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Sampling and Biostatistics

A Temperature-Dependent Phenology Model for *Liriomyza huidobrensis* (Diptera: Agromyzidae)

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Abstract

Liriomyza huidobrensis (Blanchard) is an economically important and highly polyphagous worldwide pest. To establish a temperature-dependent phenology model, essential for understanding the development and growth of the pest population under a variety of climates and as part of a pest risk analysis, *L. huidobrensis* life-table data were collected under laboratory conditions at seven constant temperatures on its host faba bean (*Vicia faba* L.). Several nonlinear equations were fitted to each life stage to model the temperature-dependent population growth and species life history and finally compile an overall temperature-dependent pest phenology model using the Insect Life Cycle Modeling (ILCYM) software. *Liriomyza huidobrensis* completed development from egg to adult in all temperatures evaluated, except at 32°C, which was lethal to pupae. Eggs did not develop at 35°C. Mean development time of all immature stages decreased with increasing temperature. Nonlinear models predicted optimal temperature for immature survival between 20–25°C (32–38% mortality of all immature stages). Life-table parameters simulated at constant temperatures indicated that *L. huidobrensis* develops within the range of 12–28°C. Simulated life-table for predicting the population dynamics of *L. huidobrensis* under two contrasting environments showed that lowland temperatures at the coast of Peru (250 m.a.s.l.) presented better conditions for a potential population increase than highland (3,400 m.a.s.l.) conditions. The presented model linked with Geographic Information Systems will allow pest risk assessments in different environmental regions to support the regulation of pest movement to prevent pest entry into not-yet invaded regions as well as to implement effective management strategies.

Key words: polyphagous pest, invasive species, pest risk assessment, life-table parameter, population dynamic

Liriomyza huidobrensis (Blanchard) (Diptera: Agromyzidae) is an economically important and highly polyphagous pest of global proportions both under open field and greenhouse conditions. *Liriomyza huidobrensis* causes direct damage to the photosynthetic tissue of host plants due to larval leaf mining, and esthetic damage by oviposition and feeding punctures (stipples) produced by adult females (Spencer 1973). Both crop yield and marketability are reduced, resulting in high economic losses to vegetable producers. Its polyphagous nature combined with high reproductive rates and rapid development of insecticide resistance contributed to the success of *L. huidobrensis* to become a highly invasive species (Shepard et al. 1998, European Food Safety Authority [EFSA] 2012).

Liriomyza huidobrensis was restricted to South America until the 1980s, and from there spread to tropical and subtropical regions of Central America, Europe, Asia, and Africa, presumably associated with the global trade of ornamental plants (Spencer 1990, Dempewolf 2004, Centre for Agricultural Bioscience International 2012). Recent records are from Israel (Weintraub and Horowitz 1995), Indonesia (Katamaya and Teramoto 1997), Kenya (Gitonga et al. 2010), Egypt, Nepal, Malaysia, and the Philippines (CABI 2012, EFSA 2012). In northern Europe, *L. huidobrensis* is mostly a pest in protected crops, but some pupae survived outdoor winter conditions in the Netherlands at a minimum temperature of −11.5°C and 30 d of frost in 1990–1991 (van der Linden 1993).

Temperature is a critical abiotic factor affecting the development, survival, and reproduction of insect species. The ability of an insect to develop at different temperatures is an important adaptation to survive in various climatic conditions, and its understanding is important for predicting pest outbreaks (Gilbert and Raworth 1996). Although *L. huidobrensis* is an invasive pest of worldwide importance, information on temperature-dependent development is limited. Minimum temperature thresholds for development have been recorded at 7.0–8.1°C, and a temperature range of 20–25°C seemed to be most suitable for population growth (Zhou et al. 2001, Lanzoni et al. 2002, Luo et al. 2002, Chien and Chang 2008). A detrimental effect of temperature on *L. huidobrensis* development and

survival was observed at 27.5 °C (Zhou et al. 2001) and 30 °C (Luo et al. 2002), with 92% and 96.1% of total mortality, respectively. However, the available information on temperature-dependent development times and survival for *L. huidobrensis* was never used to establish a temperature-driven phenology model.

Insect life-table data developed under a wide range of temperatures provide the information for developing temperature-based phenology models that are useful for understanding temperature-dependent pest population growth potentials in different agroecologies (Briere et al. 1999; Sporleder et al. 2004, 2013; Kroschel et al. 2013; Kroschel and Schaub 2013; Sporleder et al. 2016). As an example, the population dynamics of *L. huidobrensis* are well studied at the Peruvian coast, with the highest population during the winter–spring cropping season at mean temperatures of 17–20°C, whereas the lowest population occurs during the hottest months with mean temperature of 23°C (Cisneros and Mujica 1999). Instead, the population growth in the Peruvian highlands (3,200 m.a.s.l.), where it is a serious pest of faba bean, is not well understood. A temperature-driven phenology model would be helpful to forecast the pest incidence in this region and its capacity to disperse to new ecological zones.

The objective of the present study was to complement the current knowledge on temperature-dependent development and to establish an overall phenology model for *L. huidobrensis* that can be used for global pest risk assessments. For this purpose, *L. huidobrensis* fly life-table data were collected at seven constant temperatures and a phenology model was developed. The model was validated using life-table data collected at fluctuating temperatures (Sporleder et al. 2004, 2013). Finally, the established model was used to predict (and interpret) the dynamics of *L. huidobrensis* population growth potential under Peruvian lowland and highland conditions according to temperature records.

Materials and Methods

Origin and Rearing of *L. huidobrensis*

Liriomyza huidobrensis specimens used in this study were derived from a laboratory colony reared on faba bean (*Vicia faba* L.) and maintained at the International Potato Center (CIP), Lima, Peru. The flies were originally collected from infested potato leaves in the Cañete valley. Newly collected *L. huidobrensis* from different coastal potato production regions of Peru were made regularly to reduce any inbreeding effects (Haghani et al. 2006). Faba bean seeds were sown in pots (four seeds per pot of 10 by 10 cm) in a mixture of soil, sand, and moss (1:1:1 v/v/v), and the pots were placed in screen houses. Temperature in the screen houses was not regulated and varied from 12.4°C (lowest mean temperature in winter) to 28.9°C (highest mean temperature in summer). When the plants reached stem heights of ~20 cm (about 20-d-old plants in summer and about 30-d-old plants in winter), 15 pots were placed in wooden-framed cages (55 by 100 by 75 cm) covered with fine nylon gauze and ~300 newly emerged *L. huidobrensis* adults of mixed sex released for oviposition. Honey was provided as food. The oviposition cages were maintained at a temperature of 20 °C, >70% relative humidity, and a photoperiod of 12:12 (L:D) h. Four times, in a 3-d interval, the potted plants were replaced and the infested plants stored in a separate rearing room at 25°C for 4–6 d, which allowed developing flies to complete their larval stage. Thereafter, plants were cut off at the bottom and laid in plastic containers filled with fine sand as pupation medium, because under natural conditions, third-instar larvae leave the leaf to pupate in soil. Pupae were collected after 7 d for continuing the rearing cycle or were used in the life-table experiments.

Experimental Procedures for Data Collection

The effect of temperature on the development and reproduction of *L. huidobrensis* was studied in controlled incubator chambers (Thermo Fisher Scientific Inc., MA) at seven constant temperatures of 10°C, 15°C, 20°C, 25°C, 30°C, 32°C, and 35 °C. Data loggers (Hobo H8, Onset, MA) were used to monitor the temperature conditions. Relative humidity in the chambers was maintained at about 60% by placing containers with water; the photoperiod was kept at 12:12 (L:D) h.

Development of Immature Stages and Survival

Plants were placed in a wooden cage (45 by 30 by 25 cm) covered with fine nylon mesh and exposed to 50 *L. huidobrensis* 3-d-old adults of mixed sex for a 4-h oviposition period. Thereafter, plants were incubated at the required temperature. Eggs, which became clearly visible 1 d after oviposition, were individually located and marked by circling the leaf area with a felt-tip pen under binoculars. For each temperature, egg hatch of not less than 100 eggs were determined by inspecting the eggs with the microscope every 12 h. At high temperatures (30°C, 32°C, and 35 °C), the observations were made at intervals of 4–6 h. The same larvae were observed until leaf-exit to determine the larval development time. Pupae were placed individually in translucent gelatin capsule vials (7.5 by 20 mm) and maintained at the same experimental conditions. Adult emergence was recorded twice daily to determine development time of pupa and sex. This made it possible to evaluate total immature development time for males and females separately. Observations continued for 15 d until no further adults were expected to emerge. Survival in each of the life stages was recorded as the proportion of individuals that developed to the next stage deducted from the number of individuals that entered a life stage. Because no egg hatched at 35°C, an intermediate temperature of 32°C was considered and the same method applied as described above. The life-table experiment was repeated several times at 32°C (five and four times) and 35 °C (four times) owing to low survival rates at this temperature.

Adult Longevity and Reproduction

Pupae were randomly removed from the insect-rearing cages and placed individually in translucent gelatin capsule vials. One day after adult emergence, one female and one male were jointly released into a plastic cylinder (15 cm high, 10 cm diameter) that contained a faba bean plantlet (i.e., three fresh leaves placed in a flask filled with water to maintain plant turgor pressure). The cylinders were incubated at the required constant temperature, and faba bean leaflets were replaced daily until death of the female. In the event of survival of the adult male, cylinders remained without leaflets until the death of the male. The survival time was recorded separately for males and females and used to model the survival time of adults. The removed leaves containing the oviposited *L. huidobrensis* eggs were incubated under ambient temperature conditions between 18 °C and 27°C until *L. huidobrensis* eggs developed to pupae. Pupae were individually placed in gelatin capsules until adult emergence for sex determination. The number of emerged males and females and temperature were recorded daily. Female rate was always insignificantly different than 50% at any temperature, and this rate was constant throughout the life time of the female mother. In total, 30 couples were observed at each temperature.

Data for Model Validation

The influence of fluctuating temperature on the development, mortality, survival time of adults, and reproduction of *L. huidobrensis*

Table 1. Mean development time, mortality, and model fitted to development time of immature *L. huidobrensis* life stages at constant temperatures

Temp. (°C)	*n*	Immature stages						Total	
		Egg		Larvae		Pupae			
		Mean dev. time (d)	Mortality (%)	Mean dev. time (d)	Mortality (%)	Mean dev. time (d)	Mortality (%)	Mean dev. time (d)	Mortality (%)
10	100	11.70 (0.18)[a] a[b]	38.0	19.63 (0.36) a	11.3	34.28 (0.50) a	38.2	65.62 (0.35) a	66.0
15	100	5.47 (0.07) b	20.0	13.64 (0.18) b	12.5	24.13 (0.61) b	45.7	44.25 (0.61) b	62.0
20	105	3.39 (0.06) c	7.6	6.39 (0.037) c	6.2	11.92 (0.07) c	22.0	21.70 (0.07) c	32.4
25	100	2.24 (0.06) d	8.0	4.65 (0.05) d	5.4	7.97 (0.14) d	28.7	14.86 (0.10) d	38.0
30	355	1.26 (0.01) e	4.4	4.45 (0.01) d	22.7	7.76 (0.06) d	93.1	13.48 (0.27) d	97.3
32	133	1.29 (0.03) e	56.0	4.44 (0.11) d	82.4	ND[c]	100.0	—	100.0
35	220	ND	100.0						
Model[d]				$F(X) = \frac{1}{1+e^{-(a_i+b\ln x)}}$					
Commune slope		10.80 (0.426)		13.96 (0.428)		14.25 (0.639)			
P (>|z|)		<0.001		<0.001		<0.001			
AIC		467.34		341.37		388.76			
R^2/R^2 adjusted		0.838/0.809		0.981/0.979		0.91/0.904			

[a] Numbers in parenthesis are standard errors.

[b] Means followed by different letters in the same columns are significantly different ($P < 0.05$; Tukey–Kramer HSD). Egg: $F = 3907.2$; df = 5,708, $P < 0.0001$; larvae, $F = 2740.3$; df = 5,528; $P < 0.000$; pupae, $F = 845.8$; df = 4,222; $P < 0.0001$; total, $F = 5652.7$; df = 4,213; $P < 0.0001$.

[c] ND: No adults emerged from pupae at 32 °C and eggs did not hatch at 35 °C.

[d] Logit distribution: $F(X)$ is the probability to complete development at time x, e is the natural exponential, ln x is the natural logarithm of the days observed, a is the intercept corresponding to temperature i, and b is the common slope of the regression model in all cases.

was studied under natural temperature conditions at the experimental station of CIP in La Molina–Lima (12° 05′ S, 76° 57′ W, 250 m.a.s.l.) from September to November, following the same procedure as used in constant temperature studies. During this time period, a total of two generations were observed. A data logger was used to monitor the daily maximum and minimum temperature conditions.

Model Parameterization and Analysis

The development of the *L. huidobrensis* phenology model and its life-table parameter simulation was conducted using the Insect Life Cycle Modeling (ILCYM) software version 3.0 developed by CIP. It is freely available at the website of CIP https://research.cip.cgiar.org/confluence/display/ilcym/Downloads (Sporleder et al. 2013, Tonnang et al. 2013). Data collected in the life-table studies under constant temperature conditions were arranged in incomplete life-table formats as required by the "model builder" of ILCYM to process, analyze, and develop the phenology model (development time and its variation, development rate, senescence, mortality, total oviposition, and relative oviposition frequency). The "validation and simulation" module of ILCYM was applied for simulating life-table parameters and for model validation. The best-fit model was selected based on the Akaike Information Criterion (AIC), a well-known goodness-of-fit indicator (Akaike 1973) or other built in statistics (R^2, Adjusted R^2, MSE). The smaller the value of the AIC, the better the model fitted. For the selection of the best functions, statistical criteria and biological aspects of the species were considered (Sporleder et al. 2004, 2013).

Development Time and Its Distribution

The cumulative frequencies of developmental times of each life stage and temperatures were plotted against normalized developmental times by fitting a logit distribution curve for egg, larvae, and pupae (Table 1).

Development Rate

The modified version of the biophysical Sharpe and DeMichele model (Sharpe and DeMichele 1977, Schoolfield et al. 1981) was used for estimating the nonlinearity for egg development at temperature extremes. A Tb (Logan) was fitted for estimating the nonlinearity in development rate for larvae, and a modified version of Janish-1 model was applied to describe the effect of temperature on development rate of pupae stage. The expressions of the models are presented in Table 2. The choice of best-fit function in ILCYM was done as mentioned above.

Immature Mortality

Mortality was calculated from the frequency of cohort mortality. A Gompertz–Makeham model was fitted for estimating the mortality of the egg stage, and a modified version of the Wang model (Wang et al. 1982) was applied to describe the effect of temperature on mortality of larva and pupae (Table 3).

Adult Life Span

The cumulative frequencies of the adults life span and temperatures were plotted against normalized developmental times by fitting a cloglog distribution curve for female (Table 4) and logit distribution for male (Table 1) adults. The mean survival time of adults was recorded for both sexes and the inverse of it was plotted against respective temperatures. A square-root model of Ratkowsky was fitted to determine the relationship between senescence rate of female and male adults and temperature. (Table 5).

Temperature-Dependent Reproduction

A quadratic equation was fitted to *L. huidobrensis* oviposition data to determine the effects of temperature on the total number of eggs laid per female (Table 5). A Gamma model was fitted to describe the age-specific fecundity rate at each of the test temperatures. The cumulative oviposition rate was plotted against normalized female age, expressed as ratio of age in days divided by mean survival time.

Table 2. Models and their parameters fitted to describe median development rate (1 per d) for immature life stages of *L. huidobrensis*

Life stages	Models[a]	Parameters		*F* value	$df_{1,2}$	*P*	R^2 R^2_{adj}
Egg	Sharpe and DeMichele model 13 $r(T) = \frac{P*\frac{T}{T_0}*e^{\left[\frac{\Delta H_A}{R}\left(\frac{1}{T_0}-\frac{1}{T}\right)\right]}}{1+e^{\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_L}-\frac{1}{T}\right)\right]}}$	P	51.1828 (±0.207)[b]	65.5430	3,5	<0.001	0.975
		H_A	−79899.47 (±0.195)				0.960
		H_L	−101873 (±0.271)				
		T_L	306.1635 (±47.040)				
Larvae	Tb Model (Logan) $r(T) = sy * e^{\left(b(T-T_b)-e^{\left(\frac{b(T-T_b)}{DT_b}\right)}\right)}$	sy	0.0767 (±0.053)	20.4864	3,4	0.0069	0.939
		b	0.2154 (±0.089)				0.893
		T_b	6.9178 (±0.166)				
		DT_b	3.7611 (±2.131)				
Pupae	Janish-1 $r(T) = \frac{2}{D_{min}(e^{K(T-T_{opt})}+e^{-K(T-T_{opt})})}$	D_{min}	6.8409 (±0.203)	191.5274	2,2	0.0052	0.995
		T_{opt}	29.0372 (±0.837)				0.990
		K	0.1275 (±0.011)				

[a] Models: Sharpe and DeMichele model 13: R is the universal gas constant (1.987 cal degree^{-1} mol^{-1}), P is the development rate at optimum temperature T_0 (°K) assuming no enzyme inactivation, ΔH_a is the enthalpy of activation of reaction catalyzed by enzyme (cal mol^{-1}), ΔH_L is the change in enthalpy at high temperature (cal mol^{-1}), and T_L is the high temperature at which enzyme is half active; T_b model: sy, b, T_{min}, T_{max}, and DT_b are the parameters; Janish-1 model: D_{min}, K, and T_{opt} are the parameters. In all cases e is the natural exponential.

[b] Numbers in parenthesis are standard errors.

Table 3. Estimated parameters of the nonlinear model fitted to mortality rate for immature life stages of *L. huidobrensis*

Life stages	Models[a]	Parameters		*F* value	$df_{1,2}$	*P*	R^2 R^2_{adj}
Egg	Gompertz–Makeham $m(T) = a_1 * e^{(b_1*T)} + a_2 * e^{(b_2*T)} + c_1$	a_1	0.0002 (±0.00003)[b]	8.4639	4,5	0.0189	0.8713
		b_1	0.2498 (±0.0435)				0.7684
		a_2	1.9991 (±0.00879)				
		b_2	−0.0253 (±0.00128)				
		c_1	−1.1675 (±0.13825)				
Larvae	Wang 2 $m(T) = 1 - \frac{1}{e^{\left(\left(1+e^{\left(\frac{T-T_l}{B}\right)}\right)\left(1+e^{\left(\frac{T_b-T}{B}\right)}\right)*H\right)}}$	T_l	9.2068 (±5.07829)	7.2735	3,4	0.0426	0.8451
		T_b	29.1442 (±1.79771)				0.7289
		B	1.0082 (±0.38841)				
		H	0.0826 (±0.08375)				
Pupae		T_l	26.6066 (±0.0)	411.1494	3,1	0.0362	0.9992
		T_b	9.8165 (±0.0)				0.9968
		B	1.5175 (±0.0)				
		H	0 (±0.0)				

[a] Models: Gompertz–Makeham, $m(T)$ is the rate of mortality at temperature T (°C) and a_1, a_2, b_1, b_2, and c_1 are the equation parameters. Wang 2, T_l is the low temperature, T_b is the high temperature, T_{opt} is the optimum temperature for survival (°C), and B and H are the fitted parameters. In all cases, e is the natural exponential.

[b] Numbers in parenthesis are standard errors.

All submodels were compiled and implemented in an overall stochastic phenology model.

Simulation of Life-Table Parameters at Constant Temperatures

Life-table parameters—i.e., net reproductive rate (R_0), intrinsic rate of increase (r_m), finite rate of increase (λ), mean generation time (T), and doubling time (DT)—were estimated using the simulation tool in ILCYM (Southwood and Henderson 2000, Sporleder et al. 2013). The estimates were based on the phenology model formed to simulate development, mortality, and reproduction of 100 individuals for a 1-yr period. Deterministic simulation was performed over a range of 8−35 °C in 1° steps.

Model Validation

The validation tool in ILCYM allowed evaluation of the ability of the developed phenology model to reproduce the *L. huidobrensis* life-table data collected under fluctuating temperature conditions. A data logger was used to monitor the maximum and minimum temperature conditions. Experimental life-table data were compared with model outputs produced by using the same temperature records as input data. Validation of established model was done using stochastic simulations.

Life-Table Parameters of *L. huidobrensis* at Two Contrasting Agroecological Zones

In order to understand how temperature affects *L. huidobrensis* population growth potential in lowland (La Molina: 12° 05′ S, 76° 57′ W, 250 m.a.s.l., with a mean annual precipitation of 6.4 mm and mean temperature of 19.7°C) and highland (Huancayo: 12° 00′ S, 75° 22′ W, 3250 m.a.s.l., with a mean annual precipitation of 646 mm and temperature of 12.2°C) Peruvian potato agroecologies, we performed deterministic simulations using the ILCYM software for a 1-yr period at fluctuating temperatures. Historical minimum and maximum daily temperature data collected during 2008 in La Molina and Huancayo by CIP Weather Station were used to simulate life-table parameters in each region.

Table 4. Mean survival time (±SE), female reproduction, and model fitted to describe development time of *L. huidobrensis* adults at constant temperatures

Temp	Longevity (d)		Mean no. of eggs per female
(°C)	Female	Male	
10	10.75 (±1.54) a[a]	11.92 (±1.73) a	1.87 (±0.50) c
15	9.83 (±0.65) a	7.44 (±0.77) b	49.62 (±7.34) b
20	8.93 (±0.62) a	8.25 (±0.48) b	94.72 (±10.29) a
25	2.56 (± 0.19) b	2.19 (±0.18) c	87.42 (±6.85) a
30	1.92 (±0.39) b	1.67 (±0.48) c	35.32 (±4.87) bc
Model	Cloglog[b]	Logit	
Commune slope	2.367(±0.085)	3.363(±0.215)	
P (>|z|)	<0.001	<0.001	
R^2/R^2 adjusted	0.950/0.947	0.927/0.922	

[a] Means followed by different letters in the same columns are significantly different ($P < 0.05$; Tukey–Kramer HSD). Female ($F = 30.40$; df = 4,105; $P < 0.0001$), male ($F = 24.60$; df = 4,108; $P < 0.0001$), oviposition ($F = 30.69$, df = 4,242; $P < .0001$).

[b] Models: Cloglog: $F(x) = 1 - e^{(\hat{(}-e^{(\hat{a}_i + b\ln x)}))}$, $F(x)$ is the probability to complete development time x, e is the natural exponential, ln$x$ is the natural logarithm of the days observed, a is the intercept corresponding to temperature i, and b is the common slope of the regression model.

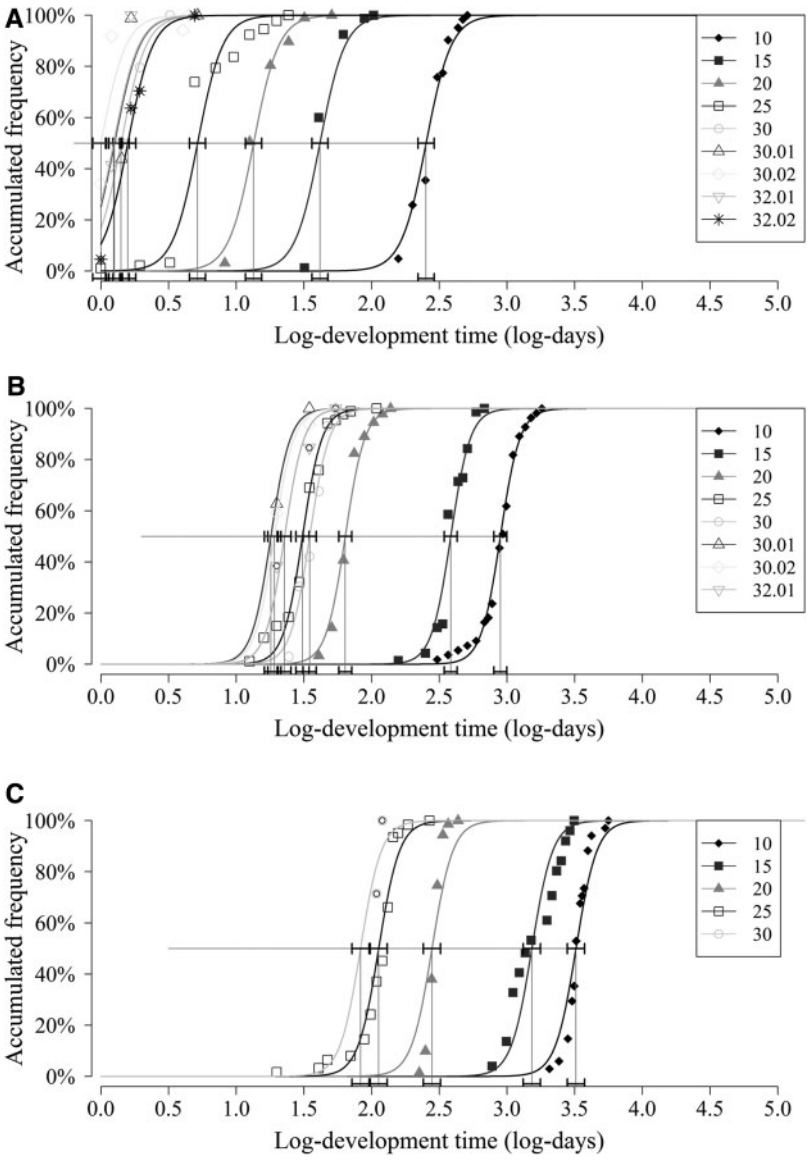

Fig. 1. Cumulative distribution of developmental times of immature *L. huidobrensis* life stages (**A**: egg, **B**: larva, and **C**: pupa). Fitted curves by logit model (Equation 1) using parallel line approach (solid lines), bars indicate 95% confidence intervals for median development rates estimated by the model.

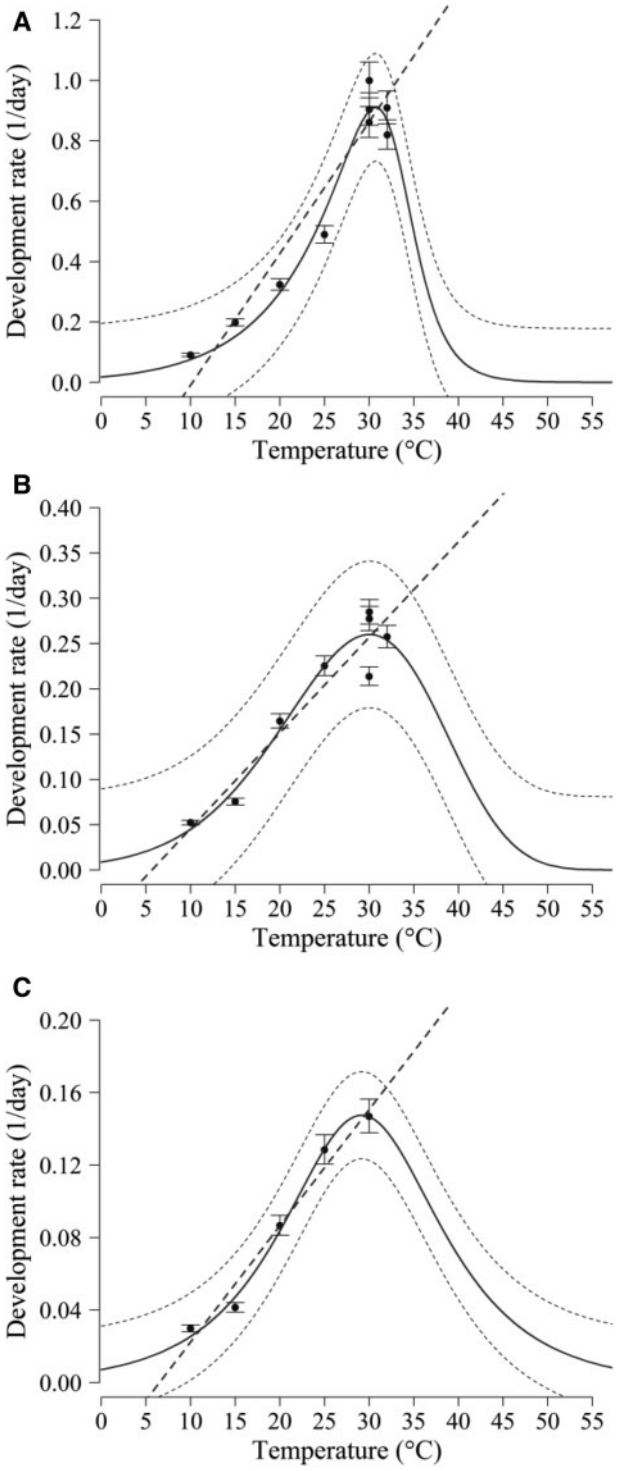

Fig 2. Temperature-dependent developmental rates for immature life stages of *L. huidobrensis*. Sharpe and DeMichelle model for egg (**A**), Tb model for larvae (**B**), and Janish-1 for pupae (**C**). The bold line is the selected model output, and dashed lines above and below represent the upper and lower 95% confidence bands. Bars represent standard deviation of the mean.

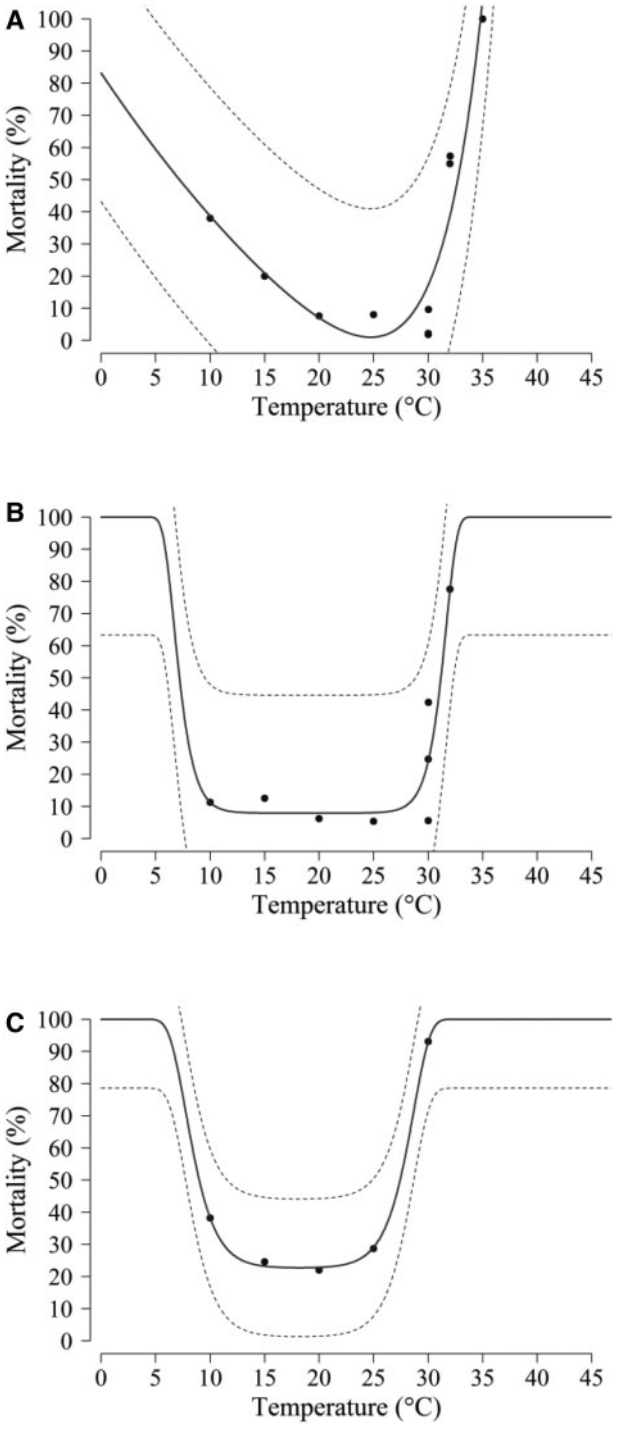

Fig. 3. Temperature-dependent mortality rates of immature life stages of *L. huidobrensis*: egg (**A**), larvae (**B**), and pupae (**C**). Fitted curves: Gompertz–Makeham model (**A**), Wang 2 model (**B**, **C**). Dashed lines above and below represent the upper and lower 95% confidence.

Complementary Analysis

The linear degree-day model (thermal summation model; Campbell et al. 1974, Sporleder et al. 2004) was used to estimate the linear relationship between temperature and the rate of development of *L. huidobrensis*. The linear relationship is $Y\,(=1/\mathrm{d}) = a + bT$, where, Y is the rate of development (1/d), T is the ambient temperature (°C), and the regression parameters are the intercept (a) and slope (b). The thermal constant $K\ (=1/\mathrm{b})$ is the number of degree-days above the threshold summed over the development period. The theoretical lower (minimum) development threshold $T_{min}\ (=-a/b)$ is the minimum temperature at which the rate of development is zero

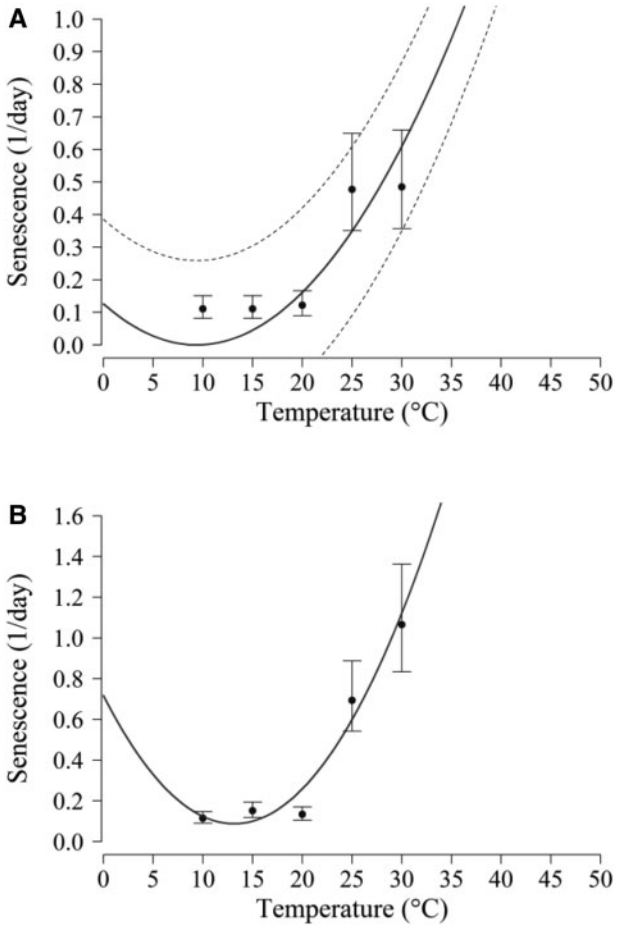

Fig 4. Temperature-dependent senescence rates (day 1) for *L. huidobrensis* adult females (**A**) and males (**B**). Fitted curves of senescence rates: Rawtosky-1 model (solid line). Bars represent standard deviation of the median senescence rate.

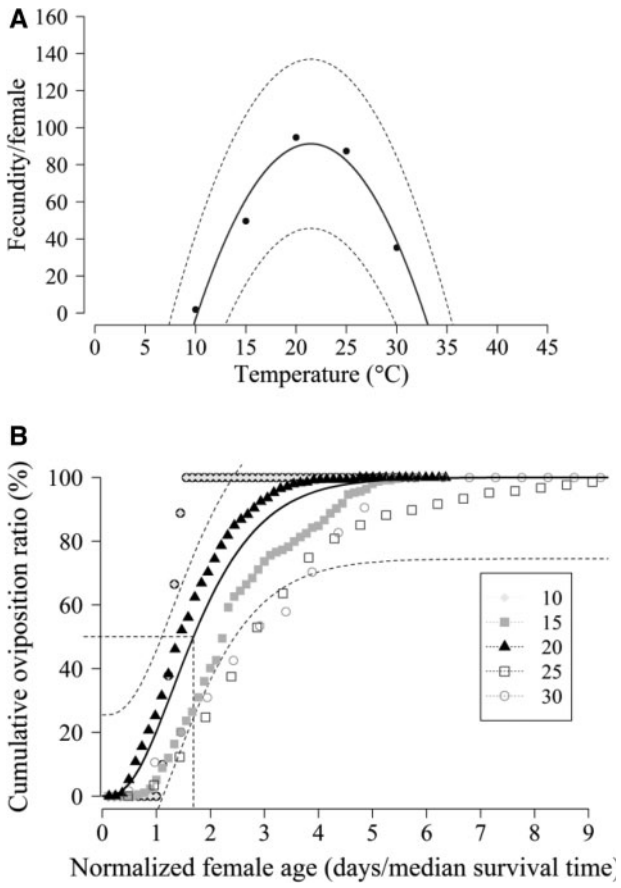

Fig. 5. (**A**) Temperature-dependent total egg production curve. Fitted curve: Taylor-1 model; the upper and lower 95% confidence intervals are indicated. The dots are observed data points. (**B**) Cumulative proportion of egg production in relation to female age expressed as normalized time (senescence/mean senescence time). Fitted curve: Gamma model; the upper and lower 95% confidence intervals are indicated. The dots are observed data point at each of the test temperatures. Age of the female at 50% oviposition is indicated.

Table 5. Estimated parameters of the non-linear models fitted to lifespan and reproduction for Liriomyza huidobrensis adults.

Response variable	Models[a]		Parameters	F value	$df_{1,2}$	P	R^2/R^2_{adj}
Adult senescence rate	Square root model of Ratkowsky $r(T) = b(T - T_b)^2$	b^2	0.0013 (±0.00019)[b]	10.1042	1,4	0.0336	0.716
		Tb^2	8.6584 (±0.0)				0.645
		b^3	0.0029 (±0.00028)	44.8173	1,3	0.0068	0.937
		Tb^3	10.601 (±0.0)				0.916
Total eggs per female	Quadratic $n(T) = c + b * T + a * T^2$	a	−0.7204 (±0.11329)	25.0948	2,2	0.0383	0.962
		b	30.9078 (±4.58093)				0.923
	$f(x) = \frac{1}{b^a * \Gamma(a)} D^{a-1} e^{-\left(\frac{x}{b}\right)}$	c	−240.2103 (±42.12375)				
Proportion of progeny production	Gamma	a	3.2421 (±0.40018)	1565.498	1, 258	<0.001	0.859
	$l(T) = \int_0^D (f(x))\partial x$	b	1.7317 (±0.22337)				0.858

[a] Models: Square root model of Ratkowsky: *r(T)* is the senescence rate at temperature T (°C), and *b* and *Tb* are equation parameters. Quadratic: *n*(*T*) represents the fecundity function at temperature *T* (°C) and *a*, *b*, and *c* are parameters of the equation. Gamma model: *D* is the normalized age of female, *a* and *b* are the equation parameters, *e* is the natural exponential, and *l(T)* is the accumulated oviposition rate.

[b] Numbers in parenthesis are standard errors.

or no measurable development occurs. Data on development time of the different life stages, adult longevity, and fecundity of females were compared across constant temperatures using a one-way ANOVA using the statistical package JMP. When significant differences were detected, multiple comparisons of treatments were made using test of Tukey ($P > 0.5$).

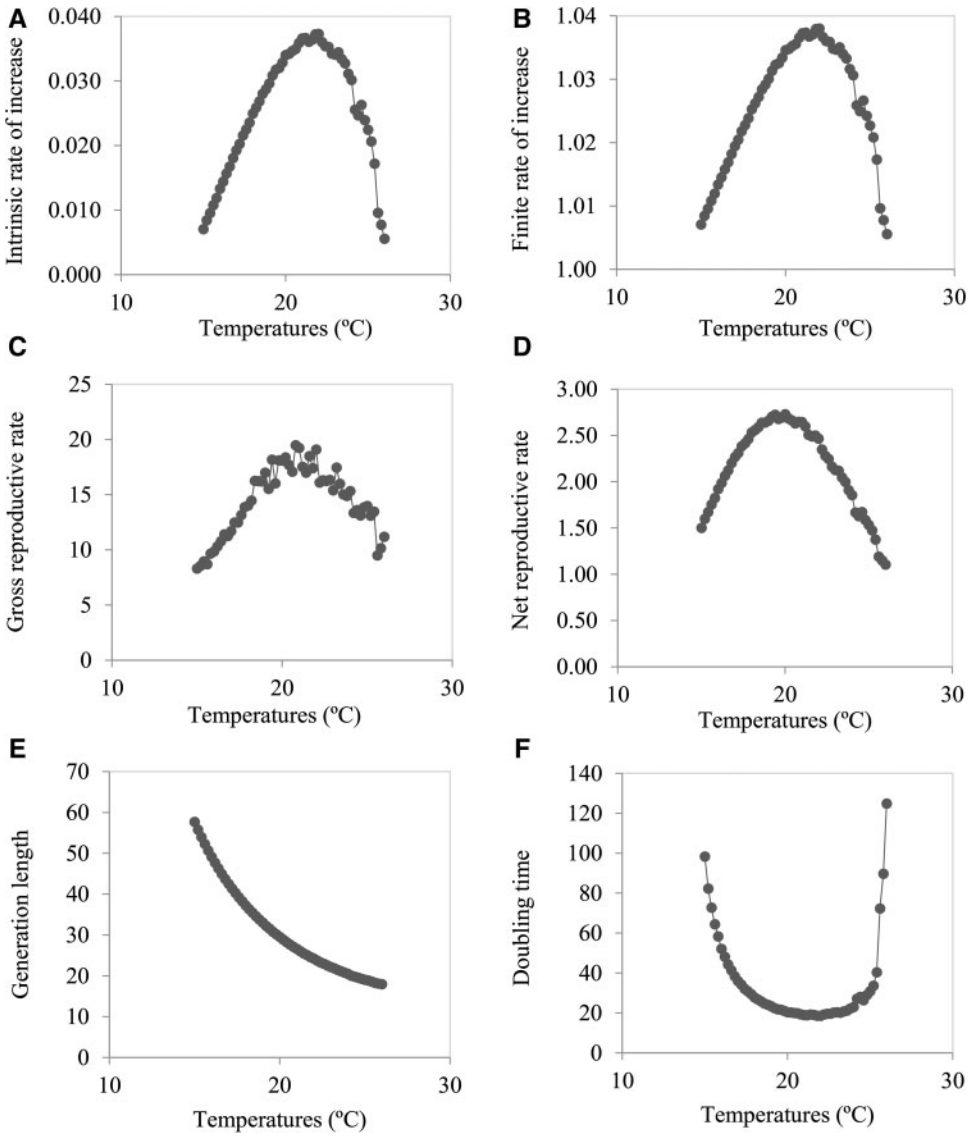

Fig. 6. Simulated life-table parameters of *L. huidobrensis* using stochastic phenology model at constant temperatures. (**A**) Intrinsic rate of natural increase (r_m), (**B**) finite rate of increase (λ), (**C**) gross reproduction rate (GRR), (**D**) net reproduction rate (R_0), (**E**) mean generation time (T), and (**F**) doubling time (Dt).

Results

Appropriateness of Temperature-Dependent Models

Development and its Distribution

The duration of the immature stages and the time required to complete the cycle from egg to adult decreased significantly with increasing temperatures within the temperature range of 10−30 °C (Table 1). *Liriomyza huidobrensis* completed development from egg to adult in all temperatures evaluated, except at 32 °C, which was lethal to pupae. Eggs did not develop at 35°C. *Liriomyza huidobrensis* total development was five times longer at 10°C (65.6 d) than at 30°C (13.5 d). The pupae stage represented >50% of the development time of *L. huidobrensis* between 10−30°C. The logit distribution model produced the best fit, based on the lowest AIC values, to describe variability in the development of eggs, larvae, and pupae according to temperature (Table 1, Fig. 1). The common slopes determined for each life stage were highly significant ($P < 0.001$) and seem adequate to describe the overall variability in the development within each immature life stage (Table 1).

Development Rate

Median developmental rate of all immature stages was adequately described by Sharpe and DeMichele 13, Tb Logan, and Janish-1 models for egg, larvae, and pupae, respectively (Table 2). Coefficient of determination values ranged from 0.94 to 0.99 for egg, larvae, and pupae stages. The curves for the three immature stages were linear from 15°C to 25°C, and consequently, a linear model would be satisfactory to describe temperature-dependent development between these temperatures (Fig. 2). However, above 25°C development is curvilinear such that the described models were more appropriate. The linear regression suitably described the relationship between temperature and development rate of *L. huidobrensis*, as corroborated by the high R^2. Estimated theoretical lower threshold temperature (estimated from the slope and intercepts of the linear regression) for development of immature stages were 9.3°C (egg), 4.1°C (larvae), 5.7°C (pupae), and 6.1°C (total immature). On the basis of these thresholds, the thermal constant (k) for the development, expressed in degree-days (DD = 1/slope), were 29.6, 113.6, 175.5, and 307.5 for egg, larvae, pupae, and total immature stages, respectively.

Immature Mortality

The effects of temperature on the mortality of *L. huidobrensis* immature stages were best described by Gompertz–Makeham model for egg, and a modified Wang model was fitted for larvae and pupae stages (Table 3; Fig. 3). The total immature mortality had the lowest value at 20°C (32.4%) and the highest at 30°C (97.3%). At 32°C, all pupae died (before adults could emerge). The larval stage had the lowest mortality (compared with other developmental stages) in the range of 10−25°C. By contrast, pupae were more vulnerable to unfavorable temperatures than the other stages. Mortality rates of pupae were lowest at 20°C (22%), then increased from 29% to 100% as the temperature changed from 25°C to 32°C. At 10°C, *L. huidobrensis* pupae showed a mortality rate of 38.2%. The models explained >85% of the variation by temperature. Nonlinear models predicted optimal temperature for survival at 20−25°C (32 − 38% survival of the entire immature stage).

Adult Longevity and Fecundity

Female and male longevity decreased significantly with increasing temperature >10°C (Table 4). Multiple comparisons revealed no significant differences in the longevity between male and female adults. Rawtosky-1 model offered a good fit to the observed mean senescence rates for both female and male (Table 5, Fig. 4). The lowest senescence rates were observed within the temperature range of 10−20°C. Oviposition was significantly affected by temperature (Table 4). The effects of temperature on fecundity were described by a quadratic function, with predicted high fecundity at around 22°C (Fig. 5A). This largely agrees with experimentally observed maximum fecundity between 20−25°C. The relationship between the cumulative proportion of progeny produced per female and normalized female age was described by the Gamma function (Table 5, Fig. 5B). The oviposition period was nearly completed (>80% of eggs are laid) before females reached their lifetime mid-point at 20−25°C. The 50% oviposition was completed by the time the female reached a normalized age of 1.7.

Life-Table Parameters

Simulations of *L. huidobrensis* population parameters show that the intrinsic rate of natural increase (r_m) augmented almost linearly with increasing temperature to reach a maximum at 24°C (0.0838), then decreased sharply at 28°C (0.0297), representing an asymmetrical dome-shaped pattern (Fig. 6A). The negative r values <12°C and >28°C indicate that population size is decreasing owing to high mortality and no reproduction. Similarly, the finite rate of increase peaked at 24°C ($\lambda = 1.087$) and was smallest when exposed to 11°C ($\lambda = 0.99992$) and 29°C ($\lambda = 0.98445$; Fig. 6B); $\lambda < 1$ indicates that the population is decreasing. The highest values for both reproductive parameters (gross reproductive rate, [GRR]; Fig. 6C and net reproductive rate, R_0, (Fig. 6D)) were found between 18°C and 22°C. The shortest mean generation time (T) and doubling time (Dt) were observed at 30°C (15.81 d; Fig. 6E) and 24°C (8.27 d; Fig. 6F), respectively. The optimum temperature for overall population growth ranged between 18°C and 24°C.

Validation of the Model

Phenology model validation of *L. huidobrensis* was carried out under fluctuating temperatures at 18−28.7°C, with an average mean temperature of 21.8°C. Population parameters were mostly well predicted when compared with observed data; the most significant discrepancy was with the mean generation time (Table 6). Simulation predicted 12% lower development time from egg to adult (19.4 d) compared with data collected at fluctuating temperatures (22.0 d).

Table 6. Statistic life-table summary from simulated and observed life-table parameters, development time, and mortality of *L. huidobrensis*

	Simulated		Observed	P
Life-table parameters				
Intrinsic rate of increase (r)	0.069	(±0.017)[a]	0.068	0.754
Net reproductive rate (R_o)	4.50	(±1.972)	7.15	0.042
GRR	21.24	(±7.274)	14.53	0.232
Mean generation time (T)	21.81	(±0.612)	28.93	0.001
Finite rate of increase (λ)	1.07	(±0.018)	1.07	0.751
Doubling time (Dt)	10.05	(±2.458)	10.20	0.836
Development time (d)				
Egg	2.745	(±0.139)	3.556	0.002
Larvae	5.748	(±0.072)	7.245	0.000
Pupa	10.928	(±0.299)	11.212	0.071
Immature stages	**19.421**		**22.013**	
Mortality (%)				
Egg	0.0	0 (±0)	0.029	0.000
Larva	0.069	(±0.088)	0.01	0.093
Pupa	0.742	(±0.117)	0.663	0.091
Immature stages	**0.811**		**0.702**	

[a] Numbers in parenthesis are standard errors.

Also, the model predicted about 11% higher overall mortality than observed.

Life-Table Parameters of *L. huidobrensis* at Two Contrasting Environments

Deterministic simulation conducted under fluctuating temperatures within a period of 1 yr showed that lowland (La Molina) presents better temperature conditions than highland (Huancayo) for *L. huidobrensis* population increase (Fig. 7). Under highland conditions, potatoes are grown from November to March/April during the rainy season. Maximum year-round temperatures range between 18–22°C, and minimum temperatures drop to 1°C during the winter months or dry season (June–August; Fig. 7H). The rainy season provides the best conditions for the increase of the *L. huidobrensis* population, as shown by the highest values of the population parameters. During the total cropping season, *L. huidobrensis* populations potentially might increase with a finite rate of about 1.034 (Fig. 7A); accordingly, populations double in <21 d (Fig. 7F). Survival of immature life stages is about 35% (Fig. 7D). It would take an average of about 59 d to complete one generation (Fig. 7C). Flight activity might be expected to be high during the cropping season. Each female adult reproduces about seven females during the cropping season and drops to less than three during the cooler months (Fig. 7B). Dry season presented adverse conditions for *L. huidobrensis* population growth, taking about 72 d to complete one generation with an immature survival of 19%. By contrast, under lowland conditions, the potato-growing season lasts from April to November. Maximum temperature fluctuates between 18–30°C within the year, whereas mean minimum temperatures drop to 14°C during the winter (June–August; Fig. 7G). Autumn season provided the best conditions for the increase of the *L. huidobrensis* population, as shown by the highest values of the population parameters compared with the other seasons. In this season, *L. huidobrensis* populations potentially might increase with a finite rate of about 1.17 (Fig. 7A); accordingly, populations double in about 6 d (Fig. 7F). Survival of immature life stages is about 62% (Fig. 7D), and it would take an average of about 29 d to complete one generation (Fig. 7C). Each female adult reproduces about 25 females during the cropping

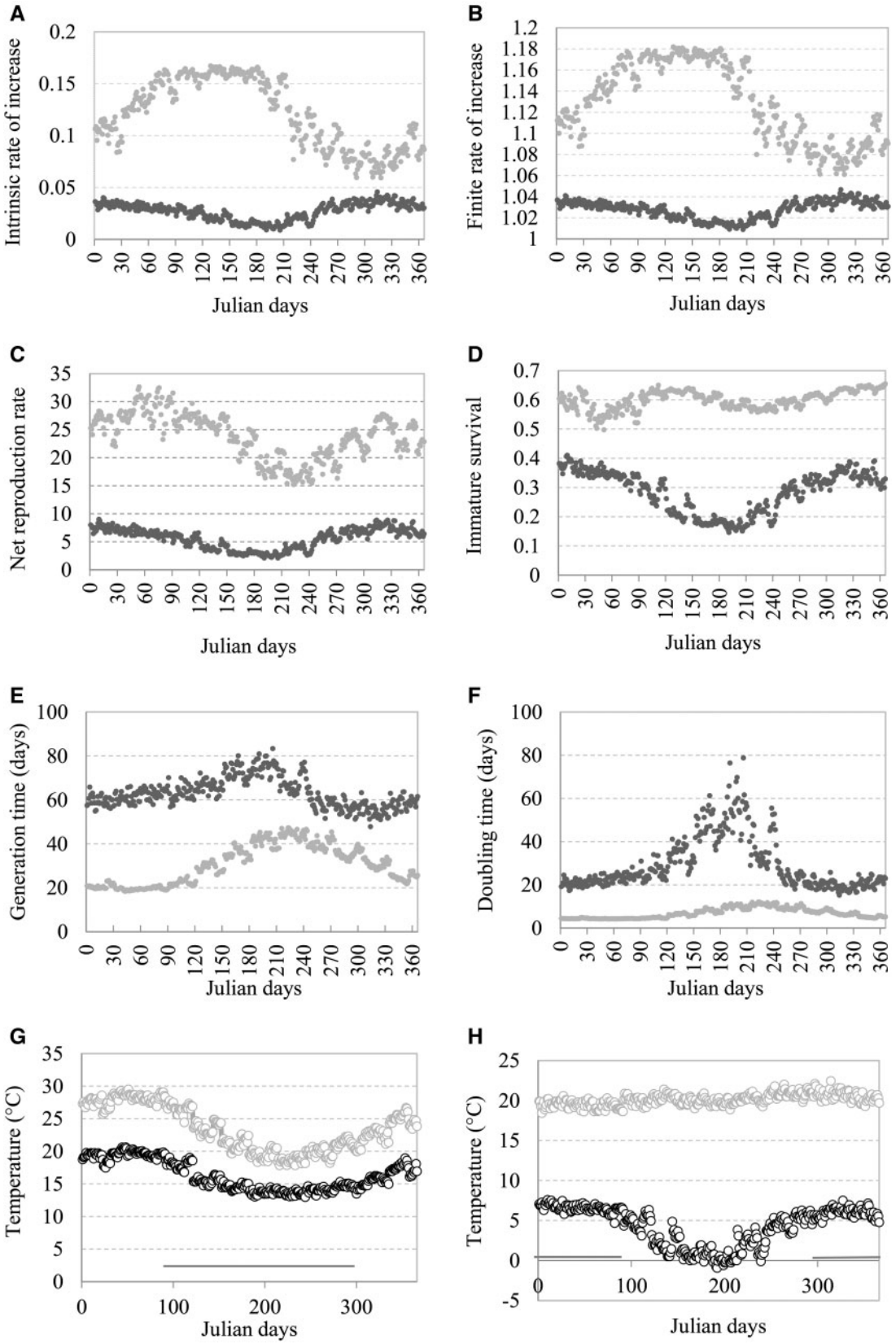

Fig. 7. Within-year variation of life-table parameters for *L. huidobrensis* simulated for lowland (La Molina) and highland (Huancayo, Mantaro Valley) Environments in Peru, using mean daily minimum and maximum temperature data from CIP Weather Station (1975–2000). Figures **A, B, C, D, E,** and **F** show the fluctuations of population life-table parameters (i.e., intrinsic rate of increase, finite rate of increase, net reproduction rate, immature survival, mean generation time, and population doubling time) in lowland (gray dots) and highland (black dots) as examples. Figures **G** (lowland) and **H** (highland) indicate daily mean maximum (open gray dots) and minimum (open black dots) temperatures. Bars above the x-axis indicate the potato-cropping season for each system.

season. According to mean generation time (T), 12 and 6 generations of the *L. huidobrensis* are able to develop per year in lowland (la Molina) and highland (Huancayo) environments, respectively.

Discussion

The development time of each immature stage of *L. huidobrensis* observed in this study in its host faba bean did not differ substantially from different host crop studies as alfalfa (*Medicago sativae* L.) (Aguilera 1972), beans (*Phaseolus vulgaris* L.) (Vercambre and De Crozals 1993, Lanzoni et al. 2002, Chien and Chang 2008), cowpea (*Vigna unguiculata* (L.) Walp.; Zhou et al. 2001), and lettuce (*Lactuca sativa* L.) (Mrtin et al. 2005). A detrimental effect of high temperature on pupa was pointed out by Zhou et al. (2001) when mortality dramatically increased from 40.7% to 84.0% as temperature rose from 25°C to 27.5°C. Similarly, Chien and Chang (2008) observed an increase of 50% in pupal mortality with increasing temperatures from 25°C to 28°C. According to our results, the highest survival of the total development occurred at $20 - 25$°C, which is consistent with previous studies on optimum survival temperature for *L. huidobrensis* (Zhou et al. 2001, Lanzoni et al. 2002, Luo et al. 2002, Chien and Chang 2008).

The established functions describing the temperature-dependent development, survival, and oviposition allowed the development of an overall *L. huidobrensis* phenology model. Life-table parameters simulated at constant temperatures indicated that *L. huidobrensis* population develops within the temperature range of $12 - 27$°C, with an optimum temperature between 18–24°C. These predictions support the finding of Zhou et al. (2001) and Chien and Chang (2008). The intrinsic rate of increase indicates the most favorable temperature for population growth (development time, survival, and reproduction; Southwood and Henderson 2000) and its highest value was reached at 24°C. Also, at 24°C, the finite rate of population growth was highest and doubling time shortest. Finite rate of population growth and doubling time are the most important parameters describing population increase.

Validation of the phenology model was conducted by comparing modeling results with experimental one-cycle life-table data obtained from fluctuating temperature studies. Development time and population parameters were properly predicted by the model, but disagreement with immature mortality and reproduction slightly overestimated the intrinsic rate of increase. In this case, we recommend that more data at extreme temperatures should be generated to increase the precision of estimated parameters.

The established model produces reasonable life-table parameters for the pest based on temperature. The model was used to estimate the annual variation of the *L. huidobrensis* population growth in two contrasting potato environments. Our biological studies suggest that low temperatures at high elevations reduce *L. huidobrensis* oviposition and fecundity, and increased its mortality as a consequence of a longer development time. Also, life-table parameters under constant temperatures showed that the capacity of natural increase (r) and net reproduction rate (R_0) increased with increasing temperature from 10 to 25°C, which is accompanied with a decrease of the mean generation time (T). Thus, the female population only increases 1.18 times in 69.2 d at 12°C (highland conditions) compared with 16.3 times in 35.6 d at 20°C (lowland conditions). The annual variation of the *L. huidobrensis* population under highland environmental conditions has also been observed by Lindo and Paucarchuco (2009), who describe a *L. huidobrensis* population increase in November and a highest flight activity from December to April coinciding with the rainy and main cropping season in the Mantaro valley (mean and minimum temperature of 12.7°C and 5.9°C). The *L. huidobrensis* population declined during the dry and cold months from June to September (mean and minimum temperature of 11.1°C and 1.3°C, respectively). The reduction of the *L. huidobrensis* population during the coldest and driest period, typical of the winter time, is attributed to the strong decrease in minimum temperature.

Under lowland conditions, the population growth of *L. huidobrensis* in autumn is consistent with field observations in the central coast of Peru (Sanchez and Redolfi 1988, Mujica et al. 1997), and in the Elqui Valley in Chile (Larrain and Muñoz 1997). The population starts becoming evident in May (autumn), rising rapidly between June and August, maintaining the highest populations in September, and then declining in November and December. The lowest activity is observed during the warmer months from January to April. February is the most critical month with almost no *L. huidobrensis* population, which coincides with the highest mean temperature (24.4°C) recorded during the year in this environmental zone. Other factors not yet accounted in the phenology model (changes in larval parasitism, end of cropping period of main host crops) also contribute in a drastic reduction of the *L. huidobrensis* population.

In conclusion, the developed phenology model and simulated life-table parameters estimated for *L. huidobrensis* at constant temperatures reflect the temperature-dependent growth potential of the pest. It could be successfully used to explain its behavior and population growth dynamics in two contrasting Peruvian environments. The established phenology model for *L. huidobrensis* produces reasonable life-table parameters for the pest based on temperature. Linked with Geographic Information Systems, it will allow the mapping of population changes in the pest distribution and abundance in response to global warming. Thus, the model discussed here might be used as a tool for country-specific pest risk assessments and for improving pest management strategies for *L. huidobrensis*.

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