Stochastic Model of Insect Phenology: Estimation and Testing

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Environ. Entomol. 15: 540–546 (1986)

ABSTRACT A biologically based phenology model is described for use in integrated pest management. The model predicts the proportion of insects in a population in various stages of development as a stochastic function of accumulated degree-days. The model is based on a logistic probability distribution with mean and variance changing through time. Maximum likelihood parameters of the estimates are easily computed with nonlinear regression packages. Appropriate statistical tests are presented for comparing models. Results should be useful to researchers and biological modelers who describe insect or plant phenology.

PREDICTING THE OCCURRENCE of developmental stages is important to insect population modeling. Because economic damage is often heaviest during a certain stage, forest or agricultural losses can be better predicted when the onset of that stage is known. Factors regulating population size, such as predation, food limitation, and weather, affect developmental stages differently. An insect population can also respond differently to pest control methods applied to different stages of the population's life cycle.

Information on developing field populations is often variable. A sample may contain insects in several developmental stages, and the relative proportions of each stage may change when new samples are drawn. Predicting variability through time is an important component of modeling because it allows calculation of the economic risk associated with various developmental stages.

Incorporating variability into insect population models is crucial but difficult. The stochastic variation should be included in a way that has biological meaning. Unfortunately, adding stochastic effects rapidly increases the complexity of the model, making it harder to use. Methods for estimating parameters and testing the model must be clear and easy to perform for the model to be practical. Stochastic modeling is often misunderstood; investigators build expensive models containing stochastic information but discard it and in the end concentrate on the mean behavior of the system. Also, modelers sometimes use probability distributions only as convenient and flexible curves (devoid of any probabilistic content) to be directly fit to data sets.

Osawa et al. (1983) recently presented a stochastic model for describing vegetative bud development in balsam fir, *Abies balsamea* (L.) Mill. We believe their approach, with the modifications described here, could be widely applied to insect phenology. Their approach can be used to predict the proportions of an insect cohort in various developmental stages as a function of accumulated degree-days (DD).

This paper describes some improvements and extensions to the bud phenology model of Osawa et al. (1983), and adapts the model for use in entomology. First, we describe the model and show how changing the original underlying probability distribution simplifies computation. Then we describe how to obtain estimates of the model parameters for a given data set on insect development. We show how maximum likelihood estimates of the parameters are easily computed using nonlinear regression packages. Finally, we present methods for conducting formal statistical hypothesis tests about the model. An appendix contains an example of a computer program for obtaining the parameter estimates, using the Statistical Analysis System (SAS; SAS Institute 1982). The program includes a data set on the development of a population of western spruce budworm (*Choristoneura occidentalis* Freeman). This paper primarily documents for entomologists the use of the model and the associated statistical inferences.

Model Description

The model assumes that the development of a given insect is a stochastic process consisting of accumulated small increments of development time. The process $S(t)$ is defined as the amount of development time an insect has accumulated by actual time t. $S(t)$ and t should be measured in DD, as indicated by results with the western spruce budworm and with balsam fir buds (Osawa et al. 1983). The process is assumed to begin with the insect in a given life stage (i.e., egg or instar) at time $t = 0$.

As the amount of development $S(t)$ increases, the insect passes through successive stages, with the stages delimited by molts. Let a_i = amount of

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development in DD necessary for the insect to undergo the ith molt. The a_i values, $i = 1, \ldots, r - 1$, are signposts separating r stages:

stage 1:	$S(t) \leq a_1$
stage 2:	$a_1 < S(t) \leq a_2$
⋮	⋮
stage $r - 1$:	$a_{r-2} < S(t) \leq a_{r-1}$
stage r:	$a_{r-1} < S(t)$.

For the western spruce budworm data used in this paper (see *Appendix*), $r = 7$, representing five instars, pupa, and adult. The a_i values are typically unknown parameters and must be estimated from the data.

The heart of the model is a probability distribution for $S(t)$ that changes as t increases. One form, suggested by Osawa et al. (1983), is a normal distribution for $S(t)$ with a mean of t and a variance of $\sigma^2 t$, where σ^2 is a positive constant. This distribution results in the limit if development $S(t)$ up to time t is the cumulative sum of many small developmental increments. The distribution is identical to that of Brownian motion with drift, in which $S(t)$ would be the position of a particle suspended in a liquid moving at a speed of one unit distance per unit time (Karlin & Taylor 1975). Strictly speaking, the Brownian motion process allows $S(t)$ to decline from time to time, which clearly does not occur for accumulated insect development. We emphasize that the normal distribution is a limiting approximation to an insect's true development.

The random variable $S(t)$ under the above normality assumption would have a probability density function (PDF) with a mean and variance proportional to time:

$$f(s, t) = (\sigma^2 t 2\pi)^{-1/2} \exp[-(s - t)^2/(2\sigma^2 t)]. \quad (1)$$

Then the probability that an insect's development at time t has not exceeded s is the cumulative area under the PDF between $-\infty$ and s:

$$Pr[S(t) \leq s] = \int_{-\infty}^{s} f(u, t)\, du = \Phi\left(\frac{s - t}{\sqrt{\sigma^2 t}}\right). \quad (2)$$

Here, $\Phi(z)$ is the cumulative area under a standard normal curve between $-\infty$ and z.

An alternative probability distribution is easier to compute and gives predictions almost identical to the normal. It is the logistic distribution, with a PDF given by:

$$f(s, t) = \exp\left(\frac{s - t}{\sqrt{b^2 t}}\right) \Bigg/ \left\{\sqrt{b^2 t}\left[1 + \exp\left(\frac{s - t}{\sqrt{b^2 t}}\right)\right]^2\right\}. \quad (3)$$

Here, b^2 is a positive constant. This distribution has a mean of t and a variance of $(\pi^2/3)b^2 t$ (Fig. 1). Computing is easier because the cumulative area under the PDF curve is a relatively simple function of s:

$$Pr[S(t) \leq s] = \int_{-\infty}^{s} f(u, t)\, du = 1 \Big/ \left\{1 + \exp\left[-\left(\frac{s - t}{\sqrt{b^2 t}}\right)\right]\right\}. \quad (4)$$

The normal integral (2), by contrast, has no simple form and must be evaluated through numerical integration or other methods.

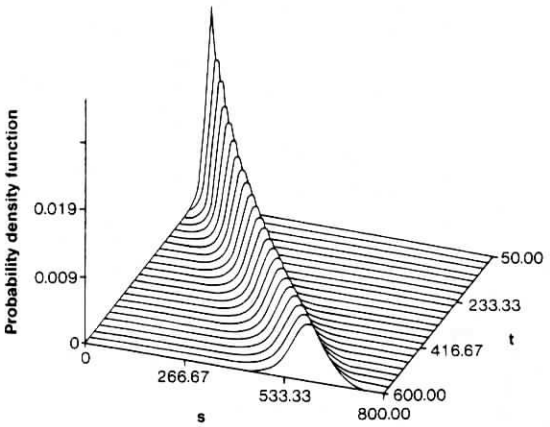

Fig. 1. Logistic PDF (3) plotted for increasing values of t. Mean and variance of the distribution increase linearly with t.

Our experience using the normal and logistic models to describe budworm data indicates that the differences between the two models are slight. The PDF curves 1 and 3 are similarly shaped, with the logistic having slightly larger kurtosis (sharper peak and heavier tails). Indeed, the two models are used interchangeably in dose/response studies for probit analysis (normal) and logit analysis (logistic) (see Bishop et al. 1975). Although Osawa et al. (1983) originally proposed the normal model of phenology, we adopt the logistic model in this paper because it is easier to use for analyzing data sets.

At any fixed time t, the a_i values divide the PDF into r parts (Fig. 2). The area under the curve between a_{i-1} and a_i gives the probability that an insect will be in stage i at time t. As t increases, the PDF moves through the a_i values, and the insect is more likely to be found in an advanced stage of development. Information for estimating the a_i values and the value of b^2 can be obtained by taking field samples of such an insect population at several fixed times. The expected frequencies of the various stages in the population can then be computed and plotted through time (Fig. 3).

Several factors affecting insect phenology are not explicitly included in the model. First, the

model does not have terms for mortality differences among various stages. Second, the model does not incorporate heterogeneity in development rates among individual insects. Finally, the model does not have distributed initial conditions for representing populations not entirely in stage 1 at $t = 0$. The model was developed, however, for describing a given type of data set commonly collected in the field. Results with the western spruce budworm (Kemp et al. 1986) suggest the model has enough parameters to account implicitly for much of the variability in such data resulting from these factors.

Parameter Estimation

Data for this model consist of samples of insects taken from a population at fixed times $t_1, t_2, \ldots, t_q$. The population is assumed to be a cohort of insects in their initial stage of development at time $t = 0$. At each time t_j, the number of insects in stage i, denoted x_{ij}, is recorded. The sample size at time t_j is then $x_{1j} + x_{2j} + \ldots + x_{rj} = n_j$. The population is considered to be an ensemble of insects developing according to the stochastic process $S(t)$. The values $x_{1j}, x_{2j}, \ldots, x_{rj}$ are then assumed to be a random sample from a multinomial distribution. The multinomial probabilities $p_{1j}, p_{2j}, \ldots, p_{rj}$ are found using the logistic curve 3:

$$\begin{aligned} p_{ij} &= Pr[a_{i-1} < S(t_j) \leq a_i] \\ &= \int_{a_{i-1}}^{a_i} f(u, t_j)\, du \\ &= 1/\left\{1 + \exp\left[-\left(\frac{a_i - t_j}{\sqrt{b^2 t_j}}\right)\right]\right\} \\ &\quad - 1/\left\{1 + \exp\left[-\left(\frac{a_{i-1} - t_j}{\sqrt{b^2 t_j}}\right)\right]\right\}. \end{aligned} \tag{5}$$

For completeness, a_0 and a_r are defined to be $-\infty$ and $+\infty$, respectively, so that $p_{1j} + p_{2j} + \ldots + p_{rj} = 1$.

This model has r unknown parameters: $a_1, a_2, \ldots, a_{r-1}$, and b^2. For large samples, maximum likelihood (ML) estimates of these parameters will have many desirable statistical properties, including small variances, unbiasedness, and normal distributions. The ML estimates, denoted $a_1, \ldots, a_{r-1}, b^2$, are the numerical values of the parameters that maximize the likelihood function, L, of the data:

$$L = C \prod_{j=1}^{q} \prod_{i=1}^{r} [p_{ij}]^{x_{ij}}. \tag{6}$$

Here, C is a combinatorial constant ($= \prod (n_j!)/[(x_{1j}!)(x_{2j}!) \ldots (x_{rj}!)]$) that does not contain the parameter values. Maximizing log L instead of L yields the identical estimates but is numerically easier:

$$\log L = \log C + \sum_{j=1}^{q} \sum_{i=1}^{r} x_{ij} \log p_{ij}. \tag{7}$$

This function can be directly maximized by using the Nelder-Mead algorithm (see Olsson & Nelson 1975) or by other methods. It can be maximized indirectly, however, using a nonlinear regression package.

Jennrich & Moore (1975) showed that maximizing L (or log L) is equivalent to performing a nonlinear least squares regression. The nonlinear regression must be "iteratively reweighted." The nonlinear regression uses the x_{ij} values as observations on the dependent variable and the $n_j p_{ij}$ values as the model to be fit, with weights of $(n_j p_{ij})^{-1}$ computed at each iteration. The resulting least squares estimates of $a_1, \ldots, a_{r-1}$, and b^2 are the desired ML estimates.

Nonlinear regression packages, such as PROC NLIN of SAS (SAS Institute 1982) or AR of BMDP (Dixon 1983), are widely available. These two packages are particularly convenient because they do not require derivatives, and their options allow properly scaled confidence intervals for the parameter estimates. A library function for evaluating the normal probability integral (PROBNORM) exists in SAS, if the normal model is desired instead of the logistic. A complete SAS program for fitting the logistic model to a western spruce budworm data set is presented and discussed in the *Appendix*.

These iterative computer packages require initial values for the parameters. The initial values should be close to the final ML values, or the routines may not converge properly. Initial values can be guessed by observing plots of the data and by using biological intuition. A variety of initial values should be explored because the likelihood function (6) is a complicated surface with possible multiple local maxima.

Hypothesis Testing

ML estimation makes possible two types of statistical hypothesis tests concerning this model. The first type, goodness-of-fit tests, allows the descriptive quality of the model to be evaluated for a given data set. The second type, parameter comparison tests, is a method for comparing the fitted models of two separate data sets. The tests described here are derived from the standard large-sample statistical theory for ML estimation (see Rao 1973, Bishop et al. 1975).

Goodness-of-fit Tests. The data for this model consist of independent samples from q multinomial distributions, one sample at each fixed time t_j. The data form a two-way table with $r \times q$ cells. The model states that knowledge of just r parameter values, $a_1, \ldots, a_{r-1}, b^2$, is sufficient to compute the p_{ij} values for all the cells. ML estimates of the p_{ij} values under the model, denoted $\hat{p}_{ij}$, are found by evaluating equation 5 with the ML estimates $\hat{a}_1, \ldots, \hat{a}_{r-1}, \hat{b}^2$. An estimate of the expected value for x_{ij} in each cell is then $n_j \hat{p}_{ij}$. If the model fits poorly, an alternate hypothesis would simply es-

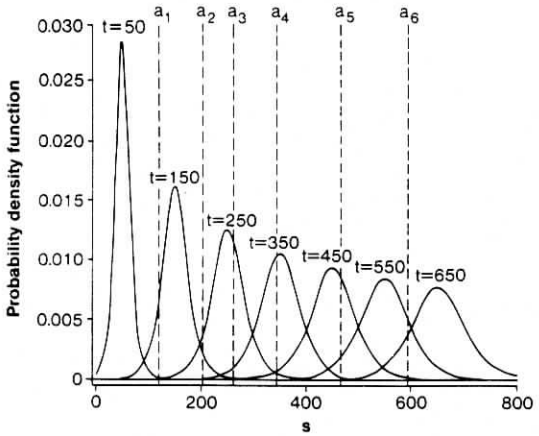

Fig. 2. Logistic PDF (3) plotted for seven fixed values of t. Area under the PDF between a_{i-1} and a_i gives expected proportion of insects in stage i at time t. Values of $a_1, \ldots, a_6$ and b^2 used in the graph are the ML estimates for the western spruce budworm data set in the *Appendix*.

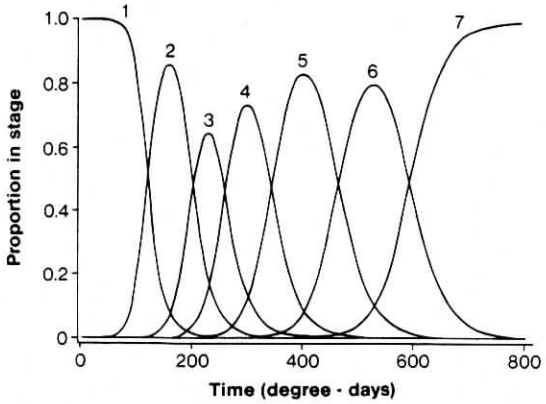

Fig. 3. Expected proportions of insects in stages 1–7 plotted as functions of t. Parameter values are the same as for Fig. 2.

timate the cell probabilities using the raw data, $\tilde{p}_{ij} = x_{ij}/n_j$, independent of any underlying common model. Denote by $\hat{L}_o$ the estimated likelihood under the null hypothesis that the model fits; that is, $\hat{L}_0$ is equation 6 computed using the $\tilde{p}_{ij}$ values. Denote by $\tilde{L}_1$ the estimated likelihood under the alternate hypothesis that the model does not fit; that is, $\tilde{L}_1$ is equation 6 evaluated using the $\tilde{p}_{ij}$ values. The ratio of these estimated likelihoods, given by $R = \hat{L}_0/\tilde{L}_1$, compares the descriptive power of each hypothesis according to the data. Large values of R support the model, while small values of R support the hypothesis that the model does not fit (R will always be between 0 and 1). From a theorem in mathematical statistics,

$$V = -2 \log R \tag{8}$$

will have (approximately) a χ^2 distribution with $q(r-1) - r$ degrees of freedom, under the null hypothesis that the model fits (see Bishop et al. 1975). The null hypothesis would be rejected if V exceeded, say, the 95th percentile of the appropriate χ^2 distribution. With a little algebraic rearrangement, V (8) can be shown to be identical to

$$V = 2 \sum_{j=1}^{q} \sum_{i=1}^{r} x_{ij} \log[x_{ij}/(n_j \hat{p}_{ij})], \tag{9}$$

a form more convenient to compute. Also, V is approximately equal to the more familiar Pearson χ^2 statistic in large samples:

$$V \cong \sum_{j=1}^{q} \sum_{i=1}^{r} [x_{ij} - n_j \hat{p}_{ij}]^2/(n_j \hat{p}_{ij}). \tag{10}$$

One possible obstacle to using V is a table with empty or nearly empty cells. For the χ^2 distribution of V to be valid, each $n_j \hat{p}_{ij}$ value should be at least five. This is ensured by pooling adjacent sparse cells within each fixed time t_j until the expected frequencies exceed five for every remaining cell. If the total number of remaining cells is m, the appropriate degrees of freedom are $m - q - r$.

Parameter Comparisons. In some studies, comparing parameter estimates resulting from two separate data sets may be desirable. Comparisons can be made, for example, between estimates from two different regions or sampling periods. A property of ML estimates allows such comparisons to be phrased as formal statistical tests. ML estimates have normal distributions for large samples.

Specifically, let $\hat{\theta} = [\hat{a}_1, \ldots, \hat{a}_{r-1}, \hat{b}^2]'$ be the $r \times 1$ vector of ML parameter estimates for a population. Let $\partial_k p_{ij}$ represent the partial derivative of p_{ij} with respect to parameter number k; that is, $\partial_2 p_{ij} = \partial p_{ij}/\partial a_2$, $\partial_r p_{ij} = \partial p_{ij}/\partial b^2$, and so on. Define the $r \times r$ "information matrix," F, as having its element in the kth row and lth column given by

$$f_{kl} = \sum_{j=1}^{q} \sum_{i=1}^{r} (n_j/p_{ij})(\partial_k p_{ij})(\partial_l p_{ij}). \tag{11}$$

Also, denote by θ the $r \times 1$ vector of the true parameter values for the population. Then, $\hat{\theta}$ has (approximately) a multivariate normal distribution with mean vector θ and variance/covariance matrix F^{-1}. In particular, each individual parameter estimate in $\hat{\theta}$ has a normal distribution, with a mean equal to the parameter's true value and a variance equal to the corresponding element on the main diagonal of F^{-1}. F^{-1} can be estimated by substituting the ML parameter estimates in F, and inverting the matrix.

The SAS or BMDP nonlinear regression packages have options for easily computing this estimate of F^{-1}. The options (SIGSQ = 1 in SAS; MEANSQUARE IS 1.0 in BMDP) set the residual mean square equal to one before the asymptotic standard deviations and correlation matrix of the parameters are calculated. The resulting standard deviations and correlations are the same obtained from the estimated information matrix. The cor-

relation matrix, G, is $G = D(1/\sigma_i)F^{-1}D(1/\sigma_i)$, where $D(1/\sigma_i)$ is a matrix ($r \times r$) containing reciprocals of the parameter standard deviations down the main diagonal, and zeros elsewhere. The estimate of F^{-1} can be directly obtained from the computer output as

$$\hat{F}^{-1} = D(\hat{\sigma}_i)\hat{G}D(\hat{\sigma}_i), \quad (12)$$

where $\hat{G}$ is the printed estimate of the correlation matrix, $\hat{\sigma}_i$ is the printed estimate of the standard deviation for the ith parameter, and $D(\hat{\sigma}_i)$ is the diagonal matrix of those standard deviations.

The following multivariate statistical test compares the model parameters for two different populations. Let $\hat{\theta}_1$ and $\hat{\theta}_2$ be the vectors of parameter estimates resulting from fitting the model to two different data sets. Also, let $\hat{F}_1^{-1}$ and $\hat{F}_2^{-1}$ be the respective estimates for the variance/covariance matrices. The hypotheses to be tested are H_0: $\theta_1 = \theta_2$ versus H_1: $\theta_1 \neq \theta_2$, where θ_1 and θ_2 are the vectors of true parameter values. Under H_0, $\hat{\theta}_1 - \hat{\theta}_2$ would have (for large samples) a multivariate normal distribution with mean vector $\theta_1 - \theta_2 = 0$ and variance/covariance matrix $F_1^{-1} + F_2^{-1}$. Then, under H_0, the statistic

$$W = (\hat{\theta}_1 - \hat{\theta}_2)'[\hat{F}_1^{-1} + \hat{F}_2^{-1}]^{-1}(\hat{\theta}_1 - \hat{\theta}_2) \quad (13)$$

will have a χ^2 distribution with r degrees of freedom. Reject H_0 if W exceeds the $100(1 - \alpha)$th percentile of the χ^2 distribution, where α is the desired significance level of the test.

Note that the sample sizes do not need to be equal (just large) nor do the sample times (t_j values) need to match up between the two data sets. The latter requirement precludes a comparison of the two frequency tables directly using loglinear models, unless the sampling times were exactly matched.

Individual parameters can be compared with the univariate version of W. Let $\hat{a}_{i1}$ be a parameter estimate in $\hat{\theta}_1$, $\hat{a}_{i2}$ be the corresponding estimate in $\hat{\theta}_2$, and $\hat{\sigma}_{i1}$, $\hat{\sigma}_{i2}$ be the computed estimates of the standard deviations (square roots of the ith elements of the diagonals of $\hat{F}_1$ and $\hat{F}_2^{-1}$, respectively). The statistic W then reduces to

$$W = (\hat{a}_{i1} - \hat{a}_{i2})^2/(\hat{\sigma}_{i1}^2 + \hat{\sigma}_{i2}^2), \quad (14)$$

with a χ^2 distribution having 1 df.

Acknowledgment

Work leading to this publication was funded in part by the Canada/United States Spruce Budworms Program, USDA, For. Serv., Pacific Northwest Res. Stn., Portland, Oreg. We thank Dale O. Everson and Kirk R. Steinhorst (Dep. of Mathematics and Applied Statistics, Univ. of Idaho); Gary A. Simmons (Dep. of Entomology, Michigan State Univ.); and Alan J. Thomson (Pacific For. Res. Centre, Canadian Forestry Serv.) for their manuscript reviews. Also, J. J. Colbert (PNW Res. Stn., USDA For. Serv.); Jery R. Stedinger (Dep. of Environmental Engineering, Cornell Univ.); W. Jan A. Volney (Dep. of Entomology, Univ. of California, Berkeley); and Akira Osawa (College of Forestry, Yale Univ.) for their manuscript reviews.

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Received for publication 16 May 1985; accepted 30 January 1986.

Appendix

This appendix contains a SAS program for computing ML estimates of the parameters a_1, a_2, . . . , a_{r-1}, and b^2 in the logistic phenology model. The program illustrates the use of nonlinear regression for obtaining such estimates. The data used in the program, which are described in Kemp et al. (1986), represent the development of a western spruce budworm population. The seven developmental stages are five instars, pupa, and adult. Samples were drawn at 12 different times. Thus, $r = 7$ (number of stages), and $q = 12$ (number of samples).

In the program, each observation contained in the resulting SAS data set corresponds to an ith developmental stage and a jth sample. The program sets up the SAS data set as shown:

SAS variable name:	T	N	I	X
Sample 1	t_1	n_1	1	x_{11}
	t_1	n_1	2	x_{21}
	$\vdots$	$\vdots$	$\vdots$	$\vdots$
	t_1	n_1	r	x_{r1}
Sample 2	t_2	n_2	1	x_{12}
	t_2	n_2	2	x_{22}
	$\vdots$	$\vdots$	$\vdots$	$\vdots$
	t_2	n_2	r	x_{r2}
	$\vdots$	$\vdots$	$\vdots$	$\vdots$
Sample q	t_q	n_q	1	x_{1q}
	t_q	n_q	2	x_{2q}
	$\vdots$	$\vdots$	$\vdots$	$\vdots$
	t_q	n_q	r	x_{rq}

SAS Program to Compute ML Estimates for Logistic Phenology Model

```
DATA;
* CONTINUOUS STREAM OF OBSERVATIONS ENTERED INTO SAS DATA SET;
INPUT T N I X @@;
CARDS;
 58  16  1  16   58  16  2   0   58  16  3   0   58  16  4   0
 58  16  5   0   58  16  6   0   58  16  7   0   82  10  1  10
 82  10  2   0   82  10  3   0   82  10  4   0   82  10  5   0
 82  10  6   0   82  10  7   0  107  30  1  23  107  30  2   7
107  30  3   0  107  30  4   0  107  30  5   0  107  30  6   0
107  30  7   0  155  47  1   3  155  47  2  44  155  47  3   0
155  47  4   0  155  47  5   0  155  47  6   0  155  47  7   0
237  64  1   0  237  64  2   6  237  64  3  45  237  64  4  13
237  64  5   0  237  64  6   0  237  64  7   0  307  74  1   0
307  74  2   2  307  74  3   9  307  74  4  48  307  74  5  15
307  74  6   0  307  74  7   0  342  72  1   0  342  72  2   0
342  72  3   1  342  72  4  34  342  72  5  37  342  72  6   0
342  72  7   0  388 104  1   0  388 104  2   0  388 104  3   1
388 104  4  10  388 104  5  87  388 104  6   5  388 104  7   0
442  74  1   0  442  74  2   0  442  74  3   0  442  74  4   7
442  74  5  53  442  74  6  21  442  74  7   0  518  76  1   0
518  76  2   0  518  76  3   0  518  76  4   0  518  76  5  10
518  76  6  65  518  76  7   1  609  40  1   0  609  40  2   0
609  40  3   0  609  40  4   0  609  40  5   0  609  40  6  14
609  40  7  26  685  42  1   0  685  42  2   0  685  42  3   0
685  40  4   0  685  42  5   0  685  42  6   0  685  42  7  42

* INVOKE NONLINEAR REGRESSION PROCEDURE;
PROC NLIN NOHALVE SIGSO=1;
* PROVIDE INITIAL PARAMETER VALUES;
```

```
PARMS A1=150 A2=230 A3=280 A4=330
    A5=440 A6=580 BB=3;
* COMPUTE PROPORTION OF POPULATION EXPECTED IN ITH DEVELOPMENTAL
* STAGE AT JTH SAMPLE;
IF I=1 THEN P=1/(1+EXP(-(A1-T)/SQRT(BB*T)));
ELSE IF I=2
THEN P=1/(1+EXP(-(A2-T)/SQRT(BB*T)))-1/(1+EXP(-(A1-T)/SQRT(BB*T)));
ELSE IF I=3
THEN P=1/(1+EXP(-(A3-T)/SQRT(BB*T)))-1/(1+EXP(-(A2-T)/SQRT(BB*T)));
ELSE IF I=4
THEN P=1/(1+EXP(-(A4-T)/SQRT(BB*T)))-1/(1+EXP(-(A3-T)/SQRT(BB*T)));
ELSE IF I=5
THEN P=1/(1+EXP(-(A5-T)/SQRT(BB*T)))-1/(1+EXP(-(A4-T)/SQRT(BB*T)));
ELSE IF I=6
THEN P=1/(1+EXP(-(A6-T)/SQRT(BB*T)))-1/(1+EXP(-(A5-T)/SQRT(BB*T)));
ELSE IF I=7
THEN P=1/(1+EXP((A6-T)/SQRT(BB*T)));
* USED TO PREVENT NUMERICAL OVERLOAD IN _WEIGHT_ STATEMENT
* WHEN P IS VERY CLOSE TO ZERO;
IF P <0.00000001 THEN P=0.00000001;
* SPECIFY THE NONLINEAR REGRESSION MODEL;
MODEL X=N*P;
* COMPUTE WEIGHT FOR EACH OBSERVATION AT EACH ITERATION;
_WEIGHT_=1/(N*P);
```