

ESTIMATING DEVELOPMENTAL AND MORTALITY RATES AND STAGE RECRUITMENT FROM INSECT STAGE-FREQUENCY DATA

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INTRODUCTION

A fundamental source of information concerning the ecology of an insect population is a cohort life-table, which consists of a record of the development of a cohort of individuals through the various life stages from egg to adult. Such data often are not difficult to collect and much attention has been given to their analysis; these analyses of single-generation stage-frequency data may be distinguished from key-factor analyses of life-table data from several generations (e.g. VARLEY and GRADWELL, 1960). Early workers were concerned primarily with extracting such information from these cohort life-tables as stage-specific mortalities or the number of individuals entering a stage (e.g. RICHARDS and WALOFF, 1954; DEMPSTER, 1961; SOUTHWOOD and JEPSON, 1962; KOBAYASHI, 1968). More recent attention has been focused on methods which can also predict population density of the various stages as the cohort develops (e.g. MANLY, 1974; BIRLEY, 1977, 1979a), and these may be used as models for population growth and development. We develop here another method which may be used as a population model, but has some advantages over methods currently in the literature. The technique allows for distributed developmental periods of the various stages (MANLY, 1974; BIRLEY, 1979a). It does not assume a constant mortality for successive stages, as do those of MANLY (1974) and KIRITANI and NAKASUJI (1967), but instead mortality rates may vary between stages. In addition, it does not require the observation of recruitment to each stage (cf. BIRLEY, 1977, 1979a). In contrast, recruitment need only be observed to the initial stage, and recruitment to subsequent stages is predicted from the estimated developmental period and mortality of each stage.

In the next section we develop the model and then demonstrate its use by applying it to a cohort life-table of *Callosobruchus chinensis* (L.), a bruchid pest of stored pulses. We then discuss the importance of the predictive ability of the model and the potential use of this technique in developing models for insect populations.

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DEVELOPMENT OF THE MODEL

This life-table model is based on the premise that the developmental period of an instar is not fixed, but may vary between individuals so that there is a distribution through time of individuals from a single cohort completing development of an instar. This distribution of the developmental period may be described by a probability distribution f_i whose elements $f_i(j)$ specify the probability of an individual in stage i moulting to stage $i+1$ at age j (age is here measured from entry to instar i) (BIRLEY, 1979 a). These probabilities $f_i(j)$ may be interpreted as the proportion of individuals of an initial cohort $x_i(0)$ which moult to the next stage upon reaching age j . The number of individuals moulting to stage $i+1$ between times t and $t+1$ (assuming for the moment that no mortality occurs) may now be described by

$$x_{i+1}(t) = x_i(0)f_i(t). \quad (1)$$

The total number of individuals of the initial cohort $x_i(0)$ which have moulted to stage $i+1$ by time t , $y_{i+1}(t)$, is given by

$$y_{i+1}(t) = x_i(0) \sum_{j=0}^t f_i(j), \quad (2)$$

and the total number of individuals remaining in stage i , $y_i(t)$, is

$$y_i(t) = x_i(0) - x_i(0) \sum_{j=0}^t f_i(j)$$

or

$$y_i(t) = x_i(0) \left[1 - \sum_{j=0}^t f_i(j) \right]. \quad (3)$$

The summation of the probability distribution f_i from zero to t in equations (2) and (3) is the value of the cumulative probability distribution $F_i(t)$,

$$F_i(t) = \sum_{j=0}^t f_i(j). \quad (4)$$

The value $F_i(t)$ is the probability that an individual in stage i will have moulted to stage $i+1$ before the time interval t to $t+1$ (time is again measured from entry to stage i). This value $F_i(t)$ may be viewed as specifying the proportion of a cohort which has moulted to stage $i+1$ up to and including the interval $t-1$ to t . The total number of individuals present in stage i may now be represented by (substituting equation (4) into equation (3))

$$y_i(t) = x_i(0) [1 - F_i(t)]. \quad (5)$$

The distribution f_i gives the proportion of the initial number of individuals in a cohort which moult to the next stage at different ages. It is well appreciated, however, that the number of individuals of a cohort in any given stage may be reduced not only through losses due to moulting but also through mortality. In order that the model may allow for mortality it is useful at this point to specify one further distribution G_i which gives the proportion of individuals in a cohort moulting to stage

$i+1$ as a function of the number of individuals of the cohort *present* in stage i , rather than as a function of the *initial* number of individuals in the cohort. The elements $G_i(j)$ of this distribution specify the conditional probability of an individual moulting to stage $i+1$ at age j given that the individual was still in stage i at age $j-1$. The distribution G_i may be derived from the distributions f_i and F_i as follows. It is necessary to define the proportion of those individuals of a cohort still in stage i at time $t-1$ which moult to stage $i+1$ at time t . Recalling from equation (5) that the number of individuals present in stage i at time $t-1$ is

$$y_i(t-1) = x_i(0)[1 - F_i(t-1)], \quad (6)$$

and that the number of individuals changing stages at time t is (from equation (1))

$$x_{i+1}(t) = x_i(0)f_i(t), \quad (7)$$

then the required proportion of individuals changing stages may be obtained by dividing equation (7) by equation (6),

$$\frac{x_{i+1}(t)}{y_i(t-1)} = \frac{x_i(0)f_i(t)}{x_i(0)[1 - F_i(t-1)]}. \quad (8)$$

The ratio of equation (8) defines the value of $G_i(t)$,

$$G_i(t) = \frac{f_i(t)}{1 - F_i(t-1)}, \quad (9)$$

and to complete the definition of the distribution G_i it is necessary only to define $F_i(-1) = 0$ (the distribution F_i was previously truncated at zero) so that $G_i(0) = f_i(0)$.

The relationships between the distributions f , F and G are shown for a hypothetical case in Fig. 1. The unimodal (singly peaked) developmental period distribution f in Fig. 1a gives rise (via equation (4)) to the sigmoid cumulative distribution F in Fig. 1b. These two distributions were combined using equation (9) to give the conditional distribution of development G in Fig. 1c. In this example G has a complex shape, but when the distribution f is narrower or symmetric the form of G is a sigmoid relationship similar to that described by F .

The use of the distribution G now permits development of a life-table model where the fate of any cohort may be described by two recursive relationships. Considering first the effects of development, the changes occurring in a cohort are specified by the two equations

$$x_{i+1}(t) = G_i(t)y_i(t-1), \quad (10)$$

$$y_i(t) = [1 - G_i(t)]y_i(t-1). \quad (11)$$

Equation (10) gives the number of individuals of the cohort moulting to stage $i+1$ between times t and $t+1$, and equation (11) accounts for these losses in the current size of the cohort (since $G_i(t)$ is the proportion of individuals changing stages at time t , $1 - G_i(t)$ is the proportion remaining in stage i). It is possible in this framework to consider additionally the effects of mortality on a cohort. The mortality will be assumed age-independent within a stage although it may differ between

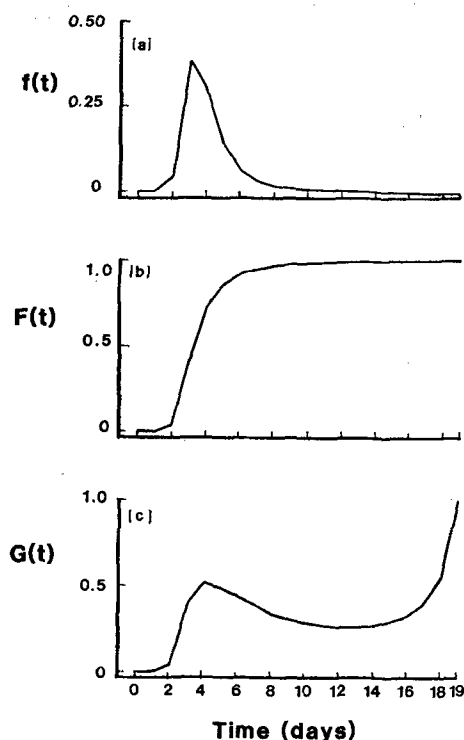


Fig. 1. Three probability distributions relating age to developmental period. (a) The distribution of individuals moulting at a given age (f) described by equation (13) when $\mu=0.3$ and $\sigma^2=0.01$. (b) The cumulative distribution of individuals which have moulted by a given age (F) (equation (4)). (c) The conditional distribution of individuals moulting at a given age (G) (equation (9)). See text for discussion.

stages. This assumption is necessary if parameters are to be estimated from data because the age-dependent developmental period would obscure any age-dependent mortality. In other words, the disappearance of individuals from a cohort may be due either to development or mortality, but only one of these processes may be assigned age-dependency during parameter estimation. A constant stage-specific survival rate s_i may be included in the model by modifying equation (11) to

$$y_i(t) = s_i[1 - G_i(t)]y_i(t-1). \quad (12)$$

Equation (12) implies that those individuals remaining in stage i suffer a proportionate mortality of $1 - s_i$ during the interval $t-1$ to t . The individuals which moult to stage $i+1$ at time t (equation (10)) form a new cohort of individuals in that stage and now have age zero; they would be subject to a mortality of $1 - s_{i+1}$ during the interval $t-1$ to t . Equations (10) and (12) complete the development of the cohort life-table model which now accounts for the processes of development and mortality. These equations may be used either in analysis or prediction of a life-table by applying them to all the cohorts present in each stage at every time step.

It remains to specify a formula for the developmental distribution f_i . A number of distributions have been used to describe the developmental period of insects. Although the normal distribution (which is symmetric) has been used by MANLY (1974) in the analysis of life-table data, a large amount of evidence indicates that developmental periods in insects are positively skewed (see the review by HOWE (1966) and also STINNER *et al.* (1975), BARFIELD *et al.* (1977) and SHARPE *et al.* (1977)). Consequently, developmental periods have often been described by skewed probability distributions such as the gamma and log-normal distributions (HOWE, 1966), special Erlangian distributions (ASHFORD *et al.*, 1970) and the beta distribution (STINNER *et al.*, 1975). In contrast to these empirical approaches, SHARPE *et al.* (1977) have described positively skewed developmental distributions by a formula which arises from the simple assumption that the developmental rates of individuals in a population are symmetrically distributed about a mean value. Transforming a symmetric distribution of developmental *rates* to developmental *periods* results in a positively skewed distribution. The approach of SHARPE *et al.* is adopted here primarily because these distributions are defined by parameters with simple biological interpretations and also because such distributions have been used successfully to describe insect development (BARFIELD *et al.*, 1977; SHARPE *et al.*, 1977). The formula used here arises from the assumption that the distribution of developmental rates in the population follows a normal distribution. This leads to a distribution of developmental period whose elements are defined by (SHARPE *et al.*, 1977)

$$f_i(j) = (k_i \sigma_i \sqrt{2\pi})^{-1} \int_j^{j+1} t^{-2} \exp [-(t^{-1} - \mu_i)^2 / 2\sigma_i^2] dt. \quad (13)$$

This distribution is specified by the two parameters μ_i , the mean developmental rate of stage i and σ_i^2 , the variance of the developmental rate. The parameter k_i is a normalizing constant which ensures that the sum of $f_i(j)$ over the range of j considered is unity. Equation (13) depicts positively skewed distributions such as that shown in Fig. 1a.

ESTIMATING THE MODEL PARAMETERS

Two approaches to estimating parameters of models are generally available, that of maximum likelihood estimation and a family of empirical approaches. The most widespread of the empirical approaches is to treat the parameters of a model as variables and find the parameter values which minimize the sum of squared deviations between model predictions and observed results (the residuals). This technique is known as "least-squares" estimation. For this life-table model, methods of maximum likelihood estimation have not been developed and all the parameter estimates have been found by a least-squares technique. The algorithm used for estimating the parameters was that of POWELL (1968).

Initially, estimates of the mean rate and variance in equation (13) for develop-

ment of eggs to first instar larvae were obtained (no egg mortality was considered, as discussed below). This provided a prediction of the number of daily recruits (the cohorts) to the first instar stage. The predicted recruitment was used together with the observed daily record of the numbers of first instar larvae present to estimate the mean and variance of the developmental rate and daily survival of first instar larvae. The result provided a prediction of the daily cohorts recruited to the second instar stage, and the analysis was repeated for the second instar and subsequently in this stepwise manner for all the other stages. This method worked well and provided reasonable estimates of the parameters. Occasionally, however, the estimate of daily survival for a particular instar would exceed unity indicating perhaps an overestimate of the mortality in the previous stage. These errors, presumably due to the nature of the sampling regime, were overcome by a simple refinement. Whenever the problem arose, the parameters for development and survival for the instar were estimated again simultaneously with the parameters for the previous instar (i. e., six parameters were estimated for the two instars together). This usually provided acceptable parameter estimates, but if the daily survival estimate again exceeded unity it was fixed arbitrarily at unity, and values for the developmental parameters for that instar were then estimated together with the developmental and survival parameters for the previous instar.

A LIFE-TABLE FOR *CALLOSOBRUCHUS CHINENSIS*

In order to illustrate the use of the model in analyzing a particular set of data, we present here a cohort life-table for *Callosobruchus chinensis*, a bruchid pest of stored pulses. The eggs of this species are laid on the surface of dried peas or beans, and upon hatching the first instar larvae burrow into the cotyledon. The four larval stages are passed entirely within a single bean. Pupation takes place in the cavity created by larval feeding, and the adults emerge from the bean a day or two after eclosion. More than one larva may develop within a bean, although there is some competition for space. The biology of *C. chinensis* has been reviewed by HOWE and CURRIE (1964).

The data for the life-table were collected by repeatedly subsampling a population of *C. chinensis* developing in a large plastic box containing cowpeas, *Vigna unguiculata* (WALP.). The population was started by isolating adult *C. chinensis* with the beans for 24 hours at 30° and 70% relative humidity, after which the adults were removed and the beans returned to these experimental conditions. A number of beans were taken from the box daily, the number of hatched eggs on each bean was recorded and each bean was then dissected in order to score the number and stage of the living individuals present. On each day sufficient beans were dissected so that a minimum of fifty living individuals were recorded. Sampling was continued until all the observed survivors were in the emerged adult stage. These data provided a

Table 1. The observed survival of *Callosobruchus chinensis* (L.) in beans with various numbers of hatched eggs (data pooled from all sampling days). The data in Table 2 were taken from beans with five or fewer hatched eggs per bean.

No. of hatched eggs per bean	Total observed hatched eggs	Total observed survivors	Percent survival	Cumulative percent survival
1	102	100	98.0	98.0
2	314	302	96.2	96.6
3	453	433	95.6	96.1
4	400	379	94.8	95.7
5	360	338	93.9	95.3
6	270	242	89.6	94.5

record of the number of individuals in each stage each day over a small range of hatched egg densities.

In order to construct a life-table from such a record it was first necessary to ensure that the observed survival was not influenced by larval density. This was done by grouping all of the data collected during the daily censusing according to the number of hatched eggs per bean. The total number of hatched eggs and the total number of survivors were pooled for sampling days five to twenty-six for each hatched egg density. An overall ratio of survival at each density was then recorded. This information is given in Table 1 for beans with six or fewer hatched eggs. It was concluded, after considering the percent survival and the cumulative percent survival at successive densities, that data from beans with five and fewer hatched eggs would provide information suitable for a density independent life-table. This provided a sample of over 1600 hatched eggs from twenty-two sampling days, or approximately 70 eggs per day, from which to construct the life-table.

The life-table (Table 2) was constructed by pooling the data from all the beans sampled on a given day. The observed number of survivors present in each stage is given as a percentage of the number of hatched eggs observed on each day. The data for days one to five (before all the eggs had hatched) represent a cohort of 100 live eggs and no egg mortality was considered here. The total number of individuals observed each day is also given as a percentage in Table 2, from which we see that the number of individuals present on successive days does not always remain constant or decrease (as would be the case if individuals from a single cohort were observed throughout their life) but occasionally increases. This is an artifact of the sampling programme where the fate of a single cohort is being approximated by the average fate of many cohorts undergoing sequentially destructive sampling. However, this did not cause serious problems when estimating the life-table parameters and no smoothing of the data was necessary (cf. SOKAL and BRYANT's (1967) life-table analysis for the house fly).

Table 2. Stage-frequency data for *Callosobruchus chinensis* (L.) per 100 hatched eggs.

Day	Eggs	I	II	III	IV	Pupae	Adults in Pea	Emerged Adults	Total
1	100.00								100.00
2	100.00								100.00
3	100.00								100.00
4	59.00	41.00							100.00
5		96.77							96.77
6		91.78							91.78
7		23.08	71.79						94.87
8		4.84	74.19	17.74					96.77
9		1.05	57.89	40.00					98.94
10		1.85	3.70	89.81	.93				96.29
11			4.76	41.67	48.81				95.24
12			.00	3.53	90.59				94.12
13			1.23	.00	96.30				97.53
14				.00	100.00				100.00
15				1.16	82.56	15.12			98.84
16					37.68	57.97			95.65
17					10.61	74.24			84.85
18					10.47	81.40		1.16	93.03
19					2.08	70.83	18.75	.00	91.66
20						22.62	72.62	1.19	96.43
21						8.22	75.34	16.44	100.00
22						4.82	38.55	53.01	96.38
23							12.68	85.92	98.60
24							8.51	91.49	100.00
25							1.96	88.24	90.20
26								88.41	88.41

Table 3. Estimates of the developmental parameters and survival rates for *Callosobruchus chinensis* (L.) from the analysis of the data in Table 2.

Instar	Developmental rate, μ_i (days ⁻¹)	Developmental variance, σ_i^2 (days ⁻²)	Proportionate daily survival	Predicted number entering stage	Predicted stage mortality(%)
Eggs	0.31684	1.9330×10^{-4}	—	100.00	0.00
1st larvae	0.46924	4.9579×10^{-4}	1.00	100.00	0.00
2nd larvae	0.48279	7.9570×10^{-4}	0.99430	100.00	1.32
3rd larvae	0.48655	5.9308×10^{-6}	1.00	98.68	0.00
4th larvae	0.22580	2.9458×10^{-4}	1.00	98.68	0.00
Pupae	0.31564	1.3752×10^{-4}	0.98662	98.68	4.79
Adults in pea	0.47338	7.0423×10^{-4}	1.00	93.95	0.00
Emerged Adults	—	—	—	93.95	—

RESULTS

The life-table model of equations (10) and (12) was fitted to the data in Table 2 and the results of this analysis are presented in Table 3. The estimated mean developmental rates of the egg, fourth instar larval and pupal stages were lower than those of the other stages. The estimated variances of the development rates were small for all stages. This is partly a reflection of the rapid development of this species in the experimental conditions used and also indicates that a sampling

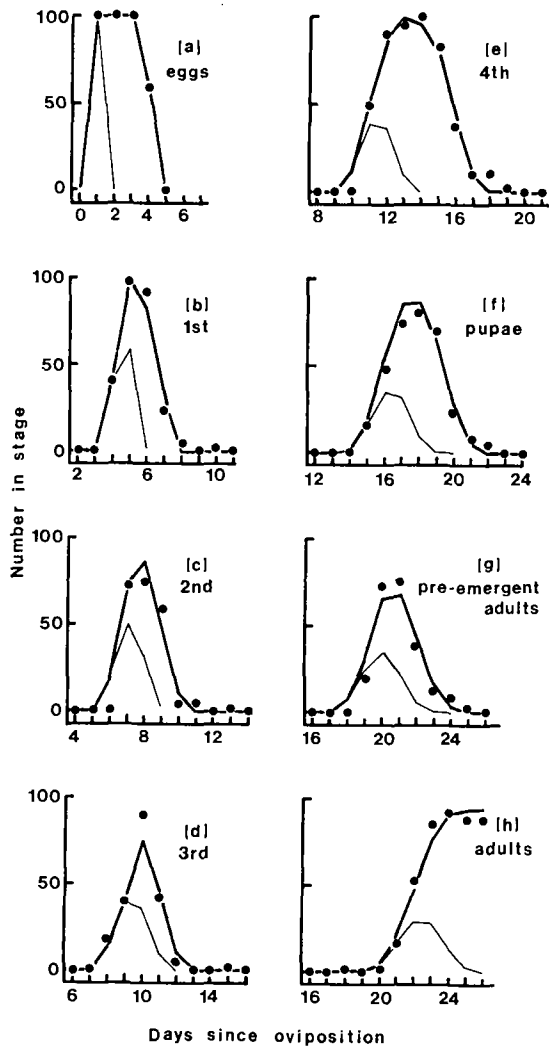


Fig. 2. The observed (●) and predicted (—) stage frequencies of *Callosobruchus chinensis* (L.) developing from oviposition (day zero) through adult emergence. Also shown are the predicted numbers entering each stage each day (—). (a) eggs; (b)–(e) first through fourth instar larvae; (f) pupae; (g) adults inside the pea; (h) adults emerged from the pea.

interval of less than one day might have been useful in determining these parameter values more accurately. In the case of the third larval instar, the estimated variance was sufficiently small that the predicted developmental period occurred entirely within one day (Fig. 3). For this stage, the estimated value of the variance parameter must be viewed only as a lower limit on the actual value as smaller variances would produce the same result. The estimates of daily survival rates for all the stages were high, resulting in a predicted overall survival of 94%. The estimated mortality of second instar larvae probably represents failure to become established in the bean. The only other stage in which survival was estimated as different than unity was the pupal stage. The estimated pupal survival was lower than that of the second instar and accounted for the largest portion of the overall mortality.

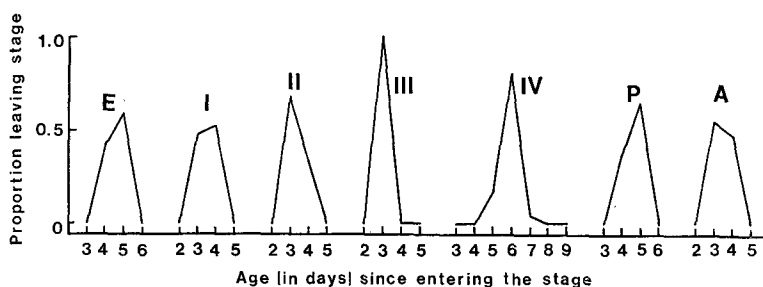


Fig. 3. The predicted distribution of the developmental period of each stage of *Callosobruchus chinensis* (L.). Ages are shown in days from entry to each stage. Stages are indicated as follows: E, eggs; I-IV, first through fourth instar larvae; P, pupae; A, adults inside the pea.

The life-table model provides a prediction of the number of individuals present in each stage through the course of a cohort's development and these predictions are presented graphically, together with the observed numbers, in Fig. 2. The model clearly described well the presence of the various stages. The distributions of the developmental periods predicted by the model are shown in Fig. 3. These distributions are all somewhat kurtotic; indeed one of them is contained entirely within one day. This emphasizes the effect of the small estimated variances of the developmental rates in Table 3.

CONCLUDING REMARKS

The model developed here has two features which, although not unique to this model, are combined here for the first time. These are the distributed developmental period (cf. MANLY, 1974) and different daily survival rates for the different stages. This combination provides a powerful tool for the analysis of data from almost any regime of insect development or life history. The analysis may be applied to data consisting of only estimates of stage densities and recruitment to the first stage, a

point of importance where recruitment to each stage cannot be observed directly (cf. RUESINK, 1975; BIRLEY, 1979 a). The model has proved useful here where initial recruitment was a pulse but also has been applied successfully to situations where recruitment occurred over several days. It has also been used in situations where mortality was higher than in the data presented here and, with slight modifications, where mortality was age-specific rather than stage-specific.

One other important property of this model is the detail with which it reconstructs a population's development. It can clearly predict stage frequencies (Fig. 2), thus permitting the development of simulation models of insect populations using parameters estimated directly from stage frequency data. In addition, the model predicts the daily recruitment to each stage. In this way the number of individuals entering each stage is estimated, and total stage mortalities are easily accounted. This predicted recruitment may be of fundamental use in discerning optimal control strategies for insect pest populations (BIRLEY, 1979 b). It may also be of considerable importance when modelling such aspects of population biology as density dependence, where the number of individuals entering a stage at a given time may affect the stage-specific survival rate. This concept of recruitment density affecting competition has been more fully developed in a further study of *Callosobruchus chinensis*, where quantifying competition within and between stages has led from simple life-table models (such as those presented here) to more detailed simulation models of population growth and development. The results of these studies will be reported in future publications.

SUMMARY

A model for the analysis of insect stage-frequency data is developed which includes stage-specific variable developmental periods and stage-specific daily survival rates. The model can predict the development of an insect population through its developmental stages and consequently may form the basis for a simulation model of the population.

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昆虫の発育ステージ別度数分布のデータから発育速度，
死亡率，発育ステージ別加入数の推定

T. S. BELLOW, JR • M. H. BIREY

昆虫の発育ステージ別度数分布のデータを分析するモデルを作成した。各ステージの発育日数の個体による変異と各ステージの生存率（各ステージで一定）をモデルに含めた。このモデルで昆虫個体群の発育ステージの予測ができ、個体群のシミュレーションモデルの基礎として役立つと考えられる。