Chapter 2

Modeling temperature-dependent development

and survival of *Otiorhynchus sulcatus*

Introduction

The black vine weevil, *Otiorhynchus sulcatus* (Fabricius), is a serious pest of many horticultural crops in most temperate regions including Europe, North America, and Australia (Moorhouse et al., 1992; Labuschagne, 1999). Between the first report of damage in North America in 1831 and the 1970's, this species spread to 26 states in the United States and six Canadian provinces, with its distribution limited to northern temperate climes in North America (Warner & Negley, 1976). Under outdoor conditions, the weevil is univoltine with considerable overlap of life stages (Schread, 1972). The timing of the appearance and duration of different stages are only approximate and additional information on the biology of *O. sulcatus* is needed to predict stage emergence more precisely (Moorhouse et al., 1992).

Insect phenology is governed by the interactions between intrinsic life-history traits and extrinsic factors such as temperature, moisture, photoperiod, and pathogens (Danks, 1994). Temperature is one of the most critical factors, and its regulatory effects on life history are fundamental to understanding insect population dynamics and managing pest populations (Ims, 1990). Current management options for *O. sulcatus* include targeting the reproducing adults with foliar insecticides throughout the summer and killing the larvae with insecticides or entomopathogenic nematode treatments in the Spring or Fall. The level of success of these measures depends on timely application, which is based on the monitoring of insect phenology. Thus, predicting the emergence time of a particular life stage is required to optimize the timing

of population monitoring and control tactics.

Several field observations and laboratory studies have shown the role of temperature in *O. sulcatus* development (Shanks & Finnigan, 1973; Montgomery & Nielsen, 1979; Stenseth, 1979; La Lone & Clarke, 1981; Masaki & Ohto, 1995). Egg development was successful at temperatures between 12 and 29 $^{\circ}$C (Montgomery & Nielsen, 1979). Pre-adult development was completed in 200 and 130 days at 15 and 24 $^{\circ}$C, respectively (Stenseth, 1979). Unfortunately, direct comparisons among published reports are complicated because information relating development to temperature is fragmented. Although the previous reports provide valuable information, additional quantitative data sets are needed to establish accurate prediction models of *O. sulcatus* populations, particularly including the development time variation among individuals. Therefore, the objective of this study was to quantify temperature effects on stage-specific development and survival of *O. sulcatus* using simple mathematical models. These models will serve as essential components in an *O. sulcatus* population dynamics model that will assist the decision-making processes in pest management by reducing the uncertainty of *O. sulcatus* phenology.

Materials and Methods

Insect rearing

The weevils from which our laboratory colony originated were collected from commercial nurseries near Blacksburg, Virginia, USA, from 2001 to 2002. Weevils were individually reared by feeding them fresh foliage of *Rhododendron* (*R. caucasium x ponticum* var. *album*) in Petri dishes (9 cm diameter, Fisher Scientific), provisioned with moist filter paper and a cotton square

to minimize desiccation stress.

Constant temperature experiment

All experiments were started with eggs or neonate larvae of *O. sulcatus* that were collected from our laboratory colony. The experimental conditions consisted of rearing each stage at a constant temperature of 11, 15, 18, 21, 24, 27, 29, or 30 ± 0.5 °C and a photoperiod of L16: D8 h. In the growth chambers that housed the experiments, the actual temperature experienced by the insects was monitored using a data logger (HOBO, OnSet Computer). The percent survival and developmental duration (in days) were recorded for eggs, larvae, and pupae.

To record egg development and hatch rate, a cohort of newly laid eggs (< 1 day old) was collected and surface-sterilized with 0.5% benzalkonium chloride solution to prevent fungal contamination. After air-drying, the eggs were transferred to a glass vial (25 mm diameter, 80 mm length) with an airtight lid and moist filter paper to provide 100% relative humidity. Fifteen eggs were placed in each vial and three vials were held at each experimental temperature. Egg hatch and mortality were checked daily under a binocular microscope.

To initiate a synchronized cohort of first instars, eggs were collected and kept at 21 °C until hatching. Ten neonate larvae (< 1 d old) were transferred using a camel's- hair brush to a rearing cup (30 ml, Bio-Serv), provisioned with a piece of carrot (4-6 g fresh weight) in autoclaved potting soil (≈ 20% soil moisture by weight). Each temperature treatment began with a total of 180 first instars. I followed the rearing method of Masaki & Sugimoto (1991). Organic carrot pieces were surface-sterilized by first rinsing with 50% ethyl alcohol and afterward in 1% sodium hypochlorite. The fresh carrot and soil were exchanged every 2-3 weeks to provide constant access to fresh food until the larvae developed to the pupal stage. As larvae matured, they were provided with individual cups. The pupae that survived from the larval experiment

were used to observe pupal development and survival. Observation of pupal development was made daily until adult eclosion. At temperatures other than those tested herein, data from Masaki & Ohto (1995) were included to improve model precision. Specifically, from Masaki & Ohto (1995), I included their measurements at 12 $^{\circ}$C and 18 $^{\circ}$C in the development rate model and 26 $^{\circ}$C in the survival model.

Temperature-dependent survival model

The effect of temperature on survival of each life stage was described by using an extreme-value distribution function (Kim & Lee, 2003). The equation is

$$S(T) = k \exp[1 + (T_{max} - T)/\rho - e^{(T_{max}-T)/\rho}],$$

where $S(T)$ is the percent survival at temperature T; k is the maximum survival rate; T_{max} is the temperature ($^{\circ}$C) at which maximum survival occurs; and ρ is a fitted constant. Percent survival of a particular stage was calculated by dividing the initial number of individuals at each stage by the number of individuals that developed successfully to the next stage.

Temperature-dependent development rate model

Development rate was expressed by the reciprocal of the mean development times of eggs, larvae, and pupae. The relationship between temperature and development rate was described by the nonlinear Logan type I model (Logan et al., 1976). The mathematical expression of this version of the Logan model is

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

where $R(T)$ is the rate of development at temperature T; ψ is a measurable rate of development at an arbitrary base temperature; ρ can be interpreted as a composite Q_{10} value for enzyme-

catalyzed biochemical reactions; T_L is the lethal maximum temperature; ΔT is the width of the decline phase in development rate above the optimum temperature.

For the linear portion of the nonlinear Logan model, a degree-day model described the relationship between temperature and development rate,

$r(T) = a + bT$,

where $r(T)$ is the rate of development at temperature T; a is the y-intercept; and b is the slope. The lower developmental threshold (T_b) and the degree-day (DD) requirement were estimated using the parameters: $T_b = -a/b$ and $DD = 1/b$ (Campbell et al., 1974).

Distribution model of development times

The variation among individuals in developmental times for each stage was described by the cumulative Weibull function (Régnière, 1984). The equation is

$f(t) = 1 - \exp[-(t/\alpha)^\beta]$,

where $f(t)$ is the cumulative frequency distribution at cohort age t; α is a scale parameter; and β is a shape parameter. Before fitting data to the Weibull equation, the cumulative emergence distribution through time was calculated in terms of percentiles for each temperature and then normalized by dividing the emergence time by the mean emergence time for each cumulative distribution (Wagner et al., 1984). The cumulative frequency distributions at different temperatures approximately coincided and thus a single temperature-independent distribution was obtained at a normalized age scale using the Weibull equation.

Stage emergence model simulation

Combining the Weibull distribution model and development rate functions simulated the

cumulative distribution of stage emergence through time at constant temperatures. According to previous studies (Curry et al., 1978; Wagner et al., 1985; Allen et al., 1995; Kim et al., 2001), the development rate function determines the daily rate of development at a given temperature, and the distribution function determines the cumulative proportion of cohort development. By incorporating the temperature-dependent survival function with these two submodels, the cumulative stage-emergence function was predicted in relation to cohort age t and at temperature T :

$$F(t,T) = S(T)\left(1 - \exp(-(tR(T)/\alpha)^\beta\right), \qquad (5)$$

where $F(t,T)$ is the cumulative emergence function; $S(T)$ is the temperature-dependent survival model; $R(T)$ is the temperature-dependent development rate model; t is cohort age (in days); and α and β are the scale and shape parameters of the Weibull function.

Data analysis

Chi-square analysis was used to compare *O. sulcatus* survival at constant temperatures for each life stage. The treatment effect on the development duration was examined using analysis of variance (ANOVA) (SAS institute, 1995). The estimates of model parameters for the linear and nonlinear regression models were obtained using TableCurve 2D Automated Curve Fitting program (Jandel Scientific, 1996).

Results

Temperature-dependent survival

Survival of egg and larval stage weevils was significantly impacted by temperature in the population sampled (egg: $\chi^2 = 84.435$, df = 8, P < 0.0001; larva: $\chi^2 = 69.792$, df = 4, P < 0.0001).

Pupal survival was not affected by temperature, but the lack of statistical significance may be due to small sample size of pupae at some temperatures. Survival was low at the high temperature extremes for all stages. Egg hatch ranged from 44 to 63% at 11-27 °C, but no or few eggs completed development at 29 and 30 °C (Table 2.1). Survival of larvae was lowest among the developmental stages (the highest survival was only 27% at 21 °C). No larvae reached pupation at 27 °C. At temperatures from 11-24 °C, most pupae developed to the adult stage and the survival rate ranged from 71.4 to 88.9%.

Temperature-dependent development

Temperature had a highly significant effect on the development duration of eggs (F = 1678.9; df = 6, 139; P < 0.0001), larvae (F = 112.9; df = 3, 136; P < 0.0001) and pupae (F = 1028.1, df = 3, 108; P < 0.0001). The development durations of *O. sulcatus* decreased with increasing temperatures up to 27, 24, and 24 °C for eggs, larvae, and pupae, respectively (Table 2.1). The duration for eggs to hatch ranged from 47.1 d at 11 °C to 9.4 d at 27 °C, with deceleration of development rate at temperatures warmer than 29 °C. The larval stage had the longest development duration at all temperatures, accounting for 78.4 ± 3.5% of total preimaginal period. The larval stage ranged from a maximum of 183.6 days at 11 °C to a minimum of 101.4 days at 24 °C. The duration of pupal development ranged from 36.0 d at 11 °C to 9.9 d at 24 °C. Total preimaginal development duration ranged from 122.6 d at 24 °C to 266.7 d at 11 °C.

Temperature-dependent survival model

The extreme value function provides a reliable description of the relationship between temperature and survival of *O. sulcatus* for all stages (Fig. 2.1 A-C). The pattern of curves for all

life stages exhibited a skewed bell shape, due to their vulnerability to high temperatures. The estimated values of parameters are shown in Table 2.2. Maximum survival (k) at the optimum temperatures (T_{max}) for each stage was estimated to be 63.7% at 19.0 ^{o}C for eggs, 32.1% at 19.0 ^{o}C for larvae and 97.0% at 17.3 ^{o}C for pupae. Coefficients of determination were higher than 0.85 for eggs and larvae but the value was 0.59 for the pupal stage.

Temperature-dependent development rate model

The relationship between incubation temperature and development rate was well described by the Logan type I model [$R(T)$], with a high coefficient of determination ($r^2 > 0.96$) for all life stages (Table 2.2). Because there was no successful completion of egg development at 30 ^{o}C or of larval development at 27 ^{o}C, the development rates at these temperatures were assumed to equal zero and estimated as the upper lethal temperatures (T_L) in the development rate models. Estimated optimal temperatures for development were 27.5, 25.1, and 24.1 ^{o}C for eggs, larvae, and pupae, respectively (Fig. 2.2 A-C). At these optimal temperatures, the shortest developmental durations for eggs, larvae, and pupae were estimated to be 8.9, 98.4, and 10.0 days, respectively. At temperatures warmer than the optima, the rates of development decreased sharply.

A linear regression analysis provided the estimation of the lower developmental threshold temperatures (T_b) and the thermal constant (DD) requirements for immature stages (Table 2.3). The estimated lower threshold temperatures were 5.9 ^{o}C for eggs, 4.1 ^{o}C for larvae, and 6.4 ^{o}C for pupae. The thermal constants for eggs, larvae, and pupae were estimated to be 195.8, 1697.6, and 178.8 DD, respectively.

Distribution model of development times

Cumulative frequency distribution against normalized age (development duration of each individual/mean development duration) for each stage is illustrated in Fig. 2.3. The shapes of distributions were similar for all stages, and described by the Weibull function (Table 2.2). A high coefficient of determination ($r^2 > 0.91$) was obtained for all developmental stages. A smaller value of the shape parameter (β) in the Weibull function indicates higher variation in the development duration for a particular stage. For example, the larval stage had a β-value of 13.8 and exhibited more variation in development time among individuals than either the pupal ($\beta = 18.1$) or egg stage ($\beta = 35.1$).

Simulation of stage emergence

Given a cohort of 1000 eggs as an input value, the predicted number of individuals in the cohort developing from one stage to the next is presented in relation to temperature and cohort age (Fig. 2.4). At optimum temperatures for development, the emergence density curve exhibits lower variance and earlier completion of development. At low and high extreme temperatures, the curve has higher variance and later developmental completion. The peak emergence was observed at the optimum temperature for survival at each stage. The curves indicate that eggs are capable of developing successfully at a broader range of temperatures than the other stages (Fig. 2.4 A-C).

Discussion

I have developed temperature-dependent development rate and survival models that describe stage-specific development of *O. sulcatus*. As expected, temperature strongly influences the

development duration and survival of all life stages of *O. sulcatus*. The effect of temperature on preimaginal mortality has been studied previously. Montgomery & Nielsen (1979) reported that egg development of *O. sulcatus* was successful at temperatures from 12-29 °C and egg survival substantially decreased at extreme temperatures > 27 °C or < 12 °C, which is similar to findings of this study. During egg development, short-term exposure to high temperature was shown to be harmful (Montgomery & Nielsen, 1979). In their study, a 12-hour exposure of newly laid eggs to 31 °C greatly reduced survival and eggs did not survive prolonged exposure to 31 °C. Low relative humidity substantially influences egg survival (Shanks & Finnigan, 1973) but no difference in egg survival was found at 93-100% RH (Montgomery & Nielsen, 1979). I found that larvae do not tolerate warm temperatures (e.g. 100% mortality at 27 °C), which is consistent with other reports: 100% mortality at 27 °C (Stenseth, 1979) and 98% mortality at 26 °C. This study demonstrates that the development of the subterranean larval stage would be seriously impaired under conditions of high temperature stress, although the mechanism by which high temperatures influence survival is not known. Stenseth (1979) observed no pupal development at 12 °C, but I observed pupal development at 11 °C. Moreover, our study shows that the developmental success of pupae is higher than that of eggs or larvae at temperatures ≤ 24 °C. The factors that influence survival of each developmental stage in the field could include the feeding status, microhabitat conditions, degree of mobility (in the case of larvae) and developmental duration.

I demonstrate that constant exposure to high temperature reduces the survival of *O. sulcatus* eggs, larvae, and pupae. Due to the fluctuation of temperatures under field conditions, a detailed study is needed to determine the effects of exposure duration of the temperatures shown to be critical in this study. The pattern of exposure to critical temperatures influences survival in many

insects. For example, the offspring of *Metopolophium dirhodum* Walker (Homoptera: Aphididae) died as third instars at a constant 27 $^{\circ}$C (Botto & Boggiatto de Pacheo, 1980) but a temperature of 31 $^{\circ}$C did not reduce survival to zero if the exposure period was less than 8 h per day for up to 6 days (Ma et al., 2004).

Overall, the extreme value function adequately described the relationship between constant temperatures and survival for each stage of *O. sulcatus* over the full range of temperatures tested. The value of parameter ρ, which was negative for all stages, indicates the poor capability of *O. sulcatus* to survive at high temperatures. In contrast, a positive value of ρ would indicate low survival at cool temperatures. The absolute value of ρ determines the spread of the survival curve. Thus larvae, which had the smallest absolute value (ρ = 4.4), are more sensitive to temperature extremes than eggs (ρ = 7.3) or pupae (ρ = 8.2). The survival model enables us to predict the survival rate of each developmental stage at constant temperatures, although direct comparison with other studies is not possible due to lack of published data. For instance, at 19 $^{\circ}$C, I would expect that 637 out of 1000 eggs would hatch and 204 larvae would pupate and finally 194 adults would eclose successfully.

The development durations for eggs and pupae that I report are similar to other studies (Montgomery & Nielsen, 1979; Stenseth, 1979; Masaki & Ohto, 1995). However, development duration for larvae is somewhat less consistent among studies. For example, larval development duration at 15 $^{\circ}$C was reported as 130, 150.4, and 142.8 days by Stenseth (1979), Masaki & Ohto (1995), and our study, respectively. The differences in larval development may result from different experimental protocols, such as the time interval between measurements or different food quality or quantity. Reports on the developmental thresholds of *O. sulcatus* also vary. Lower developmental thresholds of *O. sulcatus* for eggs, larvae, and pupae, respectively were

estimated to be 6, 2 to 6, and 12 $^{\circ}$C by Stenseth (1979) and 6.3, 2.5, and 6.1 $^{\circ}$C by Masaki & Ohto (1995). This variation among threshold temperatures probably resulted from selection of different temperature ranges on which to base the predictive linear regression. Despite the limitations of applying a linear model (VanKirk & AliNiaZee, 1981), developmental thresholds estimated in this way have proved practical for predicting insect phenology (Pruess, 1983; Roltsch et al., 1990).

The development rate curve of *O. sulcatus* in relation to temperature was typical of insect development, with nonlinearity at low and high temperatures. The nonlinear models are more accurate at extreme temperatures beyond the intermediate linear range and thus provide a better description than the linear model, including a more accurate prediction of the optimum temperature (Stinner et al. 1974). Among many nonlinear models, the Logan type I model has desirable characteristics for development models due to the simple biological meanings of its parameters (Got et al., 1997; Briere & Pracros, 1998). The parameter ΔT is the difference between the optimum temperature and the upper lethal temperature (T_L) and thus a small value for ΔT suggests that development rate declines at temperatures above the optimum temperature sharply. The value of ΔT is lowest for larvae (0.52) (Table 2.2) and the curve of development rate declines sharply at high temperatures above the optimum temperature.

No previous study has presented quantitative information on *O. sulcatus* developmental time variation among individuals. Since insect development is a stochastic process with stage transitions occurring over time (Sharpe et al., 1981), the distribution of developmental times is a key component to developing realistic models for insect development. The inherent variation of *O. sulcatus* developmental time herein is quantified by using the Weibull function. When the shape parameter (β) in the function is compared among stages, the small value for larvae

suggests that the variation in larval development time is greater than any other stage. The high variation in the duration of larval development may play a substantial role in the seasonal occurrence of different stages simultaneously in the field. For many insect species, it has been observed that developmental time variation among individuals in a cohort is skewed toward longer times and that the underlying distributions against normalized times have identical shapes irrespective of temperatures (Curry et al., 1978; Sharpe et al., 1981; Wagner et al., 1984). Therefore, the Weibull function has described the distribution of development time variation (Régnière, 1984; Wagner et al., 1984; Cockfield et al., 1994).

Although development rates under constant temperatures are frequently similar to rates under fluctuating temperatures (Campbell et al., 1974), there have been numerous reports suggesting that daily temperature cycles may play a role in insect development (Rock, 1985; Roltsch et al., 1990; Fornasari, 1995). For instance, short-term exposure to high or low temperatures in daily temperature cycles may change mortality or development rate beyond predictions based on constant temperature studies, particularly when some temperatures in the cycling regime go beyond the upper or lower thresholds (Beck, 1983). Therefore, a prerequisite for potential field use is validation of the development rate model under fluctuating temperatures. Our data quantify the development of *O. sulcatus* at constant temperatures. Under field conditions, *O. sulcatus* has only one generation per year in temperate areas. Stage-specific mortality and development in relation to temperature may result from the adaptation of each stage to different prevailing conditions of the season in which they live (Marco et al., 1997). The information on temperature-related effects on *O. sulcatus* development can be useful in designing rearing protocols, developing monitoring and management schemes, and possibly predicting the potential of this insect to colonize new geographic ranges successfully.

Table 2.1. Developmental periods (mean ± SEM) in days of *O. sulcatus* eggs, larvae, and pupae at constant temperatures

Temp.(^{o}C)	n	Egg	n	Larva	n	Pupa
11	20	47.1 ± 0.54	18	183.6 ± 4.16	15	36.0 ± 0.66
12	28	33.3[a]	33	231.1[a]	31	33.5[a]
15	27	19.7 ± 0.26	45	142.8 ± 2.28	40	21.9 ± 0.26
18	27	15.0 ± 0.12	41	127.2[a]	41	14.2[a]
21	22	12.5 ± 0.36	49	124.3 ± 2.30	35	13.2 ± 0.22
24	27	11.3 ± 0.11	25	101.4 ± 2.23	22	9.9 ± 0.17
27	24	9.4 ± 0.35		–		–
29	1	11.0		–		–
30		–		–		–

[a]: Data from Masaki and Ohto (1995) were included for temperature-dependent development rate model.

Table 2.2. Parameter estimates (value ± SEM) and coefficients of determination (r^2) to describe the temperature-dependent development rate $R(T)$, cumulative frequency distribution for development time variation $f(t)$, and temperature-dependent survival $S(T)$ of *O. sulcatus*

Model	Parameter	Egg	Larva	Pupa
$S(T)$	k	63.69 ± 6.83	32.07 ± 2.21	97.04 ± 22.03
	T_{max}	18.97 ± 1.28	19.04 ± 0.29	17.33 ± 2.92
	ρ	-7.340 ± 1.357	-4.368 ± 0.318	-8.206 ± 3.681
	r^2	0.854	0.978	0.590
$R(T)$	ψ	0.01419 ± 0.003614	0.00297 ± 0.00081	0.00977 ± 0.00347
	ρ	0.07772 ± 0.01160	0.05015 ± 0.01586	0.10188 ± 0.020417
	T_L	30.00 ± 0.06	27.00 ± 0.04	27.00 ± 0.06
	ΔT	0.8627 ± 0.2244	0.5175 ± 3.9407	1.1965 ± 0.6565
	r^2	0.963	0.964	0.980
$f(t)$	α	0.9654 ± 0.0036	0.9969 ± 0.0043	0.9849 ± 0.0039
	β	35.1806 ± 6.5187	13.8041 ± 1.0004	18.0923 ± 1.6992
	r^2	0.915	0.910	0.965

Table 2.3. Parameter estimates (value ± SEM) and coefficients of determination (r^2) of a linear model for *O. sulcatus*

Parameter	Egg	Larva	Pupa
a	-0.03002 ± 0.00554	-0.00244 ± 0.00266	-0.03573 ± 0.00702
b	0.00511 ± 0.00029	0.00059 ± 0.00017	0.00559 ± 0.00040
r^2	0.984	0.919	0.980
Developmental threshold, T_b (^{o}C)	5.9	4.1	6.4
Thermal constant, DD	195.8	1697.6	178.8

Ranges chosen for the regression were 11-27 ^{o}C for eggs, 12-18 ^{o}C for larvae, and 11-27 ^{o}C for pupae.

Fig. 2.1. Temperature-dependent survival (%) model for *O. sulcatus* (A) eggs, (B) larvae, and (C) pupae. Extreme-value function fit to the observed (●) and the data from Masaki and Ohto (1995) (○).
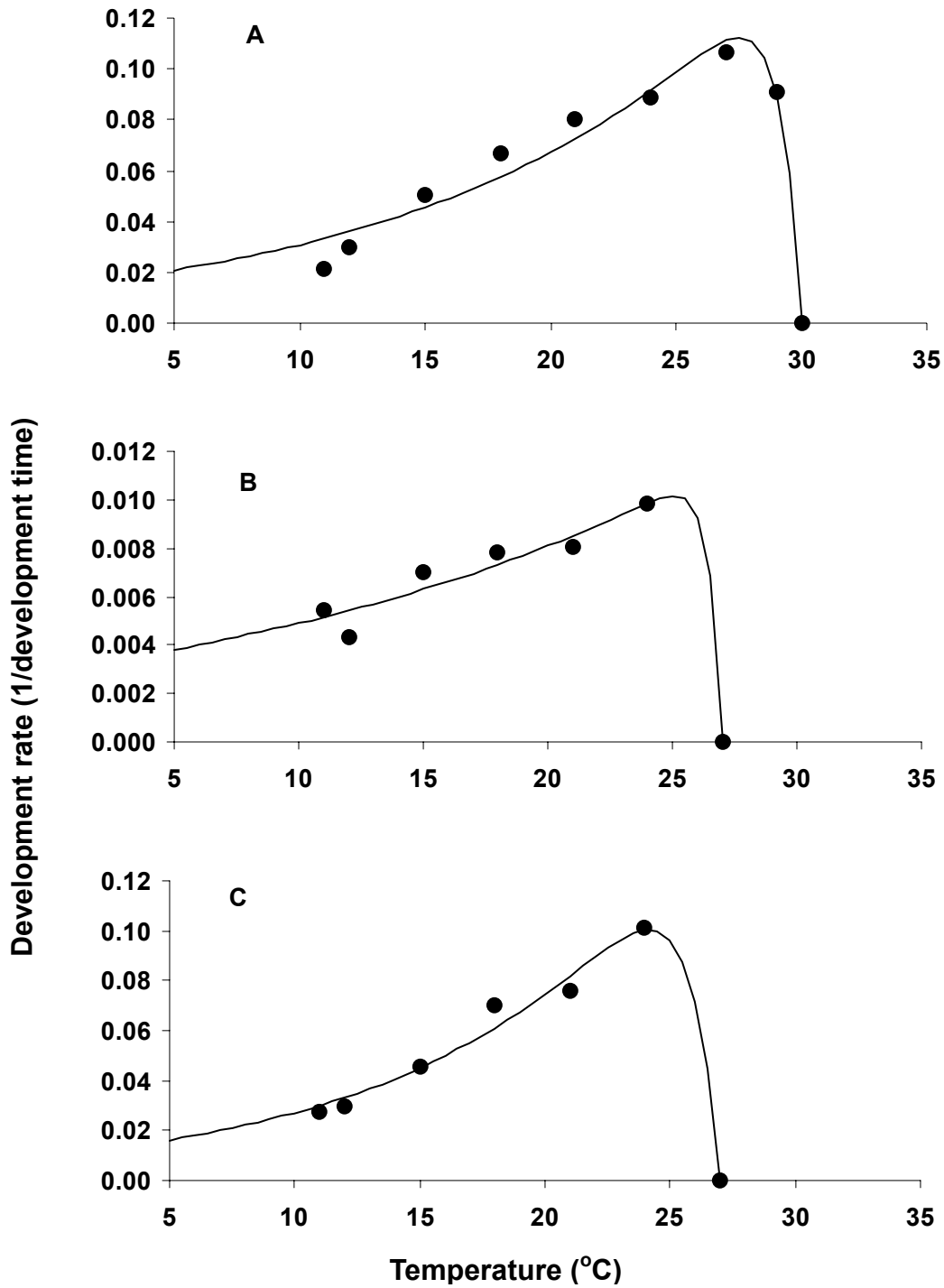
Fig. 2.2. Temperature-dependent model of development rate (1/development time) for *O. sulcatus* (A) eggs, (B) larvae, and (C) pupae. The Logan model $R(T)$ fit to the data (●).
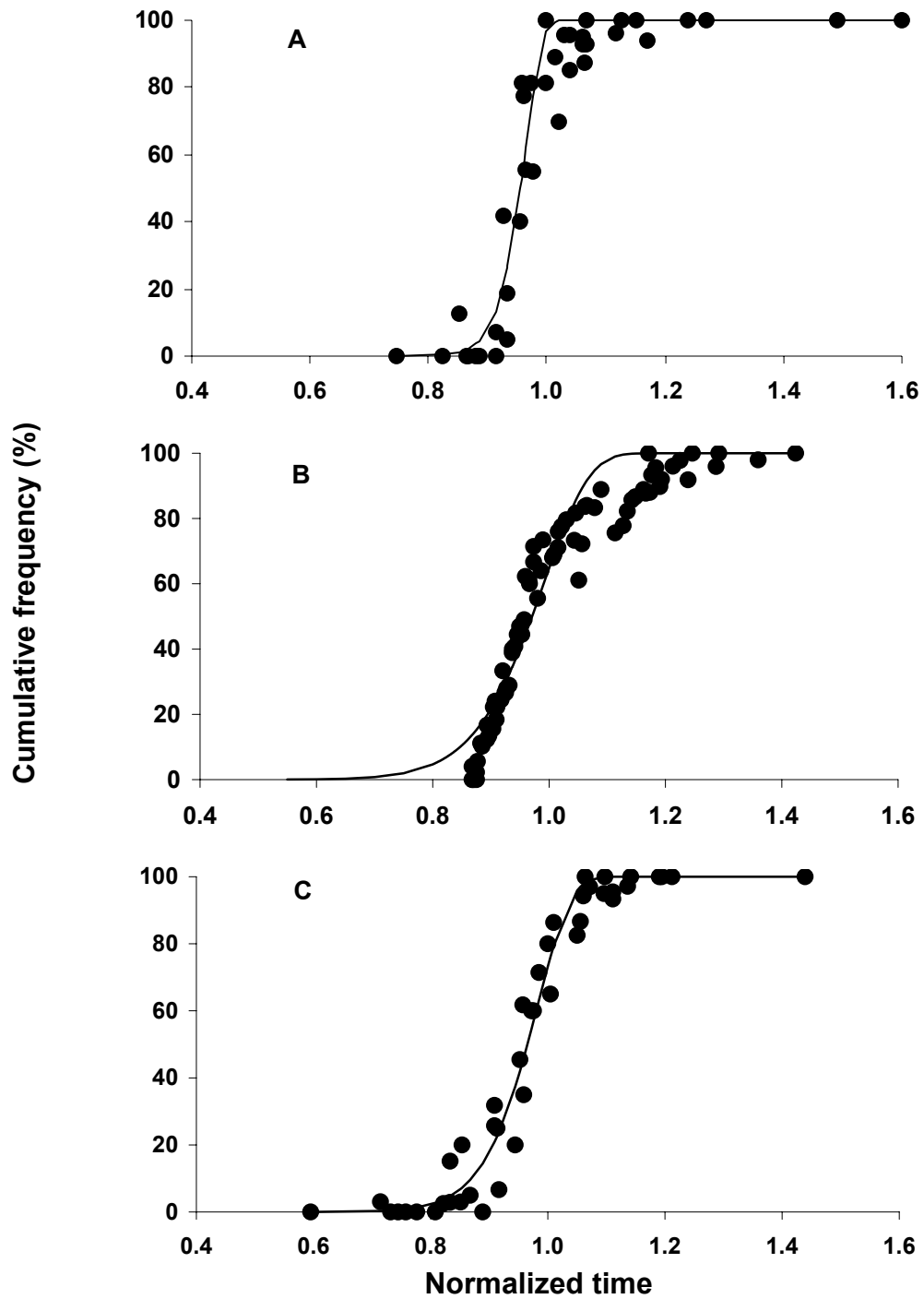
Fig. 2.3. Cumulative frequency (%) of stage emergence for *O. sulcatus* (A) eggs, (B) larvae, and (C) pupae. The Weibull function $f(t)$ fit to the cumulative frequency (●) versus normalized age (time/mean development duration).
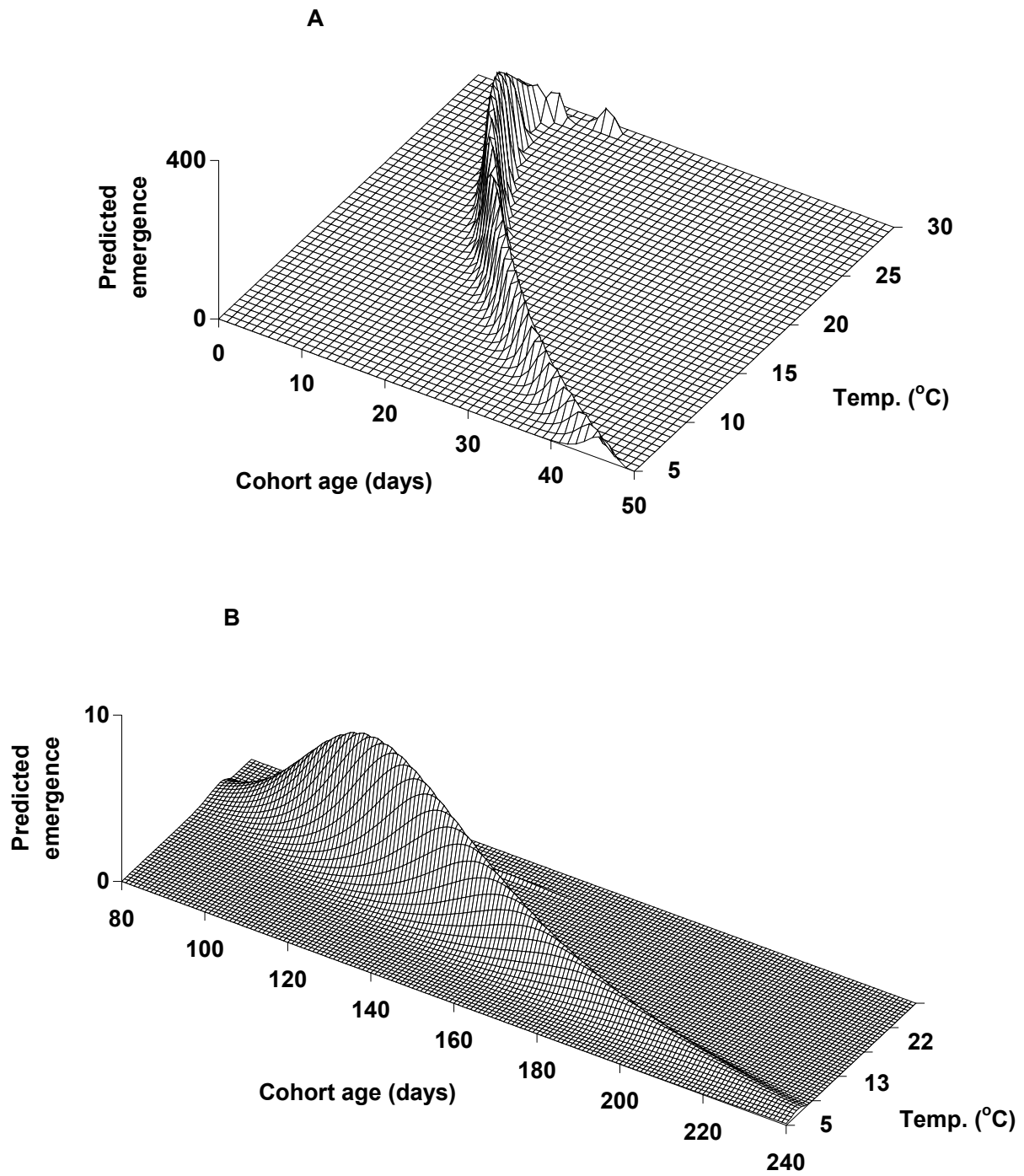
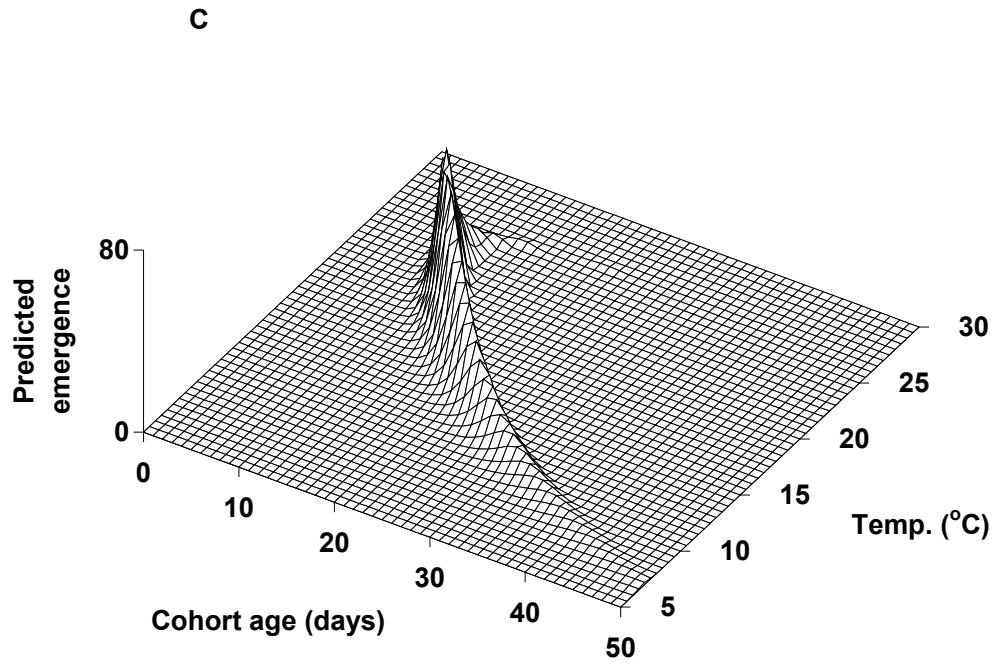**A**

B

Fig. 2.4. Continued

47

C

Fig. 2.4. Simulated density curves of stage emergence (transition) for *O. sulcatus* in relation to temperature (T, ^{o}C) and cohort age (t, days), given 1000 eggs as initial input value. (A) eggs, (B) larvae, and (C) pupae.

References

Allen JC, Yang Y & Knapp JL (1995) Temperature effects on development and fecundity of the citrus rust mite (Acari: Eriophyidae). Environmental Entomology 24: 996-1004.

Beck SD (1983) Insect thermoperiodism. Annual Review of Entomology 28: 91-108.

Botto EN & Boggiatto de Pacheco ME (1980) Resultados preliminares de estudios bioecológicos sobre el 'pulgon amarillo de los cereales' *Metopolophium dirhodum* (Walker), realizado en Castelar, Bs. As. durante 1976 a 1979. II. Estudios de laboratorio. Efecto de la temperatura sobre el desarrollo de *M. dirhodum* (Walker). Revista de la Sociedad Entomologica Argentina 39: 179-188.

Briere J-F & Pracros P (1998) Comparison of temperature-dependent growth models with the development of *Lobesia botrana* (Lepidoptera: Tortricidae). Environmental Entomology 27: 94-101.

Campbell A, Frazer BD, Gilbert N, Gutierrez AP & Mackauer M (1974) Temperature requirements of some aphids and their parasites. Journal of Applied Ecology 11: 431-438.

Cockfield SD, Butkewich SL, Samoil KS & Mahr DL (1994) Forecasting flight activity of *Sparganothis sulfureana* (Lepidoptera: Tortricidae) in cranberries. Journal of Economic Entomology 87: 193-196.

Curry GL, Feldman RM & Sharpe PJH (1978) Foundations of stochastic development. Journal of Theoretical Biology 74: 397-410.

Danks HV (1994) Diversity and integration of life-cycle controls in insects. In: Danks HV (ed) Insect Life-Cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control. Kluwer Academic Publishers, Dordrechrt. pp. 5-40.

Fornasari L (1995) Temperature effects on the embryonic development of *Aphthona abdominalis*

(Coleoptera: Chrysomelidae), a natural enemy of *Euphorbia esula* (Euphorbiales: Euphorbiaceae). Environmental Entomology 24: 720-723.

Got B, Piry S, Migeon A & Labatte JM (1997) Comparison of different models for predicting development time of the European corn borer (Lepidoptera: Pyralidae). Environmental Entomology 26: 46-60.

Ims RA (1990) The ecology and evolution of reproductive synchrony. Trends in Ecology and Evolution 5: 135-140.

Jandel Scientific (1996) TableCurve 2D. Automated Curve Fitting and Equation Discovery: Version 4.0. Jandel Scientific, San Rafael, CA.

Kim D-S, Lee J-H & Yiem M-S (2001) Temperature-dependent development of *Carposina sasakii* (Lepidoptera: Carposinidae) and its stage emergence models. Environmental Entomology 30: 298-305.

Kim D-S & Lee J-H (2003) Oviposition model of *Carposina sasakii* (Lepidoptera: Carposinidae). Ecological Modelling 162: 145-153.

Labuschagne L (1999) Black vine weevil – the millennium bug?. Bulletin of the Royal Entomological Society 23: 213-220.

La Lone RS & Clarke RG (1981) Larval development of *Otiorhynchus sulcatus* (Coleoptera: Curculionidae) and effects of larval density on larval mortality and injury to rhododendron. Environmental Entomology 10: 190-191.

Logan JA, Wollkind DJ, Hoyt SC & Tanigoshi LK (1976) An analytical model for description of temperature dependent rate phenomena in arthropods. Environmental Entomology 5: 1133-1140.

Marco V, Taberner A & Castanera P (1997) Development and survival of immature *Aubeonymus*

mariaefranciscae (Coleoptera: Curculionidae) at constant temperatures. Annals of Entomological Society of America 90: 169-171.

Ma C-S, Bernhard H & Poehling H-M (2004) Effects of pattern and timing of high temperature exposure on reproduction of the rose grain aphid, *Metopolophium dirhodum*. Entomologia Experimentalis et Applicata 110: 65-71.

Masaki M & Ohto K (1995) Effects of temperature on development of the black vine weevil, *Otiorhynchus sulcatus* (Coleoptera: Curculionidae). Research Bulletin of Plant Protection Service Japan 31: 37-45.

Masaki M & Sugimoto S (1991) Rearing method of larvae of the black vine weevil, *Otiorhynchus sulcatus* (F.) and other otiorhynchid weevils (Colopetera: Curculionidae). Research Bulletin of Plant Protection Service Japan 27: 7-11.

Montgomery ME & Nielsen DG (1979) Embryonic development of *Otiorhynchus sulcatus*: effect of temperature and humidity. Entomologia Experimentalis et Applicata 26: 24-32.

Moorhouse ER, Charnley AK & Gillespie AT (1992) A review of the biology and control of the vine weevil, *Otiorhynchus sulcatus* (Coleoptera: Curculionidae). Annals of Applied Biology 121: 431-454.

Pruess KP (1983) Degree-day methods for pest management. Environmental Entomology 12: 613-619.

Régnière J (1984) A method of describing and using variability in development rates for the simulation of insect phenology. The Canadian Entomologist 116: 1367-1376.

Rock GC (1985) Thermal and thermoperiodic effects on larval and pupal development and survival in tufted apple bud moth (Lepidoptera: Tortricidae). Environmental Entomology 14: 637-640.

Roltsch WJ, Mayse MA & Clausen K (1990) Temperature-dependent development under constant and fluctuating temperatures: comparison of linear versus nonlinear methods for modeling development of western grapeleaf skeletonizer (Lepidpoetera: Zygaenidae). Environmental Entomology 19: 1689-1679.

SAS Institute Inc. (1995) SAS User's Guide: Statistics. SAS Institute, Cary, NC.

Schread JC (1972) The black vine weevil. Connecticut Agricultural Experimental Station, Circular, No. 211.

Shanks CH Jr & Finnigan BF (1973) Temperature and relative humidity effects on eggs and first-stage larvae of the black vine weevil, *Otiorhynchus sulcatus*. Environmental Entomology 2: 855-858.

Sharpe PJH, Schoolfield RM, & Butler GD Jr (1981) Distribution model of *Heliothis zea* (Lepidoptera: Noctuidae) development times. The Canadian Entomologist 113: 845-856.

Stenseth C (1979) Effects of temperature on development of *Otiorhynchus sulcatus* (Coleoptera: Curculionidae). Annals of Applied Biology 91: 179-185.

Stinner RE, Gutierrez AP & Butler GD Jr (1974) An algorithm for temperature-dependent growth rate simulation. The Canadian Entomologist 106: 519-524.

VanKirk JR & AliNiazee MT (1981) Determining low temperature threshold for pupal development of the western cherry fruit fly for use in phenology models. Environmental Entomology 10: 968-971.

Wagner TL, Wu H, Sharpe PJH, Schoolfield RM & Coulson RM (1984) Modeling distributions of insect development time: a literature review and application of the Weibull function. Environmental Entomology 77: 475-487.

Wagner TL, Wu H, Feldman RM, Sharpe PJH & Coulson RM (1985) Multiple-cohort approach

for simulating development of insect populations under variable temperatures. Annals of Entomological Society of America 78: 691-704.

Warner RE & Negley FB (1976) The genus *Otiorhynchus* in America north of Mexico (Coleoptera: Curculionidae). Proceedings of the Biological Society of Washington 78: 240-262.