Further Statistical Inference Methods for a Stochastic Model of Insect Phenology

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ABSTRACT In 1986, B. Dennis and coworkers formulated a model describing the temperature-dependent and stochastic character of insect development in field populations. This paper presents three additional statistical inference techniques to be used in conjunction with the model. We derive a confidence interval for $p_i(t)$, the proportion of the population in development stage i at time t; confidence intervals for the times at which intermediate stage proportions peak; and a test for detecting outlying observations. Examples of each of these techniques are presented using data from the rangeland grasshopper, *Ageneotettix deorum* (Scudder).

KEY WORDS Insecta, development, phenology, stochastic model

RECENT PHENOLOGY MODELS incorporate temperature-dependent development and inherent stochastic variation (Osawa et al. 1983, Dennis et al. 1986). The model presented by Dennis et al. is useful for describing development in holometabolous and hemimetabolous insects as shown by its applications to western spruce budworm (Kemp et al. 1986) and rangeland grasshoppers (Kemp & Onsager 1986). This approach estimates the proportion of insects in a given development stage as a function of accumulated heat or degree-days (DD). Researchers and pest managers can fit the model to a given data set using a computer program listed in Dennis et al. (1986). Stedinger et al. (1985) extended this modeling approach to incorporate spatial variability.

In this paper, we explain three additional statistical inference procedures based on the Dennis et al. (1986) phenology model: a confidence interval for $p_i(t)$, the proportion of insects in stage i at time t; a confidence interval for the time, t_i^*, at which $p_i(t)$ is maximum; and a test for the deviation of an observation from its expected value under the model for a single stage and time. Implementation of these procedures requires a computer.[3] Examples of each procedure are presented using data from the rangeland grasshopper *Ageneotettix deorum* (Scudder).

Methods

Statistical Inferences in Phenology Modeling. Consider a series of samples of size $n_1, n_2, \ldots, n_q$ taken from an insect population at successive times $t_1, t_2, \ldots, t_q$. If there are r development stages, then the jth sample would consist of the counts $x_{1j}, x_{2j}, \ldots, x_{rj}$, where x_{ij} is the number of sampled insects in development stage i at time t_j, and where $\Sigma_i x_{ij} = n_j$. The counts $x_{1j}, x_{2j}, \ldots, x_{rj}$ can be described as having a multinomial distribution conditional on the sample size n_j. The underlying proportion of the population in each development stage would be expected to change with time as the individual population members develop.

Let $Y(t)$ be the stage of a randomly sampled member of the population at time t; possible values for $Y(t)$ are $\{1, 2, \ldots, r\}$. The phenology models of Dennis et al. (1986) and Osawa et al. (1983) assume that an insect's development is really a continuous stochastic process consisting of accumulated small development increments. However, $Y(t)$ is the fundamental observed random variable because a sampled insect is recorded as having reached a discrete development stage. We define $p_i(t) = Pr[Y(t) = i]$ as the proportion of the population in development stage i at time t, $i = 1, \ldots, r$.

The model of Dennis et al. (1986) takes the proportion $p_i(t)$ to be

$$p_i(t) = \begin{cases} \{1 + \exp[-(a_1 - t)/\sqrt{vt}]\}^{-1}, & i = 1; \\ \{1 + \exp[-(a_i - t)/\sqrt{vt}]\}^{-1} & \\ \quad -\{1 + \exp[-(a_{i-1} - t)/\sqrt{vt}]\}^{-1}, & i = 2, \ldots, r-1; \\ 1 - \{1 + \exp[-(a_{r-1} - t)/\sqrt{vt}]\}^{-1}, & i = r. \end{cases} \quad (1)$$

This expression arises from assuming that an insect's underlying continuous development level, denoted by $X(t)$, has a logistic probability distribution with mean t and variance $(=\pi^2 vt/3)$ proportional to t. Then $Pr[Y(t) \leq i] = Pr[X(t) \leq a_i]$ is the cumulative distribution function of a logistic distribution:

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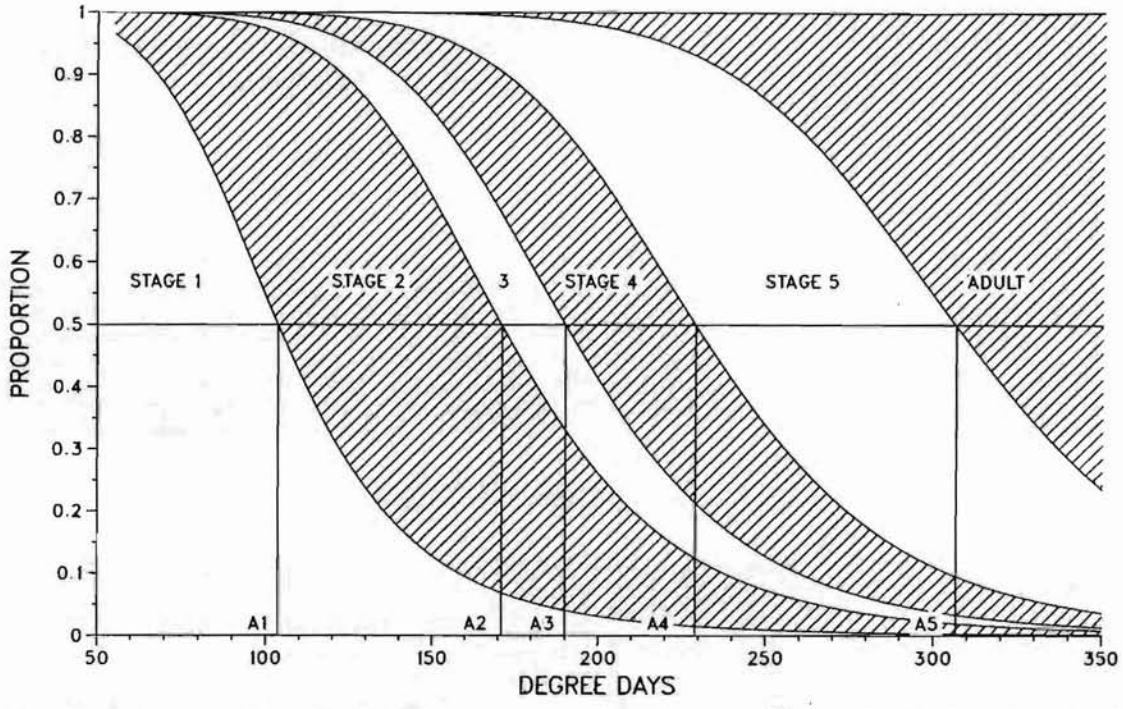

Fig. 1. Logistic cumulative distribution function, $1/\{1 + \exp[-(a_i - t)/\sqrt{vt}]\}$ (y axis), plotted as a function of t (DD: x axis), for values of a_1, a_2, a_3, a_4, and a_5 (and v) listed in Table 1. The vertical width of each region represents the proportion of insects in that stage at that time ($p_i(t)$).

$$Pr[Y(t) \leq i] = \begin{cases} 0, i = 0\ (a_0 \equiv -\infty); \\ \{1 + \exp[-(a_i - t)/\sqrt{vt}]\}^{-1}, \\ \qquad i = 1, \ldots, r-1; \\ 1, i = r\ (a_r \equiv +\infty). \end{cases} \quad (2)$$

The proportion $p_i(t)$ is obtained from Equation 2 as $Pr[Y(t) \leq i] - Pr[Y(t) \leq i - 1]$. The quantity a_i, $i = 1, \ldots, r-1$ can be interpreted as the time t at which half of the population is in stage i or below: $Pr[Y(a_i) \leq i] = Pr[Y(a_i) > i] = \frac{1}{2}$ (Fig. 1). The quantity v is a measure of the variability of development rates among insects in the population. In applications, t is usually measured in degree-days.

If there are r development stages, then the model has r unknown parameters. The unknown parameters can be written as a column vector, θ:

$$\theta = [a_1, a_2, \ldots, a_{r-1}, v]'. \quad (3)$$

Also, the proportions $p_i(t)$ defined in Equation 1 can be written as $p_i(t; \theta)$ to emphasize their dependence on θ.

These parameters can be estimated from data using the maximum likelihood (ML) method. Nonlinear regression packages can be used to perform the ML calculations as explained by Dennis et al. (1986). The resulting vector of parameter estimates, denoted by

$$\hat{\theta} = [\hat{a}_1, \hat{a}_2, \ldots, \hat{a}_{r-1}, \hat{v}]', \quad (4)$$

has a large-sample multivariate normal distribution. Specifically,

$$\hat{\theta} \xrightarrow{d} \text{multivariate normal}(\theta, \Sigma(\theta)), \quad (5)$$

in which $\xrightarrow{d}$ denotes convergence in distribution as sample size becomes large, and $\Sigma(\theta)$ is an $r \times r$ variance–covariance matrix with elements that are functions of θ (Bishop et al. 1975). The form of $\Sigma(\theta)$, as well as how to construct the ML estimate $\Sigma(\hat{\theta})$ from nonlinear regression computer output, is described by Dennis et al. (1986) and in the Appendix of this paper.

Various statistical inferences regarding functions of the parameters θ of the phenology model (Equation 1) can be derived from Equation 5 with the δ method (Bishop et al. 1975). The δ method, as used in this paper, consists of the following large-sample result. Let $g(\theta)$ be a real-valued function that is differentiable with respect to each parameter in θ. Then Equation 5 implies that

$$g(\hat{\theta}) \xrightarrow{d} \text{normal}\ (g(\theta), \beta(\theta)'\Sigma(\theta)\beta(\theta)), \quad (6)$$

where $\beta(\theta)$ is the $r \times 1$ vector of partial derivatives:

$$\beta(\theta) = [\partial g/\partial a_1, \ldots, \partial g/\partial a_{r-1}, \partial g/\partial v]'. \quad (7)$$

A large-sample, $100(1 - \alpha)\%$, confidence interval for $g(\theta)$ is constructed from Equation 6 by substituting the ML estimate $\hat{\theta}$ for θ in $g(\theta)$, $\beta(\theta)$, and $\Sigma(\theta)$:

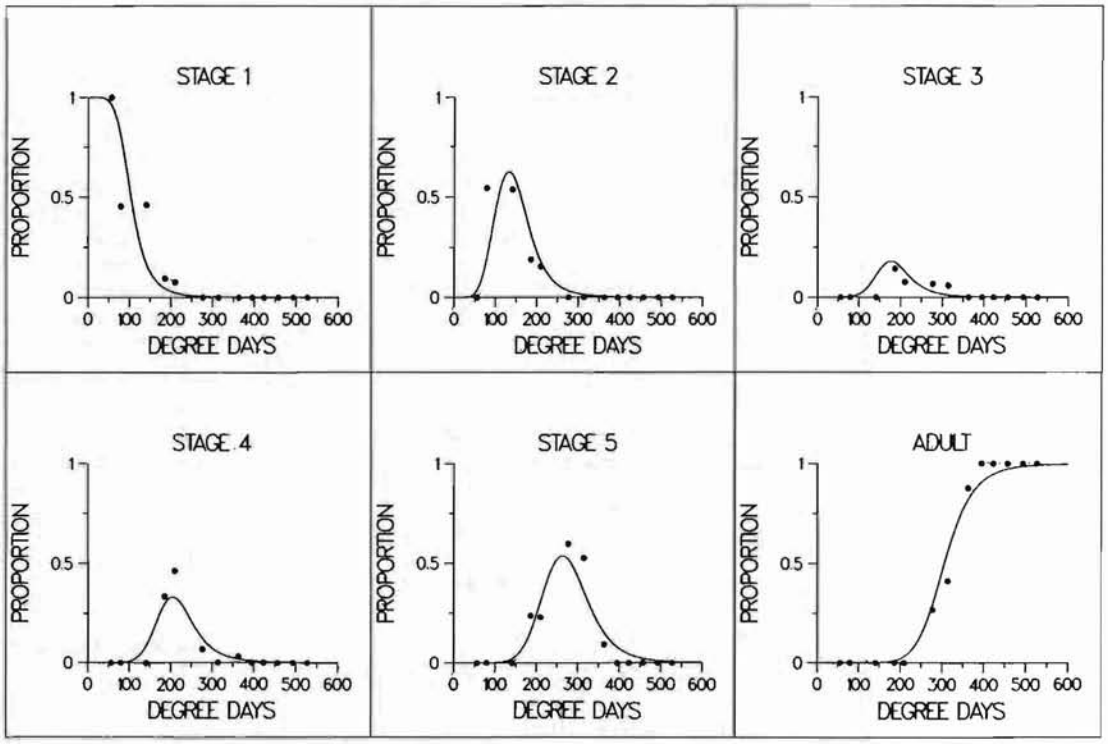

Fig. 2. Comparison of raw data (plotted points) and model results (solid line) for the proportion (y axis) of the *Ageneotettix deorum* (Scudder) population in each stage as a function of accumulated degree days (x axis); Roundup, Mont., 1975.

$$g(\hat{\theta}) \pm z_{\alpha/2}\sqrt{\beta(\hat{\theta})'\Sigma(\hat{\theta})\beta(\hat{\theta})}. \quad (8)$$

Here, $z_{\alpha/2}$ is the $100(1 - \alpha/2)$th percentile of the standard normal distribution (e.g., $z_{0.025} \cong 1.96$). The sample sizes in field phenology studies are typically very large (upper hundreds or more). The inferences obtained by means of the δ method are thus likely to be good approximations, provided the phenology model coupled with the multinomial sampling model adequately describes the system. For large study regions with spatially heterogeneous development rates, investigators should use the spatial extensions of Stedinger et al. (1985).

A Confidence Interval for $p_i(t)$. The ML estimate $\hat{p}_i(t)$ of the proportion $p_i(t)$ of the population in stage i at time t is obtained by evaluating Equation 1 with the ML parameter estimates $\hat{a}_1, \ldots, \hat{a}_{r-1}, \hat{v}$:

$$\hat{p}_i(t) = p_i(t; \hat{\theta}),\ i = 1, \ldots, r. \quad (9)$$

Thus, $\hat{p}_i(t)$ is a function of the ML parameter estimates, and the δ method can be used to find its large-sample distribution. Note, however, that if $i = 2, \ldots, r - 1$, then $\hat{p}_i(t)$ is a function of just three of the parameter estimates in $\hat{\theta}$, namely $\hat{a}_{i-1}$, $\hat{a}_i$, and $\hat{v}$. Also, note that $\hat{p}_1(t)$ and $\hat{p}_r(t)$ are each functions of just two unknown parameters. Define a column vector, $\hat{\theta}_i$, containing the estimated parameters in $\hat{p}_i(t)$:

$$\hat{\theta}_i = \begin{cases} [\hat{a}_1, \hat{v}]', & i = 1; \\ [\hat{a}_{i-1}, \hat{a}_i, \hat{v}]', & i = 2, \ldots, r-1; \\ [\hat{a}_{r-1}, \hat{v}]', & i = r. \end{cases} \quad (10)$$

Because $\hat{\theta}_i$ is formed from a subcollection of elements from $\hat{\theta}$, it also has a large sample multivariate normal distribution. Specifically, let $S(\theta_i)$ be the 3×3 (or 2×2) matrix formed by deleting from $\Sigma(\theta)$ all the rows and columns except those corresponding to the parameter estimates in $\hat{\theta}_i$. Then

$$\hat{\theta}_i \xrightarrow{d} \text{multivariate normal}(\theta_i, S(\theta_i)). \quad (11)$$

Because $\hat{p}_i(t) \equiv g(\hat{\theta}_i)$, Equations 6, 7, and 8 provide the desired confidence interval for $p_i(t)$. The following partial derivatives are required:

$$\partial p_i/\partial a_{i-1} = \begin{cases} -\exp[-(a_{i-1} - t)/\sqrt{vt}\,](\sqrt{vt}\,)^{-1} \\ \quad \cdot\{1 + \exp[-(a_{i-1} - t)/\sqrt{vt}\,]\}^{-2}, \\ \quad i = 2, \ldots, r-1; \\ \exp[(a_{r-1} - t)/\sqrt{vt}\,](\sqrt{vt}\,)^{-1} \\ \quad \cdot\{1 + \exp[(a_{r-1} - t)/\sqrt{vt}\,)]^{-2}\}, \\ \quad i = r. \end{cases} \quad (12a)$$

$$\partial p_i/\partial a_i = \begin{cases} \exp[-(a_i - t)/\sqrt{vt}\,](\sqrt{vt}\,)^{-1} \\ \quad \cdot\{1 + \exp[-(a_i - t)/\sqrt{vt}\,]\}^{-2}, \\ \quad i = 1, \ldots, r-1; \end{cases} \quad (12b)$$

$$\partial p_i/\partial v = \begin{cases} -\exp[-(a_1 - t)/\sqrt{vt}] \\ \quad \cdot (a_1 - t)(2v\sqrt{vt})^{-1} \\ \quad \cdot \{1 + \exp[-(a_1 - t)/\sqrt{vt}]\}^{-2}, \\ \quad i = 1; \\ -(a_i - t)\exp[-(a_i - t)/\sqrt{vt}] \\ \cdot (2v\sqrt{vt})^{-1} \\ \quad \cdot \{1 + \exp[-(a_i - t)/\sqrt{vt}]\}^{-2} \\ \quad + (a_{i-1} - t) \\ \quad \cdot \exp[-(a_{i-1} - t)/\sqrt{vt}](2v\sqrt{vt})^{-1} \\ \quad \cdot \{1 + \exp[-(a_{i-1} - t)/\sqrt{vt}]\}^{-2}, \\ \quad i = 2, \ldots, r - 1; \\ \exp[-(a_{r-1} - t)/\sqrt{vt}] \\ \quad \cdot (a_{r-1} - t)(2v\sqrt{vt})^{-1} \\ \quad \cdot \{1 + \exp[-(a_{r-1} - t)/\sqrt{vt}]\}^{-2}, \\ \quad i = r. \end{cases} \quad (12c)$$

The partial derivatives are collected into the column vector $\beta(\theta_i)$ as follows:

$$\beta(\theta_i) = \begin{cases} [\partial p_1/\partial a_1, \partial p_1/\partial v]', \ i = 1; \\ [\partial p_i/\partial a_{i-1}, \partial p_i/\partial a_i, \partial p_i/\partial v]', \\ \quad i = 2, \ldots, r - 1; \\ [\partial p_r/\partial a_{r-1}, \partial p_r/\partial v]', \ i = r. \end{cases} \quad (13)$$

From Equation 6, we have

$$\hat{p}_i(t) \xrightarrow{d} \text{normal } (p_i(t), \beta(\theta_i)'S(\theta_i)\beta(\theta_i)). \quad (14)$$

The large-sample, $100(1 - \alpha)\%$, confidence interval for $p_i(t)$ follows from Equation 8:

$$\hat{p}_i(t) \pm z_{\alpha/2}\sqrt{\beta(\hat{\theta}_i)'S(\hat{\theta}_i)\beta(\hat{\theta}_i)}. \quad (15)$$

A Confidence Interval for the Peak Time of $p_i(t)$. For development stages $i = 2, \ldots, r - 1$, $p_i(t)$ considered as a function of time increases to a maximum value and then declines (see Fig. 2). The "peak time" is that value of t, say t_i^*, which maximizes $p_i(t)$. The value is found by differentiating $p_i(t)$ wth respect to t and equating to zero:

$$dp_i(t)/dt \,|\, t_i^* = 0. \quad (16)$$

This equation for t_i^* is in the form $h(t_i^*, a_{i-1}, a_i, v) = 0$, where

$$\begin{aligned} &h(t_i^*, a_{i-1}, a_i, v) \\ &= -[(a_i/t_i^*) + 1]\exp[-(a_i - t_i^*)/\sqrt{vt_i^*}] \\ &\quad \cdot \{1 + \exp[-(a_i - t_i^*)/\sqrt{vt_i^*}]\}^{-2} \\ &\quad + [(a_{i-1}/t_i^*) + 1]\exp[-(a_{i-1} - t_i^*)/\sqrt{vt_i^*}] \\ &\quad \cdot \{1 + \exp[-(a_{i-1} - t_i^*)/\sqrt{vt_i^*}]\}^{-2}. \end{aligned} \quad (17)$$

Equation 16 does not have an algebraic solution for t_i^*. However, the implicit function theorem guarantees that t_i^* is defined as a differentiable function, say g, of a_{i-1}, a_i, and v (Rudin 1964, 195); that is,

$$t_i^* = g(a_{i-1}, a_i, v) = g(\theta_i). \quad (18)$$

Thus, once the ML estimate $\hat{t}_i^* = g(\hat{\theta}_i)$ is obtained, the δ method will provide the large-sample distribution for $\hat{t}_i^*$ and the large-sample confidence interval for t_i^*.

Numerical algorithms such as the secant method, false position method, or Newton's method can be used to solve Equation 16 for the ML estimate of t_i^*. The computations require a subroutine to evaluate $h(t_i^*, \hat{a}_{i-1}, \hat{a}_i, \hat{v})$ for the various values of t_i^*, an initial guess of the value of $\hat{t}_i^*$ (found by looking at a graph of $\hat{p}_i(t)$), and the ML estimates $\hat{a}_{i-1}$, $\hat{a}_i$, and $\hat{v}$. Newton's method additionally would require evaluating the partial derivative of $h(t_i^*, \hat{a}_{i-1}, \hat{a}_i, \hat{v})$ with respect to t_i^*. The derivative could be obtained analytically from Equation 17 or computed numerically. The programming of these algorithms is straightforward; details (and programs) are given by Press et al. (1986).

The partial derivatives of $t_i^* = g(\theta_i)$ (Equation 18) with respect to the parameters are needed to use the δ method (see Equation 6). These derivatives are found using the chain rule for implicit functions:

$$\begin{aligned} \partial g/\partial a_{i-1} &= -(\partial h/\partial a_{i-1})/(\partial h/\partial t_i^*); \\ \partial g/\partial a_i &= -(\partial h/\partial a_i)/(\partial h/\partial t_i^*); \\ \partial g/\partial v &= -(\partial h/\partial v)/(\partial h/\partial t_i^*). \end{aligned} \quad (19)$$

The vector $\beta(\theta_i)$ becomes

$$\beta(\theta_i) = [\partial g/\partial a_{i-1}, \partial g/\partial a_i, \partial g/\partial v]'. \quad (20)$$

The large-sample normal distribution of $\hat{t}_i^*$ is then

$$\hat{t}_i^* \xrightarrow{d} \text{normal } (t^*, \beta(\theta_i)'S(\theta_i)\beta(\theta_i)), \quad (21)$$

and the $100(1 - \alpha)\%$ confidence interval is

$$\hat{t}_i^* \pm z_{\alpha/2}\sqrt{\beta(\hat{\theta}_i)'S(\hat{\theta}_i)\beta(\hat{\theta}_i)}. \quad (22)$$

It is probably easiest to compute $\beta(\hat{\theta}_i)$ using numerical derivatives for the expressions in Equation 19, although an industrious investigator could instead obtain the derivatives analytically from Equation 17.

A Test for the Deviation from the Model of an Observation in a Single Cell. A test for significant deviation in a single cell is useful for detecting counts that are not described well by the phenology model. Although the model often gives an excellent description of the overall pattern of development in a population, there are occasional outlier cells.

A generalized residual can be defined for the phenology model as

$$\hat{w}_{ij} = (x_{ij} - n_j\hat{p}_{ij})/\sqrt{n_j\hat{p}_{ij}}, \quad (23)$$

where

$$\hat{p}_{ij} = \hat{p}_i(t_j) \quad (24)$$

is computed from Equation 9. Note that $\Sigma\Sigma\ \hat{w}_{ij}^2$ is the Pearson statistic for testing overall goodness of fit as described by Dennis et al. (1986). Using the δ method and equation 6b3.2 in Rao (1973), it can be shown that

$$\hat{w}_{ij} \xrightarrow{d} \text{normal } (0, b_j(\theta_i)) \quad (25)$$

as the jth sample size n_j becomes large, under the null hypothesis that the model fits the i, jth cell.

Table 1. Parameter estimates for *Ageneotettix deorum* from Kemp & Onsager (1986) together with estimated variance–covariance matrix generated through procedures outlined in Appendix

	a_1	a_2	a_3	a_4	a_5	ν
	103.6	170.8	190.0	229.0	306.5	3.90
a_1	50.03	8.92	1.82	−18.21	1.09	−1.52
a_2	8.92	57.12	40.94	25.92	0.70	−0.53
a_3	1.82	40.94	61.67	28.14	6.89	−0.55
a_4	−18.21	25.92	28.14	47.77	21.77	−0.86
a_5	1.09	0.70	6.89	21.77	71.32	0.06
ν	−1.52	−0.53	−0.55	−0.86	0.06	0.58

Here

$$b_j(\theta_i) = 1 - p_i(t_j) - [(n_j/p_i(t_j))\beta(\theta_i)'S(\theta_i)\beta(\theta_i)], \quad (26)$$

with $\beta(\theta_i)$ and $S(\theta_i)$ defined as in Equation 14. This variance $b_j(\theta_i)$ is estimated using the ML parameter estimates:

$$b_j(\hat{\theta}_i) = 1 - \hat{p}_{ij} - [(n_j/\hat{p}_{ij})\beta(\hat{\theta}_i)'S(\hat{\theta}_i)\beta(\hat{\theta}_i)]. \quad (27)$$

The test statistic Z is computed as

$$Z = \hat{w}_{ij}/\sqrt{b_j(\hat{\theta}_i)}. \quad (28)$$

Under the null hypothesis that the model successfully describes x_{ij},

$$Z \xrightarrow{d} \text{normal}(0, 1). \quad (29)$$

Reject the null hypothesis at level α if $|Z| > z_{\alpha/2}$, or (more informative) compute a p value as the probability that a normal(0, 1) random variable would be more extreme than the observed value of Z.

If multiple cells are tested at significance level α, then the experiment-wise Type I error is not controlled at level α. One solution to this problem is to test each cell at a more conservative level. A Bonferroni approach, for instance, would use a level of α/m for each test, where m is the number of tests being conducted. However, such tests would not be very powerful if many cells were being screened. As an alternative, we suggest that individual cells be tested each at level α or be screened for low p values, but that such analysis be performed only after a significant overall goodness-of-fit test (such as the test based on the Pearson statistic) is obtained at level α. Evidence from both parametric (Carmer & Swanson 1973) and nonparametric (Lin & Haseman 1978) multiple-comparison simulations suggests that multiple 1 degree-of-freedom tests give reasonable experiment-wise Type I error control if protected by an omnibus test.

We point out that the normal approximation (Equation 29) depends on the jth sample size, n_j, being large. Also, the omnibus Pearson χ^2 test depends on having adequate expected frequencies in most cells (the often-stated rule of thumb is no more than 20% of cells with expected frequency $n_j p_i(t_j)$ less than 5). Typical field data sets, however, are sparse; although the total number of insects caught is usually large, the bulk of the cells have zero counts and very small expected values under the model (Fig. 2). Even under such circumstances,

Table 3. Z-statistic values for testing model lack of fit to second-instar nymphs in Fig. 2

Julian date	Accumulated DD (17.8°C, base)	Total grasshoppers (all stages)	No. second instar collected	No. second instar expected	Z
176	56	6	0	$<10^{-5}$	0.51
183	79	11	6	1.15	3.71[a]
192	141	13	7	4.29	0.65
199	186	21	4	1.27	1.61
203	210	13	2	0.36	0.26
210	277	15	0	$<10^{-5}$	0.74
217	314	17	0	$<10^{-5}$	0.50
224	363	32	0	$<10^{-5}$	0.41
233	395	15	0	$<10^{-5}$	0.20
239	423	28	0	$<10^{-5}$	0.22
246	451	11	0	$<10^{-5}$	0.11
253	493	9	0	$<10^{-5}$	0.07
260	527	4	0	$<10^{-5}$	0.03

[a] Model does not fit this cell ($P < 0.01$).

Table 2. 95% confidence intervals for proportions, $p_i(t)$, of grasshoppers in a particular stage, and for peak times, t_i*, using parameters and variance–covariance matrix from Table 1

Development stage (peak time 95% CI)	DD (17.8°C, base)						
	50	100	150	200	250	300	350
Instar 1	0.98 ± 0.03	0.55 ± 0.18	0.13 ± 0.07	0.03 ± 0.02	0.01 ± 0.01	0.00	0.00
Instar 2 (132.7 ± 11.4)	0.02 ± 0.02	0.43 ± 0.17	0.57 ± 0.15	0.23 ± 0.10	0.06 ± 0.04	0.02 ± 0.01	0.01 ± 0.01
Instar 3 (176.5 ± 14.1)	0.00	0.02 ± 0.02	0.14 ± 0.09	0.15 ± 0.10	0.05 ± 0.04	0.02 ± 0.01	0.01 ± 0.01
Instar 4 (205.5 ± 12.9)		0.01 ± 0.01	0.12 ± 0.08	0.33 ± 0.13	0.21 ± 0.09	0.07 ± 0.04	0.02 ± 0.01
Instar 5 (263.4 ± 12.7)	0.00	0.00	0.04 ± 0.03	0.24 ± 0.10	0.52 ± 0.11	0.44 ± 0.12	0.20 ± 0.08
Adult	0.00	0.00	0.00	0.02 ± 0.02	0.14 ± 0.08	0.45 ± 0.12	0.76 ± 0.09

some studies have suggested that the χ^2 approximation for the Pearson statistic can remain reasonable (Larntz 1978, Koehler & Larntz 1980). The situation for the individual cell tests is more unclear. We cannot at present offer any guidelines as to how large n_j and $p_i(t_j)$ should be to insure the adequacy of the normal approximation (Equation 29). Consequently, we stress that the main purpose of the cell-by-cell analysis should not be strict hypothesis testing. Rather, the purpose should be to determine in a general way how many and which cells are discrepant.

Results and Discussion

Table 1 contains the phenology model parameter estimates computed by Kemp & Onsager (1986) for the rangeland grasshopper *A. deorum*. Also in Table 1 is the parameter variance–covariance matrix that can be generated from the output of the SAS program in Dennis et al. (1986), using the method described in the Appendix of this paper. The information in this table is needed for computing the confidence intervals and tests described in this paper.

The information can be used to estimate the proportion and associated confidence interval of insects in a particular stage, given that t DD have accumulated. Table 2 gives the results of calculating Equation 15 using the parameters and variance–covariance matrix listed in Table 1, with $\alpha = 0.05$. Note that the proportions given by Equation 1 always sum to unity at a given time t, as depicted in Fig. 1. Slight deviations from this in Table 2 result from rounding.

The times of the peak occurrences of development stage proportions may be of interest. Such peak times can be important for conducting efficient sampling or control strategies. For instance, it is suggested that density samples of rangeland grasshoppers be collected at the peak of the third instar to provide maximum management flexibility (Onsager 1987). The information in Table 1 and Equation 22 have been used to estimate the peak times of second to fifth instars of *A. deorum* (Table 2). The optimal density sampling period (i.e., the peak of third-instar proportions) is estimated at 176.5 ± 14.1 DD. If control were warranted, applications should be made near the peak time of the fourth instar for carbaryl and the peak time of the fifth instar for malathion (Onsager 1987). We emphasize that the peak times are those at which proportions, not absolute densities, are maximum. The data represent sweep-net samples with varying sampling efforts and are therefore unsuitable for estimating absolute densities.

The Pearson χ^2 goodness-of-fit test is significant for the grasshopper data in Fig. 2, even though the model appears to describe the data well graphically. In such cases, it is helpful to determine which cells (instar and date) were the outliers. The statistical test for an ill-fitted cell incorporates the information in Table 1 into the test statistic (Equation 28). As an example, Table 3 shows the specific cell for second-instar *A. deorum* (Fig. 2) that is not fit well by the model.

In conclusion, three additional statistical inference techniques have been developed to expand the utility of the Dennis et al. (1986) insect phenology model. These techniques should assist in sampling and control of insect pests.

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Appendix

The following is a matrix procedure for obtaining the estimated variance–covariance matrix from output of the SAS program, listed in Dennis et al. (1986), for computing parameter estimates in the insect phenology model.

Let $\hat{\theta}$ be a column vector of the ML parameter estimates produced by the SAS program:

$$\hat{\theta} = [\hat{a}_1, \hat{a}_2, \ldots, \hat{a}_{r-1}, \hat{v}]'.$$

Next, let $\hat{D}$ be a diagonal matrix ($r \times r$) of the asymptotic standard deviations of the parameter estimates from the output of the SAS program:

$$\hat{D} = \begin{bmatrix} \hat{\sigma}_1 & & & \\ & \hat{\sigma}_2 & \cdots & \\ & & & \hat{\sigma}_{r-1} \\ & & & & \hat{\eta} \end{bmatrix}$$

Finally, let $\hat{R}$ be the parameter correlation matrix from the output of the SAS program.

The estimated variance–covariance matrix $\Sigma(\hat{\theta})$ used in Equation 8 and throughout this paper may be found as follows:

$$\Sigma(\hat{\theta}) = \hat{D}\hat{R}\hat{D}.$$

The estimated variance–covariance matrix $S(\hat{\theta}_i)$ used in Equation 15 and throughout this paper is obtained from $\Sigma(\hat{\theta})$ by deleting all rows and columns except those corresponding to the parameters in $\hat{\theta}_i$ (see Equation 10).

As described in Dennis et al. (1986), the ML parameter estimates and the associated standard deviations and correlations can be computed with other nonlinear regression packages such as AR of BMDP.

ERRATUM

Equation 12a should read:

$$\frac{\partial p_i}{\partial a_{i-1}} = \begin{cases} -exp\left(\frac{-(a_{i-1}-t)}{\sqrt{vt}}\right)(\sqrt{vt})^{-1}\left\{1 + exp\left(\frac{-(a_{i-1}-t)}{\sqrt{vt}}\right)\right\}^{-2}, & i = 2, \ldots, r-1; \\ -exp\left(\frac{-(a_{r-1}-t)}{\sqrt{vt}}\right)(\sqrt{vt})^{-1}\left\{1 + exp\left(\frac{-(a_{r-1}-t)}{\sqrt{vt}}\right)\right\}^{-2}, & i = r. \end{cases} \tag{12a}$$