae). J. Appl. Entomol. 133: 615–625.

Khan, S. Z., M. J. Arif, C. D. Hoddle, and M. S. Hoddle. 2014. Phenology of Asian citrus psyllid (Hemiptera: Liviidae) and associated parasitoids on two species of *Citrus*, kinnow mandarin and sweet orange, in Punjab Pakistan. Environ. Entomol. 43: 1145–1156.

Koda, K., and H. Nakamura. 2010. Effects of temperature on the development and survival of an endangered butterfly, *Shijimiaeoides divinus barine* (Leech) (Lepidoptera: Lycaenidae). Entomol. Sci. 13: 29–34.

Kontodimas, D. C., P. A. Eliopoulos, G. J. Stathas, and L. P. Economou. 2004. Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae), preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various non-linear models using specific criteria. Environ. Entomol. 33: 1–11.

Kontodimas, D. C., P. G. Milonas, G. J. Stathas, L. P. Economou, and N. G. Kavallieratos. 2007. Life table parameters of the pseudococcid predators *Nephus includens* and *Nephus bisignatus* (Coleoptera: Coccinelidae). Eur. J. Entomol. 104: 407–415.

Lactin, D. J., N. J. Holliday, D. L. Johnson, and R. Craigen. 1995. Improved rate model of temperature-dependent development by arthropod. Environ. Entomol. 24: 68–75.

Li, Y. H., Y. T. Zhou, C. F. Guo, D. Ou, J. A. Qureshi, W. Sang, and B. L. Qiu. 2018. Temperature and host age effects on the life history of *Tamarixia radiata*, a dominant parasitoid of citrus psyllid *Diaphorina citri*. Crop Protect. 114: 32–38.

Liu, Y. H., and J. H. Tsai. 2000. Effects of temperature on biology and life table parameters of the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Homoptera: Psyllidae). Ann. Appl. Biol. 137: 201–206.

Logan, J. A., D. J. Wollkind, S. C. Hoyt, and K. Tanigoshi. 1976. An analytical model for description of temperature dependent rate phenomena in arthropods. Environ. Entomol. 5: 1133–1140.

Logan, J. D., W. Wolesensky, and A. Joern. 2006. Temperature-dependent phenology and predation in arthropod systems. Ecol. Model 196: 471–482.

Luhring, T. M., and J. P. DeLong. 2016. Predation changes the shape of thermal performance curves for population growth rate. Curr. Zool. 62: 501–505.

Lyons, C. L., M. Coetzee, and S. L. Chown. 2013. Stable and fluctuating temperature effects on the development rate and survival of two malaria vectors, *Anopheles arabiensis* and *Anopheles funestus*. Parasit. Vectors. 6: 104.

Marchioro, C. A., and L. A. Foerster. 2011. Development and survival of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae) as a function of temperature: effect on the number of generations in tropical and subtropical regions. Neotrop. Entomol. 40: 533–541.

Milosavljević, I., A. D. Esser, and D. W. Crowder. 2016. Effects of environmental and agronomic factors on soil-dwelling pest communities in cereal crops. Agric. Ecosyst. Environ. 225: 192–198.

Milosavljević, I., A. D. Esser, and D. W. Crowder. 2017a. Seasonal population dynamics of wireworms in wheat crops in the Pacific Northwestern United States. J. Pest Sci. 90: 77–86.

Milosavljević, I., K. A. Schall, C. D. Hoddle, D. J. W. Morgan, and M. S. Hoddle. 2017b. Biocontrol program targets Asian citrus psyllid in California's urban areas. Calif. Agric. 71: 169–177.

Milosavljevic, I., R. Amrich, V. Strode, and M. S. Hoddle. 2018a. Modeling the phenology of Asian citrus psyllid (Hemiptera: Liviidae) in urban southern california: effects of environment, habitat, and natural enemies. Environ. Entomol. 47: 233–243.

Milosavljević, I., H. A. F. El-Shafie, J. R. Faleiro, C. D. Hoddle, M. Lewis, and M. S. Hoddle. 2018b. Palmageddon: the wasting of ornamental palms by invasive palm weevils, *Rhynchophorus* spp. J. Pest Sci. (in press). DOI: 10.1007/s10340-018-1044-3

Milosavljević, I., and M. S. Hoddle. 2019. Advances in classical biological control in IPM. *In* M Kogan **and** L Higley (eds.), Integrated management of insect pests: Current and Future Developments in IPM. Burleigh Dodds Science Publishing, Cambridge, UK. (in press). DOI: 10.19103/AS.2019.0047.13

Mirhosseini, M. A., Y. Fathipour, and G. V. Reddy. 2017. Arthropod development's response to temperature: a review and new software for modeling. Ann. Entomol. Soc. Am. 110: 507–520.

Nooten, S. S., N. R. Andrew, and L. Hughes. 2014. Potential impacts of climate change on insect communities: a transplant experiment. Plos One. 9: e85987.

Obrycki, J. J., and T. J. Kring. 1998. Predaceous Coccinellidae in biological control. Annu. Rev. Entomol. 43: 295321.

Packard, G. C., and M. J. Packard, 1993. Hatchling painted turtles (*Chrysemys picta*) survive exposure to subzero temperatures during hibernation by avoiding freezing. J. Comp. Physiol. B. 163: 147–152.

Pilkington, L. J., and M. S. Hoddle. 2006a. Use of life table statistics and degree-day values to predict the invasion success of *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca coagulata* (Hemiptera: Cicadellidae), in California. Biol. Control. 37: 276–283.

Pilkington, L. J., and M. S. Hoddle. 2006b. Reproductive and developmental biology of *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca coagulata* (Hemiptera: Cicadellidae). Biol. Control. 37: 266–275.

Pilkington, L. J., and M. S. Hoddle. 2007a. Predictions of invasion success of *Gonatocerus triguttatus* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca vitripennis* (Hemiptera: Cicadellidae), in California using life table statistics and degree-day values. Biol. Control. 42: 9–15.

Pilkington, L. J., and Hoddle, M. S. 2007b. Use of life tables to quantify reproductive and developmental biology of *Gonatocerus triguttatus* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca vitripennis* (Hemiptera: Cicadellidae). Biol. Control. 42: 1–8.

Pilkington, L. J., M. Lewis, D. Jeske, and M. S. Hoddle. 2014. Calculation and thematic mapping of demographic parameters for *Homalodisca vitripennis* (Hemiptera: Cicadellidae) in California. Ann. Entomol. Soc. Am. 107: 424–434.

Quinn, B. K. 2017. A critical review of the use and performance of different function types for modeling temperature-dependent development of arthropod larvae. J. Therm. Biol. 63: 65–77.

Ratkowsky, D. A. 2004. Model fitting and uncertainty, pp 151–196. *In* R. C. McKellar **and** X. Lu (eds.), Modeling microbial responses in food. CRC Press, Boca Raton, FL.

Ratkowsky, D. A., and G. V. Reddy. 2017. Empirical model with excellent statistical properties for describing temperature-dependent developmental rates of insects and mites. Ann. Entomol. Soc. Am. 110: 302–309.

Ratkowsky, D. A., R. K. Lowry, T. A. McMeekin, A. N. Stokes, and R. E. Chandler. 1983. Model for bacterial culture growth rate throughout the entire biokinetic temperature range. J. Bacteriol. 154: 1222–1226.

Rohrig, E. A. 2010. Biology and behavior of *Diaphorencyrtus aligarhensis* (Hymenoptera: Encyrtidae), an endoparasitoid of *Diaphorina citri* (Hemiptera: Psyllidae). Doctoral dissertation, University of Florida, Gainesville, FL.

Rohrig, E., P. D. Shirk, D. G. Hall, and P. A. Stansly. 2011. Larval development of Diaphorencyrtus aligarhensis (Hymenoptera: Encyrtidae), an endoparasitoid of *Diaphorina citri* (Hemiptera: Psyllidae). Ann. Entomol. Soc. Am. 104: 50–58.

Rosso, L., J. R. Lobry, and J. P. Flandrois. 1993. An unexpected correlation between cardinal temperatures of microbial growth highlighted by a new model. J. Theor. Biol. 162: 447–463.

Roy, M., J. Brodeur, and C. Cloutier. 2002. Relationship between temperature and development rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdaniali* (Acarina: Tetranychidae). Environ. Entomol. 31: 177–187.

Schowalter, T. D. 2016. Insect ecology: an ecosystem approach, 4th ed. Academic Press, San Diego, CA.

Shi, P., and F. Ge. 2010. A comparison of different thermal performance functions describing temperature-dependent development rates. J. Therm. Biol. 35: 225–231.

Shi, P. J., M. L. Fan, and G. V. Reddy. 2017. Comparison of thermal performance equations in describing temperature-dependent developmental rates of insects: (III) Phenological applications. Ann. Entomol. Soc. Am. 110: 558–564.

Skelley, L. H., and M. A. Hoy. 2004. A synchronous rearing method for the Asian citrus psyllid and its parasitoids in quarantine. Biol. Control. 29: 14–23.

Spiess, A. N., and N. Neumeyer. 2010. An evaluation of R^2 as an inadequate measure for nonlinear models in pharmacological and biochemical research: a Monte Carlo approach. BMC Pharmacol. 10: 6. doi:10.1186/1471-2210-10-6

Spreen, T. H., J. P. Baldwin and S. H. Futch. 2014. An economic assessment of the impact of Huanglongbing on citrus tree plantings in Florida. J. Hortic. Sci. 49: 1052–1055.

[USDA NASS] United States Department of Agriculture National Agricultural Statistics Services. 2017. Citrus Production Forecast www.nass.usda.gov/Statistics_by_State/Florida/Publications/Citrus/Citrus_Forecast/index.php (accessed 10 September 2018).

Vankosky, M. A., and M. S. Hoddle. 2017a. The effects of conspecific and heterospecific interactions on foraging and oviposition behaviours of two parasitoids of *Diaphorina citri*. Biocontrol Sci. Technol. 27: 739–754. 1315

Vankosky, M. A., and M. S. Hoddle. 2017b. An assessment of interspecific competition between two introduced parasitoids of *Diaphorina citri* (Hemiptera: Liviidae) on caged citrus plants. Insect Sci., [in press]. doi:10.1111/1744-7917.12490.

Warren, J. A., and G. S. Anderson. 2013. Effect of fluctuating temperatures on the development of a forensically important blow fly, *Protophormia terraenovae* (Diptera: Calliphoridae). Environ. Entomol. 42: 167–172.

Wu, T. H., S. F. Shiao, and T. Okuyama. 2015. Development of insects under fluctuating temperature: a review and case study. J. Appl. Entomol. 139: 592–599.

Zamani, A. A., A. Talebi, Y. Fathipour, and V. Baniameri. 2007. Effect of temperature on life history of *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Braconidae), two parasitoids of *Aphis gossypii* and *Myzus persicae* (Homoptera: Aphididae). Environ. Entomol. 36: 263–271.