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Response of the Western Spruce Budworm (Lepidoptera: Tortricidae) to Temperature: The Stochastic Nature of Developmental Rates and Diapause Termination

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chemical communication in *Dendroctonus*. Contr. Boyce Thomps. Inst. 24: 283–292.

Richerson, J. V., and T. L. Payne. 1979. Effects of bark beetle inhibitors on landing and attack behavior of the southern pine beetle and beetle associates. Environ. Entomol. 8: 360–364.

Richerson, J. V., F. A. McCarty, and T. L. Payne. 1980. Disruption of southern pine beetle infestations with frontalure. Ibid. 9: 90–93.

Roelofs, W. L., and R. T. Cardé. 1977. Responses of Lepidoptera to synthetic sex pheromone chemicals and their analogues. Annu. Rev. Entomol. 22: 377–405.

Rose, W. F., III, R. F. Billings, and J. P. Vité. 1981. Southern pine bark beetles: evaluation of non-sticky pheromone trap designs for survey and research. Southwest. Entomol. 6: 1–9.

Statistical Analysis System Institute. 1982. SAS user's guide: statistics. Statistical Analysis System Institute, Cary N.C.

Texas Forest Service. 1982. Texas forest pest activity 1980–1981 and Forest Pest Control Section biennial report. Texas For. Serv. Publ. 127.

Vité, J. P., and W. Francke. 1976. The aggregation pheromones of bark beetles: progress and problems. Naturwissenschaften 63: 550–555.

Vité, J. P., and D. L. Williamson. 1970. *Thanasimus dubius:* prey perception. J. Insect Physiol. 16: 233–239.

Vité, J. P., G. Ohloff, and R. F. Billings. 1978. Pheromonal chirality and integrity of aggregation response in southern species of the bark beetle, *Ips* sp. Nature (London) 272: 817–818.

Wood, D. L., L. E. Browne, W. D. Bedard, P. E. Tilden, R. M. Silverstein, and J. O. Rodin. 1968. Response of *Ips confusus* to synthetic sex pheromones in nature. Science 159: 1373–1374.

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Response of the Western Spruce Budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), to Temperature: The Stochastic Nature of Developmental Rates and Diapause Termination

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ABSTRACT The variability in the developmental rates for the embryos, larvae, and pupae of the western spruce budworm, *Choristoneura occidentalis*, was skewed and was well described by a gamma probability density function. At extreme temperatures, the shapes of the frequency distributions for the embryos and pupae were not unimodal, suggesting the presence of thermal biotypes. Variability increased markedly towards the temperature extremes (15 and 31°C) and was greater for female than for male larvae. The shapes of the frequency distributions for larvae terminating diapause ranged from a skewed curve for second-instar larvae held in diapause at 0°C to a negative exponential curve for larvae held at 5°C. A Monte Carlo simulation model showed that the probability of synchronous emergence of male and female moths was relatively constant (ca. 66%) over a range of average minimum/maximum temperatures. During the larval developmental period, average minimum/maximum ranged from 2.3/18.1 to 6.0/21.0°C. For the pupae developmental period, average minimum/maximum temperatures ranged from 6.0/21.0 to 11.4/27.1°C. Above these temperatures, the probability of synchronous emergence decreased.

GENETIC VARIABILITY in biological processes is generally expressed by the mean and standard deviation, and only rarely is the shape of the distribution considered (Stinner et al. 1975, Sharpe et al. 1977). The shape of the distribution is critical since it reflects the potential for adaptation and the possible direction that a population could take in adaptation and survival under various environmental conditions. Thermal biotypes are often reflected in bimodal or trimodal distributions (Wilkes 1942). A continuum of genotypes exists, each with slightly different thermal requirements; consequently a population can survive under a wide variety of thermal regimes. Given the temperature range where an insect species can survive, there will be some males and females in the population with similar thermal requirements. Hence, these animals will emerge at the same time and be able to reproduce.

Spruce budworm populations are usually endemic and the species may be found at a variety of temperatures. Given several warm, dry seasons, a population of spruce budworms may increase dramatically to epidemic proportions (Morris 1963), indicating a great deal of flexibility (genetic variability) in spruce budworm populations with regard to survival in a variety of thermal regimes.

Here we consider the variability in the western spruce budworm (WSB), *Choristoneura occidentalis* Freeman, temperature-dependent developmental rates and times (1/days to complete development, and days to complete development, respectively), the termination of diapause, and the correlation between the two. Several probability density functions (pdf) were considered and a Monte Carlo simulation model was used to investigate the means, variances, and shapes of the distributions of developmental times as well as the synchronization between emergence of adult males and females at different temperatures.

Methods and Materials

Laboratory Procedures. WSB were obtained from the Forest Sciences Laboratories, Corvallis, Oreg., and were reared on McMorran's artificial diet medium (McMorran 1965). Throughout the experiments a LD 12:12 photoperiod was maintained. Six to eight temperatures in the range of 10 to 31°C were used in the experiments on developmental rates of embryos (considered on a per-egg-mass basis), larvae, and pupae. Animals were checked every day or half day depending on the life stage and temperature. We showed previously that humidity (all life stages) and sex (only in pupae) do not affect the developmental rates of the WSB (Reichenbach and Stairs 1984). Diapausing WSB larvae, which had spun hibernacula on the caps of 1-ounce plastic cups, were exposed to two temperatures (0 and 5°C) and four relative humidities (10, 43, 75, 100%). Humidity was maintained using saturated salt solutions (Greenspan 1977). After 7.5 months the caps with the diapausing larvae were fitted to 1-ounce plastic cups with the artificial diet medium and kept at 20°C. Humidity was ca. 100%. The time between removal from

the cold temperatures to the termination of diapause was recorded. Termination of diapause was defined as initiation of larval feeding on the artificial diet medium.

Statistical Methodology. Marquardt's algorithm (Statistical Analysis Systems 1979; Proc Nlin) was used to fit the truncated Gaussian curve (Taylor 1981) to the developmental rates in relation to temperature.

The variability in the developmental rates and the termination of diapause were modeled using four probability density functions: normal, quadratic, beta, and gamma.

The normal pdf is described using the first and second moments (μ, σ^2) as estimated by the sample mean and variance ($\bar{x}$, s^2)

$$f(x/\mu, \sigma^2) = 1/(\sqrt{2\pi}\sigma)\exp\{-0.5[(x - \mu)/\sigma]^2\}$$

The restriction is $\sigma > 0$ and the limits are from $-\infty$ to $+\infty$.

The quadratic pdf is described by three parameters (α, β, γ), which can be estimated from the sample mean, variance, and limits. The limits are defined as follows: $a = \bar{x} - \sqrt{5}\, s$ and $b = \bar{x} + \sqrt{5}\, s$. If a is less than 0, the lower limit is set to 0. The parameters in the model

$$f(x/\alpha, \beta, \gamma) = \alpha x^2 + \beta x + \gamma$$

can be estimated as follows: $\alpha = 6/(a - b)^3$, $\beta = -(a + b)\alpha$, $\gamma = ab\alpha$ (Sharpe et al. 1977).

The beta pdf is described by four parameters, p and q and the limits (a, b), which here are defined by the minimum and maximum of the data. The beta pdf is as follows:

$$f(x/p, q, a, b) = \frac{\Gamma(p + q)}{\Gamma(p)\Gamma(q)} \frac{(x - a)^{p-1}(b - x)^{q-1}}{(b - a)^{p+q+1}}$$

The parameters p and q are defined using the method of moments as follows, using the sample mean and variance for μ and σ^2 (Johnson and Kotz 1970)

$$p = \left(\frac{\mu - a}{b - a}\right)^2\left(1 - \frac{\mu - a}{b - a}\right)\left(\frac{\sigma^2}{(b - a)^2}\right) - \left(\frac{\mu - a}{b - a}\right)$$

$$q = \left[\left(\frac{\mu - a}{b - a}\right)\left(1 - \frac{\mu - a}{b - a}\right)\left(\frac{\sigma^2}{(b - a)^2}\right)\right] - 1 - p$$

The gamma pdf is described by two parameters (α, β), where α is the shape parameter and β is the scale parameter

$$f(x/\alpha, \beta) = \frac{(x)^{\alpha-1}\exp(-x/\beta)}{\beta^\alpha\Gamma(\alpha)}$$

or as generally given in computer systems such as SAS or International Mathematics and Statistics library (IMSL)

$$f(x/\alpha) = \frac{(x')\exp(-x')}{\Gamma(\alpha)}$$

where $x' = x/\beta$. The limits are defined from 0 to $+\infty$ and the parameters α and β are estimated using method of moments (Johnson and Kotz 1970)

$$\alpha = s^2/x^2 \text{ and } \beta = \bar{x}/\alpha$$

Alternatively, we calculated maximum likelihood estimates for α and β using tables by Greenwood and Durand (1960).

A Kolmogorov-Smirnov goodness-of-fit test was used to see which of the four pdf's described the data best (i.e., gave the smallest value of the test statistic and consistently provided a good fit to the data for the different life stages, temperatures, and humidities).

The rates were normalized to a mean of 1 using a physiological time scale in order to test whether the distributions were similar between temperatures and sexes. This was done by multiplying the different developmental times for each temperature by the average developmental rate at that particular temperature (Sharpe et al. 1981). A two-sample Kolmogorov-Smirnov goodness-of-fit test was used to make the comparisons (IMSL subroutine NKS2).

Spearman correlation coefficients were used to test whether there was a relationship between larval and pupal developmental rates (i.e., do fast larval developmental rates indicate that the pupae of those larvae will also develop quickly?) and the relationship of diapause termination to the rate of larval development.

Monte Carlo Simulation Methodology. A Fortran program was used for the calculations simulating the development of 80 males and 80 females from the termination of diapause (ca. Julian day 121; McKnight 1967) to the beginning of the adult life stage. Developmental times (means and standard deviations) were calculated for the larvae for total larval and pupal developmental time. The time to complete each life stage was estimated by integrating numerically the developmental rate equation and the Fourier series equation describing daily and seasonal temperature changes

$$\int_{x_1}^{x_2} R[T(x)]\, dx = 1.0$$

IMSL pseudo-random number generators for a gamma distribution were used to generate "animals" with different rates of development (with temperature-dependent parameters) and termination of diapause (average values of α and β used). The parameters for the gamma distribution were calculated by using the average temperature over the calculated larval and pupal life span. The average temperature was used to estimate a mean developmental rate (using the truncated Gaussian curve) and a standard deviation (using linear interpolation between the standard deviations associated with temperatures measured). The mean developmental rate and SD could then be used to calculate an α and β for the gamma pdf using the method of moments.

The random numbers, which represent the range

Table 1. Estimates (±SD) of parameters of the truncated Gaussian model describing developmental rates of the WSB

Model parameters	Embryos	Larvae		Pupae
		Male	Female	
TM^a	30.345	27.255	26.816	29.270
	0.632	0.296	0.241	0.186
TV^a	10.429	8.194	7.740	10.500
	0.436	0.299	0.257	0.181
RM^a	0.172	0.056	0.051	0.181
	0.003	0.001	0.0005	0.001
R^2	0.991	0.991	0.991	0.984

[a] $R(t) = RM \exp\{-0.5[(t - TM)/TV]^2\}$.

of developmental rates at the average temperature, were then used to modify the b_0 parameter in the temperature function (see below) in such a way as to simulate 80 animals, each with a different developmental rate. Because of the positive correlation between diapause termination and larvae developmental rates (see results) the modified b_0 values were arranged from low to high, as were the diapause termination dates, so that larvae, with early dates of diapause termination, were matched with lower b_0 values than were larvae that terminated diapause later.

A Fourier series was used to describe the minimum/maximum temperature data from Aspen, Colo., in 1983 (U.S. National Weather Center Records).

$$T(x) = \bar{T} - \frac{a_2}{2}\cos\left(\frac{2\pi}{365}t + \phi\right) - \frac{a_1}{2}\cos(2\pi t)$$

The $\bar{T}$ represents the yearly average temperature, a_2 the amplitude of the annual temperature fluctuations, a_1 the daily temperature fluctuations, and ϕ shifts the cosine curve, which usually has a maximum at 0 (1 Jan. in Julian time scale), to some other estimated time in the year (usually calculated to be in midsummer) when the annual temperature is maximal (Taylor 1981). The linear version of this formula that follows is more easily fitted using multiple regression techniques than its nonlinear counterpart

$$T(x) = b_0 + b_1\cos\left(\frac{2\pi t}{365}\right) + b_2\sin\left(\frac{2\pi t}{365}\right) + b_3\cos(2\pi t)$$

where $\bar{T} = b_0$, $a = 2b_3$, $a_2 = 2\sqrt{b_1^2 + b_2^2}$, $\phi = \arctan(-b_2/b_1)$. The yearly average temperature (b_0) was modified from 2 to 20 to test for its effect on developmental time. A b_0 of 2 corresponds to an average temperature of 10°C during the larval stage and an average minimum and maximum temperature of 2.3 and 18.1°C, respectively. For other b_0's, the average, and average minimum and maximum temperatures, are as follows: $b_0 = 8$, 14.3, 6.4, 22.1; $b_0 = 14$, 18.9, 11.0, 26.7; $b_0 = 20$, 24.2, 16.4, 32.1°C. The total time needed to complete the second-instar-to-adult time span was tested to see if it fit a gamma pdf. From these pdf's for adult male and female moth emergence times, the area of synchronous emergence could be numerically integrated.

Results and Discussion

The developmental rates of the embryos, larvae, and pupae were nonlinear in relation to temperature. At temperatures above 27 to 31°C (depending on the life stage), the developmental rates declined rapidly. At temperatures below 10°C the rates were very low. The truncated Gaussian model (Taylor 1981) described the data well (Table 1) and usually fewer than 10 iterations were required to estimate the model parameters.

The variability in the developmental rates for

Table 2. Variability of the developmental times (days) and rates (1/days) for WSB embryos reared at constant temperatures

Parameters	Temperature (°C)						
	10	15	20	25	28	29.5	31
n^a	22[b]	207	250	215	176	8[b]	6[b]
$\bar{x}$ (days)	35.5	21.5	10.4	7.6	5.9	5.6	6.8
SD	5.1	1.1	0.71	0.42	0.50	0.13	0.27
CV	14.4	5.1	6.8	5.5	8.5	2.3	4.0
Shape (α)[c]	—	374.6	214.2	316.4	151.4	—	—
Scale (β)[c]	—	0.0573	0.0484	0.0240	0.0393	—	—
$\bar{x}$ (1/days)	0.0288	0.0467	0.0969	0.1321	0.1693	0.1779	0.1484
SD	0.0049	0.0024	0.0066	0.0075	0.0132	0.0042	0.0060
CV	16.6	5.2	6.9	5.7	7.8	2.4	4.0
Shape (α)[c]	—	372.5	214.4	314.1	158.6	—	—
Scale (β)[c]	—	0.00012	0.00045	0.00042	0.00107	—	—

[a] n = No. egg masses examined (no. embryos per egg mass averaged 36).
[b] Mortality was ≫10%, sample size was too small to estimate parameters for the gamma pdf.
[c] Gamma probability density function parameters (maximum likelihood estimates).

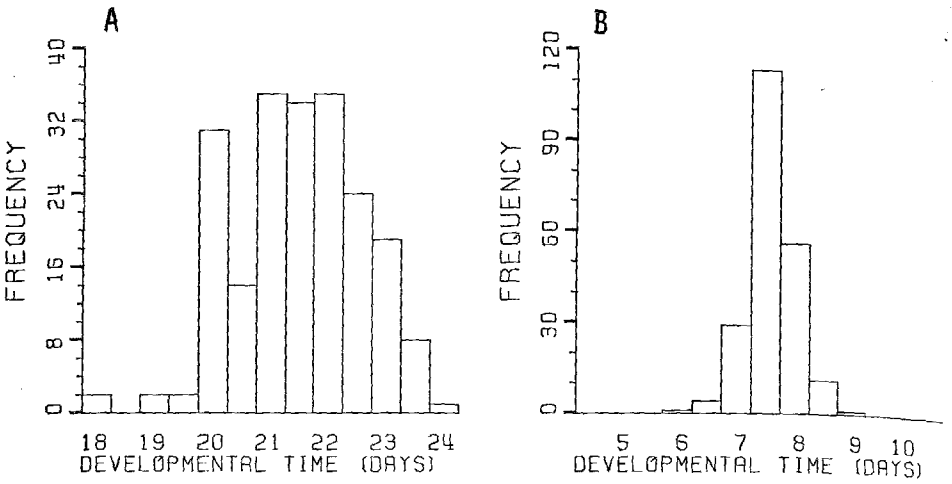

Fig. 1. Variation in the frequency distribution of developmental times for WSB embryos: (a) bimodal distribution at 15°C, and (b) unimodal distribution at 25°C.

the embryos was relatively constant over all the temperatures, as seen by a stable coefficient of variation (CV; Table 2). High mortality at both the high and the low temperatures (28 and 15°C) did not allow the fitting of the gamma pdf and the CV's were not well defined at these temperatures. At 15°C, even though a statistically good fit was obtained using a unimodal pdf, the actual data were bimodal (Fig. 1). This indicated that several thermal biotypes were present in the spruce budworm population used in the experiment.

The second-instar larvae kept in diapause at 5°C terminated diapause sooner than did those at 0°C (Table 3). At 5°C the majority of the larvae in diapause were able to complete their diapause development during the 7.5 months at 5°C and were able to break diapause rapidly. The frequency distribution for diapause termination for these animals resembled a negative exponential curve (Fig. 2). At 0°C, only a few of the larvae were able to complete diapause development during the 7.5 months. The majority of the larvae required several days at 20°C in order to complete diapause development and then terminate diapause. The frequency distribution for diapause termination for these animals was a curve skewed to the right (Fig. 2). The variance of diapause termination for larvae kept at 0°C was greater than for larvae held at 5°C. At the lower temperature (0°C), the diversity of thermal biotypes was more evident, with some of the larvae at 0°C being able to terminate diapause as rapidly as did those at 5°C. Humidity had no major effects on the average time of diapause termination, but it did have an effect on the variance (Table 3). The trends for both temperatures (0 and 5°C) showed that the variance was the smallest at 75% RH and increased towards the more extreme humidities (10 and 100% RH).

The larval developmental rates showed the least amount of variation in the temperature zone considered to be optimal for the WSB larvae (ca. 25°C; Table 4). At 28 and 15°C the variability was ca. twice that near 25°C. Similar trends were evident in the two sexes though the variability in development of the female larvae was in general greater than that of the males (most clearly seen in the standard deviations of the developmental times).

The variability in the pupae developmental rates also increased toward the temperature extremes and was minimal at ca. 20°C (Table 5). At 31 and 10°C the distribution of the times or rates showed some trends toward bimodality, indicating again the presence of thermal biotypes in the population

Table 3. Variability of the termination of diapause (days) for second-instar WSB larvae kept at constant temperatures and humidities and then removed to cups with food at 20°C

Temp (°C)	RH (%)	Sample n	Sample $\bar{x}$	Sample SD	Gamma pdf parameters Shape (α)[a]	Gamma pdf parameters Scale (β)[a]
0	10	164	6.00	2.570	4.6206	1.2998
	43	152	5.76	2.465	4.6562	1.2377
	75	230	5.82	1.908	8.6957	0.6695
	100	226	6.31	2.079	9.0845	0.6945
5	10	94	3.65	1.933	3.0406	1.2000
	43	261	2.93	1.735	2.9251	1.0020
	75	221	2.12	1.500	2.7069	0.7823
	100	55	2.13	1.711	2.1927	0.9702

[a] Probability density function parameters (maximum likelihood estimates).

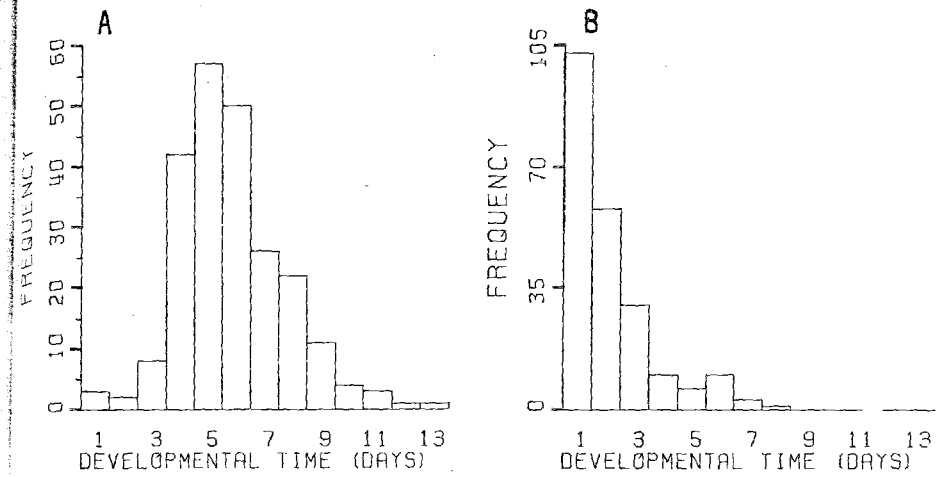

Fig. 2. Variation in the frequency distribution of diapause termination times for second-instar WSB larvae kept in diapause at (a) 0°C, a skewed distribution; and (b) 5°C, a negative exponential distribution.

of animals investigated. As noted with the embryos, the existence of two or more genetically distinct groups of animals having different thermal requirements was not evident until extreme temperatures were investigated, temperatures generally outside the linear zone of the developmental rate curve.

Of the four pdf's fitted to the data, the gamma distribution had the overall best fit, being rejected as an adequate model only three times for both developmental rate and time data (total of 54 comparisons). The beta pdf was rejected 8 times, the quadratic pdf 20 times, and the normal pdf was accepted only 5 times.

Table 4. Variability of the developmental times (days) and rates (1/days) for WSB larvae reared at constant temperatures

Parameters	Temperature (°C) 10	15	20	24	28	31
			Male larvae			
n	30[a]	263	334	283	287	22[a]
$\bar{x}$(days)	108.9	53.0	29.6	16.5	19.2	20.5
SD	13.6	8.4	2.4	1.6	1.5	4.4
CV	12.5	15.8	8.1	9.7	7.8	21.2
Shape (α)[b]	—	43.2	151.5	112.0	161.4	—
Scale (β)[b]	—	1.228	0.1955	0.1471	0.1192	—
$\bar{x}$(1/days)	0.0093	0.0193	0.0340	0.0612	0.0523	0.0505
SD	0.0011	0.0028	0.0027	0.0057	0.0042	0.0091
CV	12.0	14.6	8.0	9.3	9.7	18.1
Shape (α)[b]	—	46.0	154.6	114.7	159.2	—
Scale (β)[b]	—	0.00042	0.00022	0.00053	0.00033	—
			Female larvae			
n	23[a]	264	291	242	221	12[a]
$\bar{x}$(days)	120.9	58.0	31.2	18.1	20.4	24.4
SD	12.8	10.8	2.7	1.8	1.9	4.5
CV	10.3	18.6	8.6	9.9	9.3	18.4
Shape (α)[b]	—	32.6	136.0	113.0	115.6	—
Scale (β)[b]	—	1.776	0.2294	0.1604	0.1769	—
$\bar{x}$(1/days)	0.0084	0.0178	0.0323	0.0557	0.0493	0.0422
SD	0.0008	0.0028	0.0027	0.0050	0.0048	0.0076
CV	10.3	15.9	8.4	9.1	8.0	17.9
Shape (α)[b]	—	36.4	138.6	118.3	111.1	—
Scale (β)[b]	—	0.00049	0.00023	0.00047	0.00044	—

[a] Mortality was ≫10%, sample size was too small to estimate parameters for the gamma pdf.
[b] Gamma probability density function parameters (maximum likelihood estimates).

Table 5. Variability of the developmental times (days) and rates (1/days) for WSB pupae reared at constant temperatures

Parameters	Temperature (°C)						
	10	15	20	23	25	28	31
n	71	212	377	536	432	106	174
$\bar{x}$ (days)	27.9	20.4	8.2	7.7	6.2	5.5	5.6
SD	3.60	1.90	0.61	0.61	0.54	0.73	0.68
CV	12.9	9.3	7.4	7.9	8.7	13.2	12.1
Shape (α)[a]	60.8	114.7	177.0	155.6	123.5	127.7	73.3
Scale (β)[a]	0.4587	0.1781	0.0463	0.0497	0.0499	0.0464	0.0768
$\bar{x}$ (1/days)	0.0364	0.0494	0.1227	0.1301	0.1635	0.1845	0.1801
SD	0.0047	0.0046	0.0094	0.0109	0.0157	0.0343	0.0201
CV	12.9	9.3	7.7	8.4	9.6	18.5	11.2
Shape (α)[a]	59.8	116.0	173.9	149.4	116.7	113.8	77.4
Scale (β)[a]	0.00061	0.00043	0.00070	0.00087	0.00140	0.00150	0.00233

[a] Gamma probability density function parameters (maximum likelihood estimates).

The shape of the frequency distribution for developmental times for embryos and pupae were skewed to the left. Skewness in the developmental times for the larvae was less evident and consistent. Since developmental rates are the inverse of developmental times, the frequency distributions for the rates were skewed in the opposite direction. Skewness in developmental data is frequently observed (Stinner et al. 1975, Sharpe et al. 1977, Gagne et al. 1981), hence the symmetry of the normal and quadratic pdf's usually makes them inappropriate models of variability in biological data. The limits ($-\infty$ to $+\infty$) for the normal pdf are also usually not appropriate for biological data. The gamma and beta pdf's are flexible and can take on the shape of a negative exponential curve or curves skewed to the right or left. The beta pdf, though, has fixed limits that may be difficult to define, while the range encompassed by the gamma pdf (0 to $+\infty$) are natural limits to most, if not all, biological processes. The assignment of such small probabilities to values well outside the range of the data makes these extreme events highly improbable, but not impossible. The gamma distribution should therefore be a pdf well suited to model the variability of developmental rate phenomena.

Skewness to the left in the frequency distributions for developmental times of WSB might be due to selection for fast-developing animals, which would easily be able to complete their life cycle in the given season. Selection could act through reduced probability of encountering a mate. The individuals that develop rapidly at one temperature may also be capable of developing rapidly at other temperatures, including extreme temperatures. During seasons where extreme temperatures prevail the "normal" insects would have delayed development, potentially even past the effective season to complete development, while fast-developing insects would have sufficient time to complete their life cycle and reproduce.

Comparison of normalized data to a physiological time scale for each temperature showed that the cumulative distributions were still statistically different. This contradicts the hypothesis set forth by Curry et al. (1978) that if developmental rates are controlled by enzyme concentrations, a temperature-independent distribution function should exist on a physiological time scale. The above hypothesis was also rejected in 20% of 194 cases of developmental rates in insects examined by Shaffer (1983). Comparisons were made between every possible combination for temperature and embryonic developmental rates, sex and temperature with the larvae, temperature with the pupae, and temperature and humidity with the diapause termination of the second-instar larvae. In all, 77 comparisons were made and in only one case (20°C male larvae versus 20°C female larvae) was the hypothesis that the distributions were similar accepted. Temperature, sex, and humidity affect variability and must be considered when modeling systems or making predictions, if these factors are part of the predictor variables.

Correlations between the day of diapause termination and larval developmental rates were positive (Spearman correlation done separately for the two sexes and three temperatures, 15, 25, and 28°C; $P < 0.05$ in all cases save one where $P = 0.064$). Larvae that terminate diapause later have faster developmental rates than those larvae that terminate diapause earlier.

The rates of larval and pupal development were

Table 6. Developmental times of pupae

Temperature (°C)	Mean developmental time (days)	
	Females	Males
10	27.2 (35)[a]	27.4 (36)
15	20.0 (112)	20.9 (100)
20	7.9 (182)	8.4 (195)
23	7.5 (265)	7.9 (271)
25	6.0 (217)	6.4 (215)
28	5.5 (42)	5.6 (64)
31	5.6 (90)	5.7 (84)

[a] Sample size in parentheses.

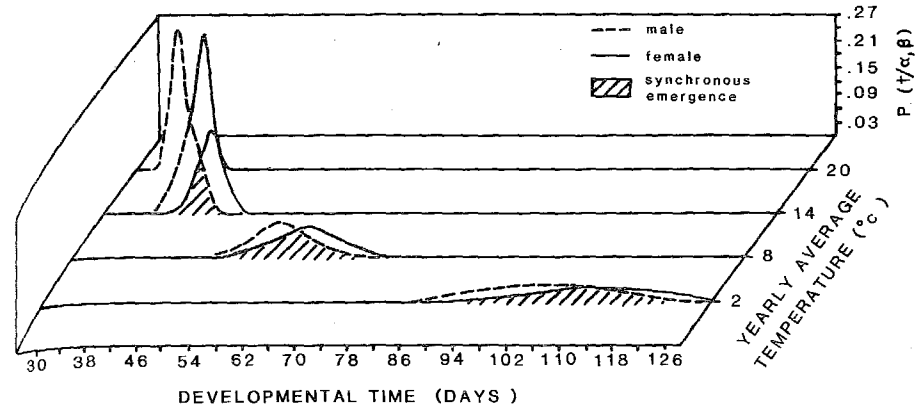

Fig. 3. The probability of emergence and overlap (showing a gamma pdf) for adult female and male WSB moths under different temperature regimes (b_0, average yearly temperature) as predicted in the stochastic simulation model.

not correlated (Spearman correlation; $P > 0.30$ in all cases except for females at 15°C, where $P = 0.011$). A fast developmental rate of larvae did not mean that the pupae would also develop quickly. Female pupae developed slightly faster than did male pupae (though they were not statistically different, Table 6), which is the reverse of the trend for development of the different sexes in the larvae.

Consequently, the trend is toward a synchronization of female/male adult emergence, shown by a positive correlation between the day of diapause termination and larval developmental rate, the fact that male larvae develop faster than do female larvae, and the fact that female pupae develop slightly faster than do male pupae.

The Monte Carlo simulation of WSB developmental times under different temperature regimes showed that as the average yearly temperature (b_0) increased, developmental times and the variances decreased (Fig. 3). An increase in b_0 results in higher temperatures (avg, avg minimum, and avg maximum) during the larval and pupal life stage. The rate of decline in the developmental times and variances was initially rapid as the environmental temperatures rose above those where low-temperature enzyme inactivation occurred (lower nonlinear zone in the developmental rate function; Sharpe and DiMichele 1977). As environmental temperatures entered into the high-temperature enzyme-inactivation zone, the rate of decline in the developmental times and variances decreased (Fig. 3).

The probability of synchronous emergence of adult male and female moths also changed under different temperature regimes. The maximum probability for the usual duration of larval and pupal developmental times in Colorado (McKnight 1967) occurred near a b_0 value of 4 (average minimum/maximum temperatures for larvae were 3.7/19.4°C and pupae were 8.2/23.0°C) where there was a 66% overlap between emergence times of male and female moths (simulation results: male larvae 67.9 ± 7.0 days; female larvae 74.5 ± 7.9 days; pupae 12.7 ± 0.6 days). Synchronous emergence of male and female moths is important since the fecundity of the WSB is greatest when males and females can copulate soon after emergence, and declines as the number of days before copulation increases (Lyon et al. 1972). The probability of synchronous emergence of male and female moths was greater than 60% in temperature regimes with an average minimum/maximum temperature ranging from 2.3/18.1 to 7.9/23.6°C for the larvae and from 6.0/21.0 to 11.4/27.1°C for the pupae. Above these temperatures the probability of synchronous emergence declined to 18.5 when average minimum/maximum temperatures during the larval life stage were 16.4/32.1 and 18.9/34.7°C for the pupae.

The consistently high probability of synchrony between male and female moth emergence, even at very low temperatures, reflects the hardiness of the spruce budworm, where the limiting factor at low temperatures is simply sufficient time to complete development, although fast-developing individuals would still be able to complete development despite low temperatures. Nevertheless, there would still be fewer individuals in the breeding population. Conversely, at high temperatures, the synchrony between adult male and female emergence declines and might result in a decrease in the number of successful matings. Consequently, populations of WSB might decline during seasons where the prevailing temperatures are unusually high because of the low probability of

synchrony between emergence of male and female moths. The population of WSB might also decline rapidly during unusually cool seasons simply because the majority of the animals would not have sufficient time to complete development.

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References Cited

Curry, G., R. Feldman, and K. Smith. 1978. A stochastic model of a temperature dependent population. J. Theor. Pop. Biol. 13: 197–213.

Gagne, J., T. Wagner, P. Pulley, J. Cover, and R. Coulson. 1981. An analysis of estimators of trends in southern pine beetle populations. Environ. Entomol. 10: 31–38.

Greenspan, L. 1977. Humidity fixed points of binary saturated aqueous solutions. J. Res. Natl. Bur. Stand. Sect. A. 81A: 89–96.

Greenwood, A., and D. Durand. 1960. Aids for fitting the gamma distribution by maximum likelihood. Technometrics 2: 55–65.

Johnson, N., and S. Kotz. 1970. Continuous univariate distribution, vol. 1 and 2. Houghton Mifflin, Boston.

Lyon, R., C. Richmond, J. Robertson, and B. Lucas. 1972. Rearing diapause and diapause-free western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae) on an artificial diet. Can. Entomol. 104: 417–426.

McMorran, A. 1965. A synthetic diet for the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Ibid. 97: 58–62.

McKnight, M. 1967. Ecology of the western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae), in Colorado. Ph.D. dissertation, Colorado State University, Fort Collins.

Morris, R. F. [ed]. 1963. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. No. 31: 1–332.

Reichenbach, N., and G. Stairs. 1984. Response of the western spruce budworm to temperature and humidity: developmental rates and survivorship. Environ. Entomol. 13: 611–618.

Shaffer, P. 1983. Prediction of variation in development period of insects and mites at constant temperatures. Ibid. 12: 1012–1019.

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

Sharpe, P., R. Schoolfield, and G. Butler, Jr. 1981. Distribution model of *Heliothis zea* (Lepidoptera: Noctuidae) development times. Can. Entomol. 113: 845–856.

Sharpe, P., G. Curry, D. DiMichele, and C. Cole. 1977. Distribution model of organism development times. J. Theor. Biol. 66: 21–38.

Statistical Analysis System. 1979. SAS Institute, Cary, N.C.

Stinner, R., G. Butler, Jr., J. Bacheler, and C. Tuttle. 1975. Simulation of temperature-dependence in population dynamics models. Can. Entomol. 107: 1167–1174.

Taylor, F. 1981. Ecology and evolution of physiological time in insects. Am. Nat. 117: 1–23.

Wilkes, A. 1942. The influence of selection on the preferendum of a chalcid (*Microplectron fuscipennis* Zett.) and its significance in the biological control of an insect pest. Proc. Soc. London 130: 400–415.

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Function of Cockroach (Orthoptera: Blattidae) Aggregation Behavior

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ABSTRACT Data were gathered to test three hypotheses concerning the function of the aggregation behavior of the German cockroach, *Blattella germanica* (L.). The first is that aggregation serves to ameliorate a harsh environment and promote individual survival. Group and individual rearing experiments demonstrated a possible reduction of survival and growth rates with increased group size, in contrast to the increases suggested in previous literature. Bioassays demonstrated that information concerning the sexual composition of a population is present in residues left by the population and that this information may be exploited by other individuals. This result is consistent with two hypotheses, i.e., that roaches aggregate for purposes of mating, and that they select habitats based on information available from conspecifics. Bioassays also showed that a natural population of roaches, which had been subject to mortality due to control efforts, displayed a stronger aggregation response than did the laboratory strain. This result is consistent with the habitat selection hypothesis.

REPORTS OF AGGREGATION pheromones have appeared frequently in recent insect literature. These substances are defined by their ability to attract individuals of the species producing them regardless of sex or age, a property which has made them attractive for control-oriented research. The German cockroach, *Blattella germanica,* has aggregated to feces and exudations of conspecifics (Ishii and Kuwahara 1968), and it was suggested that a pheromone mediated this response. This result stimulated research on the pheromone's composition, mode of action, specificity, and site of production. Results of these studies indicate that the pheromone is composed of numerous compounds (Persoons and Ritter 1979), that it is perceived by touch and causes individuals that encounter it to stop (Bell et al. 1972, Burk and Bell 1973), that it may attract other species less frequently (Ishii 1970a, Bell et al. 1972), and that glands near the anus are probably responsible for its production (Ishii and Kuwahara 1967, Ishii 1970b). This last study was conducted by determining the fractions of the insect body that produced the strongest results in a bioassay. The glands were assigned this function by default.

Ishii and Kuwahara (1967) and Ishii (1970) imply active communication in their use of the term "pheromone." In the case of an aggregation pheromone, they imply that individuals are providing information to which others respond by aggregating. Otte (1974) pointed out that such a system will evolve only when the results benefit both the presumed signaller and respondent. Demonstrations of pheromone activity often come from responses only, and really only demonstrate that information is present.

Aggregation should occur when individuals attain greater fitness by remaining in a group than they would if they were alone (Alexander 1974). This may occur when the group itself promotes individual survival, when group living increases the frequency with which an individual will mate, or when survivorship is promoted because individuals gather around a local abundance of resources. Ishii and Kuwahara (1967) provided the accepted explanation for the aggregation of the German cockroach, that is, that roaches grow more rapidly in a group due to the group's amelioration of the local environment. Ishii and Kuwahara repeated earlier experiments (von Landowski 1938, Pettit 1940, Willis et al. 1958), which evaluated the effects of individual group rearing on juvenile survival, adult weight, and age of maturity. Juvenile survival and adult weight decreased with increased group size. The conclusion of rapid growth was a misinterpretation of data showing a reduced age of maturity. Von Landowski's (1938) study of *Blatta orientalis* was the most striking. Data were recorded for groups of 1, 2, 4, 8, and 16 individuals. Trends in survival and weight gain seem to exclude the possibility of an ameliorated environment, while age of maturity (age at adult molt) showed unusual responses to increased group size. Male age of maturity plummetted when group size increased from one to two, and remained similar for all groups. Female age of maturity was reduced more gradually with increasing group size.

Another condition favoring aggregation occurs when grouping helps avoid predation (Pulliam

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