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The Effects of Constant and Fluctuating Temperatures on Development of *Diaphorina citri* (Hemiptera: Liviidae), the Asian Citrus Psyllid

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Abstract

The effects of six average daily temperatures, 15, 20, 25, 30, 32, and 35°C, that were either constant or fluctuating over 24 h on development times of California-sourced *Diaphorina citri* Kuwayama nymphs were examined. Thermal performance curves for immature stages of *D. citri* were characterized using one linear and six nonlinear models (i.e., Ratkowsky, Lobry-Rosso-Flandrois, Lactin-2, Brière-2, Beta, and Performance-2). Daily thermal fluctuations had significant effects on development times of *D. citri* nymphs, which differed across experimental temperatures. *Diaphorina citri* nymphs reared at constant temperatures completed development faster than those reared under fluctuating profiles with equivalent temperature means. Linear model estimates of degree-days required for completion of cumulative development of *D. citri* were 25% lower for constant temperatures when compared with fluctuating temperature regimens. Nonlinear model estimations of optimum developmental temperature and upper theoretical temperature bounds for development were similar for individuals reared under constant and fluctuating temperatures. Nevertheless, the estimated values of lower theoretical temperature limits above which development occurred were lower under fluctuating than constant temperatures. A meta-analysis of published *D. citri* temperature-dependent development literature, synthesizing datasets of five globally distributed populations (Brazil, California, China, Florida, and Japan) reared under different constant temperatures on six different host plants (i.e., *Citrus limonia*, *C. sinensis* cv Natal, *C. sinensis* cv. Pêra, *C. reticulata, Fortunella margarita,* and *Murraya paniculata*), together with the results of this study (*C. volkameriana*), revealed convergence in estimates of developmental parameters. These results have implications for predicting *D. citri* invasion and establishment risk and subsequent population performance across various climactic gradients and geographic regions.

Key words: development rate, *Diaphorina citri*, nonlinear regression model, thermal thresholds, meta-analysis

Candidatus Liberibacter asiaticus (CLas), the putative agent of a devastating bacterial disease of citrus, huanglongbing (Gottwald 2010), poses a significant and growing threat to citrus growers worldwide because of its ability to render citrus production unprofitable (Durborow 2012, Hall et al. 2013, Spreen et al. 2014, Bayles et al. 2017, Babcock 2018). The rapid expansion of CLas in the Americas, and the United States in particular (e.g., Alabama, California, Florida, Georgia, Louisiana, Mississippi, South Carolina, and Texas), is facilitated by *Diaphorina citri* Kuwayama, the Asian citrus psyllid, the vector of CLas. This pest can develop rapidly and sustain populations in subtropical, tropical, and arid desert environments (Taylor et al. 2019, Gomez-Marco et al. 2019). Immature *D. citri* (i.e., nymphs) acquire CLas by feeding on infected citrus trees and subsequently spread the pathogen as adults (Grafton-Cardwell et al. 2013). Once infected with CLas, psyllids remain so for their entire lifespan (Pelz-Stelinski et al. 2010). Because *D. citri* is responsible for CLas transmission to uninfected trees, and transmission rates are a function of vector population density (Grafton-Cardwell et al. 2013), an understanding of factors, such as the influence of climate, which affects vector population distribution and abundance, is important for understanding risk posed by *D. citri* (Milosavljević et al. 2017, Milosavljević and Hoddle 2019).

Climate variables (e.g., temperature) are strong predictors for which geographic locations are suitable for sustaining permanent *D. citri* populations (Wang et al. 2019), driving phenology patterns (Kistner et al. 2016, Milosavljević et al. 2018), and affecting population density levels (Taylor et al. 2019). Temperature is considered the key variable in defining the geographic and temporal distribution of *D. citri* populations across citrus-producing areas (Paris et al. 2015, Stelinski, 2019). For example, low daily minimum temperatures (<9°C) over winter may cause environmental conditions that are unsuitable for survival of *D. citri* nymphs (Liu and Tsai 2000, Fung and Chen 2006), though adults may acclimate and survive (Hall et al. 2011). In comparison to low temperatures, high temperatures (>30°C on average) may affect the ability of *D. citri* to colonize new localities and have negative impacts on population densities (Gomez-Marco et al. 2019, Milosavljević and Hoddle 2019). For example, higher temperatures increase *D. citri* development rates but reduce survival and reproductive success of surviving adults (Grafton-Cardwell et al. 2013). High temperatures strongly influence the abundance and duration of citrus flush, a growth stage of young leaves, which is an important resource required for oviposition by female *D. citri* and the development of nymphs (Gomez-Marco et al. 2019).

As a climate variable, temperature significantly influences insect population growth and life history parameters such as development times and fitness outcomes such as survivorship, fecundity rates, and longevity (Kontodimas et al. 2004; Pilkington and Hoddle 2006, 2007; Luhring and DeLong 2016; Schowalter 2016; Damos et al. 2018). Life history parameters (e.g., development times) of *D. citri* have been quantified from laboratory studies performed under constant temperature conditions (Liu and Tsai 2000; Liu and Tsai 2000; Nakata 2006; Fung and Chen 2006; Nava et al. 2007, 2010). However, exposure to constant temperatures over a 24 h period for the life times of experimental insects is unnatural and rarely occurs in nature (an exception could be stored product pests infesting dry foods stored under constant conditions; Howe 1967). Temperatures that fluctuate between daily highs and lows over 24 h are characteristic of the environment of most arthropods. Consequently, the effects of daily temperature fluctuations on immature development, adult lifespan, and reproductive output of *D. citri* are likely to be more ecologically relevant when compared to similar data collected under constant temperature exposure (Neven 2000, Rice and Allen 2009, Warren and Anderson 2013, Wu et al. 2015).

A wide variety of empirical mathematical equations have been used to model the effects of temperature on development rates of economically important insect pests (Shi et al. 2015) and natural enemy species that attack these pests (McCalla et al. 2019, Milosavljević et al. 2019). Model parameters (e.g., estimates of accumulated degree-days needed to complete development) have been used to parameterize bioclimatic species distribution models (e.g., CLIMEX and MaxEnt). Species distribution models use temperature-driven data to assess the invasive potential of species of interest and incursion vulnerability of areas of concern (Baker 2002, Fiaboe et al. 2012, Ge et al. 2015, Milosavljević et al. 2016, Kistner 2017). Studies examining the relationship between temperature and life history of *D. citri*, e.g., have focused exclusively on linear regression analyses to determine degree-days (i.e., reciprocal of the line slope) necessary for completion of development in a specific life stage and for estimating lower temperature bounds (i.e., the intercept of the line with the *x*-axis) above which development occurs (Liu and Tsai 2000; Nakata 2006; Fung and Chen 2006; Nava et al. 2007, 2010). However, development rate data as a function of temperature are typically not linear and exhibit curvilinear behavior, especially at higher temperatures. Therefore, linear equations are not capable of fitting to the curvilinear portion of response variables normally found at the higher end of thermal clines. Nonlinear models, therefore, are better suited for analyses of development rate datasets that are curvilinear (Lyons et al. 2013, Colinet et al. 2015, Quinn 2017).

Numerous nonlinear functions are available for fitting to curvilinear development rate data (Shi and Ge 2010, Sánchez-Ramos et al. 2018). Nonlinear equations can provide estimates of theoretical thermal tolerance limits (i.e., $T_{\min}$ and $T_{\max}$ [temperature bounds for development at which development rates equal zero]) and estimates of the optimal temperature for development (i.e., T_{opt} [maximum developmental rate]) (Milosavljević et al. 2019). Fitting equations and statistically comparing goodness-of-fit can provide a range of estimates for parameters of interest (i.e., T_{opt}, $T_{\min}$, and $T_{\max}$) over the entire temperature range that development studies were conducted (Ratkowsky and Reddy 2017).

The effects of constant temperatures on the life history parameters (e.g., development times, longevity) for different geographic populations of *D. citri* have been assessed several times (Liu and Tsai 2000 [Florida, United States], Nakata 2006 [Japan], Fung and Chen 2006 [China], Nava et al. 2007, 2010 [Brazil]). However, there are no studies that have investigated the effects of fluctuating temperatures typical of those that would be experienced in citrus production areas on life history traits of *D. citri* (e.g., development times). Additionally, the effects of temperature on the development of *D. citri* that invaded California in 2008 has not been investigated. Consequently, this study examined the effects of six fluctuating and constant temperature profiles on the development times of California-sourced *D. citri* nymphs.

Meta-analyses use data from multiple independent studies to statistically compare treatment effects (e.g., the influence of temperature on the development of a species of interest) with the objective of determining whether or not the treatment variable of interest has a common effect. Data from 11 studies (nine from four previously published [see below] and data from this study) were subjected to a meta-analysis to determine whether temperature affected the development (e.g., estimates of degree-days and temperature thresholds) of different *D. citri* populations in a similar manner. Development rate data were evaluated using one linear and six nonlinear thermal performance equations and model outputs were compared. Collectively, these standardized analyses on the effects of constant and fluctuating temperatures on the development of *D. citri* may improve understanding of the role temperature has on *D. citri* establishment probabilities, phenology, and population densities across differing geographic regions where citrus is grown.

Materials and Methods

Material Sources for Experiments

Diaphorina citri nymphs used for experiments were obtained from a laboratory culture maintained at the University of California Riverside Insectary and Quarantine Facility (UCR-IQF) (Hoddle and Pandey 2014, Bistline-East et al. 2015, Bistline-East and Hoddle 2016). The culture was established from CLas-free field populations of *D. citri* collected from backyard citrus trees in Riverside and Los Angeles Counties, California (United States) (California Department of Food and Agriculture [CDFA] permit no. 2870). *Diaphorina citri* were reared and maintained on CLas-free *Citrus volkameriana* V. Tenore & Pasquale (Sapindales: Rutaceae) plants (~ 1.5-yr-old). Plants and insects were contained in riser cages [15 × 15 × 30 cm (W × D × H)] constructed from two U-shaped acrylic risers (S&W Plastics F2191, Riverside, CA) with the front covered with a no-see-um sleeve (30 cm in length) to allow access into cages (Skeeta, Bradenton, FL), and the back covered with no-see-um netting (McCalla et al. 2019). Caged plants were held in a temperature controlled room within UCR-IQF at 27 ± 2°C, 40 ± 5% relative humidity [RH], and a 14:10 (L:D) h photoperiod.

Stock *C. volkameriana* plants used for insect rearing in UCR-IQF were grown in greenhouses at UCR Agricultural Operations at 27 ± 2°C, 50 ± 6% RH and natural sunlight. Plants were cultivated in 0.5 liter pots with UCR Type III potting soil mix and watered daily. Osmocote Pro 19:6:12 granular fertilizer (The Scotts Company LLC, Marysville, OH) was applied every 3 mo. Prior to movement to UCR-IQF and placement in riser cages with *D. citri* adults, plants were pruned to stimulate vigorous flush growth (i.e., newly emerging young leaves). Flushing plants stimulate *D. citri* oviposition and this growth is necessary for nymph development (Milosavljević et al. 2018, 2019).

Effects of Constant and Fluctuating Temperature Regimens on California-Sourced *D. citri* Development

The effects of six constant and six fluctuating temperatures that averaged 15, 20, 25, 30, 32, and 35°C, over 24 h on the development times of *D. citri* first-to-fifth instar nymphs were quantified. To establish experimental cohorts of *D. citri* for temperature exposure experiments, two individually-caged *C. volkameriana* with flush growth were inoculated with approximately 100 first-instar nymphs (<24 h of age) sourced from *D. citri* stock cultures held in UCR-IQF. This resulted in ~200 nymphs being reared on two plants at each experimental temperature. Caged plants containing first-instar *D. citri* were placed into climate-controlled cabinets (model I-30BLL; Percival Scientific, Perry, Indiana United States) set to one of the 12 experimental temperature regimens described above (Supp Table 1 [online only]), and maintained at 50 ± 5% RH, and a 14:10 (L:D) h photoperiod, with light intensity of 100 μE m^{-2} s^{-1}, regardless of the experimental temperature regimen. For constant temperature regimens, climate-controlled cabinets were programmed to hold the target temperature (±0.2°C) static for the duration of the study. For fluctuating temperature regimens, climate-controlled cabinets were programmed with nine temperature increments oscillating over a 24-h cycle that produced a mean target temperature equivalent to the constant counterpart. Incremental temperature changes were based on recorded field temperatures that had the desired average daily target temperature to represent realistic thermal exposure scenarios (McCalla et al. 2019).

Temperature data for programming fluctuating climate-controlled cabinets was sourced from CIMIS #44 at the UC Riverside Citrus Experiment Station, CA and ranged January 2012 to December 2016 (see Milosavljević et al. 2019 for additional details; CIMIS 2018). Target temperature regimens and relative humidity in each climate-controlled cabinet were verified by HOBO Pro V2 Temperature/RH loggers (Onset Computer Corp., Bourne, MA) programmed to record temperature and humidity at 15 min intervals for the entirety of experiments. Two riser cages with individual *C. volkameriana* infested with *D. citri* nymphs were assigned to each of 12 temperature regimens. Cages were rotated daily within cabinets to counteract potential thermal gradients (see Ashmore and Janzen 2003 for more details). Across all temperature regimens, riser cages were inspected at 24-h intervals for nymph development and emergence of adult *D. citri*. Emerged adults per cage and experimental temperature were counted and recorded by date then carefully removed using a vacuum-operated aspirator. Inspections for adult *D. citri* continued for 14 consecutive days after the last recorded emergence in each riser cage.

Statistical Methods

All statistical analyses were performed in SAS (SAS Institute Inc., version 9.4, Cary, NC [Institute SAS, 2009]). To assess whether the development of *D. citri* nymphs was affected by temperature (treated as a continuous variable), each temperature profile (i.e., 15, 20, 25, 30, 32, or 35°C) was considered separately (Streiner 2002, Pasta 2009, Milosavljević et al. 2019). For each temperature profile, a one-way analysis of variance was performed using the two treatment combinations (i.e., constant and fluctuating temperatures). Prior to analysis of variance, response variables were log-transformed to meet assumptions of homoscedasticity and normality. If the analysis of variance was significant at the 0.01 level of significance, individual pairwise comparisons were made between treatment means (Table 1), a total of two comparisons were made for each temperature profile, using the LSMEANS statement and DIFF option of the GLM procedure in SAS.

Meta-analysis of Temperature-Driven *D. citri* Development

A systematic search of Google Scholar, Web of Science, ScienceDirect, SpringerLink, and University of Florida Huanglongbing Bibliographical Database (Vanaclocha and Stansly 2009), was conducted to identify potentially relevant articles, abstracts, or conference papers on the effects of temperature on *D. citri* development rates. The following search terms were used: combinations of '*Diaphorina citri*' or 'Asian citrus psyllid' with 'development rate', 'growth', 'performance curve', or 'life history', and 'temperature' or 'thermal cline'. There were no search restrictions based on publication language. The bibliographies of all selected articles were reviewed to identify additional relevant studies. Abstracts and conference papers were included in this study if they contained complete results sections. Literature selection for use in the meta-analysis was restricted to published studies that provided complete development time of first-to-fifth *D. citri* instars across multiple temperatures. Studies were excluded if they met the following criteria: 1) provided development time of *D. citri* nymphs at room temperature only, 2) lacked data on development of *D. citri* nymphs across a range of temperatures, and 3) contained data duplicated from original studies (e.g., review articles). This literature review with the aforementioned selection criteria resulted in the selection of four papers with data from five experiments containing development data for *D. citri* nymphs derived from constant temperatures across different geographic regions: China (Fung and Chen 2006), Brazil (Nava et al. 2010), Japan (Nakata 2006), and Florida, United States (Liu and Tsai 2000).

Mathematical Models

The four papers selected for the meta-analysis that quantified development times for *D. citri* nymphs across multiple constant temperature regimens reared insects on six different rutaceous host plants: *Murraya paniculata* Jack (Liu and Tsai 2000, Fung and Chen 2006, Nakata 2006, Nava et al. 2010), *Citrus limonia* Osbeck, *C. sinensis* cv Natal, and *C. sinensis* cv. Pêra (L.) Osbeck (Nava et al. 2010), *C. reticulata* Blanco, and *Fortunella margarita* (Lour.) Swingle (Fung and Chen 2006) (all Sapindales: Rutaceae). From these published studies, the reciprocal of development time (i.e., D_r=1/D_t, development rate; where $D_t$is the mean development time in days) for *D. citri* nymphs (instars 1 to 5) was calculated and compared with results presented in this study (i.e., California-sourced *D. citri* nymphs reared on *C. volkameriana* [a seventh rutaceous host plant] under constant and fluctuating temperatures; Tables 2–6). This resulted

Table 1. Mean development times (days ± SE) of *Diaphorina citri* nymphs under constant and fluctuating temperature regimes

	Development time (mean days ± SE)					
	15°C	20°C	25°C	30°C	32°C	35°C
Constant	41.39 ± 0.61b (90)	29.91 ± 0.33b (113)	16.76 ± 0.12a (94)	10.91 ± 0.43b (34)	10.84 ± 0.25b (33)	14.95 ± 0.37b (39)
Fluctuating	58.48 ± 1.24a (59)	30.95 ± 0.37a (65)	17.35 ± 0.23a (82)	11.70 ± 0.21a (94)	12.16 ± 0.19a (56)	20.97 ± 0.33a (35)
P	<0.0001	0.0456	0.0493	0.0472	<0.0001	<0.0001

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

in a total of 11 datasets for *D. citri* nymph development times on seven different host plants and varying temperature regimens. One linear (Campbell et al. 1974) and six nonlinear (i.e., Ratkowsky, Lobry-Rosso-Flandrois, Lactin-2, Brière-2, Beta, and Performance-2) models were fitted to these datasets (Tables 2–6). Experimental temperatures for which no development data for *D. citri* nymphs were recorded were not used in model fitting.

The linear regression model,$D_r = a + bT$, was used to compute theoretical lower development thresholds ($T_{\min} = -a/b$, where *a* is the development rate at *T* = 0°C and *b* is the slope of regression [Campbell et al. 1974]) and thermal constants (i.e., degree-days necessary for completion of development [$K = 1/b$]) for each response variable (Table 2). Model integrity was evaluated on the basis of model goodness-of-fit to observed data (i.e., coefficient of determination [R^2] and its adjusted derivative [R^2_{adj}]). For linear regression analyses, each response variable was plotted in SAS (version 9.4; SAS Institute Inc., Cary, NC) with PROC SGPLOT and fit to an ordinary linear regression model (McCalla et al. 2019) using the REG procedure in SAS. Linear models with high values of R^2 and R^2_{adj}, indicated a good fit to the data (Table 2). In each analysis, Cook's *D* metric was computed to identify influential outliers with a critical value of Cook's $D > 4/n$, where *n* represents the number of observations (Bollen and Jackman 1990). Outliers exhibiting Studentized residuals greater than three standard deviations were omitted from analyses. Consequently, temperatures at which development rate did not align with the linear segment of the growth curve (i.e., 30°C [Liu and Tsai 2000], 32°C [Fung and Chen 2006; in all data sets], 32.5°C [Nakata 2006], and 35°C [this study; constant and fluctuating data sets]) were identified as influential outliers and excluded from linear analyses as they would affect estimation of the lower development threshold (Ikemoto and Takai 2000, Ganjisaffar and Perring 2015).

The performance of six nonlinear regression models were fitted to development rate data for five (i.e., China, Brazil, Japan, California, and Florida) geographically distinct *D. citri* populations reared under constant (data from this study and from publications used in meta-analyses) or fluctuating temperature (this study only) profiles (15 to 35°C) on seven different host plants. In the formulae for the six models being compared, *T* is the temperature in degrees Celsius, and D_r is the development rate. In the Ratkowsky, Lactin-2, and Performance-2 models, *e* denotes the base of the natural logarithms. Other symbols denote model parameters (see corresponding references for full description of models and parameters).

Ratkowsky model (Ratkowsky 1983):

$$\sqrt{D_r} = b\,(T - T_{min})\left(1 - e^{c(T - T_{max})}\right) \tag{1a}$$

$$D_r = \left(b\,(T - T_{min})\left(1 - e^{c(T - T_{max})}\right)\right)^2 \tag{1b}$$

Lobry-Rosso-Flandrois (LRF) model (Lobry et al. 1991, Rosso et al. 1993):

$$D_r = \mu_{opt}\frac{(T - T_{max})\,(T - T_{min})^2}{(T_{opt} - T_{min})\,[(T_{opt} - T_{min})\,(T - T_{opt}) - (T_{opt} - T_{max})(T_{opt} + T_{min} - 2T)]} \tag{2}$$

Brière-2 model (Brière et al. 1999):

$$D_r = aT\,(T - T_{min})\,(T_{max} - T)^{1/b} \tag{3}$$

Lactin-2 (Logan-Lactin) model (Logan et al. 1976, Lactin et al. 1995):

$$D_r = \lambda + e^{\rho T} - e^{(\rho T_u - (T_u - T)/\delta)} \tag{4}$$

Beta model (Yin et al. 2003, Shi et al. 2015):

$$D_r = rm\left(\frac{T_2 - T}{T_2 - T_m}\right)\left(\frac{T - T_1}{T_m T_1}\right)^{\frac{T_m - T_1}{T_2 - T_m}} \tag{5}$$

Performance-2 model (Shi et al. 2011, Wang et al. 2013):

$$D_r = b\,(T - T_{min})\left(1 - e^{c(T - T_{max})}\right) \tag{6}$$

All six nonlinear models were fit with the response variable, development rate, in its untransformed form because all datasets satisfied homogeneity assumptions (see Ratkowsky (2004) for more details). For the LRF, Lactin-2, Brière-2, Beta, and Performance-2 models no further transformation was necessary. For the Ratkowsky (square-root) model, however (equation 1a), it was necessary to square both sides of the expression, so that the left-hand side of the equation is the rate (equation 1b) rather than the square root of the rate (equation 1a) (Milosavljević et al. 2019). Nonlinear models were fit to each response variable using the PROC NLIN procedure in SAS (version 9.4; SAS Institute Inc., Cary, NC) and graphed in SigmaPlot (version 12.0; Systat Software, Inc, San Jose, CA) (Fig. 1).

The accuracy of nonlinear models was assessed based on the goodness-of-fit to observed data (i.e., *RSS*; Shi and Ge 2010), the model's nonlinear behavior (i.e., curvature measures of nonlinearity [Bates and Watts 1980, Karolczak and Mickiewicz 1995], and measures of bias [Box 1971] and skewness [Hougaard 1985, Ratkowsky 1990] in the least square estimators [Haines et al. 2004, Gebremariam 2014]), and the biological relevance of model estimations (i.e., $T_{\min}$ ['conceptual' lower development threshold] T_{opt} [optimal temperature for development] and $T_{\max}$ ['conceptual' upper development threshold]) (Tables 3–6; McCalla et al. 2019). Unless provided in the model output, theoretical thermal tolerance limits (i.e., T_{opt} [where D_r = max], and T_{min} and T_{max} [where $D_r = 0$]) were estimated in SAS for each response variable (Zahiri et al. 2010, Milosavljević et al. 2019). All nonlinear models evaluated have four parameters and therefore, the same degrees of freedom [*df*], and two 'theoretical' temperature bounds, the lower (i.e., T_{min}) and upper (i.e., T_{max}) bounds, at which development rates equal zero (Mirhosseini et al. 2017, Ratkowsky and Reddy 2017). Consequently, bias stemming from adjustments and multiple comparison criteria (e.g., *BIC*, *AIC*, and AIC_c) was eliminated (McCalla et al. 2019).

Table 2. Model comparisons among linear model using 11 datasets

Host species	a	b	$T_{\min}$	K (degree-days)	R^2	R^2_{adj}	Data set	Region
Murraya paniculata ($n = 4$)	−0.0584	0.0054	10.81	185.19	0.992	0.988	Liu and Tsai 2000	Florida, United States
Murraya paniculata ($n = 6$)	−0.0601	0.0052	11.56	192.31	0.978	0.972	Nakata 2006	Japan
Murraya paniculata ($n = 4$)	−0.0742	0.0059	12.58	169.49	0.971	0.981	Fung and Chen 2006	China
Murraya paniculata ($n = 6$)	−0.0686	0.0052	13.12	191.32	0.953	0.941	Nava et al. 2010	Brazil
Citrus limonia ($n = 6$)	−0.0877	0.0061	14.37	163.93	0.980	0.975	Nava et al. 2010	Brazil
Citrus sinensis cv. Natal ($n = 6$)	−0.0768	0.0057	13.43	174.54	0.978	0.972	Nava et al. 2010	Brazil
Citrus sinensis cv. Pera ($n = 6$)	−0.0799	0.0059	13.61	171.01	0.955	0.944	Nava et al. 2010	Brazil
Citrus reticulata ($n = 4$)	−0.0694	0.0052	13.35	192.31	0.988	0.981	Fung and Chen 2006	China
Fortunella margarita ($n = 4$)	−0.0672	0.0059	11.39	169.49	0.997	0.995	Fung and Chen 2006	China
Citrus volkameriana ($n = 5$)	−0.0541	0.0053	10.21	188.68	0.965	0.953	This study (constant)	California, United States
Citrus volkameriana ($n = 5$)	−0.0489	0.0040	12.23	250.01	0.975	0.967	This study (fluctuating)	California, United States

Table 3. Goodness-of-fit of the six nonlinear models to the 11 data sets for *Diaphorina citri* nymphs

	Model								
Host species	Sample size	Ratkowsky	LRF	Briere-2	Lactin-2	Beta	Performance-2	Data set	Region
Murraya paniculata	7 (210)	46^4	23^1	122^5	25^2	$-^6$	33^3	Nakata 2006	Japan
	5 (168)	120^1	149^3	531^6	195^4	193^5	132^2	Liu and Tsai 2000	Florida, United States
	5 (183)	85^1	87^2	350^6	220^5	132^3	213^4	Fung and Chen 2006	China
	6 (720)	67^1	68^2	76^4	90^6	85^5	71^3	Nava et al. 2010	Brazil
Citrus limonia	6 (720)	34^1	35^3	64^6	59^5	56^4	33^2	Nava et al. 2010	Brazil
Citrus sinensis cv. Natal	6 (720)	77^3	72^2	94^6	90^5	85^4	62^1	Nava et al. 2010	Brazil
Citrus sinensis cv. Pera	6 (720)	91^1	95^2	159^6	122^5	120^4	106^3	Nava et al. 2010	Brazil
Citrus reticulata	5 (149)	268^1	323^2	490^6	487^5	450^4	350^3	Fung and Chen 2006	China
Fortunella margarita	5 (157)	42^1	52^2	261^6	180^5	174^4	84^3	Fung and Chen 2006	China
Citrus volkameriana	6 (403)	58^1	71^2	$-^5$	139^4	$-^5$	93^3	This study (constant)	California, United States
Citrus volkameriana	6 (391)	15^1	27^2	$-^6$	61^4	65^5	57^3	This study (fluctuating)	California, United States
	Average rank	1.4^1	2.1^2	5.4^6	4.5^5	4.4^4	2.7^3		

All entries in the table are error mean squares (EMS) and have been multiplied by 10^6. The superscript after the entries indicates the rank position in each row (1 = best; …; 6 = worst).

RSS were used to assess the goodness-of-fit for nonlinear models to each data set (Shi et al. 2015, Ratkowsky and Reddy 2017, McCalla et al. 2019, Milosavljević et al. 2019):

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

where n represents the number of observations and y_i and $\hat{y}_i$ denote the observed and expected development rate at the i-th temperature, respectively. Nonlinear models with small values of *RSS* indicated a good fit to the data (Table 3). R^2 and R^2_{adj} were not used to assess the nonlinear model goodness-of-fit, as they do not describe accurately the fit of nonlinear models to developmental data sets, and can produce erroneous estimates (see Spiess and Neumeyer (2010) for further explanation).

In each analysis, relative intrinsic (i.e., the root-mean-square intrinsic [*RMS IN*]) and parameter-effects (i.e., the root-mean-square parameter-effects [*RMS PE*]) curvatures were used to quantify the overall nonlinearity of each nonlinear regression model tested (i.e., the full set of four parameters in each model; Table 5, Bates and Watts 1980). These two measures are scale-invariant with respect to both sample size and the number of model parameters (see Gebremariam 2014 for further explanation). A value of either curvature measure (i.e., *RMS IN* and *RMS PE*) that exceeds the critical curvature value (α = 0.05; Table 5) denotes 'poor' model behavior (Karolczak and Mickiewicz 1995). If the *RMS PE* measure exceeds the critical value, parameterizations may be found, in terms of new model parameters, yielding a good model fit (Ratkowsky and Reddy 2017). However, if the *RMS IN* exceeds the critical value, it denotes inherently 'poor' behavior that cannot be modified by re-parameterization (Gebremariam 2014). Nonlinearity measures of fitted models were assessed for each response variable using the NLINMEASURES option of the NLIN procedure in SAS.

In addition to evaluating the significance of the model's global nonlinearity, the estimation performance of a specific model parameter for each response variable was assessed using Hougaard's measure of skewness (Hougaard 1985) and Box's measure of bias (Box 1971) (see Ratkowsky and Reddy (2017) for more details). In models with low curvature, the nonlinear least squares parameter estimators have properties similar to those in linear regression models (Ratkowsky 1983, 1990). That is, they are the best linear unbiased and normally distributed estimators with minimum variance (otherwise they are asymptotically normal). Briefly, an absolute value of the standardized skewness measure (i.e., $|g_1|$) lower or equal to 0.2 indicates 'close-to-linear' or 'good' behavior, and if that measure is greater than 0.5, considerable nonlinear or 'poor' model behavior is present (Table 6; Ratkowsky 1983). Similarly, percentage bias greater than 1% indicates 'far-from-linear' behavior of a model parameter (Gebremariam 2014). These measures were estimated using BIAS and HOUGAARD options of the NLIN procedure in SAS in each analysis. The accuracy of model-predicted individual parameters was validated using profile t plots (PROFILE statement and TPLOT option of the NLIN procedure), the confidence curves (BOOTSTRAP statement and BOOTCI option of the PROC NLIN),

Table 4. Assessment of nonlinear behavior, intrinsic and parameter-effects curvatures of tested models

	Nonlinearity measure	Ratkowsky model	LRF model	Brière-2 model	Lactin-2 model	Beta model	Performance-2 model	Data set	Region
Murraya paniculata	RMS IN[a]	0.1121ns[c]	0.0679ns	0.0614ns	0.0945ns	0.0980ns	0.0925ns	Nakata 2006	Japan
	RMS PE[b]	3.0827*[d]^{5}	0.0657ns^{1}	2.8783*^{4}	1.9457*^{3}	18.2067*^{6}	0.0951ns^{2}		
	Crit. curvature	0.3312	0.3312	0.3312	0.3312	0.3312	0.3312		
Murraya paniculata	RMS IN	0.0251ns	0.0231ns	0.0246ns	0.0267ns	0.0213ns	0.0278ns	Liu and Tsai 2000	Florida, United States
	RMS PE	3.3301*^{4}	0.0462ns^{1}	15.7452*^{6}	3.6326*^{5}	1.6004*^{2}	1.6759*^{3}		
	Crit. curvature	0.0667	0.0667	0.0667	0.0667	0.0667	0.0667		
Murraya paniculata	RMS IN	0.0417ns	0.0237ns	0.0610ns	0.6118ns	0.0596ns	0.0289ns	Fung and Chen 2006	China
	RMS PE	3.0743*^{5}	0.0622ns^{1}	60.3264*^{6}	2.0792*^{4}	2.0150*^{3}	0.0635ns^{2}		
	Crit. curvature	0.0667	0.0667	0.0667	0.0667	0.0667	0.0667		
Murraya paniculata	RMS IN	0.1541ns	0.0432ns	0.2353ns	0.0876ns	0.1382ns	0.0717ns	Nava et al. 2010	Brazil
	RMS PE	2.3037*^{3}	0.1458ns^{1}	41.2918*^{6}	6.4708*^{5}	4.0606*^{4}	0.1571ns^{2}		
	Crit. curvature	0.2279	0.2279	0.2279	0.2279	0.2279	0.2279		
Citrus limonia	RMS IN	0.0815ns	0.0788ns	0.2218ns	0.1654ns	0.0682ns	0.1802ns	Nava et al. 2010	Brazil
	RMS PE	3.1234*^{4}	0.0478ns^{1}	29.0312*^{6}	3.4001*^{5}	3.0253*^{3}	1.9969*^{2}		
	Crit. curvature	0.2279	0.2279	0.2279	0.2279	0.2279	0.2279		
Citrus sinensis cv. Natal	RMS IN	0.1022ns	0.0711ns	0.1830ns	0.1709ns	0.1845ns	0.1839ns	Nava et al. 2010	Brazil
	RMS PE	2.5856*^{3}	0.1913ns^{1}	41.5112*^{6}	2.6394*^{4}	37.0526*^{5}	0.2218ns^{2}		
	Crit. curvature	0.2279	0.2279	0.2279	0.2279	0.2279	0.2279		
Citrus sinensis cv. Pera	RMS IN	0.1227ns	0.1180ns	0.4841*	0.1662ns	0.0757ns	0.2196ns	Nava et al. 2010	Brazil
	RMS PE	3.090*^{2}	1.0184*^{1}	64.1709*^{6}	12.7033*^{5}	3.4034*^{3}	3.4750*^{4}		
	Crit. curvature	0.2279	0.2279	0.2279	0.2279	0.2279	0.2279		
Citrus reticulata	RMS IN	0.0219ns	0.0308ns	0.0576ns	0.0294ns	0.0562ns	0.0396ns	Fung and Chen 2006	China
	RMS PE	3.0391*^{2}	0.6110*^{1}	18.3308*^{6}	3.2934*^{4}	5.4799*^{5}	3.1332*^{3}		
	Crit. curvature	0.0667	0.0667	0.0667	0.0667	0.0667	0.0667		
Fortunella margarita	RMS IN	0.0174ns	0.0148ns	0.1070*	0.0609ns	0.0614ns	0.0657ns	Fung and Chen 2006	China
	RMS PE	2.7976*^{5}	0.2953*^{1}	44.9621*^{6}	2.0131*^{4}	0.9939*^{3}	0.0396ns^{2}		
	Crit. curvature	0.0667	0.0667	0.0667	0.0667	0.0667	0.0667		
Citrus volkameriana	RMS IN	0.0291ns	0.1566ns	No convergence^{5}	0.1739ns	No convergence^{5}	0.1678ns	This study (constant)	California, United States
	RMS PE	2.5623*^{3}	0.2102ns^{1}		4.9148*^{4}		1.6446*^{2}		
	Crit. curvature	0.2279	0.2279		0.2279		0.2279		
Citrus volkameriana	RMS IN	0.0930ns	0.0843ns	No convergence^{6}	0.2069ns	0.2189*	0.0372ns	This study (fluctuating)	California, United States
	RMS PE	0.9591*^{2}	0.0789ns^{1}		2.8663*^{4}	16.4889*^{5}	1.1636*^{3}		
	Crit. curvature	0.2279	0.2279		0.2279	0.2279	0.2279		
	Average Rank	3.4^{3}	1.0^{1}	5.7^{6}	4.3^{5}	4.0^{4}	2.4^{2}		

[a] RMS IN-Root mean square intrinsic curvature.

[b] RMS PE-Root mean square parameter-effects curvature. The superscript after the entries indicates the rank position in each row (1 = best; …; 6 = worst).

[c] ns—Not significant, $P > 0.05$.

[d],*—Significant, $P < 0.05$.

Table 5. Assessment of nonlinear behavior for individual model parameters

	Model																									
	Ratkowsky				LRF				Briere-2				Lactin-2				Beta				Performance-2				Data set	Region
Host species	T_1	T_2	b	c	T_1	T_2	T_{opt}	μ_{opt}	a	T_1	T_2	b	λ	ρ	T_u	δ	*rm*	T_m	T_1	T_2	T_1	T_2	b	c		
Murraya paniculata	G	P	P	M	G	G	G	G	G	G	P	P	G	M	G	G	G	G	P	P	G	M	P	G	Nakata 2006	Japan
	G	P	P	M	G	M	G	G	G	G	P	P	G	P	P	P	G	G	P	P	G	P	M	P	Liu and Tsai 2000	Florida, United States
	G	M	P	P	G	G	P	G	G	P	P	P	G	M	P	P	G	G	P	M	G	P	M	P	Fung and Chen 2006	China
	M	P	P	M	G	M	G	M	P	P	P	P	G	P	P	P	M	G	M	P	G	P	P	P	Nava et al. 2010	Brazil
Citrus limonia	M	P	M	G	G	M	G	M	G	G	P	P	G	M	P	P	M	G	P	M	G	M	M	P	Nava et al. 2010	Brazil
Citrus sinensis cv. Natal	G	P	M	M	G	M	G	G	P	G	P	P	G	P	G	M	P	P	G	P	G	P	P	M	Nava et al. 2010	Brazil
Citrus sinensis cv. Pera	G	P	P	P	G	M	G	M	P	P	P	P	G	P	P	P	G	G	P	M	G	M	P	P	Nava et al. 2010	Brazil
Citrus reticulata	G	M	P	P	G	G	G	G	G	G	P	P	G	M	P	P	G	M	P	G	G	M	P	G	Fung and Chen 2006	China
Fortunella margarita	G	M	P	M	M	G	G	G	M	P	P	P	G	M	P	P	G	G	P	G	G	P	M	P	Fung and Chen 2006	China
Citrus volkameriana	G	P	P	G	G	M	G	G	-	-	-	-	G	M	P	P	-	-	-	-	G	M	P	P	This study (constant)	California, United States
Citrus volkameriana	G	P	M	G	G	M	M	G	-	-	-	-	M	P	G	G	G	M	P	P	M	P	M	G	This study (fluctuating)	California, United States

Key: G (good): $|g_1|\leq 0.2$. M (moderate): $0.2<|g_1|\leq 0.5$. P (poor): $|g_1|>0.5$.

Table 6. Comparison of parameter estimates among six nonlinear models using 11 datasets for *Diaphorina citri* nymphs

Host species	Model	T_{min}	T_{opt}	T_{max}	Data set	Region
Murraya paniculata	Ratkowsky	5.81	29.14	35.01	Nakata 2006	Japan
	LRF	6.31	29.38	33.66		
	Briere-2	11.07	29.58	32.76		
	Lactin-2	12.62	29.43	33.76		
	Beta	7.09	28.50	35.97		
	Performance-2	12.78	29.48	33.72		
Murraya paniculata	Ratkowsky	5.78	28.10	37.32	Liu and Tsai 2000	Florida, United States
	LRF	6.78	28.37	35.99		
	Briere-2	6.63	29.05	30.01		
	Lactin-2	10.50	28.76	35.83		
	Beta	1.05	28.30	36.06		
	Performance-2	10.55	28.86	35.85		
Murraya paniculata	Ratkowsky	5.62	29.52	36.81	Fung and Chen 2006	China
	LRF	6.99	29.46	35.80		
	Briere-2	6.41	31.17	32.00		
	Lactin-2	10.58	29.81	35.72		
	Beta	−10.92	29.38	35.88		
	Performance-2	10.86	29.79	35.72		
Murraya paniculata	Ratkowsky	8.17	29.11	35.44	Nava et al. 2010	Brazil
	LRF	8.83	29.22	33.14		
	Briere-2	12.32	29.27	30.93		
	Lactin-2	14.10	29.26	33.07		
	Beta	1.29	29.75	36.43		
	Performance-2	14.22	29.18	33.06		
Citrus limonia	Ratkowsky	8.01	29.34	34.53	Nava et al. 2010	Brazil
	LRF	9.84	30.71	36.51		
	Briere-2	12.20	29.54	30.51		
	Lactin-2	14.42	29.75	33.42		
	Beta	−1.68	30.44	36.89		
	Performance-2	14.56	29.95	33.41		
Citrus sinensis cv. Natal	Ratkowsky	5.76	30.79	40.33	Nava et al. 2010	Brazil
	LRF	6.43	31.07	35.36		
	Briere-2	8.26	30.55	33.59		
	Lactin-2	14.04	30.79	36.50		
	Beta	2.13	30.67	38.01		
	Performance-2	14.15	30.75	36.47		
Citrus sinensis cv. Pera	Ratkowsky	9.34	29.39	36.54	Nava et al. 2010	Brazil
	LRF	9.62	29.44	33.81		
	Briere-2	13.20	29.56	31.50		
	Lactin-2	14.54	29.55	33.78		
	Beta	−7.40	29.07	34.39		
	Performance-2	14.65	29.57	33.81		
Citrus reticulata	Ratkowsky	8.03	27.94	37.52	Fung and Chen 2006	China
	LRF	8.97	28.04	36.24		
	Briere-2	10.42	28.31	32.64		
	Lactin-2	11.14	28.37	36.06		
	Beta	−18.63	28.61	34.38		
	Performance-2	11.15	28.36	36.08		
Fortunella margarita	Ratkowsky	6.32	28.85	37.06	Fung and Chen 2006	China
	LRF	7.64	28.83	35.93		
	Briere-2	7.52	30.92	32.01		
	Lactin-2	10.93	29.19	35.81		
	Beta	−0.33	28.81	35.98		
	Performance-2	10.98	29.18	35.81		
Citrus volkameriana	Ratkowsky	5.71	32.10	37.32	This study (constant)	California, United States
	LRF	6.81	32.77	35.65		
	Briere-2	No convergence				
	Lactin-2	10.77	32.83	35.95		
	Beta	No convergence				
	Performance-2	10.95	32.77	35.90		
Citrus volkameriana	Ratkowsky	2.43	31.13	37.24	This study (fluctuating)	California, United States
	LRF	2.81	31.53	35.92		
	Briere-2	No convergence				
	Lactin-2	11.87	31.76	35.96		
	Beta	−273.15	31.05	36.46		
	Performance-2	11.99	31.81	35.94		

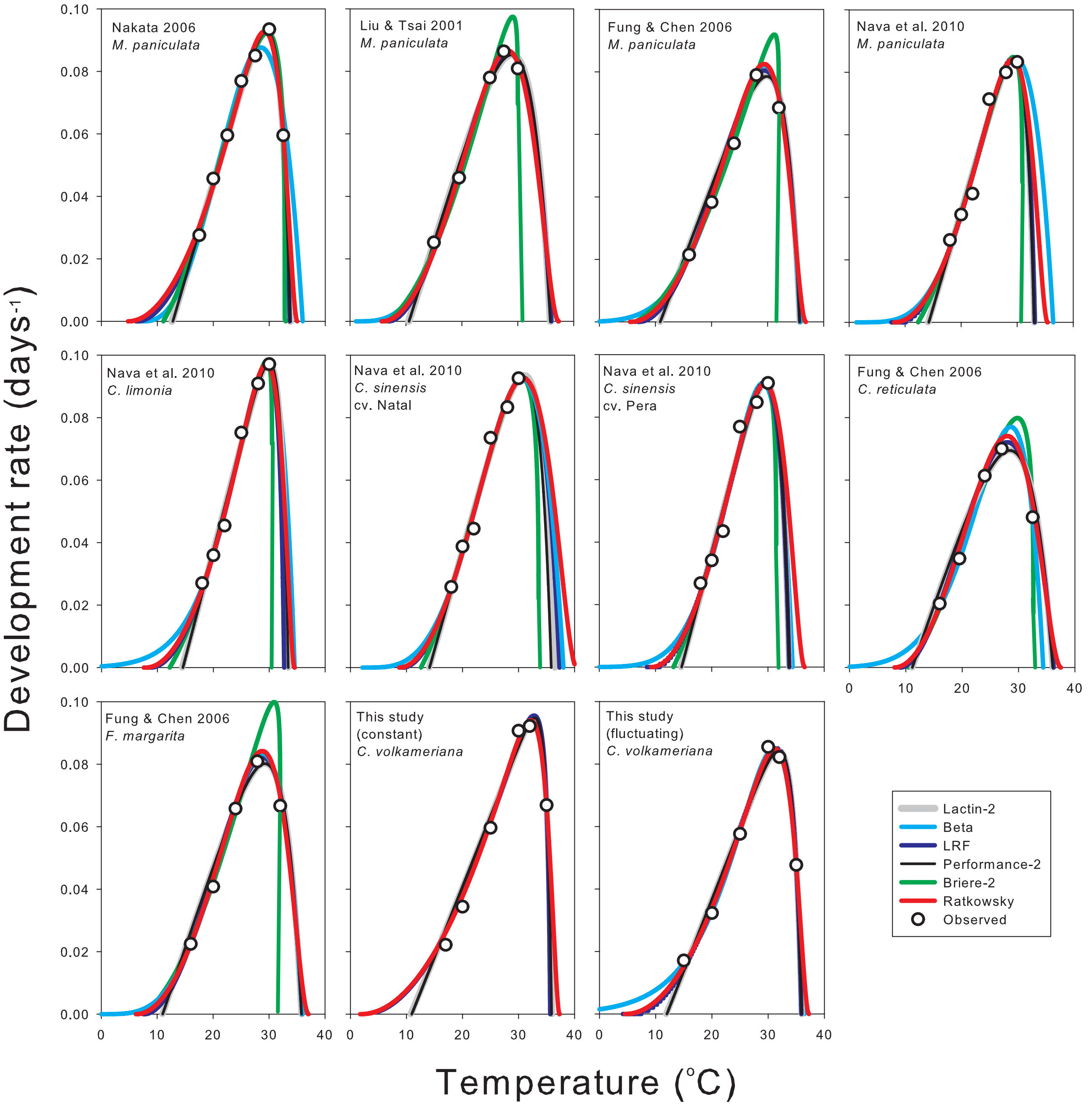

Fig. 1. Relationship between temperature (°C; *x*-axis) and development rate (days–1; *y*-axis) of *Diaphorina citri* nymphs as described by six thermal performance functions. Experimentally measured values for 11 datasets are represented by circles. Solid lines represent model predictions for constant and fluctuating temperatures: light blue (Beta model), green (Briere-2 model), dark blue (LRF model), gray (Lactin-2 model), black (Performance-2 model), and red (Ratkowsky model).

and the parameter distribution histograms (BOOTSTRAP statement and BOOTPLOTS option of the NLIN procedure) (see Ratkowsky and Reddy 2017 for details).

Results and Discussion

All experimental populations of *D. citri* completed development across all constant and fluctuating temperature profiles (Table 1). Thermal effects differed considerably between the two temperature exposure regimens (regimen effects: $P < 0.05$ for all temperature profiles). Specifically, longer development times of *D. citri* nymphs exposed to fluctuating temperatures were recorded when compared to constant temperatures with the same corresponding mean temperature. Development times for immature *D. citri* reared under constant and fluctuating temperature scenarios decreased, however, with temperatures increasing from 15 to 32°C, before increasing slightly at highest experimental temperature examined (i.e., 35°C; Table 1). This pattern is consistent with similar studies investigating the effects of constant and fluctuating temperatures on development rates for *Tamarixia radiata* (Waterston) (Hymenoptera: Eulophidae) (McCalla et al. 2019) and *Diaphorencyrtus aligarhensis* (Shafee, Alam, Argarwal) (Hymenoptera: Encyrtidae) (Milosavljević et al.

2019), two primary parasitoids that attack *D. citri* nymphs (Hoddle and Pandey 2014, Bistline-East et al. 2015, Milosavljević et al. 2017).

The largest differences between the mean development times of immature *D. citri* reared under constant and fluctuating temperatures were observed near the lower and upper extremes of experimental temperature clines (Table 1). At high temperatures (i.e., >30°C), *D. citri* reared under fluctuating temperatures completed development more slowly than those reared under constant temperatures with the equivalent mean temperatures (Table 1). This is notable, as *D. citri* reared under high fluctuating regimens appear to be at risk of accumulation of detrimental effects due to exposure to excessively high temperatures for short periods of time (i.e., 41°C for 3 h), and detrimental impacts may be further amplified by adverse temperature-induced effects on the host plants upon which they are developing (Colinet et al. 2015; Gomez-Marco et al. 2019). At constant temperatures, 30 and 32.5°C, *D. citri* completed development and these constant regimens do not expose nymphs to relatively short periods of very high temperatures (Nakata 2006; Fung and Chen 2006; Nava et al. 2007, 2010). A notable exception is *D. citri* sourced from Florida which failed to complete development at 33°C (Liu and Tsai 2000). In comparison to other published studies, our results indicate successful development at 35°C of *D. citri* nymphs sourced from California under both constant and fluctuating temperature scenarios. This result suggests that immature *D. citri* may be able to cope with high summer temperatures (i.e., >35°C for >9 h [at fluctuating 32°C], and >35°C for >11 h [at fluctuating 35°C]) that may occur in some regions in southern California where urban and commercial citrus is grown (e.g., Riverside, Indio, and the Coachella Valley). Consequently, risk assessments that include metrics of relative heat tolerance for *D. citri* may offer an important indicator of invasion risk for areas of concern.

The experimental low temperature means in this study were based on a range of prevailing winter and early spring temperatures experienced in regions where citrus is grown in California (Supp Table 1 [online only]; Milosavljević et al. 2019). Data presented here suggest that, like other poikilotherms, that cooler fluctuating temperatures delay development of immature *D. citri* when compared with constant temperature counterparts (Table 1). The lowest fluctuating temperature tested averaged 15°C and this exposed nymphs to the lowest temperature of 9°C for 3 h (Supp Table 1 [online only]), a temperature not assessed in any constant temperature studies. The effects of prolonged 'cool' temperatures below the limits investigated by constant temperature regimens (i.e., 15°C was the lowest temperature evaluated), may have significant effects on *D. citri* development rates and subsequent adult fitness (Jensen 1906, Gilbert and Raworth 1996, Kontodimas et al. 2007, Hall et al. 2011, Colinet et al. 2015). Evaluation of the effects of temperatures lower than those used in this study (e.g., 12°C fluctuating), and which are typical of citrus-producing areas in California, on the development of *D. citri* are recommended.

In this study, the linear model had R^2_{adj} values > 0.95 for both constant and fluctuating temperature regimens, specifying a good fit to the datasets (Table 2). The parameter estimates (e.g., degree-days, lower thermal thresholds) differed between models fit to constant versus fluctuating temperature datasets. Estimates of the total development time in degree-days for California-sourced *D. citri* nymphs were significantly lower for the constant temperature regimen than the corresponding fluctuating temperature scenarios, with 189 and 250 degree-days, respectively (Table 2). These findings agree with those of other similar studies suggesting that temporal predictions of population dynamics using models fit to development data from constant temperatures could produce unrealistic estimates of generation times for populations that are exposed to fluctuating daily thermal cycles in the field (McCalla et al. 2019, Milosavljević et al. 2019).

Meta-analysis of *D. citri* development data (Liu and Tsai 2000, Nakata 2006, Fung and Chen 2006, Nava et al. 2010) indicated that linear regression provided a good fit to each data set evaluated with correlation coefficients generally being greater than 0.94 (Table 2). The parameter estimates (e.g., degree-days required for completion of cumulative development [ranged 164 to 192], theoretical minimum thresholds [ranged 10.21 to 14.37°C]) were similar for *D. citri* data sets used in meta-analyses (Table 2). It is unknown whether these observed consistencies across *D. citri* populations and host plants resulted because of similar genetic composition of these geographically distinct populations (De León et al. 2011, Boykin et al. 2012, Fuentes et al. 2018), from localized adaptations to prevailing climatic conditions, or because the range of temperatures evaluated may not have been sufficiently 'extreme' at low and high ends of experimental clines for differences to be expressed. The global genetic diversity of *D. citri* from 27 different countries (including populations from Brazil, China, and United States [both California and Florida]) was assessed using mitochondrial cytochrome oxidase I (mtCOI) sequencing (Fuentes et al. 2018). This study detected very little genetic diversity among sampled populations with respect to mtCOI haplotypes. It is uncertain whether similarity in mtCOI haplotypes across *D. citri* populations represents similarities in nuclear DNA that presumably regulates fitness genes, which could influence cold and heat tolerances (Hoy 2004).

The overall best fitting nonlinear models fitted to the 11 datasets were the LRF, Ratkowsky, and Performance-2 (Tables 3–6; Fig. 1). These models include parameters of biological relevance (Ratkowsky and Reddy 2017, McCalla et al. 2019). All four parameters of the LRF model have biological meaning, notional minimum and maximum temperatures for development (T_1 and T_2, respectively), optimal temperature for development (T_{op}), and growth rate (μ_{op}). In comparison, the Ratkowsky and Performance-2 models contain two parameters that have biological significance, minimum and maximum temperatures for development (T_1 and T_2). The other two curve fitting constants (*b* and *c*) have no biological meaning. The LRF, Ratkowsky, and Performance-2 models generally yielded much lower *RSS* values than other models that were fitted to the meta-analysis datasets (Table 3). Likewise, there was very little difference between the *RSS* values for the three models when fitted to constant and fluctuating datasets for California-sourced *D. citri* used in this study. Nevertheless, the LRF, Ratkowsky, and Performance-2 functions differed in terms of their *RMS PE* values (Table 4). Off these three models, the LRF model was superior as it had significant *RMS PE* values for only three of the 11 datasets evaluated and ranked best overall (Table 4). The estimates of all four parameters of the LRF model were unbiased, had low skewness, and were close to being linear in all datasets (Table 5). Compared with the LRF function, the estimates of three of the Ratkowsky and Performance-2 model parameters, T_2, *b*, and c, were biased for most of the datasets (Table 5). The Performance-2 model provided slightly poorer fits than the LRF and Ratkowsky models (Tables 4 and 5) but gave estimates of lower theoretical thresholds within a potentially biologically realistic range (Table 6). Based on these overall results, future studies examining the temperature-dependent development of *D. citri* should consider inclusion of the LRF, Ratkowsky, and Performance-2 functions for modeling thermal performance curves.

The worst fitting model in the meta-analysis was the Brière-2 model, which deviated widely from the observed data (Tables 3–5). For example, Brière-2 often yielded much higher *RSS* (Table 3) and

RMS PE (Table 4) values than any other model used in these analyses. The estimates of two of its parameters, T_2 and *b*, displayed poor nonlinear behavior for all 11 datasets (Table 5), and parameters, T_1 and *a*, yielded poor nonlinear behavior for almost half of the datasets evaluated (Table 5). In addition, Brière-2 performed poorly in suboptimal range of the upper temperature bound for development, where, for nine datasets, the values for the *b* parameter were high. These high estimates caused the model fit to the response variable (development rate) to intersect the temperature axis with notional maximum temperature estimates that were lower than any other model (Table 6). Brière-2 also failed to converge for constant and fluctuating datasets of California-sourced *D. citri* (Table 4).

The Lactin-2 model was also a poor-fitting model in comparison to the Beta, LRF, Ratkowsky, and Performance-2 nonlinear functions (Tables 3–5). This model ranked second-worst overall in terms of both its goodness-of-fit to the 11 datasets (i.e., *RSS* values; average rank of 4.5) and *RMS PE* values (average rank of 4.3) (Tables 3 and 4). Moreover, the estimates of three of its parameters, ρ, T_u, and δ, displayed poor nonlinear behavior for half of the datasets that were compared (Table 5). The Lactin-2 model may not be particularly useful as model parameters have no biological meaning (i.e., λ, ρ, and δ) or are of no practical use (e.g., T_u or the upper 'lethal' temperature, which is higher than the 'conceptual' upper developmental threshold; Lactin et al. 1995). Interestingly, however, estimated parameter values for Lactin-2 were very similar to those of the Performance-2 model, with both models producing similar predictions for all 11 datasets (Table 6).

The Beta model performed poorly in the lower temperature region for development in comparison to the other five models used in this study, producing estimates of lower thermal thresholds for immature *D. citri* that lacked biological relevance (Table 6). For example, for the fluctuating dataset in this study, the Beta model estimate of T_1 was −273.15°C (i.e., absolute zero). It is highly unlikely that *D. citri* development occurs at temperatures below 0°C as predicted by the Beta model. In addition, the Beta model ranked third-worst overall in terms of both its *RSS* values (average rank of 4.4) and *RMS PE* values (average rank of 4.0) (Tables 3 and 4), and it did not converge for the constant temperature dataset evaluated experimentally in this study. The Beta model is unsuitable for modeling the development of immature *D. citri*, a result similar to that found for *T. radiata* development data (McCalla et al. 2019).

Nonlinear estimates of the theoretical optimum (T_{opt}) and upper (T_{max}) temperatures for development were similar among datasets (i.e., *D. citri* host plant species and geographical areas of origin) and regimens (Table 6). However, the critical lower temperature (T_{min}) above which development of immature *D. citri* occurs was generally estimated to be higher under constant regimens than at fluctuating temperatures (Table 6). This finding suggests that the use of constant temperature development data may overestimate the ability of *D. citri* to develop in cooler regions. Results from analyses completed in this study suggest that the lower thermal thresholds for *D. citri* nymphs ranged from 2.43 to 14.65°C for *D. citri* (excluding the Beta model estimates), regardless of temperature regimen (i.e., constant or fluctuating) (Table 6). These lower temperature range estimates for development overlap with reported lower temperature ranges, −5 to 12°C, for the two primary parasitoids, *T. radiata* and *D. aligarhensis*, that attack *D. citri* nymphs (McCalla et al. 2019, Milosavljević et al. 2019). Importantly, estimated values of T_{min} (and also T_{max}) do not necessarily represent the exact minimum and maximum temperatures at which development occurs (McMeekin et al. 2013, Ratkowsky and Reddy 2017). Nevertheless, these conceptual lower and upper thermal bound estimates could provide approximations of 'true' development threshold values (i.e., *MIN*t and *MAX*t) for immature *D. citri*, which most likely lie within the range of estimated parameter values predicted by several fitted models (Ratkowsky 2004). Therefore, upper, lower, and optimal temperature values predicted by models used in this study can be viewed as 'hypotheses' that are amenable to experimental investigation.

In summary, fluctuating temperature scenarios that are similar to field conditions under which citrus is grown increased development times and estimates of degree-days needed for development by *D. citri* when compared to results from constant temperature exposure studies. This finding may have significant importance for temperature-driven predictions pertaining to *D. citri* establishment and spread in regions where this pest is invasive or has high incursion likelihood. Additionally, meta-analysis results demonstrated convergence of developmental parameter estimates across five geographically distinct *D. citri* populations infesting seven rutaceous host plant species. This finding may increase confidence with respect to predictions generated by *D. citri* invasion and establishment risk assessment models that incorporate temperature-based parameters.

Supplementary Material

Supplementary data are available at *Journal of Economic Entomology* online.

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