A DISTRIBUTION MODEL FOR EGG DEVELOPMENT IN MOUNTAIN PINE BEETLE

J.A. Logan and G.D. Amman[1]

Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado, USA 80523

Abstract

Can. Ent. 118: 361–372 (1986)

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) population dynamics, as well as potential for outbreaks and resulting tree mortality, are related in part to habitat temperature. As a first step in development of a life-stage, event-oriented simulation model, we have modeled the temperature-dependent development of the egg stage. The completed model includes a full description of variation in developmental rates and is capable of predicting duration and eclosion patterns for any temperature regime. This model was parameterized using data obtained from constant-temperature experiments at temperatures of 8, 10, 12.5, 15, 20, 25, and 30°C. Validation experiments were conducted for constant temperatures of 15, 17.5, 22.5, and 27.5°C and for variable-temperature regimes of 15 ± 5 and 15 ± 10°C. Validation results indicated that the model is capable of accurately describing the emergence curve for constant temperatures below 27.5°C. The model also faithfully represents emergence under variable temperatures of 15 ± 10°C. Potential reasons for lack of model fidelity in describing emergence at constant high temperatures and for 15 ± 5°C are discussed in the text.

Résumé

La dynamique des populations du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins), de même que son potentiel épidémique et la mortalité des arbres qui en résulte, sont en partie dépendants de la température de l'habitat. Comme première étape dans le but d'élaborer un modèle de simulation du développement des stades, nous avons modélisé la relation entre le développement du stade oeuf et la température. Le modèle intégral comprend une description de la variation du taux de développement et peut prédire la durée et la courbe d'éclosion pour tout régime de température. Les paramètres du modèle ont été obtenus à partir d'expériences à température constante aux températures de 8, 10, 12,5, 15, 20, 25 et 30°C. Des tests de validation ont été effectués à 15, 17,5, 22,5 et 27,5°C et sous des régimes de température variable de 15 ± 5 et 15 ± 10°C. Les résultats de la validation indiquent que le modèle peut précisément prédire la courbe d'émergence à des températures constantes sous 27,5°C. Le modèle prévoit aussi fidèlement l'émergence à des températures variables de 15 ± 10°C. On discute des raisons possibles du manque de précision du modèle lorsqu'il s'agit de prédire l'émergence à des températures constantes plus élevées, et pour les régimes de 15 ± 5°C.

Introduction

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is one of the most destructive insects of coniferous forests in western North America (Furniss and Carolin 1977). The economic and ecological effects of this beetle are most obvious in lodgepole pine (*Pinus contorta* Douglas) forests, where outbreaks of *D. ponderosae* may result in both intensive (sometimes more than 90%) and extensive (several thousand acres if stand conditions are right) mortality (Cole and Amman 1980; Safranyik *et al.* 1974). For this reason, the combination of conditions that lead to mountain pine beetle outbreaks has been the subject of extensive research in both the United States and Canada (Berryman *et al.* 1978). Much of this work has focused on the role that beetle population dynamics play in the ecological interaction between mountain pine beetle and lodgepole pine forests (Berryman 1976; Cole *et al.* 1976). To help understand the interaction between beetle, stand, and environmental factors that lead to beetle outbreaks, we are developing a simulation model of mountain pine beetle population dynamics.

[1]Address: Intermountain Forest and Range Experiment Station, 507 25th Street, Ogden, Utah, USA 84401.

Our approach to development of a mountain pine beetle model is a life-history, event-oriented model with particular emphasis on factors that have been demonstrated to play an important role in population performance. From the life-history event point of view, the egg stage represents a logical starting point. From a key-factor point of view, an accurate model of egg development is desirable because of the importance of overwintering mortality in determining population performance. Overwintering mortality of mountain pine beetle larval populations is often high and is typically highly variable (Cole 1981), with the probability of death depending on the instar entering winter (Amman and Cole 1983). The distribution of life stages entering winter results from 2 factors: (1) the temporal ovipositional distribution and (2) individual variation in developmental rate subsequent to oviposition. Both sources of variation are highly temperature dependent.

For mountain pine beetle populations, temperature is the principal limiting factor on both the altitudinal and latitudinal geographic distribution (Safranyik 1978). Temperature also has been implicated as having a potentially important influence on outbreak probability (Thomson and Shrimpton 1984). Cold temperatures may directly result in mortality, and alteration of temperature regimes may interfere with timing of critical life-history events (Amman 1973). Conversely, high summer temperatures influence ovipositional rates and subsequent age distribution. Any mechanistic model of mountain pine beetle population dynamics clearly must include temperature as a major driving variable.

Materials and Methods

Obtaining and Incubating Eggs. To obtain beetle eggs for these experiments, lodgepole pine infested with mountain pine beetles and containing larvae were felled on the Ashley National Forest in northeastern Utah in fall 1982 and 1983. In addition, uninfested trees were also felled. Billets 45 cm long and about 25 cm in diameter were cut from the lower trunk region of the trees. The billets were taken to Ogden, where they were dipped in hot paraffin wax to slow the rate of drying, and were then stored at 2°C until needed.

Infested billets were removed from storage and placed at room temperature (21°C) for beetles to complete development. When adult beetles started to emerge, the billets were placed in cages and adults collected. Adults were placed in petri dishes containing damp sawdust and stored at 4°C until needed. Adults more than 3 days old were discarded.

To infest the green, uninfested billets, the billets were removed from cold storage and allowed to warm at room temperature for 24 h. Holes 2.5 cm deep and spaced 5 cm apart around the circumference of one end of each billet were drilled into the phloem. Adults were removed from cold storage and sexed according to characteristics of the 7th abdominal tergite (Lyon 1958). A male and female were placed in each hole. Holes were then covered with aluminum screen to prevent beetle escape.

The beetles constructed about 2.5 cm of egg gallery per day. On the fourth day following introduction of beetles into the bark, individual galleries, except the last 10 mm, and the bark surrounding them were removed from the billet. The last 10 mm of gallery contained the female beetle and was left intact. Aluminum screen was stapled over the exposed end of the gallery to prevent the female from leaving.

To obtain eggs less than 24 h old without undue disturbance to the females, eggs were removed from the most recently constructed 13 mm of egg gallery with the aid of a dissecting microscope. A teasing needle sterilized in alcohol and then a flame was used to remove eggs. Eggs were placed in numbered circles drawn on filter paper that had been placed in petri dishes and saturated with distilled water. The petri dishes containing eggs were placed over a saturated solution of K_2SO_4 in desiccators, which maintained relative humidity of about 98% (Wexler and Hasegawa 1954) and prevented rapid drying of the wet filter paper.

Data used in developing the original model were obtained during winter and early spring 1983. Twenty to 35 eggs (2 replicates of 10–18 eggs each) were incubated at each

of 7 constant temperatures (8 ± 0.25, 10 ± 0.25, 12.5 ± 0.25, 15 ± 0.25, 20 ± 2.5, 25 ± 1.1, and 30 ± 1.1°C). Eggs were examined for hatch and mortality at 24-h intervals. Data used to validate the model were obtained during late fall 1983. Thirty eggs (2 replicates of 15 eggs each) were incubated at each of 4 constant temperatures (15.0 ± 0.25, 17.5 ± 0.25, 22.5 ± 0.25, and 27.5 ± 1.1°C) and at each of 2 variable-temperature regimes (15 ± 5 and 15 ± 10°C). Variable temperatures changed gradually over each 24-h period, following a smooth ovoid cam, and yielded an average temperature of 15°C. Temperature changes in the desiccators lagged slightly behind those of the cabinet but were compensatory, yielding the same 24-h temperature regime as the cabinet. Eggs used in the model-validation tests were examined for hatch at 12-h intervals.

Model Description. The most complete model description we are aware of that accounts for both nonlinearity in developmental rates and a full distribution of developmental rates under variable temperatures was formulated by Sharpe *et al.* (1977). First, this model requires description of 4 related probability distributions:

$$f_r(x) = \text{p.d.f. (rates)}; A \leq x \leq B \quad [1]$$

$$f_t(y) = x^2 f_r(x); \text{ for } 1/B \leq y \leq 1/A \quad [2]$$

$$F_r(x) = \int_A^x f_r(x)\,dx \quad [3]$$

$$F_t(y) = 1 - F_r(x) = \int_{1/B}^{Y} f_t(y)\,dy \quad [4]$$

where $f_r(x)$ is the function describing distribution of developmental rates (x); f_t is the function describing distribution of developmental times ($y = 1/x$); F_r is the cumulative rate curve; $F_t(y)$ is the cumulative emergence curve; A and B are the slowest and fastest developmental rates, respectively; and Y is elapsed time required to complete the egg stage (i.e. $\bar{Y}$ is the median time in the egg stage). In addition to the governing equations, the Sharpe *et al.* model requires 3 assumptions: (1) temperature can be expressed as a function of time [$T = T(t)$]; (2) development under variable temperatures is an integral function of the rate curve describing development at various constant temperatures; and (3) a linear relationship exists between the mean and variance of developmental rates. A more complete description of the model and a discussion of assumptions is presented in the original paper. For alternative developments that use the Sharpe *et al.* (1977) model as a starting point, refer to Regniere (1984) or Wagner *et al.* (1984). These latter 2 methods do not explicitly require assumption (3).

Governing Eqs. (1) to (4) and relationships describing (or constrained by) the 3 assumptions provide a complete distribution model. Model development requires 4 steps: (1) parameterization of a distribution function for each empirical constant-temperature treatment; (2) least-squares fit of a developmental rate model to median rates predicted from the individual distribution models; (3) computation of a regression relationship which provides an estimate of the temperature-independent coefficient of variation; and (4) description of the full model structure.

Results and Discussion

Model Development. Distribution functions. Once parameters are known for any 1 of the 4 governing distributions, the remaining 3 are fully described. In practice, the functional form of Eq. (1) is typically hypothesized, and parameters for Eq. (4) are fit by nonlinear least squares from the observed cumulative emergence data. Several common distributions have been proposed for Eq. (4), including the Weibull distribution (Wagner *et al.* 1984), the normal distribution (Sharpe *et al.* 1977), the quadratic (Sharpe *et al.* 1977; Barfield *et al.* 1977), and the cumulative density proposed by Stinner *et al.* (1975).

Stinner *et al.* (1975) used a 4-parameter distribution to describe the cumulative distribution of time of emergence [Eq. (4)]. Apart from the specific application in their paper,

this distribution has general utility due to its straightforward mathematical form and flexibility in approximating various standard distributions. For these reasons, we used it to describe the cumulative distribution of developmental rates [Eq. (3)].

A description of the cumulative density distribution (Stinner *et al.* 1975) using our notation is given by:

$$F_z = (1 - z)^{\theta z^k}, \quad [5]$$

where θ and k are empirical constants, and z is the scaled independent variable;

$$z = (B - x)/(B - A), \quad [6]$$

where A, B, and x were previously defined. Stinner *et al.* further defined $\hat{z}$ and $\tilde{z}$ as

$$F_z(\tilde{z}) = 0.5 \text{ for } \tilde{z} = (B - \tilde{x})/(B - A), \quad [7]$$

$$F_z(\hat{z}) = 0.25 \text{ for } \hat{z} = (B - \hat{x})/(B - A), \quad [8]$$

where $\hat{x}$ and $\tilde{x}$ are the 25th and 50th developmental-rate percentile, respectively. Stinner *et al.* computed various parameter values of Eq. (5) that approximated common distribution functions. Of particular interest was their comparison with the normal distribution, where they found best results when $A = \tilde{x} - 3.688\sigma$, and $B = \tilde{x} + 3.688\sigma$. Also, because for the normal curve $\tilde{x} = \mu$ and $\hat{x} = \mu - 0.67\sigma$, both k and θ can be computed as constants equal to 2.63 and 6.192, respectively, therefore, Eq. (5) becomes a particularly simple approximation to a normal distribution with finite limits A and B, mean μ, and standard deviation σ.

Assuming that developmental rates are distributed approximately normally [the enzyme kinetic model of Sharpe and DeMichele (1977) suggests that this is reasonable; however, this assumption is not necessary, e.g. Regniere (1984)], we can obtain estimates of $\bar{x}$ and s, (mean developmental rate and standard deviation) from nonlinear least-squares fit of data from the observed emergence curve. First, the data are transformed from emergence times to developmental rates by

$$\hat{X} = 1/\hat{Y}, \quad [9]$$

$$\hat{F}_z(\hat{X}) = 1 - \text{(cumulative proportion emerged)}, \quad [10]$$

where $\hat{Y}$ is an observed elapsed time to emergence and $\hat{F}$ is the corresponding observed distribution for rates. Equation (5) is then fit to these transformed data points. Transformed data [the density distribution Eq. (3) rather than Eq. (4) directly] are used for parameter estimation because the symmetry assumption for the rate curve results in equivalence of the median and mean, whereas nonlinearity in the relationship between developmental rate and time required to complete a stadium results in an emergence curve that is typically skewed right (Sharpe *et al.* 1977). In other words, as long as Eq. (3) is used, it does not make any difference if empirical means or medians are used; however, if Eq. (4) is used, it does make a difference. Plots of Eq. (5) fit to data from our constant-temperature experiments are shown in Fig. 1, and parameter estimates are given in Table 1.

Developmental rates as a function of temperature. The developmental distributions described by Eqs. (1) to (4) completely describe development at any constant temperature. The first step in generalizing this model to account for variable-temperature regimes is to describe mean rate of development as a function of temperature. Several satisfactory relationships have recently been developed (Sharpe and DeMichele 1977; Stinner *et al.* 1975); however, for reasons of simplicity, we used the asymptotic expansion model of Logan *et al.* (1976):

$$X = p_1 \{\exp(p_2 T) - \exp(p_2 p_3 - \tau)\}, \quad [11]$$

for

$$\tau = (p_3 - T)/p_4, \quad [11a]$$

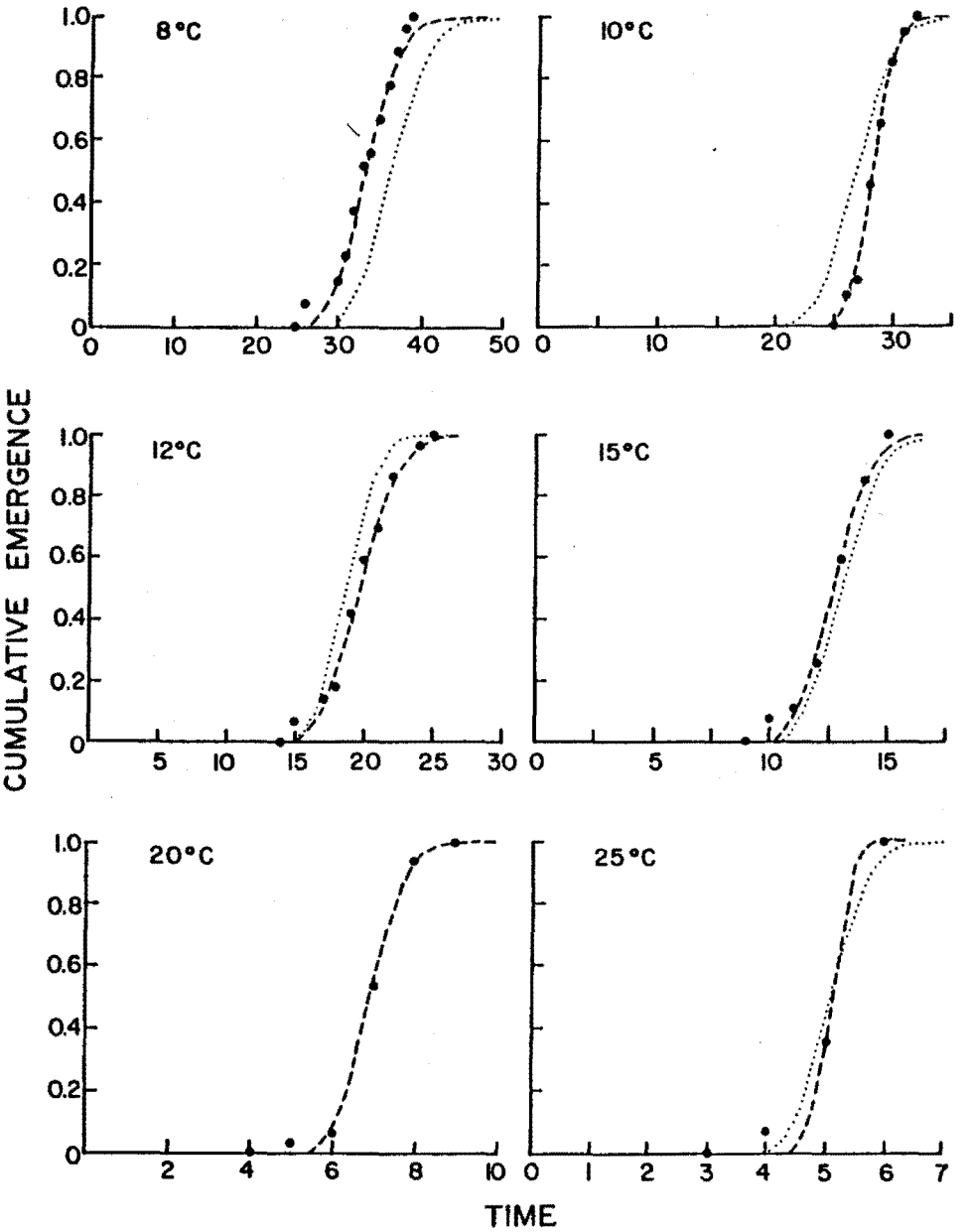

FIG. 1. Comparison of Stinner *et al.* (1975) distribution function Eq. (4) individually fit to constant-temperature data (long dash) compared with the normalized same-shape model (dotted) fit to the same data. The plots were essentially coincident for the 20°C experiment.

where T is observed temperature above an arbitrary base temperature T_b, and the p_i are parameters determined by nonlinear least-squares regression. Equation (11) was fit to the estimated mean rates listed in Table 1. Parameter values are $p_1 = 0.0282$, $p_2 = 0.156$, $p_3 = 20.859$, and $p_4 = 3.037$, for $T_b = 8.0$°C. A plot of Eq. (11) fitted to estimated

Table 1. Estimated parameters for developmental rate distribution for constant-temperature experiments. Parameters were estimated from nonlinear least-squares fit of Stinner *et al.* (1975) cumulative distribution function [Eq. (4)] to transformed emergence time data [Eqs. (8) and (9)]

Treatment	Mean	Standard deviation	Sample size	Percentage mortality
8°C	0.0301	0.00280	27	10
10°C	0.0352	0.00195	20	0
12.5°C	0.0510	0.00567	29	3.33
15.0°C	0.0788	0.00741	27	10
20.0°C	0.144	0.0134	32	8.57
25.0°C	0.196	0.0106	28	6.67
30.0°C	—	—	30	100.0

means is given in Fig. 2. A further assumption required for use of Eq. (11) in a variable-temperature environment is that development is cumulative, i.e.

$$R = \int_0^t X[T(t)]dt, \quad [12]$$

where R is the developmental index (proportion of the life stage completed by elapsed time (t) and temperature (T) is a function of time (t). We further note that

$$R(\tilde{Y}) = 1, \quad [12a]$$

where $\tilde{Y}$ is the median developmental time.

Estimation of coefficient of variation. Sharpe and DeMichele (1977) noted that, assuming Eq. (12) is valid, the concept of a developmental index can be expanded to describe a full population distribution. In particular, if

$$\sigma = c\mu, \quad [13]$$

where c is a constant. In this case, the distribution function of developmental rates can be normalized, and cumulative emergence is computed as

$$E = F_1^*(R);\ 1/B^* \leq R \leq 1/A^*, \quad [14]$$

where F_1^* is the normalized Eq. (3), and A^* and B^* are the normalized A and B of Eq. (1). The full distribution model for variable temperatures is, therefore, completely described by one additional parameter, the coefficient of variation (c).

Estimates of c were obtained by linear regression of the standard deviations on the mean developmental rate. The slope of this regression (Fig. 3) is then an estimate of c. Note that in estimating c we ignored the 25°C data. This was rationalized by the fact that as mean development rate increases, the interval over which emergence occurs is dramatically reduced. The result is that for a fixed sampling effort, we have 12 observations of emergence times at 8°C, compared with only 4 for 25°C (see Fig. 1). Estimation of a highly nonlinear 2-parameter distribution based on 4 data points seems questionable, and we decided that a better estimate of c would be obtained by ignoring this data point. The temperature-independent coefficient of variation was then estimated as

$$c = 0.0097. \quad [15]$$

This estimate of c (with nonzero intercept -0.0003) accounts for 97% of the observed variation in the data.

With the estimate of c, we now have sufficient information to develop a same-shape model (Sharpe *et al.* 1977) that provides the full distribution of emergence times under variable-temperature regimes. Comparisons of the same-shape model with individually parameterized models for describing the constant-temperature experiments are found in Fig. 1. From these comparisons there appears to be no consistent bias in predicting emergence. In fact, it could be argued that the same-shape model is a better estimator, as it

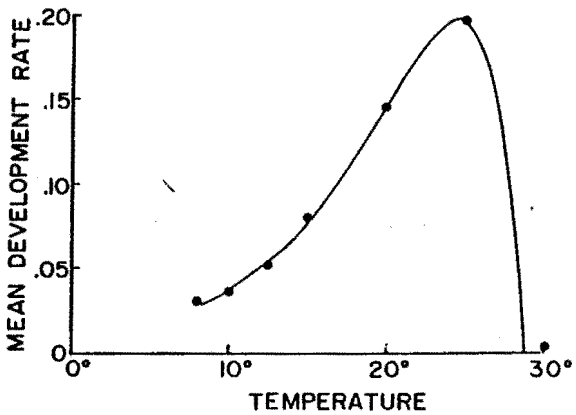

FIG. 2. Plot of developmental rate function Eq. (10) fit to estimated means (from Table 1).

includes information from the full range of constant-temperature experiments and not simply a single data point.

Complete model. The parameterized same-shape model provides the basis for a full model of egg development. The oviposition curve is represented by a collection of cohorts. A *cohort* is defined as the number of individuals entering the egg stage through oviposition over some small interval of time (Δt). Once a cohort is defined, only 2 pieces of information need to be retained: the initial number of individuals in the cohort and the developmental index [d.i. given in Eq. (12)]. The d.i. elements of the cohort matrix (order $2 \times n$, where n is the number of cohorts with d.i. $< 1/A^*$) are updated for each discrete time step Δt; and, once d.i. exceeds $1/A^*$, it is dropped from the matrix. (A generalized computer program of this algorithm can be obtained by writing to J.A.L.).

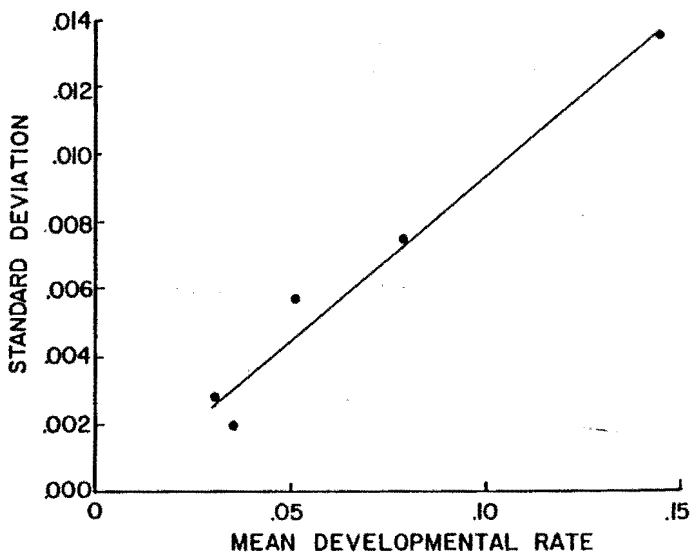

FIG. 3. Linear regression of estimated standard deviations on the mean (data from Table 1). 25°C data point ignored.

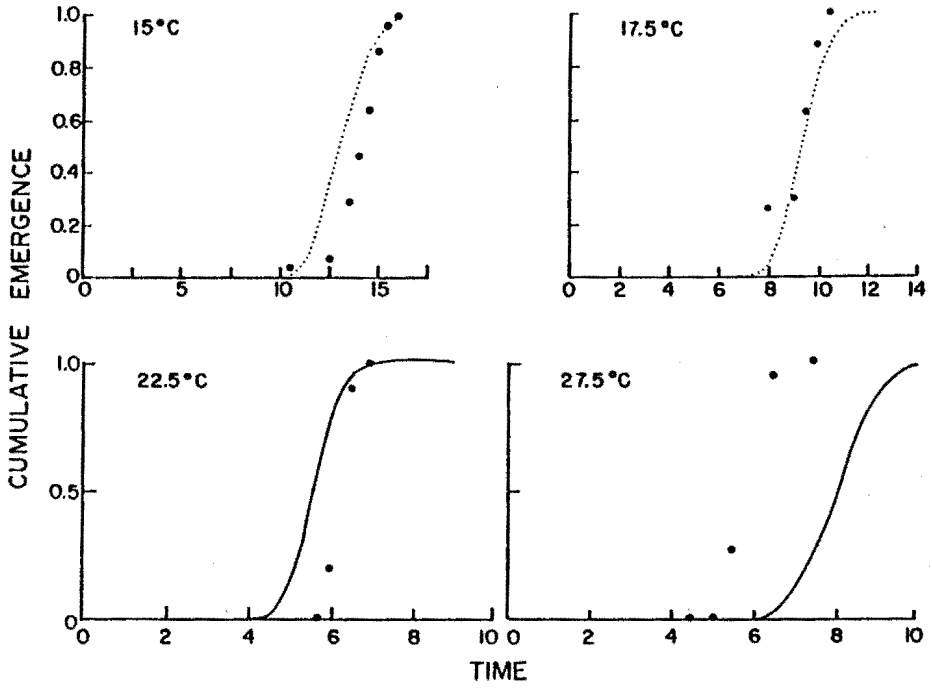

FIG. 4. Plots of the same-shape model fit to constant-temperature validation experiments.

Validation. Any model should be held suspect until some reasonable attempt is made at validation. Swartzman (1979) reserves the term validation for comparison of model predictions to data derived independently from that used to develop the model. Therefore, 2 types of data are required for validation of the egg development model, fixed-temperature experiments which correspond to the original empirical data, and variable-temperature experiments which can be used to test model assumptions explicitly stated by Eqs. (12) and (13).

Fixed-temperature validation experiments. As our original data were weighted towards lower temperatures, we selected validation experiments to be within the range of the original data but weighted toward higher temperatures. Results of validation experiments at constant temperatures of 15.0, 17.5, 22.5, and 27.5°C are shown in Fig. 4.

From inspection of Fig. 4, the model did a good job of predicting emergence curves for 15, 17.5, and 22.5°C. Predictive efficacy is indicated by the excellent job the model did at predicting the range of emergence times as well as the actual pattern of emergence. There was again no particular indication of bias, e.g. model prediction was slightly advanced at 15°C, slightly slower at 17.5°C, and again slightly advanced at 22.5°C. At any rate, model prediction for the validation experiments is well within sampling error associated with the original data (see Fig. 1).

Results from the constant 27.5°C treatment indicate that model predictions were noticeably slower than observed emergence. There are several potential explanations for model failure at this temperature. First, of course, the disparate results could simply be attributed to sampling error. However, a better phenomenological explanation is that a constant temperature this close to thermal maximum causes significant heat stress (e.g. 17% mortality). *Apparent* acceleration would then occur if the probability of mortality due to heat stress is proportional to the amount of time the organism is subjected to the stress.

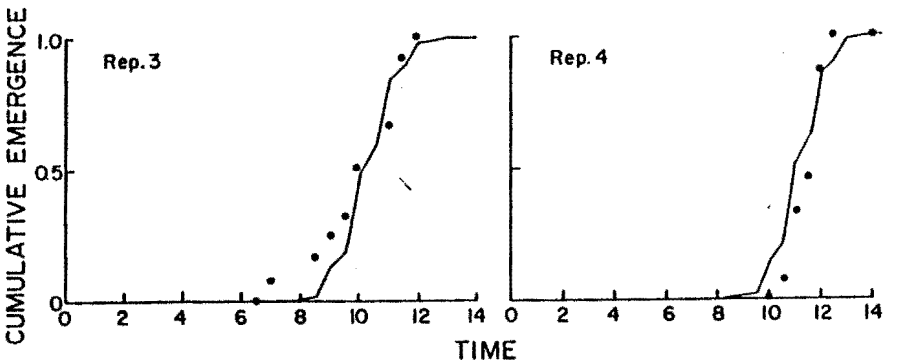

FIG. 5. Plots of 15 ± 10°C replicates 3 and 4. Model prediction is solid line.

Such differential mortality would provide a selective pressure against those individuals with a slower developmental rate. In effect, the left-hand tail of the developmental rate curve would be chopped off, resulting in an observed emergence curve (which by necessity is based on survivors) that is apparently accelerated (Ferro *et al.* 1985). Further observations and model development that explicitly models high-temperature mortality are warranted if high-temperature events are found to be of importance in mountain pine beetle ecology.

Variable-temperature validation experiments. Assumptions expressed in Eq. (12), and extended by Eq. (13) for distribution models, allow prediction of development under variable-temperature regimes from models based on fixed-temperature data. In particular the assumption of Eq. (12) has been questioned by many entomologists (see, for example, Hilbert and Logan 1983*a*; Onsager 1983; Hilbert and Logan 1983*b*). It has frequently been observed that variable temperatures lead to accelerated development when compared with that expected at a constant temperature equal to the mean. Various explanations have been offered for accelerated development under fluctuating temperatures. Acceleration may simply be an artifact of a faulty choice of functional relationship for Eq. (11) (Kaufman 1932; Tanigoshi and Logan 1979). Conversely, acceleration may be an adaptive physiological response. Therefore, the applicability of using a model based on constant-temperature data to predict events under variable-temperature regimes is controversial enough that some attempt should routinely be made to validate such models.

Based on empirical data (Powell 1967) a microhabitat temperature regime of 15 ± 5°C could be considered typical, and variation of ± 10°C is a reasonable maximum variation. We therefore designed validation experiments by programming environmental chambers for temperature cycles of

$$T = 15°C - T_A [\sin (t \cdot 2\pi/24)]$$

where T_A is the amplitude of the temperature cycle (5 or 10°C) and t is time measured in 0–24 h. Four replications were conducted for each of the 2 treatments.

Results for the 15 ± 10°C treatment are shown in Figs. 5 and 6. Because of drifting of mean temperature, and also problems with the temperature controller, each replicate was subjected to a unique temperature regime and had to be modeled separately. Results from replications 3 and 4 indicate that model predictions and observed emergence are in close agreement, well within the limits of variation under constant temperatures. During replications 1 and 2, temperature problems occurred when the temperature controller stuck at temperatures above the constant temperature maximum (temperatures above 30°C). This occurred shortly after emergence had begun (days 10, 11, and 12) for replication 1 and shortly before emergence (days 5, 6, and 7) for replication 2. The temperature anomaly

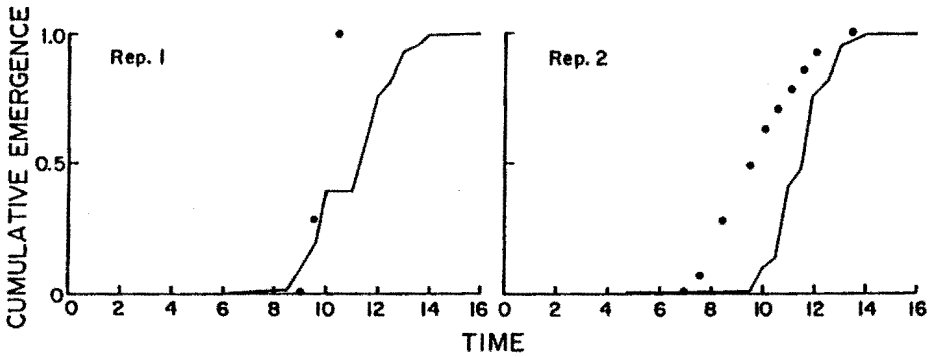

FIG. 6. Plots of 15 ± 10°C replicates 1 and 2. Model prediction is solid line.

is shown by the flat place in the emergence curve in Fig. 6*a*. The short-duration high-temperature event did not result in excessive mortality but did accelerate development beyond that predicted by the model. The same interpretation is given to results shown in Fig. 6*b*; however, the high-temperature event occurred before emergence had begun and is therefore not apparent in the predicted curve. Note that mortality was not particularly high for either replication (6% for both replicates), and that the model apparently was working satisfactorily until the high temperature problems occurred relatively late in the egg stage. Results from these 2 experiments further point out problems of confounding developmental rate with mortality.

High-temperature problems also developed during replicates 1 and 2 of the 15 ± 5°C treatment. Unfortunately, concurrent problems occurred with the thermograph and we have no record of the duration of the events. As expected, development was accelerated by the high temperatures, but because we lack a complete temperature record, there is no way to model these 2 experiments.

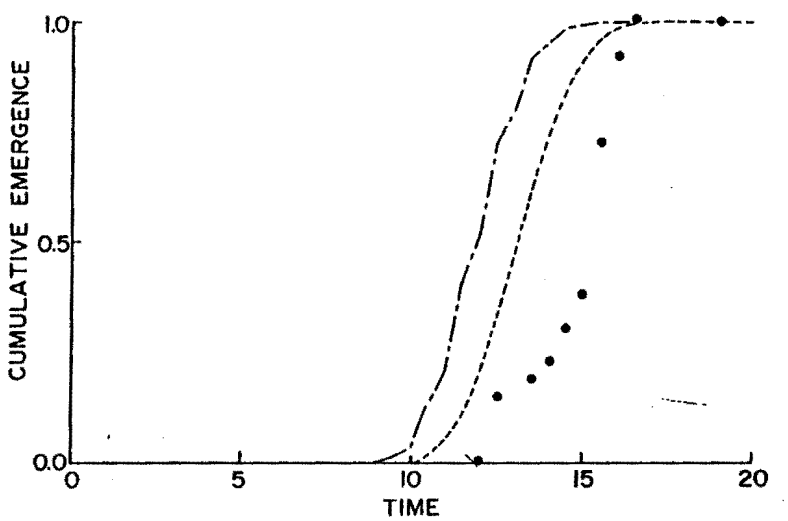

FIG. 7. Plots of model prediction for constant 15°C (short dash), 15 ± 5°C (long dash – short dash), and observed emergence.

Results from 15 ± 5°C, replicates 3 and 4, are shown in Fig. 7. Results from these 2 experiments are difficult to rationalize. Model prediction is an accelerated emergence pattern when compared with a constant 15°C temperature. The vast preponderance of empirical evidence would also lead to the same expectation. However, the observed pattern is noticeably retarded to both the fixed- and variable-temperature simulations. One possible explanation is that eggs used in these 2 replicates were obtained from females who were feeding on phloem that was noticeably drier than the other experiments. Both food quality and survival have previously been related to phloem moisture conditions (Amman and Cole 1983). However, at present we simply don't have enough evidence to indicate if the retarded emergence curve was due to sampling error, maternal habitat effect, or some consistent but unexplained physiological phenomena. Potential adaptive significance warrants further investigation.

Acknowledgments

We thank R.E. Stinner, North Carolina State University, T.L. Wagner, Texas A&M University, and 2 anonymous reviewers for their helpful comments on earlier versions of this manuscript. We considered their comments and incorporated many of their suggestions; however, we accept entirely the responsibility for opinions either expressed or implied in this paper. This publication was supported by a Cooperative Research Agreement between the Intermountain Forest and Range Experiment Station, USDA-FS, and Colorado State University.

References

Amman, G.D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environ. Ent.* **2**: 541–547.

Amman, G.D., and W.E. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II. population dynamics. *USDA For. Serv. Gen. Tech. Rep.* INT-145. 59 pp.

Barfield, C.S., P.J.H. Sharpe, and D.G. Bottrell. 1977. A temperature-driven developmental model for the parasite *Bracon mellitor* (Hymenoptera: Braconidae). *Can. Ent.* **109**: 1503–1514.

Berryman, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Ent.* **5**: 1225–1233.

Berryman, A.A., G.D. Amman, and R.W. Stark (Tech. Eds.). 1978. Theory and practice of mountain pine beetle management in lodgepole pine forests. Symp. Proc., Forest, Wildlife and Range Exp. Stn., University of Idaho, Moscow. 224 pp.

Cole, W.E. 1981. Some risks and causes of mortality in mountain pine beetle populations: A long-term analysis. *Res. Popul. Ecol.* **23**: 116–144.

Cole, W.E., and G.D. Amman. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part I. Course of an infestation. *USDA For. Serv. Gen. Tech. Rep.* INT-89. 56 pp.

Cole, W.E., G.D. Amman, and C.E. Jensen. 1976. Mathematical models for the mountain pine beetle – lodgepole pine interaction. *Environ. Ent.* **5**: 11–19.

Ferro, D.N., J.A. Logan, R.H. Voss, and J.S. Elkinton. 1985. Colorado potato beetle (Coleoptera: Chrysomelidae) temperature-dependent growth and feeding rates. *Environ. Ent.* **14**: 343–348.

Furniss, R.L., and U.M. Carolin. 1977. Insects of western forests. *USDA For. Serv. Misc. Publ.* 1339. 365 pp.

Hilbert, D.W., and J.A. Logan. 1983*a*. An empirical model of nymphal development for the migratory grasshopper (*Melanoplus sanguinipes*). *Environ. Ent.* **12**: 1–5.

——— 1983*b*. Nonlinear models and temperature-dependent development in arthropods — a reply to Dr. Jerome A. Onsager. *Environ. Ent.* **12**: *i*.

Kaufmann, O. 1932. Einige Bemerkungen über den Einfluss von Temperaturschwankungen auf die Entwicklungsdauer und Streuung bei Insekten und seine graphische Darstellung durch Kettenlinie und Hyperbel. *Z. Morphol. Ökol. Tiere.* **25**: 354–361.

Logan, J.A., D.J. Wollkind, S.C. Hoyt, and L.K. Tanigoshi. 1976. An analytic model for description of temperature-dependent rate phenomena in arthropods. *Environ. Ent.* **5**: 1130–1140.

Lyon, R.L. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. *Can. Ent.* **90**: 582–584.

Onsager, J.A. 1983. Comments on "empirical model of nymphal development for the migratory grasshopper, *Melanoplus sanguinipes* (Orthoptera: Acrididae)." *Environ. Ent.* **12**: *v–vi*.

Powell, J.M. 1967. A study of habitat temperatures of the bark beetle, *Dendroctonus ponderosae* Hopkins, in lodgepole pine. *Agric. Meterol.* **4**: 189–201.

Regniere, J. 1984. A method of describing and using the variability in development rates for the simulation of insect phenology., *Can. Ent.* **116**: 1367–1376.

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. pp 77–84 *in* Berryman, A.A., G.D. Amman, and R.W. Stark (Tech. Eds.), Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. Symp. Proc., Forest, Wildlife and Range Exp. Stn., University of Idaho, Moscow. 224 pp.

Safranyik, L., D.M. Shrimpton, and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. *Dept. Environ., Can. For. Serv., Pacific For. Res. Centre, Tech. Rep.* 1. 24 pp.

Sharpe, P.J.H., G.L. Curry, D.W. DeMichele, and C.L. Cole. 1977. Distribution model of organisms development times. *J. Theor. Biol.* **66**: 21–28.

Sharpe, P.J.H., and D.W. DeMichele. 1977. Reaction kinetics of poikilotherm development. *J. Theor. Biol.* **64**: 649–670.

Stinner, R.E., G.D. Butler, J.S. Bacheler, and C. Tuttle. 1975. Simulation of temperature-dependent development in population dynamics models. *Can. Ent.* **197**: 1167–1244.

Swartzman, G. 1979. Evaluation of ecological simulation models. pp. 295–318 *in* Patil, P., and M. Rosenzweig (Eds.), Contemporary Quantitative Ecology and Related Econometrics. Int. Co-op. Publ. House, Fairland, MD.

Tanigoshi, L.K., and J.A. Logan. 1979. Tetranychid development under variable temperature regimes. pp. 165–175 *in* Rodriquez, J.G., (Ed.), Recent Advances in Acarology, Vol. 1. Academic Press, New York.

Thomson, A.J., and D.M. Shrimpton. 1984. Weather associated with the start of mountain pine beetle outbreaks. *Can. J. For. Res.* **14**: 55–258.

Wagner, T.L., H. Wu, P.J.H. Sharpe, and R.N. Coulson. 1984. Modeling distributions of insect development time: A literature review and application of the Weibull function. *Ann. ent. Soc. Am.* **77**: 475–483.

Wexler, A., and S. Hasegawa. 1954. Relative humidity – temperature relationships of some saturated salt solutions in the temperature range 0° to 50°C. *J. Res. Natl. Bur. Stand.* **53**: 19–26.

(Date received: 1985 08 22; date revision received: 1985 10 28; date accepted: 1985 10 29)