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Comparison of Three Models Predicting Developmental Milestones Given Environmental and Individual Variation

ESTELLA GILBERT AND JAMES A. POWELL*
Department of Mathematics and Statistics,
Utah State University,
Logan, Utah 84322-3900,
USA
E-mail: powell@math.usu.edu

JESSE A. LOGAN AND BARBARA J. BENTZ
USDA Forest Service Logan Forestry Sciences Lab,
Utah State University,
Logan, Utah 84322-8000,
USA

In all organisms, phenotypic variability is an evolutionary stipulation. Because the development of poikilothermic organisms depends directly on the temperature of their habitat, environmental variability is also an integral factor in models of their phenology. In this paper we present two existing phenology models, the distributed delay model and the Sharpe and DeMichele model, and develop an alternate approach, called the Extended von Foerster model, based on the age-structured McKendrick–von Foerster partial differential model. We compare the models theoretically by examining the biological assumptions made in the basic derivation of each approach. In particular, we focus on each model's ability to incorporate variability among individuals as well as variability in the environment. When compared against constant temperature mountain pine beetle (*Dendroctonus ponderosae* Hopkins) laboratory developmental data, the Extended von Foerster model exhibits the highest correlation between theory and observation.

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1. INTRODUCTION

Many organisms are poikilothermic, that is, they have body temperatures directly tied to the temperature of the environment they live in. A consequence is that, unlike homeothermic, or warm-blooded, organisms, the speed of their metabolisms varies with temperature. The physiological clock of poikilothermic organisms does not advance at a rate directly proportional to the passage of 'lab' or 'clock' time, but runs fast or slow depending entirely on how warm or cold their habitat is.

*Corresponding address: Department of Mathematics and Statistics, Utah State University, 3900 Old Main Hill, Logan, Utah 84322-3900, USA.

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For generalist or opportunistic poikilotherms and high-R strategists, generating a broad dispersion of offspring over appropriate seasons can be a success strategy. In these cases, the more unpredictable the environment is the larger the pay off to having a built-in degree of genetic variability in developmental timing, as a bet-hedging strategy (Hopper, 1999). For opportunists taking advantage of a variety of ephemeral resources, placing offspring at broadly distributed times of year could maximize the chances that some offspring will have access to the necessary resources for survival. In this context, having clocks which progress at differing rates for all individuals is probably advantageous.

By contrast, for many specialist organisms timing and synchrony are much more important. For successful mating and reproduction an entire population of potential mates must emerge and be at similar developmental stages simultaneously. Similarly, the timing and development of resource-using life stages must coincide with the appearance of ephemeral resources for successful foraging in natural environments. Finally, most temperate, terrestrial environments are periodically lethal to poikilothermic organisms living in them due to extremes in temperature, illumination or moisture availability. Most organisms which are vulnerable to such extremes have developed one or more stage-specific mechanisms (e.g., estivation, diapause, altered biochemistry, dormancy, hardened spores) to cope, but the expression of such mechanisms must be synchronized with the environment (Logan and Bentz, 1999). It is astonishing that poikilothermic organisms do so well in temperate habitats, given the strong selective requisite for life cycle timing and the fact that their actual physiological clocks run at variable rates.

One of the answers to 'how can this work?' is provided by Jenkins *et al*. (2001) and Powell *et al*. (2000). Poikilothermic organisms have life histories characterized by a progression through several developmental phases. Development through these stages occurs at a stage-specific rate which depends directly and nonlinearly on temperature (Zaslavski, 1988). Jenkins *et al*. (2001) showed that with two or more life phases with differing developmental rates and even small environmental temperature variability, life cycles of populations are capable of synchronization. Powell *et al*. (2000) showed that quiescent periods, or temperature regimes in which development actually stops, strongly enhance the synchronization effect. Logan and Powell (2001) applied these methodologies to explain a historic outbreak of mountain pine beetle (MBP, *Dendroctonus ponderosae* Hopkins *Coleoptera:Scolytidae*) in white bark pine (*Pinus albicaulis* Engelmann) in Idaho in the early 1930s. Normally at the high altitudes (and low temperatures) of white bark stands MPB are not capable of synchronization at one generation per year, which seems to be necessary for an outbreak (Amman, 1973; Safranyik, 1978). However, Logan and Powell (2001) showed that during the 1930s unusually warm temperatures allowed a thermally feasible, univoltine (one generation per year) regime for MPB.

The MPB is poikilothermic and generally undergoes development in a series of discrete phases: eggs, several larval instars, pupae and adult. In each stage,

one may denote the fraction of the stage completed as age $a \in [0, 1]$, where $a = 0$ at the initiation of the lifestage and $a = 1$ at completion. In the simplest model for an organism's development a is directly related to the developmental rate $r(T(t))$. That is, the age of completion, $a = 1$, can also be expressed as the inverted integral function of developmental rates from the time of initiation to the time of completion (or emergence) of the lifestage. Since $r(T(t))$ is generally nonlinear and T highly variable, in practice one numerically calculates the cumulative developmental index, and then scans for the time of completion.

While this theory has the benefits of simplicity and breadth, and has been validated for the case of MPB, it does present some difficulties. The entire construction of the theory hinges on the notion that all individuals in the population have the same developmental rate, characterized by the median individual. This is clearly not the case, as variability in development is ignored. When individuals are reared at constant temperatures to parameterize rate curves, invariably there is a distribution of emergence times about the median (which is used to determine the mean rate of development at constant temperature). From an evolutionary perspective this is a logical result; any set of traits with such selective significance must have variability in phenotype expressed in order for evolution to have occurred. It is therefore necessary to develop a model which is fully cognizant of variability, both in rates of development within the population and of temperature during development.

Accounting for phenotypic variability in varying temperatures is particularly difficult. At constant temperatures the degree of trait dispersion in a population can be measured directly. In a fluctuating temperature environment, however, it is not clear how much of the potential variability which *could* be expressed at a given temperature is *actually* accumulated as the population passes through that temperature transiently. Historically two sorts of developmental models have been proposed to integrate these variabilities. The first, a distributed delay or 'boxcar' model (Forrester, 1961; Vansickle, 1977), views development as flows between a series of well-mixed chambers, so that the distribution of output is conditioned on the number of chambers and rates of flow between them (proportional to the developmental rate). Although the number of chambers can be estimated empirically from the variance, this becomes difficult for organisms with multiple lifestages. As a result the number of chambers is often arbitrary and a result of the researchers' bias/experience. Consequently, true emergence variability in fluctuating temperature regimes cannot be accurately expressed.

A second, probabilistic approach was developed by Sharpe and DeMichele (1977) and Sharpe *et al*. (1977). Distributions of cumulative rates are used to explicitly determine distributions of emergence for cohorts of individuals. To resolve the interaction between temperature fluctuation and phenotypic variability an additional assumption must be made regarding the accumulation of variance over developmental time. The usual, 'same shape' assumption is that variance accumulates linearly with cumulative development. An unfortunate consequence of this assumption is that when development stops for the median individual

(e.g., when temperatures drop below a developmental threshold) it must stop for all individuals. However, a wealth of experimental evidence indicates that, while development may be essentially zero for many or most individuals, there are usually some individuals still capable of progress at low temperatures. This is not a difficulty with the Sharpe and DeMichele approach *per se*, for which (in principle) variability is assumed around the full developmental curve, including thresholds, but it is a clear difficulty with the same-shape assumption required to apply the approach in fluctuating temperature regimes.

In this paper we develop an alternate approach, based on extending the age-structured McKendrick–von Foerster partial differential model (McKendrick, 1926; von Foerster, 1959) to account for phenotypic variability in developmental rates. The model includes variability over the full range of the rate curve. In particular, some individuals in a distribution can still develop even when median developmental rates are zero. Below we derive the Extended von Foerster (EvF) equation from minimal assumptions regarding the distribution of developmental rates in the population and show that it presents no additional burden in computation or parameterization over the distributed delay/boxcar approach or the Sharpe and DeMichele approach. We discuss how the three approaches compare and then parametrize them for MPB, using lab-derived developmental data (Bentz *et al*., 1991). Finally, all three models are compared to constant temperature, multiple stage developmental data collected separately from the parameterization data (Bentz *et al*., 2001).

2. Extended von Foerster Model

2.1. ***Derivation.*** Originally derived by McKendrick (1926) and then by von Foerster (1959) to model cell division, the McKendrick–von Foerster equation

$$\frac{\partial}{\partial t}p(a,t)+\frac{\partial}{\partial a}p(a,t)=g(a,t,p(a,t)) \tag{1}$$

has been applied to many different biological and ecological processes. For populations t is time, a is age normalized so that $0\le a\le 1$, $p(a,t)$ is the population density, and the term $g(a,t,p(a,t))$ gives the total gain, or negative loss, of individuals in the population per age per time (von Foerster, 1959). Traditionally, equation (1) is given by

$$\frac{\partial}{\partial t}p(a,t)+\frac{\partial}{\partial a}p(a,t)=-\kappa p(a,t) \tag{2}$$

$$p(0,t)=\int_0^\infty b(a,t)p(a,t)da$$

where κ is the mortality rate and $b(a,t)$ the birth rate. In this form the total gain of individuals is equivalent to the 'negative' mortality, and the integral equation for

birth is included to incorporate reproduction (Oster and Takahashi, 1974). There are many papers on the McKendrick–von Foerster type of model. Getz (1998) gives a review of the many different models used in population ecology.

If development is viewed as progression through several lifestages, an alternative form of equation (2) is needed. The partial differential equation

$$\frac{\partial}{\partial t}p(a,t) + r(T(t))\frac{\partial}{\partial a}p(a,t) = \nu(T(t))\frac{\partial^2}{\partial a^2}p(a,t) \tag{3}$$

is a variation of the von Foerster equation and will be called the Extended von Foerster (EvF) equation in this paper. Here $r(T(t))$ and $\nu(T(t))$ are interpreted as the developmental rate and variability in development, respectively. Because there is no reproduction when individuals are progressing through lifestages, there is no need for the integral equation for birth shown in equation (2). In addition, the total gain of individuals $g(a,t,p(a,t))$ in equation (3) is represented by a diffusion term instead of the negative mortality shown in equation (2). This incorporates the concept that as a population ages, its distribution 'diffuses' as the variability increases. The inclusion of the developmental rate in equation (3) adapts the original von Foerster equation for poikilotherms, for whom age and time are linked variably through temperature.

To derive an expression for ν in terms of the mean and variance of developmental rates, first assume that the developmental rates, r, of the population are normally distributed with density function

$$f(r) = \frac{1}{\sqrt{2\pi\sigma^2}}e^{-\frac{(r-r_0)^2}{2\sigma^2}}, \tag{4}$$

where r_0 is the mean developmental rate and σ^2 is the variance within the population. Consider a characteristic frame of reference $z = a - r_0 t$ which moves at the rate of development of the median individual. Now z can be interpreted as the age relative to the median individual and a as the physiological age such that $a = 0$ denotes the median initiation and $a = 1$ denotes the median completion of a developmental stage. For an arbitrary interval $[b,c]$ with $z \in [b,c]$, the change in the number of individuals at ages between b and c over a time interval Δt is given by

$$N_b^c = \int_b^c [p(z,t+\Delta t) - p(z,t)]dz.$$

The change in population density can also be given in terms of the flux. The positive flux $\varphi_+(z,t)$ is defined as the number of individuals crossing a particular developmental index, z, in the positive direction. The negative flux $\varphi_-(z,t)$ is the number crossing in the negative direction, and the total flux $\varphi(z,t)$ is the difference between the positive and negative flux. It follows that the change in population density is given by

$$N_b^c = \varphi(b) - \varphi(c) = \int_b^c -\frac{\partial\varphi}{\partial z}dz.$$

We turn now to determining how the flux at a point relates to the density and distribution of rates. The probability that an insect is in a small interval at age $b - \alpha$ and can progress past age b is

$$p(b-\alpha, t) \int_{\frac{\alpha}{\Delta t}}^{\infty} f(r) dr.$$

Individuals developing past a reference age b in a time interval Δt are those with a developmental rate r such that $r\Delta t \geq \alpha$. It follows that the positive flux per time Δt at the reference age $z = b$ is

$$\varphi_+(z=b,t) = \frac{1}{\Delta t} \int_0^{\infty} \int_{\frac{\alpha}{\Delta t}}^{\infty} f(r+r_0) p(b-\alpha, t) dr\, d\alpha.$$

Using a Taylor expansion for $p(b - \alpha)$ about the point $z = b$, the positive flux becomes

$$\varphi_+(z=b,t) = \frac{1}{\Delta t} \int_0^{\infty} \int_0^{r\Delta t} f(r+r_0) \times \left[p(b,t) - \alpha \frac{\partial}{\partial z} p(b,t) + \frac{\alpha^2}{2} \frac{\partial^2}{\partial z^2} p(b,t) - \cdots \right] dr\, d\alpha.$$

Integrating in r and using the assumption that f is a normal distribution with standard deviation σ gives

$$\varphi_+(z=b,t) = \frac{\sigma}{\sqrt{2\pi}} p(b,t) - \frac{\Delta t}{2} \frac{\sigma^2}{2} \frac{\partial}{\partial z} p(b,t) + \cdots.$$

After finding the negative flux in a similar manner, the total population flux at the reference age b is

$$\begin{aligned} \varphi(z=b,t) &= \varphi_+(b,t) - \varphi_-(b,t) \\ &= -\Delta t \frac{\sigma^2}{2} \frac{\partial}{\partial z} p(b,t) + \mathcal{O}(\Delta t^3). \end{aligned}$$

It follows that the net change in population across the interval $[b, c]$ is

$$\varphi(b) - \varphi(c) = \int_b^c -\frac{\partial}{\partial z} \varphi(z,t) dz = \int_b^c \Delta t \frac{\sigma^2}{2} \frac{\partial^2}{\partial z^2} p(z,t) dz + \mathcal{O}(\Delta t^3). \quad (5)$$

Recall that for an arbitrary interval $[b, c]$ with $z \in [b, c]$, the change in population

density is also given by $N_b^c = \int_b^c [p(z, t + \Delta t) - p(z, t)]dz$. Taylor expanding in t results in

$$\begin{aligned}\int_b^c [p(z, t + \Delta t) - p(z, t)]dz &= \int_b^c \left[p(z, t) + \Delta t \frac{\partial}{\partial t} p(z, t) \right. \\ &\qquad \left. + \mathcal{O}(\Delta t^2) - p(z, t) \right] dz \\ &= \int_b^c \Delta t \frac{\partial}{\partial t} p(z, t)dz + \mathcal{O}(\Delta t^2). \qquad (6)\end{aligned}$$

Equating (5) and (6) and simplifying gives, at leading order in Δt,

$$\int_b^c \Delta t \left[\frac{\partial}{\partial t} p(z, t) - \frac{\sigma^2}{2} \frac{\partial^2}{\partial z^2} p(z, t) \right] dz = 0.$$

Since the relation must hold for arbitrary (small) Δt, a necessary condition is that the population satisfies

$$\frac{\partial p}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 p}{\partial z^2}.$$

Because $z = a - r_0 t$, this becomes

$$\frac{\partial p}{\partial t} + r_0 \frac{\partial p}{\partial a} = \frac{\sigma^2}{2} \frac{\partial^2 p}{\partial a^2}, \qquad (7)$$

where $r(T(t))$ and $\nu(T(t))$ in equation (3) are equivalent to r_0 and $\sigma^2/2$ in equation (7), respectively. The left-hand side of equation (7) represents the change in population with respect to time and age, the change over age being affected by the mean developmental rate. The right-hand side models the diffusivity of the population over age on the increase of developmental variability in the population as development proceeds. In other words, as individuals in the population age, the variance increases or decreases proportional to the squared standard deviation of developmental rates.

An interesting and biologically disturbing consequence of the diffusion approximation (7) is that some proportion of individuals, in principle, is always aging in the *negative* direction. This is a direct result of the initial assumption that development rates are distributed normally with mean r_0 and finite variance. This means that a measurable fraction of individuals in the population will have both unrealistically large as well as negative rates of development. More generally, the EvF has the same difficulty as all diffusion approximations: extremely rapid propagation of near-infinitesimal disturbances in both positive and negative directions. These errors are negligible, as witnessed by the near-ubiquitous application of diffusion approximations in spatiotemporally extended systems [e.g., Murray (1989) for an overview]. In the next section, exact solutions will be calculated, and these will illustrate that the negatively-aging portion of the population does not unrealistically affect the distribution of predicted emergence times.

2.2. ***Solution.*** The simplest application of equation (3) is to describe the distribution of developmental milestones (eggs hatching, larvae molting, etc.) at constant temperature, given an initial population all of the same age at the same point in time. This leads to the initial value problem

$$\begin{aligned} \frac{\partial p}{\partial t} + r\frac{\partial p}{\partial a} &= \nu\frac{\partial^2 p}{\partial a^2}, \\ p(a,0) &= \delta(a), \qquad -\infty < a < \infty, 0 < t. \end{aligned} \tag{8}$$

Using the transformation $z = a - rt$ and $\tau = t$, the initial value problem becomes

$$\begin{aligned} \frac{\partial p}{\partial \tau} &= \nu\frac{\partial^2 p}{\partial z^2}, \\ p(z,0) &= \delta(z), \qquad -\infty < z < \infty, 0 < \tau. \end{aligned} \tag{9}$$

This equation is recognizable as the heat equation, the solution of which can be found in Logan (1997) and DuChateau and Zachmann (1986) as well as many other differential equation texts. After transforming the solution back into a and t, we have

$$p(a,t) = \frac{1}{\sqrt{4\pi\nu t}}\exp\left[-\frac{(a-rt)^2}{4\nu t}\right], \qquad 0 < t,$$

the solution for drift/diffusion of an initial spot, with the role of space replaced with age, a. For individuals terminating a life stage ($a = 1$), the predicted pdf is

$$p(a=1,t) = \frac{1}{\sqrt{4\pi\nu t}}\exp\left[-\frac{(1-rt)^2}{4\nu t}\right], \qquad 0 < t. \tag{10}$$

As shown in Section 2.1, if developmental rates are normally distributed we can replace r and ν with r_0 and $\sigma^2/2$, respectively, giving

$$p(a=1,t) = \frac{1}{\sqrt{2\pi\sigma^2 t}}\exp\left[-\frac{(1-r_0 t)^2}{2\sigma^2 t}\right], \qquad 0 < t. \tag{11}$$

Thus, the population density at the end of each life stage is characterized by the mean and variance of the developmental rates.

3. Distributed Delay Model

3.1. ***Derivation.*** The distributed delay model was originally derived by engineers to describe the flow of entities through a process, and has since been used in a wide variety of disciplines to express delays in development, production, etc.

(Forrester, 1961; Vansickle, 1977). One of the first to formulate and apply the distributed delay model to developmental biology, Manetsch (1976) converted an integrodifferential equation into a system of ordinary differential equations to describe the effect of maturation in an insect population (Plant and Wilson, 1986).

When applied to populations, the distributed delay model divides the length of an organism's life, or lifestage, into k discrete phases, or boxcars (Vansickle, 1977). In the ith boxcar there are P_i individuals, a fraction λ_i of which move on to the next phase per time. This leads to the differential equation describing the population change

$$\frac{dP_i}{dt} = \lambda_{i-1}P_{i-1} - \lambda_i P_i. \tag{12}$$

If a is a continuous variable representing age such that $0 \leq a \leq 1$, P_i is the population, and p is the population density, then $P_i(t) \doteq p(a_i, t)\Delta a$ for a boxcar of width Δa. Here a_i is interpreted as the age in the ith boxcar such that $a_i = i\,\Delta a$, $P_i(t)$ as the population in the ith boxcar at time t, and $p(a_i, t)$ as the population density in the ith boxcar at time t (Edelstein-Keshet, 1988). Taylor expanding $p(a_{i-1}, t)$ and assuming that development is constant throughout the lifestage ($\lambda_{i-1} = \lambda_i = \lambda_{i+1} = \lambda$), equation (12) becomes

$$\frac{\partial p}{\partial t} + \lambda\Delta a\frac{\partial p}{\partial a} = \frac{\lambda\Delta a^2}{2}\frac{\partial^2 p}{\partial a^2} + \mathcal{O}(\Delta a^3). \tag{13}$$

Thus, for a large number of boxcars the EvF and distributed delay models can be expected to behave similarly.

3.2. ***Distributed delay solution.*** Given an initial input of individuals into the first phase, or boxcar, such that $p(a = 0, t) = \delta(t)$, Manetsch (1966, 1976) and Vansickle (1977) have shown that the distribution of emergence will be given by

$$p(a = 1, t) = \frac{k(\lambda t)^{k-1}}{(k-1)!}e^{-\lambda t}, \qquad 0 < t, \tag{14}$$

where $k = 1/\Delta a$ is the total number of phases or boxcars in the process.

If we make the assumption that $\Delta a \ll 1$ (or $k \gg 1$) and that (13) describes continuous population change, the solution of the initial value problem

$$\begin{aligned} &\frac{\partial p}{\partial t} + \lambda\Delta a\frac{\partial p}{\partial a} = \frac{\lambda\Delta a^2}{2}\frac{\partial^2 p}{\partial a^2} \\ &\qquad p(a, 0) = \delta(a), \qquad -\infty < a < \infty, 0 < t, \end{aligned} \tag{15}$$

follows the solution of the initial value problem (8) in the Extended von Foerster model. But now the fundamental solution at age $a = 1$ and time t is

$$p(a = 1, t) = \frac{1}{\sqrt{2\pi\lambda\Delta a^2 t}}\exp\left[-\frac{(1 - \lambda\Delta a t)^2}{2\lambda\Delta a^2 t}\right], \qquad 0 < t, \tag{16}$$

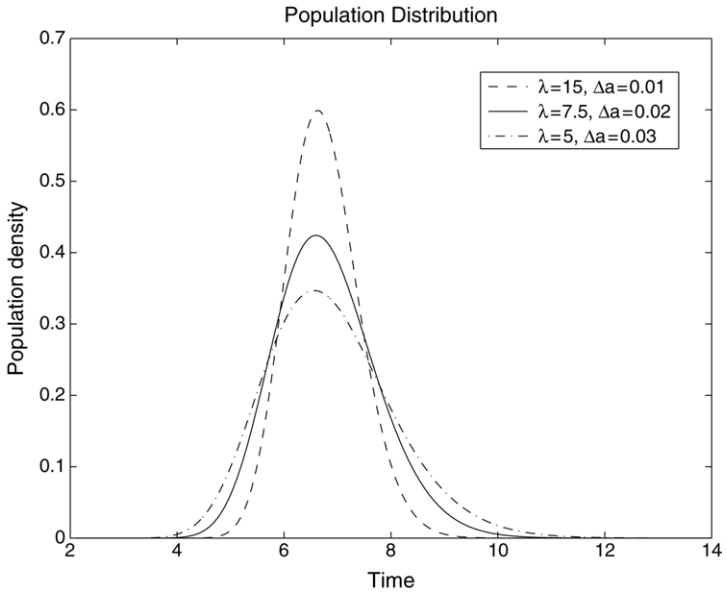

Figure 1. Population distribution estimated by the distributed delay model for individuals at age $a = 1$, where $(\lambda, \Delta a) = (15, 0.01)$, $(7.5, 0.02)$, and $(5, 0.03)$. Choices for $(\lambda, \Delta a)$ were made to maintain a constant median development time for all profiles. Although each distribution has the same median, the variance is clearly dependent on these choices.

and is dependent on the number of phases, or boxcars. λ and Δa can be easily estimated from the mean development rate r_0 of the empirical data as there are an infinite number of solutions $(\lambda, \Delta a)$ that satisfy the equation $r_0 = \lambda \Delta a$. But, as shown in Fig. 1, because the variability in the distributed delay model also varies with Δa ($\sigma^2 = \lambda \Delta a^2$), there are an infinite number of distributions with identical mean development times and different variances.

4. SHARPE AND DEMICHELE MODEL

4.1. ***Derivation.*** Sharpe *et al*. (1977) derived another model of the reaction kinetics for insect development based on several assumptions about the underlying developmental control enzymes. These assumption are: (a) a single control enzyme regulates development and hence the developmental rate of the organism (Sharpe and DeMichele, 1977); (b) the rate constant of active enzymes is temperature dependent and when multiplied by the concentration of active enzymes is proportional to the developmental rate (Sharpe and DeMichele, 1977); (c) the control enzyme can exist in an active state and two temperature dependent inactivation states (Sharpe and DeMichele, 1977); (d) the control enzyme has a symmetric distribution about some mean concentration (Sharpe *et al*., 1977). In reference to the derivation of reaction kinetics for insect development by Sharpe and DeMichele (1977), the model will be called the Sharpe and DeMichele model in this paper.

Given the pdf of rates $f(r)$ for $A \leq r \leq B$ where A and B are the minimum and maximum developmental rates, respectively, the cdf of rates is $F(r) = \int_A^r f(s)ds = \text{Prob}[R \leq r]$. In addition, the cdf of emergence times can be given by

$$G(t) = \text{Prob}[\top \leq t]. \tag{17}$$

$F(r)$ gives the probability that R, the developmental rate required to complete a lifestage, is less than or equal to the developmental rate r, and $G(t)$ gives the probability that $\top$, the time required to complete a lifestage, is less than or equal to time t. If age a is defined such that $0 \leq a \leq 1$, development is completed at age $a = 1$ and the product of developmental rate and time is equal to one ($rt = 1$). It follows that the developmental rate is inversely proportional to the emergence time and equation (17) can be written as

$$\begin{aligned} G(t) &= \text{Prob}[1/R \leq t] \\ &= \text{Prob}[R \geq 1/t] \\ &= \text{Prob}[R \geq r]. \end{aligned}$$

By definition of the cdf, this becomes

$$\begin{aligned} G(t) &= 1 - \int_A^{r=1/t} f(s)ds \\ &= 1 - F(r) \\ &= \int_{1/B}^{t} g(u)du. \end{aligned}$$

Because $f(r)dr = f(1/t)dt/t^2$, it follows that

$$\begin{aligned} g(t) &= 1/t^2 f(1/t) \qquad \text{for } 1/B \leq t \leq 1/A \\ &= r^2 f(r) \qquad\quad \text{for } A \leq r \leq B. \end{aligned}$$

Thus, if any of the following four equations are given, the remaining three can be found:

$$f(r) = \text{pdf of rates for } A \leq r \leq B, \tag{18}$$

$$g(t) = r^2 f(r) \qquad \text{for } 1/B \leq t \leq 1/A, \tag{19}$$

$$F(r) = \int_A^r f(r)dr, \tag{20}$$

$$G(t) = 1 - F(r) = \int_{1/B}^{t} g(u)du. \tag{21}$$

For the purposes of comparison with the other two models, if we assume that the developmental rates are normally distributed such that

$$f(r) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(r-r_0)^2}{2\sigma^2}}, \tag{22}$$

the pdf of emergence times becomes

$$g(t) = \frac{1}{t^2\sqrt{2\pi\sigma^2}} e^{-\frac{(1-r_0 t)^2}{2\sigma^2 t^2}}. \tag{23}$$

The nonlinear least-squares fit of the data from observed emergence gives the mean and standard deviation of development. This information completely describes equations (18)–(21), which in turn describes development at constant temperature.

5. Model Comparison

At constant temperature, the distributed delay model is essentially a numerical approximation of the von Foerster equation by the method of lines. An important difference is that the number of phases of cohorts in each developmental stage must be estimated from the data for the distributed delay model. In other words, Δa is an arbitrary interval length that must be chosen so that the term $\lambda \Delta a$ in equation (13) of the distributed delay model represents the probability that an individual will move to the next phase. In the EvF model, the probability of development is simply given by the developmental rate r, which can be approximated as the mean developmental rate r_0.

At constant temperature, with a known target population variance, it is possible to choose λ and Δa to generate the correct statistical behavior in the output distribution. The relationship between the EvF model and the distributed delay model can also be used to estimate Δa. That is, if we assume that Δa is small,

$$\begin{aligned} \frac{\nu}{r} &\approx \frac{\lambda \Delta a^2}{2\lambda \Delta a} \\ &\approx \frac{\Delta a}{2}. \end{aligned}$$

However, this implies that the developmental rate and variability depend on the size of each phase or cohort. Two types of distributed delay model were developed to address this problem: the linear chain model (Manetsch, 1976, 1980; Vansickle, 1977; MacDonald, 1978) and the modified Leslie matrix model (Slobodkin, 1953; Werner and Caswell, 1977). But these models only succeed in establishing a range of values of Δa for which each model is best suited (Plant and Wilson, 1986).

The Sharpe and DeMichele model takes a different approach to finding the developmental distribution of a population. Like the EvF model, the Sharpe and

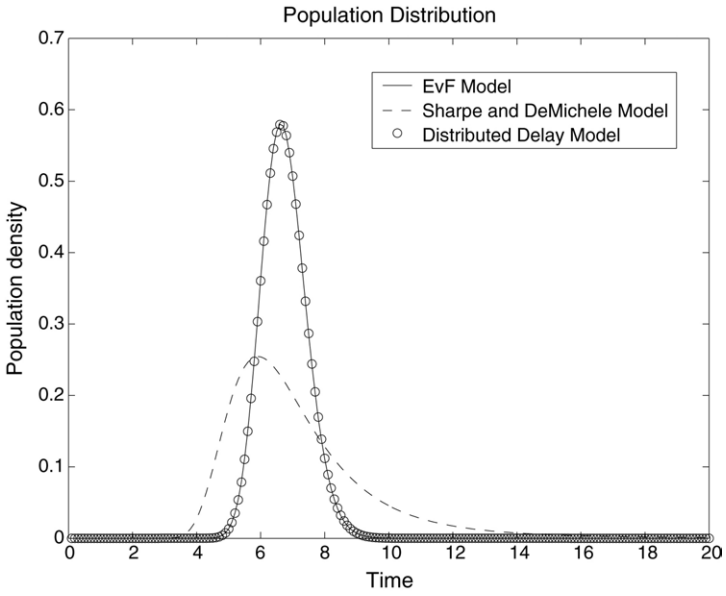

Figure 2. Distributions of emergence times estimated by the EvF model (solid) and the Sharpe and DeMichele model (dashed) for individuals at age $a = 1$ with $r_0 = 0.15$ and $\sigma = 0.04$. The distribution estimated by the distributed delay model (open circles) is equivalent to the EvF distribution with $\lambda = 14.0625$ and $\Delta a = 0.0106\overline{6}$.

DeMichele model assumes that the developmental rates follow a particular distribution. But instead of using the assumption to derive a partial differential equation based on flux and population change, the Sharpe and DeMichele model uses the pdf and cdf of rates as well as the pdf and cdf of emergence times to describe development at constant temperatures.

Assuming that the developmental rates are normally distributed, the pdf of emergence times for the Sharpe and DeMichele model is given by equation (23). When compared to equation (11), the fundamental solution of the EvF equation, we can see that although both models share the same mean developmental rate r_0, the relationship between the observed variance and the predicted variance σ^2 is different for parameter values $r_0 = 0.15$ and $\sigma = 0.04$ (Fig. 2). Now we must ask if there exists an appropriate combination of parameter values for which the EvF model and Sharpe and DeMichele model predict the same emergence distribution.

Supposing that the pdf of emergence times in the Sharpe and DeMichele model is equation (11) from the EvF model, it follows that the distribution of developmental rates in the Sharpe and DeMichele model is

$$f(r) = \frac{1}{r^2} p\left(1, \frac{1}{r}\right) = \frac{1}{\sqrt{2\pi\sigma^2 r}} e^{-\frac{(r-r_0)^2}{2\sigma^2 r}}. \tag{24}$$

Equation (24) is clearly not the normal distribution, which was used in the derivation of the EvF model in Section 2.1. In other words, emergence distributions for

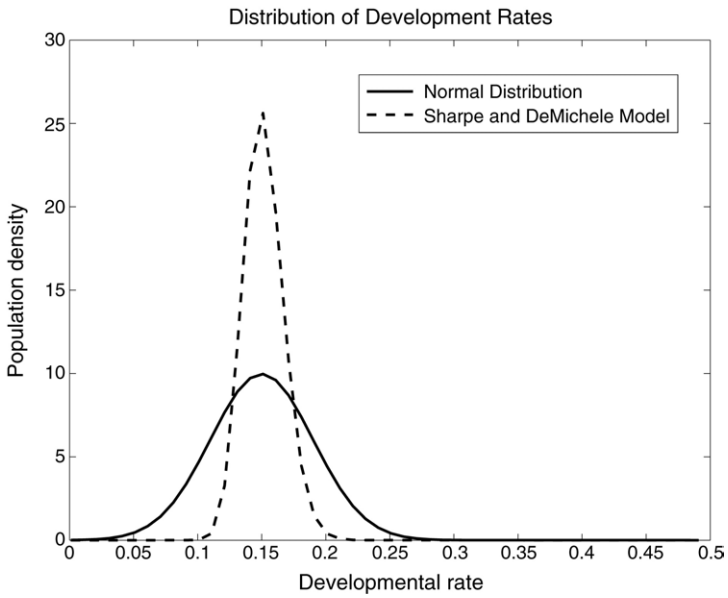

Figure 3. Distributions of developmental rates estimated by the EvF model (normal distribution, solid) and the Sharpe and DeMichele model (dashed) by assuming that both models share the same emergence distribution for individuals at age $a = 1$ with $r_0 = 0.15$ and $\sigma = 0.04$. The emergence distributions are equivalent only if the distributions of developmental rates are different.

the Sharpe and DeMichele model and the EvF model imply that the distribution of developmental rates for each model is different (Fig. 3). Like the distribution of emergence times in Fig. 2, both models share the same mean developmental rate but the relationship between the observed and predicted variances is different.

The explanation for this dichotomy between the Sharpe and DeMichele model and EvF model stems from the original derivation. The emergence distribution of the Sharpe and DeMichele model $g(t)$ is intrinsically dependent on the distribution of developmental rates $f(r)$, as $g(t) = r^2 f(r)$. In contrast, the basic structure of the EvF model, and hence the emergence distribution $p(a = 1, t)$, is not affected by the distribution of developmental rates. Only the center and spread of the emergence distribution for the EvF model will change with varying developmental rate distributions, while the center, spread, and shape of the Sharpe and DeMichele emergence distribution will all change significantly.

6. PARAMETRIZATION FOR MPB

6.1. ***Methods.*** To test the accuracy of the models, lab-derived MPB developmental data were analyzed (Bentz *et al.*, 1991). Providing emergence times at specific temperatures, the data were obtained through a laboratory experiment in

which a sample of beetles at each lifestage were held at a constant temperature and their time of emergence recorded (Logan and Amman, 1986).

Data were analyzed for six different life stages: egg, instar 1, instar 2, instar 3, instar 4, and pupae. The term instar denotes a lifestage between two successive molts. Samples of insects were held at several different constant temperatures, but mortality reduced the number of different temperatures at which successive lifestages were observed. Consequently, beetles in the egg stage were reared at 8, 10, 12.5, 15, 17.5, 20, 22.5, 25, and 27.5 °C; instar 1 at 5, 10, 15, 20, 25, and 27.5 °C; instar 2 at 10, 15, 20, 25, and 27.5 °C; instar 3 at 15, 20, 25, and 27.5 °C; and both instar 4 and pupae at 15, 20, and 25 °C (Logan and Amman, 1986; Bentz *et al.*, 1991).

Using the Nelder–Mead simplex search algorithm and the mathematical programming package (MATLAB), values of the developmental parameters were chosen that minimized the difference, or error, between the normalized cumulative frequency and the cumulative distribution function predicted by the respective model (Heath, 1997). Three different functions were used to quantify the error: the absolute value of the difference, the sum of squares, and the log of the absolute difference plus one. This served to investigate the stability of the estimates, eradicate sensitivity to variable data, and cross-check the error functions. The search was initialized by the mean developmental rate and the variance of the data divided by two. The difference between the number of observed emerged beetles and the number predicted by the models was computed for each new choice of developmental parameters.

After running the program repeatedly and analyzing the results, we found that the absolute value and log of the difference usually gave equivalent parameter values, but the parameters estimated using the sum of squares were sometimes drastically different. This was probably caused by the sum of squares' overadequate representation of errors greater than one. In this paper, results using the absolute value of the difference will be presented.

Estimates of the developmental rate r and variability ν in the EvF model were made for each lifestage and temperature by fitting the data from observed emergence to the predicted cumulative population density, the integral of equation (10). Similarly, the mean and variability ($\nu = \sigma^2/2$) of development for the Sharpe and DeMichele model were found by fitting the data from observed emergence to equation (21), the cdf of emergence times as predicted by the Sharpe and DeMichele model. The parameter values found for both models at each lifestage and temperature are given in Table 1.

6.2. ***Comparison of results.*** Although the R^2 values for the EvF model and the Sharpe and DeMichele model are equivalent, the estimated 'best fit' parameter values differ in varying degrees (Table 1). This is particularly evident in the variability parameter and re-emphasizes the conclusions drawn in Section 5 regarding the differences between the models.

Table 1. Parameters estimated by minimizing the absolute value of the error between predicted and observed emergence and their respective R^2 values. Emergence was predicted by the EvF model using r_E, ν_E and R^2_E, and the Sharpe and DeMichele model using r_S, ν_S, and R^2_S.

		Egg	Instar 1	Instar 2	Instar 3	Instar 4	Pupae
5 °C	n		5				
	r_E		0.01025774				
	r_S		0.99999983				
	ν_E		0.00000097				
	ν_S		0.00089318				
	R^2_E		0.68				
	R^2_S		0.81				
8 °C	n	11					
	r_E	0.02924079					
	r_S	0.02878648					
	ν_E	0.00019728					
	ν_S	0.00000616					
	R^2_E	0.99					
	R^2_S	0.99					
10 °C	n	7	15	11			
	r_E	0.03498788	0.06811402	0.02663810			
	r_S	0.03476382	0.06549600	0.00003548			
	ν_E	0.00000241	0.00133039	0.00999886			
	ν_S	0.00000190	0.00008633	0.00068604			
	R^2_E	0.83	0.99	0.77			
	R^2_S	0.98	0.99	0.82			
12.5 °C	n	9					
	r_E	0.05096118					
	r_S	0.04045115					
	ν_E	0.00036718					
	ν_S	0.00001699					
	R^2_E	0.98					
	R^2_S	0.99					
15 °C	n	6	10	6	4	2	2
	r_E	0.07858796	0.14139784	0.13457354	0.07974721	0.04411733	0.04210553
	r_S	0.07767692	0.12773795	0.11663893	0.99988291	0.04411733	0.04210553
	ν_E	0.00044781	0.00999144	0.00999655	0.00020856	0.00000005	0.00000004
	ν_S	0.00004071	0.00126655	0.00176600	0.00758388	0.00000005	0.00000004
	R^2_E	0.99	0.98	0.96	0	0.99	0.99
	R^2_S	0.99	0.98	0.96	0	0.99	0.99
17.5 °C	n	4					
	r_S	0.11814434					
	r_E	0.11811877					
	r_S	0.11814434					
	ν_E	0.00001804					
	ν_S	0.00000414					
	R^2_E	0.85					
	R^2_S	0.85					

Table 1. (*continued*).

		Egg	Instar 1	Instar 2	Instar 3	Instar 4	Pupae
20 °C	n	5	5	3	4	13	6
	r_E	0.14512152	0.37719247	0.30373741	0.17909991	0.09878847	0.16853505
	r_S	0.14531136	0.31964464	0.30954991	0.56831589	0.00005248	0.16237065
	ν_E	0.00047772	0.00077569	0.00405885	0.00997423	0.00999432	0.00257269
	ν_S	0.00006777	0.00348248	0.00311232	0.00999753	0.00415625	0.00045359
	R_E^2	0.99	0.95	0.79	0.80	0.95	0.98
	R_S^2	0.99	0.94	0.79	0.80	0.96	0.98
22.5 °C	n	2					
	r_E	0.16428571					
	r_S	0.16428571					
	ν_E	0.00002685					
	ν_S	0.00002685					
	R_E^2	—					
	R_S^2	—					
25 °C	n	3	6	8	9	12	7
	r_E	0.18303779	0.37508458	0.24644016	0.14330973	0.13849435	0.18614447
	r_S	0.17922628	0.33908673	0.23024597	0.05299251	0.00002384	0.09110462
	ν_E	0.00032212	0.00998743	0.00999831	0.00998595	0.00999684	0.00176397
	ν_S	0.0003068	0.00999209	0.00312535	0.00999233	0.00886165	0.00554327
	R_E^2	0.99	0.60	0.99	0.82	0.82	0.85
	R_S^2	0.99	0.64	0.99	0.94	0.93	0.85
27.5 °C	n	3	10	12	6		
	r_E	0.18713500	0.25549177	0.14698513	0.05292529		
	r_S	0.20450056	0.24693988	0.11216188	0.00003604		
	ν_E	0.00014509	0.00603980	0.00999556	0.00292613		
	ν_S	0.00013361	0.00191146	0.00267466	0.00186298		
	R_E^2	0.78	0.98	0.99	0.92		
	R_S^2	0.78	0.98	0.99	0.92		

Figs. 4–9 use information garnered from the parametrization. Although the parameters were estimated at several temperatures in all lifestages, it is important to find the developmental parameters for temperatures not studied. There are two standard ways to accomplish this: by assuming that the parameters are related and follow a particular distribution, or that one or more of the parameters remains constant over the lifestage. For the Sharpe and DeMichele model, the first approach was used. Linear regression of the estimated standard deviation σ on the estimated developmental rate r provided the slope c of the line $\sigma = cr$ for each lifestage. Computing the mean developmental rate r_0 from the data and then using r_0 and c to approximate the standard deviation σ, emergence could be estimated for all temperatures. The linear relationship between the estimated standard deviation σ and the mean developmental rate r_0 is shown in Fig. 12, where it is clear that the linear association is weak. Alternatively, the EvF model used constant values. The mean of the variability parameter ν estimated by the EvF model was taken over

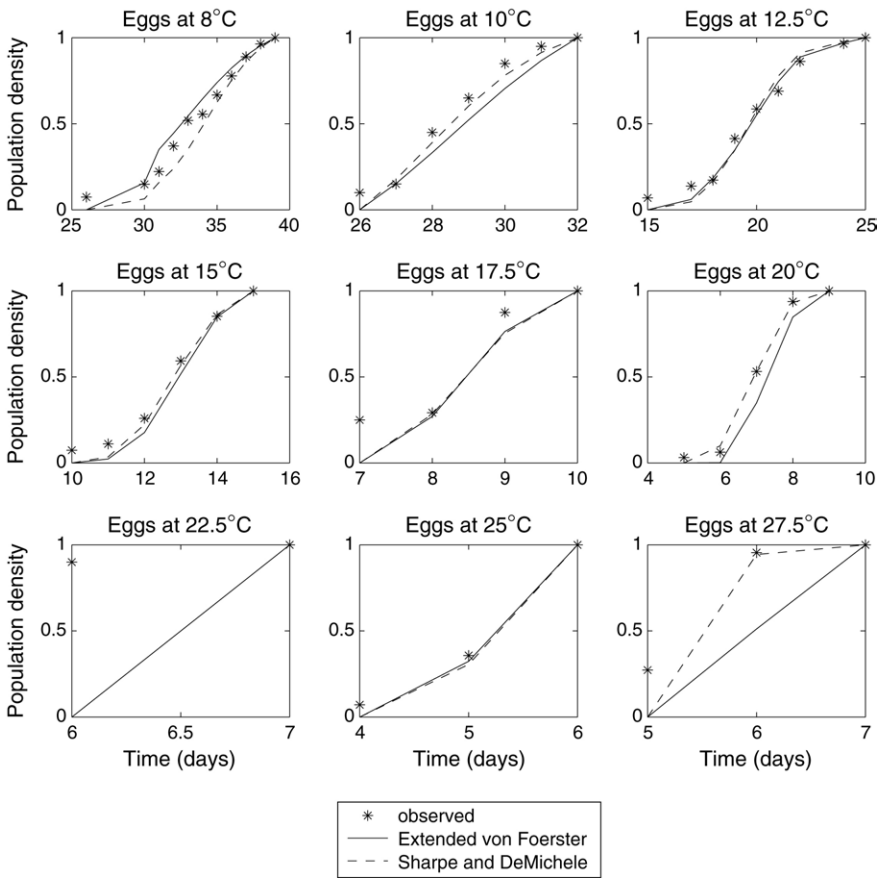

Figure 4. Observed cumulative frequency of hatched mountain pine beetle eggs and frequencies predicted by the EvF model and the Sharpe and DeMichele model. Both models occasionally make the same predictions, in which case there appears to be only one line, instead of two. The parameters used for each temperature can be found in Table 2.

all temperatures. This value was then used, as well as the mean developmental rate r_0, in equation (10) to predict emergence for each lifestage and temperature.

On examining Table 2 and Figs. 4–9, we can see that the EvF model performs as well as, if not better than, the Sharpe and DeMichele model. This is somewhat surprising given that the EvF model uses constant variability ν for all temperatures while the variability in the Sharpe and DeMichele model changes dynamically with temperature.

7. VALIDATION

Constant temperature, multiple stage developmental data for the MPB was used to compare the performance of the distributed delay, Sharpe and DeMichele, and EvF models. MPB-infested sections of lodgepole pine were held at 21 °C and adult

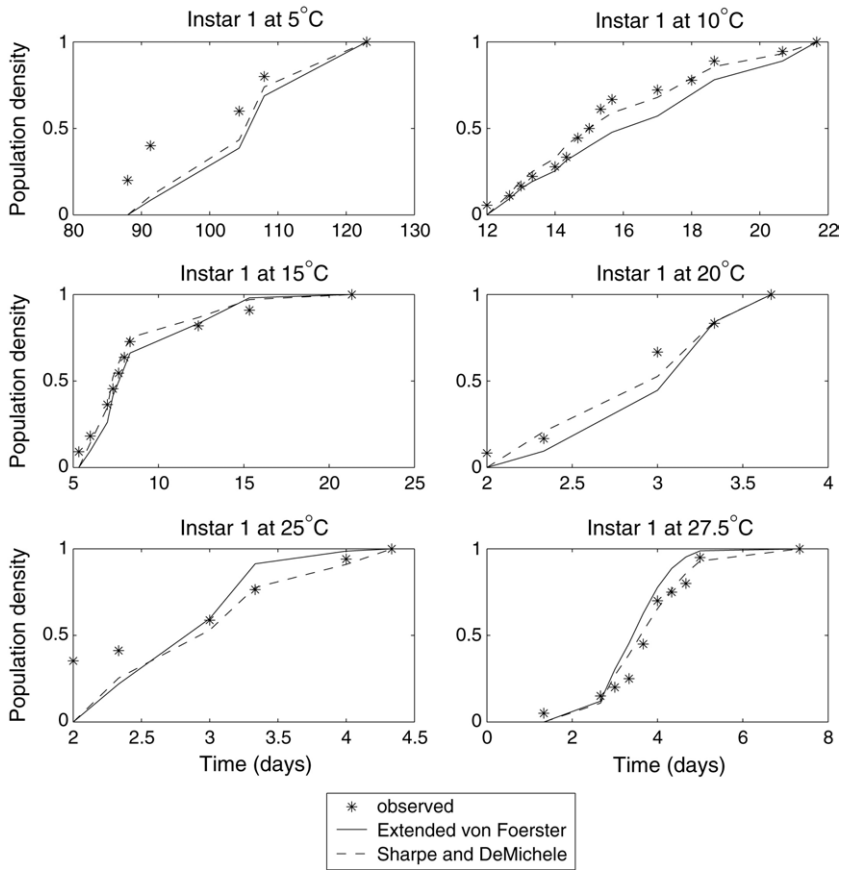

Figure 5. Observed cumulative frequency of molted mountain pine beetle instar 1 and frequencies predicted by the EvF model and the Sharpe and DeMichele model. Both models occasionally make the same predictions, in which case there appears to be only one line, instead of two. The parameters used for each temperature can be found in Table 2.

brood emergence monitored every other day, resulting in an observed distribution of total emergence time (Bentz *et al*., 2001).

Developmental rates, r, for each lifestage were approximated using methods referred to in Logan and Amman (1986), Bentz *et al*. (1991), and Jenkins *et al*. (2001). The variability, ν, used in the EvF model was estimated from the parametrization data in Section 6. This was done by averaging the variability for each lifestage over temperature, since no trend was apparent. For the Sharpe and DeMichele model, the slope c of the line $\sigma = cr$ (see Section 6.2) was found for each lifestage by linear regression on the observed parametrization data. These slopes were then used to find the standard deviation of the validation data. To approximate the optimal number of boxcars ($k = 1/\Delta a$) in the distributed delay model, the accumulated variance estimated by the EvF model was compared to the accumulated variance estimated by the distributed delay model.

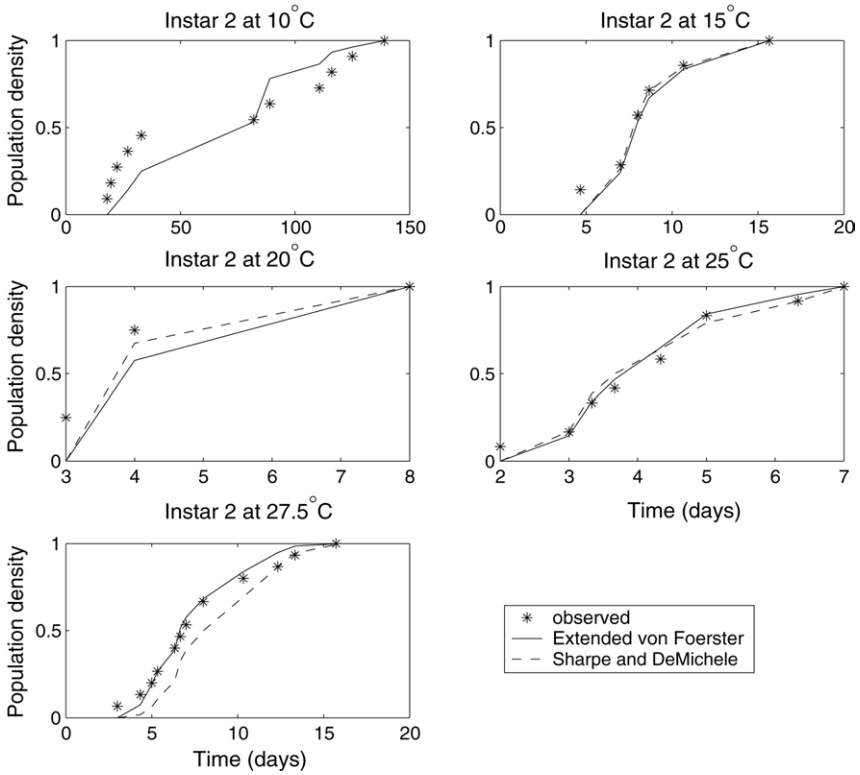

Figure 6. Observed cumulative frequency of molted mountain pine beetle instar 2 and frequencies predicted by the EvF model and the Sharpe and DeMichele model. Both models occasionally make the same predictions, in which case there appears to be only one line, instead of two. The parameters used for each temperature can be found in Table 2.

That is,

$$\begin{aligned}\nu_1 t_1 + \nu_2 t_2 + \cdots + \nu_8 t_8 &= \frac{\nu_1}{r_1} + \frac{\nu_2}{r_2} + \cdots + \frac{\nu_8}{r_8} \\ &\approx \frac{\lambda_1 \Delta a^2}{2\lambda_1 \Delta a} + \frac{\lambda_2 \Delta a^2}{2\lambda_2 \Delta a} + \cdots + \frac{\lambda_8 \Delta a^2}{2\lambda_8 \Delta a} \\ &= 4\Delta a.\end{aligned}$$

For mountain pine beetles developing at a constant 21 °C, the optimal number of boxcars was approximated as $k \approx 22$ ($\Delta a \approx 0.04445$).

The observed and predicted cumulative emergence of adult MPB at 21° are shown in Fig. 10. The EvF model with constant variance is superior to the Sharpe and DeMichele model using the same-shape assumption for variance with r^2 values of 0.985 and 0.879, respectively. Although the distributed delay model with $k = 22$ boxcars might be expected to be very similar to the EvF model, the EvF model exhibits a higher degree of accuracy with $r^2 = 0.985$ while $r^2 = 0.946$ for

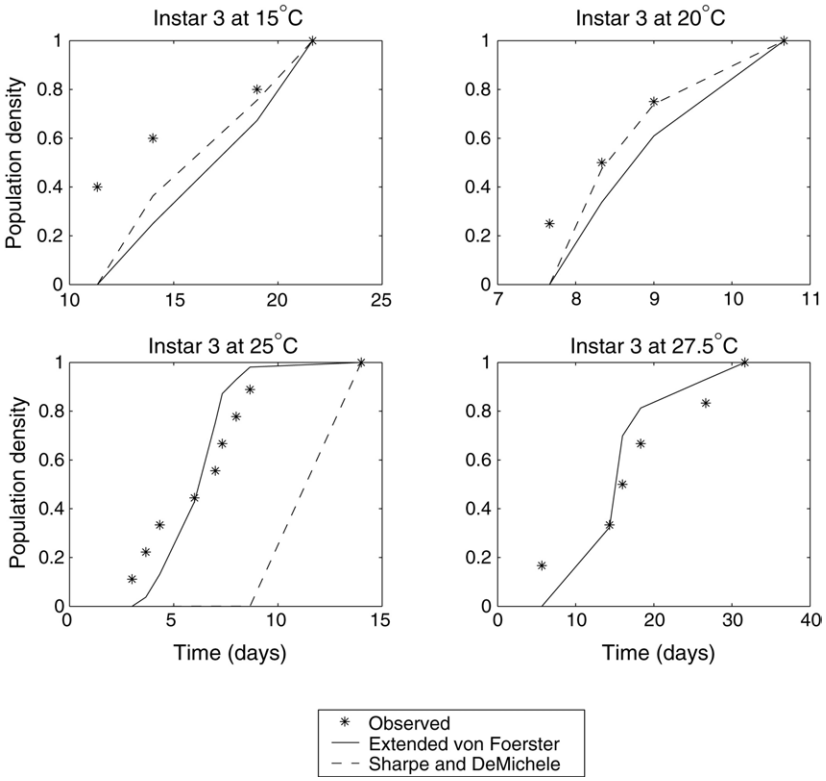

Figure 7. Observed cumulative frequency of molted mountain pine beetle instar 3 and frequencies predicted by the EvF model and the Sharpe and DeMichele model. Both models occasionally make the same predictions, in which case there appears to be only one line, instead of two. The parameters used for each temperature can be found in Table 2.

the distributed delay model. This is due, in part, to the fact that in the distributed delay model, the variance and developmental rate for each lifestage depend on Δa, which was estimated from the predicted cumulative variance in the EvF model. Thus, the distributed delay model is constrained by Δa and is less descriptive than the EvF model.

8. DISCUSSION

While the EvF approach provided a clearly superior fit to data, even the worst of the three models captured approximately 95% of the variability. To more clearly accentuate the pros and cons of the different approaches, we must consider their behavior in variable-temperature regimes. This will aid in model comparison and selection and give valuable insight for future research.

As the EvF model incorporates environmental and phenological variability into its basic structure, expanding the model to account for variable temperatures is

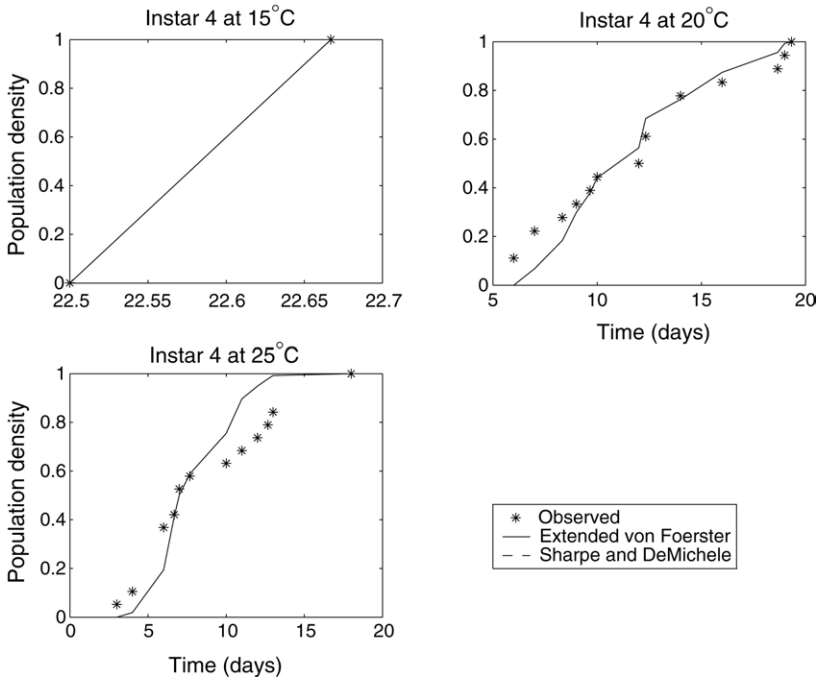

Figure 8. Observed cumulative frequency of molted mountain pine beetle instar 4 and frequencies predicted by the EvF model and the Sharpe and DeMichele model. Both models occasionally make the same predictions, in which case there appears to be only one line, instead of two. The parameters used for each temperature can be found in Table 2.

reasonably straightforward. The population distribution function of individuals completing lifestage j at time t and in a variable-temperature environment is given by

$$p_j(a=1,t) = \int_0^t p_{j-1}(a=1,t)\frac{1}{\sqrt{4\pi v_j(t-\tau)^3}} \times \exp\left[-\frac{\left(1-\int_\tau^t r_j[T(s)]ds\right)^2}{4v_j(t-\tau)}\right] d\tau, \qquad 0 < t. \tag{25}$$

This follows from replacing the δ initial condition in equation (8) with an appropriate initial distribution (the distribution of individuals from the previous lifestage) and using the convolution theorem in time. Thus, using only minimal assumptions about the distribution of developmental rates (see Sections 1 and 2.1), the EvF model describes the complexity of development in a variable-temperature environment.

The distributed delay model is more difficult to connect with constant-temperature parameters in a variable-temperature environment, primarily because

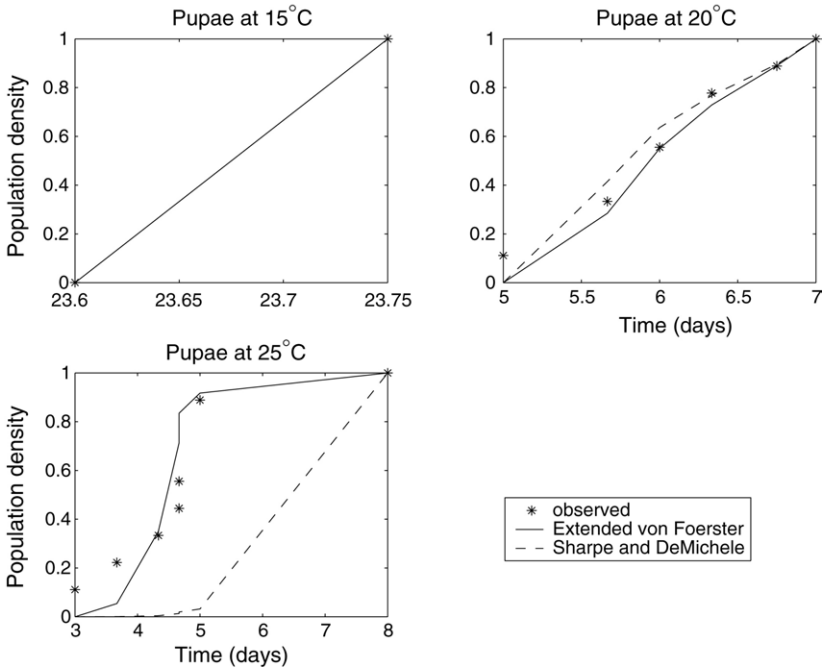

Figure 9. Observed cumulative frequency of molted mountain pine beetle pupae and frequencies predicted by the EvF model and the Sharpe and DeMichele model. Both models occasionally make the same predictions, in which case there appears to be only one line, instead of two. The parameters used for each temperature can be found in Table 2.

it is virtually impossible to determine the number of boxcars or phases for each temperature and lifestage. Based on the idea that development is akin to the flow of entities (or individuals) through a series of phases or boxcars, the output of the distributed delay model is dependent on the rates of flow ($r = \lambda \Delta a$) between the phases and the number of phases ($k = 1/\Delta a$) in the process. To achieve some target variability as rates change with temperature, we must change Δa dynamically, an unpalatable and difficult task requiring ongoing structural changes in the model.

To use the Sharpe and DeMichele model in variable-temperature regimes, two assumptions must be made: (1) the integral function of the pdf describing development at different constant temperatures gives the development at variable temperatures; (2) the mean and variance of the developmental rates are linearly proportional. The second assumption implies that σ is functionally dependent on r_0 and the pdf of the developmental rates is univariate.

If it is assumed that development is cumulative in a variable-temperature environment, then the development completed in the lifestage between time τ and time t and at temperature T is

$$\int_{\tau}^{t} r[T(s)]ds.$$

Table 2. Parameters used to generate Figs. 4–9. The mean developmental rate computed from existing data was used in both the EvF model with developmental rate r_E and the Sharpe and DeMichele model with developmental rate r_S ($r_E = r_S$). The computation of variability v_E, v_S is described in Section 6.2.

		Egg	Instar 1	Instar 2	Instar 3	Instar 4	Pupae
5 °C	n		5				
	r_E		0.00985729				
	r_S		0.00985729				
	v_E		0.00463262				
	v_S		0.04148186				
	R^2_E		0.50				
	R^2_S		0.61				
8 °C	n	11					
	r_E	0.03007893					
	r_S	0.03007893					
	v_E	0.00022272					
	v_S	0.00000291					
	R^2_E	0.96					
	R^2_S	0.93					
10 °C	n	7	15	11			
	r_E	0.03476382	0.06493120	0.02498197			
	r_S	0.03476382	0.06493120	0.02498197			
	v_E	0.00022272	0.00463262	0.00880963			
	v_S	0.00000438	0.00017795	0.0000000001			
	R^2_E	0.92	0.90	0.75			
	R^2_S	0.97	0.98	—			
12.5 °C	n	9					
	r_E	0.05034782					
	r_S	0.05034782					
	v_E	0.00022272					
	v_S	0.00000894					
	R^2_E	0.98					
	R^2_S	0.97					
15 °C	n	6	10	6	4	2	2
	r_E	0.07715618	0.12225730	0.12573322	0.06933593	0.04411733	0.04210553
	r_S	0.07715618	0.12225730	0.12573322	0.06933593	0.04411733	0.04210553
	v_E	0.00022272	0.00463262	0.00880963	0.00577372	0.00666374	0.00144556
	v_S	0.00002119	0.00067686	0.00123547	0.04147216	0.02514204	0.00018678
	R^2_E	0.97	0.95	0.95	−0.49	0.99	0.99
	R^2_S	0.98	0.97	0.96	0	0.99	0.99
17.5 °C	n	4					
	r_E	0.11823743					
	r_S	0.11823743					
	v_E	0.00022272					
	v_S	0.00004901					
	R^2_E	0.83					
	R^2_S	0.83					

Table 2. (*continued*).

		Egg	Instar 1	Instar 2	Instar 3	Instar 4	Pupae
20 °C	n	5	5	3	4	13	6
	r_E	0.13614831	0.33949560	0.23958333	0.11382502	0.09632276	0.16589709
	r_S	0.13614831	0.33949560	0.23958333	0.11382502	0.09632276	0.16589709
	ν_E	0.00022272	0.00463262	0.00880963	0.00577372	0.00666374	0.00144556
	ν_S	0.00007415	0.00423831	0.00870177	0.01339794	0.00000004	0.00277755
	R_E^2	0.95	0.91	0.68	0.65	0.94	0.97
	R_S^2	0.99	0.96	0.77	0.80	—	0.96
22.5 °C	n	2					
	r_E	0.16428571					
	r_S	0.16428571					
	ν_E	0.00022272					
	ν_S	0.00009477					
	R_E^2	—					
	R_S^2	—					
25 °C	n	3	6	8	9	12	7
	r_E	0.18214286	0.37112735	0.25568906	0.17717066	0.13576822	0.22112970
	r_S	0.18214286	0.37112735	0.25568906	0.17717066	0.13576822	0.22112970
	ν_E	0.00022272	0.00463262	0.00880963	0.00577372	0.00666374	0.00144556
	ν_S	0.00011280	0.00476958	0.00481427	0.00011659	0.000000007	0.00087443
	R_E^2	0.99	0.50	0.98	0.73	0.77	0.41
	R_S^2	0.98	0.58	0.97	−2.40	—	−1.08
27.5 °C	n	3	10	12	6		
	r_E	0.17467532	0.28278123	0.14815499	0.07206198		
	r_S	0.17467532	0.28278123	0.14815499	0.07206198		
	ν_E	0.00022272	0.00463262	0.00880963	0.00577372		
	ν_S	0.00014685	0.00252954	0.00114245	0.00000000005		
	R_E^2	0.13	0.98	0.98	0.80		
	R_S^2	0.78	0.98	0.85	—		

Assumption (2) expands this concept into a full population distribution (Sharpe and DeMichele, 1977). That is, if $f(r)$ has mean r_0 and standard deviation σ for each temperature T, then $\sigma = cr_0$ and c can be estimated by linear regression of σ on r_0. Now the distribution of emergence times for individuals completing lifestage j at time t under varying temperatures is

$$p_j(t) = \int_0^t p_{j-1}(t) \frac{1}{(t-\tau)\sqrt{2\pi c_j \int_\tau^t r_j[T(s)]ds}} \times \exp\left[-\frac{\left(1 - \int_\tau^t r_j[T(s)]ds\right)^2}{2c_j^2 \left(\int_\tau^t r_j[T(s)]ds\right)^2} \right] d\tau, \qquad 0 < t. \tag{26}$$

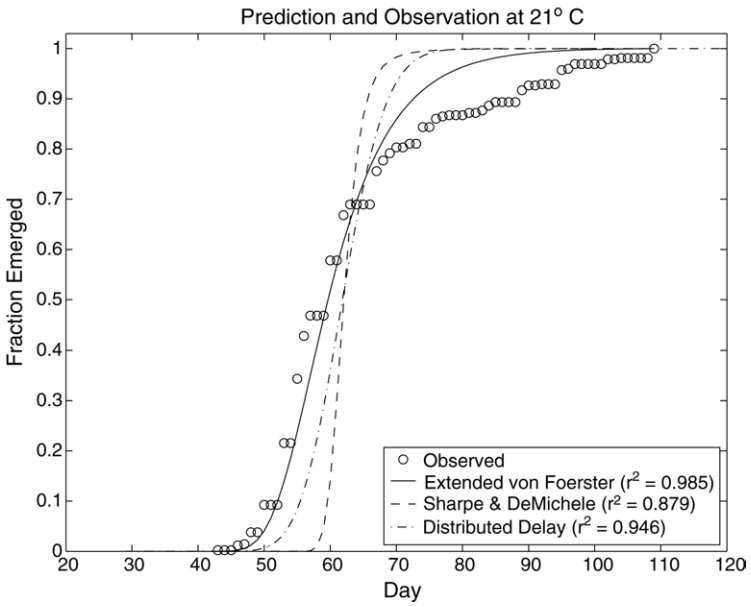

Figure 10. Observed cumulative emergence of mountain pine beetle adults and emergence predicted by the distributed delay (with $k = 22$), Sharpe and DeMichele and EvF models. Developmental rates r were predicted using the rate curves described in Jenkins *et al.* (2001). Variability for the EvF model was found by averaging ν over temperature for each lifestage [$\nu = (0.0002, 0.0046, 0.0088, 0.0058, 0.0067, 0.0014)$]. The slope c of the line $\sigma = cr$ was found using parameterization data and was used to estimate the variability in the Sharpe and DeMichele model [$c = (0.0838, 0.1869, 0.4262, 0.2880, 5.0828, 0.4590)$].

From a computational perspective, the EvF approach (25) has similar computational complexity to the Sharpe and DeMichele same-shape approach (26). Both involve convolutions of emergence distributions with probability kernels involving net development occurring between times τ and t, resulting in $O(n^2)$ computations required for n temporal increments. Consequently, the EvF approach is no more costly than the widely used Sharpe and DeMichele model. It is more mechanistically derived and is not hampered by the necessity of a same-shape assumption on the relationship between accumulation of development and variance.

In real-world environments with high thermal variability the differences between the EvF and same-shape approaches become apparent, as does the need to include the effect of phenotypic variance in phenology models. To illustrate the cumulative effect of these differing assumptions in a variable temperature environment, equations (25) and (26) were applied stage-wise to MPB developing in the Sawtooth National Recreation Area of central Idaho. An individual tree was baited with a pheromone lure and the number and timing of adult beetles attacking the tree during the summer of 2001 recorded and used to initialize the model. Phloem temperatures were recorded hourly for an entire developmental period. Results of both EvF, same-shape, and a median-individual model with no phenotypic variance are

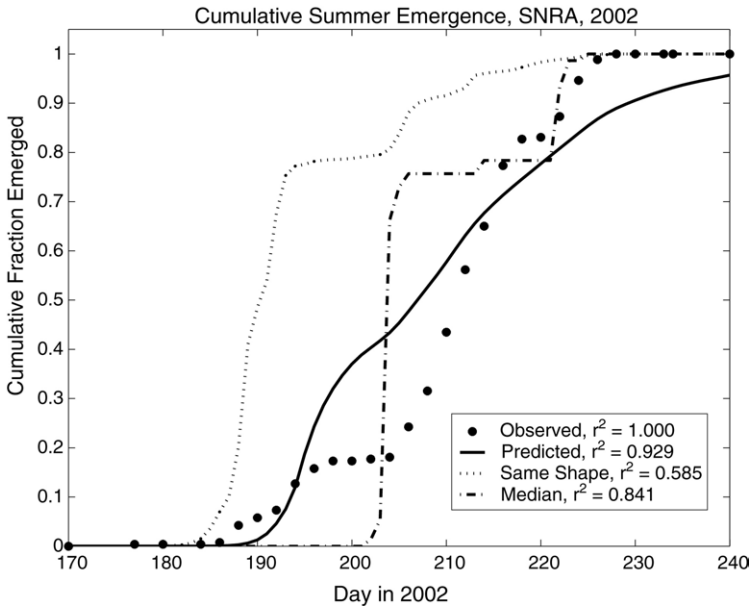

Figure 11. Observed and predicted cumulative emergence of MPB in the Sawtooth National Recreation Area. EvF (solid), same-shape Sharpe and DeMichele (dots), and median-individual models (dash–dots) were initialized using the recorded number and timing of adult beetles attacking a pheromone baited tree during the summer of 2001. Phloem temperatures were recorded hourly for an entire developmental period and emergence observed during the summer of 2002.

plotted in Fig. 11 in cumulative form, with actual cumulative observed emergence plotted for reference.

All three models are parametrized with laboratory data, as described in previous sections, not 'fit' to the observations. Nonetheless, the correspondence between the prediction of the EvF model and the data is still excellent, with an r^2 of 0.93. The same-shape Sharpe and DeMichele model exhibits a correspondence of $r^2 = 0.59$. The need to include variance is also illustrated; a median-individual model (all variances zero) is also plotted, and gives an r^2 of 0.84. This preliminary analysis indicates the need to include realistic variance in developmental timing and the superiority of the EvF approach in a variable temperature environment. More complete discussion of the field data presented here and the computational application of the EvF model in variable temperature environments will be the subject of a future paper.

9. CONCLUSION

This paper discusses three developmental models: the Extended von Foerster (EvF) model, the distributed delay or boxcar model, and the Sharpe and DeMichele model. Each model has positive and negative qualities in constant and

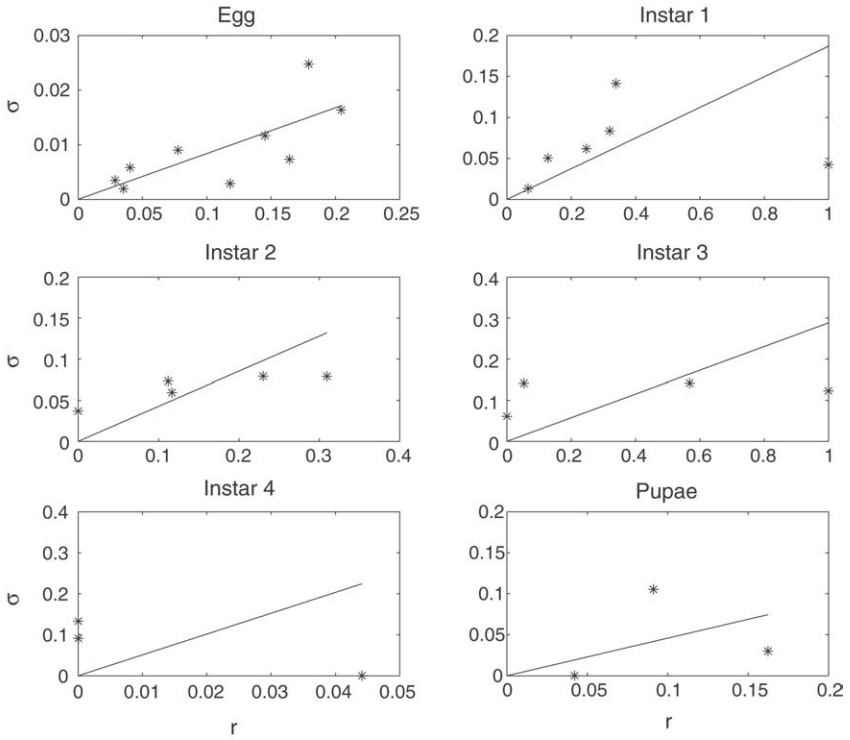

Figure 12. Estimated standard deviations vs. estimated developmental rates for each lifestage. Parameters were found using the Sharpe and DeMichele model and show only a weak linear association.

variable-temperature environments. The distributed delay model, with its compartmentalized structure, is a good way to initially envision development, and is simple to implement. Clear and straightforward, the model is easy to understand and parametrize at constant temperatures. But the underlying idea that an organism's lifestages can be divided into phases or boxcars is flawed. Choosing Δa, or the length of each boxcar, becomes difficult when examining development over all lifestages at constant temperature and virtually impossible at variable temperatures. Consequently, researchers often choose a constant Δa, either empirically or experimentally, instead of changing Δa dynamically with temperature. As a result, the accumulation of variability in fluctuating temperature regimes is largely inaccurate.

The Sharpe and DeMichele model uses the distribution of developmental rates to find the distribution of emergence times. At constant temperatures, this probabilistic methodology is relatively simple to implement and parametrize. However, at variable temperatures additional assumptions must be made to estimate the full distribution of emergence times. In particular, the 'same-shape' assumption requires the variance of developmental rates to be linearly proportional to the mean of developmental rates. This assumption is questionable both biologically and experimentally. When the MPB parametrization data from Section 6 is used to

compare the standard deviations and developmental rates predicted by the Sharpe and DeMichele model, the linear trend is weak, at best (Fig. 12). This, and the restrictive assumption that variance accumulates in direct proportion to development, makes the Sharpe and DeMichele model inaccurate in variable-temperature regimes.

The EvF model was derived by examining the relationships between the flux and the change in population density. Using only minimal assumptions about the distribution of developmental rates (namely, that the rates are symmetric about the mean, with known variance), the model incorporates phenotypic variability. The resulting model is a partial differential equation in time and age for the density of developing individuals. This model architecture allows the user to parametrize how median developmental rates and variability in the population about those rates vary with temperature. This allows for a great degree of flexibility in model construction and for variance to be accumulated in the manner that is most appropriate for a given population. In the case of MPB this results in higher correspondence with the laboratory data examined. The true test of these modelling approaches will be in predicting field observations of adult emergence made in varying temperature regimes. The results from these predictions will be presented in a future paper.

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