

## From a Descriptive Toward an Explicative Growth-Based Model on Immature *Oulema duftschmidi* (Coleoptera: Chrysomelidae) Development at Different Temperatures

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Environ. Entomol. 36(2): 245–255 (2007)

**ABSTRACT** The developmental rates of *Oulema duftschmidi* (Redtenbacher) eggs, larvae, and pupae were studied at different constant temperatures. A linear regression model was fitted to the data obtained in this and in a previous study within a temperature range where the rate proportionally increases with temperature. Ratios of SEs to the mean thermal constant and to the mean developmental threshold indicated that reliable estimates have been obtained for the three life stages. Within the framework provided by the metabolic theory of ecology, a growth-based model was evaluated to explain developmental rates in the entire temperature range permissive of development of the three life stages. The model is based on component functions describing growth patterns through time, temperature-dependent consumption rates of biomass, transformation of consumed food into body biomass change, and respiration rates with respect to temperature. Experimental data were used for the selection and validation of models and for the estimation of the parameters of different regression models. Limitations and opportunities for using the growth-based model to explain developmental rates are discussed. An empirical function was used to describe the variability of developmental rates.

**KEY WORDS** developmental rates, developmental threshold, consumption, biomass conversion, developmental rate variability

The cereal leaf beetles belong to the genus *Oulema* and infest cereal fields in Nearctic and Palearctic regions where different pest species have reduced yields by 60.9% (McPherson 1983). In cereal fields of Italy's Lombardy region, *Oulema duftschmidi* (Redtenbacher) is the most abundant among *Oulema* species (L.L., unpublished data). A series of studies were undertaken to explain the spatial and temporal distribution of *O. duftschmidi*. Densities observed in time and space are the outcomes of demographic processes such as development, mortality, fecundity, and net movement patterns that depend on environmental factors, including temperature. These dependencies are expressed as functions that, combined, eventually lead to an explanation of observed densities. The transit time through a life stage is defined as development, whereas its inverse is the developmental rate, which is the focus of this paper.

Recently, the developmental rates of immature *O. duftschmidi* life stages were observed at different constant temperatures within a restricted temperature range (Limonta et al. 2001). The developmental thresholds and developmental times for eggs, larvae, and pupae of *O. duftschmidi* were compared with the

ones obtained by Ali et al. (1977, 1979) for *O. melanopus* L. and *O. gallaeciana* (Heyden). It is noteworthy that the latter species has not yet been found in Italy's cereal fields. These studies indicate that the developmental threshold is higher and rates are lower for *O. duftschmidi* than for the other species. In the case of *O. melanopus*, the development of all immature stages was studied within the entire range of temperature permitting development (Guppy and Harcourt 1978).

Average developmental rates are considered to be important, but information is often insufficient to adequately represent poikilothermic development (Severini et al. 1990, Di Cola et al. 1999). The observed high variability in developmental rates relative to the means, reported by Limonta et al. (2001), required application of a stochastic model to temperature-dependent development (Severini et al. 2003). Development was analyzed, and a time distributed delay model was found appropriate for representing temperature dependent development of eggs. In this work, we evaluate the variability in developmental rates of all three immature life stages of *O. duftschmidi*.

The purpose of this work is to improve the predictive capability of the descriptive model that originally was developed for comparison purposes (Limonta et al. 2001). The applicability of this model is restricted to a temperature range where the rates increase linearly with increasing temperatures. To overcome this restriction, we constructed a model incorporating the developmen-

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tal rates across the entire temperature range that allows development of immature *O. duftschmidi* life stages. Thus, preference is given to a physiologically based model that explains development on the basis of growth and respiration and thereby sets the stage for analyzing multitrophic interactions. Gutierrez (1996) showed how nutrition-based models facilitate coupling of populations operating at both the same and different trophic levels. According to Agrawal (2004), the metabolic theory of ecology as presented by Brown et al. (2004), including the combination of nutrition and temperature, has compelling predictive power in explaining life history traits, population parameters, and even broader scale ecosystem processes. In this context, the growth-based model of Hilbert (1995) seems particularly promising to explain developmental rates, and we test here its applicability to explain the rates of immature *O. duftschmidi*. The passage from a linear descriptive model, which is valid in a restricted temperature range, toward a more general and explicative model that can be extended easily to interacting population systems, is an important step in the analysis of the spatio-temporal distribution of *O. duftschmidi* in Italian cereal fields.

#### Materials and Methods

**Rearing.** *Oulema duftschmidi* adults were collected in Lombardy's Po valley (Northern Italy) in wheat and barley fields, as well as on uncultivated Poaceae bordering the crops. Sampling started at the beginning of March. The adults were kept at  $24 \pm 1^\circ\text{C}$  and fed wheat seedling leaves. Each newly formed pair was placed in a petri dish (15 cm diameter) containing moist paper (distilled water added with 5% sodium hypochlorite) and wheat seedling leaves. The observations on individual development were made on three life stages: eggs, larvae, and pupae. The petri dishes were observed daily to record the life stage and the age in days at which the individual of the different experiments leave each life stage.

**Linear Descriptive Developmental Rate Model and Parameter Estimation.** The developmental rates were observed in a restricted temperature range permitting the use of a linear model (Limonta et al. 2001). The data set previously analyzed by Limonta et al. (2001) was expanded with additional observations. In six different experiments, eggs were reared to the adult stage at constant temperatures ( $T_i$  [ $^\circ\text{C}$ ],  $i = 1, 2, 3, 4, 5, 6$ ;  $T_1 = 19 \pm 1^\circ\text{C}$ ,  $T_2 = 20 \pm 1^\circ\text{C}$ ,  $T_3 = 22 \pm 1^\circ\text{C}$ ,  $T_4 = 24 \pm 1^\circ\text{C}$ ,  $T_5 = 26 \pm 1^\circ\text{C}$ ,  $T_6 = 27 \pm 1^\circ\text{C}$ ). Eggs were reared in groups, whereas newly emerged larvae were transferred individually into different petri dishes. The initial number  $N_i$  varied according to experiment ( $N_1 = 237$ ,  $N_2 = 999$ ,  $N_3 = 239$ ,  $N_4 = 396$ ,  $N_5 = 397$ ,  $N_6 = 500$ ).

In a restricted range of temperatures, development time  $D$  is often observed in units of days, and the rate  $r(T)$  is approximated by a linear regression model

$$r(T) = h(T - T_0) \quad [1a]$$

that relates, with slope  $h$ , the rates  $r$  ( $\text{day}^{-1}$ ) to the temperature  $T$  ( $^\circ\text{C}$ ) above a threshold  $T_0$  (Gilbert et

al. 1976, Gutierrez 1996, Limonta et al. 2001). According to the rates sum rule applied to 1-d intervals (Curry and Feldman 1987), development is completed if the number of degree-days accumulated by day  $D$  reach or exceed the thermal constant  $D^*$

$$\sum_{i=1}^D (T - T_0) = \frac{1}{h} = D^* \quad [1b]$$

Campbell et al. (1974) described the calculation of the SEs for  $T_0$  and  $D^*$

$$SE(T_0) = \frac{\bar{y}}{h} \sqrt{\frac{s^2}{N\bar{y}^2} + \left[\frac{SE(h)}{h}\right]^2} \quad [2a]$$

$$SE(D^*) = \frac{SE(h)}{h^2} \quad [2b]$$

where  $N$  = number of replicates,  $s^2$  = residual mean square of  $y$ , and  $\bar{y}$  = sample mean.

The ratio of the SEs to the means is used as a measure of the reliability of the estimates for  $T_0$  and  $D^*$ .

The parameter  $h$ , the threshold  $T_0$ , and their SEs were estimated by linear least square regression techniques as described by Limonta et al. (2001) and Severini et al. (2003). Importantly, only the observed rates in the temperature range  $19$ – $26^\circ\text{C}$  for eggs and larvae and  $19$ – $27^\circ\text{C}$  for pupae were used, because in this range, a linear regression model was found appropriate to describe the rate-temperature relationship (Limonta et al. 2001).

Number of observations, means, SDs, and relative frequencies of development at  $20$  and  $27^\circ\text{C}$  are reported in Table 1. Therein, the relative frequencies are reported for 10 maturation time classes.

**Growth-Based Model Description.** Hilbert (1995) assumed that temperature  $T$  and biomass  $M$  affect the rate of development  $r(T, M)$  through the growth rate  $g(T, M)$ . During development, weight of immature life stages change from an initial mass  $W_0$  to mass  $W_f$  at completion of development.

$$r(T, M) = \frac{g(T, M)}{\int_{W_0}^{W_f} \frac{dW}{f(W)}} \quad [3]$$

In equation 3, both the initial  $W_0$  and final  $W_f$  mass are constants. Growth rate  $g(T, M)$  can be expressed by a numerical response that translates biomass consumption into growth or reproduction (Baumgärtner et al. 1987, Gutierrez 1996). Accordingly, a proportion ( $\beta$ ) of the consumed food  $c(T)$  is lost as a result of egestion. From the remaining food, only the proportion  $(1 - \delta)$  is assimilated. If the assimilated food exceeds respiration costs

$$r(T, M) = \frac{c(T)(1 - \beta)(1 - \delta) - z_0 b \left(\frac{T - T_h}{10}\right)}{\int_{W_0}^{W_f} \frac{dW}{f(W)}} \quad [4]$$

**Table 1.** Development time D (days) of *O. duftschmidi* immature life stages

Temp (°C)	Stage	Classes of maturation time <sup>a</sup>										n	Mean	SD
		I	II	III	IV	V	VI	VII	VIII	IX	X			
20	Eggs	0	0.43	0.52	0.05	0	0	0	0	0	0	21	8.9	0.9
	Larvae	0	0	0	0	0.05	0.33	0.14	0.33	0.05	0.1	21	18.0	2.9
	Pupae	0	0	0	0	0	0	0.3	0.2	0.2	0.3	10	20.8	2.9
27	Eggs	0.71	0.29	0	0	0	0	0	0	0	0	38	6.2	2.6
	Larvae	0	0	0.21	0.42	0.24	0.1	0	0.03	0	0	38	12.1	2.0
	Pupae	0	0.04	0.24	0.43	0.14	0.1	0.05	0	0	0	21	11.9	2.4

Relative frequency in maturation time classes, the total no. of observations (n), the mean, and the SD are given for each temperature (20 and 27°C) and life stage (egg, larva, pupa).

<sup>a</sup> I: 5 ≤ D < 7; II: 7 ≤ D < 9; III: 9 ≤ D < 11; IV: 11 ≤ D < 13; V: 13 ≤ D < 15; VI: 15 ≤ D < 17; VII: 17 ≤ D < 19; VIII: 19 ≤ D < 21; IX: 21 ≤ D < 23; X: 23 ≤ D ≤ 25.

where  $z_0$  represents the basic respiration costs at temperature  $T_b$ , and  $b$  is the multiplier of respiration for a temperature increase of 10°C. Note that, the divisor in equation 3 represents growth that can be expressed by different models (Hilbert 1995). In the case of

exponential growth, it can be substituted by the divisor appearing in equation 5. We follow Hilbert (1995) and rely on the Beta function, in the form presented by him, to express the dependency of the consumption  $c(T)$  of biomass (mg/mg/day) on temperature  $T$

$$r(T) = \frac{\kappa(1 - \beta)(1 - \delta)(T - T_l)^\lambda(T_u - T)^\gamma - z_0 b \left(\frac{T - T_l}{10}\right)}{\ln \left[ \frac{W_f}{W_0} \right]} \tag{5}$$

where  $T_l$  and  $T_u$  are the lower and upper temperature thresholds for consumption,  $\lambda$  and  $\gamma$  are the Beta function parameters, and  $\kappa$  is the scaling factor.

**Growth-Based Model Parameter Estimation.** We followed Hilbert (1995) in using a stepwise procedure in which experimental data are used for model component selection, parameterization, and validation.

First, we measured and compared the final weights, i.e., the weight on the day before pupation, of 21 larvae at 20°C and of 38 larvae at 27°C (Table 2). Relative frequencies are reported for 10 final weight classes (Table 2).

Second, we started with larvae and tested the applicability of an exponential model for representing the divisor in equation 5. For this purpose, the growth of 236 and 228 larvae were studied at constant temperatures of 20 and 27°C, respectively. They were weighed daily on an analytical balance (CP 64; Sartorius, Göttingen, Germany) to the nearest 0.1 mg until the pupal stage. For each of the two temperatures, we evaluated the applicability of

$$\ln(W(t)) = a + qt \tag{6}$$

Third, we calculated the biomass consumed on the basis of measured leaf area eaten (Bertoldo 2003,

Jensen and Cameron 2004). Accordingly, 1 cm<sup>2</sup> corresponds to 19.9 mg fresh weight. The leaf offered daily to each larva was scanned, and the area consumed was measured with SigmaScan Pro 4.01 (SPSS, Chicago, IL) and translated into milligrams of fresh weight consumed. Consumption rate 1 and rate 2 were measured at  $T = 20^\circ\text{C}$  (21 individuals; mean consumption rate, 1.66) and  $T = 27^\circ\text{C}$  (38 individuals; mean consumption rate, 1.95), respectively. Rate 3 (mean consumption rate, 1.33) was calculated for  $T = 15^\circ\text{C}$  and reflects the observation of Trichilo and Mack (1989) and Jensen and Cameron (2004) in that herbivore consumption rates increase linearly with temperature within a restricted range. Rate 4 reflects our experience that a 10% decrease from the suspected maximum rate at  $T = 27^\circ\text{C}$  can be expected at  $T = 32^\circ\text{C}$  (mean consumption rate, 1.76). We set  $T_l = 10^\circ\text{C}$  and  $T_u = 40^\circ\text{C}$ , i.e., to values that best reflect our experience of *O. duftschmidi* requirements. Following Hilbert (1995), we used the Beta function and estimated the parameters  $\lambda$  and  $\gamma$  and the scaling factor  $k$  through linear least square regression techniques applied to the four consumption rates (mg/mg/day), as ex-

**Table 2.** Final weights  $W_f$  (mg) of *O. duftschmidi* larvae

Temp (°C)	Classes of final weight <sup>a</sup>										n	Mean	SD
	I	II	III	IV	V	VI	VII	VIII	IX	X			
20	0	0.05	0.14	0.24	0.32	0.1	0.05	0.05	0	0.05	21	8.26	1.98
27	0.08	0.13	0.37	0.16	0.13	0.08	0.05	0	0	0	38	7.07	1.61

For each class of final weights, the relative frequency is shown; for each temperature, the total no. of observations (n), the mean, and the SD are also given. The means are significantly different at  $P = 0.05$  ( $t = 2.002$ ;  $df = 57$ ) according to the Student's  $t$ -test.

<sup>a</sup> I:  $4 \leq W_f < 5$ ; II:  $5 \leq W_f < 6$ ; III:  $6 \leq W_f < 7$ ; IV:  $7 \leq W_f < 8$ ; V:  $8 \leq W_f < 9$ ; VI:  $9 \leq W_f < 10$ ; VII:  $10 \leq W_f < 11$ ; VIII:  $11 \leq W_f < 12$ ; IX:  $12 \leq W_f < 13$ ; X:  $13 \leq W_f \leq 14$ .

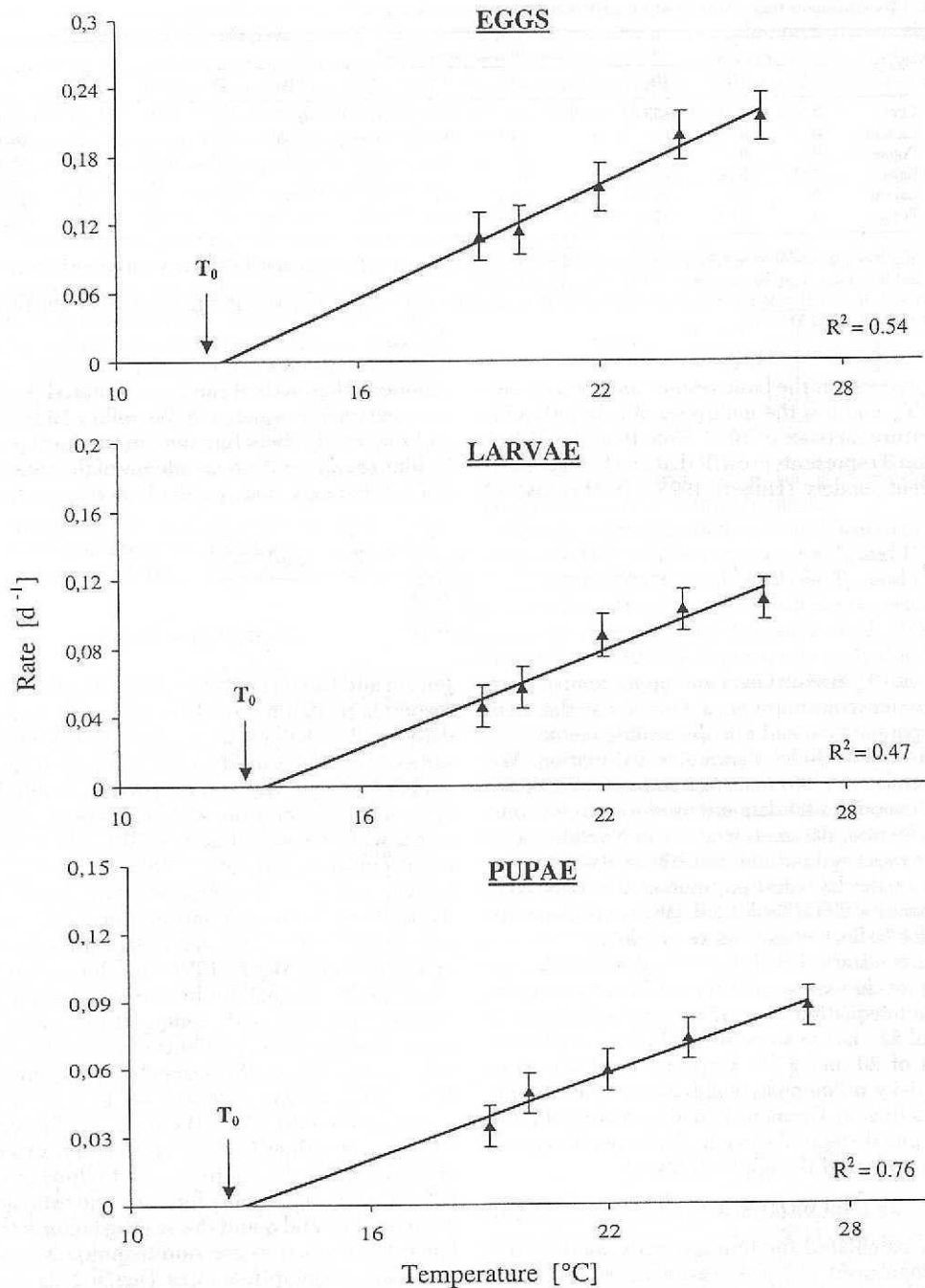


Fig. 1. Observed developmental rates (means and SEs) for immature *O. duftschmidi* life stages at different constant temperatures. A linear regression model was fitted to developmental rate data (parameters are given in Table 1).  $T_0$  indicates the lower temperature developmental threshold.

pressed by the log-transformed form of the consumption equation:

$$\ln(c) = \ln(\kappa) + \lambda \ln(T - T_l) + \gamma \ln(T_u - T), \quad [7]$$

where  $\kappa$ ,  $\lambda$ , and  $\gamma$  are the Beta parameters,  $T_l$  and  $T_u$  are the lower and the upper temperature, respectively, and  $c$  is the consumption rate.

Fourth, we measured daily larval weight changes (mg/mg of body weight) and daily consumption (mg/mg of body weight), as previously described, and assumed that the weight change (mg/mg of body weight) is related to the amount of food consumed during that day (mg/mg of body weight). The data obtained from 21 and 38 individuals were expressed as



**Table 3.** Reliability of linear regression model parameters for the development of immature *O. duftschmidi* life stages: SE of the developmental thresholds ( $T_0$ ) and thermal constants  $D^*$  (degree-days) and their ratio to the mean

Stage	n	$T_0$	SE( $T_0$ )	SE( $T_0$ )/ $T_0$	$D^*$	SE( $D^*$ )	SE( $D^*$ )/ $D^*$
Eggs	737	11.97	0.31	0.025	$62.5 \pm 1.6$	1.66	0.027
Larvae	108	13.8	0.38	0.027	$103.9 \pm 4.8$	4.83	0.046
Pupae	54	12.71	0.79	0.062	$161.3 \pm 11.9$	11.98	0.074

*n* is the no. of observations.

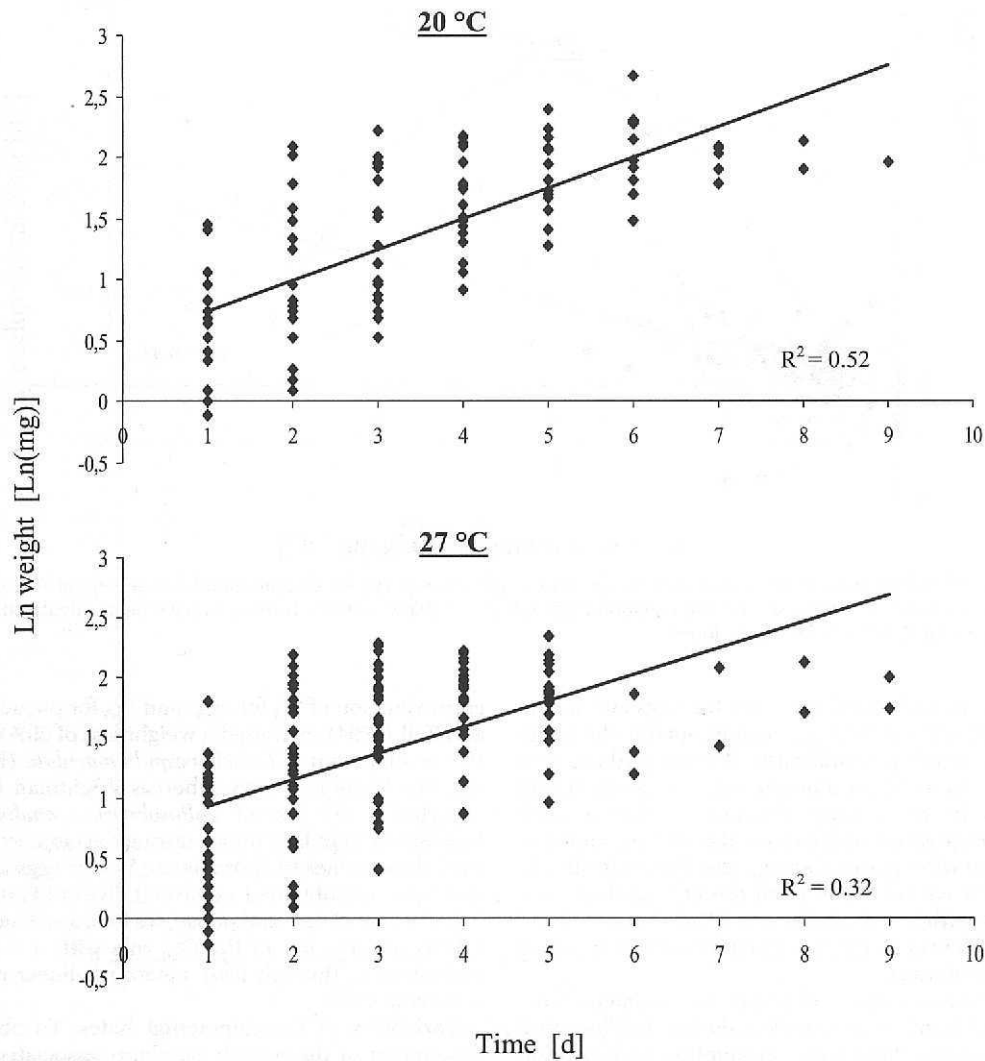
linear regressions on consumption at 20 and 27°C, respectively. The daily weighings were initiated at third instar. Larvae were cleaned of excrement before placing them on the plate balance. Weight change  $g(T)$  is expressed by

$$g(T) = -z_0 \times (T) + c(T)(1 - \varepsilon)(1 - \delta) \quad [8]$$

where  $z_0 \times (T)$  represents the respiration rate (mg/mg of body fresh weight) (Baumgärtner et al. 1987). Importantly,

we estimated the product  $(1 - \varepsilon)(1 - \delta)$ , so that we do not differentiate between egestion and assimilation. Student's *t*-test was used to test the hypotheses that the slopes  $(1 - \varepsilon)(1 - \delta)$  and the respiration rates  $z_0 \times (T)$  differ between the two experiments. Subsequently, we estimated respiration rates and the product  $(1 - \varepsilon)(1 - \delta)$  for the pooled data.

Fifth, we relied on the developmental rate data previously used to parameterize the linear regres-



**Fig. 2.** Representation of growth [ln(mg fresh weight)] of *O. duftschmidi* larvae at temperatures of 20 and 27°C by an exponential model.

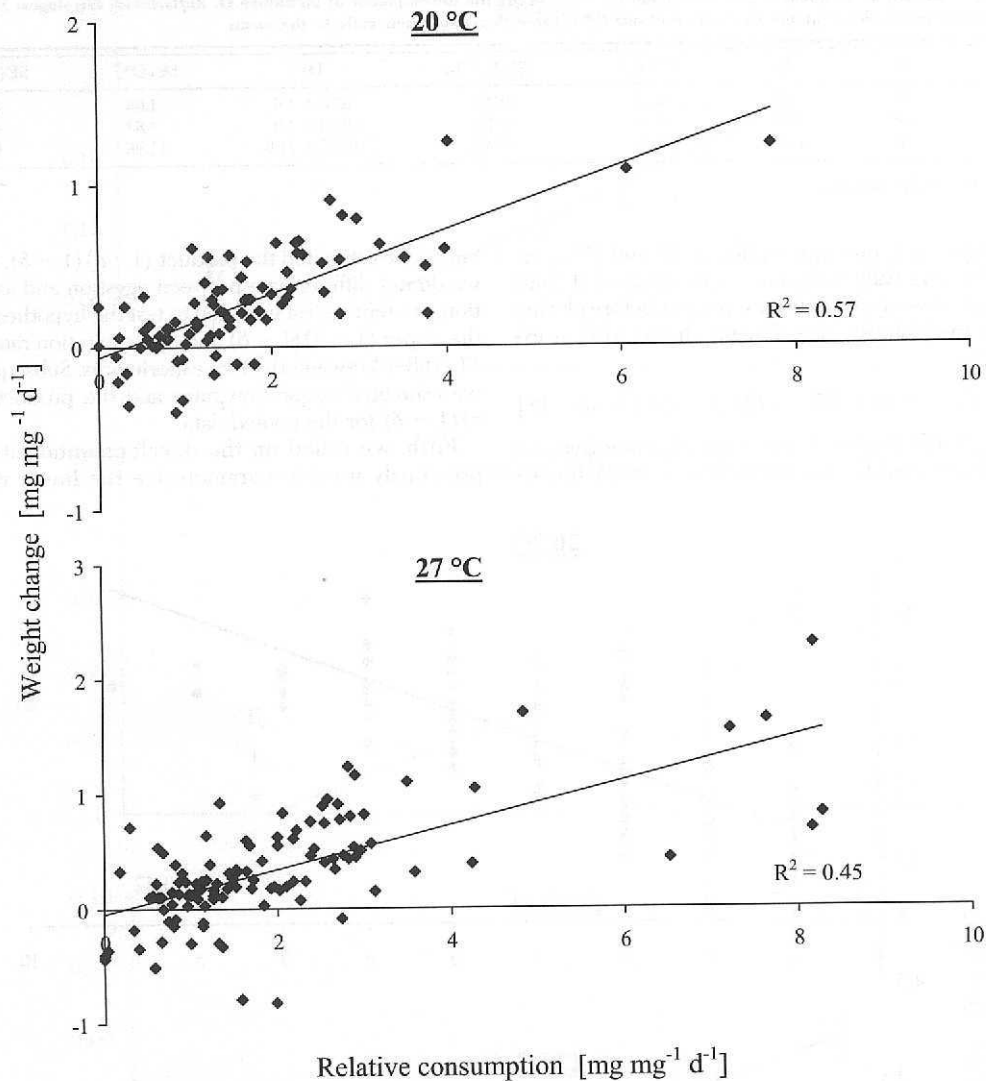


Fig. 3. Transformation of consumed biomass ( $x$ ) into weight change ( $y$ ) for *O. duftschmidti* larvae kept at 20 and 27°C. (equation 1 [20°C]:  $y = 0.1943x - 0.0564$ ; equation 2 [27°C]:  $y = 0.1935x - 0.047$ ). Intercepts have been calculated. There is no significant difference between slopes

sion model and added the rates for eggs and larvae obtained at  $T = 27^\circ\text{C}$ , i.e., the ones outside the range of linear developmental rates. We inserted the previously obtained parameters into equation 5 and used it to re-estimate, through nonlinear least square regression techniques, the scaling factor  $\kappa$ , the respiration parameters  $z_0$ , and the multiplier  $b$ . Note that we refrained from directly applying the  $Q_{10}$  rule with  $b = 2$  (Cutierrez 1996), because Kayser and Heusner (1964) reported very low  $b$  values for coleopterans.

In the case of eggs and pupae, we assumed an exponential trend in biomass loss during development. In these stages, there is no consumption, and equation 5 is reduced to respiration in relation to initial  $W_0$  and final weight  $W_f$ . Data on larval weight provide an

approximation of  $W_f$  for eggs and  $W_0$  for pupae. Stein and Fell (1994) measured a weight loss of 29% during the development of *Dolichovespula maculata* (Hymenoptera: Vespidae) eggs, whereas Wightman (1978) reported a 20% loss of *Callosobruchus analis* (Coleoptera: Bruchidae) pupae during development. We used these values to approximate  $W_0$  for eggs and  $W_f$  for pupae and obtained a constant divisor in equation 5. In the case of eggs and pupae, we followed Gutierrez (1996), making use of the  $Q_{10}$  rule with  $b = 2$  and estimating  $z_0$  through least square nonlinear regression techniques.

**Variability of Developmental Rates.** To obtain a description of the overall variability associated with developmental rates, we relied on the models of Régnière (1984).

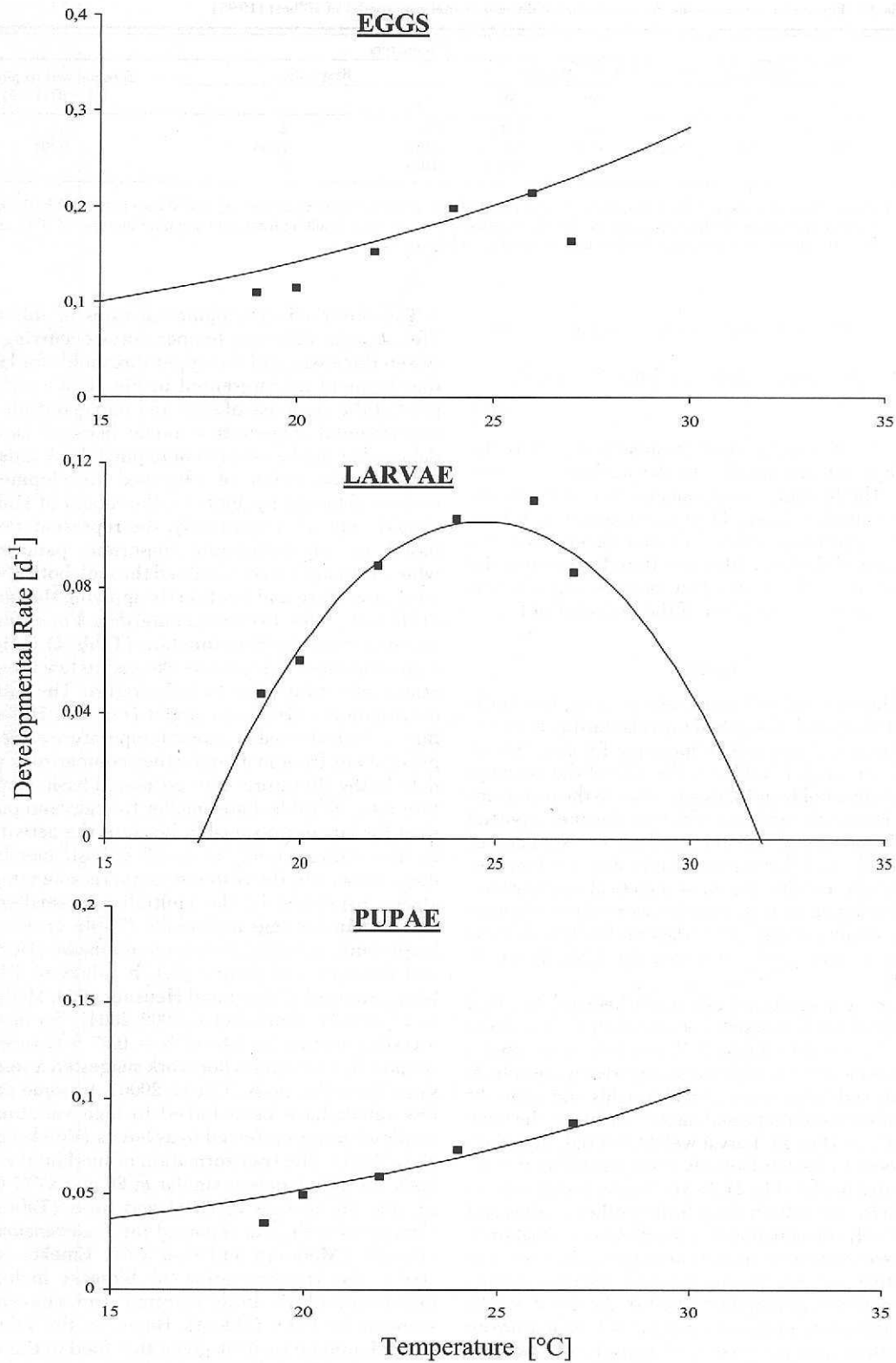


Fig. 4. Developmental rates of *O. duftschmidi* eggs, larvae, and pupae predicted by the growth-based model of Hilbert (1995) (line) and observed under constant temperature conditions (dots).

Table 4. Parameter estimates for the growth-based developmental rate model of Hilbert (1995)

Stage	Parameters							
	Consumption			Weight		Respiration		Egestion and respiration [[1-β)(1-δ)]
	κ	λ	γ	W <sub>0</sub>	W <sub>f</sub>	z <sub>0</sub>	b	
Eggs				1.6	1.265	0.02	2	
Larvae	0.685	0.486	0.322	1.265	7.7	0.915	1.146	0.194
Pupae				7.7	6.164	0.008	2	

κ, λ, and γ are the scalar and the shape parameters of the Beta function adjusted to consumption. W<sub>0</sub> and W<sub>f</sub> are initial and final weights (mg), z<sub>0</sub> is the respiration at the base temperature, b is the multiplier of respiration resulting from a temperature increase of 10°C, and (1-β)(1-γ) is the proportion of biomass lost because of egestion and conversion.

$$f = \{1 + \exp[-K(X - C)]\}^{-\frac{1}{Q}}, \quad [9a]$$

$$f = \{1 + \exp[-K(X - 1)](0.5^{-Q} - 1)\}^{-\frac{1}{Q}}, \quad [9b]$$

where  $f$  is the cumulative frequency, and  $X$  is the development rate relative to the median (rate/median). The  $X$  values were assigned to 1 of 10 classes. The parameters  $K$  and  $Q$  were estimated with least square regression techniques and determined the steepness of the sigmoid curve, thus determining the amount of variability and skew, respectively, whereas  $C$  determined the position of the midpoint of  $f$ .

### Results

Within a restricted temperature range, the linear model adequately described the relationship between developmental rate and temperature for eggs, larvae, and pupae (Fig. 1; Table 3). The SEs of the developmental thresholds and slopes relative to the means are <0.1. Hence, the addition of data to the ones reported by Limonta et al. (2001) resulted in estimates of thresholds and thermal constants that we consider sufficiently reliable for most practical applications. The developmental rate statistics were obtained under high mortality of eggs (50%), larvae (84.7), and pupae (63.8), as previously observed by Limonta et al. (2001).

There is a significant difference between the final weights of larvae measured at 20 and 27°C ( $t = 2.002$ ;  $df = 57$ ;  $P = 0.05$ ; Table 2). Nevertheless, we used a constant mean value of 7.7 mg as required by equation 6.

High variability among larval weights and a low  $R^2$  were observed for repeated measurements on the same individuals (Fig. 2). Larval weight through time does not seem to be satisfactorily represented by the exponential model (Fig. 2). Nevertheless, for the sake of simplicity, we refrain from testing other models and tentatively use equation 6 as the divisor in equation 5.

Linear regression models are appropriate for representing the relationship between relative growth and relative consumption (Fig. 3). At the  $P = 0.05$  level, there was no significant effect of temperature on respiration and conversion of consumed food into weight change ( $t = 0.33$ ;  $df = 199$ ). Hence, we used the value of 0.194 for the slope and 0.915 for respiration as obtained from the pooled data for equation 5.

The observed developmental rates of different life stages at different temperatures occurring between the lower and the upper thresholds for larval development are presented in Fig. 4. We did not predict the response of eggs and pupae outside the experimental temperature range because lack of data makes model evaluation impossible. A satisfactory representation of observed developmental rates is obtained by applying the model of Hilbert (1995) (Fig. 4). Importantly, the representation is based on physiologically important parameters whose estimates were obtained through both a stepwise procedure and by directly applying the model of Hilbert (1995) to experimental data. For example, parameters of the Beta function (Table 4) indicate a nonsymmetrical response, skewed to low temperatures, of consumption to temperature. The pattern corresponds to Hilbert's model (Fig. 2 in Hilbert), but the lack of reliable data at temperature extremes prevents us from making further comparisons with data in the literature. The estimated basic respiration rates in Table 4 are smaller for eggs and pupae than for larvae presumably because the activity of larvae requires energy in excess of basic metabolic costs. However, the response to increasing temperatures, expressed by the multiplier, is smaller for larvae than for eggs and adults (Table 4). For coleopterans, including *Tribolium castaneum* (Herbst) and *Rhizoperta dominica* (F.),  $b$  values < 2 have been reported (Kayser and Heusner 1964, Medrano and Gall 1976, Emekci et al. 2002, 2004). For insects, a resting metabolic rate of  $b = 0.67$  was recently proposed, whereas earlier work suggested a steeper slope for arthropods (Clarke 2006). In some cases, low values have been linked to high variation in respiration rates referred to as bursts (Emekci et al. 2002, 2004). The transformation of food intake into body weight change is similar at 20 and 27°C (Fig. 3), and an average of 0.194 was used (Table 4). Compared with data reported for *T. castaneum* for example (Medrano and Gall 1976, Emekci et al. 2002), the transformation of biomass including losses caused by both egestion and conversion seems to be low (Table 4). However, the value of 0.194 should be realistic given that food in this case consisted of fresh leaves with high water content.

The cumulative frequency of larvae, pupae, and adults emerging from the previous life stage is repre-



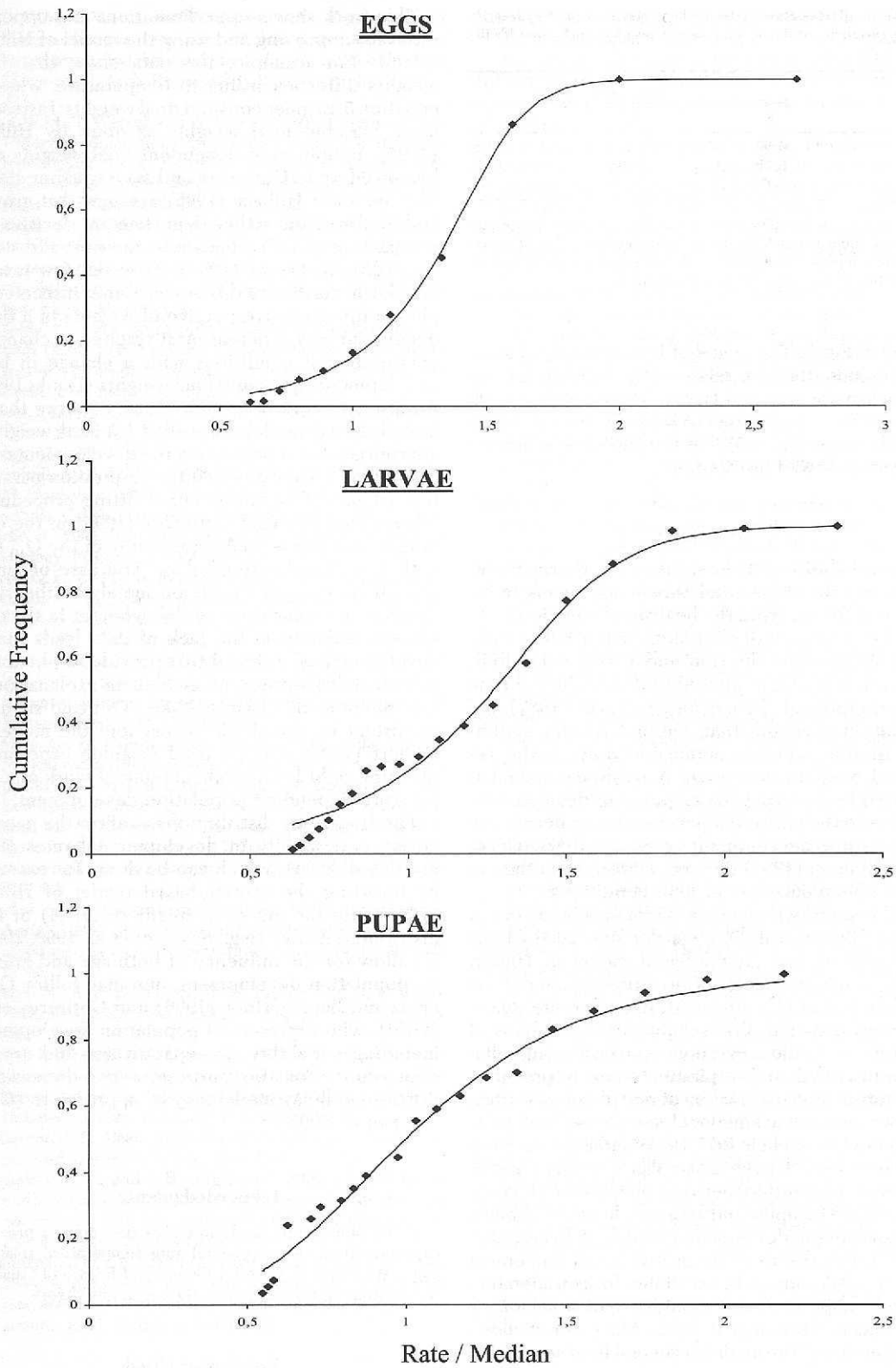


Fig. 5. Cumulative frequency distributions of *O. duftschmidi* larvae, pupae, and adults emerging from the previous life stage. The curves have been obtained by fitting the model of Régnière (1984) to observed pooled data (dots).

Table 5. Parameters of the model of Régnière (1984) describing the variability of the development rates of *O. duftschmidti*'s life stages

Stage	Parameters		
	K	Q	C
Eggs	9.365	2.62	1.526
Larvae	6.298	2.195	1.472
Pupae	3.958	1.018	—

Equation 8a has been fitted to the pooled temperature data of eggs and larvae and equation 8b to the pooled temperature data of pupae. K, Q, and C represent steepness (or the amount of variability), skew, and position of the midpoint of Y, respectively.

sented in Fig. 5. The model of Régnière (1984) satisfactorily describes the relationship: equation 9a was satisfactory for eggs and larvae, whereas equation 9b was used for pupae. Values of K and Q decreased with later life stages (Table 5). The Q value is  $>1$ , indicating a negative skewed distribution.

### Discussion

The reliability of the estimates for thermal constants and developmental thresholds seems to be sufficient for applying the heat sum (equation 1) to model *O. duftschmidti* phenology under field conditions. When using the sum under field conditions, however, the user is advised to divide the 1-d time step into intervals (Curry and Feldmann 1987) and to take into account that, without further modifications, the model is applicable only to the restricted temperature range. A nonlinear model is required to represent the response of developmental rates to the entire temperature range permissive of immature development. Among others, Curry and Feldmann (1987) derived a rate sum method to model phenologies under field conditions.

In this study, we relied on the metabolic theory of ecology (Brown et al. 2004, Van der Meer 2006, Clarke 2006) and on the growth-based model of Hilbert (1995) to obtain a mechanistic representation of the development of *O. duftschmidti* immature life stages. The representation of development on the basis of resource acquisition, egestion, conversion, and allocation to growth and respiration seems to provide a more satisfactory explanation of rate phenomena than reliance on enzyme kinetics alone (Logan et al. 1976, Sharpe and DeMichele 1977, Curry and Feldman 1987, Gutierrez 1996, Clarke 2006, Van der Meer 2006). However, relationships between metabolism and temperature are complex and seriously limit the explicative capacities of development models (Clarke 2006). Nevertheless, the use of the growth-based function of Hilbert (1995) opens the possibility for consideration of food composition and quality, i.e., of stoichiometrical aspects (Hessen et al. 2004). Moreover, it allows the extension of the model to general food acquisition and allocation functions and thereby paves the way for development of multitrophic population models (Gutierrez 1996).

This work shows some limitations and opportunities for improving and using the model of Hilbert (1995). For example, the data show that final weights differ according to temperature, whereas equation 5 assumes constant final weights. Instead of using variable final weights as done by Hilbert (1995), temperature-dependent final weights may be considered (Gutierrez and Baumgärtner 1996). The model of Hilbert (1995) assumes that growth and final weights rather than time are decisive for the passage of individuals into the next life stage. According to Danks (1994), however, few insects develop according to this model. Other insects complete a life stage irrespective of weights in a time-dependent way, whereas most respond to changing environmental conditions with a change in both developmental time and final weights (Danks 1994). Additional work is required to confirm that a growth-based model controlled by final weight is appropriate for representing the development of *O. duftschmidti*. We estimated the respiration parameters ( $b$ ,  $z_0$ ) of larvae by curve fitting procedures, whereas we followed Gutierrez (1996) in the case of eggs and pupae, making use only of the  $Q_{10}$  rule with  $b = 2$  and estimated  $z_0$ . The case of larvae reflects an attempt to rely on metabolic theory to develop an explanatory model, whereas in the case of eggs and pupae, the lack of data leads to the development of a model that provides a phenomenological description rather than an explanation of rate phenomena (Clarke 2006). To avoid such inconsistencies, metabolic theory and the model of Hilbert (1995) may be used to guide experiment planning right from the beginning of work on temperature-dependent population development.

The frequency distributions confirm the need to consider variability in developmental rates (Severini et al. 2003), which can be done, for example, by inserting the growth-based model of Hilbert (1995) into the model of Régnière (1984) or into distributed delays (e.g., Severini et al. 1990, 2003). To allow for the influence of both age and growth on population development, one may follow Gutierrez and Baumgärtner (1996) and Gutierrez et al. (2006), who represented population development, including variability, in separate age and growth dimensions. For this purpose, a two-dimensional distributed delay model may be appropriate (Gutierrez et al. 2006).

### Acknowledgments

J. Bertoldo kindly made available data from a previous experiment on developmental rate-temperature relationships. We thank C. Gilioli, University of Reggio di Calabria, for stimulating discussions on the metabolic theory.

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Received for publication 2 May 2006; accepted 30 November 2006.