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DEVELOPMENT OF A MODEL FOR ON-LINE CONTROL OF THE CEREAL LEAF BEETLE (*OULEMA MELANOPUS* (L.))

By

Winston Cordell Fulton

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ABSTRACT

DEVELOPMENT OF A MODEL FOR ON-LINE CONTROL OF THE CEREAL LEAF BEETLE (*OULEMA MELANOPUS* (L.))

By

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On-line control of insect pests requires models which are accurate for only short time spans into the future and which may be initialized using data easily gathered by a farmer or a pest management scout. Such a model is developed here by omitting certain parts of the cereal leaf beetle ecosystem which were considered unimportant in determining the amount of damage in the current crop. These factors included the parasites of the beetle, the evidence of density dependent mortalities in the first and fourth instars, and evidence of the oviposition rate being dependent on photoperiod.

The model developed is a continuous time deterministic one, using time varying distributed delays of the Erlang type to represent insect life stages.

Much of the validation work was in terms of measuring the degree of synchrony between the model and field observations for several year's data. In order to get a high degree of synchrony, one parameter, that which was considered to move the adult beetles from wheat to oats in the spring had to be chosen arbitrarily for each year. This makes the use of the model in the on-line mode at

the moment impractical. However, under the assumption that this parameter will eventually be modeled or measured, sensitivity analysis of the model continued and showed that synchrony between the model and field was little affected by sampling bias against small instars, and was little affected by changes in larval development times. Synchrony is strongly affected by even small biases in the temperature data used to drive the model with biases of greater than 1% causing serious increases in the error.

When synchrony is improved as much as possible by adjusting the rate of movement of adults from wheat to oats in the spring, field egg density estimates taken between 110 and 220 °D>9 may be used to estimate total incidence of larvae to between 1 and 4 times the actual number observed. Predicted density bounds of this order of magnitude could be acceptable in an on-line pest management mode, since bounds on the error are known.

To maintain the error within these bounds following implementation would require an accurate determination of the temperature to which the insects are exposed up to the time of the sample, and a method of measuring the rate at which adults are moving from wheat to oats when the sampling takes place. This movement rate might be determined either from the sample, or be modeled in terms of environmental factors.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Dr. Dean L. Haynes for his friendship and support throughout my tenure as a graduate student. His philosophy on pest management, expressed most strongly at the Friday afternoon seminar, will continue to affect me in my professional career.

I also wish to thank my other guidance committee members for their invaluable input into my professional development: Dr. George Bird, Dr. William Cooper, Dr. Robert Ruppel, and Dr. Lal Tummala.

Finally I want to express my great pleasure at having been associated with a very remarkable series of graduate students: Stuart Gage, Dick Casagrande, John Jackman, Emmett Lampert, Al Sawyer, and Kasumbogo Untung.

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INTRODUCTION

The cereal leaf beetle, <u>Oulema melanopus</u> (L.) was once considered to be a major threat to the small grain industry of North America (Webster, et al., 1972). Since 1975, however, interest in the insect as a major threat has declined because the cereal leaf beetle has not, for unknown reasons, become a major economic problem. This interest may again be kindled when the cereal leaf beetle invades the huge acreages of spring grains in the west, but its development as a pest there can not be predicted.

The cereal leaf beetle is still an excellent experimental animal for research use because of the great deal of information which has been accumulated on its life history. It was with these points in mind that the procedure for developing a model for on-line control (Tummala and Haynes, 1977) of the cereal leaf beetle was investigated.

Because of the amount of information available on the cereal leaf beetle, a number of models have been written concerning it, three of which have been published. Each of these models was developed for a different purpose from the present one. The model of Lee, et al. (1976) was used to test the usefulness of partial differential equation models in an ecological setting and to find a closed form solution to the equations. The model of Tummala, et al. (1975) was developed to study the between generations dynamics of the cereal leaf beetle. The model of Gutierrez, et al. (1974) is certainly the closest to the model developed here in design and intent, but it differs in being a discrete, physiological time based model as opposed to the continuous, chronological time type model developed here.

The model developed here is for on-line control and that basically implies optimizing the use of pesticides.

For long-term optimal control of the cereal leaf beetle (a model for which is currently being prepared by V. Varadarajan under the direction of Dr. R. L. Tummala at Michigan State University) it will be necessary to consider the effects of management strategies on parasites of the beetle. But for on-line control the larval parasites can be ignored, since they emerge after pupation, and thus do not greatly affect the damage caused by the larva which they infest. The egg parasite *Anaphes flavipes* (Foerster) Hymenoptera Mymaridae, would have to be included in the model were it not for the fact that it develops large populations only late in the season (Gage, 1974) after most damage has been done.

To truly optimize the use of pesticides the model would have to predict the effects of beetle populations on yield, and determine the economic implications of that, but that is a study in itself. The approach here then is merely to predict population densities in a crop, the economic implications of which must await another work.

LITERATURE REVIEW

The natural history of the cereal leaf beetle in Michigan was described by Castro, et al. (1965) who reviewed much of the European literature on the insect.

Yun (1967) did most of the basic laboratory studies on the effects of various biological and environmental factors on the beetle. His data are used extensively in the model development and are discussed in the sections in which they are used.

Yun (1967) had treated the larvae as a single life stage instead of breaking it down into its four instars. Helgesen (1967) for his work on the population dynamics of the beetle provided information on the developmental rates of the individual instars.

Wilson and Shade (1966) provided some information on the survival and development of larvae on various species of Gramineae. Similar work was performed by Wellso (1973) who also investigated (1976) feeding and oviposition of the beetle on winter wheat and spring oats.

Ruesink (1972) and then Casagrande (1975) provided information on the emergence of adults from overwintering sites and their subsequent mortality rate.

The systems approach to pest management has been discussed often in the literature in the past few years, in a published joint symposium of the Entomological Society of Canada and the

Entomological Society of Alberta (N. D. Holmes, ed., 1974) and by Giese, et al. (1975) for example. Important aspects of the approach including environmental monitoring networks (Haynes, et al., 1973) biological monitoring (Fulton and Haynes, 1977) and on-line pest management (Tummala and Haynes, 1977) have been discussed.

There is certainly nothing new in using models in ecological systems (Pielou, 1969) but recently a wide variety of modeling techniques have been applied in ecology. For example, spectral analysis in general, reviewed by Platt and Denman (1975) and transfer function models in particular (Hacker, et al., 1975). The use of flowgraph to model biological systems has recently been attempted (Wiitanen, 1976). Control theoretic approaches to control of insect and biological systems in general are now in vogue (Mitchiner, et al., 1975; Vincent, 1975). The use of modeling and systems analysis in defining agricultural research needs has been evaluated by DeMichele (1975).

As discussed in the introduction, 3 models written specifically for the cereal leaf beetle have already been published (Gutierrez, 1974; Tummala, et al., 1975; and Lee, et al., 1975) but again these purposes were different from that of the model developed here.

The validation procedure is an integral part of modeling in the systems approach (Manetsch and Park, 1972; Shannon, 1975), but techniques and procedures for validation of complex ecological models are not well developed (Caswell, 1976; Miller, 1976).

PROBLEM DESCRIPTION

In the context of a sampling problem, any given population is composed of two types of individuals--those which can be observed with a given technique, and those which cannot be observed with this technique. The proportion which can be observed will depend on a number of factors, notably on the technique itself, the timing of the estimate in relation to population development, and intrinsic population parameters relating to the distribution of the individuals with respect to maturity (see Fulton and Haynes, 1977, for details of this development).

Briefly, referring to Figure 1A, the distribution of ages of the population at the initial value of maturity, f is shown. The dotted line indicates the position of the mean maturity, μ. Figure 1B shows the distribution of ages after some interval Δf and so on to Figure 1E. The two vertical lines from a_i and a_j represent the limits of integration, i.e., the ages which are observable with the sampling method being used. The proportion counted, therefore, lies between a_i and a_j.

In the earlier work (Fulton and Haynes, 1977) it was assumed that σ^2, the variance of the age distribution, remains constant with changes in f. It was also assumed that changes in population level were negligible or constant in rate through all ages. These assumptions were reasonable in the context of that work, but for pest

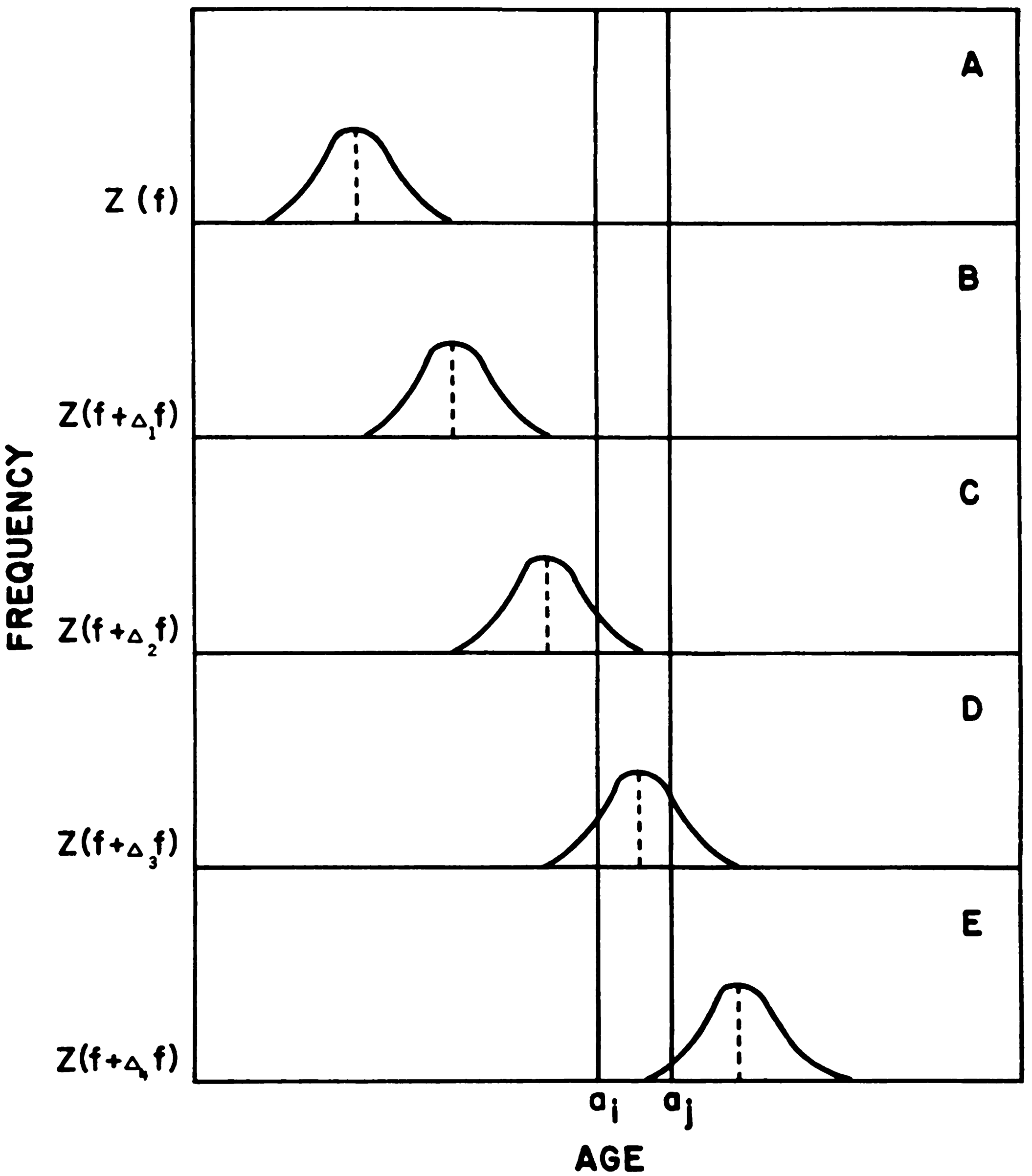


Figure 1.--Frequency distributions of ages of individuals in the population being sampled. A is at an initial value of maturity f. B-E are at subsequent values of f as the population ages.

management on an individual field basis, our interests are different. Here, a dynamic model capable of mimicking changes from field to field, and not just average conditions is essential.

The static model points out three factors that affect the proportion of the total population which is counted in any type of population. These are indicated in Figure 2. The effect on the proportion counted of changes in the observable ages is shown in Figure 2A, where it is clear that if more extreme ages can be sampled, a higher proportion of the whole population will be sampled. The effect of the distance of the population mean age from the age class observed is shown in Figure 2B. Obviously a much higher proportion of the whole can be sampled when the mean age is in the sampling interval. The effects of different degrees of dispersion in the population is shown in Figure 2C. A larger variance leads to a smaller proportion being counted.

It is clear, then, that the maturity of the population can affect the proportion of that population which is counted at a specific point in time. Not only will it affect the counts of the primary organism, but in cases where parasitized individuals are concerned, it affects the estimates of seasonal parasitism. The effects of maturity on the population density estimate can be minimized by choosing a sampling method which collects all age classes present or alternatively by sampling a life stage which is so long and stable that essentially all of the individuals in the population are in that life stage at one time. Slightly less effective is to attempt to take the population sample when the mean age of

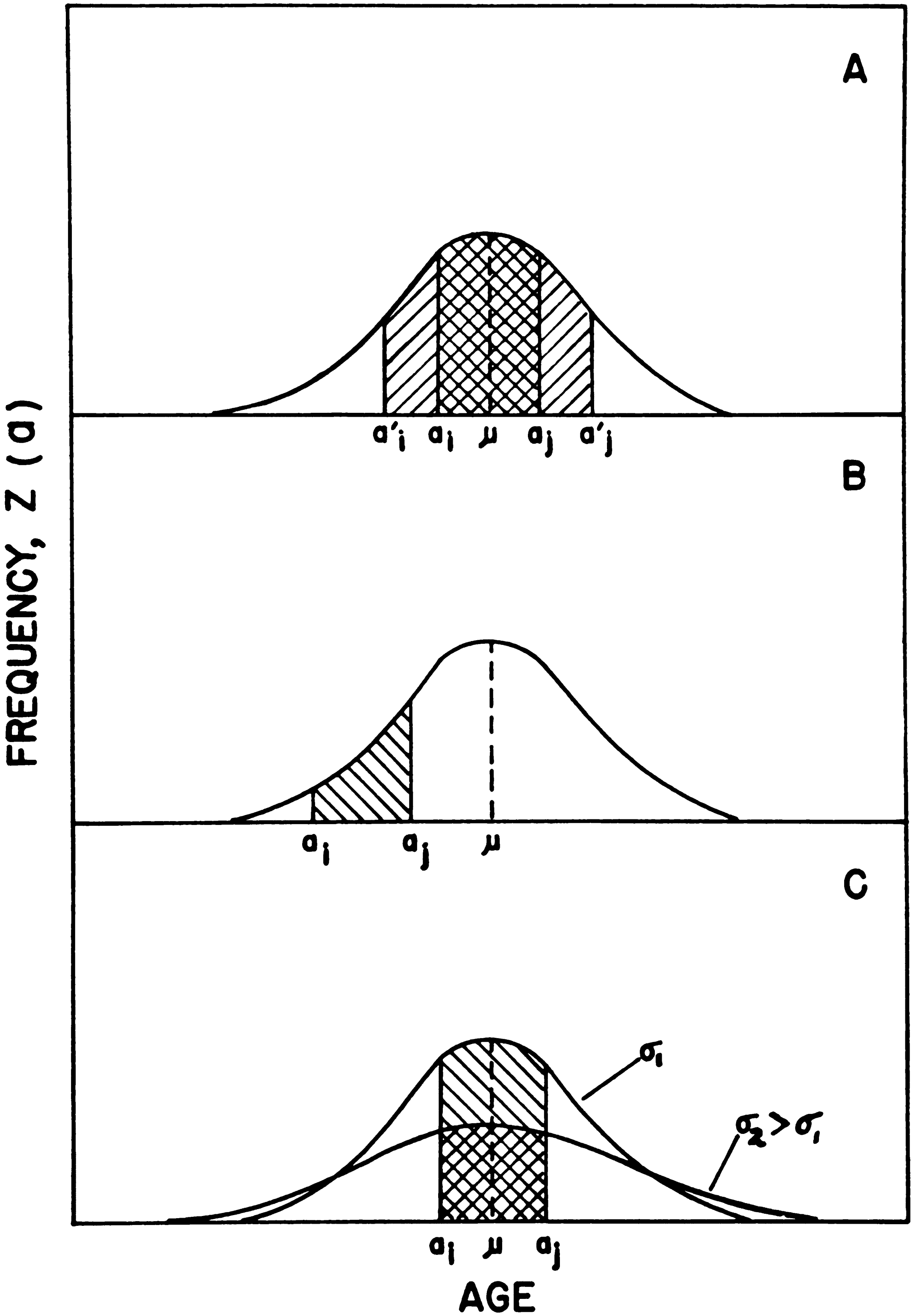


Figure 2.--Three factors which affect the proportion of the population counted. The a_i to a_j and a'_i to a'_j are observable ages, μ is the mean population age and σ is the standard deviation of ages.

individuals is near the midpoint of the observable age interval, so that the largest portion of the individuals can be observed.

In on-line pest management peak damage is likely to occur at peak density of certain life stages. Sampling, therefore, must precede the occurrence of that peak.

We have therefore to establish both population density and time synchrony to initialize a pest management model. Furthermore, sampling must be early enough so that control measures can be effectively applied after sampling and evaluating the management alternatives. That will constrain our choice of sampling techniques. Trade-offs exist between sampling early to get a longer time to implement a control procedure and the accuracy of model predictions over an increasingly future time. Models to predict the immediate future can be much simpler than those needed to predict the far future with the same degree of accuracy.

ANALYTICAL APPROACH

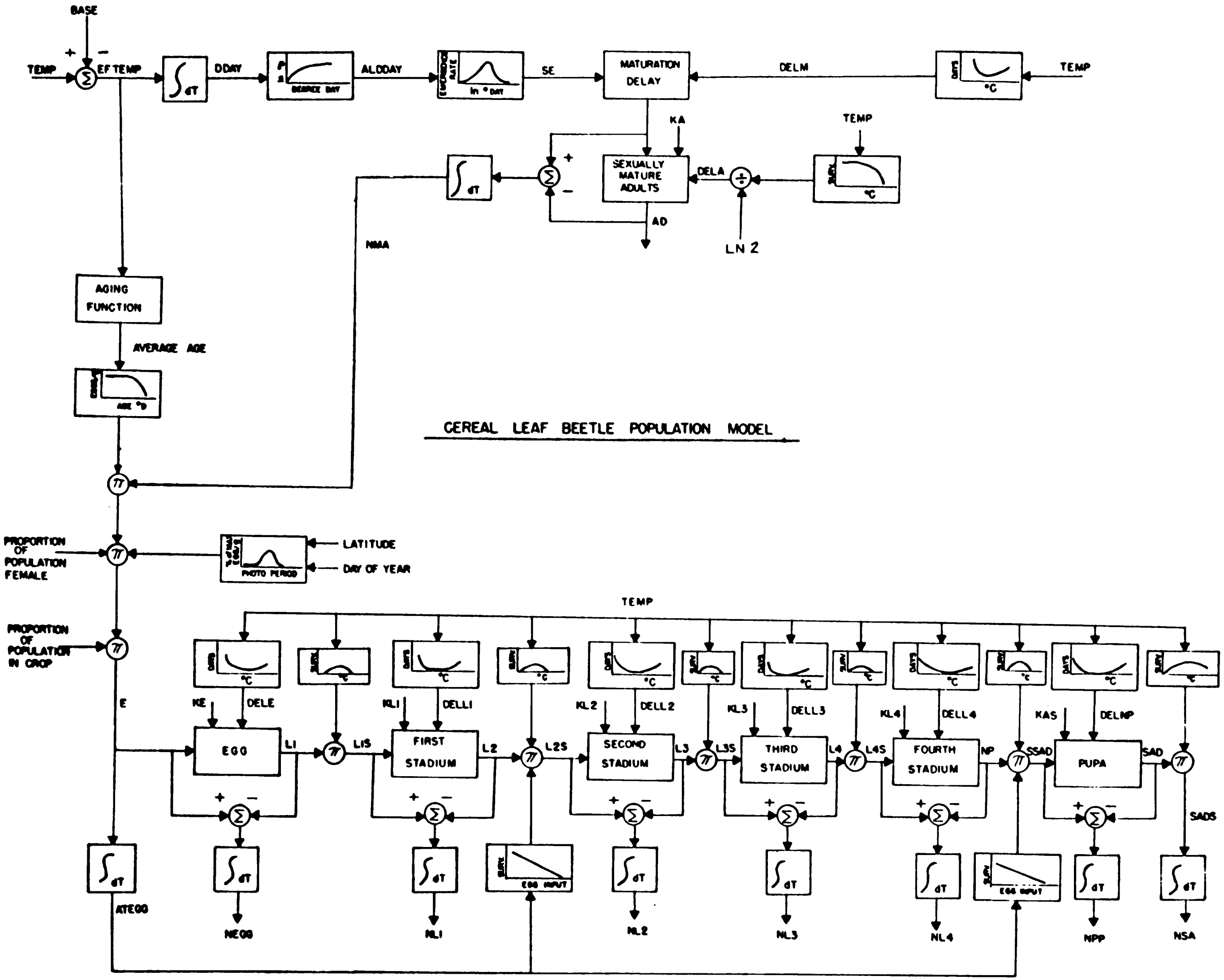
The Model

Since the age structure of the population is important in interpreting population density, and field samples will be used to initialize a population model for the cereal leaf beetle, a pest model was constructed in which the age distribution of the population at any point in time is available as output (Figure 3).

This model was constructed mainly from a structural rather than a black box point of view. System components are broken down to a level which shows their functioning in relation to physical factors. A black box approach would show the functioning of the components in relation to time only. The structural approach offers more insight into the workings of the natural system.

Temperature (TEMP) has the most widely distributed effects in this model. It is used (directly or indirectly) to drive a number of functions which affect adults leaving overwintering sites, survival, oviposition, and length of a life stage. Other inputs are the latitude and day of the year so that photoperiod can be determined, the proportion of the population which is female, the proportion of the population which is in the crop being considered, and K values for the distributed delays (see below) used to represent life stages.

Figure 3.--A functional block diagram model of the cereal leaf beetle.



CEREAL LEAF BEETLE POPULATION MODEL

Model outputs are the number of individuals in each life stage at any time.

The usual temperature data available from the National Weather Service are daily maximums and minimums. Assuming that temperature changes within a day are sinusoidal with maximum and the minimum 12 hours apart, degree-day accumulations with errors on the order of 5% over a growing season can be computed (Baskerville and Emin, 1969). Equation 1 is used in the model for temperature at any time of day (HTIME).

$$\text{TEMP} = \frac{(\text{AMAX} + \text{AMIN})}{2} + (\text{AMAX} - \text{AMIN})* \qquad (1)$$

$$\{\text{Sin } (\text{HTIME} - 9)* (2\pi/24)\}$$

Where AMAX is the maximum temperature and AMIN the minimum for that day. The factor 9 causes AMIN to occur at 3 a.m. and AMAX to occur at 3 p.m.

Since development is not linearly related to temperature (Fulton, 1975) the use of degree-day values to determine developmental times is not, strictly speaking, valid. Despite this, degree-days were used as a predictor of spring movement of adults from their overwintering sites and the oviposition rate of females.

Model Parameterization

In this section of this thesis the parameterization of the various components of the model will be developed, beginning with the emergence of adults in the spring and ending with the emergence of summer adults from the pupae.

Spring Adult Emergence

Referring to the upper left-hand corner of Figure 3, the base temperature of 9°C for CLB aging is subtracted from the instantaneous temperature TEMP to give the temperature EFTEMP which is effective in CLB aging. This value is integrated over time to give the °Day accumulation (DDAY) which is transformed to natural logs (ALDDAY). ALDDAY determines the rate (SE) at which adults move from their overwintering sites.

Data on the spring movement of adults from their overwintering sites for 1971, 1972 (Ruesink, 1972), and 1973 (Casagrande, 1975) at Gull Lake were the basis for a probit-regression model for this movement. The relation between the probit for emergence of adults and the natural logarithm of accumulated degree-days > 9 for these three years is linear (Figure 4). The regression line for the pooled data is:

$$Pr = -2.90974 + 1.98964 \ln A \qquad (2)$$

where Pr is the probit of spring emergence and A is the accumulated degree-days > 9.

A probit is defined by Finney (1971) as Y in 3:

$$P = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{Y-5} \exp\{-\tfrac{1}{2}u^2\}\ du \qquad (3)$$

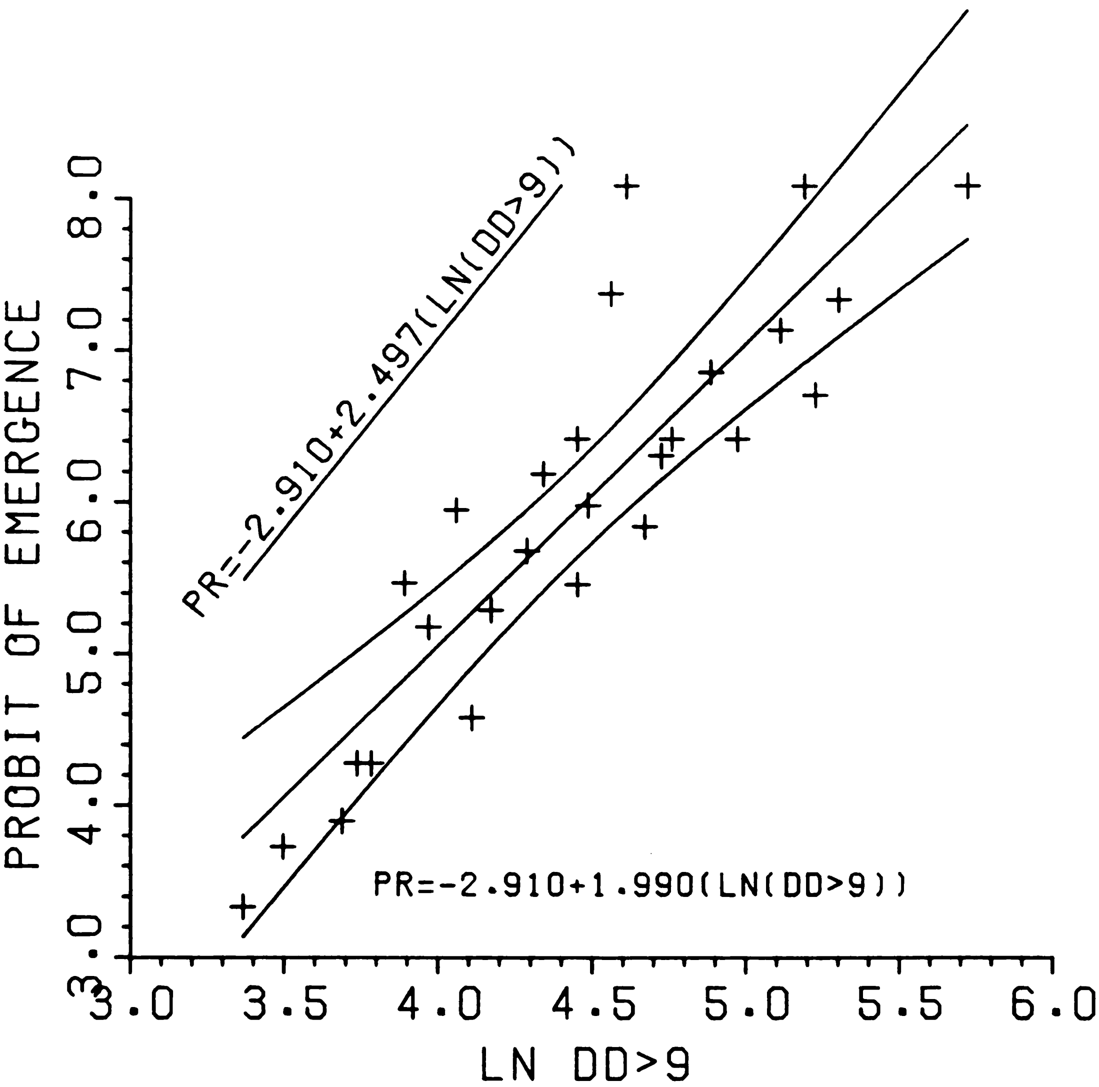


Figure 4.--The regression of the probit of cereal leaf beetle adult emergence on the natural logarithm of °D>9C. The line above the data was used in later model runs. Data from Ruesink (1972) and Casagrande (1975).

that is, it is 5 more than the abscissa corresponding to a probability P in a normal distribution with mean 0 and variance 1. Emergence data were transformed to cumulative percent and then to probit values. The last observation was assumed to represent 99.9 percent emergence rather than 100 percent emergence, since the probit of 100 percent is + ∞.

Solving equation 2 for A when Pr = 5 gives 50% spring emergence at 53 °D > 9. The standard deviation of the normal distribution is given by the reciprocal of the slope in equation 2:

$$S = \frac{1}{b} = \frac{1}{1.98964} = 0.5026 \qquad (4)$$

The other line in Figure 4, with its defining equation, is used in the model development and will be discussed in a later section. Having moved from their overwintering sites, spring adults undergo a maturation process the length of which, DELM, is temperature dependent (Figure 5). Adults leaving this delay at a rate DM, enter the sexually mature adult stage then die at a rate AD.

<u>Adult Survival</u>

Yun (1967) showed that at the extreme temperatures of -18° and 43°C spring adult mortality reached 100% in well under 1 hour. Unfortunately this is the extent of the information from controlled environments on the survival of adult CLBs as a function of temperature. Adult mortality in the field over various finite time periods were presented by Casagrande (1975). Those data are confounded by the fact that temperatures fluctuated over the period when mortalities were being measured, and the possibility of seasonal changes

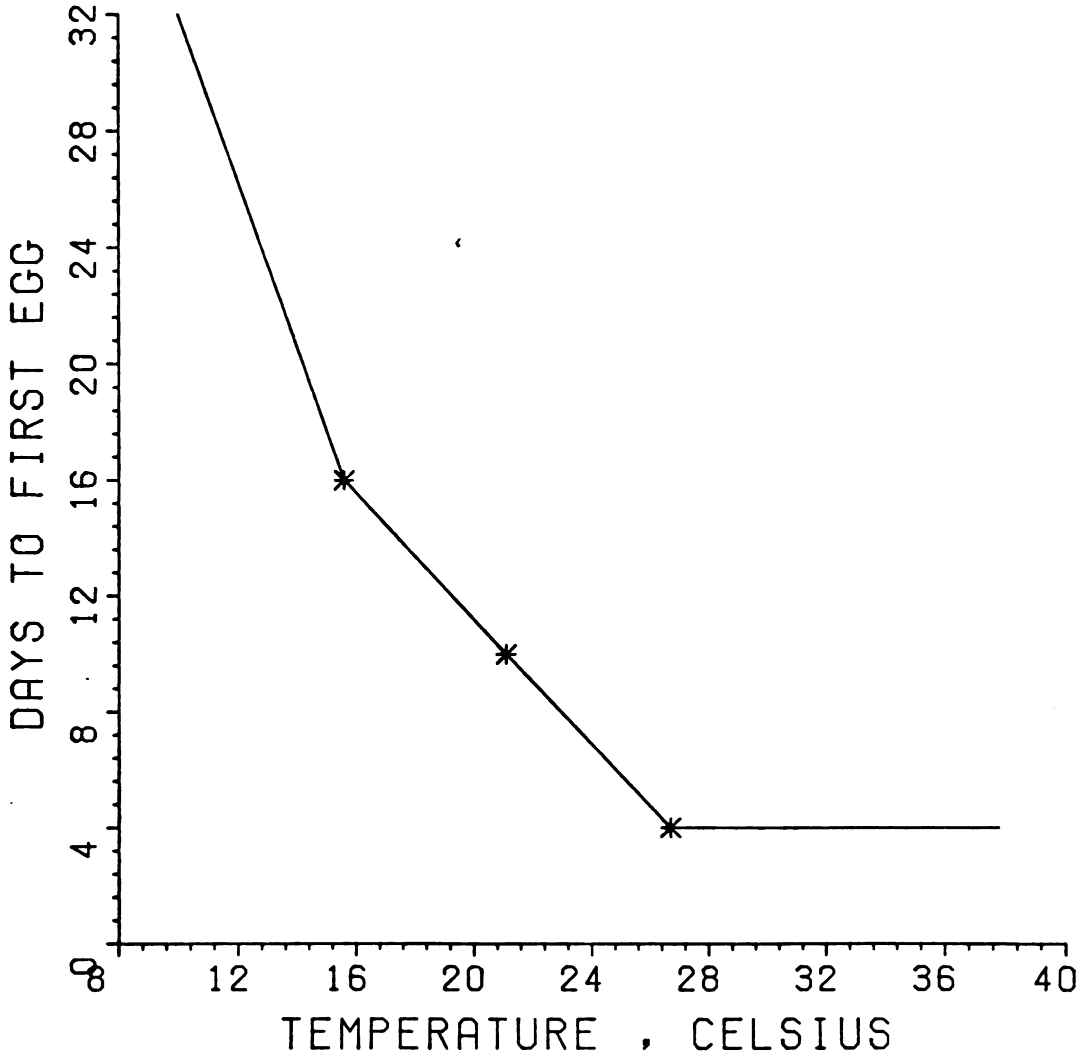


Figure 5.--Days from adult emergence from overwintering sites to time of first oviposition as a function of temperature. Data from Yun (1967).

in the mortality rate of adults which was not determined by temperature.

The model is a continuous as opposed to a discrete one, and the assumption was made that temperature dependent mortalities operated continuously. This implies that:

$$P_t = P_o\, e^{at}$$

where; t = time
P_t = population at time t.
P_o = initial population.
and a = instantaneous survival rate.

A more thorough treatment of this subject will be undertaken in the section of egg and larval survival, below.

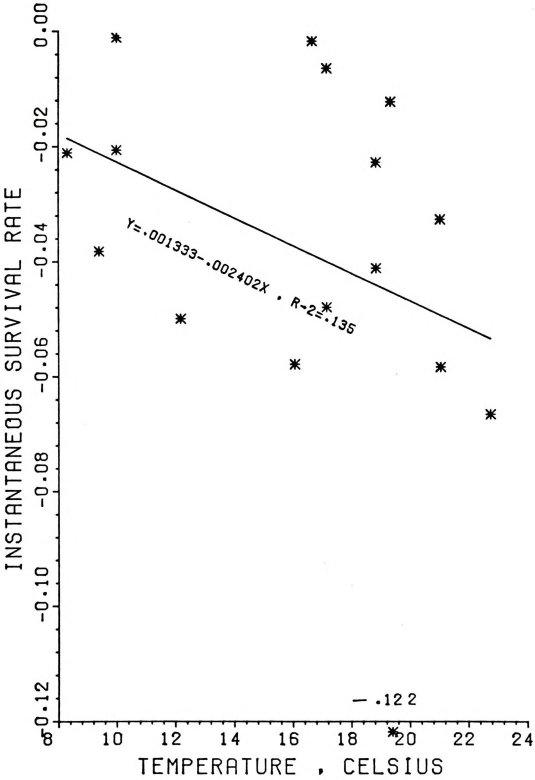
Instaneous survival rates for adults were computed from Casagrande's data and are plotted over temperature in Figure 6. Excluding the aberrant point (19.4, -12.2) made little difference in the position of the regression line, so the line is for all of the data.

The survival rate is used to compute the half-life of adults under the existing temperature regimen;

$$P_t = P_o \quad e^{at}$$

$$\frac{P_t}{P_o} = e^{at}$$

Figure 6.--Instantaneous survival rate of adult cereal leaf beetles as a function of temperature. (Data derived from Casagrande, 1975, Table 9.)


INSTANTANEOUS SURVIVAL RATE
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
Y=.001333-.002402X , R-2=.135
— .122
8
10
12
14
16
18
20
22
24
TEMPERATURE , CELSIUS

setting this equal to ½;

$$\frac{P_t}{P_o} = e^{at} = \tfrac{1}{2}$$

$$t = \frac{-\ln 2}{a}$$

This half-life, t, while it is a median and not a mean, is used as an estimate of the mean survival time, DELA, and fed into the sexually mature adult stage represented by a time varying delay.

Time Varying Delays

A basic element of this model is the use of time varying delays to represent the life stages of the CLB. Manetsch and Park (1972) show that these delays represent an aggregative approximation to the response of individuals in a population undergoing a pure time lag in the input variable. The time lag of individuals in the population are assumed to be random variates from a probability density function, $f(\tau)$. In this case, $f(\tau)$ is assumed to be the Erlang function:

$$f(\tau) = \frac{(\alpha K)^{K} (\tau)^{(K-1)} e^{-K\alpha\tau}}{(K-1)!} \tag{5}$$

The mean for this distribution is:

$$\varepsilon[\tau] = 1/\alpha \tag{6}$$

its variance is given by:

$$\mathrm{Var}[\tau] = \frac{1}{K\alpha^2} \tag{7}$$

The strictly positive integer valued parameter K determines the member of the Erlang family of density functions desired. When K = 1, the density function is the exponential (Figure 7). When K increases without bound, the Erlang distribution approaches the normal distribution with mean $1/\alpha$ and zero variance.

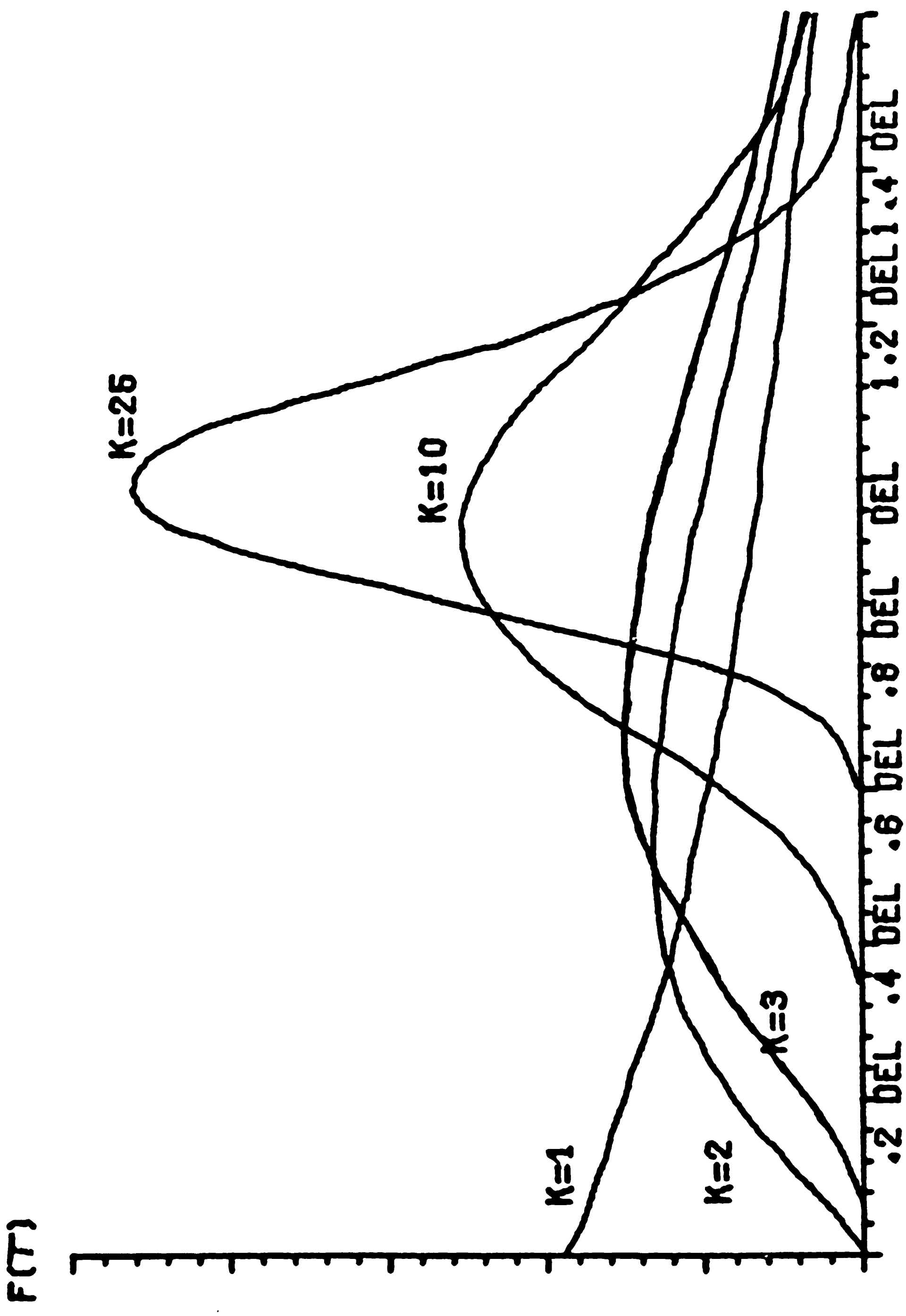
The Erlang function was selected because different values for K allow the same function to be used as an approximation for many different density functions. Manetsch and Park (1972) have shown that the aggregative delay characterized by a K^{th} order Erland function are represented by a K^{th} order linear differential equation. The output from such a delay is easily simulated by delay routines presented by these authors.

Computing an estimate of K from the data is shown in Appendix A. The number of individuals in any life stage is now computed in the delay routine itself and passed back to the main program (see Appendix B).

Oviposition

Unpublished data from S. G. Wellso on the oviposition by CLB in oats and wheat in 1972 at East Lansing indicated that the oviposition rate on Genesee wheat and Clintland oats are essentially the same during the initial period of oviposition. Figure 8 shows the pooled wheat and oat data for the first 222 °D>9 after

Figure 7.--Several members of the Erlang family of curves used in the time varying delays in the simulation model.


F(T)
K=1
K=2
K=3
K=10
K=25
.2 DEL
.4 DEL
.6 DEL
.8 DEL
DEL
1.2 DEL
1.4 DEL

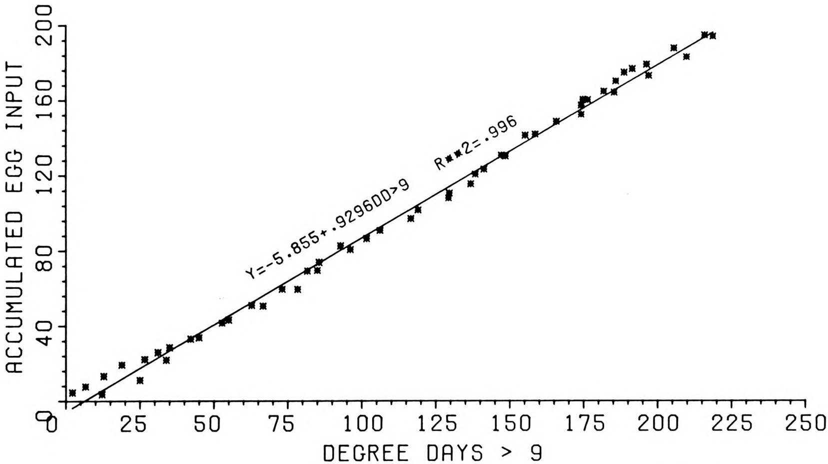


Figure 8.--Accumulated cereal leaf beetle egg input as a function of accumulated °D>9C. Pooled data for wheat and oats. Unpublished data from Dr. S. G. Wellso.

subtracting the degree-day value at the beginning of the experiment from each data set. The equation for the line is:

$$E = -5.855 + .9296\ D,\ r^2 = .996 \tag{8}$$

where E is the accumulated number of eggs per female and D is the accumulated °Days > 9 value from the start of the experiment.

Figure 9 shows the oviposition data for wheat (lower curve) and oats after 222 °D>9 had been accumulated. The relationship is nearly linear on a log scale, but clearly the slopes of the lines for wheat and for oats are different. The equations for the lines are:

$$\text{Wheat:}\quad E = -630.79 + 153.606\ \ln D,\ r^2 = .998 \tag{9}$$

$$\text{Oats:}\quad E = -820.05 + 189.253\ \ln D,\ r^2 = .996 \tag{10}$$

In the model, it is the oviposition <u>rate</u> which is needed; hence, the derivatives of equations 8, 9, and 10 were used.

$$dE/dD = .9296 \tag{11}$$

for pooled linear part.

$$dE/dD = 153.606/D \tag{12}$$

for wheat when D is more than 165 °D>9.

$$dE/dD = 189.253/D \tag{13}$$

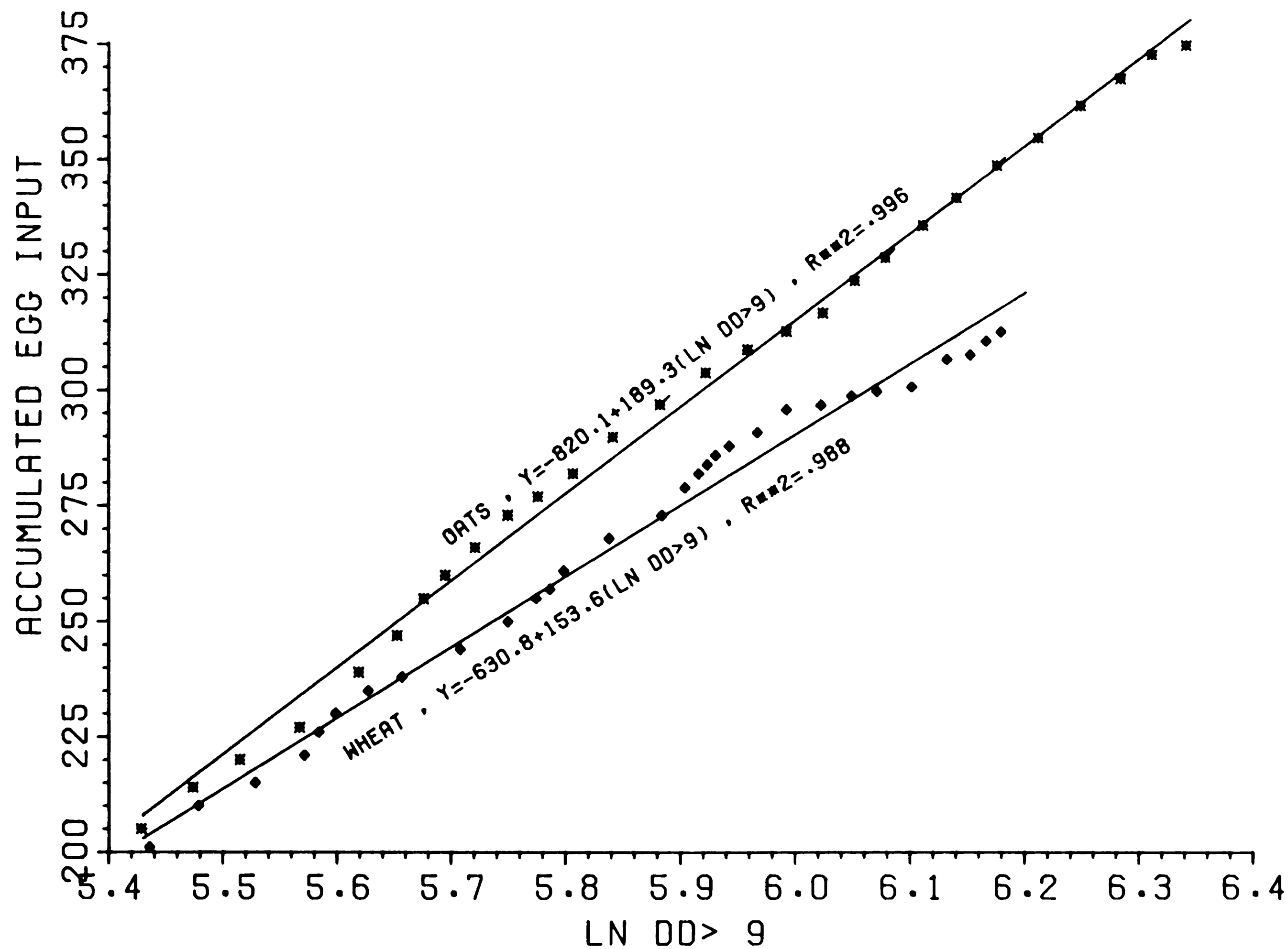


Figure 9.--Accumulated cereal leaf beetle egg input into wheat and oats as a function of the natural logarithm of °D>9C. Unpublished data from Dr. S. G. Wellso.

for oats when D is more than 203 °D>9. Although equation 8 is based on pooled data from 0 to 222 °D>9, and equation 9 and 10 on data from 222 °D>9 and greater, the rate equations 11, 12, and 13 are used over a slightly different range. This was necessary in order to have a single valued function for oviposition in each case. For, solving for the point at which the pooled data rate equals the curvilinear rate on oats, one has:

$$189.253/D = .9297 \Rightarrow D = 203.6 \tag{14}$$

and for wheat:

$$153.606/D = .9297 \Rightarrow D = 165.2 \tag{15}$$

Figure 10 shows the oviposition rate functions as used in the models. The vertical axis is eggs/female/°D>9; the horizontal axis is "age" of the female in °D>9.

Yun (1967, pp. 47, 48) showed that the CLB oviposition rate is strongly related to photoperiod. This function is present in the model, however, its output is set to one because the degree of refinement of the model does not permit its use.

Movement from Wheat to Oats

Of the eggs laid some will go into the crop of concern, e.g., oats or wheat, and only those are considered in each simulation.

An initial estimate of the rate at which adults moved from wheat to oats was computed as follows:

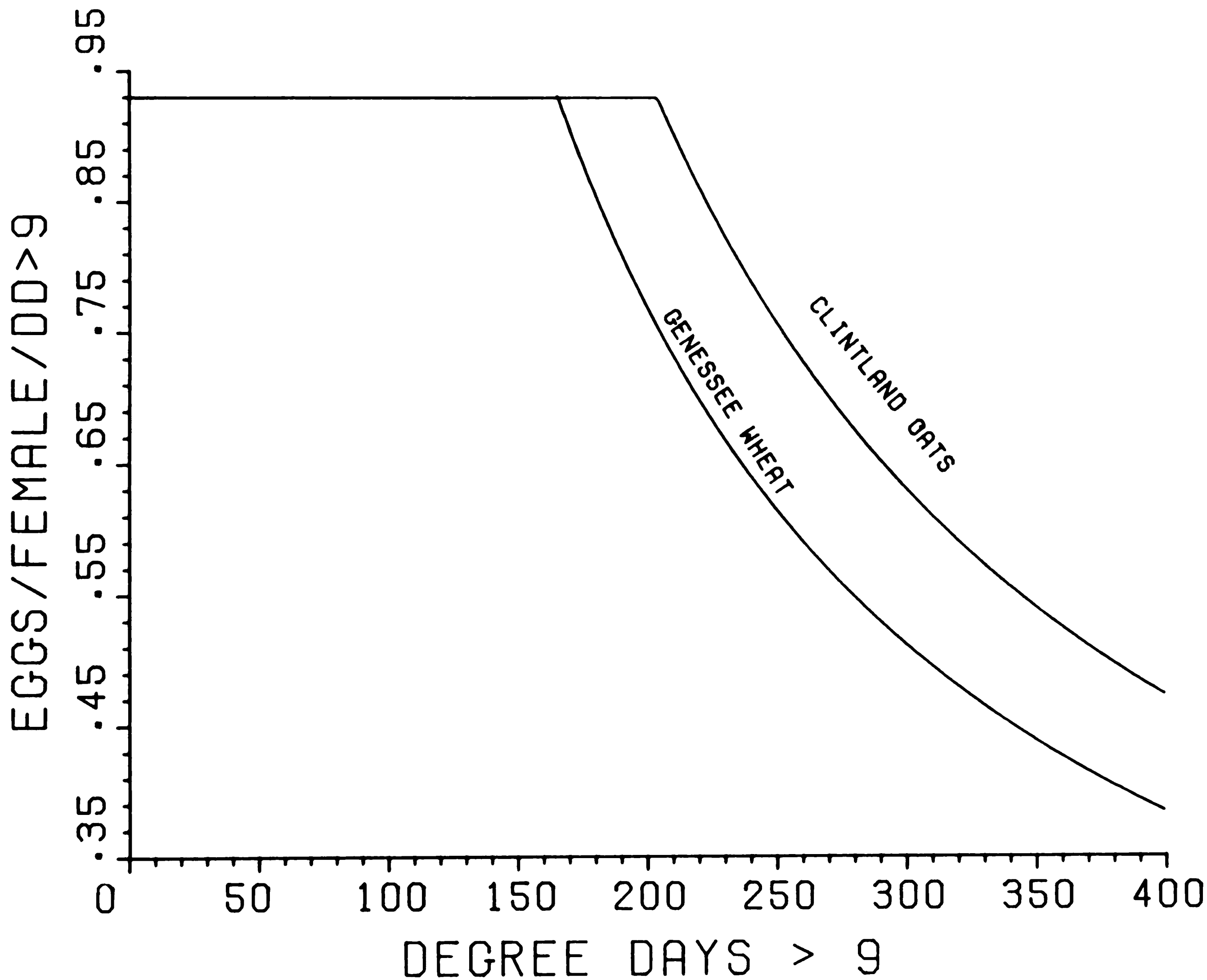


Figure 10.--Cereal leaf beetle oviposition rate as a function of age in accumulated °D>9C.

The last eggs in wheat at Gull Lake were typically observed at about 700 °D>48 (Gage, 1974, pp. 77, 78; Fulton, 1975, p. 60). Assuming that on the average these were half developed when found, then they were laid at about 580 °D>48, or ≃ 840 °D>42. Assuming adults start to move as soon as oats emerge, first eggs in oats are found at about 193 °D>48 (Gage, 1974) and would have been slightly developed, say they were laid at 145 °D>48 (≃ 240 °D>42).

Assume all adults move from wheat, etc., to oats, etc., (or die) during that 600 °D>42. Peak eggs in oats occur at about 485 °D>48 (467, Gage, 1974; 503, Fulton, 1975) ≃ 710 °D>42, again assume they were half developed when found, they were then laid at about 365 °D>48 ≃ 540 °D>42, that is about halfway between time of first egg in oats and last egg in wheat.

If it is further assumed that the movement between crops follows a normal distribution, and that at the first observation of an egg in oats, about 1% are there, then the proportion of the adult population which is in oats is given by the equation;

$$Y = .8625 + \begin{array}{l} .00766\ ^{\circ}D{>}42F \\ (.01379\ ^{\circ}D{>}5.6C) \end{array} \qquad (16)$$

where Y is the probit of the proportion of adults in oats at any value of °D>42 (in Fahrenheit) or °D>5.6 (in Celsius).

Total egg input (ATEGG) is computed as the integral of net oviposition rate (E). This value is the "egg input" used to estimate density-dependent survival in the first and fourth instars by Helgesen and Haynes (1972). Density-dependent survival is not incorporated into this model, but it would be very easily added (Figure 3). It is not currently there because the evidence for density-dependent mortality is sketchy, and certain of the scaling procedures developed during model validation can not be used if density dependent functions are used in the model.

The Egg Stage

Eggs enter the egg stage or delay at a rate E and remain there for a length of time (DELE) which is dependent on temperature (Figure 11) and survival, which is a function of temperature (Figure 12).

Survival as a function of temperature can be represented in a number of ways. In Figure 12 we have survival over the whole stage, but since the time spent in the stage is also a function of temperature, there is an interaction there. That interaction can be removed using the instantaneous survival rate for eggs (Figure 13). In the model, the equation used for egg survival is:

$$P_{t+Dt} = P_t \, e^{-.0423 - .002975 \, TEMP} \tag{17}$$

where, t = time

Dt = the simulation time increment

P = population

$TEMP$ = temperature, in Celsius.

The form of the exponent has been assumed linear throughout this work. A longer series of experiments on survival and development

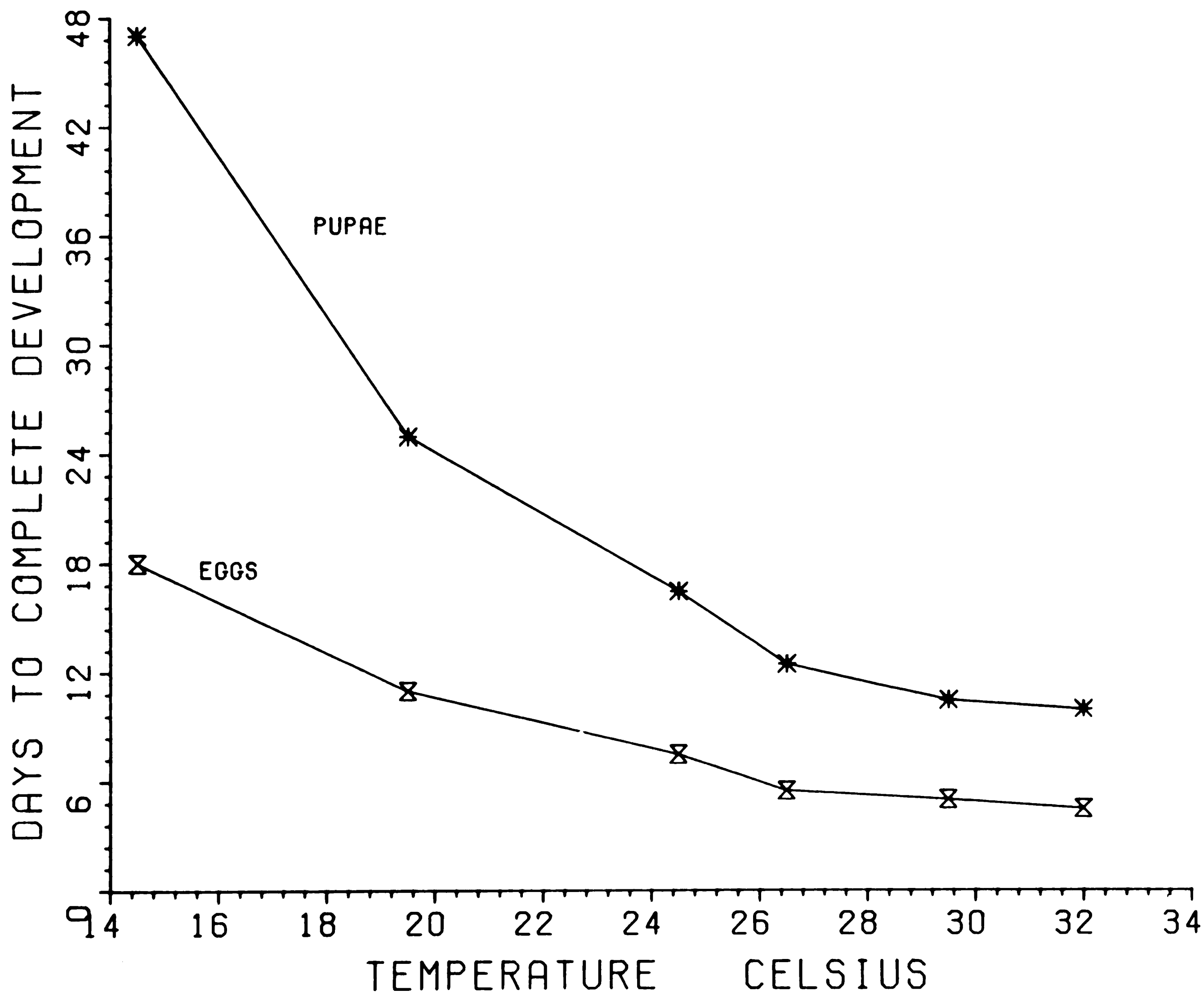


Figure 11.--Development times for cereal leaf beetle eggs and pupae as a function of temperature. (Data from Yun, 1967.)

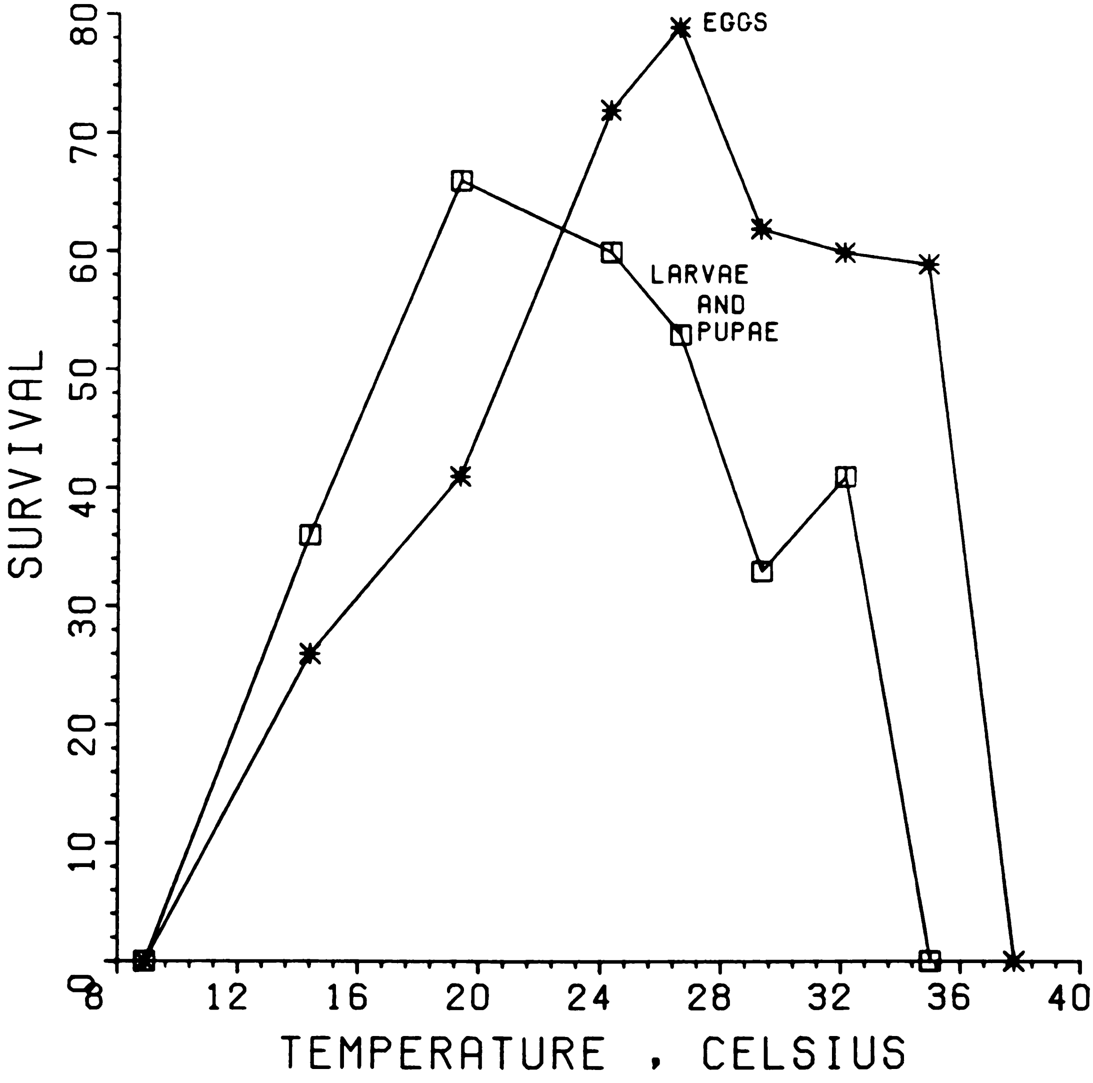
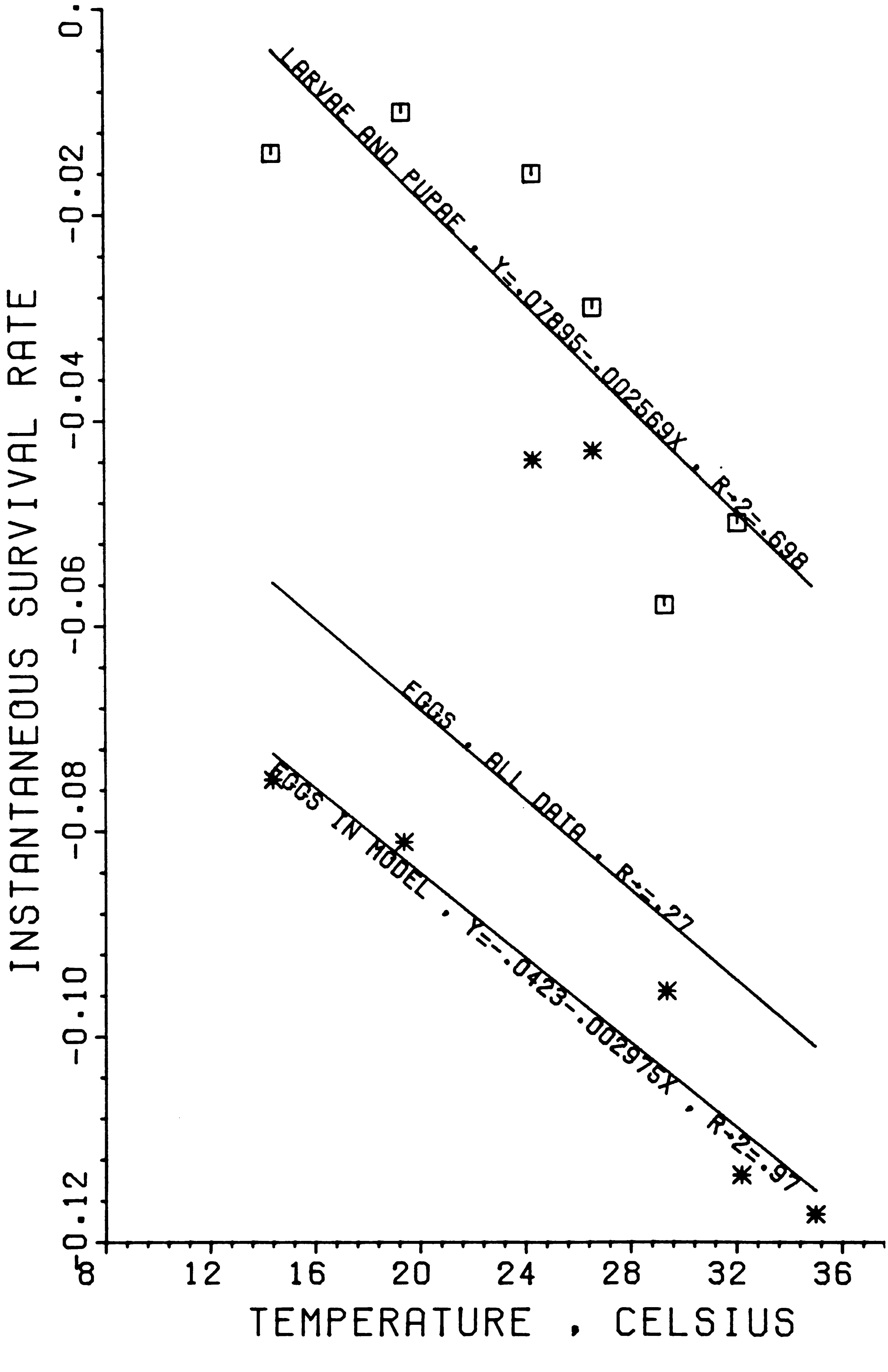


Figure 12.--Survival of eggs, larvae and pupae as a function of temperature. (Data from Yun, 1967.)

Figure 13.--Instantaneous survival rates for eggs and for larvae and pupae as a function of temperature. (Derived from data presented by Yun, 1967, and Table 12.)



INSTANTANEOUS SURVIVAL RATE
0.
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
LARVAE AND PUPAE , Y=-.07895-.002569X , R-2=.698
EGGS , ALL DATA , R-2=.27
EGGS IN MODEL , Y=-.0423-.002975X , R-2=.97
8
12
16
20
24
28
32
36
TEMPERATURE , CELSIUS

as a function of temperature would be necessary to determine the exact relation. The aberrant points (near -0.04) in the data were excluded from determining the function used in the model since they affect the position of the line considerably, yet the slope of the line is essentially the same for both lines.

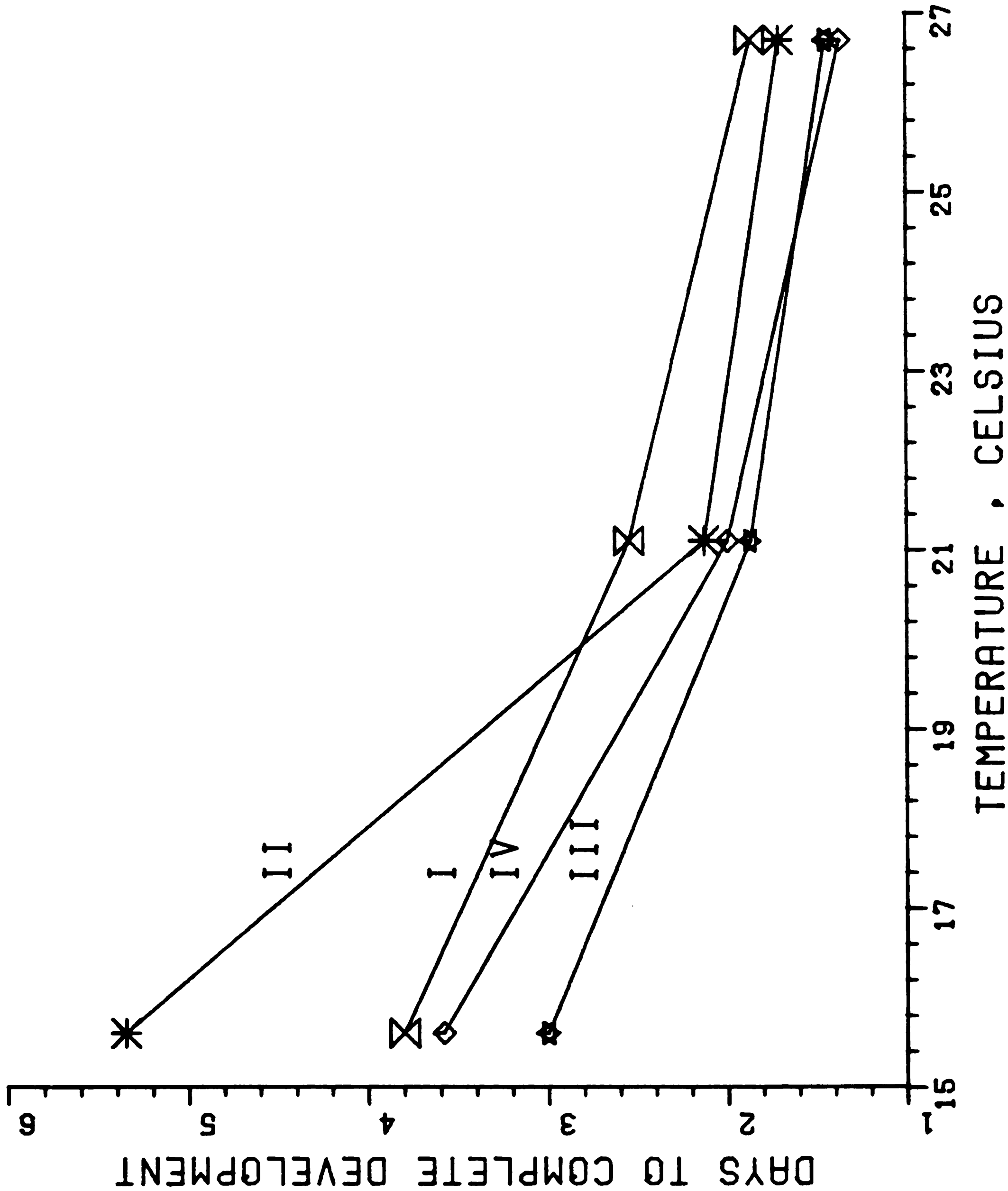
In the block diagram model, mortality of the various immature stages is shown as taking place between the stages. That is for eggs at the time of eclosion, and for larvae at the time of the moult. This is a reasonable approach under the assumption of discrete periods of mortality, but under the assumption of continuous mortality used herein, mortality must take place within the growth stage, that is within the delay. When the change was made to this type of mortality, it was found that the delay function with attrition provided by Manetsch and Park (1972) was in error. A modification to another of these routines (VDEL) was made in order to implement the continuous mortality function. The modified routine is included in Appendix B.

The Larval Stage

Eggs hatch and enter the first larval stage at a rate L1S. Survival as a function of temperature for larvae and pupae was shown in Figures 12 and 13. Development times as a function of temperature were given for pupae in Figure 11. They are given in Figure 14 for the individual larval instars.

The approach used for egg development and survival is continued through each of the larval instars and the pupa, ending with

Figure 14.--Developmental times for the 4 instars of the cereal leaf beetle as a function of temperature (after Helgesen and Haynes, 1972).


DAYS TO COMPLETE DEVELOPMENT
TEMPERATURE , CELSIUS
1
2
3
4
5
6
15
17
19
21
23
25
27
I
II
III
IV

the rate at which summer adults are being produced (SADS) and the number of summer adults (NSA).

New survival functions could easily be added as multipliers if the survivals are multiplicative, or by modification of existing survival functions when two or more of these are additive (Morris, 1965). Pupae which survive to become summer adults are accumulated and stored since there is no diapause function in the model.

FORTRAN Implementation

Table look-up functions TABLIE and TABLI from Llewellyn (1965) are used in the FORTRAN version of this model (Appendix B). These routines use linear interpolation between data points on each entry, and both restrict the value of the function returned to certain limits. Values for arguments below the minimum are set to the functional value for the minimum, and values for arguments above the maximum are set to the functional value for the maximums. TABLIE requires that the functional values be given for equally spaced arguments, and is, therefore, efficient for smooth, regular functions. TABLI does not require equally spaced arguments, and is, therefore, more efficient for irregular functions.

These function subroutines are used extensively in this model since they allow one to emphasize the structure of the model rather than curve fitting. Also, frequently the quality of the data does not warrant extensive curve fitting efforts.

Function VDEL returns the output rate when the input rate is XVIN. The distribution of the delay is Erlang with mean $\frac{1}{\text{DEL}}$ and variance related to K (equation 7). The time-varying aspect of the function is reflected in the parameter DELP, which is the previous value of DEL.

Function DAY computes the length of the photoperiod on day I at latitude PHI. The accuracy of this function is related to the latitude and the time of year. In the worst case tested (PHI = 54°N), the average error was about one minute, while the worst was about 15 minutes in September. The logic was developed by R. Brandenburg.

Function NDTR is from the IBM Scientific Subroutine Package Version III (anonymous, 1968). It computes the normal probability density (D) and distribution (P). This function is used to estimate the rate at which spring adults move from their overwintering sites.

As was mentioned earlier, the effects of photoperiod on oviposition are not yet included in the model. The mechanism for doing this is included in function DAY and function PEG. PEG uses TABLI to find the percent of maximum response which can be expected under the current photoperiod and reflects the data presented in Yun (1967).

Sampling to Initialize the Model

Extensive use was made of the sampling data in Helgesen (1969, square yard and square foot samples for larvae); Ruesink (1970, sweepnet sampling for adults and larvae); Gage (1972, 1974, square foot samples, planting date, number of stems per square foot); Jackman (1976 and unpublished, planting date, square foot samples, number of larvae per stem, number of stems per foot through the season); Fulton (1975, sweepnet sampling of larvae through the season); Sawyer (1976, square foot samples, stem densities, relation of mean and variance in square foot samples); Logan (1977 and unpublished, sweepnet samples and square foot samples).

If the information to initialize the model is to be provided by the farmer or scout from individual fields, it would be desirable, if indeed not essential, that the data provided be gathered cheaply and with little technology. Data of this type include: (a) planting data, (b) plant height at sampling time, (c) number of eggs per stem and number of larvae per stem, (d) number of stems per foot.

The sampling for this dissertation was primarily the number of eggs and larvae per stem. Data were taken from three fields at Niles, Michigan from the area studied by Sawyer to determine the effect of pubescent wheat on cereal leaf beetle populations.

Several times through the season one hundred single stem samples were collected from randomly chosen locations within each of three fields and the numbers of eggs and of larvae on each stem were recorded. The variance plotted over the mean for those three fields (designated 10-2-4, 1-3-6, 3-3-3 by Sawyer) is shown in Figure 15 for eggs (r^2 = .86), and in Figure 16 for larvae (r^2 = .96), and in Figure 17 for combined eggs and larvae (r^2 = .96). These relationships can be used to determine the sample size required to achieve a given degree of precision in the estimate of the mean density.

Figure 15.--The variance-mean relationship for single oat stem samples of cereal leaf beetle eggs.

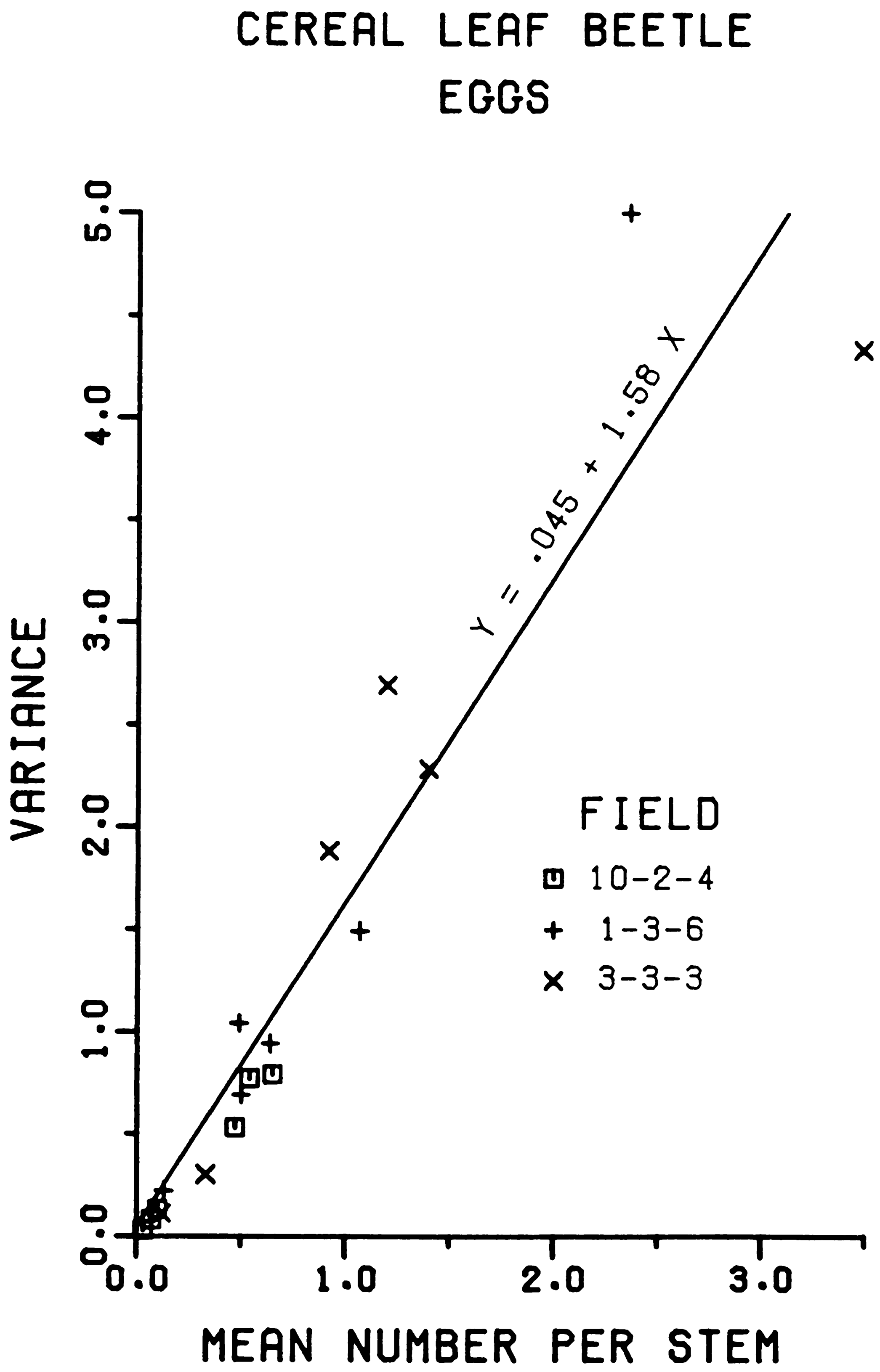

CEREAL LEAF BEETLE
EGGS
VARIANCE
MEAN NUMBER PER STEM
Y = .045 + 1.58 X
FIELD
10-2-4
1-3-6
3-3-3
0.0
1.0
2.0
3.0
4.0
5.0
0.0
1.0
2.0
3.0

Figure 16.--The variance-mean relationship for single oat stem samples of cereal leaf beetle larvae.

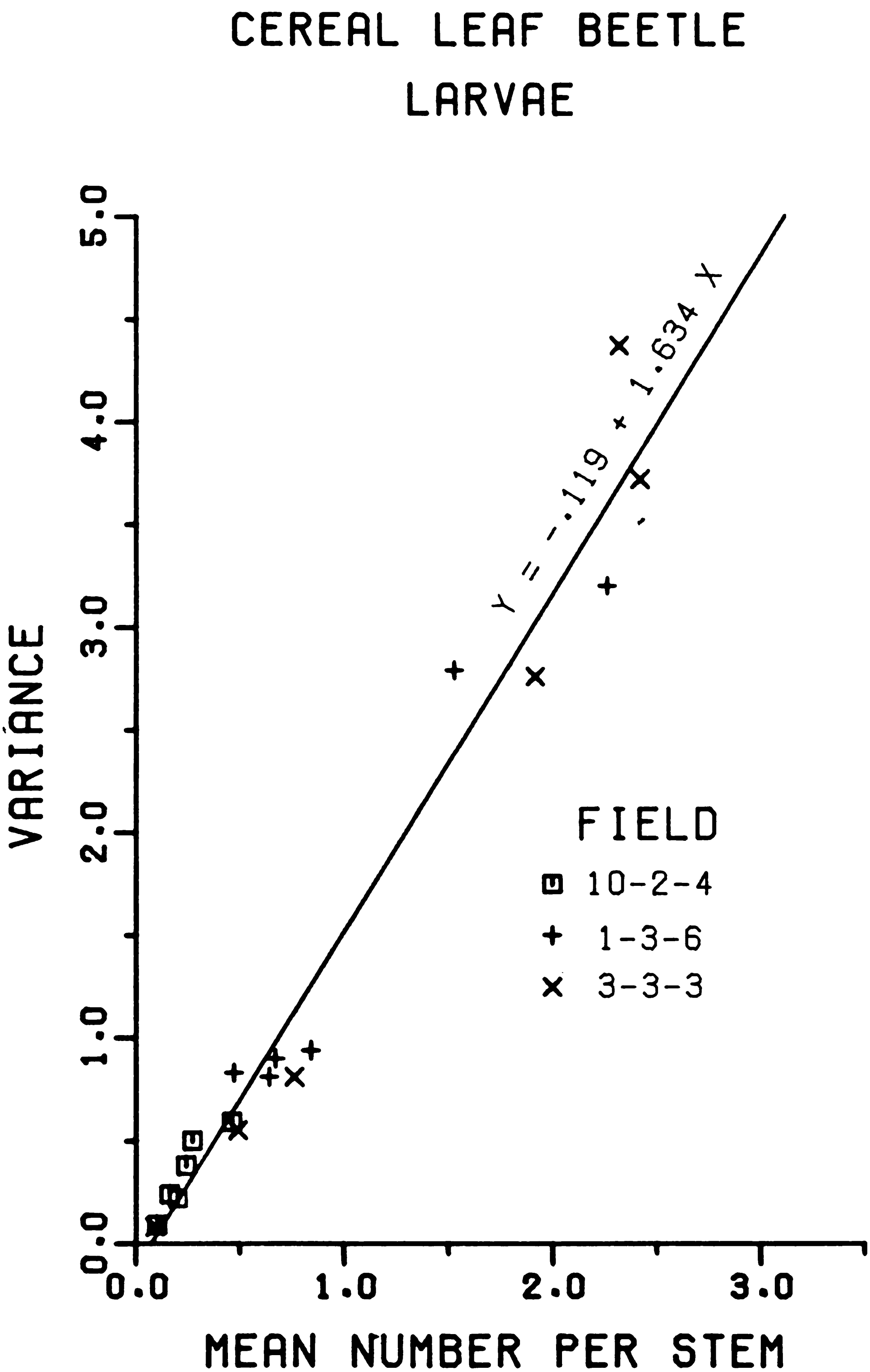
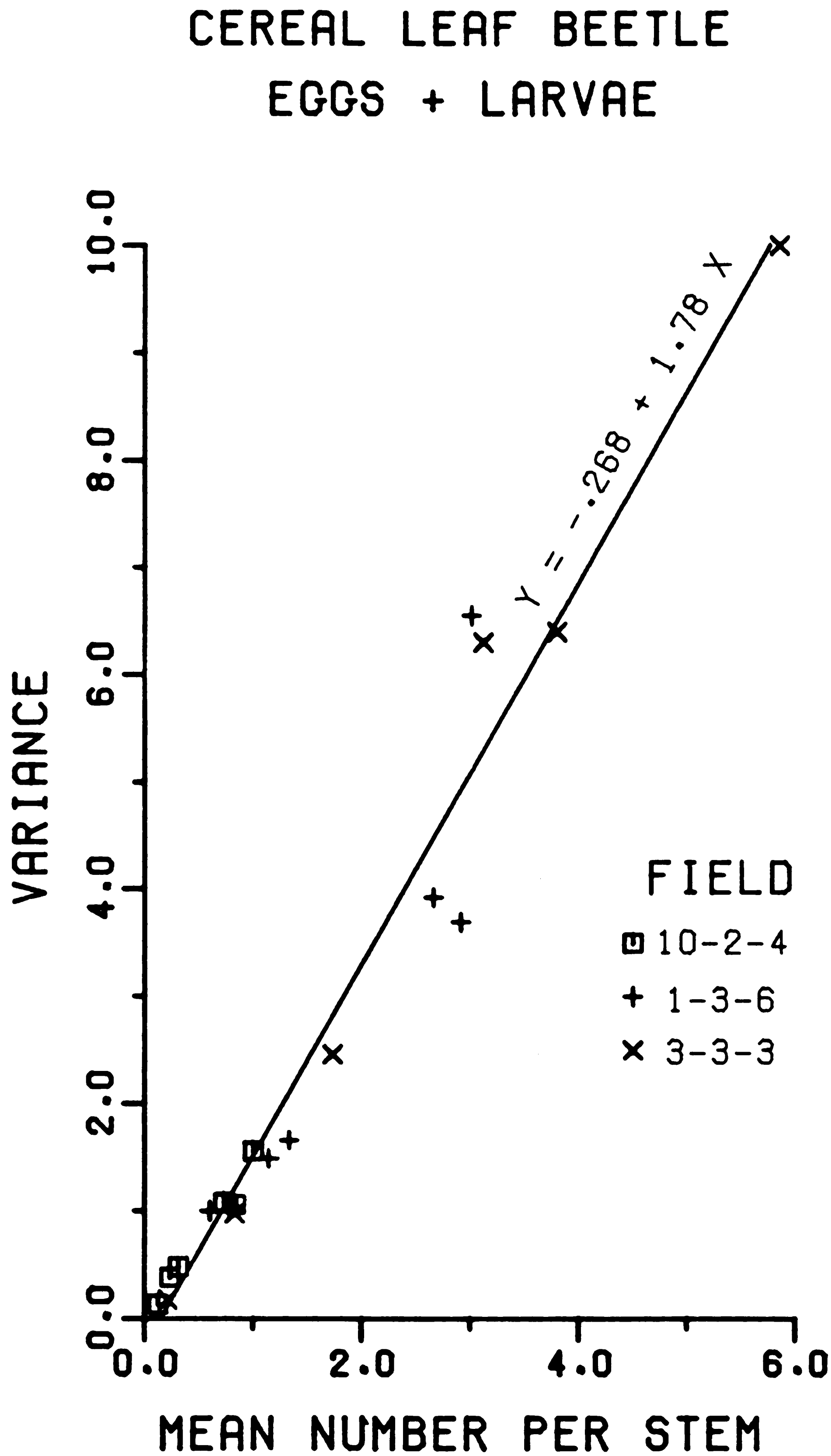

CEREAL LEAF BEETLE
LARVAE
VARIANCE
MEAN NUMBER PER STEM
Y = -.119 + 1.634 X
FIELD
10-2-4
1-3-6
3-3-3
0.0
1.0
2.0
3.0
4.0
5.0

Figure 17.--The variance-mean relationship for single oat stem samples of eggs + larvae of the cereal leaf beetle.


CEREAL LEAF BEETLE
EGGS + LARVAE
VARIANCE
MEAN NUMBER PER STEM
0.0
2.0
4.0
6.0
8.0
10.0
0.0
2.0
4.0
6.0
Y = -.268 + 1.78 X
FIELD
10-2-4
1-3-6
3-3-3

The mean number of eggs and of larvae per stem, and the mean number per square foot (from Sawyer) are listed in Table 1. Square foot samples were not always collected on the same date as stem samples, but data from the nearest such sampling date was used. Also given are the ratios of the two observations. These ratios are quite variable and tend to be higher at times of higher population densities. In the regressions of number per square foot on number per stem for eggs, the regression line was $Y = 2.276 + 3.154X$, $r^2 = .48$. This poor fit was due in large part to one point (1.2, 15.5) the deletion of which yielded the equation $Y = 1.910 + 2.886X$, $r^2 = .71$. A log-log transformation of the data gave a much poorer fit ($r^2 = .35$) than did the straight regression.

In the regression of number per square foot on number per stem for larvae, the regression line was $Y = .3937 + 11.13X$, $r^2 = .59$. Here a log-log transformation gave marginal improvement in the fit ($r^2 = .65$), but it is not sufficient to justify the additional complexity of interpretation, in view of the fact that the transformation does poorly for eggs.

Even a casual glance shows that there are huge discrepancies between the number per square foot in Table 1 and the number per stem multiplied by the number of stems per square foot. That will be considered later.

TABLE 1.--A comparison of population estimates made by stem counts and by square foot counts in three fields at Niles, Michigan in 1976.

		Field:	10 - 2 - 4				1 - 3 - 6				3 - 3 - 3			
Date	°D>48	°D>42	Stem	Sq.Ft.	ratio	Stems/ Sq.Ft.	Stem	Sq.Ft.	ratio	Stems/ Sq.Ft.	Stem	Sq.Ft.	ratio	Stems/ Sq.Ft.
EGGS														
6/1	474	718	--	--	--		--	--	--		3.52	12.6	3.6	
6/2	487	736	.65	1.4	2.2		2.37	6.7	2.8		--	--	--	
6/8	591	875	.54	2.1	3.9	32	1.07	6.5	6.1	48	1.40	7.7	5.5	37
6/11	666	968	.47	4.9	10.4		.64	5.4	8.4		1.20	15.5	12.9	
6/15	786	1112	.07	3.5	50.0		.49	.9	1.8		.92	5.7	6.2	
6/17	815	1152	.10	1.6	16.0		.50	2.6	5.2		.33	2.1	6.4	
6/21	879	1240	.03	0.0	--	36	.13	4.9	37.7	32	.12	.4	3.3	39
LARVAE														
6/1	474	718	--	--	--		--	--	--		2.33	8.5	3.7	
6/2	487	736	.20	1.3	6.5		.67	9.1	13.6		--	--	--	
6/8	591	875	.46	3.5	7.6		1.53	17.6	11.5		2.43	24.5	10.1	
6/11	666	968	.27	9.6	35.6		2.27	43.1	19.0		1.92	26.9	14.0	
6/15	786	1112	.24	4.8	20.0		.84	2.1	2.5		.76	22.7	30.0	
6/17	815	1152	.16	1.7	10.6		.64	1.1	1.7		.49	3.8	7.8	
6/21	879	1240	.10	.6	6.0		.47	2.3	4.9		.09	.5	5.6	

MODEL VALIDATION

During the construction of the model each of its components was compared to the data used in its construction to ensure against logical errors in the development of the component. That was done by operating the model components with constant temperature input, or by using pulse inputs to the different stages.

Following that it was necessary to validate the whole model. That was done by comparing model output to field data.

This field data was from the intensive population studies at Gull Lake and contained in the various theses written on the cereal leaf beetle at MSU.

While it would have been useful to compare model-generated densities of each of the life stages to those observed in the field, that could not be done because of the lack of appropriate field data. Estimates of adult densities were not available for the same field-year combinations as were larval and egg density estimates. Further, classification of the larvae by instar had been done subjectively (and unreliably, Fulton, 1975) and could not be used. The densities that could be compared then were total larvae (all four instars) and eggs.

Since there are no density-dependent parameters in the model at the present time, the relative shape of the model-generated curves is constant for a given temperature regime and set of model parameters. It should be possible then to somehow "normalize" the model output so that it is on the same scale as the field data. It would then be much easier to visually compare the curves. In this validation procedure, sequences of maximum and minimum temperatures from Gull Lake for the year in question were used to drive the model. Then the number of eggs and the number of larvae present in the model on those days in which field data were collected were used for comparison with the field data.

Three ways of comparing these two sets of observations, field and model, were chosen. They are: a linear regression between the observed values, the slope of that regression, and by a comparison of the areas under the seasonal density curves.

The regression approach involves reading values from the regression line. It gives excellent results when the correlation coefficient is high (> .6), but with poor fits it distorts the shape of the curve. Even with a good fit, the right end of the curve tends to be too high (Figure 18). When the slope alone is used to make the adjustment, the shape is closer to that of the field, but it is still very difficult to compare model output to field observation.

When the model output is adjusted by a factor equal to the ratio of the total incidences of the two sets of data, a visual determination of the goodness of fit can be made (Figure 18). This method was adopted for most of the validation procedure.

This method of adjusting the model output for comparison to the field data was very effective for making visual comparisons, but

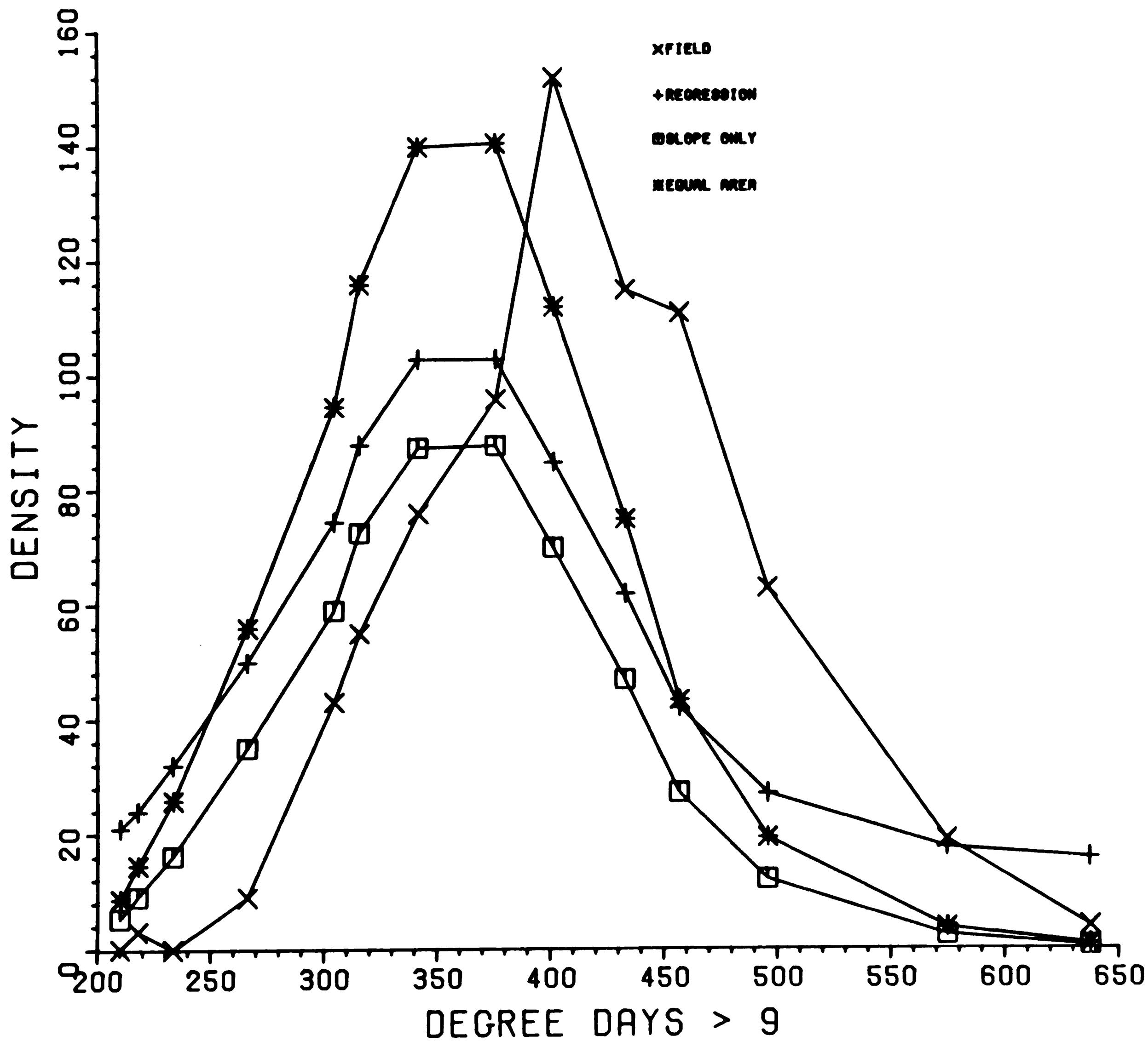


Figure 18.--Three different methods for comparing model output to field observation.

a quantitative measure of the degree of similarity was needed in order to objectively compare different simulation runs. The first measure used for this was the squared differences between field observation and adjusted model output, summed over the season. While this statistic worked well for comparing the effects of different values of a parameter on the match between field and model for any one year, it did not work well for evaluating the effects of parameter changes across all field-year changes since it is data-dependent. That is, the possible size of the error is related to the observed density. This led to the result that one or two years with high densities were determining the optimum value for the parameter.

Two methods were used to overcome this problem. The first was to choose as the optimum value for a parameter that value which gave the best fit to the largest number of field-year combinations. The second procedure, used only in later simulations, was to compute a chi-square-like statistic as:

$$\chi^2 = \frac{(\text{Adjusted model density - field density})^2}{\text{Adjusted model density}} \tag{18}$$

This statistic is relatively stable over all values of density, except very small ones (<1). Because of the way in which this statistic was calculated, it was deemed inappropriate to use the value in a significance test. Instead it is the magnitude of this statistic and its rate of change under manipulation of the model parameters which should be considered.

In Figures 19 through 22 a comparison is made of the match between model output and field data for several different year-field combinations with optimum values of several parameters (vertical axis). The topmost comparisons in each figure are from the initial simulation with all parameter values set at the best estimate possible from field and laboratory data, as described earlier. In all of these figures the points represented by squares are for eggs, model; triangles are eggs, field; X is for larvae, model; + is for larvae, field.

First consider the graphs for the initial base run in Figures 19 - 22. The correspondence between larvae for 1967 was very good, but that for eggs was poor. In this case, however, the problem may be with the field data, since judging from that data, peak eggs apparently occurred after peak larvae, a very unlikely possibility.

For 1968, correspondence between larvae was again excellent, but that between eggs was not good. The general shape of the model egg curve seems all right, but it occurs later in the season than the actual egg curve.

For 1969 we have good correspondence between the egg curve, except that the tail end of the distribution drops off too quickly. The larvae match but poorly for 1969.

For 1970, two different fields were used, with an excellent match of both eggs and larvae in each field. There was a slight tendency for the model values to be more peaked than the field data.

Figures 19 - 22.--Comparisons of model output and several years' field data. The digits in the corner of the figure indicate the year (first 2 digits) and different fields within the same year (third digit) eg. 713 indicates data are from field 3 of 1971.

Squares - eggs, model; triangles - eggs, field; X - larvae, model; + - larvae, field. Top series of graphs are for the basic parameter set of the model. The second series is with the optimum value for the mean of YP. The third set has optimum YP and egg development time increases by 25%. The bottom set of graphs has YP the same as the top series, egg development as the third series, but the optimum value for adult emergence. See the text for details.

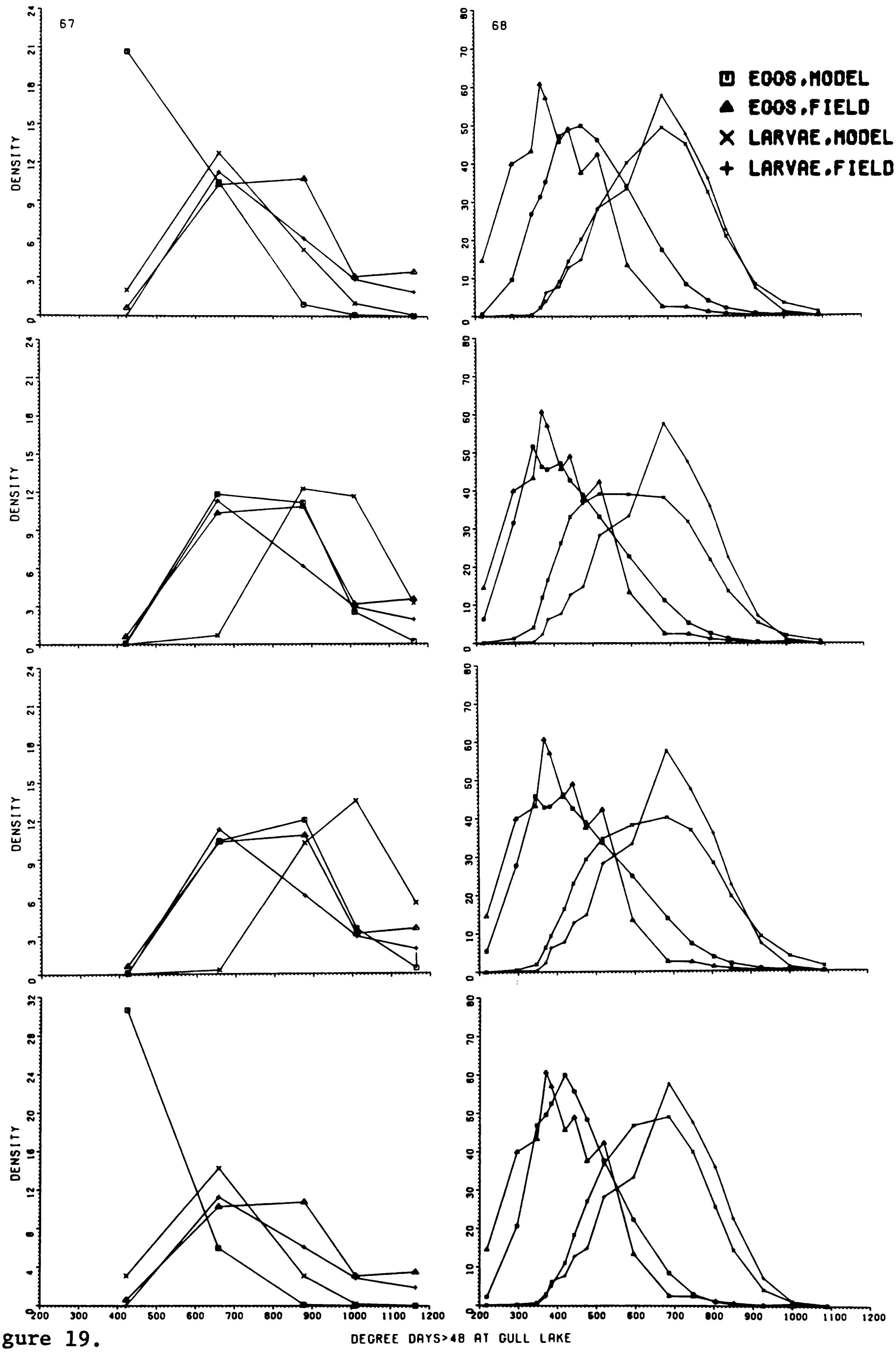

67
68
EGGS,MODEL
EGGS,FIELD
LARVAE,MODEL
LARVAE,FIELD
DENSITY
DEGREE DAYS>48 AT GULL LAKE

Figure 19.

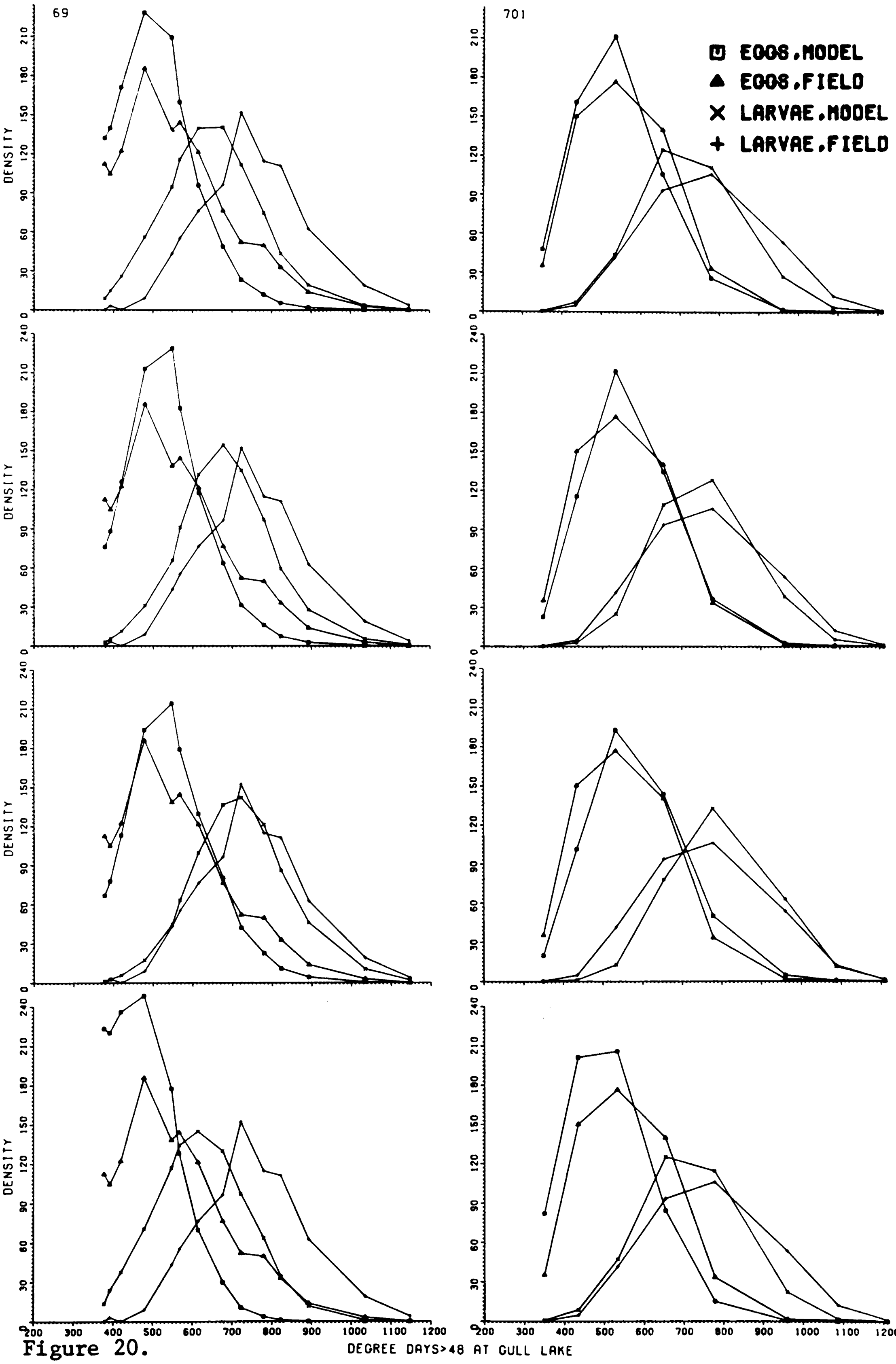

69
701
EGGS,MODEL
EGGS,FIELD
LARVAE,MODEL
LARVAE,FIELD
DENSITY
DEGREE DAYS>48 AT GULL LAKE

Figure 20.

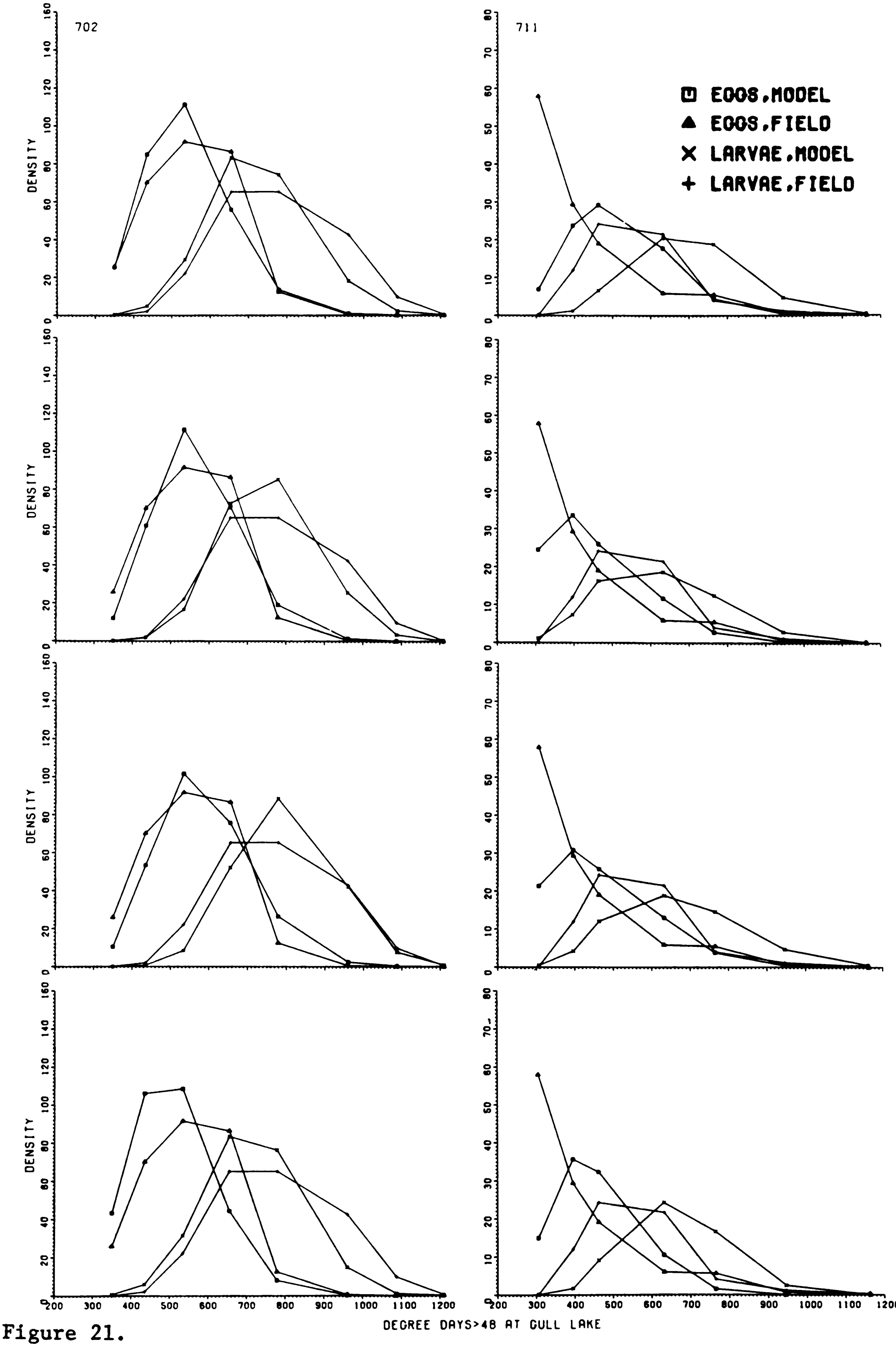

702
711
EGGS,MODEL
EGGS,FIELD
LARVAE,MODEL
LARVAE,FIELD
DENSITY
DEGREE DAYS>48 AT GULL LAKE

Figure 21.

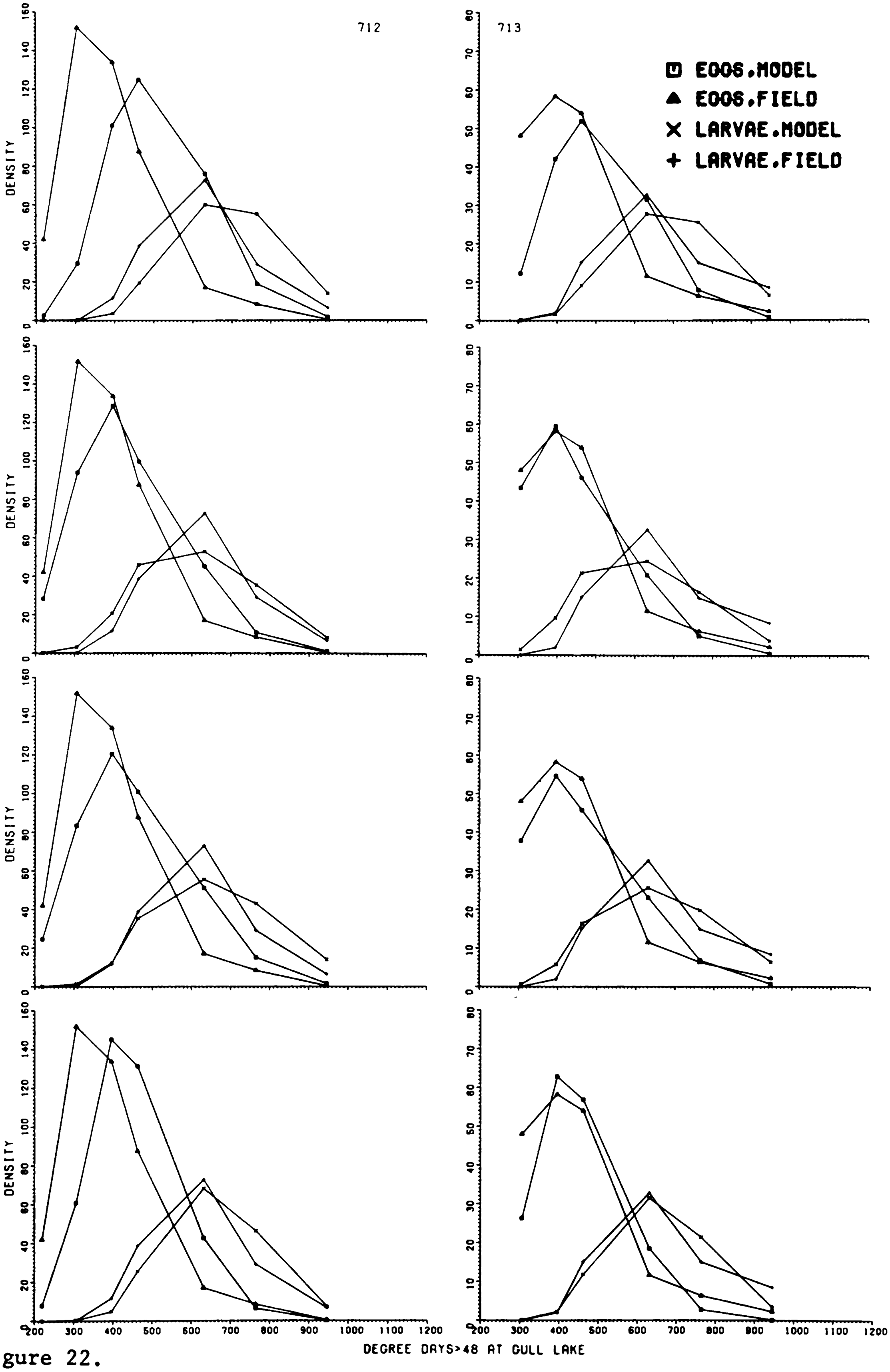

712
713
EGGS.MODEL
EGGS.FIELD
LARVAE.MODEL
LARVAE.FIELD
DENSITY
DEGREE DAYS>48 AT GULL LAKE

Figure 22.

For 1971, three different fields were used. Development in those fields seemed to be unusually early in that year, and that is reflected in the fact that for both eggs and larvae, simulated values occur later than the observed values, although larvae match more closely than do eggs.

While it is ultimately the larvae which one is interested in for pest management purposes, good correspondence between the curves for both eggs and larvae ought to be sought for the model. Since the distribution of larvae depends to a great extent on the distribution of eggs, it seemed reasonable to first try to bring the curves for eggs from the field and the model into close correspondence for all years.

From a consideration of the model structure, it is clear that two features would have the most influence on the time relationships of the egg curve. They are the emergence from overwintering sites and the rate of movement of adults from wheat to oats in the spring. Because the latter is a more immediate influence, it was the first factor considered.

As was previously stated, adults were assumed to move from wheat to oats at a rate such that the probit of the proportion of eggs going into oats at any value of °D>5.6 was given by:

$$YP = \text{Probit of Proportion} = .8625 + .01379 * {}^\circ D{>}5.6C \qquad (19)$$

This represents a normal distribution with mean equal to 300 °D>5.6 and standard deviation equal to $\frac{1}{b}$ = 72.5 °D>5.6.

Therefore there are two parameters involved here which might affect the distribution of eggs.

Several preliminary simulations indicated a greater sensitivity of the error between model and field to changes in the mean than to changes in the standard deviation, so the mean was varied.

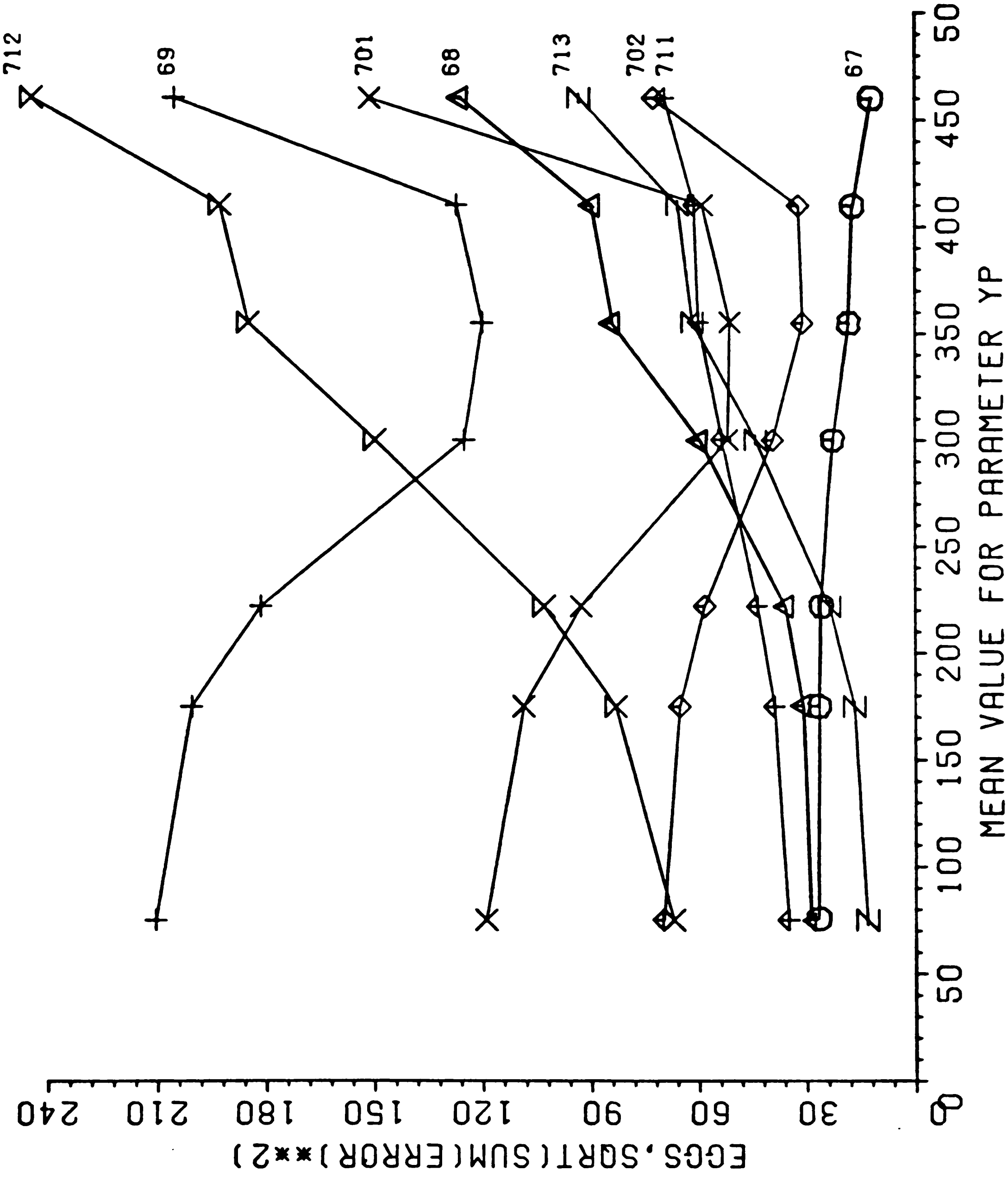
Since the synchronization of eggs was good for the 1969 data, but poor for 1967 (model too early) and 1968 and 1971 (model too late) it was anticipated that no single value of YP would be optimal for all fields.

In Figure 23 the square root of the sum of the squared differences between model and field for several fields are plotted over the YP (the mean). For three fields true optima do exist, that is a point of minimum error. Those fields are 69, 701, and 702, each with a minimum error near 350 °D>5.6. For the other fields, with the exception of 1967, the best value of YP is a very low one, unrealistically low when it is remembered that YP is the time (°D>5.6) when half of the eggs being laid are going into oats.

Data for the year 1967 were peculiar in the distribution of eggs being later than larvae, and this is reflected in a large value of YP being best for that year.

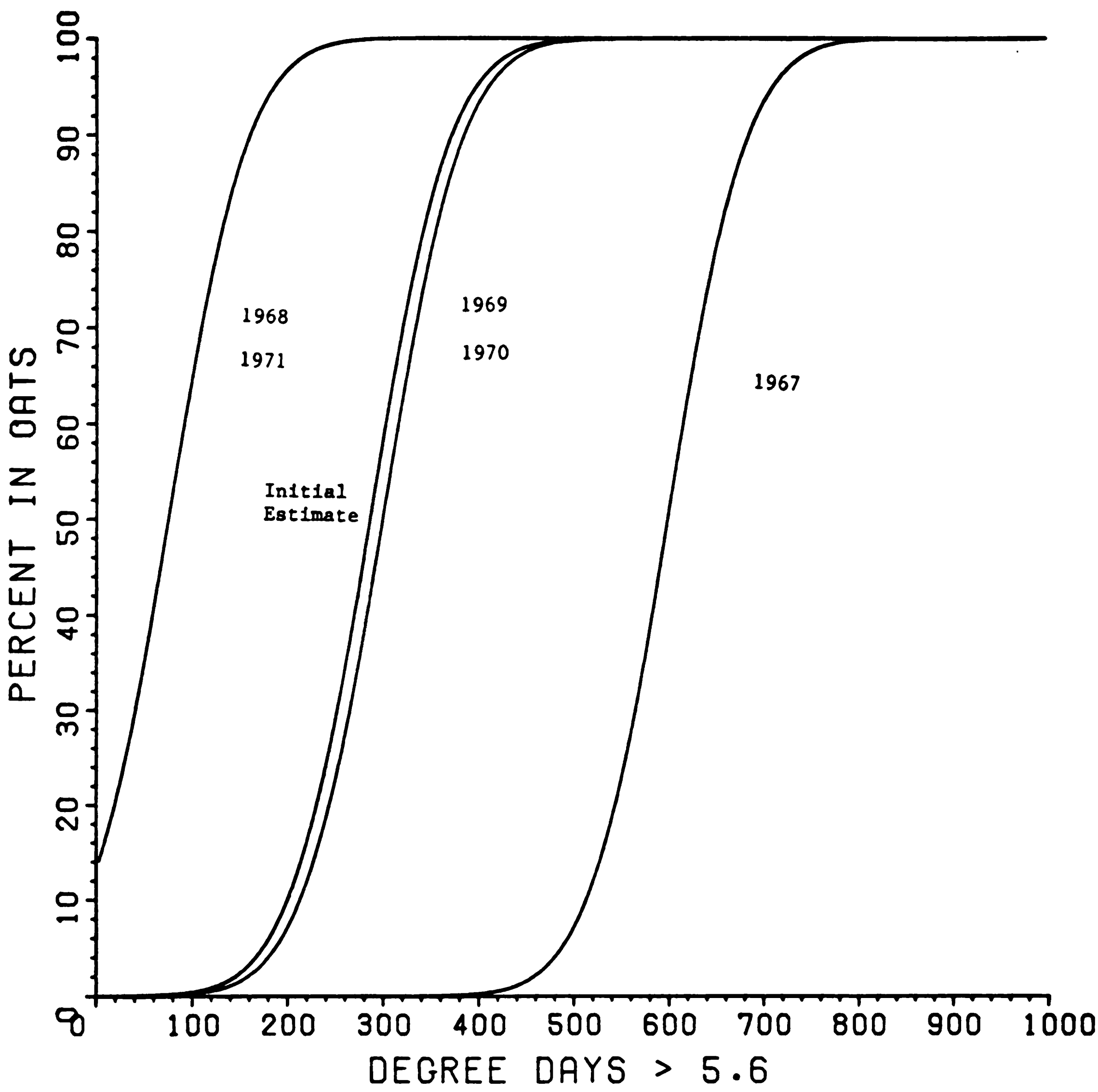
As anticipated, no one value of mean YP gave best results for all fields. The optimal curve for each year is shown in Figure 24. A comparison of field with model, with the best value of YP used for each year (all fields for one year used the same value of YP) are shown as the second row of graphs in Figures 19 - 22.

Figure 23.--The square root of the sum of the squared deviations between model and field values for different years (first 2 digits) and different fields (3rd digit) plotted over the mean value for YP, the parameter which moves adults from wheat to oats in the spring.



EGGS,SQRT(SUM(ERROR)**2)
0
30
60
90
120
150
180
210
240
MEAN VALUE FOR PARAMETER YP
0
50
100
150
200
250
300
350
400
450
500
712
69
701
68
713
702
711
67

Figure 24.--The percent of eggs being laid in oats as a function of °D>5.6C (42°F). The different curves are those that minimize the error in the comparison of field and model incidence curves for eggs in the year indicated.


PERCENT IN OATS
DEGREE DAYS > 5.6
1968
1971
1969
1970
1967
Initial
Estimate
0
10
20
30
40
50
60
70
80
90
100
0
100
200
300
400
500
600
700
800
900
1000

Clearly adjusting this one parameter allows a remarkably good correspondence between egg curves from the field and from the model. Even in the case where the data are questionable (1967), the fit is remarkable.

For 1970 the slight change in mean YP to get the best fit does not disturb the good fit for larvae in that year. The fits for larvae appear to be improved for fields in 1969 and 1971, however results are poor for 1968 and much worse for 1967.

With the fits for eggs established, it appeared that the length of time from peak eggs to peak larvae was lower in the model than was observed in the field. There are a number of possible causes for this, two of which were considered likely and were investigated with the model. The first of these is that eggs on the surface of leaves are experiencing temperatures different from those at the standard weather station from which data were obtained, and were therefore developing at a rate different from what the model would predict. The second possibility is that the development rates are different in the field than those determined in the laboratory (Figure 11).

The first possibility was investigated by multiplying the temperature input to the egg time delay function by a constant for a number of simulations. The second possibility was investigated by multiplying the output from the egg time delay function by a constant. Of the two methods, the second, which is equivalent to changing the actual developmental time curve, gave the best results, with an optimal value for the development time of 1.25 times the

values suggested by Figure 11. (While it is possible for the average developmental time of a population to change from year to year (Morris and Fulton, 1970) that possibility was not admitted here.)

The third series of graphs in Figures 19 - 22 show the comparison of model and field when this adjustment to DELE, the time spent in the egg stage, is applied to distributions with their optimal value for mean YP. While this adjustment causes slightly poorer fits in 1970 and for field 711, the overall effect is an improvement in the larval fit, particularly for 1968 and 1969.

By adjusting two parameters then, mean YP and egg development time, DELE, it is possible with the model to mimic well the time sychrony of the cereal leaf beetle in the field. The adjustment to DELE constituted no great difficulty to the further development of this work along the lines which were originally intended, but if a parameter must be determined anew each year, then it does constitute a problem. The value for the parameter must be observed in the field, or the factors causing the change in the parameter must be determined, and the changes themselves modeled from a measurement of those causal factors. The first solution is undesirable in the context of a pest management scheme if it involves sampling more than once, a high possibility when a rate is involved as here with YP. The second solution--modeling the process, could not be attempted here because of a lack of data.

Because of these difficulties with using the optimal value of mean YP the possibility of a single value for adult emergence which would give improved fits for all fields was investigated. Here

the intercept of the probit regression line was kept constant while the slope was changed. The value for YP was set to its original value, but development time of eggs, DELE, was left at 1.25 times the original DELE value. The emergence line which gave best overall fit is shown in Figure 4, and the comparison of the simulation output with field data is shown as the bottom set of graphs in Figures 19 - 22. While the overall effect is an improvement on the original parameter values, the results for 1969 and 1970 were slightly worse than they were for the original parameter sets. In any case, this single alteration to emergence rate is not as effective in reducing the error as is the yearly adjustment of YP.

These conclusions are shown more objectively in Table 2 where the chi-square statistic discussed earlier is tabulated for the different fields under the different parameter sets. The values for 1967 are included for reference, but were not used in computing the mean or the standard deviation. Reference to the means and standard deviations shows very clearly the tremendous superiority of adjusting YP and changing DELE over the other approaches, but again that approach requires a different value for YP for each year. It was thought necessary therefore to test the alterations to spring emergence rate and to egg development rate on data which were not used in the optimization procedure. That was done using data from 7 fields from the years 1972 to 1977 provided by E. Lampert and A. Sawyer. Table 3, which is similar in structure to Table 2, contains the computed chi-square values for these fields for the

TABLE 2.--Values for Chi-square from the comparison of model and field densities of cereal leaf beetle eggs and larvae when simulations were run with different sets of parameters.

Year	Base Set		YP		YP + DELE		Emergence + DELE		DELE	
	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae
67	1853	35	62	163	30	367	3238	790	928	15
68	537	9	40	96	57	40	144	29	657	37
69	482	504	309	235	185	52	2670	1419	246	179
701	26	57	26	34	45	87	135	137	9	18
702	26	65	30	30	41	34	65	134	16	14
711	395	156	62	15	73	38	157	98	471	384
712	1234	56	63	17	99	16	317	24	1487	162
713	127	10	13	18	13	7	104	11	163	29
68-713 (Mean)	404	122	78	64	73	39	526	265	436	118
Std. Dev.	423	175	104	81	56	26	988	512	520	136

TABLE 3.--Values for chi-square when simulations using optimal parameter values for years 1967-71 were applied to new data.

Year	Base		Base + DELE		Emergence + DELE	
	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae
72	1346	82	764	182	3056	92
731	95	1.3	52	.4	774	2.9
732	230	.5	127	.4	885	.9
74	114	2.3	66	.9	673	7.6
75	43	.7	23	1.6	269	.7
76	258	1.0	164	1.6	2972	.9
77	5492	14	2835	5.5	9274	51
Mean	1083	15	576	27	2558	22
Std. Dev.	1996	30	1029	68	3170	36

comparison of field to simulation with the optimal values of DELE and emergence used, as well as with the initial parameter values.

The results listed in Table 3 cast strong doubt on the reality of the improvement in fit caused by the alteration of the emergence function and by modification of DELE. Although modification of DELE here leads to consistent and major improvements in the fit, that was not true when that modification alone was applied to the initial set of data (Table 2).

Part of the problem here is that larval densities were extremely low for 1973, 1975, 1976 and 1977, generally under one per square foot. That made a precise estimate of their value difficult to accomplish. In fact I ought to have chosen about every other year's data for the initial development, then used the remaining years to test the conclusions on. This would also have minimized the effects of the introduction of parasites in the later years, as well as the effects of different sampling teams and field supervisors.

Despite the fact that changes in the emergence or in the rate of egg development don't provide improvement in the fit of simulation to field data, and that YP must at this point be determined from the data, the model can still be used to test the effects of altering inputs on the goodness of fit. To do that it seemed reasonable to use the best fit available as a reference set, that being the simulation with mean YP optimal and the egg delay increased by 25%. Also no further consideration will be given to the 1967 data.

MODEL SENSITIVITY

When temperature data from Gull Lake for 1968 through 1971 and the basic set of parameters were used in the model (with the exception of using the optimum values for mean YP and having egg development time increased by 25%) oviposition and survival in oats and in wheat were as listed in Table 4.

The number of eggs per female (sum of the number laid in oats and in wheat for a given year) ranges from about 110 to 150. While the oviposition function was based on data from Wellso, these values are in agreement with several values listed in Yun (1967, Table II). In addition, for the 4 years 1968-71 the percentage of eggs in oats is 99.4, 38.1, 43.0, and 99.0 (Table 4). If one computes corresponding values from the total incidence of eggs in oats and in wheat recorded in Gage (1974, Table 19a) the values are: 96.0, 47.8, 50.6, and 91.9. The significant correlation between the two sets of values is .998. Thus while the change in mean YP was undertaken to achieve an improvement in synchrony between model and field, its effects on oviposition in the wheat and oat crops is sufficient to explain observed yearly differences in the proportion of the beetle population found in these two crops.

Egg survivals are somewhat less than those generally reported. They are quite naturally less than those reported by Yun (1967) since the instantaneous survival regression line ignored two

TABLE 4.--Oviposition and survival for the simulation with YP optimal and DELE = 1.25 * DELE.

		SURVIVAL							
Year	Eggs/female	Eggs	L1	L2	L3	L4	Larval	Immature Stages	Eggs*
OATS									
1968	109	.341	.894	.891	.916	.910	.664	.226	.426
1969	43	.339	.897	.888	.918	.909	.665	.225	.423
1970	54	.366	.890	.892	.914	.914	.663	.243	.542
1971	122	.367	.893	.892	.915	.910	.663	.243	.448
Mean		.353	.916	.891	.916	.911	.664	.234	.460
WHEAT									
1968	.6	.313	.911	.890	.923	.913			
1969	69.8	.334	.904	.892	.922	.913			
1970	71.5	.359	.893	.891	.916	.910			
1971	1.2	.345	.906	.896	.922	.914			
Mean		.338	.904	.892	.921	.912			

* Using all data regression equation from Figure 13.

points at intermediate temperatures whose inclusion would have raised egg survival values to those given in the rightmost column of Table 4. The average value for egg survival for that column, .46, is similar to a value of .48 reported by Shade, et al. (1970) for field populations of cereal leaf beetles but very different from the value of .90 reported by Helgesen and Haynes (1972).

By contrast the larval survivals in Table 4 are higher than those usually reported of .10 to .35 (Ruesink, 1972, Table 2; Wellso, 1973), but near that reported by Wilson and Shade (1966) for cereal leaf beetles on favorable hosts. The overall effect in the model is for a slightly higher survival to the beginning of the pupal stage than is usually reported.

Some Effects of Sampling Bias on Synchrony Between Model and Field

Previous work (Fulton, 1975; Logan, 1977) had shown a bias in sweepnet samples of the cereal leaf beetle against the early instars. To check for the effect of this bias on the synchrony between the model and field, a systematic bias was applied to samples from the model. The chi^2 values for different amounts of bias are listed in Table 5 along with the values for no bias. Obviously the synchrony of the curves is very little affected by even a strong bias against small larvae. This is perhaps made clearer by Figure 25 where for three years the effects of the strongest bias imposed, 0.5 x number of L1's and 0.6 x number of L2's, in the bottom set of graphs is compared to the output without bias in the top set of graphs.

TABLE 5.--Chi-square values for the correspondence between model and field data when the number of first (L1) and second (L2) instar larvae in the model are multiplied by the factors shown before the total incidence was adjusted and compared.

Year	.5L1 .6L2	.6L1 .65L2	.7L1 .75L2	.8L1 .5L2	L1 L2
68	32	33	35	36	40
69	30	33	38	41	52
701	144	126	112	104	87
702	58	50	44	41	34
711	51	48	44	43	38
712	20	19	18	18	16
713	6	6	6	7	7
Sum	341	316	297	289	274

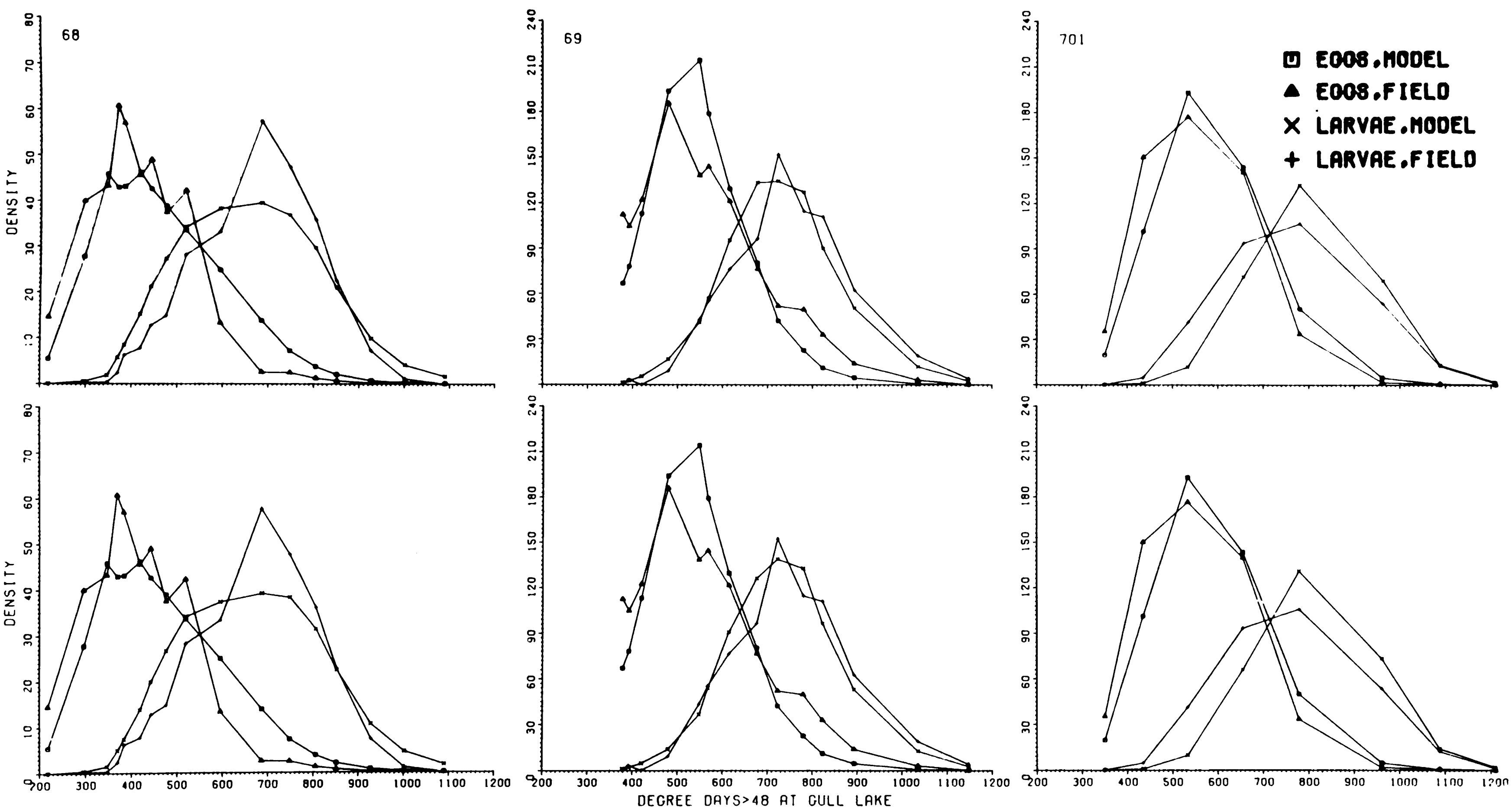


Figure 25.--The effects of sampling bias on synchrony. Top row YP optimal and DELE = 1.25 * DELE (standard set). Second row - standard set with number of first instar larvae in the model decreased by 50% and the number of second instar larvae decreased by 40%.

The effect of this degree of bias on the number that would be counted at each of the sampling times for 1969 is shown in Figure 26 where the ratio of the total number in the biased model sample over the total number in the unbiased model sample is plotted over the appropriate °D value. Here the bias has an obviously serious effect, and worse, its effect changes with the season.

Sensitivity to Biases in Temperature Data

Previous work (Fulton and Haynes, 1976) had indicated that relatively small differences between the temperature measured near an experimental plot and the temperature to which the insect is exposed have profound effects on the interpretation of experimental results. Therefore temperature within the model was multiplied by a series of constants and the generated density curves were compared to the field data, ignoring these temperature biases. The chi^2 values for the correspondence between model and field for the egg and larval curves when the temperature affecting the insect ranged from 80% to 120% of that observed are given in Table 6. Anything beyond a 1 - 5% bias causes a rapid rise in the chi^2 value but this translates into only about 1°C! That kind of accuracy is extremely difficult to attain in field work and yet the effects are quite striking (Figures 27 and 28). Section A of Figure 27 and 28 is with unbiased temperature data. Section B has a bias of .95, for Section C it is 1.01, and for Section D it is 1.05. Again, a 5% bias might be too great to tolerate for pest management!

Figure 26.--The effect of a 50% bias against first instar larvae and a 40% bias against second instar larvae on the fraction of the whole population that would have been sampled at the sampling times which were used in 1969.

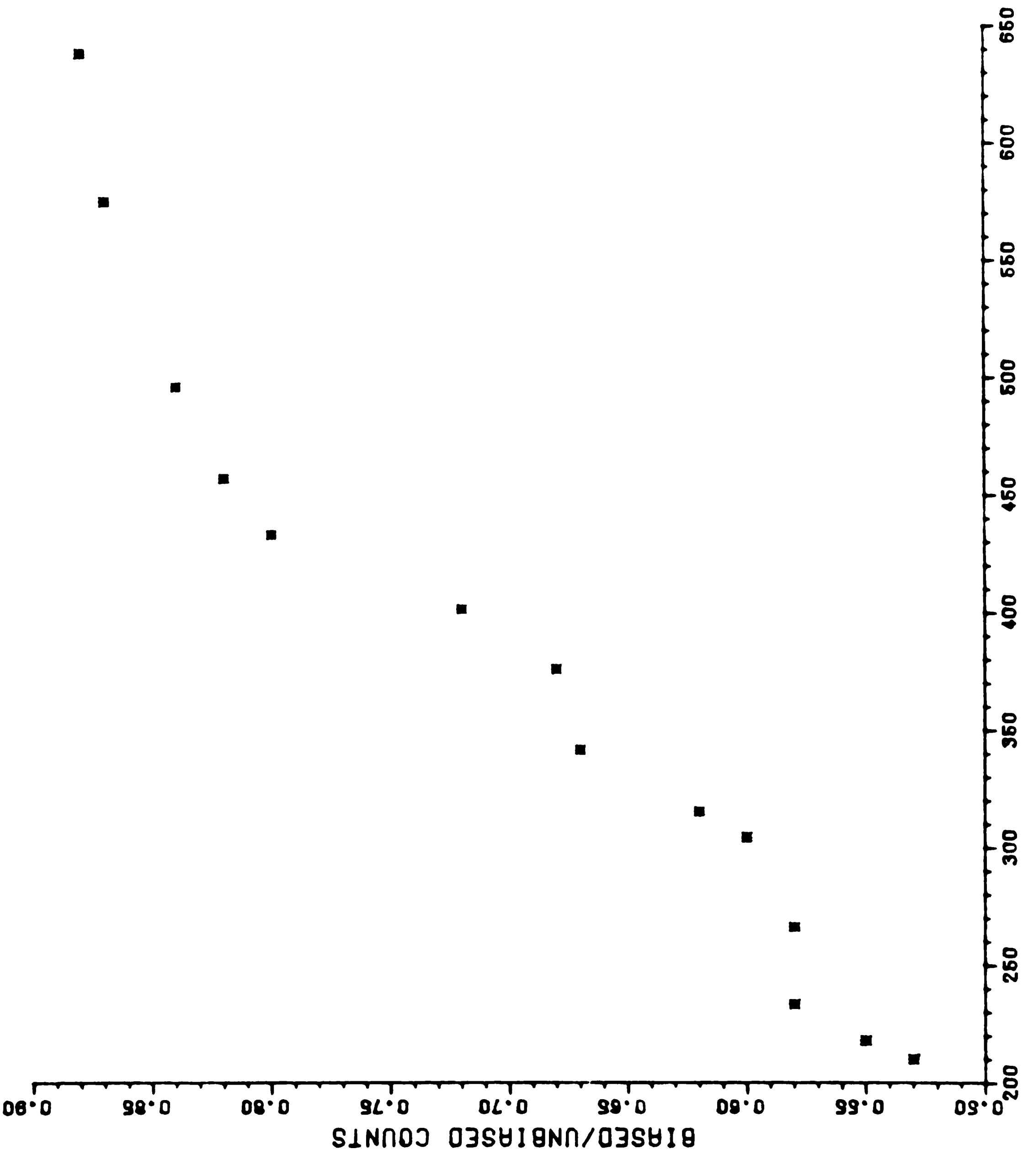

1969 SAMPLING TIMES OD>9
BIASED/UNBIASED COUNTS
200
250
300
350
400
450
500
550
600
650
0.50
0.55
0.60
0.65
0.70
0.75
0.80
0.85
0.90

TABLE 6.--Chi-square values for the correspondence between model and field density values when the temperature affecting the insect differs from that recorded at a standard weather station by the factor given.

Year	.8	.9	.95	.99	1.0	1.01	1.05	1.1	1.2
EGGS									
68	6699	673	214	75	57	43	24	74	555
69	49151	2583	569	186	185	219	759	2898	19731
701	27668	1581	374	78	45	24	37	272	2255
702	19848	1020	243	61	41	28	33	143	1118
711	2460	384	162	85	73	65	58	107	406
712	5278	841	315	128	99	75	20	26	400
713	1156	179	55	17	13	12	26	112	840
Sum	112259	7262	1931	629	513	465	956	3635	25304
LARVAE									
68	895	135	41	34	40	51	141	440	3903
69	16281	968	121	28	52	94	509	2171	25231
701	48118	3488	624	135	87	56	70	476	7957
702	22610	1531	276	54	34	24	73	445	7395

TABLE 6--Continued.

Year	.8	.9	.95	.99	1.0	1.01	1.05	1.1	1.2
711	2107	312	115	48	38	29	9	5	63
712	621	153	57	20	16	12	17	68	592
713	161	39	13	6	7	9	27	98	965
Sum	90793	6625	1248	325	274	276	845	3702	46107

Figure 27.--1968. The effect of a bias in the temperature recorded at a weather station in comparison to the temperature affecting the insect temperature. A. TEMP = temperature. B. TEMP = .95 * temperature. C. TEMP = 1.01 * temperature. D. TEMP = 1.05 * temperature.

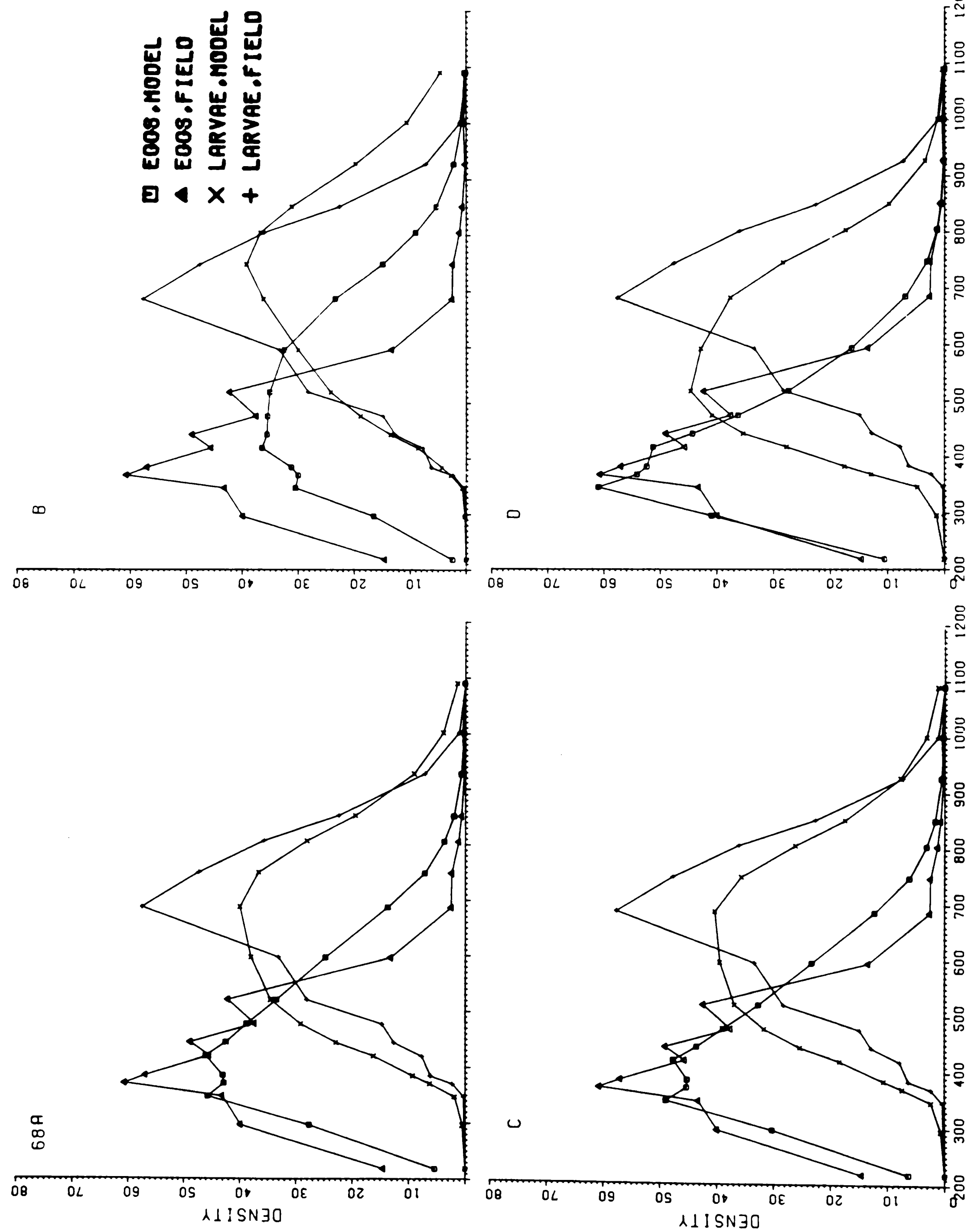
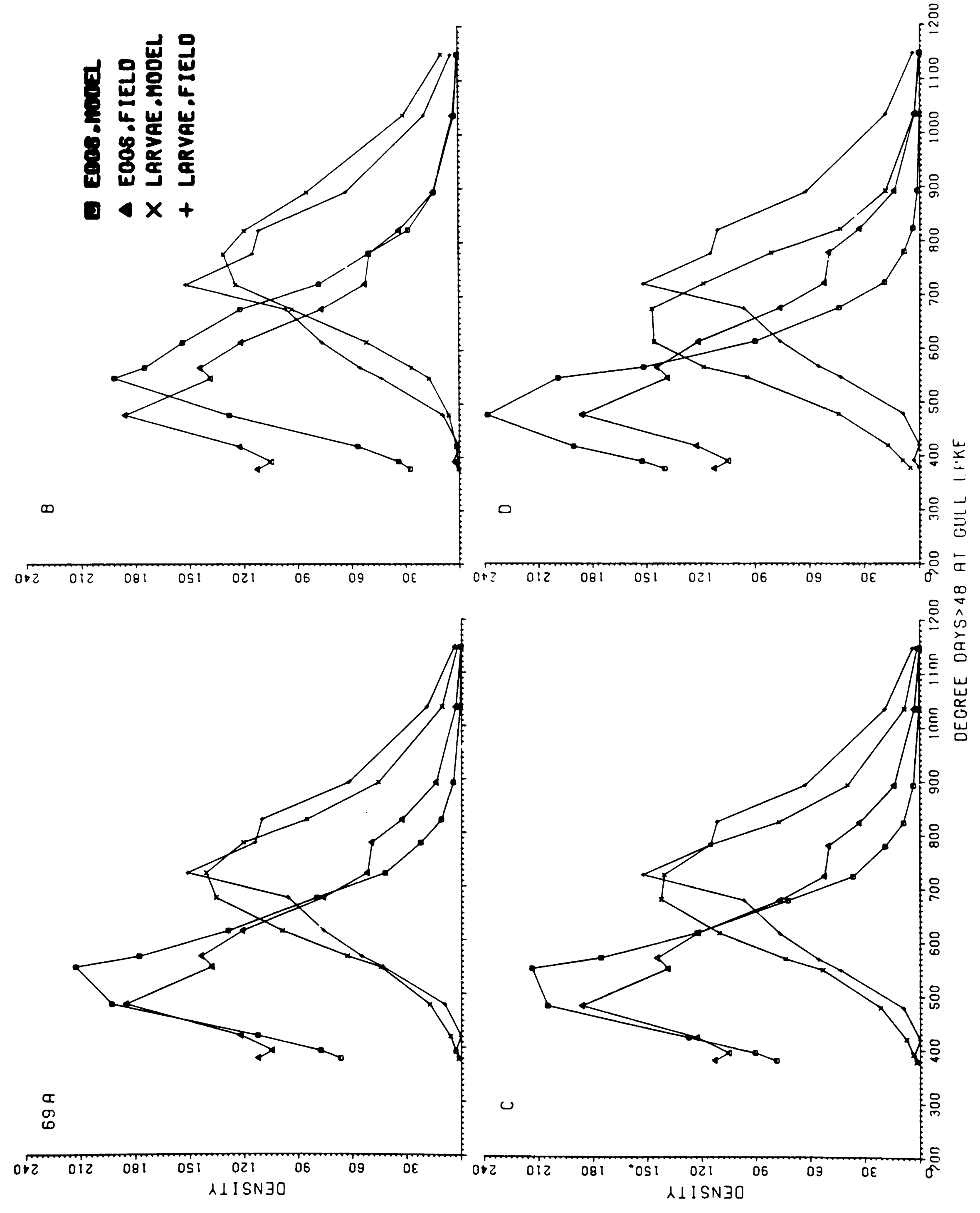

EGGS.MODEL
EGGS.FIELD
LARVAE.MODEL
LARVAE.FIELD
68A
B
C
D
DENSITY
DEGREE DAYS>48 AT GULL LAKE
10 20 30 40 50 60 70 80
200 300 400 500 600 700 800 900 1000 1100 1200

Figure 28.--1969. The effect of a bias in the temperature recorded at a weather station in comparison to the temperature affecting the insect TEMP. A. TEMP = temperature. B. TEMP = .95 * temperature. C. TEMP = 1.01 * temperature. D. TEMP = 1.05 * temperature.


EGGS.MODEL
EGGS.FIELD
LARVAE.MODEL
LARVAE.FIELD
A 69
B
C
D
DENSITY
DEGREE DAYS>48 AT GULL LAKE

There are other factors which might be affected by a difference between the recorded temperature and the temperature affecting the insect. For example, fecundity, egg survival, and larval survival. Fecundity and egg survival in the model with several values for the temperature bias are listed in Table 7 for the years 1968-71. Clearly these factors are little affected by the temperature bias. A similar conclusion holds for larval survival.

Variation in Larval Development Times

The developmental time of a species can be difficult to determine. For instance cereal leaf beetle larval development time was found to be about 1.7 times faster by Helgesen ahd Haynes (1972) than the value found by Yun (1967). The effects of such great differences were not investigated, but development rates from 0.8 to 1.2 times those reported by Helgesen and Haynes (1972) were tested (Table 8). Within these bounds the effects are certainly not serious. Extreme cases existed in 1968 and 1969 (Figure 29). The top sections, labeled "A" were generated with the larval development times decreased by 20% compared to the standard, sections "B." Sections "C" had the development times increased by 20%. Note that development times in sections C are 1.5 times longer than those in sections "A" without serious disruption of the synchrony between model and field.

Egg and Larval Survival Functions

The automatic scaling factor was always greater for the eggs than for the larvae. That indicated either that egg survival is

TABLE 7.--Eggs per female laid in oats when the temperature affecting the insect differs from that recorded by the factor shown.

EGGS/FEMALE	FACTOR						
Year	.8	.9	.99	1.0	1.01	1.1	1.2
1968	106	105	108	109	110	118	125
1969	43	44	43	43	43	42	44
1970	55	56	55	54	54	51	49
1971	117	117	121	122	123	128	130
EGG SURVIVAL							
1968	.307	.340	.342	.341	.340	.339	.358
1969	.298	.315	.336	.339	.341	.363	.377
1970	.315	.344	.363	.366	.369	.400	.425
1971	.340	.358	.367	.367	.368	.379	.399

TABLE 8.--Chi-square values for the comparison of field and model when larval development times were changed by the factors shown.

Year	FACTOR .8	.9	1.0	1.1	1.2
68	61	46	40	37	35
69	107	75	52	37	27
701	63	74	87	101	117
702	29	30	34	39	46
711	49	32	38	44	50
712	11	13	16	18	21
713	9	8	7	7	6
Sum	328	277	274	283	301

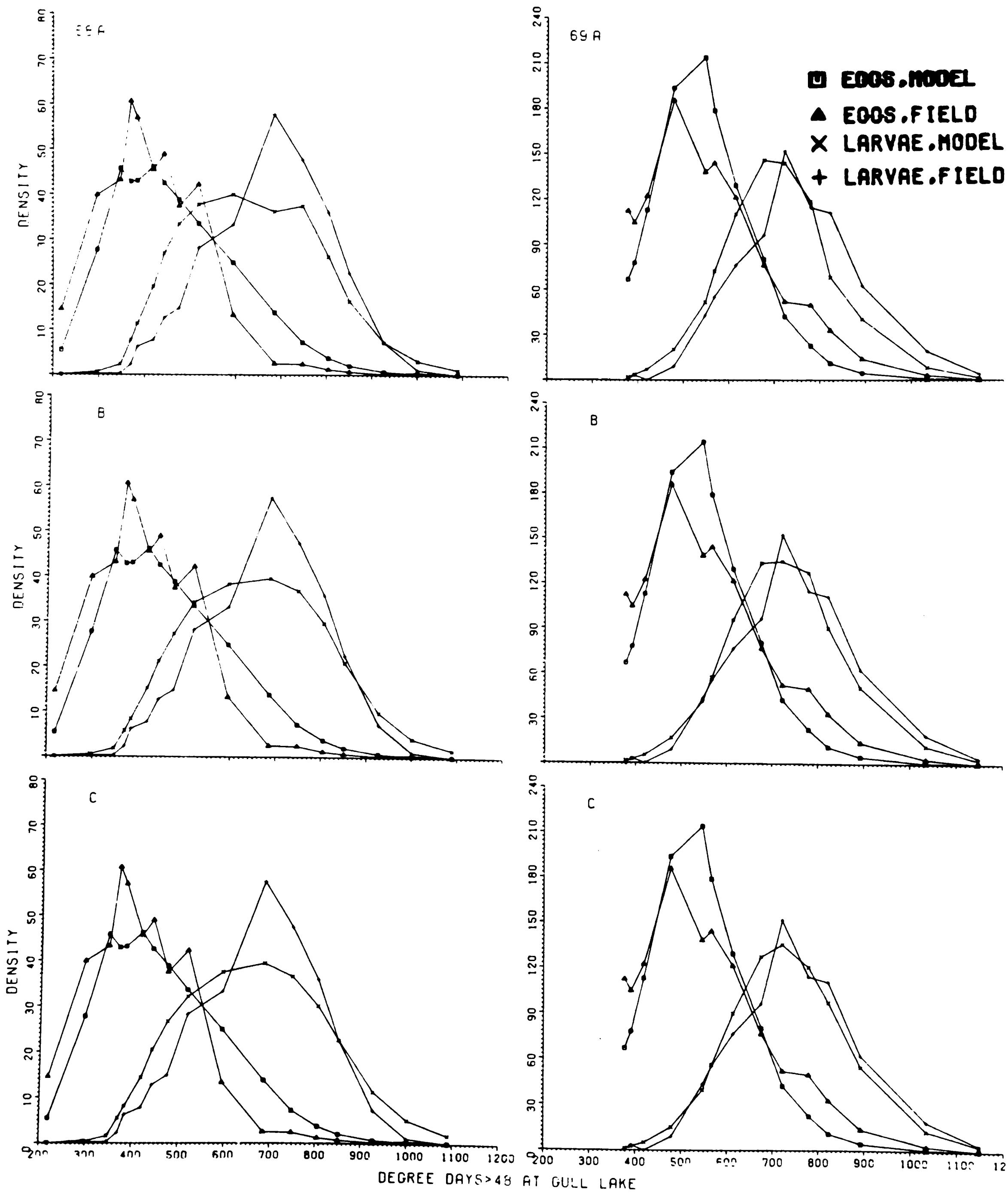


Figure 29.--The effects of larval development times on synchrony for two years, 1968 and 1969.

A - development times decreased by 20%
B - standard development times
C - development times increased by 20%

higher in the field than in the model, which has been indicated; or the sampling for eggs in the field is less efficient than is the sampling for larvae; or both of these effects may be operating. Those effects can not be sorted out here, but the effects of changes in survival on these ratios can be considered.

In Table 9 are listed the total incidence ratio for eggs and for larvae with 5 different sets of survival functions, A - E, and the ratio of those values for eggs over those for larvae. The general trend is for increases in the survival rate to cause the ratio of eggs over larvae to decrease, with the value being near 1.0 for some years (1971) when average egg survival is about .65 to .70 (column B). For other years however, this ratio is near 1 only when both egg and larval survival are set to 1. Reference to the chi^2 values in Table 9, which are again for the correspondence between field and model, show that these kinds of changes in survival have little effect on synchrony.

TABLE 9.--Total incidence ratio - model/field from simulations with YP optimal, DELE = 1.25 * DELE, and survivals as indicated.

	A			B			C			D			E		
Year	Eggs	Larvae	Eggs/ Larvae	Eggs	Larvae	Eggs/ Larvae	Eggs	Larvae	Eggs/ Larvae	Eggs	Larvae	Eggs/ Larvae	Eggs	Larvae	Eggs/ Larvae
68	38.6	16.3	2.37	55.9	34.2	1.63	60.2	39.2	1.54	67.1	48.1	1.40	67.1	58.8	1.14
69	4.6	2.4	1.95	6.7	3.7	1.81	7.2	5.7	1.26	8.1	7.1	1.14	8.1	8.7	.93
701	6.4	3.7	1.76	8.9	6.9	1.29	9.5	7.8	1.22	10.8	10.0	1.08	10.8	12.2	.89
702	12.2	5.5	2.23	16.8	10.3	1.63	18.0	11.7	1.54	20.5	14.9	1.38	20.5	18.3	1.12
711	71.9	43.4	1.66	102.0	84.0	1.21	108.7	94.3	1.15	123.5	117.7	1.05	123.5	144.9	.85
712	18.4	14.8	1.24	25.5	28.8	.88	27.2	32.5	.84	30.5	40.3	.76	30.5	49.3	.62
713	40.6	32.0	1.27	57.5	62.1	.93	61.3	70.4	.87	69.4	87.0	.80	69.4	106.4	.65
Mean			1.78			1.34			1.20			1.14			.89
Mean Survival	0.35	0.66		0.71	0.66		0.80	0.66		1.0	0.66		1.0	1.0	
χ^2	513	274		661	295		710	300		824	312		824	348	

A - Standard survival equations.
B - Egg instantaneous survival, a = .01-.002075 * TEMP°C.
C - Egg instantaneous survival, a = .02-.002075 * TEMP°C.
D - Egg survival = 1.0.
E - Egg survival = 1.0, Larval survival = 1.0.

THE ON-LINE MODE

The original intent of this work was to provide a model for use in the on-line control of the cereal leaf beetle. The development of YP as a parameter which at this time must be determined for each year, or modeled in future work, make that objective unattainable. The model can be used however to evaluate certain approaches to using a model in on-line control.

For example, in Table 6 and Figures 27 and 28 sensitivity of the model to a systematic bias in the measured temperature was considered. But for on-line control it isn't a systematic distortion of the type used there which needs to be considered. Rather it is the effects of using historical weather data in the model to make predictions about the current year's population trend after the initial sample. There are an infinite number of ways in which this historical data might be used but here two approaches will be considered. In the first approach one merely uses the daily temperature records from a previous year to run the simulation. In the second, one uses current weather information up to the time of a sample (here May 10) and then uses monthly maximum and minimum temperatures as estimates of future weather. Results for these two approaches are presented in terms of the chi^2 values for the comparison of field and model (Table 10), and graphically for two years' data (Figure 30). The interpretation of these results is somewhat complex. The model

TABLE 10.--Chi-square values for the correspondence between model and field data when three different temperature regimes are used as input to the model.

Year	Eggs A*	Eggs B*	Eggs C*	Larvae A	Larvae B	Larvae C
68	57	392	55	40	17	37
69	185	2604	620	52	521	353
701	45	3377	462	87	3908	858
702	41	1702	222	34	1782	391
711	73	279	151	38	138	86
712	99	556	253	16	62	15
713	13	85	41	7	12	10
Sum	513	8994	1804	274	6441	1779

A - Standard run.

B - With 1967 temperatures used for all years.

C - With actual temperatures to May 10, thereafter longterm mean maximum and minimum temperatures for the month in question.

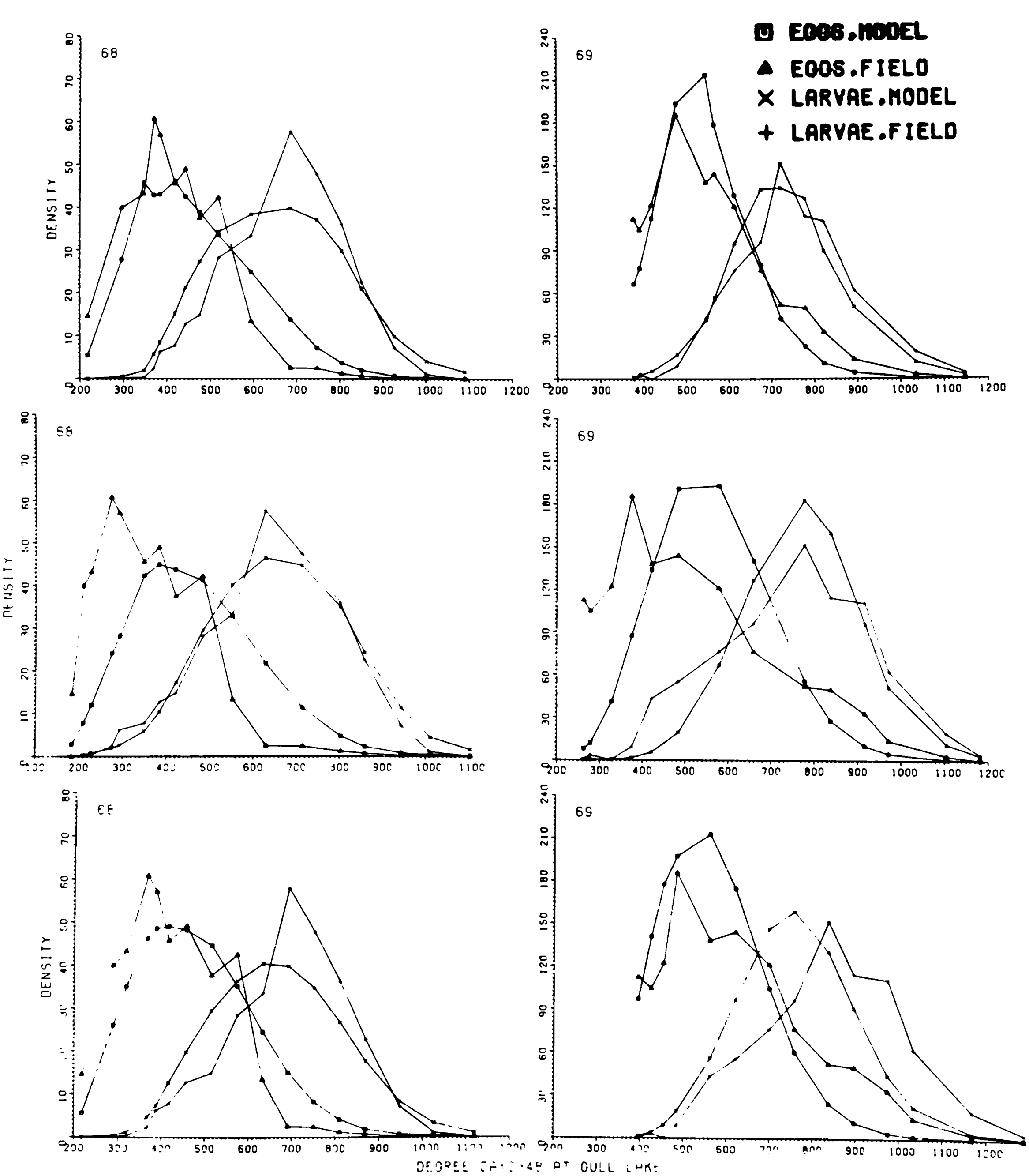


Figure 30.--The effects of using different temperature regimens after May 10 on the synchrony between model and field. Top row - actual temperatures. Middle row - using 1967 temperatures. Bottom row - using long-term weekly means.

output is generated by the input temperatures, but the field data are those values which would have been (and actually were) observed on a particular calendar data. The approach of using a sequence of temperatures from a previous year (column B in Table 10 and the second row of graphs in Figure 30) actually gave an improvement in fit when compared to the values for the basic set for larvae in 1968 (column A of Table 10, and the top row of graphs of Figure 30). This resulted in a much poorer fit. But a poorer fit was more usual. Temperature near the time of sampling initiated the synchrony and provided a considerably better overall fit than did the previous approach (Table 10, column C; Figure 30, bottom row). This suggests that very accurate temperature information up to the time of sampling to initialize the model might establish synchrony between model and field at that point and allow historical data to be used to make reasonable predictions for the rest of the season.

Essentially all of the previous discussion has been concerned with synchrony because it is the match between the shapes of the curves which reflects so many important aspects of the biology of the insect. But in more refined management plans it may be the density at a particular time during the development of the crop which is important rather than the total incidence of the insect. For on-line control we must consider the problem of whether samples taken early in the season, together with temperature data up to that point, are sufficient information for the model to predict this season's field population (in this case, given the YP value).

The ratio of eggs to larvae in the model is the same as that in the field only when mortalities are adjusted downward from the basic values (Table 9). The adjustment in mortalities needed to achieve that correspondence is different for different years, however. It is possible that the buildup of the egg parasite, _Anaphes flavipes_, released in 1967 at Gull Lake and recovered in 1968 (Maltby, et al., 1971) is responsible, at least in part, for this change in survival needed to equate model and field ratios. Unfortunately no information on _A. flavipes_ parasitism is available for years prior to 1971.

If egg and larval survivals are set to 1.0 in the model, then the ratio of eggs to larvae in the model are similar to those observed in the field except for 2 fields in 1971. Then any sample which will determine the total incidence of eggs will also determine the total incidence of larvae.

The first approach is to use current weather information to establish synchrony between the model and field, and then collect a sample. If the synchrony were truly exact and the field samples were taken without error, then the ratio of any field sample to the model value could be used to adjust model densities so that it would from that time on track field densities (neglecting for a moment the need to predict field densities using historical weather data). But of course the synchrony isn't perfect and the samples have error.

The ratio of observed densities to model values for each of the sampling times below 700 °D>48 should be compared to the ratios of the two areas under the density curves (Table 11).

TABLE 11.--The ratio of model values to field densities on the sampling day for two years. Model egg and larval survivals set to 1.0.

1968	Density Ratio		1969	Density Ratio	
°D>48	Eggs	Larvae	°D>48	Eggs	Larvae
218	18	--	378	3.6	76
296	35	97	392	4.9	5.5
347	53	266	420	6.2	--
370	45	120	479	6.8	13
384	50	67	548	11.2	7.2
419	68	103	568	10.2	8.1
443	63	94	615	10.3	9.5
476	77	111	677	10.8	11
519	59	76			
595	137	74			
686	397	43			
Area ratio	67	59		8.1	8.7

The 1968 density ratios for samples between 600 and 700 °D>48 become very large (Table 11). This is very apparent in the values for the other years not contained in Table 11. Assuming we restrict the sampling to the interval 200 to 600 °D>48, the number of eggs appears to be a better estimator of the ratio between total populations (model/field) than does the number of larvae or the total of the number of eggs and the number of larvae. This would give estimates from 0.31 to 2.32 times the actual values that do occur (Table 11). For all of the standard data set, 67 - 713 the range is 0.24 to 2.32. In fact for that data with the egg samples taken below 400 °D>48 the range is 0.24 to 1.0. That means that from egg samples taken in the range 200 to 400 °D>48 the seasonal larval population can be estimated to between 1 and 4 times its actual value. Using several samples does not seem to provide any additional information in the range 200 - 400 °D>48 and therefore need not be done.

SUMMARY AND CONCLUSIONS

A continuous time dynamic simulation model for the cereal leaf beetle was constructed. Initial adult densities were not available for the validation data, therefore a number of procedures were tested for equating field and model populations. The method which was finally accepted was to equate the egg and larval total incidence curves of the model to those of the field.

It became obvious during validation studies that either through sampling or through the development of a sub-model, the rate at which adult beetles moved from wheat to oats in the spring had to be determined. That is because synchrony between model and field depends to a very great degree on this rate. The rate of adult emergence in the spring also affects synchrony, but it is not nearly as effective in decreasing the error in synchrony between the model and field, as measured by a chi^2 like statistic computed from adjusted densities.

Although the rate at which adults move from wheat to oats could not be determined from the existing data, it was possible to establish an empirical relationship for each year. Oviposition rates into wheat and into oats under these empirical relationships were sufficient to explain the observed year-to-year differences in the percent of the beetle larvae found in oats as compared to wheat,

even though the relationships were developed by considering synchrony only.

Sampling bias against the first and second instar larvae of as much as 50% and 40%, respectively, had little effect on the synchrony but continued to have a strong effect on the population estimate, which was still only about .66 of the true value at peak density.

The model was very sensitive to biases in the temperature used to establish the synchrony. Biases greater than 1% caused serious errors. Oviposition rates and egg and larval survival are not greatly affected by temperature.

Changes in larval development times of as much as ± 20% had little effect on synchrony, but a 25% increase in the development time for eggs gave an overall improvement.

Egg and larval survival values had to be increased in order to have model values correspond more closely with field values, especially for use of the model to predict populations for management purposes.

When estimated temperatures instead of actual temperatures are used in the model, synchrony is disrupted far less if actual temperatures up until May 10 are used and then long-term monthly extrema are used rather than by using the daily temperature extrema from a previous year for the whole growing season. The conclusion is that very accurate temperature information up to the time of the density sample accurately establishes the synchrony which is not then easily distorted.

Egg population density estimates taken between 200 and 400 °D>48 make it possible to estimate the total incidence of larvae to follow to between 1 and 4 times the actual value. These large error bounds are due largely to problems in establishing the synchrony between model and field. The solution to this problem would involve a more accurate determination of the temperature affecting the insect, and an accurate estimate of the rate at which beetles move from wheat to oats. Work currently being done at MSU to develop satellite oriented environmental monitoring systems may increase the precision of temperature estimates. Research currently being done by Alan J. Sawyer (MSU Ph.D. proposed date 1978) on the between field movement of beetles may lead to methods for modeling the spring movement from wheat to oats. Neither of these efforts would be necessary if the synchrony could be determined from the sample; however, two previous efforts to do this have failed (Fulton, 1975; Logan, 1977), and that must await future investigations.

APPENDICES

APPENDIX A

COMPUTING AN ESTIMATE OF κ FOR THE ERLANG DISTRIBUTION FROM DATA

These estimates are based on mean development times and the relations for the Erlang distribution:

$$E(\tau) = 1/\alpha \tag{A1}$$

and

$$V(\tau) = 1/\kappa * \frac{1}{\alpha^2} \tag{A2}$$

$$f(\tau) = \frac{(\alpha\kappa)^k \; (\tau)^{(k-1)} e^{-k\alpha\tau}}{(k-1)!} \tag{A3}$$

Table A1 lists the means and variances for the development times of larvae at different temperatures. The variances were unpublished in Helgesen and Haynes (1972).

Table A2 presents κ values computed by solving equation A2 for κ for each treatment. The overall mean, computed as the mean of the individual κ values is also presented in Table A2. No attempt was made to determine if this procedure is an unbiased estimator of κ. In practice the value of 5 turned out to be too small and an empirically determined value of 15 was used in the model.

TABLE A1.--Means and variances for CLB larval development times. (Unpublished variances from Helgesen's work.)

	Temperature, °F					
	60°		70°		80°	
Instar	mean	var	mean	var	mean	var
1	3.81	2.66	2.55	.83	1.86	.93
2	5.33	3.06	2.12	.86	1.71	.71
3	3.00	3.63	1.87	.84	1.44	.40
4	3.59	3.26	2.00	.71	1.36	.26

TABLE A2.--K values for the Erlang distribution computed from the data in TABLE A1.

Instar	Temperature, °F 60°	70°	80°
1	5	8	4
2	9	5	4
3	3	4	5
4	4	6	7
Mean	5.25	5.75	5.00
Grand Mean	5.00		

APPENDIX B

SIMULATION MODEL FOR CEREAL LEAF BEETLE

```
      PROGRAM POPDIS(OUTPUT=129,TAPE6=129,TAPE63=129,INPUT=129,TAPE60=IN
     +PUT,
     +TAPE61=OUTPUT,TAPE64=129,TAPE65=129,TAPE66=129,TAPE67=129,TAPE62=1
     +29,TAPE87=129)
C NMM=NUMBER OF REPRODUCING ADULTS.
C ATEGG=NUMBER OF EGGS LAID TO DATE.
C NEGG=NUMBER OF EGGS NOW PRESENT.
C NL1=NUMBER OF FIRST INSTAR LARVAE.
C NL2=NUMBER OF SECOND INSTAR LARVAE.
C NL3=NUMBER OF THIRD INSTAR LARVAE.
C NL4=NUMBER OF FOURTH INSTAR LARVAE.
C NPP=NUMBER OF PUPAE
C NIA=NUMBER OF SEXUALLY IMMATURE ADULTS.
C ATN=TOTAL NUMBER OF LARVAE PRODUCED TO DATE.
C TL=TOTAL NUMBER OF LARVAE PRESENT.
C NA=TOTAL NUMBER OF MATURE AND
C      IMMATURE ADULTS PRESENT.
C ATA=TOTAL NUMBER OF MATURE AND IMMATURE
C      ADULTS PRODUCED TO DATE.
C E=EGG PRODUCTION RATE FOR THE POPULATION.
C L1S= NUMBER OF EGGS SURVIVING TO ENTER
C      THE 1ST INSTAR DELAY.
C L2S=NUMBER OF L1"S SURVIVING TO ENTER THE 2ND INSTAR.
C L3S=NUMBER OF L2"S SURVIVING TO ENTER THE 3RD INSTAR.
C L4S=NUMBER OF L3"S SURVIVING TO ENTER THE 4TH INSTAR.
C NPS=NUMBER OF L4"S SURVIVING TO ENTER THE PUPAL STAGE.
C HOUR=NUMBER OF RADIANS REPRESENTED BY 1 HOUR
C ON A 24 HOUR CLOCK.
C Q1=NUMBER OF HOURS REPRESENTED BY A TIME CHANGE OF 1 DT.
C AMAX=MAXIMUM TEMPERATURE FOR THE DAY.
C AMIN=MINIMUM TEMPERATURE FOR THE DAY.
C DAILY TEMPERATURES ARE ASSUMED TO FLUCTUATE IN A
C SINUSOIDAL MANNER WITH MINIMUM=AMIN AND MAXIMUM=AMAX.
C HTIME IS 24 HOUR CLOCK TIME.
C MAXIMUM AND MINIMUM TEMPERATURES ARE ASSUMED TO BE
C 12 HOURS APART, WITH MINIMUM OCCURING AT 3 AM
C AND MAXIMUM AT 3 PM.
C DELLVF IS A TIME VARYING DELAY FUNCTION
C MODIFIED SLIGHTLY FROM MANETSCH, T.J. AND
C G.L. PARK 1973.  SYSTEM ANALYSIS AND SIMULATION
C WITH APPLICATIONS TO ECONOMIC AND SOCIAL SYSTEMS.  PART II
C PRELIMINARY.  MICHIGAN STATE UNIVERSITY.
C THESE ARE TIME VARYING DELAY VALUES
C USED AS INPUTS TO FUNCTION DELLVF
C THE MATURATION DELAY FOR EACH STAGE
C IS A FUNCTION OF TEMPERATURE WHICH IS
C IN THIS CASE A FUNCTION OF TIME.
C M=THE RATE(NO./DAY)AT WHICH SEXUALLY
C MATURE LOCAL ADULTS ARE ENTERING THE POPULATION.
C RATE(NO./DAY)AT WHICH PUPAE
C  ARE BECOMING ADULTS.
C NP =RATE (NO./DAY) AT WHICH 4TH INSTAR
C LARVAE ARE BECOMING PUPAE.
```

```
C L4=RATE AT WHICH 3RD INSTAR LARVAE ARE
C BECOMING 4TH INSTAR LARVAE.
C L3=RATE AT WHICH 2ND INSTAR LARVAE ARE
C BECOMING 3RD INSTAR LARVAE.
C L2=RATE AT WHICH 1ST INSTAR LARVAE ARE
C BECOMING 2ND INSTAR LARVAE.
C L1=RATE OF EGG HATCH.
C AD=SEXUALLY MATURE ADULT MORTALITY RATE, WHICH IS
C TEMPERATURE DEPENDENT.
C TABLIE IS A TABLE LOOK UP FUNCTION FROM
C FORDYN. BY R.W.LLEWELLYN, 1965.  RALEIGH
C , NORTH CAROLINA.
C TABLI IS A TABLE LOOK UP FUNCTION FROM
C FORDYN.  BY R.W.LLEWELLYN, 1965.  RALEIGH, NORTH CAROLINA.
C SET THE ARRAYS FOR INTERMEDIATE RATES FOR
C THE DELLVF DELAY ROUTINE TO THEIR INITIAL VALUES.
C THESE K VALUES ARE THE ORDER OF THE
C DELAY USED TO REPRESENT VARIOUS STAGES
C THEY ARE RELATED TO THE VARIANCE OF DELAY
C (DEVELOPMENT, LIFETIME) TIMES OF INDIVIDUALS
C IN THE POPULATION.
C KA=ADULT LONGEVITY.
C KM=ADULT PREMATING PERIOD.
C KE=EGG DEVELOPMENT PERIOD.
C KL1=L1 DEVELOPMENT PERIOD.
C KL2=L2 DEVELOPMENT PERIOD.
C KL3=L3 DEVELOPMENT PERIOD.
C KL4=L4 DEVELOPMENT PERIOD.
C KP=PUPAL DEVELOPMENT PERIOD
      DIMENSION AYE(10)
      DIMENSION DEGG(7),DL1(5),DL2(5),DL3(5),DL4(5),DP(7)
      DIMENSION MATT(4)
      DIMENSION RL1(15),RL2(15),RL3(15),RL4(15),RSA(15)
      DIMENSION RE(15)
      DIMENSION RA(15),RM(15)
      DIMENSION YEAR67(20),YEAR68(20),YEAR69(20),YEAR70(20),YEAR71(20)
      DIMENSION YEAR(20)
      DIMENSION YEAR72(20),YEAR73(20),YEAR74(20),YEAR75(20)
      DIMENSION YEAR76(20),YEAR77(20)
      LOGICAL WHEAT
      REAL NL1,NL2,NL3,NL4,NPP,NEGG
      REAL NIA
      REAL L1,L2,L3,L4,NP
      REAL NA,NSA
      REAL MATT
      REAL NMA,NMM
      DATA AYE/-3.274,3.966,.1046,.1046,3.966,5*.1046/
      DATA YEAR71/34.,41.,42.,48.,55.,62.,70.,76.,83.,90.,10*0./
      DATA YEAR70/31.,43.,48.,52.,58.,65.,71.,78.,85.,91.,10*0./
      DATA YEAR67/27.,38.,46.,63.,73.,82.,89.,97.,12*0./
      DATA YEAR68/26.,29.,37.,44.,47.,52.,54.,57.,60.,63.,66.,69.,72.,
     +75.,78.,81.,85.,89.,93.,0./
      DATA YEAR69/50.,53.,56.,59.,63.,66.,70.,73.,77.,80.,84.,87.,93.,
     +98.,6*0./
```

```
      DATA MATT/32.,16.,10.,4./
      DATA DEGG/16.5,12.5,9.7,7.7,5.5,5.0,4.5/
      DATA DL1/3.8,3.2,2.5,2.2,1.9/
      DATA DL2/5.3,3.7,2.2,1.9,1.7/
      DATA DL3/3.,2.4,1.9,1.7,1.4/
      DATA DL4/3.6,2.8,2.0,1.7,1.4/
      DATA DP/42.,30.,22.5,17.5,12.5,10.5,10./
      DATA YEAR72/47.,52.,55.,63.,69.,75.,82.,89.,96.,11*0./
      DATA YEAR73/46.,53.,61.,68.,73.,79.,82.,88.,96.,11*0./
      DATA YEAR
     +74/47.,51.,55.,59.,64.,68.,73.,78.,82.,86.,89.,93.,96.,7*0./
      DATA YEAR75/50.,53.,59.,64.,67.,71.,74.,78.,81.,85.,88.,9*0./
      DATA YEAR
     +76/33.,47.,51.,54.,58.,61.,65.,68.,72.,79.,82.,86.,89.,92.,
     +6*0./
      DATA YEAR77/47.,50.,54.,57.,61.,64.,68.,71.,75.,78.,
     +82.,85.,89.,92.,6*0./
      REWIND 6
      DO 347 IU=60,67
      REWIND IU
347   CONTINUE
4711  CONTINUE
      TITX=TIME(ZZ)
      TITY=DATE(JO)
      FACTOR=1.05
      DDAY2=0.
      WHEAT=.F.
      DT=.1
      HALFDT=DT/2.
C IKO DETERMINES THE PRINT FREQUENCY
      IKO=5
C PROPFEM IS THE PROPORTION OF FEMALES IN THE MATURE ADULT POPULATION
      PROPFEM=0.5
      IRLLGT=110
      TIMEX=0.
      IDTR=1./DT+1.
      Q1=DT*24.
      PIE=3.1415926
      TOPIE=2.*PIE
      HOUR=TOPIE/24.
      AMAX=0.
      AMIN=0.
      DO12 J=1,15
      RA(J)=0.
      RM(J)=0.
      RE(J)=0.
      RL1(J)=0.
      RL2(J)=0.
      RL3(J)=0.
      RL4(J)=0.
      RSA(J)=0.
12    CONTINUE
      CO=1.
      EGSUR=1.
```

```
      DDAY=0.
      DD5=0.
      PROB=0.
      PROB1=0.
      TPOP=100.
      DM=0.
      DELPA=1.
      DELPM=1.
      DELPE=1.
      DELPL1=1.
      DELPL2=1.
      DELPL3=1.
      DELPL4=1.
      DELPAS=1.
      NSA=0.
      TL=0.
      NEGG=0.
      NL1=0.
      NL2=0.
      NL3=0.
      NL4=0.
      NPP=0.
      E=0.
      ATEGG=0.
      NIA=0.
      NP=0.
      L1=0.
      L2=0.
      L3=0.
      L4=0.
      SE=0.
      NMA=0.
      NMM=0.
      KA=15
      KM=15
      KE=15
      KL1=15
      KL2=15
      KL3=15
      KL4=15
      KAS=3
      ATL1=0.
      ATL2=0.
      ATL3=0.
      ATL4=0.
      ATP=0.
      SKIP=10.
      EFTEMP=0.
      SKP=10.
      READ(6,21)ISTATE,INDEXNO,IDIV,IYEAR
      IF(EOF(6))1111,1101
1101  CONTINUE
```

```
      IV=1
      JP=IYEAR-66
      IF(IYEAR.LT.67.OR.IYEAR.GT.77)JP=12
      DO 1102 IM=1,20
      GO TO (1104,1105,1106,1107,1108,1112,1113,1114,1115,1116,1117
     +,1109)JP
1104  YEAR(IM)=YEAR67(IM)
      GO TO 1102
1105  YEAR(IM)=YEAR68(IM)
      GO TO 1102
1106  YEAR(IM)=YEAR69(IM)
      GO TO 1102
1107  YEAR(IM)=YEAR70(IM)
      GO TO 1102
1108  YEAR(IM)=YEAR71(IM)
      GO TO 1102
1112  YEAR(IM)=YEAR72(IM)
      GO TO 1102
1113  YEAR(IM)=YEAR73(IM)
      GO TO 1102
1114  YEAR(IM)=YEAR74(IM)
      GO TO 1102
1115  YEAR(IM)=YEAR75(IM)
      GO TO 1102
1116  YEAR(IM)=YEAR76(IM)
      GO TO 1102
1117  YEAR(IM)=YEAR77(IM)
      GO TO 1102
1109  YEAR(IM)=0.
1102  CONTINUE
21    FORMAT(I2,I4,I1,I2)
      WRITE(62,22)ISTATE,INDEXNO,IDIV,IYEAR,TITX,TITY,WHEAT
      WRITE(61,22)ISTATE,INDEXNO,IDIV,IYEAR,TITX,TITY,WHEAT
      WRITE(63,22)ISTATE,INDEXNO,IDIV,IYEAR,TITX,TITY,WHEAT
      WRITE(66,22)ISTATE,INDEXNO,IDIV,IYEAR,TITX,TITY,WHEAT
      WRITE(67,22)ISTATE,INDEXNO,IDIV,IYEAR,TITX,TITY,WHEAT
      WRITE(64,22)ISTATE,INDEXNO,IDIV,IYEAR,TITX,TITY,WHEAT
      WRITE(64,555)
      WRITE(66,555)
555   FORMAT(* 10AE1234LPS*)
      WRITE(65,22)ISTATE,INDEXNO,IDIV,IYEAR,TITX,TITY,WHEAT
      WRITE(65,556)
      WRITE(67,556)
556   FORMAT(*  9AE1234PS*)
22    FORMAT(*1WEATHER ,STATE *I3*STA.NO.*I5
     +* DIV. *I2* YEAR=19*I2,* TIME *A10* DATE *A10* WHEAT= *L1)
      WRITE(61,6)
6     FORMAT(* DAY*,2X,*DD>48*2X*EMER*1X,*IM.AD.*,1X,*MAT.AD*,
     +3X,*EGGS*,4X,*EGG INPUT*1X,*T.LARVAE*1X,*N.PUPAE*,1X,* DD 42  *)
      WRITE(63,66)
66    FORMAT(5X* DAY*2X*DD>48*2X*DD>9*3X*F I E*3X* ONE*3X*TWO*1X*THREE*
     +2X*FOUR*1X*S.ADULTS*)
```

```
      DO1 I=1,IRLLGT
      HTIME=0.
      READ(6,29)AMAX,AMIN
29     FORMAT(2F3.0)
      AMAX=.555555555*(AMAX-32.)
      AMIN=.555555555*(AMIN-32.)
C     AMAX=18.5
C     AMIN=12.5
      HRANG=(AMAX-AMIN)/2.
      TMEAN=(AMAX+AMIN)/2.
      DO 3 J=1,IDTR
      HTIME=HTIME+Q1
      THETA=(HTIME-9.)*HOUR
      TEMP=TMEAN+HRANG*SIN(THETA)
      TEMP=TEMP*FACTOR
      TIMEX=TIMEX+DT
      DELM=TABLIE(MATT,10.,5.56,3,TEMP)
      CERN=.00164-.00242*TEMP
      DELA=-.69315/AMIN1(-.000069315,CERN)
C COMPUTED AS LN(2)/INSTANTANEOUS SURVIVAL RATE
      DELE=TABLIE(DEGG,15.5,2.75,6,TEMP)
C     DELE=DELE*1.2
      DELE=1.25*DELE
C     DELE=DELE*1.3
C     DELE=DELE*.8
C     DELE=DELE*.9
      DELL1=TABLIE(DL1,15.5,2.75,4,TEMP)
      DELL2=TABLIE(DL2,15.5,2.75,4,TEMP)
      DELL3=TABLIE(DL3,15.5,2.75,4,TEMP)
      DELL4=TABLIE(DL4,15.5,2.75,4,TEMP)
      DELNP=TABLIE(DP,15.5,2.75,6,TEMP)
50    FORMAT(* *7G10.3,/* *7G10.3)
      SAD=DELLVF(NP,RSA,NPP,CO,DELNP,DELPAS,DT,KAS)
      NP=DELLVF(L4,RL4,NL4,CO,DELL4,DELPL4,DT,KL4)
      L4=DELLVF(L3,RL3,NL3,CO,DELL3,DELPL3,DT,KL3)
      L3=DELLVF(L2,RL2,NL2,CO,DELL2,DELPL2,DT,KL2)
      L2=DELLVF(L1,RL1,NL1,CO,DELL1,DELPL1,DT,KL1)
      L1=DELLVF(E,RE,NEGG,EGSUR,DELE,DELPE,DT,KE)
      AD=DELLVF(DM,RA,NMM,1.,DELA,DELPA,DT,KA)
C FOR PULSE INPUT
C     IF(TIMEX.GT.2.*DT)SE=0.
      DM=DELLVF(SE,RM,NIA,1.,DELM,DELPM,DT,KM)
      AAE=PROB*TPOP
      NA=NMM+NIA
      ATEGG=ATEGG+DT*E
      ATL1=ATL1+DT*L1
      ATL2=ATL2+DT*L2
      ATL3=ATL3+DT*L3
      ATL4=ATL4+DT*L4
      ATP=ATP+DT*NP
      FIE=1.*NL1+3.1*NL2+8.9*NL4+12.5*NL4
C DATA FROM WELLSO , 1973 ANN. ENT. SOC. AMER. 66:1201-8
      NSA=NSA+DT*SAD
```

```
      TL=NL1+NL2+NL3+NL4
      EFTEMP=AMAX1(0.,TEMP-9.)
      EFTEMP2=AMAX1(0.,TEMP/FACTOR-9.)
      PDD5=AMAX1(0.,TEMP-5.6)
      DD5=DD5+PDD5*DT
C COMPUTE DISTRIBUTION BETWEEN OATS AND WHEAT
C USING THE FOLLOWING PROBIT EQUATION
C     YP=.2552+.01819*DD5
C     YP=.8625+.01379*DD5
C     YP=1.939+.01379*DD5
C     YP=2.539+.00820*DD5
C     YP=-6.64+.00820*DD5
C     YP=-.291+.01764*DD5
C     YP=3.055+.00648*DD5
C     YP=3.055+.00648*DD5
C     YP=.1046+.01379*DD5
C     YP=-.0654+.01379*DD5
C     YP=3.412+.00648*DD5
C     YP=2.587+.01379*DD5
C     YP=3.966+.01379*DD5
C     YP=-1.343+.01379*DD5
C     YP=-2.033+.01379*DD5
C     YP=-3.274+.01379*DD5
      YP=AYE(JP)+.01379*DD5
      YP=YP-5.
      CALL NDTR(YP,PROB2,DENS)
      Y1=PROB2
C     IF(DD5.LT.105.)Y1=0.
      DDAY=DDAY+EFTEMP*DT
      DDAY2=DDAY2+EFTEMP2*DT
      IF(DDAY.LE.0.)DDAY=1.E-5
      ALDDAY=ALOG(DDAY)
C EMERGENCE IS LOG NORMALLY DISTRIBUTED WITH MEAN=3.97546DD>9
C AND STANDARD DEVIATION =.5026
      XNORM=(ALDDAY-3.97546)/.5026
C     XNORM=(ALDDAY-5.048)/.6382
C     XNORM=(ALDDAY-3.278)/.4145
C     XNORM=(ALDDAY-3.429)/.4334
C     XNORM=(ALDDAY-3.593)/.4543
C NEXT VALUE WAS BEST IN VALIDATION RUNS.
C     XNORM=(ALDDAY-3.167)/.4004
C     XNORM=(ALDDAY-3.886)/.2884
      CALL NDTR(XNORM,PROB,DENS)
      PROBD=PROB-PROB1
      PEM=TPOP*PROBD
      PROB1=PROB
      SE=PEM/DT
C NEXT LINE FOR PULSE INPUT
C     SE=5000.
      RDT=DT*(DM-AD)
C RDT IS THE INTEGRAL OVER ONE DT AND IS THEREFORE THE CHANGE
C IN THE NUMBER OF MATURE ADULTS IN THIS DT
C
```

```
      NMA=NMA+RDT
      E=EFTEMP*PROPFEM*NMA*FEC(DDAY,WHEAT)
      IF(WHEAT)Y1=1.-Y1
      E=E*Y1
C USE  Y1=1.-Y1 TO GENERATE THE WHEAT CURVES
      EGSUR=AMIN1(EXP(DT*(-.0423-.002075*TEMP)),1.)
      CO=AMIN1(EXP((.00775-.002569*TEMP)*DT),1.)
      FA=1.8*DDAY2
      DD42=DD5*1.8
      IF(FA.LT.SKIP)GO TO 3
      IF(FA.GT.500.)SKP=50.
      IF(FA.GT.1000.)SKP=100.
      IF(FA.GE.1500.)SKP=1000.
      IF(NEGG.GT.1.)ELRAT=TL/NEGG
      WRITE(87,704)FA,ELRAT
704   FORMAT(* *F5.1,*,*F16.8)
      SKIP=SKIP+SKP
      WRITE(64,666)FA,NA,NEGG,NL1,NL2,NL3,NL4,TL,NPP,NSA
      WRITE(65,666)FA,AAE,ATEGG,ATL1,ATL2,ATL3,ATL4,ATP,NSA
666    FORMAT(* *10F7.0)
3     CONTINUE
      WRITE(66,666)TIMEX,NA,NEGG,NL1,NL2,NL3,NL4,TL,NPP,NSA
      WRITE(67,666)TIMEX,AAE,ATEGG,ATL1,ATL2,ATL3,ATL4,ATP,NSA
      XTIME=TIMEX+HALFDT
      IF(IFIX(XTIME).NE.IFIX(YEAR(IV)))GO TO 84
      IV=IV+1
      WRITE(62,87)TIMEX,FA,IYEAR,WHEAT,NEGG,NL1,NL2,NL3,NL4,TL
87    FORMAT(* *F5.1,F5.0 ,I2,L2,6(F6.1,1X))
84    CONTINUE
      IT=I/IKO
      IT=IKO*IT
      IF(IT.NE.I)GO TO 1
      WRITE(61,4)TIMEX,FA,PROB,NIA,NMM,NEGG,ATEGG,TL,NPP,DD42
      WRITE(63,5)TIMEX,FA,DDAY,FIE,NL1,NL2,NL3,NL4,NSA
5     FORMAT(* *9(1X,F6.0))
4     FORMAT(* *F4.0,F6.0,1X,F5.3,F6.0,3(3X,F6.0),4X,F6.0,3X,F6.0,4X,F5.
     +0)
1     CONTINUE
      EPF=ATEGG/(TPOP*PROPFEM)
      WRITE(61,457)EPF
457   FORMAT(* EGGS / FEMALE =*F5.1)
      SURE=ATL1/ATEGG
      SURL1=ATL2/ATL1
      SURL2=ATL3/ATL2
      SURL3=ATL4/ATL3
      SURL4=ATP/ATL4
      WRITE(61,349)SURE,SURL1,SURL2,SURL3,SURL4
349   FORMAT(* SURVIVAL ,EGG=*F5.3,1X*L1=*F5.3,1X*L2=*F5.3,1X*L3=*F5.3,1
     +X*L4=*F5.3,1X)
      ATL=ATL1+ATL2+ATL3+ATL4
      ENDFILE 62
      ENDFILE 64
```

```
      ENDFILE 65
      ENDFILE 66
      ENDFILE 67
      ENDFILE 87
      GO TO 4711
1111  CONTINUE
      CALL EXIT
      END
```

```
      FUNCTION DELLVF(RIN,R,STRG,SURVR,DEL,DELP,DT,K)
      DIMENSION R(1)
C SURVR MUST BE COMPUTED ON A PER DT BASIS
      VIN=RIN
      FK=FLOAT(K)
      B=1.+(DEL-DELP)/(FK*DT)
      A=FK*DT/DEL
      DELP=DEL
      DO 10 I=1,K
      DR=R(I)
      R(I)=DR+A*(VIN-DR*B)
      VIN=DR
10    CONTINUE
      STRG=0.
      DO 30 I=1,K
      R(I)=R(I)*SURVR
      STRG=STRG+R(I)*DEL/FK
30    CONTINUE
      DELLVF=R(K)
      RETURN
      END
```

```
      FUNCTION TABLIE(VAL,SMALL,DIFF,K,DUMMY)
      DIMENSION VAL(1)
      DUM=AMIN1(AMAX1(DUMMY-SMALL,0.),FLOAT(K)*DIFF)
      I=1.+DUM/DIFF
      IF(I.EQ.K+1)I=K
      TABLIE=(VAL(I+1)-VAL(I))*(DUM-FLOAT(I-1)*DIFF)/DIFF+VAL(I)
      RETURN
      END



      FUNCTION TABLI(VAL,ARG,DUMMY,K)
      DIMENSION VAL(1),ARG(1)
      DUM=AMAX1(AMIN1(DUMMY,ARG(K)),ARG(1))
      DO 1 I=2,K
      IF (DUM.GT.ARG(I))GO TO 1
      TABLI=(DUM-ARG(I-1))*(VAL(I)-VAL(I-1))/(ARG(I)-ARG(I-1))+VAL(I-1)
      RETURN
1     CONTINUE
      RETURN
      END



      FUNCTION FEC(RNDT,WHEAT)
      LOGICAL WHEAT
      FEC=.9297
      IF(WHEAT)2,1
1     IF (RNDT.LT.204.)RETURN
      FEC=189.25/RNDT
      RETURN
2     CONTINUE
      IF(RNDT.LT.166.)RETURN
      FEC=153.606/RNDT
      RETURN
      END
```

```
      FUNCTION DAY(I,PHI)
C THIS FUNCTION COMPUTES THE LENGTH OF DAY (SUNRISE TO SUNSET)
C FOR ANY LATITUDE .THE LOGIC WAS DEVELOPED BY R. BRANDENBURG
C AND PROGRAMMED BY W. C. FULTON
C "TO" IS MARCH 21  , 1974
C SEE MY FILE "FPHOTOPERIOD"
      DATA TO/127./,Y/.0172020236/,X/.39795/,Z/-.0145439/,R/7.63944/
      T=I+48
      XL=Y*(T-TO)
      SD=X*SIN(XL)
      D=ASIN(SD)
      CT=(-.0145439-SIN(PHI)*SD)/(COS(PHI)*COS(D))
      ACT=ACOS(CT)
      DAY=R*ACT
      RETURN
      END



      SUBROUTINE NDTR(X,P,D)
      AX=ABS(X)
      T=1./(1.+.2316419*AX)
      D=.3989423*EXP(-X*X/2.)
      P=1.-D*T*(((1.330274*T-1.821256)*T+1.781478*T-
     +.3565638)*T+.3193815)
      IF(X)1,2,2
1     P=1.-P
2     RETURN
      END



      FUNCTION PEG(T)
      DIMENSION PHO(8),PHE(8)
      DATA PHO/0.,9.,13.5,14.5,15.5,16.5,20.,23.5/
      DATA PHE/.02,.005,.02,.36,1.,1.,.65,.06/
      PEG=TABLI(PHE,PHO,T,8)
      RETURN
      END
```

APPENDIX C

VALIDATION PROGRAM

```
      PROGRAM COMPARE (OUTPUT,TAPE61=OUTPUT,TAPE62,TAPE80,TAPE81)
      DIMENSION IDAY(20,2),EGG(20,2),AL1(20,2),AL2(20,2)
     +,AL3(20,2),AL4(20,2)
      DIMENSION ATL(20,2),IYEAR(11),JYEAR(11)
      DIMENSION KDAY(7)
      DIMENSION X(20,11),Y(20,11),IIYER(20)
      DIMENSION IDDAY(20)
      DIMENSION CHI(20,2)
      INTEGER TIMEX,DATEX
      REWIND 62
      REWIND 80
      REWIND 81
      REWIND 61
      DATA KDAY/0,0,0,0,30,61,91/
      DATA IYEAR/8,19,14,10,10,9,9,13,11,14,14/
      DATA JYEAR/1,1,1,2,3,1,2,1,1,1,1/
      IIYER(19)=4HMEAN
      IIYER(20)=4HS.D.
      KY=0
45    READ(62,1)IYER,TIMEX,DATEX
1     FORMAT(47X,I2,2(6X,A10))
      IF(EOF(62))6,7
7     WRITE(61,3)TIMEX,DATEX
3     FORMAT(* VALIDATION DATA FOR RUN OF *A10,2X,A10)
      II=IYEAR(IYER-66)
      DO 10 I=1,II
      READ(62,4)IDAY(I,1),IDDAY(I),EGG(I,1),AL1(I,1),AL2(I,1),AL3(I,1)
     +,AL4(I,1),ATL(I,1)
4     FORMAT(I4,2X,I4,5X,6(F6.1,1X))
10    CONTINUE
55    FORMAT(* *6F6.0)
      READ(62,55)
      IF(EOF(62))347,347
347     CONTINUE
      II=JYEAR(IYER-66)
      DO11 K=1,II
      KY=KY+1
      IIYER(KY)=IYER
      READ(80,13)TIEGG,TATL1,TATL2,TATL3,TATL4,TATL
13    FORMAT(6F6.1)
      J=0
23    J=J+1
      READ(80,22)MO,JDAY,EGG(J,2),AL1(J,2),AL2(J,2),AL3(J,2),
     +AL4(J,2),ATL(J,2)
      IF(EOF(80))24,25
22    FORMAT(2I2,13X,6F5.1)
25    IDAY(J,2)=KDAY(MO)+JDAY
      ATL(J,2)=AL1(J,2)+AL2(J,2)+AL3(J,2)+AL4(J,2)
      GO TO 23
24    J=J-1
      PRINT*,"*******************************************************"
```

```
      PRINT*,"****************************************************"
      PRINT*,"****************************************************"
      PRINT*,"EGGS","19",IYER
      IW=1
      CALL REGRESS(J,IDAY,EGG,IDDAY,X1,Y1,IW,ZX)
      CHI(KY,1)=ZX
      IW=0
      X(KY,1)=X1
      Y(KY,1)=Y1
      PRINT*,"****************************************************"
      PRINT*,"FIRST INSTAR","19",IYER
      CALL REGRESS(J,IDAY,AL1,IDDAY,X1,Y1,IW,ZX)
      X(KY,2)=X1
      Y(KY,2)=Y1
      X(KY,3)=X(KY,2)-X(KY,1)
      Y(KY,3)=Y(KY,2)-Y(KY,1)
      PRINT*,"****************************************************"
      PRINT*,"SECOND INSTAR","19",IYER
      CALL REGRESS(J,IDAY,AL2,IDDAY,X1,Y1,IW,ZX)
      X(KY,4)=X1
      Y(KY,4)=Y1
      X(KY,5)=X1-X(KY,1)
      Y(KY,5)=Y1-Y(KY,1)
      PRINT*,"****************************************************"
      PRINT*,"THIRD INSTAR","19",IYER
      CALL REGRESS(J,IDAY,AL3,IDDAY,X1,Y1,IW,ZX)
      X(KY,6)=X1
      Y(KY,6)=Y1
      X(KY,7)=X1-X(KY,1)
      Y(KY,7)=Y1-Y(KY,1)
      PRINT*,"****************************************************"
      PRINT*,"FOURTH INSTAR","19",IYER
      CALL REGRESS(J,IDAY,AL4,IDDAY,X1,Y1,IW,ZX)
      X(KY,8)=X1
      Y(KY,8)=Y1
      X(KY,9)=X1-X(KY,1)
      Y(KY,9)=Y1-Y(KY,1)
      PRINT*,"****************************************************"
      PRINT*,"TOTAL LARVAE","19",IYER
      IW=1
      CALL REGRESS(J,IDAY,ATL,IDDAY,X1,Y1,IW,ZX)
      CHI(KY,2)=ZX
      X(KY,10)=X1
      Y(KY,10)=Y1
      X(KY,11)=X1-X(KY,1)
      Y(KY,11)=Y1-Y(KY,1)
      PRINT*,"****************************************************"
11    CONTINUE
      GO TO 45
6     CONTINUE
      DO 900 IS=1,11
      SUMX2=0.
      SUMY2=0.
```

```
      SUMX=0.
      SUMY=0.
      YK=KY
      YK1=KY-1
      DO 901 IY=1,KY
      SUMY=SUMY+Y(IY,IS)
      SUMY2=SUMY2+Y(IY,IS)**2
      SUMX=SUMX+X(IY,IS)
      SUMX2=SUMX2+X(IY,IS)**2
901   CONTINUE
      Y(19,IS)=SUMY/YK
      X(19,IS)=SUMX/YK
      Y(20,IS)=SQRT((SUMY2-SUMY**2/YK)/YK1)
      X(20,IS)=SQRT((SUMX2-SUMX**2/YK)/YK)
900   CONTINUE
      PRINT*," MODEL OUTPUT"
      WRITE(61,907)
907   FORMAT(* YEAR  EGG    L1   DIF    L2   DIF    L3   DIF*
     +*    L4   DIF  TOTAL   DIF*)
      DO 300 IB=1,KY
      WRITE(61,803)IIYER(IB),(X(IB,IY),IY=1,11)
803   FORMAT(3X,I2,11F6.0)
300   CONTINUE
      WRITE(61,903)IIYER(19),(X(19,IY),IY=1,11)
      WRITE(61,903)IIYER(20),(X(20,IY),IY=1,11)
      PRINT*," FIELD OBSERVATIONS"
      WRITE(61,907)
      DO 904 IS=1,KY
      WRITE(61,803)IIYER(IS),(Y(IS,IY),IY=1,11)
903   FORMAT(1X,A4,11F6.0)
904   CONTINUE
      WRITE(61,903)IIYER(19),(Y(19,IY),IY=1,11)
      WRITE(61,903)IIYER(20),(Y(20,IY),IY=1,11)
      WRITE(61,333)TIMEX,DATEX
333   FORMAT(*1RUN OF *2A10)
      WRITE(61,918)
918   FORMAT(* YEAR     EGGS  LARVAE*)
      CHIL=0.
      CHIE=0.
      DO915 IPS=1,KY
      WRITE(61,914)IIYER(IPS),CHI(IPS,1),CHI(IPS,2)
      CHIL=CHI(IPS,2)+CHIL
      CHIE=CHI(IPS,1)+CHIE
914   FORMAT(* 19*I2,1X,2F8.1)
915   CONTINUE
      WRITE(61,334)CHIE,CHIL
334   FORMAT(*-TOTAL*2F8.0)
      END
      SUBROUTINE REGRESS(J,IDAY,STAGE,IDDAY,XMDD,XFDD,IWR,S5)
      DIMENSION IDAY(20,2),STAGE(20,2),A(20),B(20)
      DIMENSION IDDAY(20),JDDAY(20)
      REAL MEANX,MEANY
```

```
      K=0
      TIM=0.
      TIF=0.
      DO 1 I=1,J
      A(I)=STAGE(I,2)
4     IF(IDAY(I+K,1).EQ.IDAY(I,2))GO TO 3
      K=K+1
      GO TO 4
3     B(I)=STAGE(I+K,1)
      JDDAY(I)=IDDAY(I+K)
1     CONTINUE
      SUMX=0.
      SUMY=0.
      SUMX2=0.
      SUMY2=0.
      SUMXY=0.
      N=J
      N1=1
      KL=0
      J1=J-1
      DO 75 IW=1,J1
      IF(A(IW).GT.0..OR.A(IW+1).GT.0.)KL=1
      IF(KL.EQ.1)GO TO 75
      N1=N1+1
75    CONTINUE
      DO13 IV=2,N
      DDT=JDDAY(IV)-JDDAY(IV-1)
      TIM=TIM+(B(IV)+B(IV-1))/2.*DDT
      TIF=TIF+(A(IV)+A(IV-1))/2.*DDT
13    CONTINUE
      TIM=TIM/220.
      TIF=TIF/220.
      RATIO=TIF/TIM
      DO 5 JIM=N1,N
      X=B(JIM)
      Y=A(JIM)
      SUMX=SUMX+X
      SUMY=SUMY+Y
      SUMX2=SUMX2+X**2
      SUMY2=SUMY2+Y**2
      SUMXY=SUMXY+X*Y
    5 CONTINUE
      N=N-N1+1
      SX2=SUMX2-SUMX**2/FLOAT(N)
      SY2=SUMY2-SUMY**2/FLOAT(N)
      SXY=SUMXY-SUMX*SUMY/FLOAT(N)
      BORIGIN=SUMXY/SUMX2
      SLOPEB=SXY/SX2
      SE=SQRT((SY2-SXY**2/SX2)/FLOAT(N-2))
      SB=SQRT(SE**2/SX2)
      TZERO=SLOPEB/SB
```

```
      R2=SXY**2/SX2/SY2
      R=SQRT(R2)
      MEANX=SUMX/FLOAT(N)
      MEANY=SUMY/FLOAT(N)
      YINTER=MEANY-SLOPEB*MEANX
      WRITE(61,445)
445   FORMAT(*OLINEAR REGRESSION STATISTICS - INDEPENDENT VARIABLE IS MO
     +DEL*)
      PRINT 100,N
100   FORMAT(*ONUMBER OF OBSERVATIONS = *,I6)
      PRINT 199,YINTER
199   FORMAT(*OY INTERCEPT = A = *20X,G15.6)
      PRINT 200,SLOPEB,TZERO,SE
      PRINT 201,BORIGIN
201   FORMAT(* SLOPE THRU THE ORIGIN = *F10.4)
200   FORMAT(* SLOPE = B = *26XG15.6,/,*OT VALUE FOR NULL HYPOTHESIS*
     +* (HO:B=0)= *,G15.6,/,* STANDARD ERROR = *21XG15.6)
      PRINT 300,R2,R
300   FORMAT(* COEFFICIENT OF DETERMINATION   R2 = *2XG15.6,/,
     +* CORRELATION COEFFICIENT  R= *10XG15.6)
      WRITE(61,14)TIM,TIF,RATIO
14    FORMAT(*OTOTAL INCIDENCE , MODEL =*F6.1* FIELD = *F6.1* RATIO
     +=F/M= *
     +F6.4)
      WRITE(61,943)
943   FORMAT(*ODD>48  MODEL   FIELD EXPECTED   DEV  MODEL.B    DEV  *
     +*MODEL.TIR    DEV  CHI SQ*)
      Z9=0.
      S5=0.
      Z5=0.
      Z6=0.
      S1=0.
      S2=0.
      S3=0.
      XMD=B(N1)
      XFD=A(N1)
      DO 107 KX=N1,J
      VAL=YINTER+SLOPEB*B(KX)
      Z=VAL-A(KX)
      Z1=B(KX)*ABS(SLOPEB)
      Z2=B(KX)*RATIO
      Z3=Z1-A(KX)
      Z4=Z2-A(KX)
      Z5=Z5+Z3
      Z6=Z6+Z4
      S1=S1+Z**2
      S2=S2+Z3**2
      Z42=Z4**2
      S3=S3+Z42
      IF(Z2.NE.0.)GO TO 930
      Z9=0.
```

```
      GO TO 927
930   CONTINUE
      Z9=Z42/Z2
      S5=S5+Z9
927   CONTINUE
      IF(B(KX).LT.XMD)GO TO 925
      XMDD=JDDAY(KX)
      XMD=B(KX)
925   CONTINUE
      IF(A(KX).LT.XFD)GO TO 926
      XFDD=JDDAY(KX)
      XFD=A(KX)
926   CONTINUE
      WRITE(61,944)JDDAY(KX),B(KX),A(KX),VAL,Z,Z1,Z3,Z2,Z4,Z9
944   FORMAT(* *I4,F8.1,3F8.1,5F8.1)
      IF(IWR.EQ.1)WRITE(81,900)JDDAY(KX),Z2
900   FORMAT(1X,I4,*,*,F8.1)
107   CONTINUE
      WRITE(61,19)Z5,Z6
19    FORMAT(38X,*TOTAL= *F8.1,8X,F8.1)
      WRITE(61,23)S1,S2,S3,S5
23    FORMAT(* SUM OF SQUARED DEVIATIONS = *2(F8.0,8X),2F8.0)
      IF(IWR.NE.1)RETURN
      ENDFILE 81
      WRITE(81,900)(JDDAY(IQ),A(IQ),IQ=N1,J)
      ENDFILE 81
      RETURN
      END
```

LITERATURE CITED

LITERATURE CITED

Anonymous, 1968. System/360 Scientific Subroutine Package (360A-CM-03X) Version III programmer's manual. White Plains, New York: International Business Machines Corporation.

Baskerville, G. L., and Emin, P., 1969. "Rapid Estimation of Heat Accumulation from Maximum and Minimum Temperatures." Ecology 50:514-517.

Casagrande, R. A., 1975. "Behavior and Survival of the Adult Cereal Leaf Beetle, *Oulema melanopus* (L.)." Ph.D. thesis, Michigan State University, 174 pp.

Castro, T. R.; Ruppel, R. F.; and Gomulinski, M. S., 1965. "Natural History of the Cereal Leaf Beetle in Michigan." Michigan Quarterly Bulletin 47, No. 4:623-653.

Caswell, H., 1976. "The Validation Problem." In Systems Analysis and Simulation in Ecology. Edited by B. C. Patten. pp. 313-325. New York: Academic Press.

DeMichele, D. W., 1975. "An Evaluation of Modeling, Systems Analysis and Operations Research in Defining Agricultural Reserach Needs and Priorities in Pest Management." Iowa State Journal of Research 49:597-621.

Finney, D. J., 1971. Probit Analysis. Cambridge University Press. 333 pp.

Fulton, W. C., 1975. "Monitoring Cereal Leaf Beetle Larval Populations." M.S. thesis, Michigan State University, 108 pp.

Fulton, W. C., and Haynes, D. L., 1977. "The Influence of Population Maturity on Biological Monitoring for Pest Management." Environ. Entomol. 6:174-180.

Gage, S. H., 1974. "Ecological Investigations on the Cereal Leaf Beetle, *Oulema melanopus* (L.), and the Principal Larval Parasite, *Tetrastichus julis* (Walker). Ph.D. thesis, Michigan State University.

Giese, R. L.; Peart, R. M.; and Huber, R. T., 1975. "Pest Management." Science 187:1045-1052.

Gutierrez, A. P.; Denton, W. H.; Shade, R.; Maltby, H.; Burger, T.; and Moorhead, G., 1974. "The Within Field Dynamics of the Cereal Leaf Beetle (Oulema melanopus (L.)) in Wheat and Oats." Journal Anim. Ecol. 43:627-640.

Hacker, C. S.; Scott, D. W.; and Thompson, J. R., 1975. "A Transfer Function Forecasting Model for Mosquito Populations." Can. Ent. 107:243-249.

Haynes, D. L.; Brandenburg, R. K.; and Fisher, P. D., 1973. "Environmental Monitoring Network for Pest Management Systems." Environ. Entomol. 2:889-899.

Helgesen, R. G., 1969. "The Within-Generation Population Dynamics of the Cereal Leaf Beetle, Oulema melanopus (L.)." Ph.D. thesis, Michigan State University, 96 pp.

Helgesen, R. G., and Haynes, D. L., 1972. "Population Dynamics of the Cereal Leaf Beetle, Oulema melanopus (Coleoptera: Chrysomelidae): A Model for Age Specific Mortality." Can. Ent. 104:797-814.

Holmes, N. D., ed., 1974. "Systems Approach to Pest Management." Quaestiones Entomologicae 10:153-186.

Lee, K. Y.; Barr, R. O.; Gage, S. H.; and Kharkar, A. N., 1976. "Formulation of Mathematical Model for Insect Pest Ecosystems--the Cereal Leaf Beetle Problem." Journal Theor. Biol. 59:33-76.

Llewellyn, R. W., 1965. FORDYN, An Industrial Dynamics Simulator. Raliegh, North Carolina, 1965.

Logan, P. A., 1977. "Development of Improved Density Estimators for Larvae of the Cereal Leaf Beetle, Oulema melanopus (L.)." Ph.D. thesis, Michigan State University, 111 pp.

Maltby, H. L.; Stehr, F. W.; Anderson, R. C.; Moorehead, G. E.; Barton, L. C.; and Paschke, J. D., 1971. "Establishment in the United States of Anaphes flavipes (Foerster), an Egg Parasite of the Cereal Leaf Beetle, Oulema melanopus (L.)." Journal Econ. Entomol. 64:693-697.

Manetsch, T. J.; and Park, G. L., 1972. "System Analysis and Simulation with Applications to Economic and Social Systems." Department of Elec. Eng. and Syst. Sci., Michigan State University.

Miller, D. R.; Butler, G.; and Bramall, L., 1976. "Validation of Ecological System Models." Journal Environ. Manag. 4: 383-401.

Mitchiner, J. L.; Kennish, W. J.; and Brewer, J. W., 1975. "Application of Optimal Control and Optimal Regulator Theory to the 'Integrated' Control of Insect Pests." IEEE Transactions on Systems, Man and Cybernetics, January 1975, pp. 111-116.

Morris, R. F., 1965. "Contemporaneous Mortality Factors in Population Dynamics." Can. Ent. 97:1173-1184.

Pielou, E. C., 1969. An Introduction to Mathematical Ecology. New York: Wiley - Interscience.

Platt, T.; and Denman, K. L., 1975. "Spectral Analysis in Ecology." Annual Rev. Ecol. and Systems 6:189-210.

Ruesink, W. G., 1972. "The Integration of Adult Survival and Dispersal into a Mathematical Model for the Abundance of the Cereal Leaf Beetle, Oulema melanopus (L.)." Ph.D. thesis, Michigan State University, 80 pp.

Sawyer, A. J., 1978 (in preparation). Ph.D. thesis, Michigan State University.

Shanon, R. E., 1975. Systems Simulation, the Art and Science. Englewood Cliffs, New Jersey, Prentice-Hall, Inc., 387 pp.

Tummala, R. L.; Ruesink, W. H.; and Haynes, D. L., 1975. "A Discrete Component Approach to the Management of the Cereal Leaf Beetle Ecosystem." Environ. Entomol. 4:175-186.

Tummala, R. L.; and Haynes, D. L., 1977. "On-line Pest Management Systems." Environ. Entomol. 6:339-349.

Vincent, T. L., 1975. "Pest Management Programs via Optimal Control Theory." Biometrics 31:1-10.

Webster, J. A., Smith, D. H.; and Lee, C., 1972. "Reduction in Yield of Spring Wheat Caused by Cereal Leaf Beetles." Journal Econ. Ent. 65:832-835.

Wellso, S. G., 1973. "Cereal Leaf Beetle: Larval Feeding, Orientation, Development, and Survival on Four Small-Grain Cultivars in the Laboratory." Ann. Ent. Soc. Amer. 66: 1201-1208.

Wellso, S. G., 1976. "Cereal Leaf Beetle: Feeding and Oviposition on Winter Wheat and Spring Oats." Environ. Entomol. 5: 487-491.

Wiitanen, W., 1976. "Modeling Biological Systems by Means of Flowgraphs." Simulation, June 1976, pp. 185-192.

Wilson, M. C.; and Shade, R. E., 1966. "Survival and Development of Larvae of the Cereal Leaf Beetle, *Oulema melanopus* (Coleoptera: chrysomelidae), on Various Species of Gramineae." *Ann. Ent. Soc. Amer.* 59:170-173.

Yun, Young Mok, 1967. "Effects of Some Physical and Biological Factors on the Reproduction, Development, Survival, and Behavior of the Cereal Leaf Beetle, *Oulema melanopus* (Linnaeus), under Laboratory Conditions." Ph.D. thesis, Michigan State University, 153 pp.