Estimating Temperature-Dependent Developmental Rates of *Diorhabda elongata* (Coleoptera: Chrysomelidae), a Biological Control Agent of Saltcedar (*Tamarix* spp.)

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ABSTRACT   Developmental times and survival rates of the immature stages of *Diorhabda elongata* Brullé (Coleoptera: Chrysomelidae), a biological control agent of saltcedar (*Tamarix* spp.), were studied in the laboratory at six constant temperatures (15–40°C). At 15 and 40°C, eggs did not develop and sustained 100% mortality. Similarly, larvae at 15°C and pupae at 40°C did not develop and sustained 100% mortality. For all three larval stages, the developmental time decreased with increasing temperature between 20 and 35°C and increased at 40°C. Developmental times also decreased with increasing temperature between 20 and 35°C for the pupal stage as did total developmental time from egg to adult. Both linear and nonlinear models were used to describe the relationship between developmental rates (1/d) and temperature (°C) and to determine stage-specific lower and upper developmental thresholds, respectively. The lower developmental thresholds, calculated using the linear model, ranged from 6 to 15°C for all life stages. Using the nonlinear model, the lower developmental thresholds ranged from 15 to 18°C for all life stages. Likewise, the high temperature thresholds for the first-, second-, and third-instar larvae, pupae, and total development ranged between 40 and 42°C. Results from this study were used to enhance the efficiency of mass-rearing methods for open field releases of *D. elongata* in California. More importantly, this study is the first step in the construction of a detailed population simulation model to predict field phenology and density of *D. elongata* to further optimize the use of this biological control agent in managing saltcedar in the western United States.

KEY WORDS   *Diorhabda elongata*, development, developmental model, developmental thresholds, degree-days

SALTCEDAR (*Tamarix* spp.), an exotic and invasive shrub, was introduced to the western United States in the early 1800s as an ornamental and to prevent stream bank and wind erosion (DeLoach et al. 2003). However, it is now considered a pest plant, because it invades riparian areas where it outcompetes and replaces native vegetation. It is speculated that as a result of saltcedar invasions, populations of riparian wildlife such as birds, rodents, and fish may have significantly declined (Dudley et al. 2000). To aid in the management of this invasive shrub, an Asian leaf beetle, *Diorhabda elongata* Brullé (Coleoptera: Chrysomelidae), was released in 2001 in the western United States (California, Colorado, Nevada, Texas, Utah, and Wyoming) for the biological control of saltcedars (Lewis et al. 2003). Significant beetle impact to plant

growth and development has been documented in some release sites (Carruthers et al. 2004).

Life history studies of *D. elongata* have been performed both in the laboratory and in the field (Herrera 2003, Lewis et al. 2003). Female beetles lay egg masses on saltcedar's scale-like leaves. On hatching, the larvae feed on the leaves where they complete three larval stages. Third instars cease feeding when fully grown and crawl or drop from the plant to the ground, where they burrow into the leaf litter or soil and build a pupal case of sand, soil, and organic matter. Inside the pupal case, the larvae enter an immobile prepupal stage before pupating. Adults emerge from the ground, move back to the foliage, and resume feeding on saltcedar leaves. The beetles typically complete three generations per season in their native habitat in Fukang, China, before overwintering as an adult (Baoping et al. 2000). At field study sites in the United States, it has been determined that photoperiod alters the number of generations that occur each season, with beetles in some areas producing only two (Lewis et al. 2003, DeLoach et al. 2004). The ultimate adult generation feeds on saltcedar and overwinters in aggregations in sites similar to where it

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pupates. Overwintering adults emerge in early spring in synchrony with the new saltcedar foliage. They feed, mate, and initiate oviposition in May and June (Lewis et al. 2003).

Preliminary studies relating temperature to developmental rates of immature *D. elongata* stages were conducted by Lewis et al. (2003), but only a single constant temperature of 24 ± 2°C and natural, fluctuating, field temperatures were examined. The lower developmental threshold for total development from egg to adult, and degree-days required for development of each stage were roughly estimated by fitting a linear degree-day model to these data. This model was tested against various field observations and was shown to only grossly predict field phenology. Errors were especially evident during warm summer months. To improve the prediction of field phenology of *D. elongata* in biological control release sites, more comprehensive temperature-dependent developmental rate studies were required across the full range of expected and observed temperatures.

It is well documented that the effect of temperature on insect development is often more complex than that represented by a simple degree-day model and typically nonlinear (Taylor 1981, Gordon 1984, Briere et al. 1999). That is, developmental rates tend to steadily increase at intermediate temperatures to an optimum rate while decreasing to zero at lower and higher extreme temperatures. Therefore, to better describe the influence of temperature on the developmental rates of the immature stages of *D. elongata,* laboratory development studies must encompass a broad range of temperature conditions to improve phenology prediction under variable field conditions and to aid in more accurately estimating stage-specific survival.

Temperature is a dominant factor affecting developmental rates of insects (Howe 1967). As such, linear and nonlinear mathematical models have been constructed to describe the relationship between ambient temperature and developmental rates of many insects. The linear degree-day model is widely used to estimate lower developmental thresholds and day-degree day requirements to complete stage-specific development (Hanula et al. 1987, Woodson and Jackson 1996, Mazzei et al. 1999). Although linear models are popular because they are simple to apply and require minimal data, they have limitations. For many insects, the model is applicable only over intermediate temperatures, because it does not adjust for the nonlinearity of developmental rates at low and high temperatures (Wagner et al. 1984). Also, because lower developmental thresholds are estimated by extrapolating a straight line to the temperature axis, linear models will underestimate development at temperatures near and below the lower threshold for development and overestimate development at high temperatures (Hilbert and Logan 1983).

Curvilinear models were developed to address the nonlinearity of developmental rates at low and high temperatures. For example, Logan and Sharpe and DeMichele models describe the response of developmental rates over a wider range of temperatures, and have been successfully used to estimate lower and upper thresholds for development of many insects (Logan et al. 1976, Wagner et al. 1984, Wermelinger and Seifert 1998, López et al. 2001, Roy et al. 2002). While the Logan models are empirical and composed of parameters that can be interpreted biologically, the Sharpe and DeMichele model is theoretical and based on enzyme reaction rate theory, with little direct linkage to actual threshold values (Logan et al. 1976, Sharpe and DeMichele 1977).

Because developmental models can be incorporated into insect population simulation models, and these in turn can be used to make predictions about the occurrence of insects in the field, it is important to describe and predict the relationship between temperature and developmental rates as accurately as possible (Legaspi et al. 1998). Phenological models have been constructed to predict stage specific emergence times or outbreaks (Johnsen et al. 1990, Bentz et al. 1991), fecundity, and mortality rates (Rochat and Gutierrez 2001). In the field of biological control, population models have also been used to estimate population growth, reproduction, and mortality of both insect (Gutierrez et al. 1981, Throne et al. 2000) and pathogen (Carruthers et al. 1992, Larkin et al. 1993) biological control agents.

The purpose of this study was to determine stage-specific, temperature-dependent developmental times and survival rates of the immature stages of *D. elongata* over a range of constant temperatures and fit linear and nonlinear models to the data to estimate developmental rates and lower and upper thresholds. In all, one linear and three nonlinear models were evaluated and compared with select the most appropriate model for *D. elongata* phenology prediction. This study is the first step in the construction of a detailed population simulation model to predict field phenology and density of *D. elongata* to help optimize the use of this biological control agent in controlling saltcedar at various locations throughout the western United States.

Materials and Methods

Developmental rate studies of *D. elongata* immature stages (eggs and larvae) were conducted in controlled environment chambers at six constant temperatures (15, 20, 25, 30, 35, and 40°C) to simulate a realistic range of conditions during the growing season. One chamber per temperature treatment was used, and the study was not replicated. The photoperiod setting for all experiments was 16:8 (L:D) h to ensure no compounding diapause effects (D. W. Bean et al., unpublished data). Relative humidity was not controlled, but ambient humidity conditions were kept well below dew point through extensive ventilation of the experimental chambers.

Eggs and larvae used in these studies were the offspring of an adult colony originally collected from Fukang, Xinjiang Province, China, and recollected from biological control release sites in Nevada (Love-

lock) and California (Owens Valley) to ensure accurate representation of field-released material. This stock laboratory colony was kept in an environmental chamber at 25°C and 16:8 (L:D) h photoperiod. Twenty to 30 reproductive adults were kept inside 2.8-liter (3 qt) plastic containers and given bouquets of fresh saltcedar foliage every other day on which to feed and oviposit. Foliage was inspected daily for the presence of eggs, and if found, these were collected for use in developmental studies.

Egg Development Study. *Diorhabda elongata* adults lay their eggs in clusters on saltcedar leaves in small branchlets; only clusters composed of 2–10 eggs were used to facilitate handling and counting. Multiple branchlets containing egg clusters were transferred with forceps onto a piece of tissue paper located inside a 236-ml (8 oz) plastic container. Each container received 20 eggs. Eggs less than 1 d old were used, and the egg clusters were not removed from the saltcedar branchlets to which they were attached. A total of 100 eggs (five plastic containers with 20 eggs each) were placed into each temperature treatment. Egg development was monitored daily and hatching date and total survival recorded.

Larval Development Study. Eggs laid within a single day were collected from the adult colony and monitored daily for hatching. Newly hatched first instars (<24 h) were placed singly in 236-ml (8 oz) plastic containers. The center of the plastic container lid was removed and replaced with a piece of fine mesh cloth to allow air circulation to prevent condensation within the container. Fifty individually maintained larvae were placed in temperature-controlled incubators that were maintained at 15, 20, 25, 30, 35, and 40°C. The larvae were supplied fresh saltcedar bouquets in 2-ml plastic centrifuge tubes, with water inside the tubes to keep the saltcedar cuttings as fresh as possible. The saltcedar bouquets were replaced every other day for larvae incubated at 15–25°C. In days when the saltcedar was not replaced, water was added to the centrifuge tubes. The saltcedar bouquets were replaced daily for those larvae incubated at 30–40°C because plant desiccation was faster than at lower temperatures.

The larvae were monitored daily for stage of development and acute mortality until they reached the adult stage. When third instars were two days old, sand was added to the plastic containers to provide material for constructing pupal cases. To gather further development data on the prepupal stage, half of the third instars were not supplied with sand, allowing direct observation of pupation, which could not be seen under normal case bearing conditions. The beetles in sand cases were considered adults when they fully emerged.

Developmental Models. Both linear and nonlinear models were fitted to all of the developmental data of each *D. elongata* immature stage (eggs and three larval stages) and for total development from egg to the adult stage. However, only developmental data of beetles reared in sand cases were considered for the final models because in nature, beetles pupate inside cases under the ground litter.

Linear Model. The relationship between temperature (T) and developmental rates (r = 1/d) was modeled using linear regression, where $r(T) = a + bT$, within the temperature range in which the relationship is linear (15–35°C). The model was fitted using the statistical program JMP, version 4.0 for Windows (SAS Institute 2000). The lower developmental threshold temperature was estimated by extrapolating the regression line to the temperature axis, $t_b = -a/b$. In addition, degree-day estimations for development were calculated using the formula $K = (T - t_b) \cdot Dev$; where K is degree-days, Dev is the mean number of days to complete development at a constant temperature (T), and t_b is the lower threshold temperature (Gordon 1984). The required accumulated degree-days for development at each experimental temperature were calculated for each immature stage. From these data, the stage-specific mean degree-days for development were estimated.

Nonlinear Models. The relationship between temperature (T) and developmental rates (r = 1/d) was determined using a Logan type III nonlinear model (Hilbert and Logan 1983). The model was developed by Logan et al. (1976), and is composed of two functions, each describing a separate phase of the developmental rate curve. Phase 1 is represented by a sigmoid function. This function describes the ascending rate of development as temperature increases to an optimum temperature for development. Phase 2 is represented by a second function that describes the descending portion of developmental rate curve, after having reached the optimum temperature for development, as temperatures increase to a lethal maximum.

To determine if the Logan type III model gave the best fit to the data, another version of a Logan model and a polynomial function were fitted to the developmental data of third instars (Logan et al. 1976).

Logan Type III Model. The model formula was as follows:

$$r(T) = \psi\{(T - T_b)^2/[(T - T_b)^2 + D^2]$$
$$- \exp[-(T_m - (T - T_b)]/\Delta T]\},$$

where r(T) is the developmental rate (1/d), T is temperature (°C), T_m is the lethal maximum temperature threshold, ΔT is the width of the high-temperature boundary area (where "thermal breakdown" occurs), T_b is an arbitrary base temperature (not necessarily the developmental threshold temperature), and ψ and D are empirical constants. Nonlinear regression methods required that initial parameter values be estimated directly from the data. This was accomplished using the program Graphing Calculator version 1.5 for Windows. The final parameters were estimated using a Gauss-Newton iterative nonlinear regression method using the statistical program JMP, version 4.0. The best fit of the model was assessed and decided on by comparing the residual sum of square error (SSE) of each iteration result. Lower and upper

developmental thresholds were estimated from the equation. Because developmental rates asymptotically approach a value of zero at lower temperatures, the developmental thresholds cannot be estimated as an absolute value. Rather, we estimated the development thresholds to be within a small temperature range. This was compared with the results of linear and polynomial regression estimates of predicted base temperatures of third instars.

Early Logan Model. The model formula was as follows:

$$r(T) = \psi\{\exp(\rho T) - \exp[\rho T_m - (T_m - T/\Delta T)]\},$$

where $r(T)$ is the developmental rate $(1/d)$, T is temperature (°C), T_m is the lethal maximum temperature threshold, ΔT is the width of the high-temperature boundary area (where "thermal breakdown" occurs), ψ is the developmental rate at some base temperature above the lower developmental threshold, and ρ is the rate increase to an optimum temperature where the development rate is at a maximum. The initial and final parameters were estimated using the same techniques employed to estimate the parameters of the Logan type III model (Logan et al. 1976).

Polynomial Equation. A fourth degree polynomial was fitted to the data using the graphical program SigmaPlot, version 9.0 for Windows (Systat Software 2004). Although polynomials have no biologically meaningful parameters, this type of function was included in the model comparative analysis because polynomials approximate curvilinear data better than linear functions, they are simple to apply, and they have been used to model developmental rates (Logan et al. 1976). The equation was as follows:

$$r(T) = aT^4 + bT^3 + cT^2 + d\,T + e$$

where $r(T)$ is the developmental rate, T is temperature (°C), and a, b, c, d, and e are constants.

Results

Survivorship. The percentage mortality for all the developmental stages of *D. elongata* is described by a U-shape pattern over the range of temperatures used for this study (Fig. 1). Eggs failed to survive at 15 and 40°C but experienced the lowest mortality at 25 (3%), 30 (1%), and 35°C (5%). Similarly, all larvae failed to survive at 15°C, with 95% dying within a period of 5 d. Although all three larval stages survived at 40°C, they suffered high mortality at this temperature. At 40°C, third instars sustained the highest percentage mortality (44%) compared with first (22%) and second (18%) instars. The pupae, however, incurred 100% mortality at 40°C. In all, the data show that all stages are more sensitive to the extreme temperatures (15 and 40°C), and all attained the highest survival at temperatures between 30 and 35°C.

Developmental Time. At 15°C, complete development of larvae was not observed, and after several weeks, all individuals died at varying larval instars. For the purpose of modeling developmental rates versus temperature, development rate was assumed
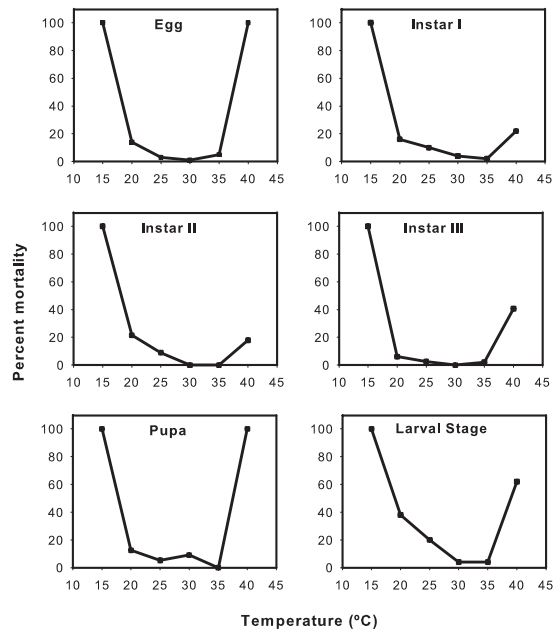

Fig. 1. Percent mortality of immature *D. elongata* stages at various constant temperatures (°C).

to be zero at 15°C for all stages. Developmental times decreased with increasing temperatures within the range of 20–35°C for all stages, including total development from egg to adult (Table 1). At 40°C, no pupae reached the adult stage (Table 1), so pupal and total developmental rates were assumed to be zero at 40°C when fitting the model to the data. Prepupae were monitored outside of their pupal sand cases, and 100% mortality also was observed at 40°C. Complete mortality of the prepupae at 40°C might explain why the pupal stage within cases was not completed. Mean developmental times of prepupae and pupae without sand cases are shown in Table 2.

Developmental Models. Both linear and nonlinear models were used to describe the relationship between developmental rates $(1/d)$, and temperature (°C). To select the most appropriate model for *D. elongata* development prediction, a comparative analysis among the models was performed.

Linear model. As shown by the high coefficient of determination ($r^2 > 0.822$) obtained for all immature developmental stages of *D. elongata*, the linear model adequately described the lower temperature threshold (t_b) and degree-days required for development (Table 3). The linear regression was applied to the temperature range in which the relationship between developmental rates and temperature is linear for all stages (Fig. 2). The estimated lower temperature threshold (t_b) for eggs (6.13°C) and pupae (11°C) were lower than those of the larvae (>13.76°C).

Logan Type III Model. The parameter estimates for the Logan type III model are shown in Table 4. Although laboratory studies showed that larvae did not survive at 15°C, the lower temperature thresholds for

Table 1. Mean development time (days ± SE) required for development of *D. elongata* immature stages at various constant temperatures

Stage	Temperature (°C)					
	15	20	25	30	35	40
Egg	—[a]	9.94 ± 0.06	6.92 ± 0.03	5.06 ± 0.04	4.78 ± 0.05	—
		(86)[b]	(97)	(99)	(95)	
Instar 1	—	8.29 ± 0.28	4.51 ± 0.15	2.06 ± 0.04	2.00 ± 0.03	2.82 ± 0.10
		(42)	(45)	(48)	(49)	(39)
Instar 2	—	8.24 ± 0.20	4.76 ± 0.13	2.60 ± 0.08	2.08 ± 0.06	3.81 ± 0.16
		(33)	(41)	(48)	(49)	(32)
Instar 3	—	9.26 ± 0.20	5.73 ± 17	3.81 ± 0.10	3.13 ± 0.11	5.05 ± 0.21
		(31)	(40)	(48)	(48)	(19)
Pupa	—	22.29 ± 0.59	13.17 ± 0.25	9.65 ± 0.21	8.00 ± 0.18	—
		(14)	(18)	(20)	(20)	
Total[c]	—	58.16 ± 0.60	34.25 ± 0.24	23.01 ± 0.23	19.97 ± 0.14	—
		(14)	(18)	(20)	(20)	

[a] —, 100% mortality.
[b] Number of individuals monitored.
[c] Egg to adult developmental time.

eggs, first instars, second instars, third instars, pupae, and total development were estimated to be within a range of 17–18, 16–17, 15–16.5, 15–16.5, 17–18, and 17–18°C, respectively (Fig. 2; Table 5). The lower temperature thresholds estimated for all the stages by this model were higher than those calculated by the linear degree-day model.

The optimal developmental temperatures where the developmental rate reaches a maximum were estimated as 39, 35, 35.5, 35, 39, and 39°C for eggs, first instars, second instars, third instars, pupae, and total development stages, respectively. After the optimum temperature, the developmental rate decreases as temperatures approach the high temperature threshold. Similarly, and in the same stage order, the high temperature thresholds were estimated to be 40, 42.5–43, 41–41.5, 41–41.5, 40, and 40°C, respectively (Table 5). For eggs, pupae, and total development, the optimal developmental rate rapidly decreased to a value close to zero as the temperature approached 40°C. The drop from the optimal developmental temperature to the lethal temperature is not as fast for the larvae.

Early Logan Model. The model did not adequately predict development rates as well the Logan type III model at lower temperatures (Fig. 3A). Developmental rates are overestimated at this temperature range, and the lower temperature threshold is estimated to

be between 8 and 10°C, lower than that estimated by the Logan type III model (Table 6). The optimum developmental temperature and high temperature threshold estimates, however, were similar to those estimated by the Logan type II model (Table 6).

Polynomial Equation. Similar to the early Logan model, the polynomial model did not adequately describe developmental rates for the third instars in the low temperature range but did well at temperatures >25°C (Fig. 3B). The developmental rate rapidly declines to an absolute zero value at 15°C. This estimate was lower than that estimated by the Logan type III model. The optimum developmental temperature and high temperature threshold, estimates for the third instars, however, were similar to those estimated by the Logan type III model (Table 6).

Discussion

Survival Rates. The percentage mortality curve versus the whole range of temperatures resembled a U-shaped pattern for all the immature stages of *D. elon-*

Table 2. Mean development time (days ± SE) required for development of *D. elongata* prepupal and pupal stages that developed without sand cases at various constant temperatures

Temperature (°C)	Life stages			
	Prepupa	N[a]	Pupa	N
15	—[b]	—	—	—
20	7.20 ± 0.35	15	14.00 ± 0.46	8
25	4.05 ± 0.33	21	7.90 ± 0.10	21
30	2.77 ± 0.11	26	5.54 ± 0.10	26
35	2.78 ± 0.13	23	5.22 ± 0.19	23
40	—	—	—	—

[a] N, no. of individuals monitored.
[b] —, 100% mortality.

Table 3. Parameter estimates (a and b) and coefficients of determination (r^2) for linear regressions [r(T) = a + bT] describing the relationship between constant temperatures (15–35°C) and developmental rates (1/d) of *D. elongata* immature stages

Stage	a (±SE)	b (±SE)	r^2	t_b[a]	DD[b] (±SE)	N[c]
Egg	−0.049 (0.005)	0.008 (0.000)	0.853	6.13	131.53 (0.61)	377
Instar 1	−0.417 (0.016)	0.028 (0.000)	0.898	14.9	39.61 (0.67)	184
Instar 2	−0.390 (0.018)	0.026 (0.000)	0.872	15.0	42.25 (0.65)	171
Instar 3	−0.017 (0.000)	0.234 (0.015)	0.822	13.76	63.01 (0.97)	167
Pupa	−0.066 (0.006)	0.006 (0.000)	0.914	11.0	189.35 (2.19)	72
Total	−0.028 (0.001)	0.002 (0.000)	0.965	14.0	299.86 (2.23)	72

[a] t_b, lower development threshold.
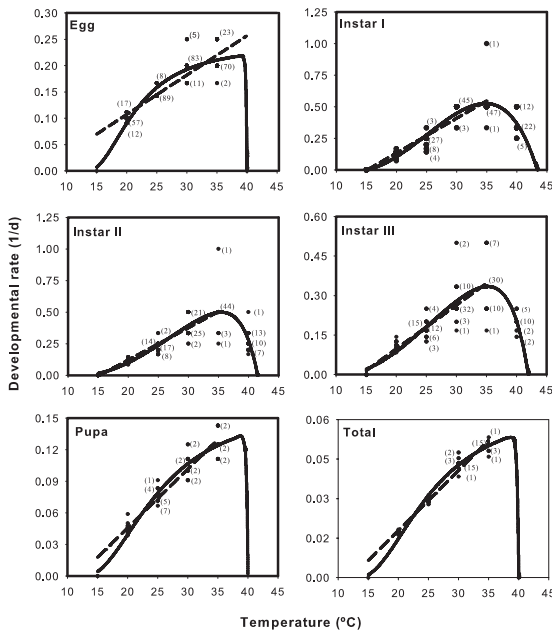[b] DD, mean developmental time in degree-days above t_b.
[c] N, no. individuals monitored.

Fig. 2. Developmental rates (1/d) of *D. elongata* versus temperature (°C). Observed and predicted values by linear model (dashed line) and the Logan type III nonlinear model (solid line). Numbers in parentheses next to the plotted data indicate the number of observations for each point.

Table 5. Lower threshold (LT), optimum temp (OT), and upper threshold (UT) for the development of *D. elongata* immature stages, as estimated by the Logan type III nonlinear model

Stage	Temperature threshold (°C)		
	LT	OT	UP
Egg	17–18	39	40
Instar 1	16–17	35	42.5–43
Instar 2	15–16.5	35.5	41–41.5
Instar 3	15–16.5	35	41–41.5
Pupa	17–18	39	40
Total	17–18	39	40

some third instars of *D. elongata* survived at 40°C, they all eventually perished early in the pupal stage regardless if they were encased in a pupal sand case or not; of 15 prepupae, only 1 constructed a sand case before dying. Lewis et al. (2003) also reported high pupal mortality in outdoor mesh bags and attributed this to low humidity. Because pupae are adapted to develop inside pupal cases burrowed deep in the leaf litter or soil, they are probably protected from naturally occurring high air temperatures and desiccation. Also, they are not continuously exposed to such high temperatures for 24 h each day. Additionally, the temperature range of 30–35°C, where survival during larval and total development was highest, is consistent with the warm temperature regimens the immature stages are exposed to in their native habitat in China and experience in the U.S. release sites (Lewis et al. 2003). Although these results are directly applicable to rearing technologies, further research on the effects of fluctuating temperatures must be studied before being used to predict mortality in the field.

Developmental Rates. For all the immature stages of *D. elongata*, developmental rates increased with temperature and eventually slowed down after an optimum temperature for development was reached. The temperature optimum, where the minimum developmental times were recorded, was within a range of 30–35°C for all stages (Table 1). These are common temperature conditions the beetles experience during summer in their native Fukang, China, and also in many areas of the western United States, where they have been released as biological control agents. Additionally, this temperature range is that at which all

gata. High or complete mortality was documented at extreme cold and high temperatures. In contrast, low and sometimes constant mortality occurred at intermediate temperatures. This U-shaped curve of mortality versus temperature has been previously documented for the immature stages of other coleopterans (Wagner et al. 1987, Fornasari 1995, Marco et al. 1997, Roy et al. 2002).

In this study, *D. elongata* eggs failed to hatch and larvae did not survive at 15°C. At the highest temperature, 40°C, third instars were more sensitive than first and second instars. Smith and Ward (1995) obtained similar results showing increased mortality, and/or incomplete development, at extreme temperatures (40.8 and 42.1°C) by the various larval stages of a chrysomelid beetle, *Bruchus pisorum* L. Although

Table 4. Parameter estimates (ψ, D, ΔT, T_m, and T_b),[a] for the Logan type III nonlinear equations describing the relationship between constant temperatures (15–40°C) and developmental rates (1/d) of *D. elongata* immature stages

Stage	Parameters						
	Ψ	D	ΔT	T_m	T_b	SSE[b]	N[c]
Egg	0.242	8.30	0.142	26.422	15.590	0.115	577
Instar 1	2.947	33.931	6.788	36.503	12.227	0.993	261
Instar 2	1.655	31.516	2.842	31.677	12.014	1.035	233
Instar 3	0.998	30.212	3.205	33.432	10.630	0.579	231
Pupa	0.164	12.497	0.210	27.060	12.981	0.007	93
Total	0.067	12.231	0.236	26.583	13.463	0.000	93

[a] ψ and D, empirical constants; r(T), developmental rate (1/d); T, temp (°C); T_m, lethal max temp threshold; ΔT, width of the high-temp boundary area; T_b, base temp.

[b] SSE, residual sum of square error.

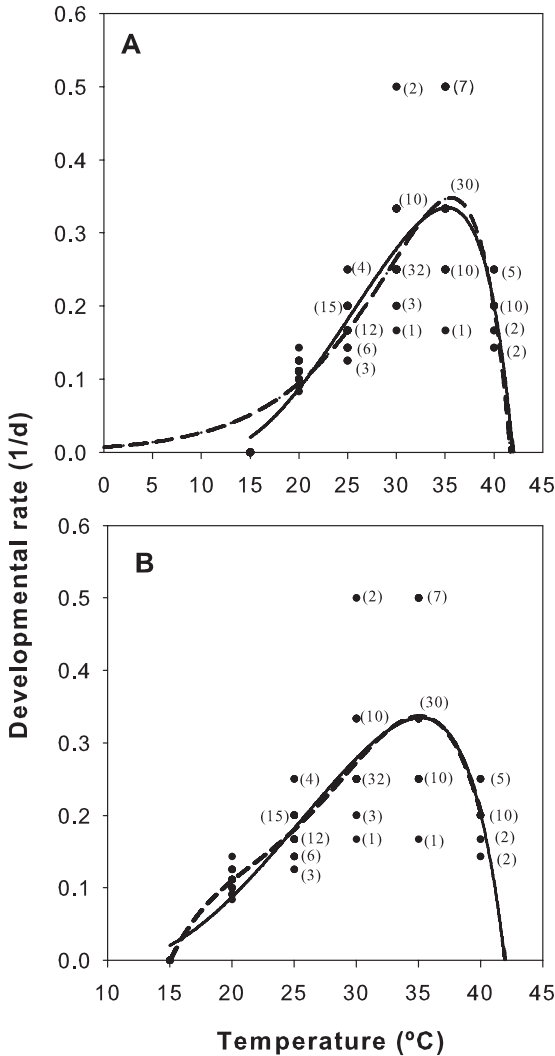[c] N, no. individuals monitored.

Fig. 3. Developmental rates (1/d) of third-instar *D. elongata* larvae versus temperature (°C). Comparison of Logan type III nonlinear model fit (solid line) to fits (dashed line) of (A) earlier Logan model and (B) fourth-degree polynomial. Numbers in parentheses next to the plotted data indicate the number of observations for each point.

stages attained the highest survival (Fig. 1). As the development curves for each *D. elongata* stage showed, development rates slowed at temperatures higher than 35°C (Fig. 2). Similar patterns in devel-

Table 6. Lower threshold (LT), optimum temp (OT), and upper threshold (UT) for *D. elongata* third-instar larvae estimated by the early Logan model and fourth-degree polynomial function

Stage	Temperature threshold (°C)	
	Early Logan model	Polynomial
LT	8–10	15
OT	35.5	35
UP	41–41.5	41–41.5

opment rates have been observed in temperature-dependent developmental studies of other coleopterans (Wagner et al. 1987, Fornasari 1995, Smith and Ward 1995, Woodson and Jackson 1996, Mazzei et al. 1999) and noncoleopteran insects (Lysyk 1998, López et al. 2001).

As indicated by the different shape of the developmental rate curves, the way in which development was affected by temperature varied by life stage (Fig. 2). All three larval instars developed faster than the other stages (Table 1). This stage-specific variation of temperature response has also been documented for the different life stages of curculionid (Ryoo and Cho 1988, Marco et al. 1997) and scolytid (Wagner et al. 1987) beetles.

It is currently unknown how shorter periods of exposure to 40°C or higher temperatures affect development and survival of *D. elongata,* but such studies are of critical importance as peak daytime temperatures often surpass 40°C in many areas where saltcedar is now considered a pest. Also, the larvae may possess behavioral adaptations to avoid high temperatures. Field observations indicate that larvae move beneath saltcedar leaves to avoid direct exposure to sun during peak noon temperatures at the Owens Valley, CA, study site. We suggest further research in this area be conducted to more accurately characterize the biological implications of these higher temperatures.

Developmental Models. Of the three nonlinear models and the linear degree-day model fitted to the development data of the third instar, the Logan type III model described the relationship between developmental rates and temperature best over the entire range of constant temperatures used in this study. Although all three nonlinear models were almost identical in predicting developmental rates at temperatures >20°C, they did not show similar patterns at lower temperatures. The Logan type III model described developmental rates at temperatures close to, or below, the minimum temperature for development better than the other two nonlinear models. The developmental rate curve declines rapidly as it asymptotically approaches the lower temperatures and therefore minimizes overestimating developmental rates (Fig. 3). In contrast, while the early Logan model also approaches the temperature axis asymptotically, it is not a rapid decline, and it eventually overestimated the development rates at lower temperatures. Additionally, the model predicted development at temperatures <10°C. This contradicts laboratory results showing that larvae failed to develop at 15°C.

The fourth-degree polynomial function performed worse than the early Logan model in predicting developmental rates at lower temperatures (Fig. 3). Although the polynomial curve rapidly declines to a zero development rate value at 15°C, it overestimated developmental rates at temperatures between 15 and 25°C compared with the other two nonlinear models. Also, its prediction of zero development at 15°C may not be correct. Although in this study most of the larvae died at 15°C within 5 d after the experiment was initiated, it is possible for development, although slow,

to occur at low temperatures and not be noticed (Howe 1967). Prolonged exposure to low temperatures, caused by slow developmental rates, is what eventually kills insects. Therefore, because development is extremely slow at temperatures close to the lower threshold, it may not be possible to identify an absolute temperature at which development ceases.

The Logan type III model predicted different temperature ranges where the lower developmental thresholds occur for the various *D. elongata* stages. The developmental thresholds were much lower for the larval stages (15–16.5°C) than for the eggs and pupae (17–18°C), indicating that eggs and pupae are the most sensitive to both low and high extreme temperatures. Differences in developmental thresholds among the various life stages have been shown for other insects (Hughes et al. 1984, Hanula et al. 1987, López et al. 2001). More specifically, these differences also can vary greatly. For example, lower developmental thresholds ranging from 7.3 to 15.2°C were reported by Marco et al. (1997) for the egg and pupal stages of another coleopteran, *Aubeonymus mariaefranciscae* Roudier, respectively. In the case of *D. elongata*, this reduced thermal range may be caused in part by the fact that the beetle pupates in the litter or upper portion of the soil where temperature is probably highly buffered compared with highly fluctuating air temperature.

The lower developmental thresholds estimated using the Logan type III nonlinear model were higher than those calculated using the degree-day linear model; the estimates also varied by stage (Table 3). The differences were not as large for the larval as they were for the egg and pupal stages. The linear model clearly underestimated the lower threshold for eggs because laboratory data showed that eggs died at 15°C, and although it was not possible to monitor pupae at this temperature, it is possible that the linear model also underestimated the pupal lower developmental threshold. Nevertheless, the *D. elongata* larval and total development lower thresholds estimated by this degree-day model were higher than the 12.5°C lower developmental threshold Lewis et al. (2003) estimated using a linear model fitted to the limited developmental data available in their study.

Additionally, the Logan type III nonlinear model estimates were higher than those from the linear model because of the method used to calculate lower thresholds. That is, unlike the extrapolation method used in the linear model, the lower threshold from the nonlinear model was estimated to be within a small temperature range rather than an absolute temperature value where developmental rate [r(T)] equals zero. Discrepancies between estimates of lower thresholds using linear and nonlinear models have been shown by other insect development studies, and authors have concluded that the nonlinear models were better at predicting developmental rates (Marco et a1. 1997, López et al. 2001). However, the lower threshold estimates reported by these studies were lower for nonlinear models than the linear models

because they were estimated to occur when r(T) = 0 in both model types.

Developmental Models and Biological Control. Modeling developmental rates of biological control agents of plants or insects as a function of temperature is not a new practice. Linear models have been used to model development of insects released to control plant (Godfrey and Anderson 1994, Fornasari 1995, Mazzei et al. 1999) and insect pests (Lysyk 1998), and other studies have started to implement nonlinear models as well (Flinn and Hagstrum 1995, Parajulee et a1. 1995, Loni 1997, Throne et al. 2000, Roy et al. 2002). The latter studies, however, have focused on biological control agents used to control insect pests of economically important crops or stored products. Our nonlinear model is based on an insect biological control agent used to control a pest plant. Regardless of what type of biological control agent is involved, biological control scientists have recognized the use of developmental models for determining ideal conditions for the mass rearing of agents (Fornasari 1995, Pickett et al. 1999) and to parameterize insect population models that can be used to improve the success rate of biological control programs in the field (Wermelinger and Seifert 1998).

The use of temperature-dependent developmental data and its application in insect population models has long been recognized as a key tool to help solve pest problems. Insect population and phenological models have historically been used to help insect pest management programs to predict seasonal emergence, density, and survival of insect pests under field conditions and to further help farm managers and entomologists optimize pesticide use (Ruesink 1976, Lampert and Haynes 1985, Johnsen et al. 1990, Meikle et al. 1999).

Scientists have applied insect population models in biological control programs to help control insect or plant pests. Such population models, however, have typically been used to simulate parasitoid–host interactions in crop (Barlow and Goldson 1993, van Roermund et al. 1997, Rochat and Gutierrez 2001) or stored grain systems (Flinn and Hagstrum 1995, Legaspi et al. 1998, Throne et al. 2000) of economic importance to understand parasitoid– host dynamics and improve release strategies of parasitoids. Population models to simulate predator–prey interactions also have been constructed to control insect pests in crop systems to explore and/or improve integrated pest management (IPM) programs (Gutierrez et al. 1981, O'Neil et al. 1995, Cividanes and Gutierrez 1996) and to simulate insect pathogens– host dynamics (Feng et al. 1988, Carruthers et al. 1992, Larkin et al. 1993).

For the saltcedar biological control program, a *D. elongata* population dynamics model has been created to improve the effectiveness of *D. elongata* releases (N.T.-C., unpublished data). The Logan type III model, with the parameter estimates obtained in this study, was incorporated into this population model. The model is being used to predict population phenology and synchrony with target plant growth and

to estimate the population dynamics of *D. elongata* in the field so that density, survival, and impact can be assessed under variable environmental conditions across complex spatial environments. These models and the information they provide will be used to more accurately determine the optimal range of conditions for *D. elongata* population growth in the United States. They also will be used to assess other life history characteristics of this insect and similar biotypes and species now under consideration by the United States Department of Agriculture in this multi-state biological control effort.

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