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Author(s): Leigh J. Pilkington , Michael Lewis , Daniel Jeske , and Mark S. Hoddle
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Calculation and Thematic Mapping of Demographic Parameters for *Homalodisca vitripennis* (Hemiptera: Cicadellidae) in California

LEIGH J. PILKINGTON,[1,2] MICHAEL LEWIS,[1] DANIEL JESKE,[3] AND MARK S. HODDLE[1,4,5]

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ABSTRACT The reproductive and developmental biology, including life tables, for *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), the glassy-winged sharpshooter, were quantified at four constant temperatures in the laboratory: 20, 25, 30, and 33°C. Mean time from egg oviposition to adult death and mean female adult longevity was greatest at 25°C. Mean total progeny production was greatest at 25°C at 214 eggs per individual. The percentage of females ovipositing at each experimental temperature was relatively low at 22, 46, and 56% at 20, 25, and 30°C, respectively. No oviposition occurred at 33°C. Upper, lower, and optimal developmental thresholds were calculated for all life stages, and for egg to adult emergence these were 35.95, 13.99, and 29.45°C, respectively. Key demographic parameters were calculated and intrinsic rate of increase and net reproductive rate were highest at 30 and 25°C at 0.04 and 40.21 d, respectively. Mean generation times and population doubling times were lowest at 25 (97.66 d) and 30°C (15.51 d). Modeling of demographic parameters indicated that approximately three generations of *H. vitripennis* per year are needed for the existence of permanent populations. Historical weather data were used to map the number of generations and estimate net reproductive rates for *H. vitripennis* throughout California. Data presented here will be useful for modeling and estimating the possible invasion success of *H. vitripennis* in areas other than California.

KEY WORDS degree–day, demographic, developmental biology, GIS mapping, invasive pest

Understanding the reproductive and developmental biology of an organism is critical in estimating its potential to establish a population in an invaded area (Pilkington and Hoddle 2006a). Degree–day accumulation is the acquisition of thermal units above a critical minimum for which development is required over time, and with respect to different temperature regimens, this phenomenon has been used to predict aspects of insect developmental and reproductive biology (Baskerville and Emin 1969). For invasive pests, environmental conditions of the receiving area, acting independently of other important factors such as host availability and natural enemies, may assist in the prediction of how vulnerable that region is to invasion (Sutherst 2000, Baker 2002). Further, climatic conditions in the receiving area may cause incursions to be temporary due to unfavorable conditions for prolonged periods (Jarvis and Baker 2001, Hoddle 2004, Hatherly et al. 2005) or potentially permanent due to a compatible year-round environment for the pest (Sutherst 2000, Baker 2002, Hoddle 2004). After establishment, favorable climatic conditions in turn drive pest phenology, population dynamics, abundance, and spread (Gutierrez et al. 2011).

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), is an invasive pest native to the southeastern United States and northeastern Mexico, and has high agricultural importance because it transmits the xylem-dwelling bacterium *Xylella fastidiosa*, which causes numerous lethal maladies in various plants, including Pierce's disease of grapes (Pilkington et al. 2005). *H. vitripennis* is xylophagous and females lay eggs in clusters, often referred to as egg masses, on the undersides of leaves. Nymphs hatch from these eggs and pass through five nymphal instars before reaching the adult stage (Sétamou and Jones 2005). After its accidental introduction into California and French Polynesia, *H. vitripennis* demonstrated high rates of population growth and rapidly spread throughout the invaded regions (Pilkington et al. 2005, Grandgirard et al. 2009, Petit et al. 2009). In California, *H. vitripennis* has established itself in much of the southern part, including the counties of Los Angeles, Riverside, Orange, San Bernardino, and Ventura, and parts of Santa Barbara, Kern, Fresno, and Santa Clara Counties (California Department of Food and Agriculture [CDFA] 2013; Fig. 2A). In some areas where populations are highly localized, as in San Luis Obispo, Tulare, Fresno, and

[1] Department of Entomology, University of California, Riverside, Riverside, CA, 92521.
[2] Current address: NSW Department of Primary Industries, Central Coast Primary Industries Centre, Ourimbah, NSW, 2258 Australia.
[3] Department of Statistics, University of California, Riverside, CA 92521.
[4] Center for Invasive Species Research, University of California, Riverside, CA 92521.
[5] Corresponding author, e-mail: mark.hoddle@ucr.edu.

Santa Clara Counties, eradication programs are ongoing and tentatively appear to have been successful in certain locations (e.g., San Luis Obispo; CDFA 2013). Favorable climatic conditions, a lack of effective natural enemies in the receiving range, abundant host plants, and no significant competitors in California and other invaded areas (e.g., French Polynesia) contributed to the high invasion success of *H. vitripennis* (Hoddle 2004, Grandgirard et al. 2009, Petit et al. 2009).

Incursion success may be predicted a priori by examining how climatic variables, such as prevailing year-round temperatures, affect estimates of population growth, and subsequently, the likelihood that an organism will successfully spread to new areas by indicating geographical regions where climatic conditions are conducive to the establishment of permanent populations (Hoelmer and Kirk 2005). Estimations of degree–day requirements coupled with measures of reproductive biology, such as net reproductive rates (R_o), can be used to determine the temperature at which ranges are suitable for persistent year-round populations and the subsequent intensity of population growth. For example, laboratory studies across a range of temperatures on the development and reproduction of two species of mymarid egg parasitoid associated with *H. vitripennis* were used to develop thematic maps using climate data to determine potential geographic ranges of these natural enemies in California (Pilkington and Hoddle 2006b, 2007). Similar studies are lacking for *H. vitripennis* and represent a significant deficit in our fundamental understanding of the developmental and reproductive biology of this pest.

The aim of this work was to examine the developmental and reproductive biology of *H. vitripennis* under controlled temperatures in the laboratory and to generate estimates of key demographic parameters (e.g., net R_o) across a variety of temperatures. Using these demographic data and long-term climate records, the invasion potential of *H. vitripennis* in areas of California where this pest has not yet established was determined. These data were used to predict and map the number of *H. vitripennis* generations and subsequent net R_os for this pest using long-term historical weather data with geographic information system models. In addition, these laboratory-derived data for *H. vitripennis* are applicable to modeling for areas outside of California, especially major grape producing areas, to determine their suitability for invasion.

Materials and Methods

***H. vitripennis* Colony Maintenance for Experiments.** Potted, insect-free "Eureka" lemon trees, *Citrus limon* (L.) Burm., a cultivar preferred by *H. vitripennis* for egg laying (Irvin and Hoddle 2004), were planted in 1-liter pots, watered twice during the first week with fertilizer solution (Dynamite plant food; Enviro-Safe Laboratories Inc., Miami, FL) and subsequently refertilized every 6 mo. Trees were placed in two large (2.4 by 1.8 by 1.8 m) mesh-screened, walk-in cages located within a temperature controlled glasshouse (6.5 by 3.8 by 3.8 m) maintained at 15–28°C at the Ag-Ops Field Station, University of California, Riverside, CA. Plants were watered every 2 d. Monthly field collections of *H. vitripennis* adults were made from unsprayed citrus at Ag-Ops and ≈500–1000 adults were added to these caged plants immediately after collection. Between April 2006 and May 2008, *H. vitripennis* females of undetermined age and mating status were harvested from these cages when needed and eggs laid by these females at each experimental temperature were used to initiate the experiments detailed here (see below).

Experimental Cage Set-Up, Temperatures, and Number of Females Used for Experiments. Four individual growth cabinets (Percival Scientific Inc., Perry, IA) were set at 20°C (±0.6°C; 18 females), 25°C (±0.5°C; 22 females), 30°C (±0.5°C; 22 females), and 33°C (±0.3°C; 17 females) under long days (a photoperiod of 14:10 [L:D] h) and 50% relative humidity (RH). Temperatures and RH in cabinets were measured every 30 min with HOBO data loggers (Onset Computer Co., Bourne, MA). Host plants used in this study were greenhouse-grown cowpeas (Black Eye #5, Ferry Morse, Mountain View, CA), a host plant previously demonstrated to be suitable for these types of studies (Sétamou and Jones 2005, Sisterson 2008), grown in 10-cm-diameter pots with Kellogg Amend Garden Soil for Flowers and Vegetables (Kellogg Garden Products, Carson, CA). Plants were maintained at ≈25–30°C under a photoperiod of 14:10 (L:D) h. Plants were watered daily and fertilized weekly with MiracleGro (The Scotts Company, Marysville, OH). Female *H. vitripennis* sourced from colony maintenance cages (see above) and assumed to have mated were introduced onto potted cowpea plants enclosed by 3-liter clear plastic soda bottle cages (Boyd et al. 2007) and allowed to oviposit. Bottle cages were observed daily, and females were removed once eggs had been laid. Egg hatch rates across temperatures were determined by daily observations for nymphal eclosion. Developmental times for 1,016 fertile eggs laid by *H. vitripennis* females across all experimental temperatures were recorded and used to calculate mean egg hatch times in days for each experimental temperature. At 20°C, data from 465 eclosed eggs were used to determine the average egg hatch times; at 25°C, 212 eggs eclosed; at 30°C, 202 eggs hatched; and at 33°C, 137 eggs eclosed. If additional nymphs were needed for nymphal developmental studies, eggs were hatched at specific experimental temperatures but time to eclosion was not recorded. In total, 945 individual *H. vitripennis* nymphs that hatched from eggs laid by females at each experimental temperature were set-up individually on cow pea plants enclosed by a bottle cage to determine nymphal developmental times for each experimental temperature; 156 nymphs were set up at 20°C, 197 at 25°C, 323 at 30°C, and 269 at 33°C. Nymphs were monitored daily and developmental stage and survivorship rates were recorded for each temperature. Nymphs successfully reared to adults were sexed and kept at the same experimental

temperature to calculate daily and lifetime fecundity and survivorship rates (both females only) on potted cowpea plants enclosed by bottle cages. Cowpea plants were replaced if they showed evidence of deterioration and *H. vitripennis* were transferred to these new plants.

Calculation of Demographic Growth Parameters. Time from oviposition to nymphal emergence, time of duration in each of five nymphal instars, daily adult survivorship rates and fecundity, and sex ratio of offspring at each experimental temperature were used to construct $l_\chi m_\chi$ life tables from which demographic growth parameters were calculated. Only reproductive output data from adults that died naturally were used for calculation of demographic growth parameters. At 20°C data from 44 females were used, at 25°C from 90 females, and at 30°C from 113 females. At 33°C, only three *H. vitripennis* nymphs (≈1%) of the 269 nymphs set-up on plants survived to adult emergence and this temperature was discarded from further analysis. Nymphs that passed successfully through life stages were used to calculate developmental times for each instar even if they did not develop to adults.

The following demographic parameters were calculated from $l_\chi m_\chi$ life tables (Pilkington and Hoddle 2006a, 2007):

1. Net R_o ($R_o = \Sigma l_\chi m_\chi$, where $l_\chi m_\chi$ is the net female maternity, l_χ is the fraction of females alive at age χ, and m_χ is the number of daughters born to surviving females at age χ; Carey 1989).
2. Mean generation time ($T_c = \Sigma \chi l_\chi m_\chi / R_o$; Carey 1989).
3. The intrinsic rate of natural increase, r_m. The value of r_m is iterated until the Equation $1 = \Sigma l_\chi m_\chi \exp(-r_m)$ is solved (Birch 1948).
4. Finite rate of increase, $\lambda = \exp(r_m)$ (Birch 1948).
5. Population doubling time, $T_d = \ln(2)/r_m$ (Carey 1989).

Mean demographic parameter estimates with SEs were generated using bootstrap pseudoreplication of $l_\chi m_\chi$ life table data. At each temperature, life tables and associated demographic parameters were constructed for each possible outcome for the random selection, removal, and replacement of individual females from the cohort of females that died from old age for each specific experimental temperature. Females dying prematurely from other causes (e.g., drowning) or "disappeared" prematurely were discarded from these analyses.

The new dataset that was calculated by bootstrapping contains many pseudoreplicates and no adjustment for the removed individual is necessary, although bias in the generated mean R_o value ($R_{o.adj}$) is reduced with the equation:

$$R_{o.adj} = 2 \times R_{o.all} - R_{o.bootstrapped} \text{ (Meyer et al. 1986)}$$

From this bootstrap analysis, mean and variance estimates for each demographic parameter of interest were calculated for *H. vitripennis.*

Mean adult longevity, preoviposition, total and mean daily progeny, mean development time, and sex ratio were compared across temperatures with analysis of variance using Genstat (2009). Quadratic regression lines were fitted to the pseudoreplicates for the demographic parameter means to estimate the affect of different temperatures outside the experimental temperature range using Microsoft Excel 2003 (Microsoft Corporation, 2010; Microsoft Corporation, Redmond, WA).

Fitting the Modified Logan Model to *H. vitripennis* Data Sets. The modification by Lactin et al. (1995) to the Logan model (Logan et al. 1976) was used to regress developmental rate (1/d) with temperature for developmental data from individually reared *H. vitripennis* life stages at each experimental temperature,

$$r(T) = e^{\rho T} - e^{(\rho T_{max} - [T_{max} - T])/\Delta)} + \lambda. \quad [1]$$

where r(T) is the developmental rate at temperature T (°C); and ρ, T_{max}, Δ, and λ are fitted parameters (Lactin et al. 1995). In the original Logan model, which has no λ parameter, T_{max} was the upper developmental threshold. The Lactin modification used the λ parameter to estimate the lower developmental threshold. With the Lactin model in (1), the lower and upper developmental thresholds (LDT and UDT) can be found as the two solutions to the equation:

$$e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\rho]} + \lambda = 0\,. \quad [2]$$

The optimal developmental temperature (T_{opt}) was solved for:

$$T_{opt} = T_{max} - \Delta \log(\Delta\rho)/\Delta\rho - 1\,. \quad [3]$$

Consequently, Equations 1, 2, and 3 were used to estimate minimum, maximum, and optimal temperatures for the development of each *H. vitripennis* life stage. The thermal constant K, or degree–day requirements for development of each life stage (Campbell et al. 1974), was found as the reciprocal of the slope of the line joining the points (LDT, 0) and (T_{opt}, $r[T_{opt}]$). This value can be shown to be

$$K = (T_{opt} - LDT)/r(T_{opt}). \quad [4]$$

SE estimates for K were determined using the Delta Method (Casella and Berger 2002). Lactin models (1) were fitted to all observations for each temperature by iterative nonlinear regression using PROC NLIN in SAS (SAS Institute 2008, SAS Institute, Cary, NC) using the Marquardt algorithm, where a grid of alternative starting values was used to select the optimal starting value, and nonnegative constraints on ρ, T_{max}, and Δ were set at each iteration.

Calculation of the Number of *H. vitripennis* Generations by Location for Geographic Information System (GIS) Mapping. Two estimates of the number of *H. vitripennis* generations in a given year were calculated for each weather station. The first was the number of generations based on degree–day accumulation (UC IPM 2005, Pilkington and Hoddle 2006a) and the second was calculated using an adaptation of the fitted model equation for T_c; see results):

$$T_c = -3.0264\chi^2 + 147.92\chi - 1616.2$$

where χ is the daily average temperature at each weather station.

The value for T_{num}, the proportion of a generation that was completed at the prevailing average temperature for each weather station, was calculated for each 24-h period by taking the reciprocal of that day's value for generation time calculated from the daily mean temperature at that weather station and then summing over 365 d (Pilkington and Hoddle 2006b). Temperatures below 16.5°C (the minimum developmental threshold for *H. vitripennis* across all life stages [see results]) were considered too cold and development would temporarily cease, returning a value of zero at that weather station at that specific time. The formula for calculating the total number of yearly generations, T_{num}, for *H. vitripennis* was:

$$T_{num} = \Sigma_{\chi \text{ day } 1 \ldots 365} \left(1/\left(-3.0264\chi^2 + 147.92\chi - 1616.2\right)\right)$$

where χ is equal to the daily average temperature at each weather station.

Calculation of Net R_o for GIS Mapping. When the value for R_o is >1.0, the population increases in size. In contrast, when R_o is <1.0, populations contract; R_o of one indicates a stable population (Deevey 1947). The persistence of *H. vitripennis* populations in a given area in California was estimated by calculating the average R_o, for each weather station from daily maximum and minimum temperature values. The model used for estimating R_o across a range of temperatures was:

$$R_o = -1.113\chi^2 + 57.481\chi - 701.19$$

where χ is equal to the daily average temperature at each weather station. Owing to the fact that R_o is an instantaneous estimate (as opposed to T_{num}, which accumulates over time, daily estimates for R_o were averaged over the entire year to calculate R_o for *H. vitripennis* populations in specific locations). It was assumed that any area where the calculation of the yearly value for R_o resulted in a negative value would not allow *H. vitripennis* populations to persist year-round, although temporary establishment for specific periods may have been possible. Means for a geographic point that were returned as negative values were converted to zeroes (indicating that permanent establishment was unlikely) and mapped accordingly.

Construction of GIS Maps to Assess Invasion Potential of *H. vitripennis* in California. Historic daily maximum and minimum temperatures from 121 Californian weather stations maintained by the California Irrigation Management Information System (CIMIS, http://www.cimis.water.ca.gov) and 260 Californian weather stations maintained by the Western Regional Climate Center (WRCC, http://www.wrcc.dri.edu/) were used for GIS modeling of *H. vitripennis* demographic parameters. Daily maximum and minimum temperatures were averaged over 5 to 10 yr of complete weather data between 1 January 1995 and 31 December 2004. The biofix point for generating demographic estimates for GIS modeling was 1 January of the year of interest. These were the same data used in previous mapping studies of life table parameters for two mymarid egg parasitoids of *H. vitripennis, Gonatocerus ashmeadi* Girault, and *Gonatocerus triguttatus* Girault, that had been used in biological control programs against this pest in California (Pilkington and Hoddle 2006b, 2007). Consequently, climate-driven predictions from models developed here for *H. vitripennis* are directly comparable to data sets generated previously for natural enemies of this pest.

The number of generations estimated by degree–day accumulation and generational turnover using the R_o model as calculated for *H. vitripennis* from all weather stations were compiled into an Excel spreadsheet along with the location of the station in decimal degrees of latitude and longitude. The spreadsheet was imported into ArcGIS 10.1 (Environmental Systems Research Institute [ESRI], Redlands, CA) and used for analyses. The estimated number of generations (T_c), and R_o for *H. vitripennis* for each weather station were converted into an ArcGIS shapefile and latitude–longitude coordinates were used to perform Teale Albers projections (ESRI 2012).

The ArcGIS extension Geostatistical Analyst (ESRI, Redlands, CA) was used to generate interpolated grids for estimated values of the number of generations using degree–days, and R_o using an inverse-distance weighting algorithm that covered the entire state of California. The input parameters for the inverse-distance weighting analysis were:

1. For each interpolation, 15 weather station sites were used.
2. The spatial shape for including neighboring weather stations was designated to be circular as a directional influence in the data cannot be assumed a priori in these analyses.
3. The default Power Optimization in the Geostatistical Analyst was chosen. The "Power Value" is the distance weight given to a station used in the interpolation and is inversely weighted so that the contribution of more distant input stations to interpolation values at any given location is lessened with increasing distance.

Results

Partial Life Tables and Developmental and Reproductive Estimates. Life tables were constructed for the number of *H. vitripennis* individuals entering each life stage after emergence from eggs and their realized and actual mortality rates were calculated (Table 1). Mean longevity (the time from oviposition to the natural death of an adult) was significantly higher at 25°C (189.43 d on average), intermediate at 20°C (159.71 d), and lowest at 30°C (129.94 d; $F = 6.182$; df = 2, 150; $P < 0.01$; Table 2). Mean adult longevity was highest at 25°C at 153.35 d, intermediate at 20°C (104.13 d), and lowest at 30°C (99.02 d; $F = 6.33$; df = 2, 141; $P < 0.05$; Table 2).

The preoviposition period (Table 2) was longest at 25°C (104.45 d on average, minimum = 14 d, maximum = 308 d, median = 98 d) and shortest at 20 and 30°C (33.85 and 33.62 d, respectively; $F = 14.15$; df = 2, 72; $P < 0.001$). Total progeny and mean daily prog-

Table 1. Partial life table for *Homalodisca vitripennis* reared at three constant temperatures (°C) based on age from emergence (Day 0) to death

Age class (days)	l_x			d_x			q_x			M_r		
	20°C	25°C	30°C	20°C	25°C	30°C	20°C	25°C	30°C	20°C	25°C	30°C
0–20	42	84	105	20	28	42	0.48	0.33	0.40	0.48	0.33	0.40
21–40	22	56	63	0	0	2	0.00	0.00	0.03	0.00	0.00	0.02
41–60	22	56	61	1	3	10	0.05	0.05	0.16	0.02	0.04	0.10
61–80	21	53	51	4	2	9	0.19	0.04	0.18	0.10	0.02	0.09
81–100	17	51	42	0	7	6	0.00	0.14	0.14	0.00	0.08	0.06
101–120	17	44	36	2	7	7	0.12	0.16	0.19	0.05	0.08	0.07
121–140	15	37	29	0	4	7	0.00	0.11	0.24	0.00	0.05	0.07
141–160	15	33	22	2	6	3	0.13	0.18	0.14	0.05	0.07	0.03
161–180	13	27	19	3	2	2	0.23	0.07	0.11	0.07	0.02	0.02
181–200	10	25	17	3	2	1	0.30	0.08	0.06	0.07	0.02	0.01
201–220	7	23	16	4	1	1	0.57	0.04	0.06	0.10	0.01	0.01
221–240	3	22	15	2	4	8	0.67	0.18	0.53	0.05	0.05	0.08
241–260	1	18	7	1	2	1	1.00	0.11	0.14	0.02	0.02	0.01
261–280	0	16	6		3	2		0.19	0.33		0.04	0.02
281–300		13	4		3	1		0.23	0.25		0.04	0.01
301–320		10	3		5	3		0.50	1.00		0.06	0.03
321–340		5	0		1			0.20			0.01	
341–360		4			1			0.25			0.01	
361–380		3			1			0.33			0.01	
381–400		2			0			0.00			0.00	
401–420		2			1			0.50			0.01	
421–440		1			0			0.00			0.00	
441–460		1			1			1.00			0.01	
461–480		0										

l_x = the number entering stage, d_x = no. dying in stage, q_x = apparent mortality (the proportion dying within that particular age class), and M_r = real mortality (the proportion dying within the age class calculated against the no. that entered the first age class). *H. vitripennis* failed to reproduce at 33°C.

eny (Table 2) was lowest at 20°C (45.29 and 11.74 eggs, respectively). Total progeny was greatest at 25°C (213.58 eggs) and intermediate at 30°C (169.14 eggs). Mean daily progeny did not differ significantly between 25 and 30°C (16.86 eggs and 16.36 eggs, respectively; total progeny: $F = 3.197$; df = 2, 71; $P < 0.05$; mean daily progeny: $F = 3.397$; df = 2, 825; $P < 0.05$). Oviposition by adult females was lowest at 20°C (21.9%, or 7 of 32 females laid eggs), intermediate at 25°C (46.3%, 31 of 67 females), and highest at 30°C (56.2%, 36 of 64 females). There was no evidence of oviposition at 33°C.

Mean development time (Table 2), from oviposition to adult emergence, was shortest at 30°C (31.88 d), intermediate at 25°C (35.26 d), and longest at 20°C (63.10 d; $F = 529.96$; df = 2, 323; $P < 0.001$). Temperature did not influence the sex ratio of offspring ($F = 2.19$; df = 2, 355; $P > 0.1$; Table 2).

Mean time (days) spent as an egg (Table 3) decreased significantly as temperature increased ($F = 2.614$; df = 3, 1012; $P < 0.001$). Time spent in all other life stages, including egg to adult, was significantly affected by temperature (first to second instar: $F = 57.24$; df = 3, 664; $P < 0.001$; second instar: $F = 25.47$; df = 3, 568; $P < 0.001$; third instar: $F = 28.13$; df = 3, 499; $P < 0.001$; fourth instar: $F = 41.65$; df = 3, 360; $P < 0.001$; fifth instar: $F = 58.54$; df = 3, 306; $P < 0.001$; egg to adult: $F = 568.47$; df = 3, 353; $P < 0.001$; Table 3).

Mean net R_o ($F = 75423$; df = 2, 247; $P < 0.001$), intrinsic rate of increase (r_m) ($F = 133616$; df = 2, 247; $P < 0.001$), and finite rate of increase (λ) ($F = 135854$; df = 2, 247; $P < 0.001$) were all significantly different

Table 2. Mean longevity (days ± SE; i.e., time in days from oviposition to adult death), mean adult longevity (days ± SE; i.e., time in days from emergence as an adult to death), mean preoviposition period (days ± SE), total progeny (± SE), mean daily progeny (± SE), mean developmental time (egg to adult emergence, days ± SE) and female sex ratio of progeny of female *Homalodisca vitripennis* at each experimental temp

Demographic parameters	Temperature		
	20°C	25°C	30°C
Mean longevity (oviposition to death as an adult)	159.71±14.10a	189.43 ± 12.75b	129.94 ± 10.97c
Mean adult longevity (emergence as an adult to death)	104.13±13.27a	153.35 ± 13.31b	99.02 ± 10.29a
Mean preoviposition period (days)	33.86± 5.29a	104.45 ± 13.20b	33.62 ± 7.17a
Mean total progeny	45.29±18.06a	213.58 ± 32.41b	169.14 ± 25.86c
Mean daily progeny	11.74± 0.98a	16.86 ± 0.47b	16.36 ± 0.54b
Mean developmental time (days)	63.10± 1.12a	35.26 ± 0.41b	31.88 ± 0.55c
Sex ratio (% female offspring)	0.46a	0.52a	0.40a

Mean values between temperatures with different letters were significantly different.

Table 3. Mean time (days ± SE) individuals spent in each life stage, from egg to adult

Life stage	Temperature							
	20°C		25°C		30°C		33°C	
	Mean time (days)	*n*	Mean time (days)	*n*	Mean time (days)	*n*	Mean time (days)	*n*
Egg - first instar	14.00 ± 0.03a	465	8.74 ± 0.07b	212	6.27 ± 0.04c	202	5.39 ± 0.05d	137
First - second Instar	13.46 ± 0.41a	92	9.46 ± 0.30b	164	7.93 ± 0.21c	252	8.15 ± 0.30c	159
Second - third instar	11.44 ± 0.61a	84	6.48 ± 0.32bc	153	5.84 ± 0.26c	216	7.85 ± 0.72b	118
Third - fourth instar	11.28 ± 0.65a	80	6.42 ± 0.54b	140	6.23 ± 0.29c	202	13.05 ± 1.31a	81
Fourth - fifth instar	12.32 ± 0.62a	68	6.52 ± 0.32b	111	6.58 ± 0.30b	163	13.95 ± 2.11a	22
Fifth instar - adult	15.84 ± 0.63a	64	8.91 ± 0.32b	106	8.05 ± 0.34b	137	13.33 ± 3.84a	3
Egg - adult	77.13 ± 1.12a	70	44.34 ± 0.36b	125	38.04 ± 0.55c	159	48.00 ± 5.69b	3

Rows with different letters are significantly different between temperatures.

between temperatures and were highest for individuals reared at a constant 25 (40.21), 30 (0.04), and 30°C (1.05), respectively. Mean T_c ($F = 111029$; df = 2, 247; $P < 0.001$) and T_d ($F = 3061$; df = 2, 247; $P < 0.001$) were significantly different across temperatures and were lowest when individuals were reared at 25°C (97.66 d) and 30°C (15.51 d), respectively. Quadratic lines were fitted to the means for each life table parameter (Fig. 1) and these equations, where appropriate, were used in thematic mapping (see below).

Developmental Thresholds for *H. vitripennis*. Estimates of the lower developmental threshold, optimal

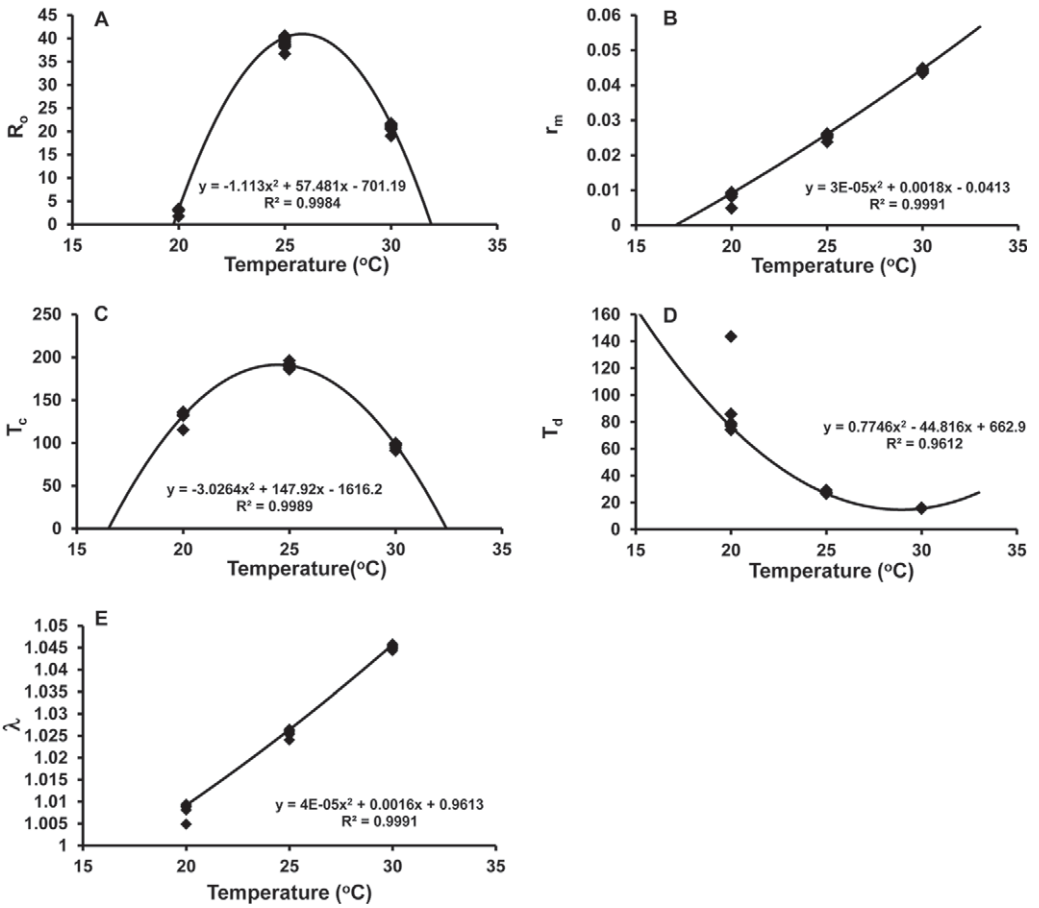

Fig. 1. Fitted quadratic lines for life table statistics (A) net R_o (mean R_o, 3.23 ± 0.04 at 20°C; 40.21 ± 0.08 at 25°C; 21.55 ± 0.03 at 30°C), (B) mean r_m (mean r_m, 0.009 ± 0.0001 at 20°C; 0.026 ± 0.0003 at 25°C; 0.045 ± 0.0003 at 30°C), (C) mean generation time (mean T_c, 131.65 ± 0.40 at 20°C; 190.31 ± 0.11 at 25°C; 97.66 ± 0.08 at 30°C), (D) mean T_d (76.39 ± 1.57 at 20°C; 26.59 ± 0.03 at 25°C; 15.51 ± 0.01 at 30°C), and (E) finite rate of increase (mean λ, 1.01 ± 0.001 at 20°C; 1.03 ± 0.00003 at 25°C; 1.05 ± 0.00003 at 30°C) for *H. vitripennis* at each experimental temperature: 20, 25, and 30°C. *H. vitripennis* failed to reproduce at 33°C.

Table 4. Estimates of the lower, optimal and upper developmental threshold (estimated by the Logan model [Logan et al. 1976]), $T_{max\text{-}modified}$ (estimated by the Lactin model [Lactin et al. 1995]) temp thresholds for male and female *H. vitripennis* life stages combined, together with the parameter estimates for the modified Logan model (Lactin et al. 1995), the thermal constant, K (± SE) was estimated from Equation 4, and the Campbell estimate of K (Campbell et al. 1974) was the reciprocal of the slope through the linear portion of the data

H. vitripennis life stage	*n*	Lower threshold (°C)[a]	Optimal temp. (°C)[b]	Upper lethal threshold (°C)[a]	$T_{max\text{-}modified}$ (°C)[b]	ρ^b	Δ^b	λ^b	K (± SE)[c]	Campbell K (± SE)[c]
Egg	1,016	11.55	41.63	50.08	55.39	0.008	3.75	−1.09	126 (±13)	113 (±2)
First instar	668	11.67	31.57	41.46	51.78	0.009	6.92	−1.11	135 (±49)	123 (±13)
Second instar	572	16.18	29.30	37.80	46.29	0.041	12.41	−1.35	47[d]	39 (±8)
Third instar	503	16.06	27.58	35.18	43.26	0.046	11.58	−1.39	43[d]	37 (±8)
Fourth instar	364	14.86	28.52	34.59	39.80	0.017	3.83	−1.28	61 (±23)	55 (±12)
Fifth instar	310	12.49	32.45	33.05	33.25	0.010	0.12	−1.13	84[d]	82 (±19)
Egg to adult[e]	357	13.99	29.45	35.95	47.10	0.002	3.61	−1.03	574 (±42)	521 (±15)

[a] Solved by allowing $r(T) = 0$.
[b] Solved by iteration.
[c] Determined by linear regression with SE's estimated via the Delta Method.
[d] SE unable to be calculated.
[e] Data from 196 males and 161 females were combined and used for egg to adult estimates.

temperature, and the upper lethal threshold were estimated using the Logan model (Logan et al. 1976; Table 4). Another estimation of the upper developmental threshold, $T_{max\text{-}modified}$, for male and female life stages combined (Table 4), was estimated by the Lactin model (Lactin et al. 1995) with parameter estimates from the modified Logan model (Lactin et al. 1995) also presented. Two estimates of the thermal constant (Equation 4 and Campbell et al. [1974]) represent the calculated degree–days required for each life stage to reach completion and cumulatively across all immature stages (i.e., egg to adult; Table 4).

Mapping of Estimated Life Table Statistics. Maps delineating *H. vitripennis* actual (known for southern California) or potential (for central and northern California where this pest has not established permanent populations because of quarantine and eradication programs) establishment status (total, partial, or no establishment) in Californian counties were generated from California Department of Food and Agriculture records (Fig. 2A). The estimated number of generations of *H. vitripennis* throughout California were calculated by degree–day accumulation (Fig. 2B) and were highest in southeastern California in Riverside and Imperial counties with a predicted maximum of 6–8.89 generations per year. A second estimate of the number of generations of *H. vitripennis* was calculated from the modified life table statistic T_{num} (Fig. 2C) and indicated 3.5–4.95 in generations in eastern Riverside County and the coastal counties of Santa Barbara and Ventura. Estimates of net R_o were maximal at 40–50 in the important grape growing regions of Fresno, Tulare, and Kern Counties (Fig. 2D).

Discussion

This study has provided the first parameter estimates for *H. vitripennis* developmental and reproductive biology across four constant temperatures (20, 25, 30, and 33°C). These data now enable the use of modeling tools to more accurately predict invasion likelihood and establishment success of *H. vitripennis* in California and elsewhere. We used these data to calculate the potential number of generations a population may undergo in any given area of California (i.e., phenology) and potential net R_o in these same areas, which is a measure of pest population growth and subsequent pressure (Hart et al. 2002).

Prevailing climatic conditions strongly influence the ability of an invading insect to spread across a new geographic range, and incursion success, in the absence of temperature-derived demographic data, may initially appear unpredictable (Crawley 1987). Although there is potential for the biological responses of an invading population to be difficult to predict, the impact of adverse weather conditions, especially extreme high or low temperatures, are known to have deleterious effects on incursion success and population permanency (Jarvis and Baker 2001). The utility of laboratory-derived demographic parameters to model pest or natural enemy distributions using long-term weather records for an area of interest has been shown to reflect the known distribution of mymarid egg parasitoids of *H. vitripennis* (Pilkington and Hoddle 2006b, 2007). In the absence of demographic data across a variety of temperatures for *H. vitripennis*, climate-driven ecological niche models (Hoddle 2004) or weather-driven physiologically based demographic models have been used to predict distributions of this pest in California (Gutierrez et al. 2011) and elsewhere (Hoddle 2004).

Current establishment of *H. vitripennis* in California (Fig. 2A) shows areas where climatic conditions clearly favor permanent populations, especially in southern California where this pest is widely distributed and persistently problematic. Estimates for the yearly number of generations based on degree–day calculations (Fig. 2B) indicate that the possible number of generations produced by *H. vitripennis* is reduced as populations move north out of the warmer southern counties of Riverside and San Diego and into areas with average annual temperatures that are lower, such as Mendocino, Napa, and Sonoma Coun-

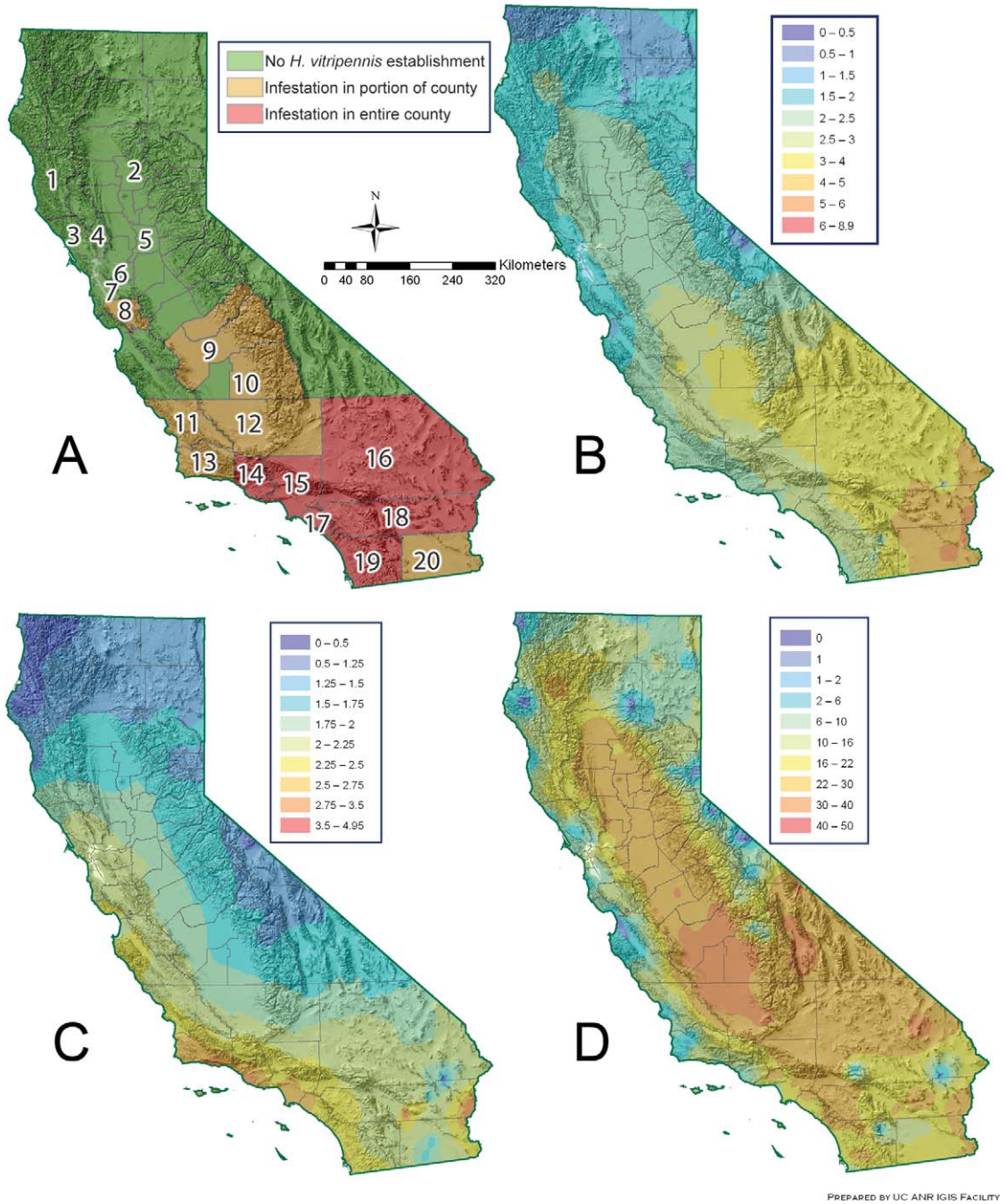

Fig. 2. Maps of estimated life table statistics for *H. vitripennis* in California; (A) Counties in California and the status of *H. vitripennis* populations in each of the following area: 1) Mendocino, 2) Butte, 3) Sonoma, 4) Napa, 5) Sacramento, 6) Contra Costa, 7) Alameda, 8) Santa Clara, 9) Fresno, 10) Tulare, 11) San Luis Obispo, 12) Kern, 13) Santa Barbara, 14) Ventura, 15) Los Angeles, 16) San Bernardino, 17) Orange, 18) Riverside, 19) San Diego, 20) Imperial; (B) estimated number of generations of *H. vitripennis* in each area calculated by dividing the year's accumulated degree–days by the total degree–days required for development; (C) estimated number of generations that hypothetical populations of *H. vitripennis* in each area calculated by applying historical weather data to the formula for yearly generations, T_{num}, derived from the life table statistic for generation time, T_c. and; (D) estimation of the yearly value for net R_o derived by applying historical weather data to the formula for R_o. The colored legend indicates the value of the particular statistic of interest for an entire year. (Online figure in color.)

ties (major wine-producing regions) or Fresno and Tulare Counties (production areas for table grapes and raisins in the San Joaquin Valley). Estimates presented here indicate that in winter, populations of *H. vitripennis* may not be permanent in some northern areas of California. These findings, especially those pertaining to major wine-producing regions of northern California, support results from weather-driven physiologically based demographic models that also suggest that these regions are marginal for *H. vitripennis* (Gutierrez et al. 2011).

The estimated number of generations per year based on the equation for T_{num}, which was calculated using the daily average temperature indicates that *H. vitripennis* can range from zero to 4.95 generations (Fig. 2C). This estimation of the number of generations differs considerably from estimations using degree–days, which were calculated using maximum and minimum temperatures for each 24-h period, and indicated a maximum of 8.9 generations may be possible in some areas of southern California, in particular, the very warm regions of eastern and central Imperial County and eastern Riverside County. These discrepancies may be because of reproductive responses by *H. vitripennis* to shorter winter days, rather than the effects of suitable average daily temperatures on egg laying (see below).

The values returned for R_o (Fig. 2D) range from 0 to >40 and indicate that most counties in California may be suitable for *H. vitripennis* population growth for certain periods of the year, but rates may be reduced because of low nonlethal winter temperatures in northern California such as some coastal areas of Mendocino and southern areas of Sonoma Counties. The minimum number of generations required to produce a stable, persistent, *H. vitripennis* population was calculated to be 2.9 per year with more generations contributing to population growth. This figure of approximately three generations is consistent with work conducted by Hummel et al. (2006) where populations of *H. vitripennis* in Riverside, CA, were collected, dissected, and assigned an ovarian rank to assess local vitellogenesis cycles. Dissection results suggested that there are two distinct generations per year with an occasional third (Hummel et al. 2006). Modeling work by Gutierrez et al. (2011) also predicted 2–3 *H. vitripennis* generations per year in southern California. Consequently, three different approaches (dissections; [Hummel et al. 2006], physiological modeling [Gutierrez et al. 2011], and demographic modeling [this work]) assessing the number of *H. vitripennis* per year in southern California are in accordance predicting 2–3 generations per year. Importantly, the figures produced in this model reflect estimated demographic values across California based on averaged annual temperature data used in previous studies on natural enemies attacking the eggs of this pest (Pilkington and Hoddle 2006b, 2007), thereby enabling direct comparisons to previous studies.

This study estimated that the number of generations in Riverside, CA, would be approximately three when using the T_{num} formula. Calculation of the number of generations using degree–days was slightly higher with 4–5 generations in the Riverside area. However, even though temperatures are theoretically favorable, *H. vitripennis* responds to shortening days over winter and largely ceases to lay eggs, thus it is unlikely 4–5 generations per year occur (Hummel et al. 2006). In southern California, most *H. vitripennis* females dissected between August and January (i.e., late summer and early winter) are either postvitellogenic (percentage in category ≈50–60%), previtellogenic (≈20–40%), or vitellogenic (<10%; Hummel et al. 2006). This suggests that there is a very small proportion of the *H. vitripennis* population (≈10%) that can lay eggs over the winter producing very low densities of *H. vitripennis* nymphs. Given this low occurrence, small population spikes over winter resulting from these reproductively active females would be extremely difficult to detect given the gross sampling techniques employed for monitoring *H. vitripennis* (i.e., yellow sticky cards or beat sampling). Difficulty of detection would be further amplified by parasitism of eggs by *G. ashmeadi*, the key natural enemy of *H. vitripennis* in southern California (Pilkington and Hoddle 2006a,b), which would reduce nymph densities further, possibly subjecting these localized low-density winter populations to extinction because of unfavorable stochastic events (e.g., winter storms).

Previous studies using cowpeas have shown that oviposition by laboratory-reared *H. vitripennis* females on this host plant can be as high as 88% at a constant 27°C (Sétamou and Jones 2005). Approximately 56% of laboratory-reared females oviposited at temperatures averaging ≈25°C when greenhouse temperatures in which females were maintained fluctuated from lows of ≈18°C to highs of ≈32°C (Sisterson 2008). Although temperature ranges differed in these studies, they are supportive of similar data generated in this study, where successful oviposition from emerged adult females was in the range of 22–56%. Further, our study supports results reported by Sisterson (2008) that in the laboratory, *H. vitripennis* females are long-lived and that oviposition is discontinuous during the female life span.

Preoviposition periods for females in this study were unexpectedly high at 25°C, with females, on average, laying their first eggs after 104 d. Sisterson (2008) reported similar results at temperatures averaging ≈25°C where 44% of females never oviposited, 19% oviposited within 40 d, and 37% oviposited after 40 d with a mean preoviposition period for this group being 124.4 d (Sisterson 2008). In this study, at a constant 25°C, 54% of females never oviposited, 9% oviposited within 40 d, and 37% oviposited 40 d post-adult-emergence. Results presented here reinforce the proposition that laboratory-reared *H. vitripennis* may demonstrate different ovarian maturation rates and oviposition propensities to field populations. Further, egg-laying may be influenced, in part, by host plant (Chen et al. 2010), mating status, and possibly the timing of mating and quality of males (Sisterson 2008). Oviposition behavior and developmental and reproductive biology may be further affected by host

plant species (Chen et al. 2010). Three studies (Sétamou and Jones 2005, Sisterson 2008, and this study) investigating aspects of *H. vitripennis* developmental and reproductive biology in the laboratory used cowpeas as host plants. Sisterson (2008) indicated that cowpea was likely a better host plant than sorghum for these types of studies, while Chen et al. (2010) indicated sunflowers are good hosts. In the laboratory, only four plant species are known to support complete development of *H. vitripennis* from egg to adult with subsequent reproduction by adults on the same host plant on which they were raised, namely, these are cowpeas, sunflowers, chrysanthemum, and soybean (Chen et al. 2010).

H. vitripennis females enter the adult stage with zero mature eggs to oviposit (Sisterson 2008), hence they are synovigenic (i.e., egg production continues over the life of the female as opposed to proovigenic where females emerge with a full complement of mature eggs) suggesting that adult resources are important for maturing eggs after emerging as adults (Sisterson 2008). Therefore, it is possible that choice of host plant for these types of studies with *H. vitripennis* may have significant effects on parameter estimates across different temperatures and results from laboratory studies using cowpeas may not be representative of field-based population growth.

Despite using highly regulated temperature and light-controlled conditions in greenhouses and temperature cabinets, laboratory-reared *H. vitripennis* populations used in this study may have been subjected to uncontrollable seasonal influences that impacted results in undetermined ways. For example, longevity can be affected by up to 100% between summer and winter field populations, a trait that does not appear to be influenced by the controlled environments (Lauzière and Sétamou 2010). This study was run continuously between April 2006 and May 2008 and could have been affected by unrecognized seasonal fluctuations. This variation because of seasonal changes may also be evident in preoviposition rates, but not in estimates of overall female fecundity (Lauzière and Sétamou 2010).

In conclusion, modeling of laboratory-derived demographic parameters indicated that in addition to southern California, much of coastal and central California is susceptible to invasion and the establishment of permanent populations of *H. vitripennis* may be possible. These results support ongoing management practices by the California Department of Food and Agriculture to maintain these susceptible areas as pest-free via inspections of nursery shipments that originate in southern California and eradication of incipient *H. vitripennis* populations in vulnerable areas when detected. Data presented here on the developmental and reproductive biology of *H. vitripennis* across a range of temperatures will be useful for modeling and estimating the possible invasion success of *H. vitripennis* in areas other than California, especially incursion susceptibility in areas with important grape producing industries, which has been estimated previously using ecological niche modeling in the absence of biological data (Hoddle 2004).

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