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POPULATION MODELING OF GREENBUG APHIDS

IN SPRING WHEAT

BY

MARIE ANN COFFIN

A thesis submitted in partial fulfillment
of the requirements for the degree
Master of Science
Major in Mathematics
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1988

POPULATION MODELING OF GREENBUG APHIDS

IN SPRING WHEAT

This thesis is approved as a creditable and
independent investigation by a candidate for the degree,
Master of Science, and is acceptable for meeting the
thesis requirements for this degree. Acceptance of this
thesis does not imply that the conclusions reached by the
candidate are necessarily the conclusions of the major
department.

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Abstract

A computer model was developed which used weather data and
initial field counts of green-bug aphids to predict the
behavior of the aphid population throughout the season. The
model considered the effects of heat, food supply, predation
and rainfall on the population. Data were obtained on the
life-cycle of aphids grown in a controlled laboratory
setting. These data were used to postulate a stochastic
model of aphid growth which could be applied to a population
in the field. A modified Leslie matrix model was used to
predict the population's future behavior. Factors were then
added to this basic model to account for mortality due to
old age and predation, and the fecundity of the adult
population. The completed model was compared with the
actual field data obtained for several years. This
comparison showed that the model generally performed well.
As a last step, sensitivity analysis was done to determine
which factors in the model would most profit by closer
scrutiny. It was found that predation, in particular,
needed to be analyzed more carefully.

Chapter One

Literature Review

Population modeling proceeds in the following general manner. A cohort of aphids is reared in the laboratory under controlled conditions and constant temperature. Regular observation of the aphids' development yields data on the length of time each individual spends in each life-stage. This is used to postulate the behavior of the aphids in a natural environment.

The crudest estimation methods utilize only the observed mean development time to estimate the development time in nature. It is possible, however, to get much better estimates by using more of the information that the laboratory study yields.

Two different methods exist for doing this. Manetsch [3] proposed setting up a system of differential equations which describe the changes in the population. Solving the system at time t will yield the size of the population at that time.

Leslie [1] devised a different approach. His is based on the assumption that population growth is controlled by a small number of factors acting on the present population. The cumulative effect of these factors can be expressed as survival and reproductive probabilities on the present

population. Thus, the survival and reproductive

probabilities, when multiplied by the current size of the

population, will yield the future population size.

Manetsch proved that solutions to the set of

differential equations he proposed would necessarily be

distributed as a gamma random variable. For this reason, it

was decided that incorporating the gamma distribution into

the Leslie model would be more efficient and require less

computer time than repeatedly solving differential

equations.

Chapter Two

The Model

We are attempting to model a greenbug aphid population. Aphids do not over-winter in South Dakota, because the cold is too intense. Instead, winged aphids migrate in on the southerly winds of spring. They land on small grain plants and start feeding and reproducing.

The aphid life-cycle can be summarized as follows. Newborn aphids begin to feed on plant juices and grow. As they grow, they must occasionally shed their exoskeletons for larger ones. The period between two such molts is called an instar. Greenbugs have four immature instars before reaching adulthood. Shortly after adulthood, the aphids begin reproducing, and continue to do so until death.

When the aphid population begins to experience crowding, some of the aphids produced will be winged (alatae). Alate aphids are winged when they reach adulthood, and immediately ride the winds to a new area. Upon landing at a new site, their wing muscles degenerate, and the aphids begin reproducing.

When the cereal plants mature in summer, the aphids migrate to later-growing crops and non-crop grasses.

It should be noted that cereal crops will be harmed only if aphid populations become sufficiently large in the early season, while the plants are still small. In larger

plants, it is not possible for the aphids to remove enough of the plant's nutrients to affect crop growth and yield.

The Model

This model attempts to consider all aspects of the aphid life-cycle. Since aphids do not over-winter in South Dakota, the life-cycle can be considered to begin when aphids are first sighted in the field. At this time, an initial count or estimate is made, and is used to start the model.

Leslie's matrix model was chosen. Leslie [1] assumed that the age-structure of the population at some time t was known. He then used this information to predict the age-structure of the population at a future time.

In practice, however, the age structure is usually not known; the stage-structure is much more easily obtained. Woodward [2] suggested that Leslie's method could be modified to be used on a population where only the stage-structure was known. Woodward began by assuming that development times in each stage were normally distributed. This was done so that the age-structure of the population could be "recovered" (actually estimated) from the stage-structure. Woodward proceeded by dividing each life-stage into a number of sub-stages. This is done so that one can approximate the amount of time that an individual has spent in its current life-stage. Then the Leslie matrix is modified to include all of these

sub-stages.

For our purposes, it did not seem necessary to estimate the age-structure of the population, and so normality assumptions were unnecessary. In fact, they are probably unwarranted, since visual examination of developmental data show that development times are markedly skewed to the left. (Manetsch [3], using a distributed delay method, derives the result that development times have a gamma distribution.)

When constructing the model it is necessary first to estimate how many sub-stages will be needed. Clearly, too few sub-stages will lead to a crude approximation, while too many will make the model cumbersome to operate. Matetsch suggested that good results could be obtained by choosing the number of sub-stages to be equal to the shape parameter of the gamma distribution. This proved to be feasible, since the gamma distributions we modeled all had shape parameters between one and ten.

The model is based on the Leslie matrix model. Briefly, the Leslie matrix is a modified Markov Chain in which the diagonal elements represent the probabilities of an individual's surviving to the next time-step. In addition, the first row of the matrix contains the average numbers of female births to individuals in each age class in the time-step that survive until the next time-step.. The remaining elements of the matrix are zero. This matrix is

called the A matrix. We also define a vector whose elements
are the numbers of individuals in each life-stage. This is
called the F vector. If we take the matrix product
F* = A x F, the F* will contain the number of individuals in
each life-stage after one time-step.

Example: Suppose the numbers of aphids in each of five
life-stages are 5, 3, 2, 1 and 6, respectively. Also
suppose the average number of females born to a female in
age-class 5 is 0.78, and the average number of females born
to younger females is 0. Finally, suppose that the
probability of surviving to the next age-class is 0.95 for
all age classes. Then

$$
A = \begin{bmatrix} 0 & 0 & 0 & 0 & 0.78 \\ 0.95 & 0 & 0 & 0 & 0 \\ 0 & 0.95 & 0 & 0 & 0 \\ 0 & 0 & 0.95 & 0 & 0 \\ 0 & 0 & 0 & 0.95 & 0 \end{bmatrix} \qquad F = \begin{bmatrix} 5 \\ 3 \\ 2 \\ 1 \\ 6 \end{bmatrix}
$$

and

$$
F* = \begin{bmatrix} 4.68 \\ 4.75 \\ 2.85 \\ 1.90 \\ 0.95 \end{bmatrix}
$$

For our purposes, it was considered more realistic to

modify the model in several ways. The original Leslie model assumes that survival and fecundity probabilities are constants which are known or estimated. In fact, it appears that the probabilities (e.g. 0.78 and 0.95 in the example above) are functions which may depend upon the present size and structure of the population, as well as the quantity and quality of food available. Although this is only a small change in theory, it necessitates a major change in the computations, since the elements of the A matrix must be re-calculated at each time-step, to reflect changes in the population and environment. Some of the necessary considerations are discussed below.

Time Measurements

Aphid developmental rate is known to be linearly related to temperature [11]. This linear relationship holds true over a wide range of temperatures. An aphid has a base temperature, below which no development will occur, and an upper limit temperature beyond which no additional increase in developmental rate will result from higher temperatures. Between these two, developmental rate is essentially linear. However, since temperatures in nature fluctuate greatly in time, aphid developmental rate is not in any sense linear, or indeed predictable, with respect to time. Because of this, a "time scale" in degree-days (DD) was used. One degree-day is defined to be a temperature of one degree

celcius above base temperature, experienced for 24 hours.
The total degree-days accumulated in a day can be estimated
from the maximum and minimum temperatures for the day.
Degree-day estimation was done by the method of Allen [4].
For details, see Appendix A.

Laboratory Study

A cohort of aphids was reared in the laboratory under
constant temperature and infinite food supply. The constant
temperature made the calculation of accumulated degree-days
particularly simple. It is known that a cohort of aphids
that enter a life-stage simultaneously will emerge
distributed in time, where "time" is measured in
degree-days. Thus, the time at which an individual matures
to the next life-stage can be considered a random variable.

To construct the model, we need to know the
distribution of that random variable. Previously, this has
often been assumed to have a gamma-type distribution. On
the other hand, Wagner, et. al. [5] postulated a Weibull
distribution and obtained good results from it. There is
some theoretical justification for this, since the Weibull
distribution was developed specifically to model
failure-time data. The gamma distribution has density
function

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

while the Weibull distribution has density function

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

Preliminary examination of the laboratory data suggested that either a Gamma or Weibull distribution might be appropriate (the two are similar in shape), but no method was found to evaluate which distribution would provide a better description. In fact, no adequate method was found to estimate the parameters of such a Weibull distribution. This estimation is decidedly non-trivial, and it may be that the Weibull is not commonly used for just such computational reasons. In contrast, the parameters of a Gamma distribution can be easily estimated from the sample mean and standard deviation of the population in question.

Such estimates were made from the laboratory data, and the resulting Gamma distribution was tested against the laboratory data, in an attempt to measure how well the proposed distribution fit the facts. A value of R^2 was calculated for each life-stage. This is usually interpreted as representing the fraction of the total variation in the random variable which can be accounted for by the distribution. In five of the six life-stages, the value of R^2 was in excess of 0.90. This was felt to be an excellent fit; therefore, the Gamma distribution was used to construct the model.

The poor fit of the fifth set of parameters can be explained by the fact that we are attempting to predict when an individual moves from the fifth life-stage

(pre-reproductive adult) to the sixth (reproducing adult).
The time that an individual spends in the fifth life-stage
is typically quite short -- often only a few hours. Since
the aphids were monitored at eight-hour intervals, it is
likely that the data collected were not very accurate on
this point. However, it was also felt that even a poor
estimate would be adequate, since the estimate would not be
wrong by more than a few hours. Table 1 contains a list of
the parameters and R^2 values for all six life-stages.

Maturation Probabilities

Aphids have four immature life-stages, and a mature
life-stage. For ease in computation, the mature life-stage
was divided into two: pre-reproductive matures, and
reproducing matures. This gives us a total of six
life-stages. Since individuals who enter a life-stage at
the same time will leave it at different times, each
life-stage is divided into a number of sub-stages, so that a
better estimate could be made of the length of time an
individual had spent in its present life-stage. Knowing the
parameters of the underlying distribution enables us to
estimate how many of the individuals in any sub-stage will
mature to the next life-stage in a time-step. These
individuals are transferred by the model to the first
sub-stage of the next life-stage. Figure 1 shows
graphs of the empirical distribution functions, and the
gamma curves that were fitted to them.

Table One

Parameters of the Gamma Distribution

Life-stage	Scale Parameter	Shape Parameter	R^2
1	3.16987	9.19488	0.901
2	2.47643	8.96503	0.924
3	3.78789	4.14873	0.915
4	3.08195	7.29780	0.976
5	6.73449	1.97160	0.604
6	59.7507	9,85034	0.956

Figure 1a
Gamma Curve for the First Life-Stage
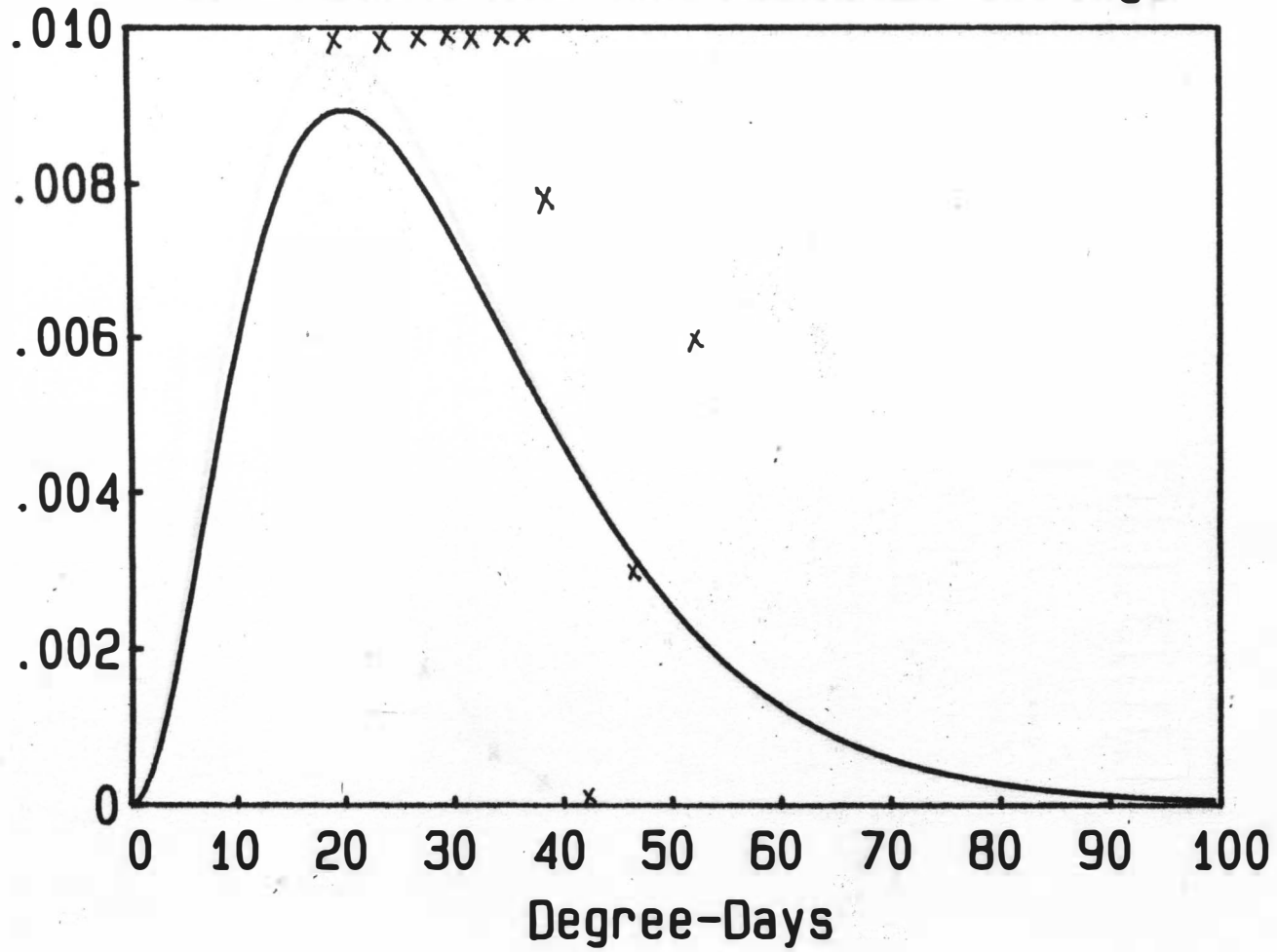
Figure 1B

Gamma Curve for the Second Life-Stage
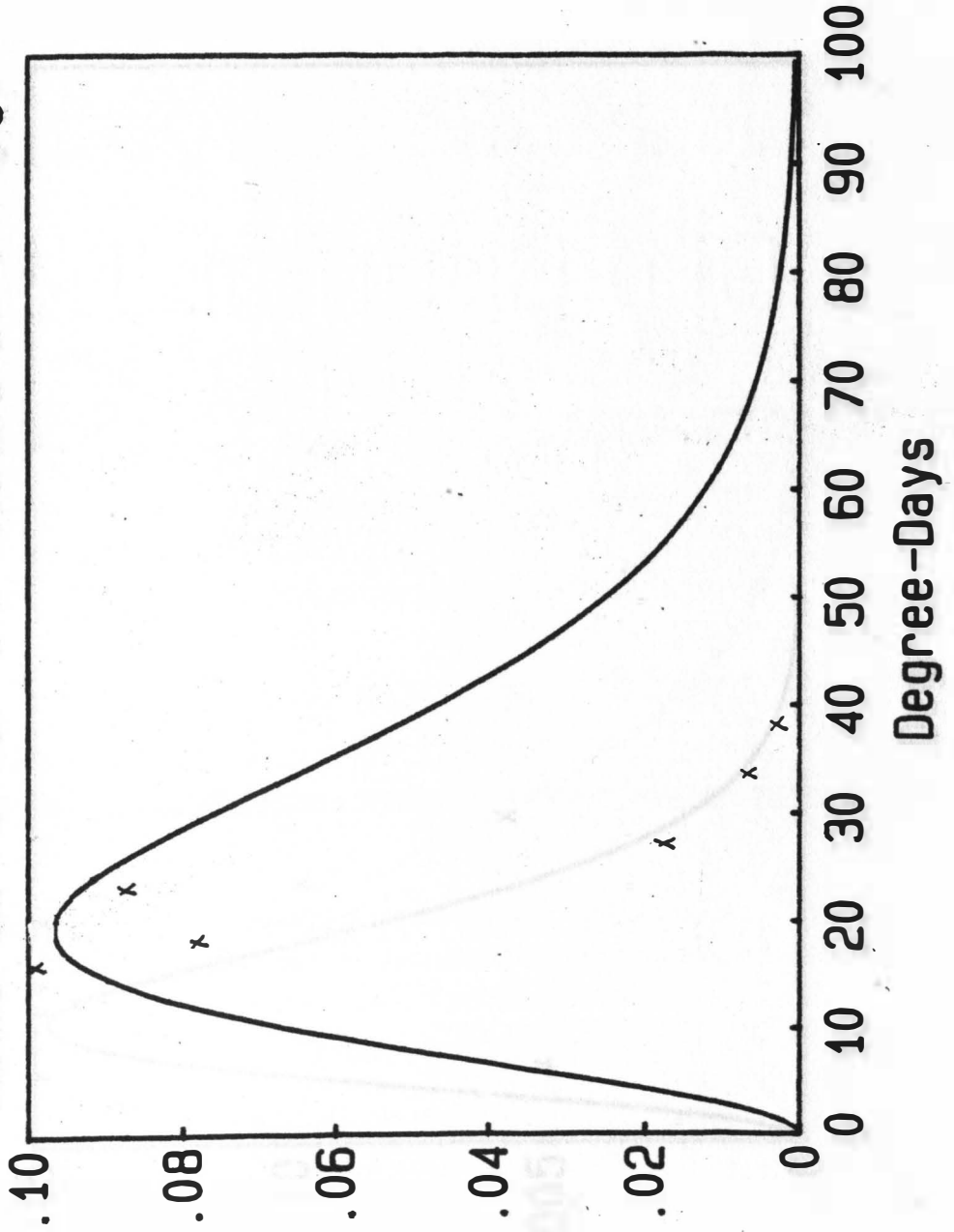
Figure 1c

Gamma Curve for the Third Life-Stage
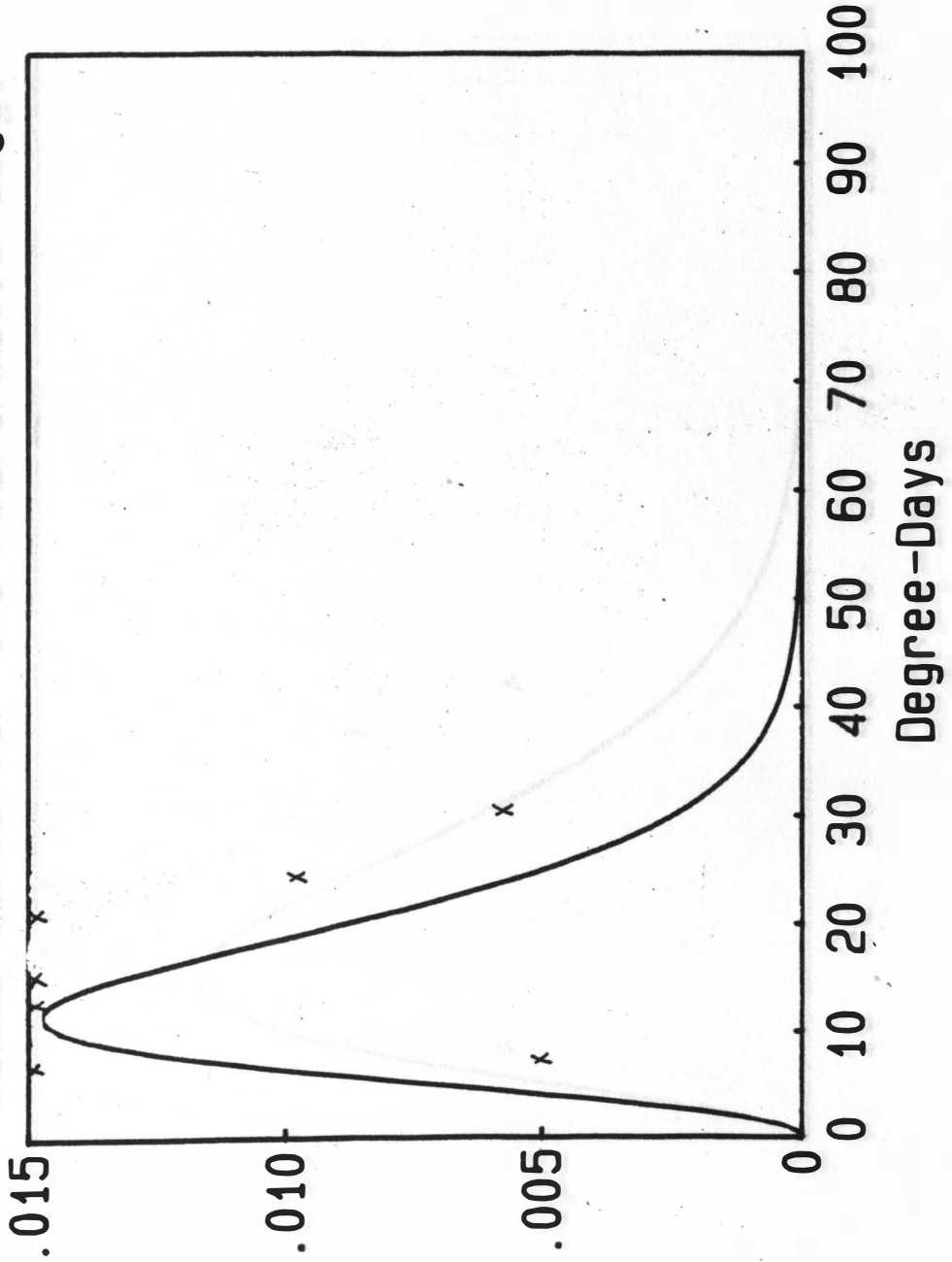
Figure 1d

Gamma Curve for the Fourth Life-Stage
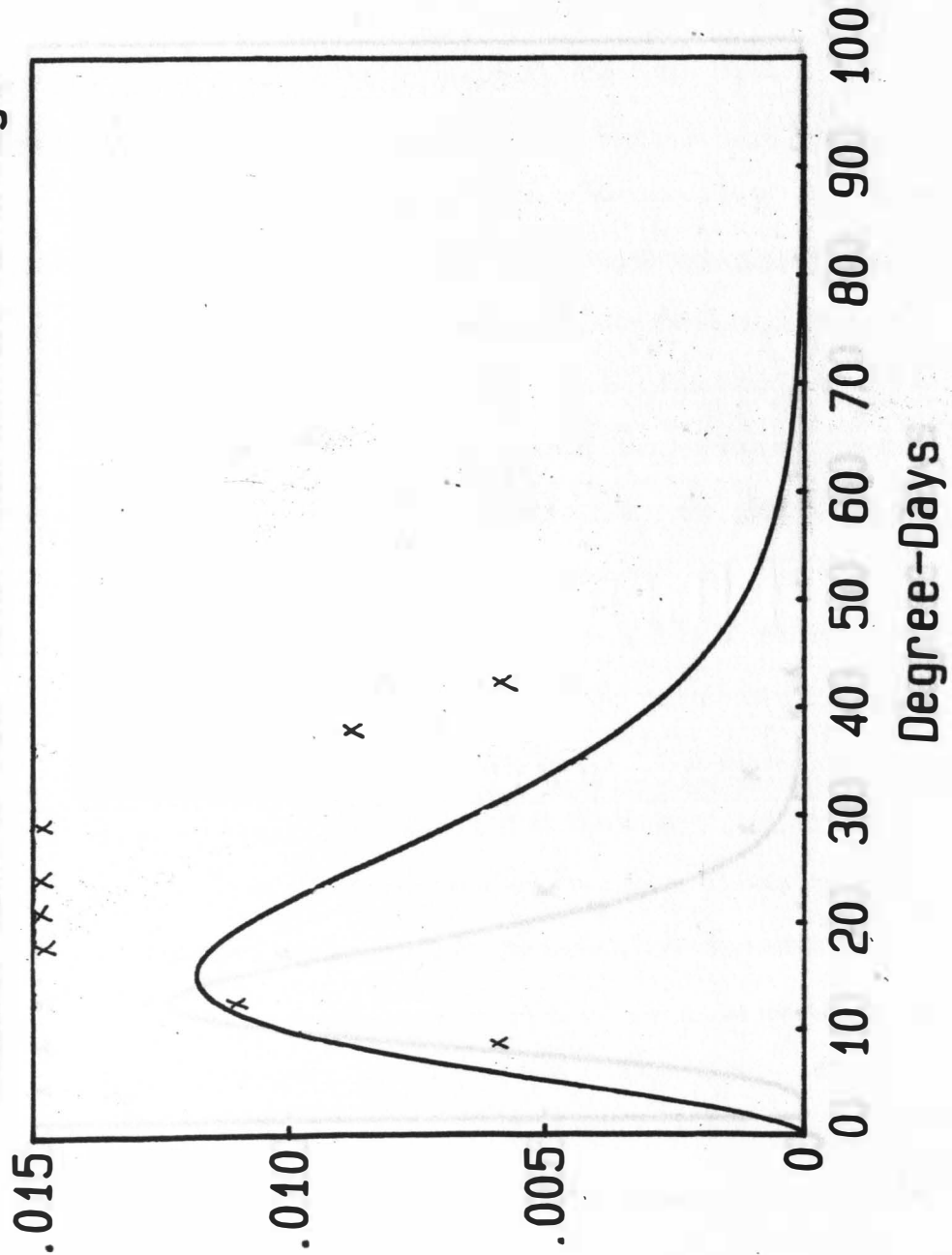
Figure 1e
Gamma Curve for the Fifth Life-Stage
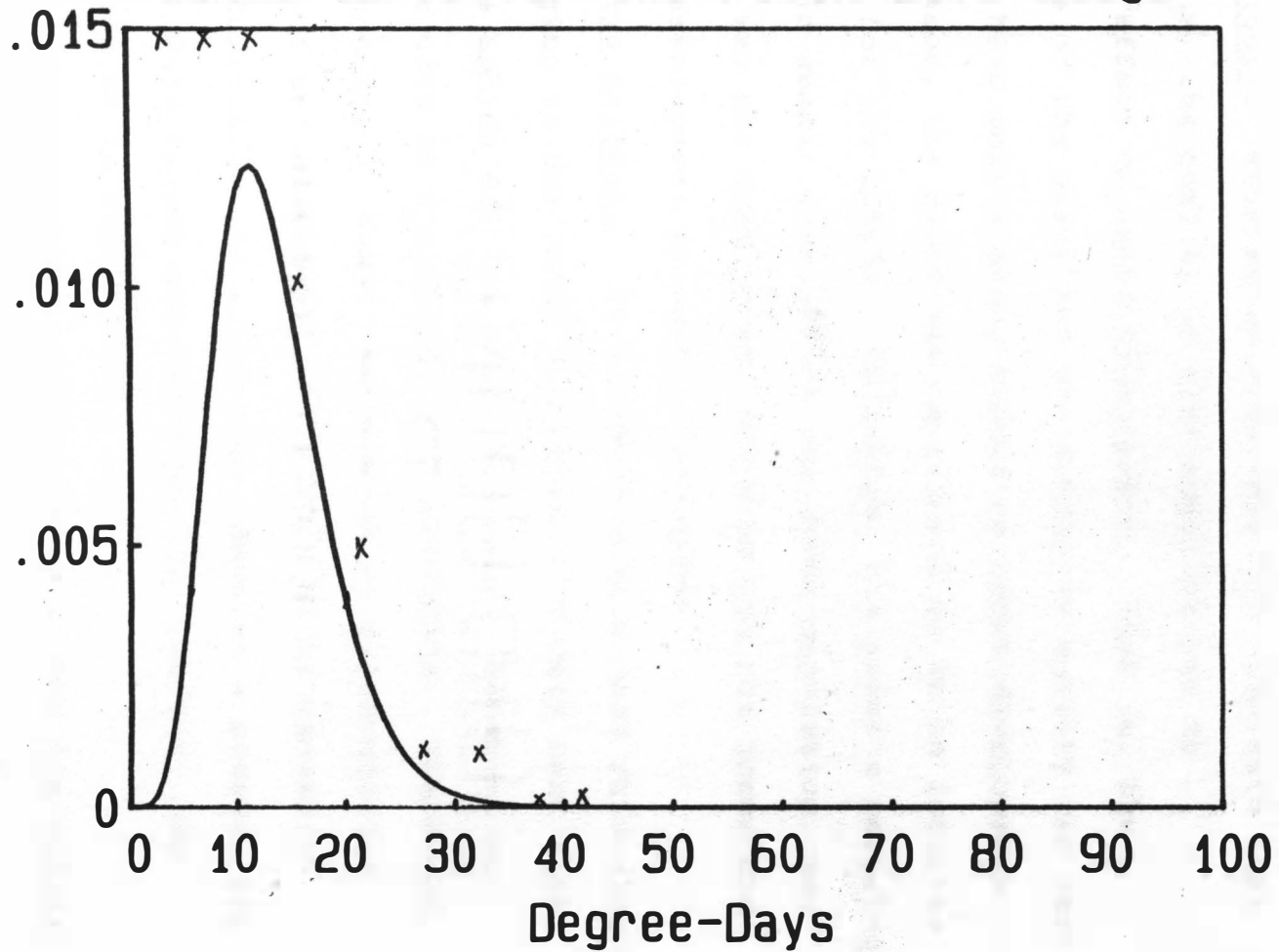
Mortality

Aphid mortality is caused by several factors: predation, inadequate food supply, old age and excessive rainfall. In the model, each of these factors needs to be considered separately.

Food Supply. Studies by Kiekiefer [12] indicate that within limits, the quality of food supplied has no significant effect on aphid development. That is, the growth stage of the plant and the nutritive quality can vary greatly and have only a minor effect on aphid development. For this reason, the plant was considered to be an infinite food source for the aphids. Of course, the plant's maturing and drying in summer does affect the aphid population, but this effect was not considered, since we are not concerned with aphid development at such a late date.

Excessive Rainfall. It is known that a hard rain-storm can be damaging to the aphid population. A very hard rain can wash the aphids off the plant entirely. However, no quantitative data on the effect were available. Therefore, the model contains a "dummy" subprogram to calculate the probability of an individual's being killed by excessive rainfall. Currently, the subprogram computes a probability of zero. If data become available on this subject, the subprogram can be re-written

Age-Specific Mortality. A cohort of aphids was raised

in the laboratory, and careful counts were made of how many died in any given time-span. Non-linear regression was used to fit this data to a curve, using an equation described by Graf, et.al. [6]. The equation is:

MORT = 1 - a * EXP[b * EXP(c * DD))].

This method appeared to yield a very good fit. The estimated parameters are a = 0.908589, b = -0.006861, c = 0.006561

Predation. Aphids have two major predators: Hippodamia convergens and H. tridecimpunctata tibialis (abbreviated HC and HT in the program). It was not considered practical or necessary to model the entire predator life-cycle, since in the early part of the season, predator numbers remain essentially constant. Since there was very little data on which to base any assumptions, the simplest possible functional model was used. A Type I functional response [7] was chosen, in which the amount (in weight) of aphids eaten is assumed to be a linear function of the size of the aphid population, unless the population is effectively infinite, in which case the amount eaten is constant.

Data were obtained in the following manner. Counts were taken of how many aphids of a particular life-stage were eaten in one day by a starved predator. This was considered to be the maximum amount that a predator could

eat in one day. Aphids of different life-stages were weighed to determine their relative average weights.

Since aphids of different life-stages have greatly different average weights, a new measurement of "aphid units" was introduced into the model. An aphid unit (AU) is defined to be the average weight of a first instar aphid. The average weights of all the instars, expressed as aphid units, appear in Table 3. Thus for predator purposes, the population can be considered to consist of a certain number of aphid units. In addition, the predators' "appetites" can also be expressed in aphid units. Then only two cases can occur.

Case 1: The aphid population is so large that the predators can eat as much as they wish. In this case, the predators will eat a constant amount of aphid units. Then for any individual aphid, the probability of being preyed upon is simply the fraction of the total population that is eaten. Unfortunately, we do not know how large the aphid population must be for these conditions to exist. An estimate of 25 adult aphids per predator per day was used. This is called the critical number of aphids, and is abbreviated in the program as NCA.

Case 2: The predators cannot eat as much as they wish. The number of aphids eaten when the aphid population is zero will, of course, be zero. The number of aphids eaten when

the aphid population reaches the critical number is also known. Between these two values, consumption is assumed to be a linear function of the size of the population. Hence, the probability of an individual aphid's falling prey to a type HT predator during one degree-day is proportional to $TUNITS / NCA_1$. Similarly, the probability of an individual aphid's falling prey to a type HC predator is proportional to $TUNITS / NCA_2$. Here TUNITS is the total weight of the aphid population, in aphid units; NCA_1 and NCA_2 are the critical numbers of aphids for type HT and HC predators respectively.

Now, if the number of HT predators is NHT, and the number of HC predators is NHC, the probability of an individual aphid's not being preyed upon (i.e., surviving) is

$$P(survival) = (1 - P_1)^{NHT} (1 - P_2)^{NHC}$$

Then, the probability of being preyed upon is

$$PRED = 1 - (1 - P_1)^{NHT} (1 - P_2)^{NHC},$$

where P_1 and P_2 represent the probability of being eaten by an HT and HC predator, respectively. We assume that all of the predators are acting independently. Now for any individual in the population, if we let M represent age-specific mortality, P represent predation, and R represent rainfall mortality (all expressed as probabilities), and we assume that these factors operate independently on the

population, then the probability of the individual's
surviving to the next time-step is

P(survival) = 1 - M - P - R + M*P + M*R + P*R

- M*P*R.

Fecundity.

The same cohort used to model mortality above was also
used to model the fecundity function. This was also modeled
according to Graf's equation:

Fertility = [a * DD] / [b^{DD}].

The estimated parameters were a = 0.008, b = 1.001.

Chapter Three

Testing the Model

Field data were gathered over a period of years at a number of experimental sites in South Dakota. Information gathered included the number of nymphs, adult alate and adult apterate aphids of four different species present, as well as the number of predators sighted. These were recorded as number present in a quadrat. At each location, 40 quadrats were sampled at weekly intervals, beginning in early spring and continuing through the summer.

Four of these sampling periods were chosen to test the model. These four periods were felt to represent particularly complete and accurate sampling. Those chosen were Site I, 1963; Site II, 1963; Site I, 1966 and Site I, 1967. For each sampling period, the counts were averaged over the 40 quadrats sampled, and the averages were then converted from number per quadrat to number per 500 tillers. The first aphid counts and corresponding predator counts for the year were then used as initial conditions to start the model running. The model would then predict the future behavior of the population, which could be compared to the observed behavior. This comparison is useful in assessing the utility of the model.

The model runs made in this way showed several

discrepencies in the program. The model consistently
underestimated the observed population. This suggests that
some factor, such as predation or age-specific mortality,
may be given too much weight in the model. Also, adult
aphids in the model die off much more quickly than is
consistent with observed behavior. Clearly, these are areas
deserving of more attention. Graphs of the actual and
predicted population growth appear in Figure 2.
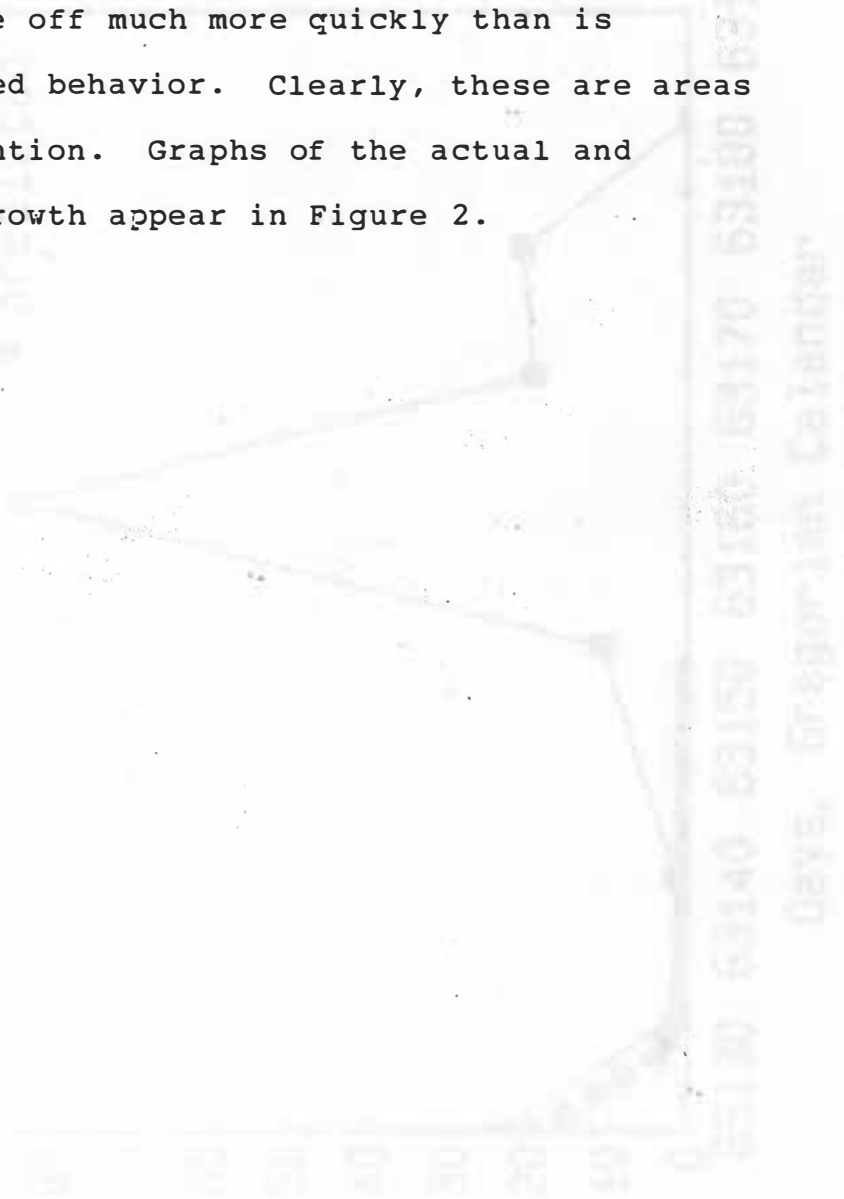
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Site I, 1963
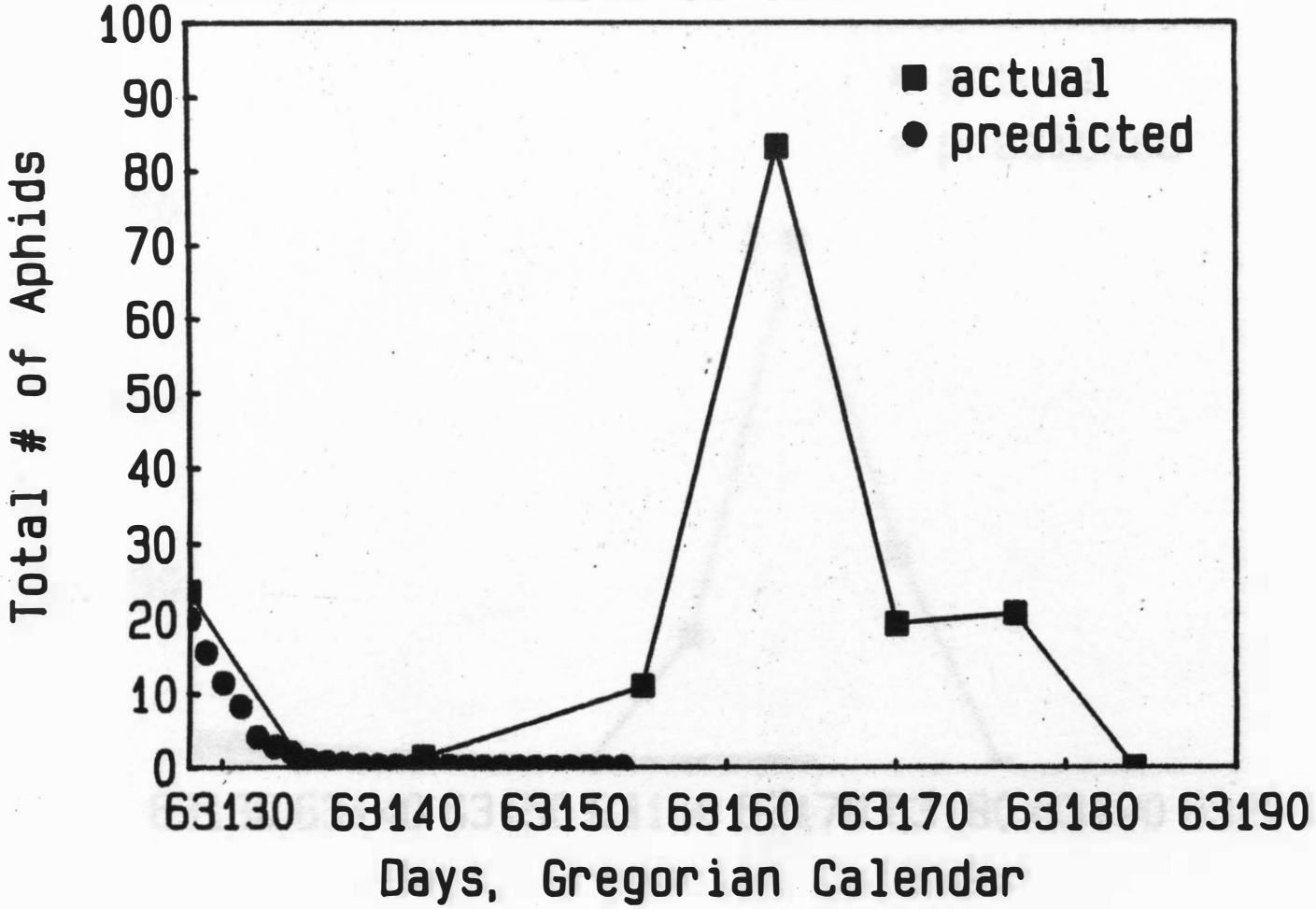
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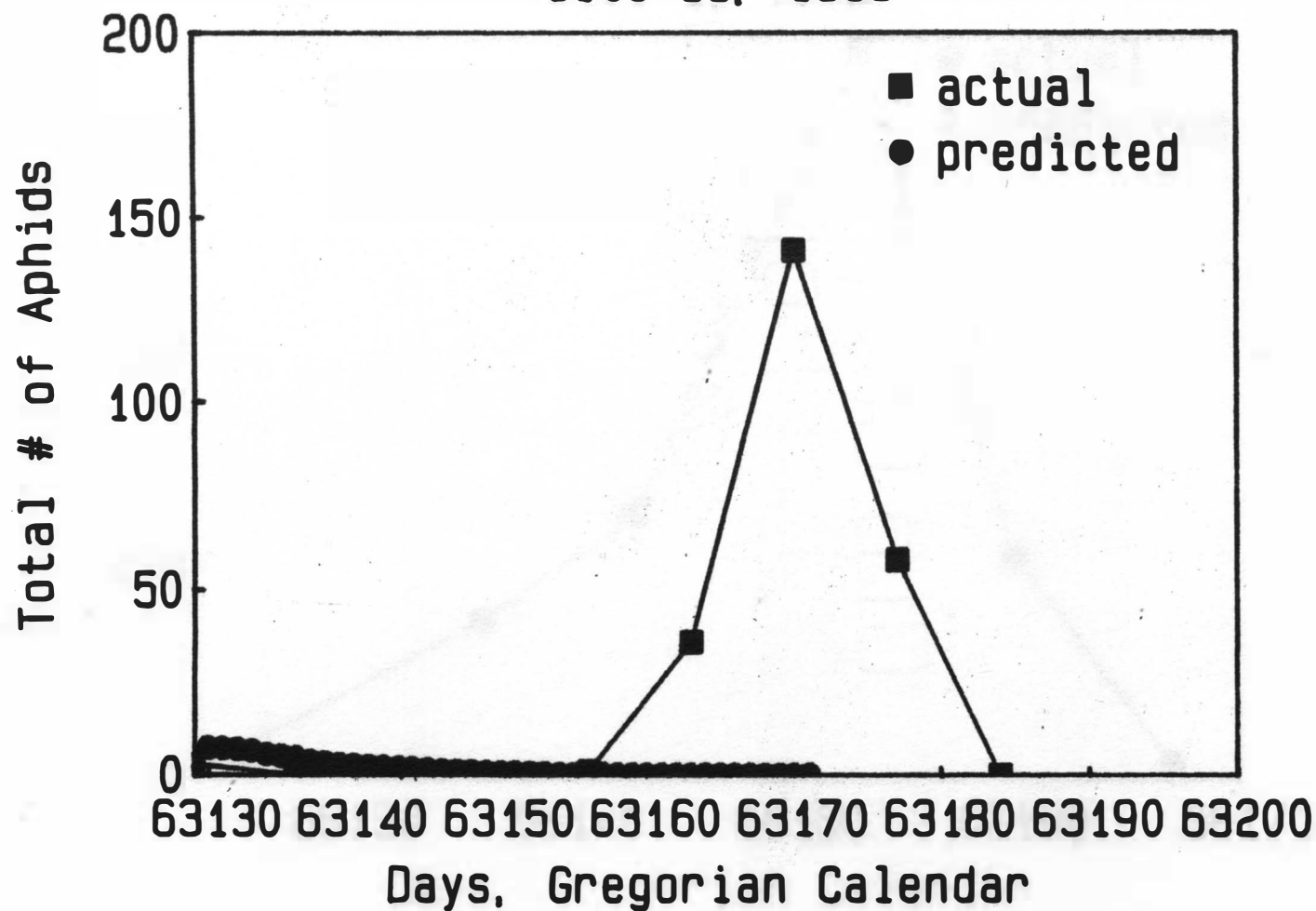
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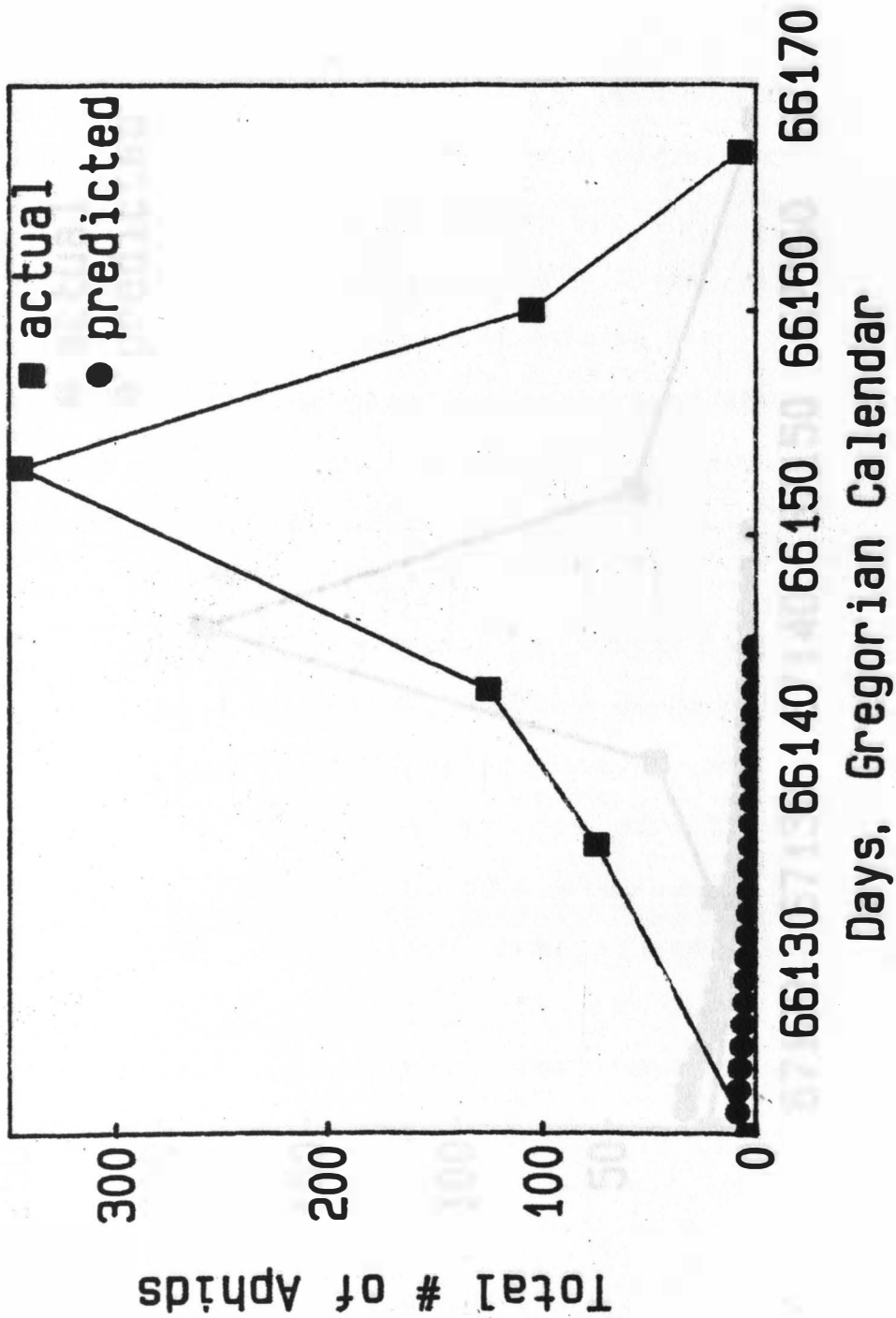
Figure 2d
Site I, 1967
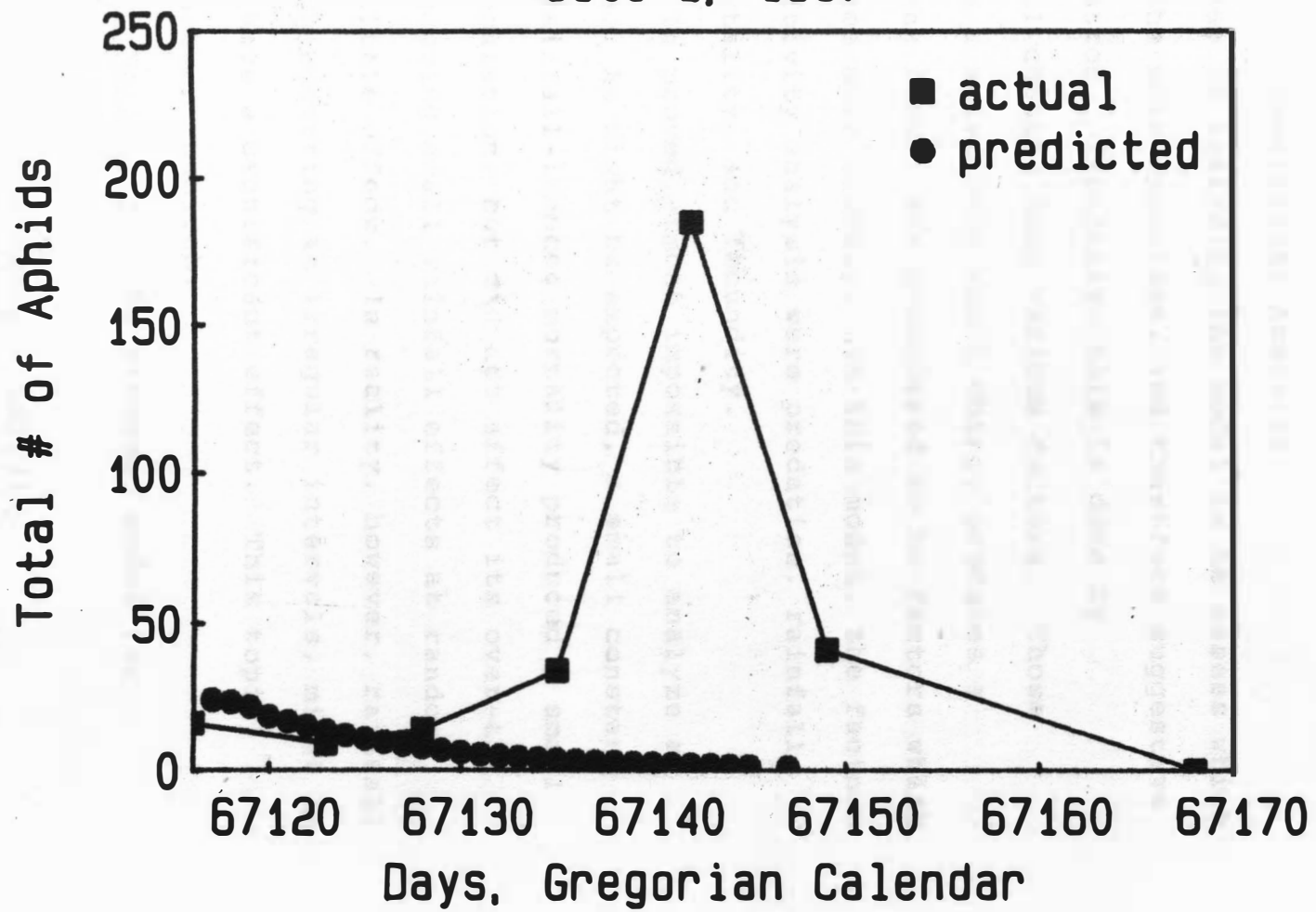
Chapter Four

Sensitivity Analysis

The next step in analyzing the model is to assess which factors may be the most important, and therefore suggestive of further attention. Typically, this is done by introducing small changes into various factors. Those factors in which a relatively small change produces a markedly different result are considered to be factors which should be examined more closely. In this model, the factors chosen for sensitivity analysis were predation, rainfall, age-specific mortality, and fecundity.

Rainfall. It proved almost impossible to analyze a dummy subroutine. As might be expected, a small constant probability of rainfall-induced mortality produced a small change in the population, but did not affect its over-all behavior. Introducing small rainfall effects at random seemed to have little effect. In reality, however, rainfall effects, although occurring at irregular intervals, might be quite large and have a significant effect. This topic clearly needs further research.

Age-Specific Mortality. The proposed model for age-specific mortality is

MORT = 1 - a * EXP[b * EXP(c * DD))].

Even slight changes in the parameters affect the population

size. Also, since this function has three parameters, the
interaction of changes in the three parameters must be
investigated. Furthermore, if age-specific mortality is
over-estimated for adults, this affects the reproductive
capability of the population, and hence the age structure as
well as the size of the population.

Fecundity. The proposed fecundity function is

$$FERT = [a * DD] / b^{DD}.$$

Again, it appears that slight changes in the parameters have
a significant effect. It would be worthwhile to estimate
these parameters more precisely, if only because they have
extremely small values, so that a small change produces a
large effect.

Predation. In examining the predation function, a
number of problems come to light. The number of predators
present in the early season appears to be quite high in
relation to the number of aphids available for consumption.
This suggests one of two situations: 1. We have estimated
how many aphids must be present for the population to be
effectively infinite. Perhaps our estimate is much too
high. 2. There may be other insects at the site which also
serve as food for the predators. In this case, we must be
able to make some sort of estimate of how many of these
"other" insects the predators are consuming, or incorporate
some sort of correction factor into the model.

Clearly, both of the above possibilities need to be investigated further. It must also be considered that the aphid model in use is very crude. It does not take into consideration the searching time, eating time, resting time, etc. which are generally considered important in estimating predation.

In summary, it appears that these problems are causing predation to be over-estimated, which produces a damping effect on population growth. The whole predation function undoubtedly merits further attention.

Chapter Five

Sugegestions for Further Research

Predation.· It is generally felt that either a Type II or Type III predator/prey model is a better predictor than a Type I model. [7] These models take into account such factors as searching time, resting time and feeding time. They also allow for the fact that at very low prey densities, predation is generally lower than a linear model would predict.

It is also necessary to explore the predator/prey interaction more deeply. For instance, does the number of prey eaten per day depend only on the biomass of the prey? We have assumed this to be true.

Finally, some way must be found to quantify the presence of other prey in the field. Perhaps there is some way to estimate this from available data.

Hypothesis Testing. Frequently, it is assumed that development times for the first three instars come from the same underlying distribution. This hypothesis should be tested. If we are assuming a gamma distribution, this is equivalent to testing the hypothesis that three means are equal and that at the same time, three standard deviations are also equal. One possibility for this would be a Kolmogorov-Smirnov Test [8].

It should also be noted that a separate base

temperature was found for each life-stage. Since these temperatures are fairly close together, the hypothesis that all or several of the life-stages have the same base temperature should be tested.

Choosing the Underlying Distribution. In this model the underlying distribution of development times was assumed to be gamma. A more rigorous approach to choosing a distribution could be used.

The data should be fitted to a generalized three-parameter gamma distribution [9]. This distribution may be: Gamma, Lognormal or Weibull depending on the choice of parameters.

Fitting the data to this model would provide a way quantitatively assessing the goodness-of-fit. Unfortunately, we found no way to fit the parameters of such a model, but feel sure that some numerical method could be found.

Rainfall. Some way must be found to work deaths due to excessive rainfall into the model. There is also some suggestion in the literature that prolonged periods of high humidity may make the aphids more succeptible to fatal fungal infections.[10]

Appendix A

Degree-Day Approximations

If we let y(t) = temperature (in ^{O}C) at time t,
(0 ≤ t ≤ 24), and if y is a continuous function, then the
accumulated degree-hours for the day will be the area between
the curve y = y(t) and y = t_b, where t_b is the base
temperature (i.e. the temperature below which no development
will take place). Then we can obtain degree-days by dividing
degree-hours by 24. That is,

$$DD = (1/24) \int_0^{24} (y - t_b)dt$$

In actual practice, the function y = y(t) is not known.
Instead, we must find an approximation for y, and several
methods exist for doing this. The methods discussed here have
in common that they require knowing only the maximum and
minimum temperatures for the day.

Method 1: We assume that y = (MAX + MIN)/2. That is, we
use a rough approximation of the average temperature for the
day as an estimate for y. Note that although this is a very
crude approximation for y, it may yield a good approximation
for accumulated degree-days. This method has the advantage of
quick and easy calculation, and has long been used with good

results. The formula is:

DD = (MAX + MIN)/2 - t_b.

Method 2: Temperature appears to vary in a generally
sinusoidal fashion. We can assume that y is a sine wave with
minimum at t = 0 (midnight) and maximum at t = 12 (noon). We
obtain

y(t) = (MAX - MIN)/2 * [sin(($12/\pi$)t + 6)]

+ (MAX + MIN)/2.

If we assume that $y(t) \geq t_b$ for all values of t, this will
exactly the same approximation as Method 1. However, if
$y(t) \leq t_b$ for any value of t, the graphs look like this:
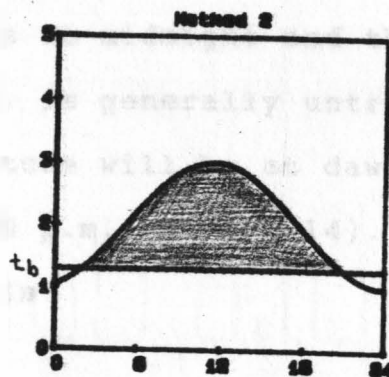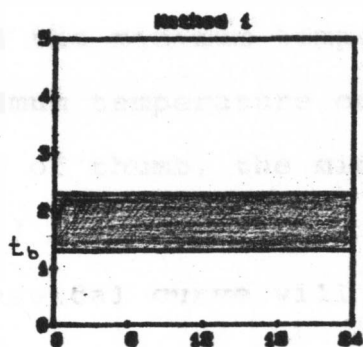
The desired degree-days will be only the shaded areas It
appears that the two methods may not yield the same result. To
obtain degree-days, we must first find t_1 and t_2. We can
find t_1 by observing that $y(t_1) = t_b$, or

$$t_b = (MAX - MIN)/2 * [sin((12/\pi)t_1 + 6)]$$
$$+ (MAX + MIN)/2.$$

Solving for t_1 yields:

$$t_1 = (\pi/12) * sin^{-1}\left[\frac{(t_b - (MAX + MIN)/2}{(MAX - MIN)/2}\right] - 6$$

This equation has infinitely many solutions, and we must choose one such that $0 \leqslant t_1 \leqslant 12$. Then, by symmetry of the curve, $t_2 = 24 - t_1$. Thus, we can calculate

$$DD = (1/24)\int_{t_1}^{t_2}(y(t) - t_b)dt.$$

Method 2 is also fairly easy to compute, and has been in general use until recent times.

Method 3: Allen [4] noted that an assumption of Method 2, that the minimum temperature occurs at midnight and that the maximum temperature occurs at noon, is generally untrue. As a rule of thumb, the minimum temperature will be at dawn (about 6 a.m.) and the maximum at about 2:00 p.m. (or $t = 14$). Then the sinusoidal curve will look like this:
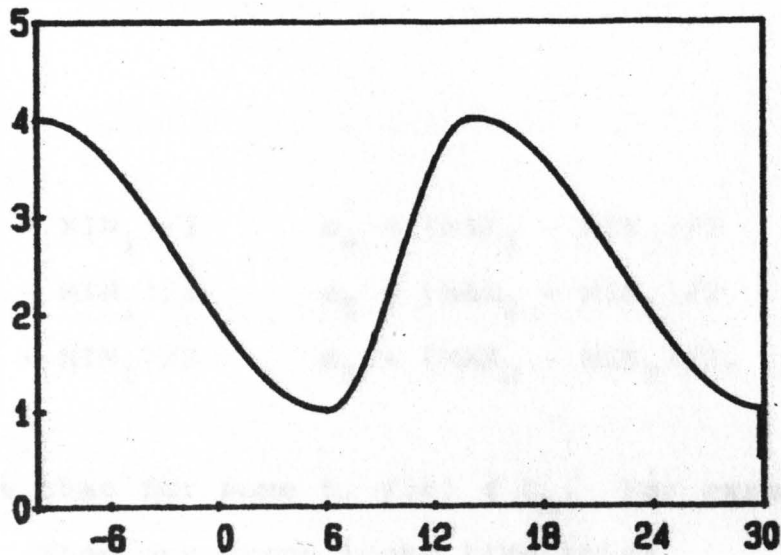
Note that we have constructed the wave by assuming that the maximum and minimum temperatures do not vary from one day to the next. If we allow these to vary from day to day, the curve becomes:
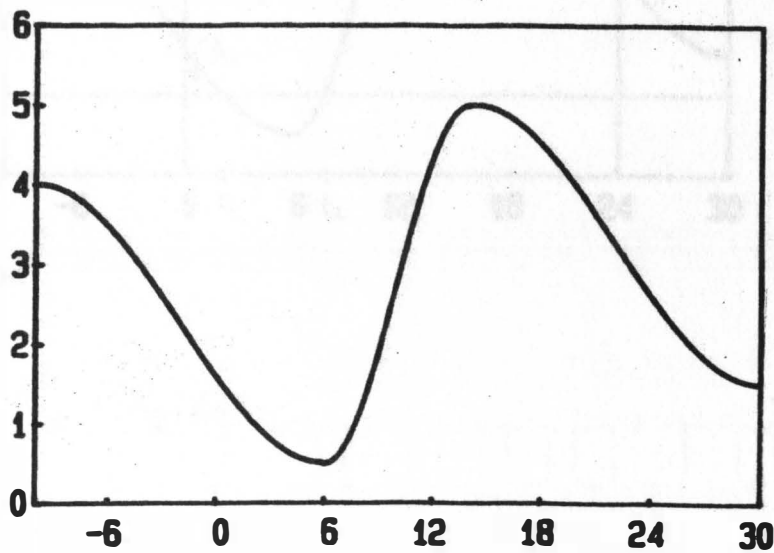
Then

$$
y = \begin{cases}
m_1 + m_2[\sin(\ (t + 48)/16] & 0 \leq t \leq 6 \\
m_3 + m_4[\sin(\ (t + 6)/8] & 6 \leq t \leq 14 \\
m_5 + m_6[\sin(\ (t - 6)/16] & 14 \leq t \leq 24
\end{cases}
$$

where

$$m_1 = (MAX_1 + MIN_1)/2 \qquad m_4 = (MAX_2 - MIN_2)/2$$

$$m_2 = (MAX_1 - MIN_1)/2 \qquad m_5 = (MAX_2 + MIN_2)/2$$

$$m_3 = (MAX_2 + MIN_1)/2 \qquad m_6 = (MAX_2 - MIN_2)/2.$$

Now suppose that for some t, $y(t) \leqslant t_b$. For example, suppose $MIN_1 \leqslant t_b$. Then our curve looks like this:
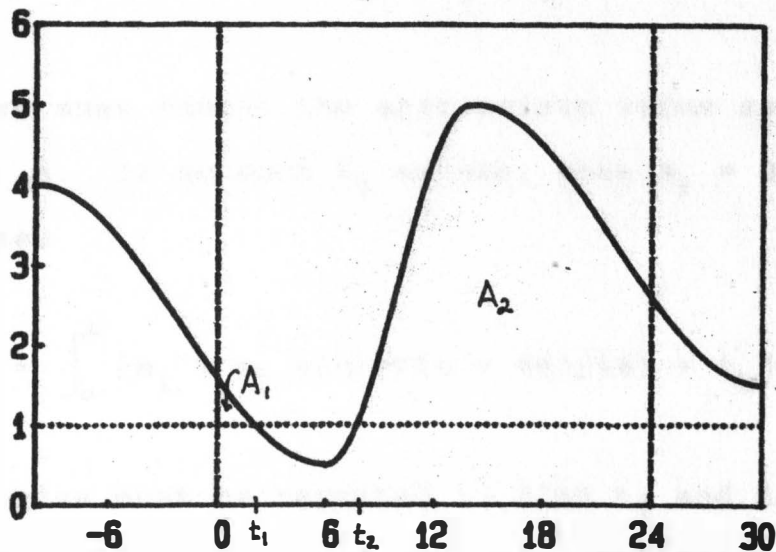
and we have

$$DD = (A_1 + A_2)/24.$$

To find this area, we must first find t_1 and t_2. To find t_1, note that

$$t_b = m_1 + m_2 \sin[\pi(t_1 + 48)/16]$$

Solving for t_1:

$$t_1 = (16/\pi) \sin^{-1}[t_b - m_1)/m_2] - 48.$$

Again, we must choose the appropriate value so that $0 \leq t_1 \leq 6$. If no such t_1 exists, then $A_1 = 0$. Otherwise,

$$A_1 = \int_0^{t_1} [m_1 + m_2 \sin(\pi(t + 48)/16) - t_b] dt.$$

This process must be repeated to find t_2 and A_2.

The situation becomes further complicated if either MAX_1 or MAX_2 falls below t_b.

At this point, the algorithm is not practical to use "by hand". As Allen points out, however, the method can be easily adapted to a computer. A subroutine to utilize this method is cumbersome to write, since so many different possibilities must be considered, but it will be quite efficient to run.

Appendix B

Model Program

```
//MA12 JOB 1099967025,MARIE,CLASS=J,MSGCLASS=M
/*ROUTE PRINT N2.MUSIC
// EXEC WATFIV,OUT=M
$JOB
C ***********************************************
C *                                             *
C *        THIS IS A FORTRAN PROGRAM            *
C *        TO MODEL APHID DEVELOPMENT TIMES     *
C *                                             *
C *        NAME:  MODEL                         *
C *        WRITTEN BY:  MARIE COFFIN            *
C *        FIRST ATTEMPT:  2/11/87              *
C *        LATEST REVISION: 3/20/88             *
C *                                             *
C ***********************************************
C
      INTEGER TAU,DD,NDAYS,STAGE,SUBSTG,GDD,DAY,MN,DY,YR,CONJUL,JDATE
      INTEGER YTEMP,MTEMP,DTEMP,HTEMP,LTEMP
      REAL A,F,FTEMP,FIN,TOTAL,FERT,MORT,EXTRA,M,P,R,HIGH,LOW
      DIMENSION A(60,60),F(60),FTEMP(60),FIN(60),HIGH(60),LOW(60)
      DIMENSION BASTMP(7),RELDD(6),TOTALS(7),ATEMP(60),INIT(6)
      DIMENSION DEGDAY(7)
C
      DATA A,ATEMP,DEGDAY/3600*0.0,60*0.0,7*0.0/
      DATA BASTMP/6.29,6.54,10.36,7.59,6.56,8.17,0.0/
C
C ***********************************************
C *        THIS IS THE INITIAL COHORT           *
C ***********************************************
C
      READ 5,MN,DY,YR
    5 FORMAT (T40,3(I2,1X))
      JDATE = CONJUL(MN,DY,YR)
      PRINT 7
    7 FORMAT ('1')
      PRINT 40,JDATE
C
      READ 10,INIT
   10 FORMAT (27X,6I5)
C
      READ 15,NHT,NHC
   15 FORMAT (54X,2I5)
C
      READ 20,NDAYS
   20 FORMAT (29X,I3/)
C
      READ 25,YTEMP,MTEMP,DTEMP,HTEMP,LTEMP
   25 FORMAT (5X,3(I2,1X),2(I3,1X))
      WHILE (MTEMP.LT.MN.OR.DTEMP.LT.DY) DO
          READ 25,YTEMP,MTEMP,DTEMP,HTEMP,LTEMP
      ENDWHILE
C
      HIGH(1) = CENTIG(HTEMP)
      LOW(1) = CENTIG(LTEMP)
      DO 110 I = 2,NDAYS
          READ 30,HTEMP,LTEMP
   30     FORMAT (T15,I3,1X,I3)
          HIGH(I) = CENTIG(HTEMP)
          LOW(I) = CENTIG(LTEMP)
  110 CONTINUE
C
      NEWDAY = NDAYS - 1
      DO 120 I = 2,NEWDAY
          DO 115 J = 1,7
```

```fortran
                ADD = ACCDD(HIGH(I),LOW(I),HIGH(I-1),LOW(I+1),BASTMP(J))
                DEGDAY(J) = DEGDAY(J) + ADD
  115       CONTINUE
            ATEMP(I-1) = DEGDAY(7)
  120 CONTINUE
C
      NSTEPS = INT(DEGDAY(7)/12.0)
      DO 130 I = 1,6
         RELDD(I) = DEGDAY(I)/FLOAT(NSTEPS)
  130 CONTINUE
      RELDD(6) = RELDD(6) * 24.0
      ABSDD = 12.0
C
      CALL DIST(F,INIT,RELDD,TOTALS)
C
      PRINT 50,(TOTALS(I),I = 1,6)
      PRINT 60,TOTALS(7)
C
      DAY = 1
      DO 210 TAU = 1,NSTEPS
C
C **********************************************
C *     THIS SECTION CALCULATES THE NUMBER     *
C *  THAT HAVE MATURED TO THE NEXT LIFESTAGE    *
C **********************************************
C
         DO 140 I = 1,60
            FIN(I) = 0.0
            FTEMP(I) = 0.0
  140    CONTINUE
C
         DO 150 I = 1, 50
C
            CALL CALSTG(I,STAGE,SUBSTG)
C
            GDD = INT(RELDD(STAGE) * SUBSTG)
            PROMAT = PMAT(STAGE,GDD)
            NMAT = PROMAT * F(I)
C
            LSTAGE = NXTSTG(I)
C
            F(I) = F(I) - NMAT
            FIN(LSTAGE) = FIN(LSTAGE) + NMAT
  150    CONTINUE
C
C **********************************************
C *    THIS SECTION CALCULATES THE FERTILITY    *
C *   AND MORTALITY ELEMENTS OF THE A MATRIX     *
C **********************************************
C
         DO 160 J = 51,60
            CALL CALSTG(J,STAGE,SUBSTG)
            A(1,J) = FERT(SUBSTG,RELDD(6))
            BABIES = A(1,J) * F(J)
            FTEMP(1) = FTEMP(1) + BABIES
  160    CONTINUE
C
         DO 170 I = 2,60
            J = I - 1
            CALL CALSTG(J,STAGE,SUBSTG)
            M = MORT(STAGE,SUBSTG,RELDD(STAGE))
            P = PRED(J,STAGE,TOTALS,F,ABSDD,NHT,NHC)
            R = RAIN(J)
            A(I,J) = 1 - M - P - R + M*P + M*R + P*R - M*P*R
```

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```
C
               SURVIV = A(I,J) * F(J)
               IF (I.LT.51) THEN
                  FTEMP(I) = FTEMP(I) + SURVIV
               ELSE
                  FRACT = SURVIV/24.0
                  FTEMP(I) = FTEMP(I) + FRACT
                  FTEMP(J) = FTEMP(J) + 23.0 * FRACT
               ENDIF
  170     CONTINUE
C
          DO 180 I = 1,60
             F(I) = FTEMP(I) + FIN(I)
  180     CONTINUE
C
          TOTALS(7) = 0.0
          DO 200 I = 1,6
             TOTALS(I) = 0.0
             DO 190 J = 1,10
                K = (I - 1) * 10 + J
                IF (F(K).LE.0) F(K) = 0
                TOTALS(I) = TOTALS(I) + F(K)
  190        CONTINUE
             TOTALS(7) = TOTALS(7) + TOTALS(I)
  200     CONTINUE
C
          TEMP = TAU * ABSDD
          IF (TEMP.GE.ATEMP(DAY)) THEN
             DAY = DAY + 1
             JDATE = JDATE + 1
             PRINT 40,JDATE
   40        FORMAT ('0','DATE = ',I5)
             PRINT 50,(TOTALS(I),I = 1,6)
   50        FORMAT (' ',6(F8.1,2X))
             PRINT 60,TOTALS(7)
   60        FORMAT (' ','TOTAL = ',F12.1)
          ENDIF
C
  210     CONTINUE
       STOP
       END
       FUNCTION PMAT(STAGE,TIME)
C
C ************************************************
C *   THIS FUNCTION CALCULATES THE PROBABILITY  *
C *   OF MATURING TO THE NEXT LIFE-STAGE, AS    *
C *   A FUNCTION OF ACCUMULATED DEGREE-DAYS     *
C ************************************************
C
          INTEGER STAGE,TIME
C
          IF (STAGE.EQ.1) THEN
             B = 3.16987
             C = 9.19488
          ELSEIF (STAGE.EQ.2) THEN
             B = 2.47643
             C = 8.96503
          ELSEIF (STAGE.EQ.3) THEN
             B = 3.78789
             C = 4.14873
          ELSEIF (STAGE.EQ.4) THEN
             B = 3.08195
             C = 7.2978
          ELSEIF (STAGE.EQ.5) THEN
```

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```fortran
            B = 6.73449
            C = 1.9716
         ELSE
            B = 59.7507
            C = 9.85034
         ENDIF
C
         PMAT = 0.0
         DO 100 I = 1,TIME
            PMAT = PMAT + F(I,B,C)
  100    CONTINUE
         RETURN
         END
         FUNCTION F(N,B,C)
C
C **********************************************
C *   THIS FUNCTION CALCULATES THE PROBABILITY   *
C *      DENSITY FUNCTION (GAMMA DISTRIBUTION)    *
C **********************************************
C
         F = (N/B) ** (C-1) * EXP(-N/B)/(B * GAMMA(C))
         RETURN
         END
         FUNCTION FERT(SUBSTG,RELDD)
C
C **********************************************
C *   THIS FUNCTION CALCULATES THE FERTILITY      *
C *      ASSOCIATED WITH THE NUMBER OF DD         *
C **********************************************
C
         INTEGER SUBSTG
         DD = RELDD * SUBSTG
         FERT = (0.008 * DD)/(1.001 ** DD)
         RETURN
         END
         REAL FUNCTION MORT(STAGE,SUBSTG,RELDD)
C
C **********************************************
C *   THIS FUNCTION CALCULATES THE MORTALITY      *
C *      ASSOCIATED WITH THE NUMBER OF DD         *
C **********************************************
C
         INTEGER STAGE,SUBSTG
         REAL DD
         DIMENSION AVGDD(5)
         DATA AVGDD/29.1466,22.2013,15.7149,22.4915,13.2777/
C
         LAST = STAGE - 1
         DD = 0.0
         I = 1
         WHILE (I.LE.LAST) DO
            DD = DD + AVGDD(I)
            I = I + 1
         ENDWHILE
C
         DD = DD + RELDD * SUBSTG
         IF (DD.GE.1500) THEN
            MORT = 1.0
         ELSE
            MORT = 1.0 - 0.908589 * EXP(-0.006861*EXP(0.006561*DD))
         ENDIF
C
         RETURN
         END
```

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```
          FUNCTION ACCDD(MAX2,MIN1,MAX1,MIN2,TB)
C
C ****************************************************
C *      THIS FUNCTION CALCULATES ACCUMULATED        *
C *          DEGREE-DAYS FOR THE DAY.                 *
C ****************************************************
C
          REAL MIN1,MIN2,MAX1,MAX2,TB,M1,M2,M3,M4,M5,M6
          DATA PI/3.14159/
C
          IF (MIN1.GE.TB) THEN
              Y1 = 3*(MAX1 + MIN1) - 1.5719925*(MAX1 - MIN1) - 6*TB
              Y2 = 4*(MAX2 + MIN1) - 8*TB
          ELSE
              IF (MAX1.LT.TB) THEN
                  Y1 = 0.0
              ELSE
                  M1 = (MAX1 + MIN1)/2.0
                  M2 = (MAX1 - MIN1)/2.0
                  X1 = 16.0/PI * ARSIN((TB - M1)/M2) - 48.0
                  CALL QUAD(X1)
                  FACTOR = 1 + COS(PI/16.0 * (X1 + 48.0))
                  Y1 = X1 * (M1 - TB) - 16.0/PI * M2 * FACTOR
              ENDIF
C
              IF (MAX2.LT.TB) THEN
                  Y2 = 0
              ELSE
                  M3 = (MAX2 + MIN1)/2.0
                  M4 = (MAX2 - MIN1)/2.0
                  X2 = 8.0/PI * ARSIN((TB - M3)/M4) - 6.0
                  CALL QUAD(X2)
                  IF (X2.LT.6.0) X2 = 12.0 - X2
                  FACTOR = COS(PI/8.0 * (X2 + 6.0))
                  Y2 = (14 - X2) * (M3 - TB) + 8.0/PI * M4 * FACTOR
              ENDIF
          ENDIF
C
          IF (MIN2.GE.TB) THEN
              Y3 = 5*(MAX2 + MIN2) + 2.35264*(MAX2 - MIN2) - 10*TB
          ELSE
              IF (MAX2.LT.TB) THEN
                  Y3 = 0.0
              ELSE
                  M5 = (MAX2 + MIN2)/2.0
                  M6 = (MAX2 - MIN2)/2.0
                  X3 = 16.0/PI * ARSIN((TB - M5)/M6) + 6.0
                  CALL QUAD(X3)
                  IF (X3.LT.14.0) X3 = 36.0 - X3
                  X3 = AMIN1(24.0,X3)
                  FACTOR = -COS((PI/16.0) * (X3 - 6.0))
                  Y3 = (24 - X3) * (M5 - TB) + 16.0/PI * M6 * FACTOR
              ENDIF
          ENDIF
C
          ACCDD = (Y1 + Y2 + Y3)/24.0
C
          RETURN
          END
          FUNCTION PRED(J,STAGE,TOTALS,APHIDS,DD,NHT,NHC)
C
C ****************************************************
C *      THIS FUNCTION COMPUTES THE PROBABILITY      *
C *          THAT AN INDIVIDUAL WILL BE KILLED        *
```

```
C *          BY PREDATION.                              *
C ********************************************************
C
        REAL NAU,NCON
        INTEGER STAGE
        DIMENSION APHIDS(60),UNITS(6),TOTALS(7),AU(6)
        DATA AU/1.0,2.26,5.08,7.63,12.2,12.2/
C
        NCA = 305.0 * (NHC + NHT)
C
        IF (APHIDS(J).LT.0.01.OR.TOTALS(STAGE).LT.0.01) THEN
          PRED = 0.0
        ELSE
          TUNITS = 0.0
          DO 100 I = 1,6
            UNITS(I) = TOTALS(I) * AU(I)
            TUNITS = TUNITS + UNITS(I)
100       CONTINUE
C
          IF (TUNITS.GE.NCA) THEN
            NAU1 = 0.85 * DD
            NAU2 = 1.13 * DD
          ELSE
            NAU1 = 0.85 * DD * TUNITS / NCA
            NAU2 = 1.13 * DD * TUNITS / NCA
          ENDIF
C
          PRED = 1.0-(1.0-NAU1/TUNITS)**NHT*(1.0-NAU2/TUNITS)**NHC
C
        ENDIF
        RETURN
        END
      FUNCTION RAIN(I)
C
C ********************************************************
C *    THIS FUNCTION COMPUTES THE PROBABILITY    *
C *       THAT AN INDIVIDUAL WILL BE KILLED      *
C *          BY EXCESSIVE RAINFALL.              *
C ********************************************************
C
        RAIN = 0.0
C
        RETURN
        END
      SUBROUTINE DIST(F,INIT,LENGTH,TOTALS)
C
C ********************************************************
C *        THIS SUBROUTINE DISTRIBUTES THE        *
C *       INITIAL COHORT THROUGHOUT THE ARRAY.    *
C ********************************************************
C
        REAL LENGTH(6)
        INTEGER TIME
        DIMENSION F(60),CDF(10),INIT(6),TOTALS(7)
C
        TOTALS(7) = 0.0
        DO 200 J = 1,6
          TOTALS(J) = FLOAT(INIT(J))
          DO 100 I = 1,10
            K = (J - 1) * 10 + I
            TIME = INT(I * LENGTH(J))
            CDF(I) = PMAT(J,TIME)
C
            IF (I.EQ.1) THEN
```

```
                      F(K) = CDF(I) * INIT(J)
                  ELSE
                      F(K) = (CDF(I) - CDF(I-1)) * INIT(J)
                  ENDIF
      100         CONTINUE
                  TOTALS(7) = TOTALS(7) + TOTALS(J)
      200     CONTINUE
C
          RETURN
          END
      INTEGER FUNCTION CONJUL(MONTH,DAY,YEAR)
C
C *************************************************
C *     THIS FUNCTION CONVERTS AN ORDINARY         *
C *       (GREGORIAN) DATE TO A JULIAN DATE.       *
C *************************************************
C
          INTEGER MONTH,DAY,YEAR,DAYSUM
          DIMENSION NDAYS(12)
          DATA NDAYS/31,28,31,30,31,30,31,31,30,31,30,31/
C
          IF (MOD(YEAR,4).EQ.0) NDAYS(2) = NDAYS(2) + 1
C
          DAYSUM = 0
          I = 1
          WHILE (I.LT.MONTH) DO
              DAYSUM = DAYSUM + NDAYS(I)
              I = I + 1
          ENDWHILE
          DAYSUM = DAYSUM + DAY
          CONJUL = 1000 * YEAR + DAYSUM
C
          RETURN
          END
      SUBROUTINE CALSTG(I,STAGE,SUBSTG)
C
C *************************************************
C *     THIS SUBROUTINE TAKES THE SUBSCRIPT FROM   *
C *       THE F ARRAY AND CALCLUATES THE STAGE     *
C *       AND SUBSTAGE CORRESPONDING TO IT.        *
C *************************************************
C
          INTEGER STAGE,SUBSTG,REM
C
          REM = MOD(I,10)
C
          IF (REM.EQ.0) THEN
              STAGE = I/10
              SUBSTG = 10
          ELSE
              STAGE = I/10 + 1
              SUBSTG = REM
          ENDIF
C
          RETURN
          END
      FUNCTION NXTSTG(I)
C
C *************************************************
C *     THIS FUNCTION CALCULATES WHAT STAGE THE    *
C *       INDIVIDUALS FROM ANY STAGE WILL MATURE   *
C *       TO (J-VALUES ARE CALCULATED, NOT STAGES) *
C *************************************************
C
```

```
              J = 0
              WHILE (J*10.LT.1) DO
                  J = J + 1
              ENDWHILE
              NXTSTG = J * 10 + 1
C
              RETURN
              END
          SUBROUTINE QUAD(X)
C
C **************************************************
C *     THIS SUBROUTINE CONVERTS AN ANGLE X, IN    *
C *       RADIANS, TO AN EQUIVALENT ANGLE IN THE   *
C *           FIRST REVOLUTION.                     *
C **************************************************
C
              FRACT = X/6.2832
              X = FRACT - INT(FRACT)
              IF (X.LT.0) X = X + 6.2832
              RETURN
              END
          FUNCTION CENTIG(FTEMP)
C
C **************************************************
C *     THIS FUNCTION CONVERTS A FAHRENHEIT         *
C *         TEMPERATURE TO CENTIGRADE.              *
C *     THE FAHRENHEIT TEMPERATURE IS INTEGER       *
C *         AND THE RESULT OF CONVERSION            *
C *             IS REAL.                            *
C **************************************************
C
              INTEGER FTEMP
C
              CENTIG = 5.0/9.0 * (FTEMP - 32)
              RETURN
              END
```

Appendix C

SAS Program to Fit Gamma Curves

```
//MA12 JOB 1099967025,ELLIOT,CLASS=J,MSGCLASS=M
/*ROUTE PRINT N2.MUSIC
// EXEC SAS,OUT=M
TITLE 'MODELS OF GREEN-BUG APHID DEVELOPMENT';
DATA A;
  INPUT  MO DAY YEAR SP $ TEMP I1 I2
         I3 I4 B MORPH $;
  T2 = I2 - I1;
  T3 = I3 - I2;
  T4 = I4 - I3;
  T5 = B - I4;
  DD1 = TEMP - 6.29;
  DD2 = TEMP - 6.54;
  DD3 = TEMP - 10.36;
  DD4 = TEMP - 7.59;
  DD5 = TEMP - 6.56;
  DEV1 = I1/24 * DD1;
  DEV2 = T2/24 * DD2;
  DEV3 = T3/24 * DD3;
  DEV4 = T4/24 * DD4;
  DEV5 = T5/24 * DD5;
  KEEP TEMP DEV1-DEV5 MORPH;
  CARDS;
PROC SORT DATA=A;
  BY DEV1;
DATA B;
  SET A;BY DEV1;
  IF DEV1 = . THEN DELETE;
  IF FIRST.DEV1 THEN NMAT = 1;
    ELSE NMAT + 1;
  IF LAST.DEV1 THEN OUTPUT;
PROC MEANS MEAN STD SUM N NOPRINT;
  VAR DEV1 NMAT;
  OUTPUT OUT = STATS MEAN = MEANA MEANB
                     STD = STDA STDB
                     SUM = NA NB
                     N = NOBSA NOBSB;
DATA VARBLS; SET STATS;
  MEAN = MEANA;STD = STDA;N = NB;NOBS = NOBSA;
  B = STD**2/MEAN;
  C = (MEAN/STD)**2;
  KEEP MEAN STD B C N NOBS;
PROC PRINT DATA = VARBLS;
  TITLE2 'PARAMETERS FOR FIRST LIFE-STAGE:  GAMMA MODEL';
DATA C;
  IF _N_ = 1 THEN SET VARBLS;
  SET B;
PROC PRINT DATA = C;
DATA COMPLETE;
  SET C;
  CF + NMAT/N;
  PCF = 0;
  DO X = 1 TO DEV1;
    PCF +  (X/B)**(C-1) * EXP(-X/B)/(B*GAMMA(C));
    END;
  OSQR = (CF - PCF) ** 2;
  SSE + OSQR;
  YSUM + CF;
  YSQR + CF ** 2;
  IF _N_ = NOBS THEN DO;
    SST = YSQR - (YSUM ** 2)/NOBS;
    RSQR = 1 - SSE/SST;
    OUTPUT;
    END;
```

```
        PROC PRINT DATA = COMPLETE;
        PROC SORT DATA=A;
          BY DEV2;
        DATA B;
          SET A;BY DEV2;
          IF DEV2 = . THEN DELETE;
          IF FIRST.DEV2 THEN NMAT = 1;
            ELSE NMAT + 1;
          IF LAST.DEV2 THEN OUTPUT;
        PROC MEANS MEAN STD SUM N NOPRINT;
          VAR DEV2 NMAT;
          OUTPUT OUT = STATS MEAN = MEANA MEANB
                           STD = STDA STDB
                           SUM = NA NB
                           N = NOBSA NOBSB;
        DATA VARBLS; SET STATS;
          MEAN = MEANA;STD = STDA;N = NB;NOBS = NOBSA;
          B = STD**2/MEAN;
          C = (MEAN/STD)**2;
          KEEP MEAN STD B C N NOBS;
        PROC PRINT DATA = VARBLS;
          TITLE2 'PARAMETERS FOR SECOND LIFE-STAGE:  GAMMA MODEL';
        DATA C;
          IF _N_ = 1 THEN SET VARBLS;
          SET B;
        PROC PRINT DATA = C;
        DATA COMPLETE;
          SET C;
          CF + NMAT/N;
          PCF = 0;
          DO X = 1 TO DEV2;
            PCF +  (X/B)**(C-1) * EXP(-X/B)/(B*GAMMA(C));
            END;
          DSQR = (CF - PCF) ** 2;
          SSE + DSQR;
          YSUM + CF;
          YSQR + CF ** 2;
          IF _N_ = NOBS THEN DO;
            SST = YSQR - (YSUM ** 2)/NOBS;
            RSQR = 1 - SSE/SST;
            OUTPUT;
            END;
        PROC PRINT DATA = COMPLETE;
        PROC SORT DATA=A;
          BY DEV3;
        DATA B;
          SET A;BY DEV3;
          IF DEV3 = . THEN DELETE;
          IF FIRST.DEV3 THEN NMAT = 1;
            ELSE NMAT + 1;
          IF LAST.DEV3 THEN OUTPUT;
        PROC MEANS MEAN STD SUM N NOPRINT;
          VAR DEV3 NMAT;
          OUTPUT OUT = STATS MEAN = MEANA MEANB
                           STD = STDA STDB
                           SUM = NA NB
                           N = NOBSA NOBSB;
        DATA VARBLS; SET STATS;
          MEAN = MEANA;STD = STDA;N = NB;NOBS = NOBSA;
          B = STD**2/MEAN;
          C = (MEAN/STD)**2;
          KEEP MEAN STD B C N NOBS;
        PROC PRINT DATA = VARBLS;
          TITLE2 'PARAMETERS FOR THIRD LIFE-STAGE:  GAMMA MODEL';
```

```
DATA C;
  IF _N_ = 1 THEN SET VARBLS;
  SET B;
PROC PRINT DATA = C;
DATA COMPLETE;
  SET C;
  CF + NMAT/N;
  PCF = 0;
  DO X = 1 TO DEV3;
    PCF + (X/B)**(C-1) * EXP(-X/B)/(B*GAMMA(C));
    END;
  DSQR = (CF - PCF) ** 2;
  SSE + DSQR;
  YSUM + CF;
  YSQR + CF ** 2;
  IF _N_ = NOBS THEN DO;
    SST = YSQR - (YSUM ** 2)/NOBS;
    RSQR = 1 - SSE/SST;
    OUTPUT;
    END;
PROC PRINT DATA = COMPLETE;
PROC SORT DATA=A;
  BY DEV4;
DATA B;
  SET A;BY DEV4;
  IF DEV4 = . THEN DELETE;
  IF FIRST.DEV4 THEN NMAT = 1;
    ELSE NMAT + 1;
  IF LAST.DEV4 THEN OUTPUT;
PROC MEANS MEAN STD SUM N NOPRINT;
  VAR DEV4 NMAT;
  OUTPUT OUT = STATS MEAN = MEANA MEANB
                    STD = STDA STDB
                    SUM = NA NB
                    N = NOBSA NOBSB;
DATA VARBLS; SET STATS;
  MEAN = MEANA;STD = STDA;N = NB;NOBS = NOBSA;
  B = STD**2/MEAN;
  C = (MEAN/STD)**2;
  KEEP MEAN STD B C N NOBS;
PROC PRINT DATA = VARBLS;
  TITLE2 'PARAMETERS FOR FOURTH LIFE-STAGE:  GAMMA MODEL';
DATA C;
  IF _N_ = 1 THEN SET VARBLS;
  SET B;
PROC PRINT DATA = C;
DATA COMPLETE;
  SET C;
  CF + NMAT/N;
  PCF = 0;
  DO X = 1 TO DEV4;
    PCF + (X/B)**(C-1) * EXP(-X/B)/(B*GAMMA(C));
    END;
  DSQR = (CF - PCF) ** 2;
  SSE + DSQR;
  YSUM + CF;
  YSQR + CF ** 2;
  IF _N_ = NOBS THEN DO;
    SST = YSQR - (YSUM ** 2)/NOBS;
    RSQR = 1 - SSE/SST;
    OUTPUT;
    END;
PROC PRINT DATA = COMPLETE;
PROC SORT DATA=A;
```

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```
    BY DEV5;
DATA B;
  SET A;BY DEV5;
  IF DEV5 = . THEN DELETE;
  IF FIRST.DEV5 THEN NMAT = 1;
    ELSE NMAT + 1;
  IF LAST.DEV5 THEN OUTPUT;
PROC MEANS MEAN STD SUM N NOPRINT;
  VAR DEV5 NMAT;
  OUTPUT OUT = STATS MEAN = MEANA MEANB
                    STD = STDA STDB
                    SUM = NA NB
                    N = NOBSA NOBSB;
DATA VARBLS; SET STATS;
  MEAN = MEANA;STD = STDA;N = NB;NOBS = NOBSA;
  B = STD**2/MEAN;
  C = (MEAN/STD)**2;
  KEEP MEAN STD B C N NOBS;
PROC PRINT DATA = VARBLS;
  TITLE2 'PARAMETERS FOR FIFTH LIFE-STAGE:  GAMMA MODEL';
DATA C;
  IF _N_ = 1 THEN SET VARBLS;
  SET B;
PROC PRINT DATA = C;
DATA COMPLETE;
  SET C;
  CF + NMAT/N;
  PCF = 0;
  DO X = 1 TO DEV5;
    PCF +  (X/B)**(C-1) * EXP(-X/B)/(B*GAMMA(C));
    END;
  DSQR = (CF - PCF) ** 2;
  SSE + DSQR;
  YSUM + CF;
  YSQR + CF ** 2;
  IF _N_ = NOBS THEN DO;
    SST = YSQR - (YSUM ** 2)/NOBS;
    RSQR = 1 - SSE/SST;
    OUTPUT;
    END;
PROC PRINT DATA = COMPLETE;
DATA DEATH;
  INPUT T6 @@;
  DEV6 = T6 * 13.84;
  CARDS;
PROC SORT DATA = DEATH;
  BY DEV6;
DATA B;SET DEATH;
  BY DEV6;
  IF FIRST.DEV6 THEN NDEAD = 1;
    ELSE NDEAD + 1;
  IF LAST.DEV6 THEN OUTPUT;
PROC MEANS MEAN STD SUM N NOPRINT;
  VAR DEV6 NDEAD;
  OUTPUT OUT = STATS MEAN = MEANA MEANB
                    STD = STDA STDB
                    SUM = NA NB
                    N = NOBSA NOBSB;
DATA VARBLS; SET STATS;
  MEAN = MEANA;STD = STDA;N = NB;NOBS = NOBSA;
  B = STD**2/MEAN;
  C = (MEAN/STD)**2;
  KEEP MEAN STD B C N NOBS;
PROC PRINT DATA = VARBLS;
```

```
       TITLE2 'PARAMETERS FOR SIXTH LIFE-STAGE:  GAMMA MODEL';
DATA C;
   IF _N_ = 1 THEN SET VARBLS;
   SET B;
PROC PRINT DATA = C;
DATA COMPLETE;
   SET C;
   CF + NDEAD/N;
   PCF = 0;
   DO X = 1 TO DEV6;
     PCF +  (X/B)**(C-1) * EXP(-X/B)/(B*GAMMA(C));
     END;
   DSQR = (CF - PCF) ** 2;
   SSE + DSQR;
   YSUM + CF;
   YSQR + CF ** 2;
   IF _N_ = NOBS THEN DO;
     SST = YSQR - (YSUM ** 2)/NOBS;
     RSQR = 1 - SSE/SST;
     OUTPUT;
     END;
PROC PRINT DATA = COMPLETE;
```

Bibliography

1. Leslie, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika. 33:182-212.

2. Woodward, I.O. 1982. Modeling population growth in stage-grouped organisms: a simple extension of the Leslie model. Austr. Jour. Ecol. 7:389-394.

3. Manetsch, T.J. 1976. Time-varying distributed delays and their use in aggregate models of large systems. IEEE Trans. Systems, Man. Cybern. 6:547-553.

4. Allen, J.C. 1975. A modified sine wave method for calculating degree days. Florida Agric. Exp. Stn. Journal Series No. 6064.

5. Wagner, T.L., H. Wu, P.J. H. Sharpe, and R.N. Coulson. 1984. Modeling distributions of insect development time: A literature review and application of the Weibull function. Ann. Entomol. Soc. Amer. 77:475-487.

6. Graf, B., J. Baumgartner and V. Delucchi. 1985. Simulation models for the dynamics of three apple aphids, Dysaphis plantaginea, Rhopalosiphum insertum, and Aphis pomi (Homoptera, Aphididae) in a Swiss apple orchard. Z. ang. Ent. 99:453-465.

7. Hassell, M.P. 1978. Arthropod Predator Prey Systems. Princeton Univ. Press, Princeton, New Jersey.

8. David, H.T. 1958. A three-sample Kolmogorov-Smirnov test. Annals of Mathematical Statistics: 842-851.

9. Lawless, J. 1981. Statistical Models and Methods for Lifetime Data, J.P. Wiley.

10. Vickerman, G.P. and S.D. Wratten, 1979. Ecology and pest status of cereal aphids (hemiptera: Aphididae) in Europe: a review. Bull. Entomol. Tes. 69:1-32.

11. Bieri, M., J. Baumgartner, G. Bianchi, B. Delucchi, R. von Arx. 1983. Development and fecundity of pea aphid (Acyrthosiphum pisum Harris) as affected by constant temperatures and by pea verieties. Mitt. Schweiz. Ent. Ges. 56:163-171.

12. Keickhefer, R.W. and B.H. Kantack. 1980. Losses in yield in spring wheat in South Dakota caused by cereal aphids. J. Econ. Entomol. 73:582-585.