THE WITHIN-GENERATION POPULATION DYNAMICS OF THE CEREAL LEAF BEETLE, OULEMA MELANOPUS (L.)

Thesis for the Degree of Ph. D

MICHIGAN STATE UNIVERSITY

ROBERT GORDON HELGESEN

1969

This is to certify that the

thesis entitled

THE WITHIN-GENERATION POPULATION
DYNAMICS OF THE CEREAL LEAF
BEETLE, OULEMA MELANOPUS (L.)

presented by

Robert Gordon Helgesen

has been accepted towards fulfillment
of the requirements for

Ph.D **degree in** Entomology

Dean L Haynes
Dean L. Haynes
Major professor

Date October 20, 1969

O-169

ABSTRACT

THE WITHIN-GENERATION POPULATION DYNAMICS OF THE CEREAL LEAF BEETLE, *OULEMA MELANOPUS* (L.)

BY

Robert Gordon Helgesen

The cereal leaf beetle, *Oulema melanopus* (L.), has rapidly increased its numbers and range since it was discovered in Michigan in 1962. It was hypothesized that intraspecific density-dependent mortality was the major constraint on the survivorship of this foreign pest as its density increased.

In order to quantify fecundity and age specific survivorship the density of three different populations was censused from April to July in 1967, 1968 and 1969. Populations were established in cages where age specific survivorship could be investigated at specific densities.

Fecundity was the same at all densities and affected mainly by temperature. Mortality in the first and fourth instar was found to increase with an increase in the logarithm of density. There was a significant difference in fourth instar mortality between host plants but no difference in first instar mortality between host plants. Two different mortality factors appeared to be involved in the density-dependent mortality of these two instars. Second and third instar mortality, as well as pupal mortality was relatively constant with respect to density. The cereal leaf beetle has the requisite for population regulation -- a density-dependent feedback system.

THE WITHIN-GENERATION POPULATION DYNAMICS OF THE CEREAL LEAF BEETLE, *Oulema melanopus* (L.)

By

Robert Gordon Helgesen

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Entomology

1969

ACKNOWLEDGEMENTS

To Dr. Dean L. Haynes I extend my sincerest appreciation for the personal guidance, unselfish contribution of time and wealth of scientific inspirations he offered throughout my program and the preparation of this thesis.

Dr. Gordon Guyer's enthusiasm, optimism and support were a constant source of encouragement during my entire program. Some discerning suggestions by Dr. William Cooper enhanced the quantitative aspects of this study.

I am grateful for my wife's encouragement, patience and toil in the preparation of this thesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES -- Cont.

INTRODUCTION

Many foreign insects have been introduced into North America. Future technological advances in transportation will intensify this phenonomenon. We can assume that many introduced insects never survived for various reasons, while others, like the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), were eradicated after successful establishment. However, a few insects like the gypsy moth, *Porthetria dispar* (L.), European corn borer, *Ostrinia nubilalis* (Hübner), the codling moth, *Carpocapsa pomenella* (L.), and the japanese beetle, *Popillia japonica* Newman, were able to establish themselves. Once established, they found very little environmental resistance and greatly expanded their distribution and abundance.

Like other successfully introduced insect pests, the cereal leaf beetle (CLB), *Oulema melanopus* (L.), has rapidly increased its number and range. Its preferred host is the succulent growth of small grains, and its success threatens the economic production of oats in Michigan. Therefore, population control is necessary before a certain economic damage threshold is reached. However, before a population control program can be logically designed and evaluated, the dynamics of a population should be quantified. Initial research on the

CLB dealt with damage control and biology instead of population dynamics. Unfortunately, this type of research does not provide very much useful information to design a program in population management. Turnbull and Chant (1961) most aptly suggest that economic entomologists have classically limited their ability to understand the total pest management problem by equating damage control to population control.

This study was an investigation of the within-generation population dynamics of the cereal leaf beetle. Natural mortality factors of the population were isolated and quantified in order to construct a mathematical model which would explain natural population changes of the cereal leaf beetle and perhaps expose certain features of the population which are susceptible to control. Castro (1965) and Yun (1967) showed that no parasites or predators significantly affect the cereal leaf beetle in Michigan. Therefore, it was hypothesized that most mortality occurring within a generation was a direct cause of intrinsic and climatic or physical mortality factors. By accepting the almost axiomatic assumption that a population has an upper limit of density in any given area, certain mortality factors must function through a density-dependent feedback system, at least above certain densities. This density-dependent mortality would tend to hold the population at some variable and unknown upper limit. Given the somewhat constant planting practices for small grains in Michigan, the most obvious factor which could produce this density-dependent mortality is competition for food which could express itself through direct mortality and qualitative changes in the population.

REVIEW OF LITERATURE

An excellent account of the history, distribution, general biology and literature of the cereal leaf beetle is given by Yun (1967). From the literature he reviewed, Yun concluded that the cereal leaf beetle has been recorded as a pest of small grains since the mid-eighteenth century. It is presently acknowledged as a general, but sporadic, pest throughout its native range of Europe, parts of north Africa, Turkey, Iran and from central Siberia eastward (Yun 1967).

It was first identified in North America from specimens collected in Michigan in 1962. However, from our present knowledge of the insect the abundance at that time indicates it was probably introduced at least ten years previously.

Castro, *et al.*, (1965) described the natural history of the cereal leaf beetle in Michigan. A graphic representation of the life cycle of this insect is diagrammed in Figure 1.

```
                            MONTH
  J    F    M    A    M    J    J    A    S    O    N    D
  aaaaaaaaaaaaaaaaaaaaaaaaaa     aaaaaaaaaaaaaaaaaaaaaaaaa
                   eeeeeeeeeee
                       lllllll                  a = adult
                             pppppp             e = egg
                                                l = larvae
                                                p = pupae
```

Figure 1. Life cycle of the cereal leaf beetle, *Oulema melanopus* (L.).

They reported that the overwintering adult could be found in forest litter, grass stubble, under tree bark, or any site well protected from temperature extremes. Overwintering adults become active in March when daytime temperatures and solar radiation raise their temperature above 55°F. Once active, the beetles are arbitrarily called spring adults.

Spring adults feed on winter grains as well as native and cultivated grasses for a few days after emergence. Females generally mate very soon after leaving the overwintering site and continue to mate throughout the ovipositional period. Oviposition occurs from mid-April to June in Michigan, usually on the basal one third of the upper leaf surface. Generally, smaller more succulent grain plants are preferred for food and oviposition.

Larvae feed on the upper surface of the leaf and chew through to the lower cuticle. When development is complete the prepupa drops or crawls from the plant and enters the soil to pupate. Merritt (1967) reported that mortality in the pupal stage ranged from 4% to 24% with mortality probably related to soil moisture. Adults, arbitrarily called summer adults, emerge in July and feed on grasses and corn for two to four weeks. Responding to some environmental or physiological cue the summer adults seek an overwintering site and enter a state of reduced activity until the following spring. Under laboratory conditions Yun (1967) reported 65% mortality for overwintering adults held at 43°F for 90 days.

POPULATION THEORY

Several theories have been constructed to render numerical population change understandable (Nicholson 1933; Thompson 1939; Andrewartha and Birch 1954; Milne 1957). Underlying all of these theories is an almost axiomatic assumption that population size cannot increase indefinitely without some upper limit. Exactly how and why populations change numerically is the major source of controversy among these theories. This review will deal with those features of each theory which contribute most to understanding the population dynamics of the cereal leaf beetle.

Nicholson (1933) was the first to construct a logical and detailed theory of population dynamics and it is the basis for most subsequent theories. Nicholson (1954) used the observations of Howard and Fiske (1911) and Chapman (1928), and the mathematical models of Lotka (1925) and Volterra (1926) to postulate that a population and its environment exist in a state of dynamic balance because of density-related resistance to infinite population growth. The following quotation summarizes his point of view:

> "Populations are self-governing systems. They regulate their densities in relation to their own properties and those of their environment. This they do by depleting and impairing essential things to the threshold of favorability, or by maintaining reactive inimical factors, such as the attack of enemies, at the level of tolerance.
>
> The mechanism of density governance is almost always intraspecific competition, either amongst the animals for a critically important requisite, or amongst natural enemies for which the animals concerned are requisites.
>
> .
> .

> Far from being a stationary state, balance is commonly a state of oscillation about the level of equilibrium density which is forever changing with environmental conditions.
>
> .
> .
> .
>
> Although population densities can be governed only by factors which react to density change, factors which are uninfluenced by density may produce profound effects upon the density."

Nicholson's theory can be summarized quite accurately by an oversimplified mathematical model (after Cole 1957):

$$N_{x+1} = N_x R_o g(x),$$

where the present population density (N_{x+1}) is equal to the product of the previous generation density (N_x) times the net reproductive rate (R_o) times a "governing" factor ($g(x)$). This model is restricted to populations with non-overlapping generations. Since Nicholson concluded that population change was a result of both the density of the existing population (N) and the environment (E), then, the "governing" factor, g, must be a function of both density and environment and since the full effect of the environment determines the carrying capacity or mean density (N_{max}), then:

$$g = f(N,E) = \left(1 - \frac{N}{N_{max}} \right), \quad 0 \leq g < 1$$

Nicholson's theory has received both widespread acceptance and criticism among population ecologists. For example, Thompson (1956) accurately points out that the factor of chance plays a much greater part in population dynamics than Nicholson eludes. In a statistical sense, Nicholson has used a deterministic model where a stochastic model would be most accurate to describe population dynamics. Following this stochastic argument, Thompson (1956) suggests that environmental conditions met by any population vary tremendously in both time and space, and the mean density defined for a population is not a single event, but a distribution of events in a probability set.

Andrewartha and Birch (1954) observed frequent and extreme fluctuations in Australian grasshoppers and concluded that these insects as well as many others were regulated by environment and not by density-dependent factors. However, in a Nicholsonian sense they have simply stressed the importance of the environment as the determinant of the carrying capacity (N_{max}).

Milne (1957) emphasizes the incomplete nature of Nicholson's dogmatic classification of density-dependent and density-independent factors responsible for numerical population change. Milne (1957) concluded that natural enemies of a population are imperfectly density-dependent and can only control increase of a population in combined action with density-independent factors.

EFFECT OF DENSITY ON POPULATION CHANGE

Andersen (1957) compiled a review of the effects of density on the birth and death rate of a population. He investigated Kostitzin's (1939) assumption that the birth and death rates of a population are linear functions of its density. Bøggild and Keiding (1958) clarified Kostitzin's (1939) assumption on the relationship of mortality and density by stating that above a certain density the fraction of the population dying between birth and the adult is a linear function of its initial density. That is,

$$\frac{y}{x} = a - bx,$$

where x is the initial density, y is the number surviving and a and b are constants of the equation. By a simple algebraic manipulation of this equation Bøggild and Keiding (1958) showed that the survival process may be divided into two components:

$$y = ax - bx^2$$

where the number surviving is equal to some constant mortality factor (ax), such as genetic or intrinsic death, and a parabolic component (bx^2) showing that mortality is due to mutual influence of individuals proportional to the second power of density (x). The square of density expresses mutual influence because at a specific density (x) each individual is affected by x-1 individuals so mutual influence in the total population is x(x-1). However, as $x \to \infty$, $x(x-1) \to x^2$, or the second power of density.

Andersen (1957) concluded from several important laboratory findings that the assumption of Kostitzin (1939) and Bøggild and Keiding (1958) was correct. In the laboratory, Yun (1967) showed that there was a linear relationship between the logarithm of the number of larvae placed on a grain plant and the survival of those larvae.

Unlike mortality, fecundity is not a linear function of density as Kostitzin (1939) assumed. Andersen (1957) concluded, after an exhaustive review of literature, that: "Above a certain limit of density the fecundity (n) is a linear function of the reciprocal of the density (N)." Mathematically, that is:

$$n = a + b/N$$

where a and b are constants. Biologically, the reciprocal of density (b/N) can be interpreted as (from Andersen 1957):

1) amount of food available per female
2) the number of oviposition sites per female
3) amount of space per female

Yun (1967) showed a similar relationship between adult density and fecundity, but the densities were so unnaturally high that unrealistic interference must have occurred. Most studies reviewed by Andersen (1957) were from homogeneous laboratory conditions and populations with uniform age distributions.

Aside from the quantitative changes in response to density a population can also exhibit certain density-related qualitative changes. Ullyett (1950) showed that the size of adult *Chrysomia chloropyga* decreased with increasing initial larval density and that fecundity increased with increasing female size. Greenbank (1956) showed that fecundity increased linearly with increasing size of the female pupal spruce budworm.

EFFECT OF CLIMATE AND WEATHER ON POPULATION CHANGE

The influence of climate and weather on animal populations is considered by Andrewartha and Birch (1954), Birch (1957), Greenbank (1956), Klomp (1962) and Wellington (1954). In these studies climatic factors are considered as they affect insect fecundity, growth and survival.

Yun (1967) showed that a day length in excess of 8 hours is necessary for cereal leaf beetle oviposition and a maximum rate is obtained at 16 hours. Oviposition also increases with increased temperature. However, his data did not support his conclusion that fluctuating temperatures had an adverse effect on oviposition because he compared a constant temperature treatment of 80°F to a day-night temperature of 70°F to 50°F. Under these conditions a comparison is not possible.

Yun (1967) also showed that developmental time of the cereal leaf beetle decreased with increasing temperature according to Davidson's (1944) logistic equation:

$$Y = \frac{1+e^{a+bx}}{K}$$

where, Y = developmental time
x = temperature
a, b & K = constants

The effect of this relationship is such that under a constant temperature of 58°F larval development is complete after 27 days while at 90°F only 8 days is required. In the field situation direct solar radiation can raise the body temperature of some insects 10° to 15°F (Wigglesworth 1965). This makes application of laboratory results to natural conditions somewhat difficult.

Dickler (unpublished) and Yun (1967) showed how extreme temperatures affect survival of eggs, larvae and pupae of the cereal leaf beetle. Their data showed that survival in these age classes is little affected by the temperature regimes found in lower Michigan from April through July. Greenbank (1956) points out that a decrease in temperature not only prolongs developmental time, but it increases the amount of time the immature insect is exposed to mortality factors, or increases the probability of death.

The desiccating action of low humidity and wind must have some effects on survival of young larvae at the time of eclosion and ecdysis, but this can only be inferred from the literature (Wigglesworth 1965).

DESIGN OF FIELD STUDIES

Sampling efficiency seems to be a universal problem in population studies and has received considerable attention by Embree (1965), Harcourt (1961a, 1961b, 1962, 1963, 1964), Hughes (1963), LeRoux, *et al.* (1963), Lyons (1964), Morris (1960, 1963). In all cases the objective of the design was to accurately and efficiently estimate absolute field densities in time and space. Most of the concern in estimating absolute density has been in determining the optimal sample unit size, number of samples, and sample frequency and efficiency.

The problem is to define the universe to be sampled and select an appropriate sample unit (Morris 1960, 1955; Southwood 1966). Morris (1955) offered the following six considerations for the selection of a sample unit:

> "1. In order for the sample to be representative of the universe, the sample unit should be of such a nature that all units in the universe have an equal chance of selection.
> 2. The sample must have stability. That is, the number of units available to the insect population must not be affected by changes in growth habit of the plant caused either by intrinsic factors or by repeated insect damage.
> 3. The proportion of the insect population using the sample unit as a habitat must remain constant.
> 4. The sample unit should be reasonably small so that enough units can be examined on a given plot and date to provide an adequate estimate of variance.
> 5. In absolute population work, where estimates of population per acre are required, the sampling unit must lend itself to quantitative assessments of the number of units per acre.
> 6. An important practical consideration is the facility with which the sample unit can be delineated in the field and collected without serious loss of disturbance of the insect population."

Methods for determining the most efficient sample units are suggested by Southwood (1966), Lewis and Taylor (1967), Lyons (1964) and Morris (1963). Lyons (1964) used precision, and the time required to collect one sample unit, as the most important criteria in designing an efficient sample plan.

Most of the authors mentioned above agree that the standard error should be maintained around 10% of the mean, because at this level variance of the mean estimate due to sampling is minimal. The sample size required to lower the standard error below 10% of the mean often becomes so large that efficient sampling is no longer feasible. Embree (1965) showed that the estimation of sample size, N, can easily be obtained by the formula:

$$N = s^2/s_{\bar{x}}^2 :$$

where $s_{\bar{x}}$ is 10% of $\bar{x}$.

However, he showed that if there is a relationship between the magnitude of the mean and the variance, a table or graph of sample size (which maintains SE = 10% of $\bar{x}$) versus the mean is helpful in determining the adequate sample size for a certain sample area.

Harcourt (1961, 1963, 1964) and Richards (1961) considered the problem of sample frequency in terms of the insect's developmental rates. They made effective use of the insect's developmental curve to predict the optimal sampling frequencies of a certain insect species.

ANALYTICAL TECHNIQUES FOR POPULATION DATA

In addition to estimating population size, changes in density through time must be evaluated in such a way that survival probabilities may be assigned to specific age classes. Life tables conveniently summarize these survival probabilities. Various population parameters which can be calculated from one life table (Birch 1948) can be compared to those of other life tables by variance analysis and/or regression analysis.

Numerical change within one instar can be accounted for by recruitment from the preceding instar, moulting and age specific mortality. This is complicated in the cereal leaf beetle because eggs are laid over an eight week period and all age classes occur simultaneously. It is not possible to follow one uniformly aged cohort in a natural field situation. Separating age specific mortality in such a population is an analytical problem studied by the following authors: Dempster 1961; Kiritani and Najasuji 1967; Richards and Waloff 1954; Richards, Waloff and Spadbury 1960; Southwood 1966.

Southwood (1966) explains a simple, yet very basic, method to calculate age specific mortality from this type of data. If the population is censused frequently enough an occurrence curve of each instar can be established. The area under each curve is the total number of instar-days. From this the actual number of individuals entering the instar (N_I) can be calculated by dividing average developmental time (d) into instar-days (N_T):

$$N_I = \frac{N_T}{d}$$

Southwood (1966) showed that the method is most accurate when the distribution of mortality is light at the beginning and heavy toward the end of the instar. If this procedure is repeated for each instar the number entering each instar can be compared to determine age specific survivorship.

Richards and Waloff (1954) used the "Y"-intercept of a regression line fitted to the negative slope of the total instar occurrence curve to approximate the number of individuals entering that instar. This assumes a constant mortality and developmental time and requires a well defined peak in the total instar occurrence curve.

Richards, Waloff and Spadbury (1960) offer another method for analysis of instar survival. They reasoned that the total incidence (instar-days) of an instar (N) is expressed as:

$$N = n \int_{o}^{a} K^t \, dt = \frac{n(K^a - 1)}{\ln K}$$

where n = total entering the instar
K = daily survival rate
a = duration of stage
t = time

And, if the observed N could be compared with what should have occurred, a·n, this difference would reflect mortality within that age class:

$$\frac{N}{an} = \frac{K^a - 1}{\ln K^a}$$

In contrast to the previous method this method assumes much of the mortality takes place early in the instar development. The method, however, is very sensitive to accurate estimation of developmental time.

Dempster (1961) treats census data as a series of simultaneous equations

$$\Delta N = P_a - \frac{(I_o + I_t)}{2} \, t\mu_I \ldots . - \frac{(Ad_o + Ad_t)}{2} \, t\mu_{ad}$$

where population change (ΔN) during a certain sample interval (t) is equal to the fraction of the total eggs hatching during that interval (P_a) minus the average occurrence of each age class ($I_o + I_t/2$) times the mortality during the sample interval ($t\mu_i$). The only unknowns in this equation are $\mu_I \ldots \mu_{ad}$, the age specific daily mortality rates. If there are more samples than unknowns the unknowns can be solved by a system of simultaneous equations. Unlike the other methods age specific developmental time is not required. However, to be most efficient the sample interval should be close to the average age specific developmental time. The method appears to be the most efficient of all the methods reviewed.

DEVELOPMENT OF THE LIFE TABLE

Pearl, *et al.* (1941) were the first to seriously apply life table analysis to the study of insect populations. As early as 1947 Deevey (1947) criticizes ecologists for leaving the construction and analysis of life tables to statisticians and laboratory ecologists. He gives a comprehensive discussion of the various types of life tables and the meaning of the various parameters which may be calculated. Deevey (1947) described a life table in the following way:

> "A life table is a concise summary of vital statistics of a population. Beginning with a cohort, real or imaginary, whose members start life together, the life table states for every interval of age the number of deaths, the survivors remaining, the rate of mortality, and the expectation of further life. These columns are symbolized by d_x, l_x, q_x, and e_x, respectively, where x stands for age."

Birch (1948) improves the versatility of the life table by integrating the age specific life table and the age specific fecundity table of the female population. From this table additional parameters, such as net reproduction rate

(R_o) and mean length of the generation can be calculated.

Morris and Miller (1954) suggest several modificatiions of the life table to make it more applicable to insect population studies. They suggest that the age column (x) should emphasize that stage where mortality occurs rather than strict adherence to chronological age. The age column might then have unequal age intervals. They also suggest another column d_xF that summarizes the factors causing the mortality in that age interval. They also noted that there is little use for a summarization of life expectation (e_x) in insect populations of one generation per year.

Ives (1964) discusses the problems encountered in the development of life tables for insect populations. He accurately concludes that the single most important problem in developing life tables for insect populations is sampling.

Yun (1967) constructed life tables for a laboratory population and a field population of the cereal leaf beetle. These tables were important in indicating where high mortality could be expected in the cereal leaf beetle, and what age classes needed the most detailed study. However, one life table for one generation of an insect in one environment hardly describes its population dynamics. Morris and Miller (1954) conclude that, "More valuable information can be shown, ... by continuous life tables for many generations and for different environments." It is interesting to note that in the spruce budworm study, Morris (1963) used 81 life tables to establish population trends and Embree (1965) developed 35 life tables to study the population dynamics of the winter moth.

POPULATION MODELS

Morris (1963) states that population models "... reveal in a quantitative way exactly how much is understood about the population dynamics of a species..." The population model quantitatively explains the dynamic processes of population change.

The equation reviewed in population theory $N_{x+1} = N_x R_o g(x)$ is such a model. However, there are many other models which describe population phenomena. Watt (1961) proposes an approach to modeling the within-generation survivorship of an insect population. He begins with a series of submodels developing the probability of survival for each age class being studied. These are constructed by serially adding the percentage values of the most important mortality factors, in the age class being considered, until the majority of the mortality in an age class is accounted for. This value is subtracted from one to give the survival of the age class. A typical submodel is:

$$S_{egg} = (M_1 + M_2 + M_3 \ldots M_n) - 1;$$

where M_n equals a mortality factor percentage.

In the case of a life table the survival for the age class can be computed directly, but how mortality came about will not be understood. Then he explains total generation survival as the product of the series of probabilities of survival for each of these submodels:

$$S_{Gen} = S_{Egg}\ S_{I}\ S_{II}\ S_{III}\ S_{IV}\ S_{P}\ S_{A}\ PF;$$

where generation survivorship (S_G) equals the product of age specific survival (S) times the proportion of adults that are females (P) times the mean fecundity (F). Morris (1963) and Embree (1965) use this model to explain the dynamics of the populatons they studied. Watt's basic model, of course, must be modified according to the various interactions and properties of a particular population which might affect total survival. In developing this model, Watt (1961) discusses the history, philosophy and techniques of building inductive and mixed inductive-deductive population models.

METHODS AND MATERIALS

FIELD STUDY

The object of the field study was to quantify numerical population change of the cereal leaf beetle within a generation. One method of measuring this change is by frequent estimation of the absolute population density throughout a generation. Accuracy of the absolute density estimate can be optimized with the selection of an appropriate sample universe, sample unit and sample size (n).

Sample universe. A one acre sample universe was selected because an acre of oats or winter wheat was small enough to be reasonably sampled, but large enough to reflect the variance inherent in most grain fields. Since within field variance was also of interest the one acre plot was systematically subdivided into ten equal subplots from which random samples were taken.

Sample unit. The sample unit could have been a portion of the grain plant, the whole plant or an area unit of several plants. However, wheat and oats are relatively small plants and at lower beetle densities (e.g., one egg/400 plants) a large number of plants would have to be collected to obtain a reasonable estimate of the absolute density. The most efficient method of sampling large numbers of plants was using an area sample unit that included several plants. A sample unit of one square yard was arbitrarily selected for the 1967 field study. During this study square foot samples were also used to estimate densities in the field. Table 1 shows a comparison of the efficiency of the two sample units.

TABLE 1.

EFFICIENCY OF YD^2 AND FT^2 SAMPLE UNITS IN 1967 GALIEN WHEAT

Sample Unit	Statistics			$\Sigma\ ft^2$ needed in sample
	$\bar{x}$	s^2	N*	
ft^2	140	3,432	17	17
yd^2	980	52,900	5.5	49.5

*for SE = 0.1 $\bar{x}$

When the square yard sample unit is used three times as much plant material is required to maintain the same efficiency (SE = .1 $\bar{x}$) as the square foot sample unit.

Sample size. Figure 2 shows that the variance increased proportionately with the mean in the 1967 field study. In order to maintain the standard error at 10% of the mean the sample size (N) had to be adjusted to cover most of the means expected in the field. Using the variances from Figure 2, at a mean of 10 CLB/ft^2, the sample size is 25 units and at a mean of 160 CLB/ft^2 the sample size is 19 units. Therefore it was adequate to remove two to three square foot samples at random from each subplot, or a total of twenty to thirty square foot samples per plot.

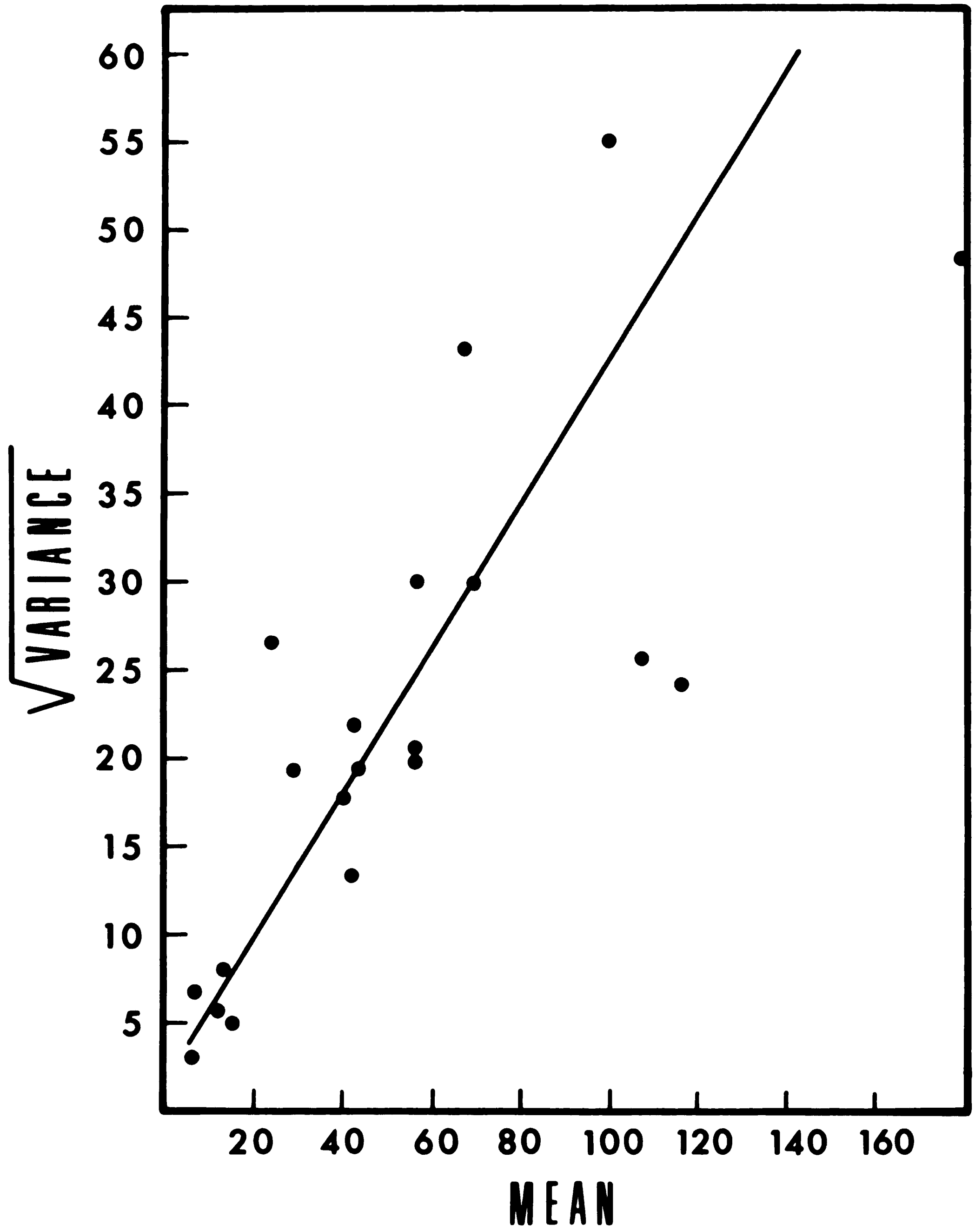

Figure 2. The relationship of the mean and variance in square foot samples of Galien wheat in 1967.

Sample frequency. In 1967 a sample frequency of one sample per week was selected. However, it was found that too much development had occurred in the population to accurately develop age specific population curves. Therefore, a sample frequency of three days was chosen for the 1968 and 1969 studies because this frequency was close to the average developmental time of one larval instar.

Field procedures. The 1967 field study included a low density area at Gull Lake and a high density area at Galien, Michigan. One acre plots in larger fields of oat and winter wheat were established at each location. The sample unit consisted of the grain plants in one square yard. Each sample unit was randomly located and removed from each of the 10 subplots once a week during the egg and larval stages. The samples were returned to the laboratory in plastic bags for counting. The pupal stage was sampled by taking a one half square yard soil sample 2 1/2" - 3" deep from each subplot. The soil was washed through 1/8" screen which separated the soil from the pupal cells (see Figure 4). Before the summer adults began to emerge, 3 one-milliacre cages were placed at random throughout the plot (Figure 3). Newly emerged adults were removed from these cages at two to three day intervals.

The 1968 and 1969 field studies were similar to the 1967 study but included three Michigan locations; a low density area at East Lansing, a medium density area at Gull Lake, and a high density area at Galien. Three 1 ft^2 samples in 1968, and two in 1969, were randomly selected from each subplot at 3-4 day intervals during the egg and larval stages. The processing of these samples and sampling for pupae and emerging summer adults was the same as in 1967.

An additional sample was added to the 1968 and 1969 field studies. In order to obtain an independent estimate of oviposition during the sample interval, a series of plants consisting of 2 linear row-feet were marked off in each subplot in both oats and wheat. At each sampling the eggs were counted and pinched so that no eggs remained after counting. This was continued until oviposition had ceased.

Temperature and humidity were recorded on hygrothermographs placed on one of the plots at each location. Solar radiation was recorded on pyroheliographs at Gull Lake and Galien in 1968 and 1969.

EXPERIMENTAL CAGE STUDY

To quantify the effect of density on age specific survival, a gradient of very low to very high density populations was established in 6-milliacre cages. These cages were placed in oats at the MSU Entomology Research Facility in East Lansing. This study was very similar to the field study except many more densities could be studied at one time and place with a minimum of variance. The cages exclosed any native predators and moderated the influence of meteorological events on survival.

In 1967, populations of 100, 200, 500, 1000, 2000 and 4000 spring adults were established in each of six 6-milliacre cages. In 1968 and 1969 twelve cages were available so four different densities (100, 500, 2000, 5000 spring adults/cage) were replicated three times. In each cage twenty-five one row-foot sample sites (15 in 1969) were staked out at random. Unlike the field study, the phenology of the organism in each sample site was followed in time. Therefore, the number occurring in each age class at the sample sites was recorded at a sample frequency of four days. No plants or larvae were removed. After pupation all plants were removed from the cage. The soil from each row-foot sample site was removed, and processed in the same way as the field study. Emerging adults were collected from the cage three times during the emergence period. In 1969 three oviposition sites, similar to the 1968 and 1969 field studies, were established in each cage in order to estimate oviposition during the sample interval.

QUALITATIVE EFFECTS OF DENSITY

Size. To test the qualitative effects of density on the cereal leaf beetle the sizes and weights of newly emerged adults from all the field studies and the 1967 caged density studies were compared. Thirty individuals from each population were placed in a laboratory oven at 106°C for 48 hours and the dry weight of each individual was measured on a Kahn Electrobalance with an accuracy of ±0.0005 mg. The elytral length was measured with an optical micrometer.

Fecundity. Several studies have shown a relationship between the size of female pupae, or resultant adults and the number of eggs they are capable of laying. To test this relationship in the cereal leaf beetle two experiments were performed. Newly emerged spring adults from a high density area (Galien), a medium density area (Gull Lake), and a low density area (East Lansing) were placed in cages in the laboratory and in the field under natural conditions. The number of eggs laid by each female was followed at various intervals throughout the life of the female.

In the laboratory, twenty pairs of beetles from each of the three density areas were placed in cellulose acetate cylinders atop a 2-inch pot of small barley plants. The pots were replaced every three days, when the eggs were counted. Counts continued until the female died. Males were not replaced if they died before the female. The laboratory was maintained at a constant temperature of 78°F and 50% R.H. with a 16 hour day.

In the field fecundity study, sixty pairs of beetles taken from the same areas as those in the previous experiment were placed in separate sleeve cages. The cage enclosed an individual wheat plant. This test was set up during the last week of April, 1969. Egg counts were made at weekly intervals. The evaluation procedure was the same as in the laboratory study.

The sleeve cages were constructed of nylon screen formed in an eight inch cylinder, 32" tall. The top was formed by an 8" embroidery hoop which was attached to the top of a 36" stake. The seam of the cylinder was stapled to this stake for support. Destruction of the eggs after counting was accomplished with a long dissecting needle.

One plant provided sufficient food for the entire life of the adult female.

DEVELOPMENTAL RATE

Larval developmental rates were observed at different temperatures so temperature-dependent developmental curves could be constructed for each instar over the range of temperatures studied. Twenty-four larvae on individual 4-inch pots, were placed in each of three Sherer-Gillette table top growth chambers maintained at 60°F, 70°F, and 80°F (with 70 to 80% R.H. and 16 hour day). The age class status of larva, established by exuviae and head capsule width, was recorded daily.

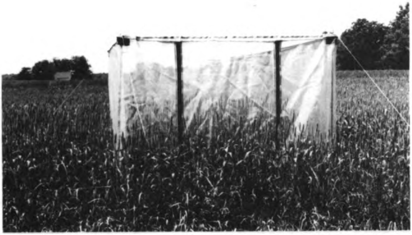

Figure 3. One milliacre emergence cages used for summer adult cereal leaf beetles.

Figure 4. Left. Screening technique used to separate CLB pupae from soil.

Figure 5. Right. A CLB ovary showing seven ovarioles.

RESULTS

FECUNDITY OF THE CEREAL LEAF BEETLE

Southwood (1966) defines fecundity as the total egg production and fertility as the number of viable eggs laid by a female. Since fecundity is the numerical input of a population system, the factors which determine this input are of a major importance in population studies. It was hypothesized that ovarian composition, temperature and adult size were the most important factors influencing egg production in the cereal leaf beetle.

Ovarian composition. The insect ovary is composed of a number of ovarioles responsible for egg production. Since the number of ovarioles can directly determine fecundity, ovaries were dissected from sixty spring adults from Galien, Gull Lake and East Lansing to determine variation in numbers of ovaries and ovarioles. The size of these spring adults varied considerably. Figure 5 shows a dissected ovary with seven ovarioles and eggs in various stages of development. All females had two ovaries each containing seven ovarioles or a total of fourteen ovarioles per female.

Temperature. Yun (1967) showed large differences in egg production at two different temperature regimes in the laboratory. However, more information was needed to establish the influence of temperature on egg production in the field. The ovipositional activity of the cereal leaf beetle was measured every three days at oviposition sites in the field. When these results were plotted against the mean maximum daily temperature measured during the three day sample interval a definite linear trend was observed. Figure 6 shows that the rate of oviposition increased linearly from 50° to 75°F. The linear relationship cannot be extrapolated beyond the endpoints of this range because the rate of oviposition quickly becomes non-linear at low and high temperatures. The cereal leaf beetle does not oviposit during the night, so maximum daily temperature was used as an indicator of daily temperature influence. Other meteorological events, such as solar radiation and wind influence body temperature and, hence, oviposition. However, the strong relationship between temperature and rate of oviposition shows that these factors are relatively minor. Table 2 shows the fecundity of three differert populations reared in the laboratory and field. In the laboratory, at a constant temperature of 78°F, mean fecundity ranged from 205 to 360 eggs per female. In the field mean fecundity ranged from 53 to 61 eggs per female. The mean daily temperature during the field experiment was 62°F. The relationship between temperature and oviposition rate suggest that this suboptimal temperature regime was probably responsible for the large difference in mean fecundity between the laboratory and field experiment. The fecundity of the field fecundity experiment was lower than that which expected in natural populations, as in Figure 6, because the cages modified the warming effect of direct solar radiation.

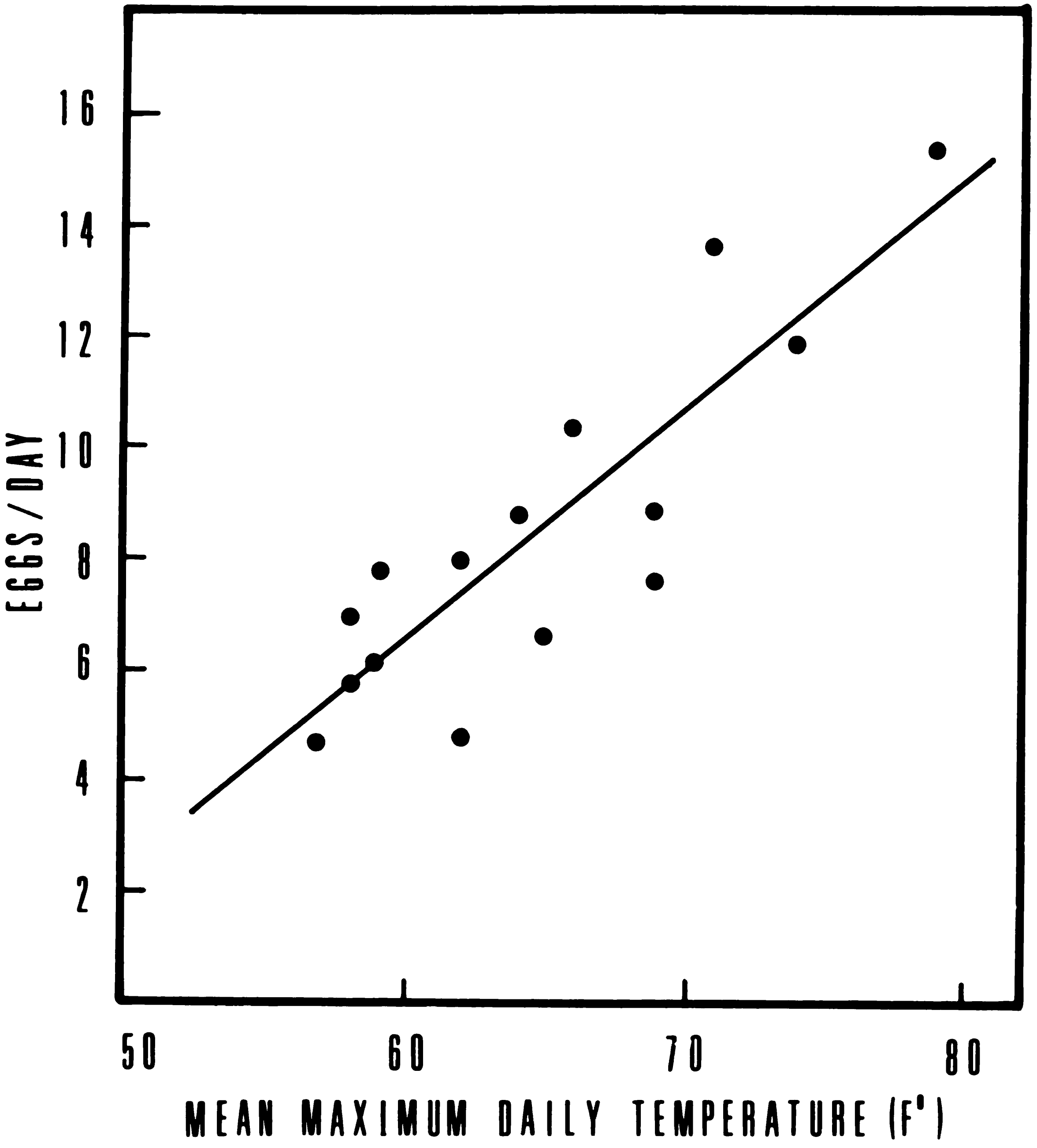

Figure 6. The relationship between egg production per female and maximum daily temperature in the cereal leaf beetle.

TABLE 2.

A COMPARISON OF FECUNDITY IN THREE POPULATIONS WITH DIFFERENT MEAN ELYTRAL LENGTH

	Galien	Gull Lake	East Lansing	F-value	Sign.
mean elytral length(mm)	3.648 ±.019†	3.705 ±.035	3.770 ±.017	7.76 2,37*	P<.01
		LABORATORY			
mean fecundity (eggs)	359.20 ±49.06	302.75 ±43.34	205.29 ±53.19	2.33 2,51*	P>.10
mean life span (days)	37.10 ±4.69	37.50 ±4.35	23.43 ±4.44	2.67 2,51*	P>.10
		FIELD			
mean fecundity (eggs)	53.07 ±5.13	54.31 ±5.49	60.77 ±5.32	0.59 2,152*	P>.10
mean life span (days)	30.66 ±2.59	29.86 ±2.54	34.85 ±2.38	1.07 2,152*	P>.10

*degrees of freedom

†± standard error

Adult size. Since studies of other insects have shown that fecundity decreases as female size decreases, it was hypothesized that there may be a similar relationship in the cereal leaf beetle. To test this the fecundity of three different populations, each with a different mean elytral length, was observed in the field and laboratory as described earlier. Table 2 shows that there was a significant difference in the mean elytral length of these three populations: East Lansing having the largest and Galien the smallest. The East Lansing population had the lowest fecundity. However, an analysis of variance showed that there was no significant difference in the mean fecundity of these three populations within the laboratory or field experiment. No difference could be shown using an analysis of variance of log transformed data or using a non-parametric test.

Adult survival. Survival of spring adults could be influenced by size. Since fecundity is also affected by the longevity of the female, the mean female life span of these three populations was compared. For convenience the origin of their life span was the first day of the experiment. All populations were collected and experiments started within a three day span. Table 2 shows that there was no significant difference in the mean female life span of the three populations either in the field or laboratory.

AGE SPECIFIC DEVELOPMENTAL RATES

Age specific developmental rates at various temperatures were required in the survival analysis of the field and caged populations. Although Yun (1967) gave estimates of total larval development at different temperatures, he did not quantify developmental rates by instar. Therefore, the number of days required for complete development of each larval instar of the cereal leaf beetle was followed in the laboratory at 60°F, 70°F and 80°F. Table 3 summarizes these data.

TABLE 3.

DEVELOPMENTAL TIME (IN DAYS) FOR INSTARS OF THE CEREAL LEAF BEETLE AT VARIOUS TEMPERATURES

Instars	Temperature		
	60°F	70°F	80°F
egg*	12.00	5.50	5.00
I	3.81 ± 0.36	2.55 ± 0.19	1.86 ± 0.21
II	5.33 ± 0.41	2.12 ± 0.23	1.71 ± 0.18
III	3.00 ± 0.46	1.87 ± 0.24	1.44 ± 0.16
IV	3.59 ± 0.44	2.00 ± 0.22	1.36 ± 0.16
Σ_L	16.24 ± 0.85	8.53 ± 0.34	5.91 ± 0.25

*Dickler (unpublished)

Although Davidson's (1944) logistic developmental equation is useful in describing developmental curves over a wide range of temperatures, the mean field temperatures affecting the larval cereal leaf beetle ranged from 62°F to 72°F so the corresponding developmental rates were read directly from the data plotted in Figure 7.

SURVIVAL ANALYSIS

Age class survivorship. In order to evaluate natural age specific mortality in the cereal leaf beetle the

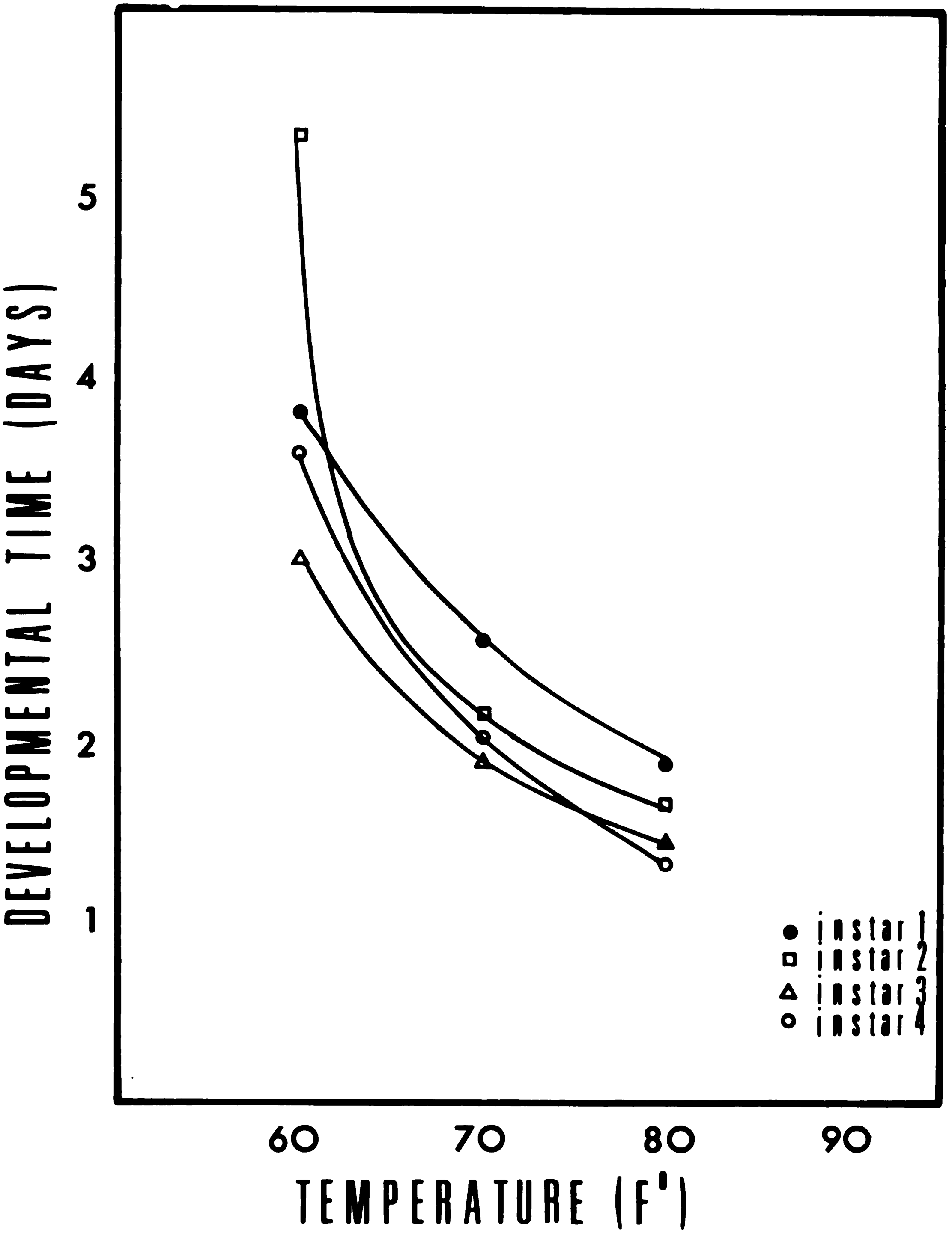

Figure 7. Temperature related developmental curves for the four instars of the cereal leaf beetle.

absolute density of each age class was estimated at frequent intervals in the field until all larvae had pupated. Tables 14 through 23 in the Appendix list these data and the descriptive statistics for the field and cage studies.

Since the age classes occur simultaneously over a relatively long period of time, a population curve for each age class was made by plotting the absolute densities from these tables against time, as in Figure 8.

The area under these curves is the total incidence of the age class during the census period. These values are listed for eggs and larvae at the end of Tables 14 through 23 in the Appendix. The actual number to enter an age class per sample unit was calculated by dividing the total incidence of that age class by its median developmental time. Developmental time was estimated by determining the average temperature to affect the age class during the generation and reading the corresponding developmental time in Figure 7.

When the total number entering each instar is known, survival for age class (x) may be calculated by dividing the number entering age class (x+1) by the number entering age class (x):

$$S_x = \frac{\#\text{ entering instar}_{x+1}}{\#\text{ entering instar}_x}$$

However, the total incidence method was not used for all age classes, so the specific survival analysis used for each age class is outlined below.

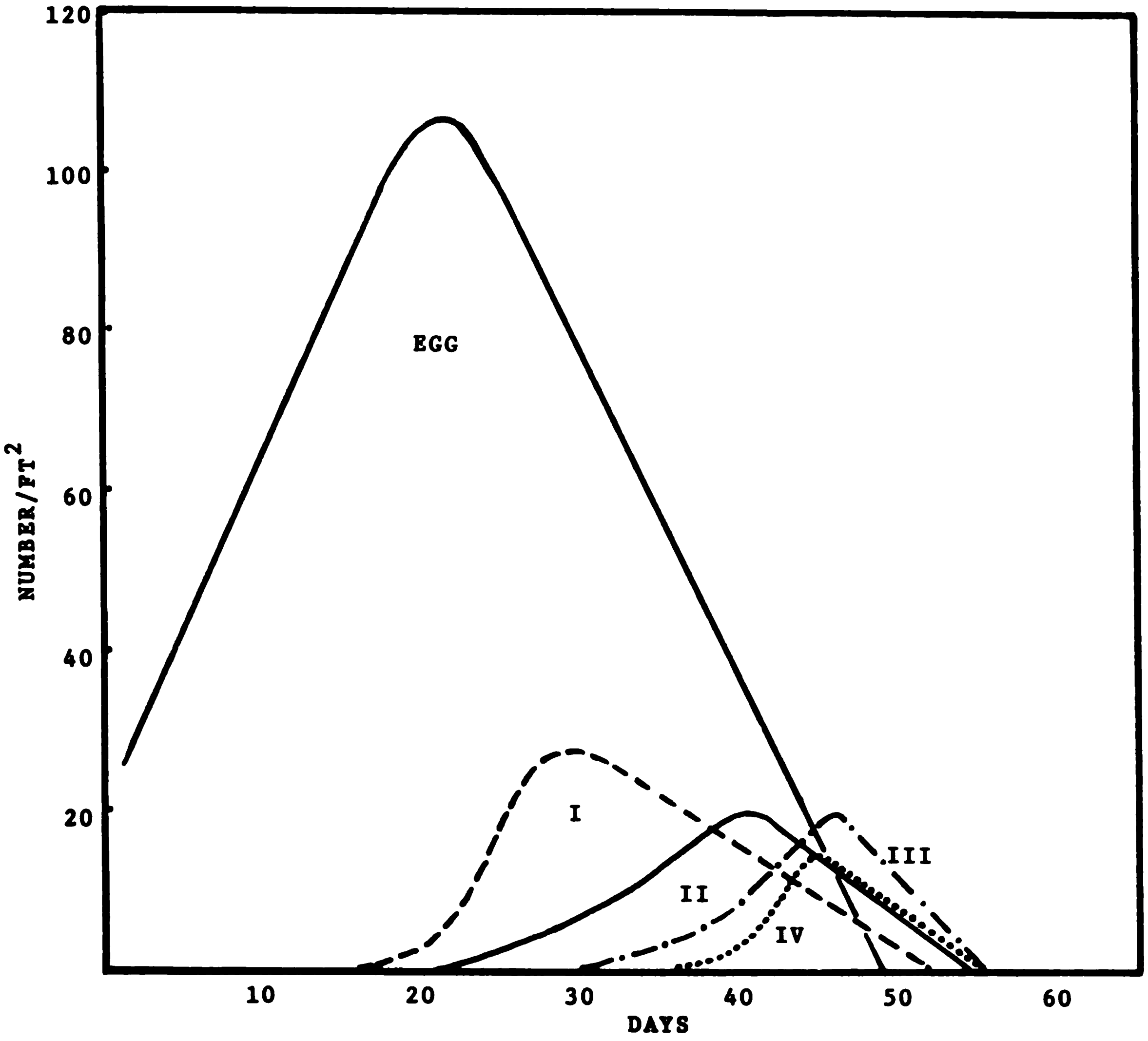

Figure 8. Population curves for egg and larvae of the cereal leaf beetle in Galien wheat, 1967.

Egg. The total number of eggs laid in a sample unit was measured directly in 1968 and 1969, but in 1967 the number laid per sample unit was calculated by the total incidence method. Survivorship of the egg was measured directly in the laboratory. As samples came into the laboratory for counting, eggs were placed in petri dishes on moist filter paper and incubated at 80°F. Results are presented in Table 4. Some mortality in Table 4 was unnatural because of dessication and fungal growth in a few petri dishes.

TABLE 4.

SURVIVORSHIP OF CEREAL LEAF BEETLE EGGS

Locality	Year	Host Plant	% Survival
Galien	1967	oats	85
		wheat	69
Gull Lake	1967	oats	93
		wheat	100
Galien	1968	both	91
Gull Lake	1968	both	78

Dickler (unpublished) found similar values for eggs laid in the laboratory.

For purposes of the survival analysis egg survival was accepted as a 90 percent constant.

First instar. The number of individuals entering instar I was calculated by multiplying the total number of eggs laid by egg survivorship or 0.90. The number entering instar I could also be calculated by dividing the total incidence of the first instar by its developmental time. However, using the formula below, the survival values of the first instar were plotted according to their egg densities along the median development line in Figure 9. A hypothetical distribution line was drawn from the origin of development to total development through the cluster of high density points on the median developmental line. This distribution suggests that mortality is high early in the instar at high densities. Therefore, the actual number entering the first instar (100% level in Figure 9) would be considerably underestimated using the total incidence method.

$$S_I = \frac{\text{total incidence II/dev. time II}}{\text{\# eggs} \times 0.90}$$

Second and third instar. Survivorship for these instars was calculated by the total incidence method outlined above:

$$S_{II} = \frac{\text{total incidence III/dev. time III}}{\text{total incidence II/dev. time II}}$$

$$S_{III} = \frac{\text{total incidence IV/dev. time IV}}{\text{total incidence III/dev. time III}}$$

Fourth instar. Survival of the fourth instar was calculated by dividing the total number to pupate by the total number to enter the fourth instar:

$$S_{IV} = \frac{\text{absolute density of pupae}}{\text{total incidence IV/dev. time IV}}$$

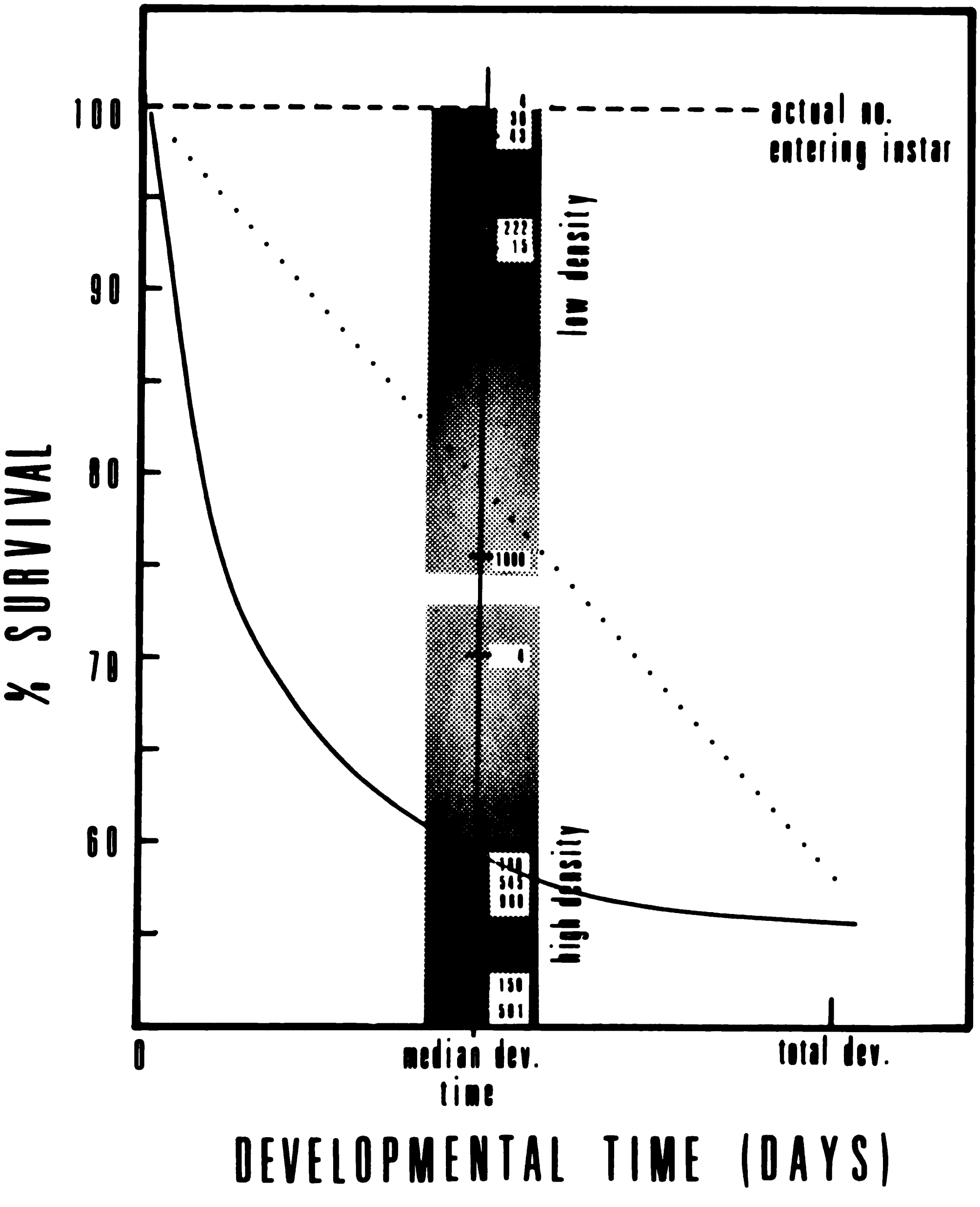

Figure 9. The distribution of first instar survival (solid line) calculated by the total incidence method. The survival values corresponding to egg density are plotted along the median line.

Pupae. Pupae were sampled after all larvae had entered the ground. Adult emergence prior to pupal sampling did not affect the estimate of absolute density because empty as well as full pupal cases were recovered. Pupal survivorship was calculated by dividing the absolute density of pupae into the absolute density of adults recovered in the emergence cages.

$$S_P = \frac{\text{absolute density of summer adults}}{\text{absolute density of pupae}}$$

Total larval survival. Total larval survival was calculated by dividing the absolute density of pupae by the absolute density of eggs:

$$S_L = \frac{\text{absolute density of pupae}}{\text{absolute density of eggs}}$$

Egg survival, included in this calculation, was defined as part of total larval survival. Although within-generation survival (i.e., the fraction surviving from egg to adult) is easily calculated by dividing the egg density by the adult density, the total larval mortality was of most interest in development of the population model.

The results of the preceding calculations for age specific survival in the field and cage studies are tabulated in Tables 5 and 6. Mortality, rather than survivorship, was used in these tables, but the transformation back to survivorship is simple ($S_x = 1-M_x$). There were two causes for the negative mortalities seen in these tables:

TABLE 5.

AGE SPECIFIC MORTALITY OF THE CEREAL LEAF BEETLE IN 1967, 1968 AND 1969 FIELD STUDIES

Location	Year	Crop	Total eggs*	AGE CLASS MORTALITY (X100)					
				I	II	III	IV	Total Larval	Pupal
Galien	69	W	150	28	22	41	89	97	00
		O	1005	37	43	35	61	92	41
	68	W	222	44	32	41	65	93	00
		O	960	63	36	34	65	95	48
	67	W	350	50	56	81	-53	95	00
		O	96	-7	33	73	1	85	45
Gull Lake	69	W	545	43	25	21	80	94	14
		O	591	40	22	-3	86	94	25
	68	W	4	59	38	30	25	88	55
		O	160	35	-1	27	25	68	51
	67	W	1	12	63	77	-58	73	56
		O	17	-76	53	57	23	78	67
East Lansing	69	W	30	-30	20	17	73	79	--
		O	43	-16	34	-17	58	66	21
	68	W	4	70	26	69	-50	79	--
		O	15	16	6	58	9	73	00
Mean					29.9	40.1			30.2
Standard error					4.7	7.1			6.5

*per square foot

TABLE 6.

AGE SPECIFIC MORTALITY OF THE CEREAL LEAF BEETLE IN THE 1969 CAGE DENSITY STUDY

Cage Number	Number Spring Adults	Total Eggs*	AGE CLASS MORTALITY (X100)					
			I	II	III	IV	Total Larval	Pupal
H1	5000	324	31	33	22	88	96	82
H2	5000	388	39	13	9	95	98	40
H3	5000	212	37	7	-15	88	92	76
K1	2000	226	5	-17	-8	60	56	89
K2	2000	236	43	-12	-7	72	56	93
K3	2000	196	28	-44	1	89	90	44
M1	500	80	-2	-72	-7	75	57	65
M2	500	64	29	-7	-12	65	48	79
M3	500	96	24	-77	-26	74	60	74
L1	100	36	-5	-49	-29	72	40	80
L2	100	15	-8	-8	-20	86	49	62
L3	100	19	-10	-115	-9	72	23	61

*per square foot

1) inaccurate estimate of age specific developmental time,
2) random sample error as mortality approaches zero, and
3) underestimates of total incidence (e.g., in some cases field sampling did not begin until third instar larvae were present, so the incidence of first and second instar larvae previous to this time was lost).

VARIANCE ANALYSIS OF TOTAL LARVAL MORTALITY

Variance of mortality in the field study. Total larval mortality ranged from 66% to 97% in the field studies. It was hypothesized that, of the factors that caused this variance, host plant and population density were the most significant.

Total larval mortality from Table 5 was classified by host plant and density in Table 7. Density was defined as the number of eggs laid per square foot in a sample plot; high = 201 to 1000 egg/ft^2 and low = 1 to 200 egg/ft^2. A two-way analysis of variance of the mortality in Table 7 showed that there was no significant difference in total larval mortality between host plants. However, there was a very significant difference in total larval mortality between the high and low densities. The influence of these broad density classifications on the conclusion of host plant difference will be considered later.

Variance of mortality in the cage study. Total larval mortality was also variable in the cage density study. All densities were observed in cages of oats in East Lansing at the same time so the variation caused by location, crop and time were removed. Within field variance was kept at a minimum by placing the cages six feet apart in a homogeneous area of the oat field.

TABLE 7.

TWO-WAY ANALYSIS OF VARIANCE OF % TOTAL LARVAL MORTALITY IN 1967-1969 CLB FIELD STUDY

Host Plant	Density	
	High	Low
Oats	92 95 94 -- --	85 68 78 66 73
Wheat	93 95 94 -- --	97 88 73 79 79
Source of Variance	F Value*	Significance
Host Plant	2.77	P>.10
Density	17.47	P<.01
Interaction	1.47	P>.10

*with 1,14 degrees of freedom

Therefore, it was hypothesized that the variability of total larval mortality was attributable to the differences in density from cage to cage. The densities in the 1969 cage density study were designated by the initial number of adults placed in each cage as described earlier: 5000 adults, 2000 adults, 500 adults, 100 adults. The total larval mortality values from Table 6 were classified according to these lettered densities in Table 8. A one-way analysis of variance of these values showed that there was a significant difference in total larval mortality amongst these four densities.

TABLE 8.

ONE-WAY ANALYSIS OF VARIANCE OF TOTAL LARVAL MORTALITY IN THE 1969 CAGE DENSITY STUDY

rep	Density			
	H	K	M	L
1	96	90	57	48
2	98	56	48	49
3	92	56	60	23

$F_{3,8} = 10.14$; $P<.01$

Relationship of host specific mortality to density. The results of the field and cage studies indicated that much of the variance in total larval mortality could be explained if the relationship between larval mortality and density was understood. Because of the convincing laboratory studies discussed earlier it was hypothesized that there was a linear relationship between density and larval mortality.

In order to investigate this hypothesis total larval mortality in wheat and oats was plotted against the total number of eggs laid per square foot for each population in the field and cage studies (Figure 10). It was shown earlier that there was no significant difference in total larval mortality between oats and wheat. However, upon closer inspection of Table 7 it was discovered that the broad classification of high and low density used to test this hypothesis masked a real survival difference in the two host plants. Figure 10 shows that total larval mortality in wheat was higher than in oats over all densities. Figure 10 also shows that total larval mortality is a linear function of the logarithm of density and increases with increasing density.

VARIANCE OF AGE SPECIFIC MORTALITY

The components of total larval mortality must be analyzed separately in order to understand the relationship between mortality and density. The simplest hypothesis to explain this relationship is that mortality in each instar increases as density increases.

It is important to first investigate the relative importance of mortality in each instar to the variance of total larval mortality. Table 9 shows the correlation analysis between total larval mortality and instar mortality from the field study (Table 5) and cage study (Table 6). The negative mortality values of the fourth instar in Table 5 were adjusted to zero for this analysis because the total incidence of the fourth instar, in these cases, was underestimated due to very long sample intervals (in the 1967 field study, Table 5). From this analysis it appears that the first and fourth instar were the most highly correlated with and account for 29% to 68% of the variance of total larval mortality in the field and cage studies (Table 9).

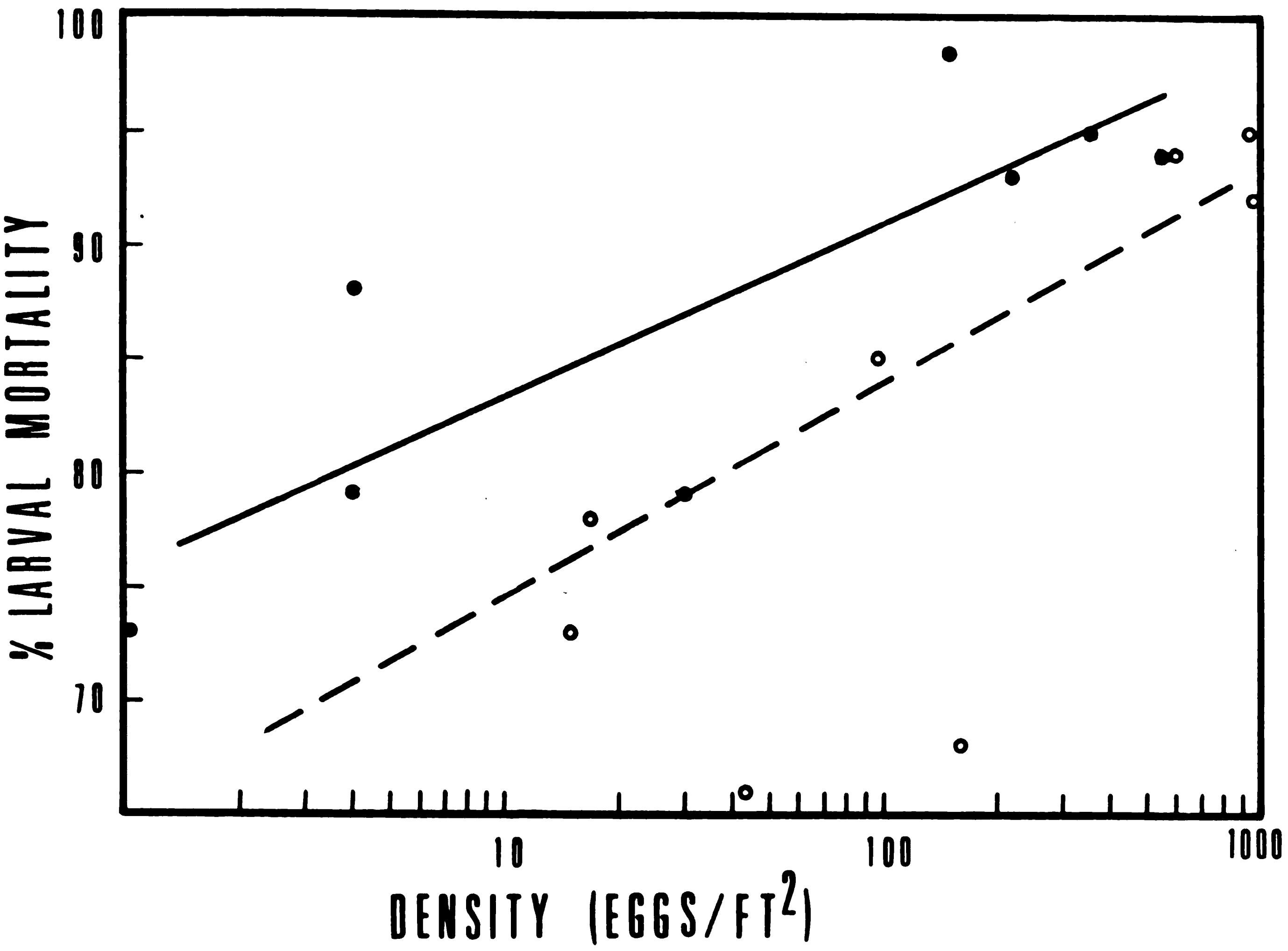

Figure 10. The relationship of host-specific larval mortality and density in the field study.

TABLE 9.

CORRELATION ANALYSIS BETWEEN INSTAR AND TOTAL LARVAL MORTALITY IN THE CEREAL LEAF BEETLE

Age Class	r^2	Significance
Field		
I	0.29	$.01<P<.05$
II	0.04	$P>.10$
III	0.003	$P>.10$
IV	0.20	$.05<P<.10$
Cage		
I	0.68	$P<.01$
II	0.43	$.01<P<.05$
III	0.40	$.01<P<.05$
IV	0.56	$P<.01$

However, even though these instars may be significantly correlated with total larval mortality, it does not directly follow that their mortality increases with increasing density nor that the relationship is linear. For this reason the relationship between first and fourth instar mortality and density from the field study (Table 5) was investigated in Figure 11. On an arithmetic density scale the relationship between mortality and density was curvilinear. These curves were not fitted mathematically. The first and fourth instar curves were essentially similar except the magnitude of mortality was higher in the fourth than in the first. A logarithmic transformation (common logs) of density removed the curved characteristic of the lines in Figure 11 and produced an essentially linear relationship between mortality and density (Figure 12). The transformation shows that mortality in these two instars increased linearly with an increase in log density, except for the fourth instar in the cage study.

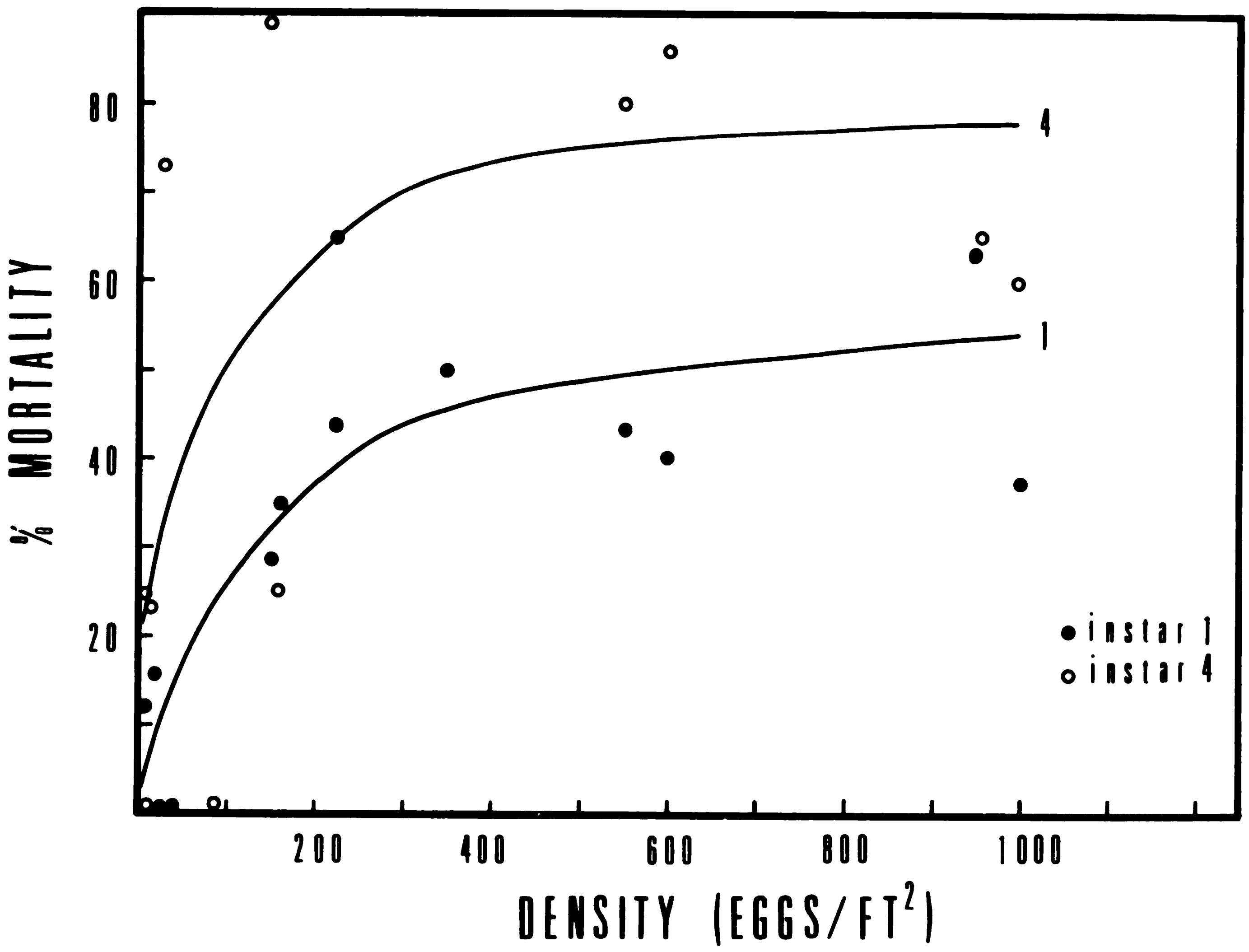

Figure 11. The relationship between density and mortality in the first and fourth instar of the field study. Closed circles represent first instar. Open circles represent fourth instar.

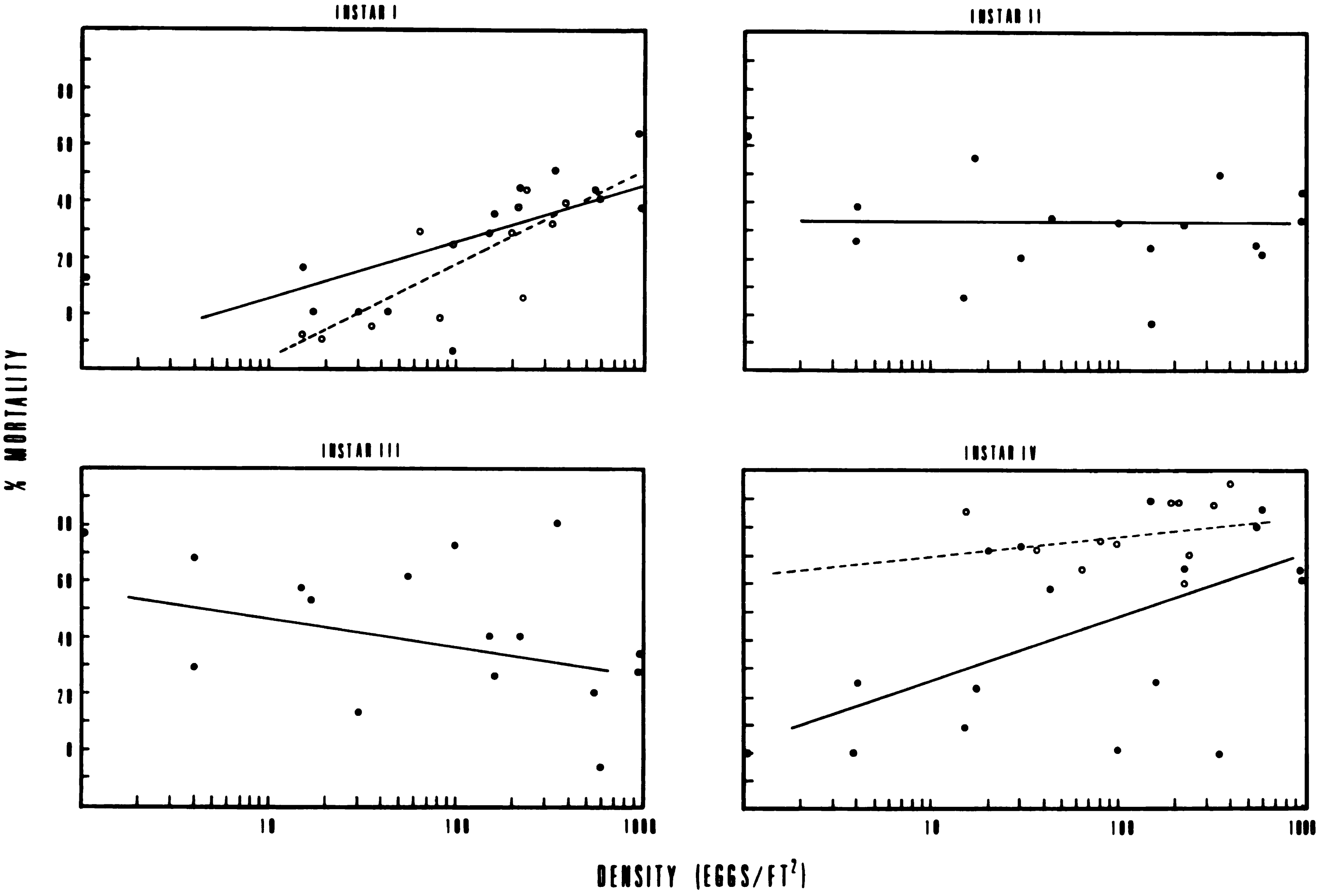

Figure 12. The relationship between percent mortality and log density in each larval instar of the cereal leaf beetle. The open circles in A and D represent the 1969 cage study.

The relationship between log density and mortality was also graphed for the second and third instar in Figure 12. However, data from the cage study was not used because sampling problems caused gross underestimation of second and third instar mortality. These lines show that second instar mortality is relatively constant over all densities in the field. There is a slight tendency for third instar mortality to decrease with increasing density. Regression and correlation statistics of the graphs in Figure 12 are listed in Table 10.

TABLE 10.

THE RELATIONSHIP BETWEEN INSTAR MORTALITY AND LOG_{10} DENSITY IN THE CEREAL LEAF BEETLE

Age Class	a	b	r^2	Sign.
Field				
I	-14.1	19.4	0.51	$P<.01$
II	30.8	0.004	0.008	$P>.10$
III	58.8	-10.0	0.11	$P>.10$
IV	6.7	21.3	0.26	$.05<P<.10$
Cage				
I	-50.3	33.7	0.65	$P<.01$
IV	64.9	6.5	0.08	$P>.10$

Only the correlations between log density and first instar mortality were significant at greater than the 1% probability level in the field and cage studies. In the cage study as much as 65% of the variance in first instar mortality could be accounted for by density.

Figure 13 shows that relationship between age specific mortality and density in oats and in wheat. There is no difference between host plants and no significant correlation between density and mortality in the second and third instar (Table 11). However, Table 11 shows that 67% and 56% of the variance in first instar mortality could be explained by density in oats and wheat respectively. In the fourth instar the slopes were similar in both host plants but mortality was 30% higher in wheat than in oats. Table 11 shows that 48% and 66% of the variance in fourth instar mortality could be explained by density in oats and wheat respectively.

TABLE 11.

THE RELATIONSHIP BETWEEN DENSITY AND AGE CLASS MORTALITY CLASSIFIED BY HOST PLANT IN THE FIELD STUDY

Instar	coefficient of determination (r^2)	
	Oats	Wheat
I	0.67*	0.56*
II	0.01	0.10
III	0.16	0.09
IV	0.48*	0.66*

*Significant correlation: $P<.01$

MODEL OF WITHIN-GENERATION SURVIVORSHIP

Within-generation survival (S_{WG}) was defined as that fraction of the population which survived from the egg to the adult. In the cereal leaf beetle this includes survival within the egg, four larval instars and pupa. The equation proposed earlier serves as a generalized model for within-

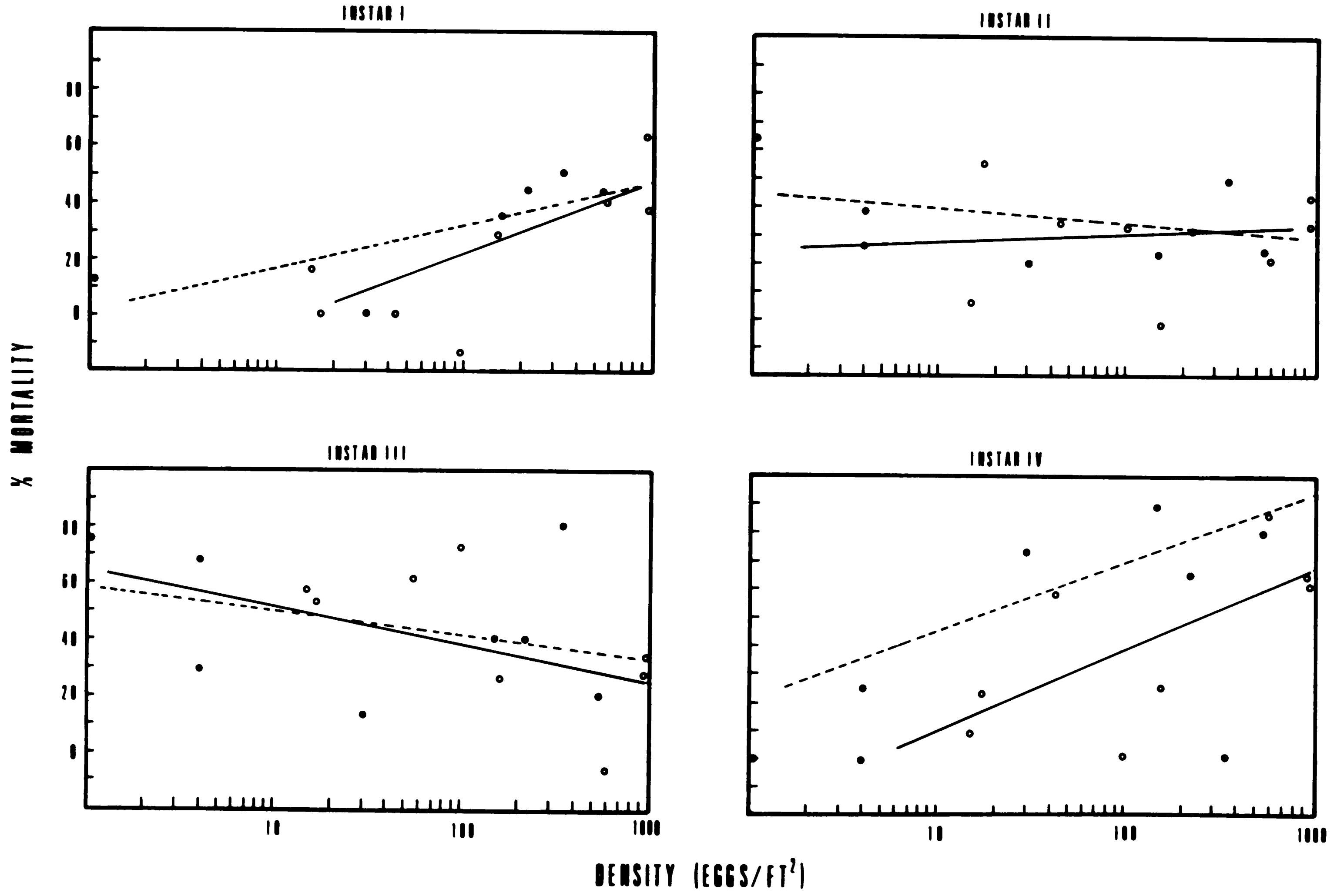

Figure 13. The relationship between percent mortality and log density in each larval instar of the cereal leaf beetle.

generation survivorship of the cereal leaf beetle:

$$S_{WG} = S_E \cdot S_I \cdot S_{II} \cdot S_{III} \cdot S_{IV} \cdot S_P$$

Survivorship in the egg, second instar and pupa were constant, with random variance, over all densities:

S_E = 0.90 (from laboratory results)
S_{II} = 0.68 (from field study)
S_P = 0.70 (from field study)

However, survivorship in the first, and fourth instars varied predictably with density and host plant. The regression statistics from Figure 13 were used to form regression equations for field populations which would predict S_I, S_{IV} at the densities and host crops studied. The regression statistics were divided by 100 to transform them from percent to fractional values:

$$\begin{aligned} S_{I(oats)} &= 1-(-.31 + .26 \log x) \\ S_{I(wheat)} &= 1-(.02 + .15 \log x) \\ S_{IV(oats)} &= 1-(-.11 + .26 \log x) \\ S_{IV(wheat)} &= S_{IV(oats)} + .30 \end{aligned}$$

where, x is the density in total eggs per square foot

when these components are combined the two-factor model takes this form:

$$\begin{aligned} S_{G(oats)} &= (0.9)\cdot(1-(-.31+.26 \log x))\cdot(0.70)\cdot(0.60)\cdot \\ &\quad (1-(-.11+.26 \log x))\cdot(.70) \\ S_{G(wheat)} &= (0.9)\cdot(1-(.02+.15 \log x))\cdot(0.70)\cdot(0.60)\cdot \\ &\quad (S_{IV(oatsP} +.30)\cdot(.70) \end{aligned}$$

Although total within-generation survivorship was measured, only the accuracy of the most dynamic portion of the model, total larval mortality, need to be tested. Pupal mortality was considered constant. Using the same type of model, total larval survivorship (including egg survival) was calculated as:

$$S_L = S_E \cdot S_I \cdot S_{II} \cdot S_{III} \cdot S_{IV}$$

Figure 14 shows the predictive value of this model. The observed values are from the field study and the calculated values from the above model, using the density values in Table 5.

A regression analysis of the observed and calculated total larval mortality showed that host plant and density accounted for 63% of the variance in total larval mortality. Climate, locality, time of planting and sample error probably account for most of the remaining 37%. However, only sixteen populations were studied over the three year study period and any attempt to factor mortality beyond host plant and density would lead to very tenuous results.

The analysis of the relationship between observed and calculated total larval mortality, in Figure 14, indicates that the calculated mortality at low densities is consistently overestimating the observed, but approaches reality at higher densities.

Another weakness of the model is that it lacks the feature of time. It treats age classes as total entities and does not explain the interactions of age classes as

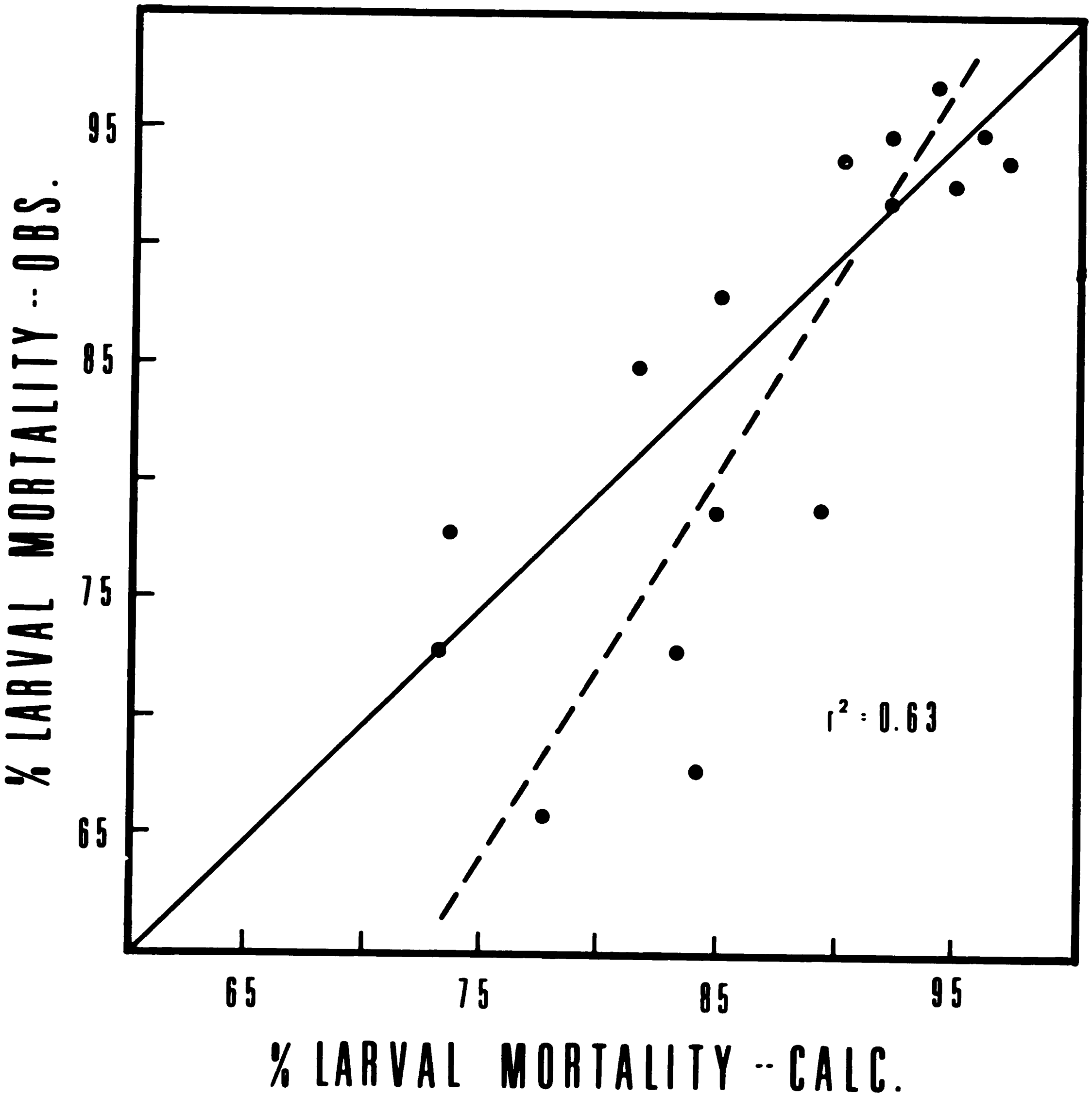

Figure 14. Comparison of observed and calculated total larval mortality of the cereal leaf beetle using the two-factor model.

they progress in time. At high densities the probability of survival for a first instar is greater early in May when there are no other instars present than in June when second, third and fourth instar larvae are feeding. Also, developmental time is faster at warmer temperaturres later in the generation so exposure to physical mortality factors is less than for instars occurring early in the generation.

QUALITATIVE EFFECTS OF DENSITY

Aside from the strictly numerical relationship of mortality and density, qualitative changes in the population can result from the effects of density. The mean elytral length and dry weight of 30 emerging female adults from different populations was plotted against the logarithm of density of that population, in Figure 15. The graph shows that the mean elytral length and dry weight of the female cereal leaf beetle decreases as log density increased. The same results were seen in emerging male adults, although males were generally smaller. These results account for the difference in mean elytral length for beetles from Galien, Gull Lake and East Lansing in the fecundity experiment. The relationship between density and larval head capsule size and dry weight was also investigated. Unfortunately, the larval samples were taken from each study area at one point in time and were not representative of the total instar population.

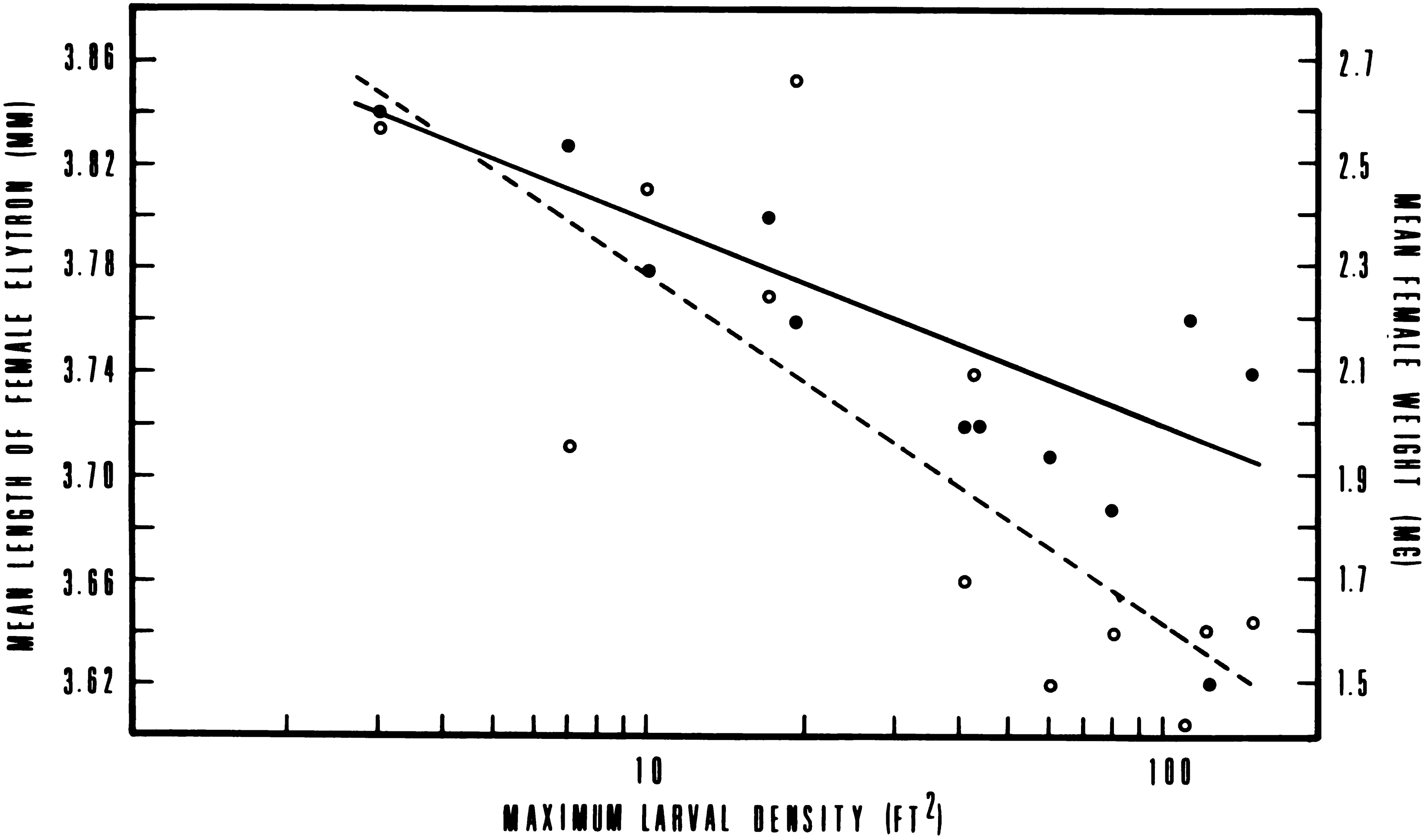

Figure 15. The relationship between mean weight and mean elytron length of the emerging adult female cereal leaf beetle and its preceding maximum larval population.

DISCUSSION

SURVIVAL ANALYSIS

Accurate estimation of age specific survivorship for the cereal leaf beetle depended on: 1) an accurate census of the population density at frequent intervals throughout the generation, and 2) selection of an appropriate method to analyze these census data.

Sampling. The relatively high variances in Table 13 through 21, in the Appendix, indicated that the distribution of eggs and larvae was not random in wheat and oats. In populations with an aggregate distribution, the ratio of variance to mean always exceeds one and as the density increases this ratio increases (Lewis and Taylor 1967). Figure 2 (in Methods section) shows this relationship for the cereal leaf beetle, and the problems of sampling this aggregate distribution were discussed in Methods and Materials. The sampling design for the field study was designed to maintain the standard error at 10% of the mean. However, the sample size needed to maintain this ratio at low densities was too large to be efficient. A sample size was selected that maintained the SE at 10% of the mean for all densities above ten organisms per square foot. Consequently, inflated standard errors were expected at low densities. A review of Tables 13 through 21 shows that below densities

of 5 organisms/ft^2 standard errors rose as high as 200% of the mean.

Also, the type of sampling used in the field study inherently underestimated survival because a constant percentage of individuals were lost as square foot samples were clipped in the field, packed in plastic bags and then unpacked again for laboratory counting.

The sample design proved to be very efficient for estimating the absolute density of the various age classes in the populations at all but low densities.

The most significant errors in the cage study were instar determination and the onset of sampling. If sampling began after eclosion the incidence of organisms previous to this time was missed and the total incidence curve was underestimated. Instar determination was more difficult in the cage study because individuals could not be disturbed and therefore could not be viewed at close range. However, this error was constant and did not affect the relationship of mortality factors and survivorship.

<u>Analytical methods.</u> Richards and Waloff (1954) showed that when a population has a well defined peak after which no recruitment takes place, the fall-off in numbers is the mortality rate of that population. When the regression of this fall-off is extended back to the origin (the time when the stage was first found) the Y-intercept is the number of organisms actually entering that age class. Biologically, the method has much appeal because it is easily interpreted: the extension of the regression line is merely the reversal

of mortality to its origin. However, the method was not adequate for this study because peaks were not well defined, (see Figure 8) and in many cases the regression would be calculated from only three or four points.

Richards *et al.*, (1960) reasoned that the total incidence (N) of an age class (expressed as instar-days) was the integral of the daily survival rate over the duration of that age class times the number entering that age class.

$$N = n\int_{o}^{a} k^{t}\,dt = \frac{n(k^{a}-1)}{\ln k}$$

If no mortality occurred then the total incidence would be equal to the developmental interval times the number entering the age class (N = an). Therefore, the ratio of N, (observed in the field) and, an, (calculated) is an expression of mortality. Unfortunately, the method is very sensitive to the accuracy of developmental time interval and an error of one half day affected the estimate of mortality as much as 30% (Table 12).

TABLE 12.

MORTALITY OF 1st INSTAR IN GALIEN WHEAT, 1967

Developmental Time	Mortality	
	Richards	Southwood
2.5	0.423	0.555
3.0	0.595	0.465
3.5	0.873	0.400

Since the standard error of the developmental times in Table 3 was as much as one half day at lower temperatures the method was considered inefficient.

Dempster's (1961) method of treating census data as a series of simultaneous equations, with the unknowns as daily mortalities of each instar seemed to be the most mathematically sound. However, an accurate estimate of the fraction of the total number of eggs to hatch during the sample interval and the number of pupae at each sampling was required. Pupal density was not measured at each sampling, and egg hatch could only be inferred from the loss of eggs during each sample interval.

Southwood's (1966) total incidence method, presented in detail earlier, was the most appropriate analytical technique for this study. Only a reasonable estimate of developmental time and density for each age class were required. The accuracy of this method did not depend on the peak or regression of the population curve as did Richard and Waloff's method. Also, Table 12 shows that the accuracy of Southwood's total incidence method is less affected by the accuracy of the estimate of developmental time than Richards, Waloff and Spadbury's method.

The accuracy of estimating the number entering an instar by the total incidence method did depend on the distribution of mortality within each age class. The number of organisms to reach the median age of an age class is estimated by dividing the total incidence of the age class by its mean developmental line. When mortality is constant during the developmental period (Figure 16a) or heavy at the beginning of the period (Figure 16b) the total incidence method will significantly underestimate the total number entering the age class. When mortality is heavy at the end of the developmental period (Figure 16c) the method closely approximates the total number entering that age class. It has already been shown in the results how heavy mortality early in the first instar affected the estimate of the number entering the first instar. There is no way to check the distribution of mortality in the other instars. For the analysis it had to be assumed that this distribution had little affect on the survival analysis. This assumption will have to be tested in future research.

Accuracy of the total incidence method also depends on the magnitude of mortality during the age class. The age distribution of a population with a five day developmental period is uniform when subject to no mortality. However, when this population is subject to a mortality rate of 20% per day or a total of 67% the age distribution is skewed so that the frequency of younger individuals is higher than that of the older individuals. This shifts the median age from 2.5 days to 1.75 days. In the total incidence method the total incidence is divided by the median developmental time because the occurrence of an individual is redundant in a census that is more frequent than the individuals developmental time. With no mortality median developmental time is an accurate index of redundancy. However, when the age distribution is skewed by heavy mortality the median developmental time is too large and, hence, underestimates the number entering the instar. Table 12 shows that in

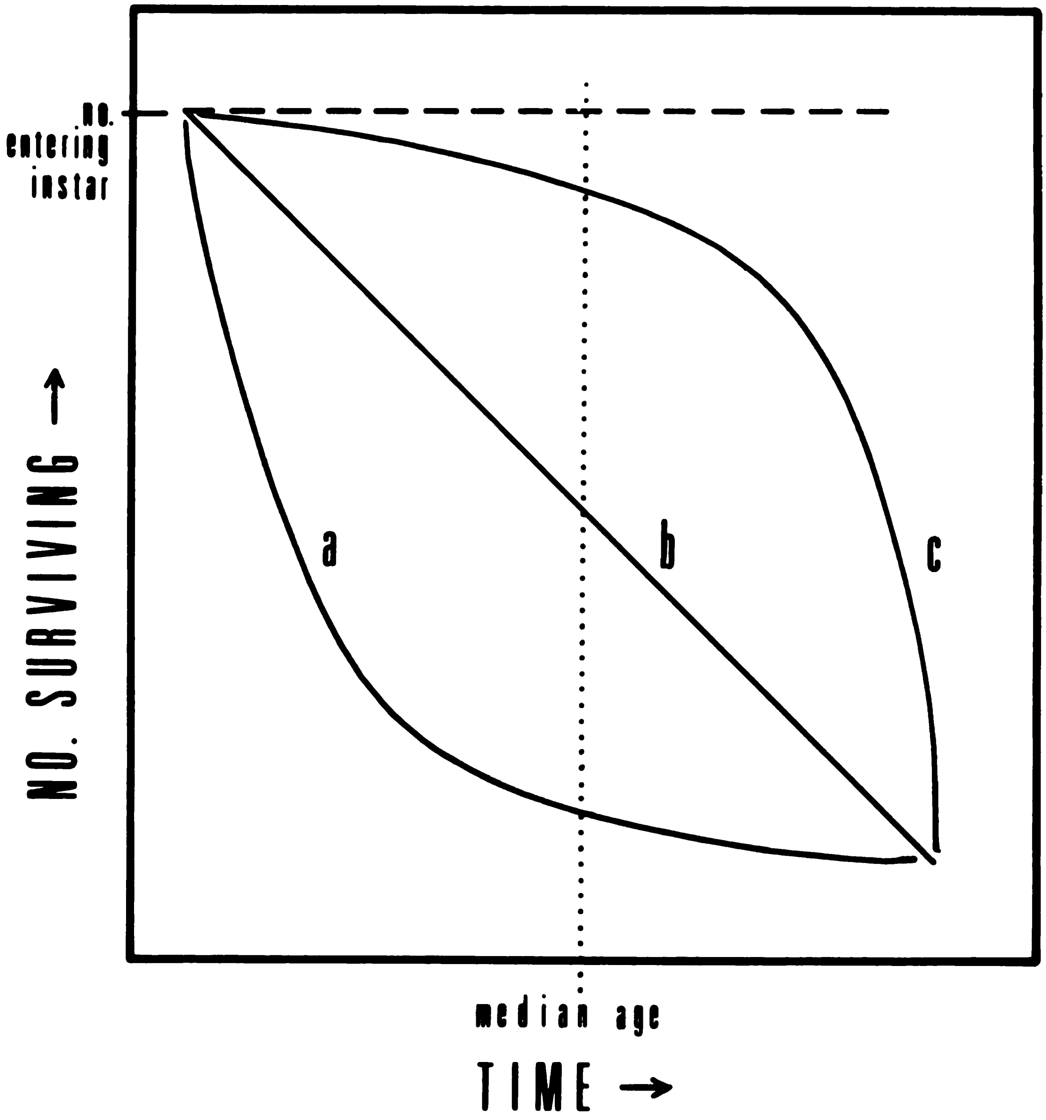

Figure 16. Distribution of survival in a hypothetical instar a) constant, b) heavy at onset, c) heavy at end.

Southwood's method an error of one-half day can affect the estimate of mortality as much as 9% in the first instar larvae from Galien wheat, 1967. However, from Figure 13, it appears that this bias in the developmental time would be most significant in the fourth instar when total mortality exceeds 80% at high densities. If competition for some resource is occurring in this instar then it is possible that the developmental time is prolonged and this error is not as great.

FACTORS AFFECTING WITHIN-GENERATION SURVIVAL

Cage study. The cage study was designed to remove as many variables from total larval survival as possible in order to test the hypothesis of density-dependent mortality. A review of the curves in Figure 12 shows that total larval mortality was lower in the cage study than in the field study at low densities. This decrease in mortality was attributable to a decrease in generation time, and protection from extreme weather conditions. Cage populations developed much more quickly than field populations because they were established in a warmer part of the season. The faster development left less time for mortality factors to operate, thus lowering mortality in each age class. Since the contribution to age specific mortality by each of the above factors is not quantified, the importance of each of these factors can only be inferred.

Parasities and predators. The influence of predators and parasities on within-generation survivorship was considered insignificant. No parasites were recovered from some 20,000 larvae reared in the laboratory in 1967. Although several species of coccinellids were found in both oats and wheat, it is believed there major prey was aphids.

Physical environment. Total larval mortality is decreased 25% at low densities by modification of mortality factors in the cage study. Since predators and parasites were not important mortality factors, physical factors probably accounted for this 25%. However, the difference in wind velocity, rain impact and solar radiation inside and out of the cage was not measured. There was no difference in temperature, but humidity was 10% to 20% higher in the cage. In the field both wind and rain are physically damaging and at times can wash or brush an individual from the host plant. The larva is not always successful in getting back to the plant. Once on the ground it is exposed to ground predators (i.e., carabids and spiders) and disease agents. High evaporation because of low humidity and high wind can desiccate a larva during eclosion or ecdysis.

Host plant. Figure 10 shows that total larval mortality is about 10% higher in wheat than in oats. The lines in this figure were not mathematically fitted. Since larvae feed only on the leaf surface of the grain plant, the leaf surface area of oats and wheat were compared. To avoid the confusion as to what actually constitutes a single grain plant the amount of leaf tissue per stem was compared in these two host plants. There was an average of 50 stems per square foot in both wheat and oats. The leaf surface area of 30 oat stems and 30 wheat stems was calculated after the plants had matured. There was a total of 4780 ± 160 mm^2 ($S_{\bar{x}}$) of leaf surface area on an average oat stem and only 3400 ± 120 mm^2 ($S_{\bar{x}}$) on an average wheat stem, or 70% of that in oats. Also, the first leaf developed on a wheat plant usually yellows and withers early in the history of the population. Therefore, there was less food available to the developing larvae in wheat than in oats. There could also be a difference in food quality between oats and wheat. However, the nutritional requirements of the cereal leaf beetle and available nutrients in wheat and oats will have to be investigated to establish the importance of food quality.

Population density. The laboratory studies, reviewed by Andersen (1957), investigated the relationship between mortality and density under entirely artifical conditions. The conclusions in these studies are restricted by assumptions, such as uniform age classes, so they cannot be tested in or applied to natural populations. The relationships between density and mortality measured in this study are completely applicable to natural populations of the cereal leaf beetle.

The relationship between total larval mortality and density was demonstrated in Figure 10. Total larval mortality increases linearly with an increase in the logarithm of density. This relationship can be interpretted as a density-dependent feedback system which could regulate the cereal leaf beetle population similar to the model described earlier:

$$\Delta N = N_o R \left(1 - \frac{N_o}{N_{max}} \right)$$

where $(1 - N_o/N_{max})$ is a constraint on the reproductive rate defined by the population density (N_o) and the carrying capacity (N_{max}) which is probably most influenced by the difference in host plants (see Figures 10 and 13).

The relationship of mortality and log density in the cereal leaf beetle does not agree with Andersen's (1957) conclusion that mortality is a linear function of initial density. However, his conclusion was based on laboratory populations with uniform age classes. Instars occur simultaneously in the cereal leaf beetle. Thus, the two conclusions are not necessarily contradictary.

It is obvious at this point that a single life table for the cereal leaf beetle is not really possible because survival in the larval age class is dependent on host plant and population density. For this reason the dynamics of the cereal leaf beetle was expressed in the form of a model dependent on these two factors.

WITHIN-GENERATION DYNAMICS

Fecundity. Results of the fecundity experiment showed that the size of the female had no influence on egg production. Also, there was no relationship between females size and egg size. Therefore, reduction in the size of adults at high densities, shown in Figure 15, would not affect fecundity of the cereal leaf beetle in the following generation. Most experiments that showed a decrease in fecundity as female size decreased involved lepidopterous or dipterous species that depended on a large fat store, from larval feeding, for egg production. These species do little feeding as adults and the feeding they do is inconsequential to egg production. It is possible, since the cereal leaf beetle feeds throughout the ovipsoitional period and derives the energy for egg production from this feeding that fecundity is not a function of size.

In the laboratory, under optimal conditions the average Galien female laid 360 eggs with a standard error ($S_{\bar{x}}$) of 50 eggs (Table 2). This was assumed to be the potential fecundity of the cereal leaf beetle. In the field fecundity experiment (Table 2) only one sixth of this potential was realized where the fecundity of the Collins Road population was 60 eggs with a standard error ($S_{\bar{x}}$) of 5 eggs per female. Several factors, such as food, quality and cage effects could be responsible for this decreased fecundity. However, Figure 6 suggests that temperature was probably the most significant factor reducing fecundity in the field fecundity experiment was related to temperature.

Temperature certainly affects egg production over short periods of time, but the cereal leaf beetle lays eggs over an eight week interval. The mean temperatuare from year to year over a two month period tends to be very similar, so temperature would not account for much variance in fecundity.

As Yun (1967) observed crowding of females can reduce fecundity in the cereal leaf beetle. Figure 17 shows that above a certain density of spring adults, in the 1967 cage study, fecundity began to decrease. A similar trend was seen in the 1968 and 1969 cage study. However, the values in these studies are not comparable because the populations were started at different times. In the high density cages (20/ft^2) it was observed that there was a much higher proportion of adults resting on the walls of the cages indicating an interaction between adults. However, this factor was not considered an important influence on fecundity because the density of spring adults has never been recorded in excess of 5 to 7/ft^2, even in the highest density areas. Some behavioral mechanism must limit spring adult density because as the season progressed the adult density in oats remained fairly constant until the end of May. The beetles produce an audible sound which could be involved in regulation of adult densities. However, the behavior of the cereal leaf beetle must be studied before this interpretation can be proven. Obviously, as adults died in the oat field new ones moved in to take their places, but never in excess of a certain maximum density. Food at these densities is definitely not a limiting factor in fecundity.

In fact, this density is so closely regulated that, if wheat and oats are treated as one population, the number of eggs laid per square foot in the combined population was almost identical in the three high density populations studied:

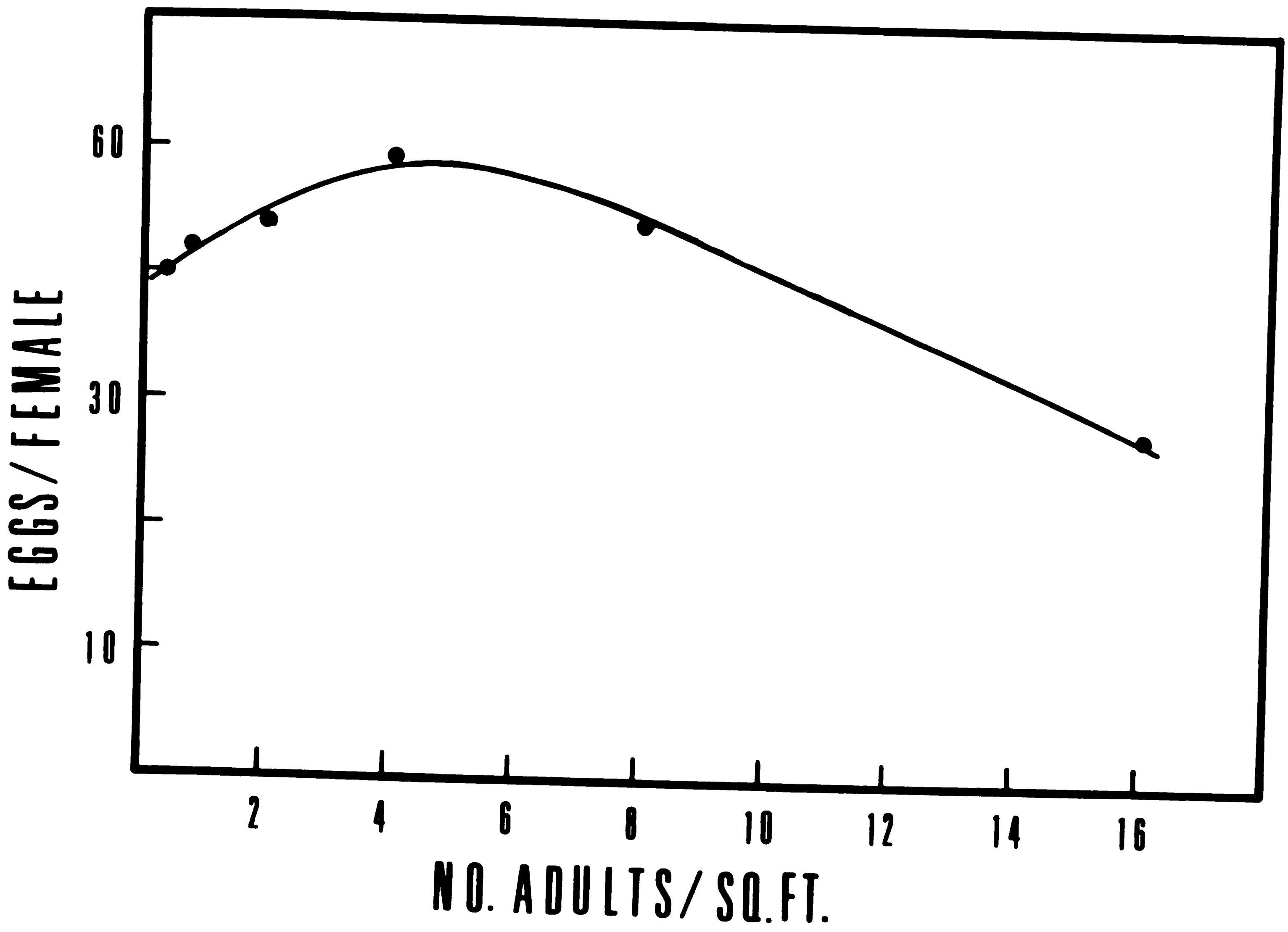

Figure 17. Effect crowding on fecundity of CLB in 1967 cage study.

Galien 1968 - 1182/ft^2
1969 - 1155/ft^2
Gull Lake 1969 - 1136/ft^2

The egg density at high densities could also be a function of the available oviposition sites, or number of stems per unit area. However, field and laboratory observations suggest that, although the beetle prefers to lay eggs on the leaf surface near the node, they will lay eggs on any green tissue on the plant. If some form of regulation is taking place it adds another dimension to the regulatory features of the cereal leaf beetle.

Egg mortality. There is no reason to suspect any relationship between the density of eggs and egg mortality. Dickler (unpublished) showed that the egg can undergo extreme temperature changes without increased mortality. The eggs are so well attached to the leaf surface that wind cannot dislodge them. Humidity might have an important influence on egg mortality, but this has not yet been shown. Perhaps the greatest climatic mortality factor in eggs is "puddling" of water and soil at the leaf nodes where eggs are often placed. Water collects at these nodes during rains and drowns the egg, at times causing from 1-2% mortality (by observation). The egg is preyed upon by some coccinellids but their contribution to mortality is so small and variable it is difficult to quantify. Aphids are the preferred food of these coccinellids and they apparently turn to CLB eggs only when aphids are not available. There is absolutely no evidence of egg cannibalism by larvae or adults.

Incubation of healthy field collected eggs showed that egg mortality was approximately 10%. The low intensity of mortality factors just discussed indicates that the 0.90 survival used in the model for eggs is liberally realistic.

First instar mortality. Early survivorship of the first instar larva depends largely upon successful establishment within the first few minutes after eclosion. Heavy mortality early in the development of the first instar, discussed earlier, indicates the importance of this critical period. Climatic conditions and physical condition of the leaf area surrounding the egg are probably the major factors affecting establishment. In the laboratory at 80°F and 70% R.H. approximately 2% of the larvae encountered mechanical difficulties and died as they were leaving the egg. However, inspection of Figure 13 shows that mortality of the first instar in oats is relatively low until the egg density approaches $20/ft^2$. So, the importance of density-dependent factors is very small. Mortality began to increase above densities of 20 $eggs/ft^2$ in oats and 2 $eggs/ft^2$ in wheat. It was noticed that the first instar larva always fed on a small area of leaf near the egg immediately after eclosion and then moved to a new area to feed. If this feeding is critical, then, as the density rises, the chance of disturbance of the area around the egg increases and the probability of establishment decreases. Also, as egg density increases the female is forced to lay eggs in sites less favorable for eclosion and establishment. Figure 9 shows that there was a large amount of mortality early in the development of the first instar at high densities which supports this explanation.

Since the fourth instar was the only other age class to have a strong correlation with density it was thought there might be some relationship between mortality of first instar larvae and fourth instar larvae. However, no such relationship was detectable.

First instar mortality could be very important in the population management of the cereal leaf beetle. If establishment is critical, as suggested earlier, mortality throughout the range of densities studied could be intensified by a feature of the host plant, such as a thicker or more dense upper cuticle, or a more sclerotic leaf tissue. However, before research on such features in host plant resistance can be investigated, the actual mechanism involved in the density-dependent mortality of the first instar must be investigated. Also, an effective predator or parasite of small larvae that responds well numerically would intensify mortality over the density range. Removing the larvae early would relieve the number reaching the fourth instar where most growth and feeding occurs.

Second and third instar mortality. These larvae are well established and difficult to dislodge from the plant. However, migrations from leaf to leaf and plant to plant intensifies during these two instars and thus they are exposed to an increased risk of falling from or being shook from the plant. Also, a certain percent encounter mechanical difficulties during ecdysis.

There is not much difference between host plants in the third instar, but a very interesting relationship exists between density and mortality of third instar larvae. Mortality decreases as log density (x), in eggs/ft^2, increases. Intense selection for highly competitive individuals (hardy individuals) during the first instar might explain this phenomenon. However, it must be emphasized that the correlation between density and third instar mortality is not significant in either host plant so this phenomenon may not be real. Also, if selection for hardy individuals is increasing with density this negative trend shoudl be detected in the second instar as well.

Fourth instar mortality. In Figure 13, mortality increased linearly with an increase in the logarithm of density in the fourth instar, as it did in the first instar. These two instars are responsible for the density-dependent feedback system explained earlier. However, the factors responsible for density-dependent mortality in these two instars appear to be different. Unfortunately, the factors responsible for larval mortality were not measured and can only be inferred from field data.

The large weight gain in the fourth instar suggests that competition for food is responsible for density-dependent mortality in this instar. The average dry weight of a third instar larva from the 1967 Gull Lake oat population was 0.50 mg and that of the fourth instar was 2.17 mg. If it takes the same amount of food to add a unit of body weight in the fourth instar as it does in the third, then the fourth instar had to eat three times as much as the three preceding instars. The developmental time of the fourth instar is approximately the same as that in each of the preceding instars, so competition for food probably becomes critical in this age class. In fact, feeding becomes so intense at high densities that on several occasions it was observed that relatively undamaged oat or wheat plants were defoliated in a 24 hour period and desiccated fourth instar larvae appeared to be dying on defoliated plants.

The relationship between mortality and density, in Figure 13, is similar for both host plants except at any given density mortality in wheat is 30% higher than in oats. If competition for food is important in the fourth instar then the 30% lower amount of leaf surface in wheat probably accounts for this difference in mortality.

Density could be expressed as the total number entering an instar, as well as total eggs per unit area. Therefore, the relationship of density and mortality in each instar was investigated using the number entering each instar as the density. The relationship between mortality and density was the same in all instars as it was by expressing density as the total number of eggs laid. However, there was an interesting shift in the correlation of density and mortality in the fourth instar. When density is expressed as the total number of eggs 66% (Table 10) of the variation in fourth instar mortality can be explained by density in wheat. However, if density is expressed as the number of fourth instar larvae only 28% of the variation in fourth instar mortality can be explained by density in wheat. This suggests that the densities of previous instars have a considerable affect on fourth instar survival. An opposite trend is seen in oats. When density is expressed as total number of eggs, only 48% (Table 10) of the variation in fourth instar mortality in oats is explained by density. But when density is expressed by the number of fourth instar larvae 71% of the variance in fourth instar mortality can be explained by density. The increased correlation when the number of fourth instars and mortality was analyzed indicates the densities in previous instars had little influence on fourth instar mortality. The decreased correlation for the same analysis in wheat indicates that, perhaps because of the smaller leaf surface in wheat, densities in previous instars influenced fourth instar mortality significantly.

If competition for food is important in the fourth instar a logical population management technique would be to intensify this competition by manipulation of plant nutrition and quantity. However, the exact nature of fourth instar density-dependent mortality must be described before such techniques can be considered. Any attempt to decrease the density of the fourth instar by predators or partial chemical control would alleviate this competition and enhance survival of the fourth instar larvae. Perhaps the most promising control agent would be a parasite that completes development in the pupa of the cereal leaf beetle. The parasite egg is placed in a third or fourth instar larva and does not kill the beetle until it reaches the pupal stage. Mortality related to competition for food is allowed to function normally. Mortality from parasitism is added to that in the preceding fourth instars.

CONCLUSIONS

Fecundity and mortality contribute to the numerical population changes within a generation of the cereal leaf beetle. This change is not a constant factor among populations.

In the field fecundity is a linear function of temperature between 55°F and 75°F. Egg production is not influenced by changes in adult size. Although fecundity decreases when adult densities exceed ten beetles per square foot in a cage, these densities are never reached in the field. Thus, fecundity has a somewhat constant influence among populations of the cereal leaf beetle.

However, larval mortality varies among populations. Density-dependent mortality, caused by intraspecific competition, accounts for most of the variation of within-generation survival of the cereal leaf beetle in wheat and oats. Mortality in the first and fourth instar is a linear function of the logarithm of total egg density. Establishment of the first instar appears to become more difficult as density increases because leaf surface disturbance and interference with larger larvae increases. Competition for food probably accounts for the increase in mortality of the fourth instar as density increases. There is 30% less available leaf tissue in a unit area of wheat than oats and fourth instar mortality is 30% higher in wheat than in oats. Egg survival, survival in the second and third instar and pupal survival are constant with respect to density and host plant.

The cereal leaf beetle has the requisite for pupulation regulation -- a density-dependent feedback system. Whether regulation is actually occurring in local populations is open to question because winter survival of field adults has not been accurately measured. The total number of eggs laid per unit area was constant in high density areas. However, spring adult behavior may be density-dependent so that adults are forced to emigrate if they enter a field with a certain maximum density. Whether the loss in numbers is due to emigration and/or winter mortality, a very effective regulation of numbers is taking place in local populations.

Since the population dynamics of the cereal leaf beetle have been quantified population control measures can be directed at a strategic stage in the development of the population. Mortality can be intensified at that stage which is most vulnerable to control measures. For example, density-dependent mortality in the first instar might be intensified by modification of the leaf cuticle and by predation and parasitism. Predation of fourth instar larvae would most likely enhance survival of the fourth instar and intensify feeding. However, a parasite completing development in the cereal leaf beetle pupa would not disrupt the density-dependent mortality of the fourth instar, but would intensify within-generation mortality. Manipulation of host plant quality and quantity could also intensify density-dependent mortality in the fourth instar.

Although numerical change within the generation of cereal leaf beetle populations has been quantified, the factors causing this mortality have not been established. The factors causing density-dependent mortality in the first and fourth instar must be investigated. Also, the nutritional requirements of the cereal leaf beetle and the nutritional levels of its host plants must be studied in relation to beetle survival. Egg laying behavior of the cereal leaf bettle could be important in regulation of fecundity, but it is relatively unknown. The effect of mortality on the age distribution and better estimates of developmental time must be investigated to support the survival analysis used in this study.

LITERATURE CITED

Andersen, F. S. 1957. The effect of density on the birth and death rate. Annual Report. 1954-55. Govt. Pest. Inf. Lab. (Spring forbi, Denmark). 26 pp.

Andrewartha, H. G. and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press. Chicago. 782 pp.

Birch, L. C. 1957. The role of weather in determing the distribution and abundance of animals. Cold Spring Harbor Symposium. 22:203-218.

__________. 1948. The intrinsic rate of natural increase of an insect population. J. Animal. Ecol. 17:15-26.

Bøggild, O. and J. Keiding. 1958. Competition on house fly larvae. Experiments involving a DDT-resistant and a susceptible strain. Oikos. 9:1-25.

Castro, T. R., R. R. Ruppel and M. S. Gomulinski, M. S. 1965. Natural history of the cereal leaf beetle in Michigan. Mich. Agr. Expt. Sta., Michigan State University Quart. Bull. 47:623-653.

Chapman, R. N. 1928. The quantitative analysis of environmental factors. Ecology. 9:111-122.

Cole, L. C. 1957. Sketches of general and comparative demography. Cold Spring Harbor Symposium. 22:1-15.

Davidson, J. 1944. On the relationship between temperature and the rate of development of insects at constant temperatures. J. Animal Ecol. 13:26-38.

Deevey, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.

Dempster, J. P. 1961. The analysis of data obtained by regular sampling of an insect population. J. Animal Ecol. 30:429-432.

Dickler, E. 1968. The influence of temperature on the survival and development of cereal leaf beetle (*Oulema melanopus* (L.)) eggs and adults. Cereal Leaf Beetle Project Report. Michigan State University.

Embree, D. G. 1965. The population dynamics of the winter moth in Nova Scotia, 1954-1962. Mem. Entomol. Soc. Can. No. 46. 57 pp.

Greenbank, D. O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. I. The role of climate. Can. J. Zool. 34:453-476.

Harcourt, D. G. 1964. Population dynamics of *Leptinotarsa decimlineata* (Say) in eastern Ontario: II. Population and mortality estimation during six age intervals. Can. Entomologist. 96:1190-1197.

__________. 1963. Population dynamics of *Leptinotarsa decimlineata* (Say) in eastern Ontario: I. Spatial pattern and transformation of field counts. Can. Entomologist. 95:813-820.

__________. 1962. Design of a sampling plan for studies on the population dynamics of the imported cabbage worm, *Pieris rapae* (L.) (Lepidoptera: Pieridae). Can. Entomologist. 94:849-858.

__________. 1961a. Design of a sampling plan for studies of the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). Can. Entomologist. 93:820-831.

__________. 1961b. Spatial pattern of the imported cabbage worm, *Pieris rapae* (L.) Lepidoptera: Pieridae) on cultivated cruciferae. Can. Entomologist. 93:945-951.

Hughes, R. D. 1963. Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). J. Animal Ecol. 32:393-424.

Howard, L. O. and W. F. Fiske. 1911. The importation into the United States of parasites of the gipsy moth and the brown-tail moth. Bull. U. S. Bur. Ent. No. 91: 312 pp.

Ives, W. G. H. 1964. Problems encountered in the development of life tables for insects. Proc. Entomol. Soc. Manitoba. 20:34-44.

Kiritani, K. and F. Nakasuji. 1967. Estimation of the stage specific survival rate in the insect population with overlapping stages. Res. Popul. Ecol. 9:143-152.

Klomp, H. 1962. The influence of climate and weather on the mean density level, the fluctuations and the regulation of animal populations. Archives Neerlandaises de Zool. 15:68-109.

Kostitzin, V. A. 1939. Mathematical Biology. Harrap. London.

LeRoux, E. J., *et al.* 1963. Population dynamics of agricultural and forest insect pests. Mem. Entomol. Soc. Can. No. 32. 103 pp.

Lewis, T. and L. R. Taylor. 1967. Introduction to experimental ecology. Academic Press. London. 400 pp.

Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins. Baltimore. Reprinted by Dover Publications, 1956. 465 pp.

Lyons, L. A. 1964. The spatial distribution of two pine sawflies and methods of sampling for the study of population dynamics. Can. Entomologist. 96:1372-1407.

Merritt, D. L. 1967. Mortality of the cereal leaf beetle within pupal cells. Proc. North Central Branch, Entomol. Soc. Amer. 22:97-97.

Milne, A. 1957. The natural control of insect populations. Can. Entomologist. 89:193-213.

Morris, R. F. 1963. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. No. 31. 332 pp.

__________. 1960. Sampling insect populations. Ann. Rev. Entomol. 5:243-264.

__________. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. Can. J. Zool. 33:225-294.

Morris, R. F. and C. A. Miller. 1954. The development of life tables for the spruce budworm. Can. J. Zool. 32:283-301.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Australian J. Zool. 2:9-65.

__________. 1933. The balance of animal populations. J. Animal Ecol. 2:132-178.

Pearl, R., T. Park and J. Miner. 1941. Experimental studies on the duration of life. XVI. Life tables for the flour beetle, *Tribolium confusum* Duval. Am. Naturalist. 75:5-19.

Richards, O. W. 1961. The theoretical and practical study of natural insect populations. Ann. Rev. Entomol. 6:147-162.

Richards, O. W., N. Waloff and J. P. Spadbury. 1960. The measurement of mortality in an insect population in which recruitment and mortality widely overlap. Oikos. 11:306-310.

Richards, O. W. and N. Waloff. 1954. Studies on the biology and population dynamics of British grasshoppers. Anti-Locust Bulletin. 17:1-182.

Scuthwood, T. R. E. 1966. Ecological methods: with particular reference to the study of insect populations. Metheun and Co. London. 391 pp.

Thompson, W. R. 1956. The fundamental theory of natural and biological control. Ann. Rev. Entomol. 1:379-402.

__________. 1939. Biological control and the theories of interactions of populations. Parasitology. 31:299-388.

Turnbull, A. L. and D. A. Chant. 1961. The practice and theory of biological control of insects in Canada. Can. J. Zool. 39:697-753.

Ullyett, G. C. 1950. Competition for food and allied phenomena in sheep blow-fly populations. Phil. Trans. Roy. Soc. London. Ser. B. 234:77-174.

Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. Accad. Lincei. Ser. 6. 2:31-112.

Watt, K. E. F. 1961. Mathematical models for use in insect pest control. Can. Entomologist. Supp. 19. 62 pp.

Wellington, W. G. 1954. Atmospheric circulation processes and insect ecology. Can. Entomologist. 86:312-333.

Wigglesworth, V. B. 1965. The principles of insect physiology. 6th. ed. Methuen and Co. London. 741 pp.

Yun, Y. M. 1967. Effects of some physical and biological factors on the reproduction, development, survival and behavior of the cereal leaf beetle, *Oulema melanopus* (L.) under laboratory conditions. Ph.D. thesis. Michigan State University. 153 pp.

APPENDIX

TABLE 13.

1967 CLB FIELD STUDY

GALIEN

wheat

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total
18 Apr	$\bar{X}$	2.70	0.00	0.00	0.00	0.00	0.00	2.70
	SD	1.05	0.00	0.00	0.00	0.00	0.00	1.05
	SE	0.33	0.00	0.00	0.00	0.00	0.00	0.33
26 Apr	$\bar{X}$	6.20	0.00	0.00	0.00	0.00	0.00	6.20
	SD	2.79	0.00	0.00	0.00	0.00	0.00	2.79
	SE	0.88	0.00	0.00	0.00	0.00	0.00	0.88
03 May	$\bar{X}$	39.74	0.00	0.00	0.00	0.00	0.00	39.74
	SD	17.59	0.00	0.00	0.00	0.00	0.00	17.59
	SE	5.56	0.00	0.00	0.00	0.00	0.00	5.56
09 May	$\bar{X}$	56.23	0.00	0.00	0.00	0.00	0.00	56.23
	SD	20.46	0.00	0.00	0.00	0.00	0.00	20.46
	SE	6.47	0.00	0.00	0.00	0.00	0.00	6.47
17 May	$\bar{X}$	108.93	0.00	0.00	0.00	0.00	0.00	108.93
	SD	25.60	0.00	0.00	0.00	0.00	0.00	25.60
	SE	8.09	0.00	0.00	0.00	0.00	0.00	8.09
23 May	$\bar{X}$	178.96	0.00	0.00	0.00	0.00	0.00	178.96
	SD	48.37	0.00	0.00	0.00	0.00	0.00	48.37
	SE	15.29	0.00	0.00	0.00	0.00	0.00	15.29
31 May	$\bar{X}$	100.47	26.69	7.36	0.66	0.02	0.00	135.20
	SD	55.59	27.04	6.78	0.79	0.07	0.00	80.26
	SE	17.58	8.55	2.14	0.25	0.02	0.00	25.38
08 Jun	$\bar{X}$	41.62	14.89	41.44	16.17	2.16	0.00	116.28
	SD	13.09	4.86	15.57	4.77	1.14	0.00	24.71
	SE	4.14	1.54	4.92	1.51	0.36	0.00	7.81
15 Jun	$\bar{X}$	13.57	0.31	2.24	6.41	2.08	0.00	24.62
	SD	8.24	0.37	1.91	2.32	1.78	0.00	9.06
	SE	2.61	0.12	0.62	0.73	0.56	0.00	2.86
22 Jun	$\bar{X}$	11.86	0.02	0.07	0.12	0.22	0.00	12.29
	SD	6.39	0.04	0.18	0.21	0.66	0.00	6.00
	SE	2.02	0.01	0.05	0.07	0.21	0.00	1.89
22 Jun	$\bar{X}$	00.00	0.00	0.00	0.00	0.00	57.04	57.04
	SD	0.00	0.00	0.00	0.00	0.00	30.38	20.38
	SE	0.00	0.00	0.00	0.00	0.00	6.44	6.44
Total Incidence		1057.00	246.00	206.00	137.00	37.00	--	--

oats

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total
24 May	$\bar{X}$	43.08	0.00	0.00	0.00	0.00	0.00	43.08
	SD	22.27	0.00	0.00	0.00	0.00	0.00	22.27
	SE	7.04	0.00	0.00	0.00	0.00	0.00	7.04
31 May	$\bar{X}$	58.90	9.34	0.00	0.00	0.00	0.00	68.24
	SD	36.87	6.49	0.00	0.00	0.00	0.00	43.08
	SE	11.66	2.05	0.00	0.00	0.00	0.00	13.62
08 Jun	$\bar{X}$	41.23	15.58	12.84	0.44	0.00	0.00	70.10
	SD	20.11	11.03	8.18	0.48	0.00	0.00	30.80
	SE	6.36	3.49	2.59	0.15	0.00	0.00	6.96
15 Jun	$\bar{X}$	9.96	6.64	12.66	11.93	2.98	0.00	44.17
	SD	5.19	3.13	6.77	6.02	2.16	0.00	19.04
	SE	1.64	0.98	2.14	1.90	0.69	0.00	6.02
22 Jun	$\bar{X}$	3.30	0.47	2.66	56.90	1.99	0.00	14.73
	SD	2.47	0.31	1.35	6.32	1.06	0.00	7.29
	SE	0.78	0.10	0.43	1.21	0.34	0.00	2.31
30 Jun	$\bar{X}$	0.73	0.07	0.11	0.19	0.12	0.00	1.22
	SD	0.72	0.08	0.09	0.17	0.14	0.00	0.89
	SE	0.23	0.02	0.03	0.05	0.05	0.00	0.28
30 Jun	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	28.91	28.91
	SD	0.00	0.00	0.00	0.00	0.00	19.66	19.66
	SE	0.00	0.00	0.00	0.00	0.00	6.22	6.22
Total Incidence		3876.00	307.00	350.00	156.00	29.00	--	--

GULL LAKE

wheat

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Tota
27 Apr	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	0.00	0.10
	SD	0.16	0.00	0.00	0.00	0.00	0.00	0.16
	SE	0.05	0.00	0.00	0.00	0.00	0.00	0.05
08 May	$\bar{X}$	0.79	0.00	0.00	0.00	0.00	0.00	0.79
	SD	0.49	0.00	0.00	0.00	0.00	0.00	0.49
	SE	0.15	0.00	0.00	0.00	0.00	0.00	0.15
16 May	$\bar{X}$	1.63	0.00	0.00	0.00	0.00	0.00	1.63
	SD	0.93	0.00	0.00	0.00	0.00	0.00	0.93
	SE	0.29	0.00	0.00	0.00	0.00	0.00	0.29
02 Jun	$\bar{X}$	0.42	0.50	0.17	0.00	0.00	0.00	1.09
	SD	0.38	0.47	0.13	0.00	0.00	0.00	0.75
	SE	0.12	0.15	0.04	0.00	0.00	0.00	0.24
12 Jun	$\bar{X}$	0.09	0.06	0.42	0.13	0.02	0.00	0.72
	SD	0.11	0.11	0.56	0.15	0.05	0.00	0.77
	SE	0.04	0.03	0.18	0.05	0.01	0.00	0.24
21 Jun	$\bar{X}$	0.43	0.00	0.00	0.02	0.01	0.00	0.47
	SD	0.70	0.00	0.00	0.05	0.04	0.00	0.72
	SE	0.22	0.00	0.00	0.01	0.01	0.00	0.23
28 Jun	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	0.78	0.78
	SD	0.00	0.00	0.00	0.00	0.00	1.20	1.20
	SE	0.00	0.00	0.00	0.00	0.00	0.38	0.38
Total Incidence		16.00	0.80	2.50	0.90	0.20	--	--

oats

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total
02 Jun	$\bar{X}$	0.63	0.01	0.00	0.00	0.00	0.00	0.64
	SD	0.86	0.04	0.00	0.00	0.00	0.00	0.89
	SE	0.27	0.01	0.00	0.00	0.00	0.00	0.28
12 Jun	$\bar{X}$	10.27	3.90	5.98	1.43	0.00	0.00	21.58
	SD	6.22	2.21	4.00	0.96	0.00	0.00	11.64
	SE	1.97	0.70	1.26	0.30	0.00	0.00	3.68
21 Jun	$\bar{X}$	10.81	2.12	2.10	1.44	0.54	0.00	17.02
	SD	4.66	1.14	0.80	0.77	0.84	0.00	4.72
	SE	1.48	0.36	0.25	0.24	0.26	0.00	1.49
28 Jun	$\bar{X}$	3.08	0.72	0.79	0.70	0.69	0.00	5.97
	SD	1.11	0.37	0.49	0.39	0.59	0.00	2.06
	SE	0.35	0.12	0.16	0.12	0.79	0.00	0.65
06 Jul	$\bar{X}$	3.49	0.12	0.53	0.69	0.56	0.00	5.40
	SD	1.93	0.13	0.23	0.49	0.32	0.00	2.47
	SE	0.61	0.04	0.07	0.15	0.10	0.00	0.78
06 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	7.24	7.24
	SD	0.00	0.00	0.00	0.00	0.00	2.39	2.39
	SE	0.00	0.00	0.00	0.00	0.00	0.76	0.76
Total Incidence		181.00	44.00	58.00	28.00	12.00	--	--

TABLE 14.

1968 GALIEN FIELD STUDY

wheat

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
23 Apr	X̄	18.93	0.00	0.00	0.00	0.00	0.00	18.93	0.00
	SD	8.68	0.00	0.00	0.00	0.00	0.00	8.68	0.00
	SE	1.58	0.00	0.00	0.00	0.00	0.00	1.58	0.00
30 Apr	X̄	52.07	0.00	0.00	0.00	0.00	0.00	52.07	42.40
	SD	20.35	0.00	0.00	0.00	0.00	0.00	20.35	15.25
	SE	3.72	0.00	0.00	0.00	0.00	0.00	3.72	4.82
07 May	X̄	78.37	0.03	0.00	0.00	0.00	0.00	78.40	35.80
	SD	25.14	0.18	0.00	0.00	0.00	0.00	25.19	17.49
	SE	4.59	0.03	0.00	0.00	0.00	0.00	4.60	5.53
14 May	X̄	106.50	3.33	0.03	0.00	0.00	0.00	109.87	63.80
	SD	38.51	3.83	0.18	0.00	0.00	0.00	40.48	27.91
	SE	7.03	0.70	0.03	0.00	0.00	0.00	7.39	8.83
16 May	X̄	82.93	9.80	1.80	0.00	0.00	0.00	94.53	24.80
	SD	37.48	7.99	1.71	0.00	0.00	0.00	42.09	7.74
	SE	6.84	1.46	0.31	0.00	0.00	0.00	7.68	2.45
19 May	X̄	79.13	24.80	2.63	0.00	0.00	0.00	106.57	4.00
	SD	28.09	10.61	2.47	0.00	0.00	0.00	35.47	3.97
	SE	5.13	1.94	0.45	0.00	0.00	0.00	6.48	1.26
22 May	X̄	69.80	15.70	6.13	0.00	0.00	0.00	91.63	14.30
	SD	21.23	6.86	4.49	0.00	0.00	0.00	26.49	6.85
	SE	3.88	1.25	0.82	0.00	0.00	0.00	4.84	2.17
24 May	X̄	92.67	25.67	7.57	1.47	0.00	0.00	127.37	7.70
	SD	27.45	11.44	5.16	1.43	0.00	0.00	38.28	5.68
	SE	5.01	2.09	0.94	0.26	0.00	0.00	6.99	1.80
27 May	X̄	57.63	21.10	9.43	1.03	0.00	0.00	89.20	10.80
	SD	15.88	9.51	5.08	1.40	0.00	0.00	21.52	7.07
	SE	2.90	1.74	0.93	0.26	0.00	0.00	3.93	2.24
30 May	X̄	61.67	20.00	18.40	6.50	0.83	0.00	107.40	8.60
	SD	21.64	10.41	10.34	4.12	1.15	0.00	36.30	5.06
	SE	3,95	1,90	1,89	0,75	0.21	0.00	6,63	1.60
02 Jun	X̄	39.17	18.60	12.50	6.07	1.67	0.00	78.07	5.60
	SD	28.48	8,26	7.28	4.73	1.99	0.00	42.97	4.84
	SE	5.20	1.51	1.33	0.86	0.36	0.00	7.85	1.53
05 Jun	X̄	25.63	10.20	11.87	16.20	15.37	0.00	79.27	1.10
	SD	12.96	7.21	5.20	9.48	10.61	0.00	24.07	1.52
	Se	2.37	1.32	.95	1.73	1.94	0.00	4.39	0.48
30 May	X̄	61.67	20.00	18.40	6.50	0.83	0.00	107.40	8.60
	SD	21.64	10.41	10.34	4.12	1.15	0.00	36.30	5.06
	SE	3.95	1.90	1.89	0.75	0.21	0.00	6.63	1.60
02 Jun	X̄	39.17	18.60	12.50	6.07	1.67	0.00	78.07	5.60
	SD	28.48	8.26	7.28	4.73	1.99	0.00	42.97	4.84
	SE	5.20	1.51	1.33	0.86	0.36	0.00	7.85	1.53
05 Jun	X̄	25.63	10.20	11.87	16.20	15.37	0.00	79.27	1.10
	SD	12.96	7.21	5.20	9.48	10.61	0.00	24.07	1.52
	SE	2.37	1.32	0.95	1.73	1.94	0.00	4.39	0.48
08 Jun	X̄	7.70	10.83	16.80	19.30	10.73	0.00	65.37	0.80
	SD	7.01	7.27	7.54	7.20	7.18	0.00	21.67	1.48
	SE	1.28	1.33	1.38	1.31	1.31	0.00	3.96	0.47
11 Jun	X̄	0.53	1.80	5.87	8.77	6.10	0.00	65.37	0.00
	SD	1.36	1.86	3.15	5.51	4.67	0.00	10.15	0.00
	SE	0.25	0.34	0.57	1.01	0.85	0.00	1.85	0.00
14 Jun	X̄	0.13	0.43	1.60	2.90	1.17	0.00	6.23	0.00
	SD	0.43	0.77	1.79	2.41	1.74	0.00	3.88	0.00
	SE	0.08	0.14	0.33	0.44	0.32	0.00	0.71	0.00
17 Jun	X̄	0.10	0.17	0.47	1.03	1.37	0.00	3.13	0.00
	SD	0.31	0.38	1.17	1.40	1.67	0.00	2.87	0.00
	SE	0.06	0.07	0.21	0.26	0.31	0.00	0.52	0.00
20 Jun	X̄	0.00	0.00	0.00	0.00	0.00	15.71	15.71	0.00
	SD	0.00	0.00	0.00	0.00	0.00	4.75	4.75	0.00
	SE	0.00	0.00	0.00	0.00	0.00	1.50	1.50	0.00
Total Incidence		2887	467	278	189	112	--	--	220

oats

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
30 Apr	X̄	32.43	0.00	0.00	0.00	0.00	0.00	32.43	0.00
	SD	15.91	0.00	0.00	0.00	0.00	0.00	15.91	0.00
	SE	2.90	0.00	0.00	0.00	0.00	0.00	2.90	0.00
07 May	X̄	157.00	0.00	0.00	0.00	0.00	0.00	157.00	234.80
	SD	52.14	0.00	0.00	0.00	0.00	0.00	52.14	53.50
	SE	9.52	0.00	0.00	0.00	0.00	0.00	9.52	16.92
14 May	X̄	222.10	23.97	0.00	0.00	0.00	0.00	246.07	169.50
	SD	62.63	11.54	0.00	0.00	0.00	0.00	64.52	30.00
	SE	11.44	2.11	0.00	0.00	0.00	0.00	11.78	9.49
16 May	X̄	268.83	31.43	0.00	0.00	0.00	0.00	300.27	84.90
	SD	69.94	13.01	0.00	0.00	0.00	0.00	74.79	31.26
	SE	12.77	2.38	0.00	0.00	0.00	0.00	13.65	9.89
19 May	X̄	237.73	45.10	2.40	0.00	0.00	0.00	285.23	36.80
	SD	115.35	30.69	5.68	0.00	0.00	0.00	137.36	6.92
	SE	21.06	5.60	1.04	0.00	0.00	0.00	25.08	2.19
22 May	X̄	282.23	47.73	4.53	0.00	0.00	0.00	334.50	57.90
	SD	93.08	23.26	5.25	0.00	0.00	0.00	115.31	17.12
	SE	16.99	4.25	0.96	0.00	0.00	0.00	21.05	5.41
24 May	X̄	243.07	52.87	7.37	0.00	0.00	0.00	303.30	34.90
	SD	62.86	17.49	5.83	0.00	0.00	0.00	78.76	9.10
	SE	11.48	3.19	1.07	0.00	0.00	0.00	14.38	2.88
27 May	X̄	280.90	57.00	53.73	5.97	0.00	0.00	397.60	77.10
	SD	71.98	23.23	19.26	5.80	0.00	0.00	96.71	31.68
	SE	13.14	4.24	3.52	1.06	0.00	0.00	17.66	10.02
30 May	X̄	270.67	61.60	58.97	10.40	0.30	0.00	401.93	52.00
	SD	79.82	23.86	20.55	5.70	0.65	0.00	103.50	17.81
	SE	14.57	4.36	3.75	1.04	0.12	0.00	18.90	5.63
02 Jun	X̄	129.20	40.83	36.47	5.90	0.00	0.00	212.40	98.50
	SD	48.83	14.31	13.11	4.01	0.00	0.00	65.34	18.58
	SE	8.91	2.61	2.39	0.73	0.00	0.00	11.93	5.88
05 Jun	X̄	141.03	38.53	36.50	21.90	14.10	0.00	252.07	85.50
	SD	68.41	23.21	20.47	12.29	8.75	0.00	118.27	21.55
	SE	12.49	4.24	3.74	2.24	1.60	0.00	21.59	6.82
08 Jun	X̄	18.97	16.73	31.83	39.00	44.40	0.00	150.93	18.40
	SD	15.95	9.58	12.31	13.05	19.03	0.00	44.08	7.41
	SE	2.91	1.75	2.25	2.38	3.47	0.00	6.05	2.34
11 Jun	X̄	0.40	2.23	19.10	41.63	22.83	0.00	86.23	8.70
	SD	1.10	2.37	10.28	13.86	9.03	0.00	27.06	5.36
	SE	0.20	0.43	1.88	2.53	1.65	0.00	4.94	1.69
14 Jun	X̄	0.17	1.27	11.27	23.40	12.67	0.00	48.77	1.90
	SD	0.91	2.79	8.62	15.28	9.02	0.00	31.63	1.37
	SE	0.17	0.51	1.57	2.79	1.65	0.00	5.78	0.43
17 Jun	X̄	0.30	1.03	7.97	19.17	9.83	0.00	38.30	0.00
	SD	0.75	1.96	9.76	14.92	9.84	0.00	27.78	0.00
	SE	0.14	0.36	1.78	2.72	1.80	0.00	5.07	0.00
20 Jun	X̄	0.87	0.30	1.70	4.87	3.10	0.00	10.83	0.00
	SD	1.74	0.60	1.93	4.20	3.32	0.00	8.08	0.00
	SE	0.32	0.11	0.35	0.77	0.61	0.00	1.47	0.00
24 Jun	X̄	0.13	0.00	0.30	0.70	0.17	0.00	1.30	0.00
	SD	0.73	0.00	0.53	0.79	0.46	0.00	1.24	0.00
	SE	0. 3	0.00	0.10	0.15	0.08	0.00	0.23	0.00
27 Jun	X̄	0.00	0.00	0.00	0.00	0.00	44.82	44.82	0.00
	SD	0.00	0.00	0.00	0.00	0.00	18.62	18.62	0.00
	SE	0.00	0.00	0.00	0.00	0.00	5.89	5.89	0.00
Total Incidence		7439	1232	812	522	324	--	--	961

TABLE 15.

1968 GULL LAKE FIELD STUDY

wheat

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
22 Apr	$\bar{X}$	0.53	0.00	0.00	0.00	0.00	0.00	0.53	0.00
	SD	1.25	0.00	0.00	0.00	0.00	0.00	1.25	0.00
	SE	0.23	0.00	0.00	0.00	0.00	0.00	0.23	0.00
29 Apr	$\bar{X}$	1.23	0.00	0.00	0.00	0.00	0.00	1.23	0.90
	SD	1.79	0.00	0.00	0.00	0.00	0.00	1.79	1.52
	SE	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.48
07 May	$\bar{X}$	0.97	0.00	0.00	0.00	0.00	0.00	0.97	1.00
	SD	0.89	0.00	0.00	0.00	0.00	0.00	00.89	1.15
	SE	0.16	0.00	0.00	0.00	0.00	0.00	0.16	0.37
14 May	$\bar{X}$	0.87	0.00	0.00	0.00	0.00	0.00	0.87	1.40
	SD	1.04	0.00	0.00	0.00	0.00	0.00	1.04	1.96
	SE	0.19	0.00	0.00	0.00	0.00	0.00	0.19	0.68
17 May	$\bar{X}$	0.20	0.00	0.00	0.00	0.00	0.00	0.20	0.00
	SD	0.55	0.00	0.00	0.00	0.00	0.00	0.58	0.00
	SE	0.10	0.00	0.00	0.00	0.00	0.00	0.10	0.00
22 May	$\bar{X}$	0.77	0.13	0.00	0.00	0.00	0.00	0.93	0.30
	SD	1.01	0.35	0.00	0.00	0.00	0.00	1.20	0.67
	SE	0.18	0.06	0.00	0.00	0.00	0.00	0.22	0.21
24 May	$\bar{X}$	1.60	0.80	0.03	0.00	0.00	0.00	2.43	0.00
	SD	1.50	1.10	0.18	0.00	0.00	0.00	2.34	0.00
	SE	0.27	0.20	0.03	0.00	0.00	0.00	0.43	0.00
27 May	$\bar{X}$	1.07	0.23	0.13	0.00	0.00	0.00	1.43	0.00
	SD	1.34	0.57	0.35	0.00	0.00	0.00	0.79	0.00
	SE	0.24	0.10	0.06	0.00	0.00	0.00	0.33	0.00
30 May	$\bar{X}$	1.20	0.43	0.20	0.00	0.00	0.00	1.83	0.00
	SD	1.68	0.68	0.48	0.00	0.00	0.00	2.00	0.00
	SE	0.30	0.12	0/09	0.00	0.00	0.00	0.37	0.00
02 Jun	$\bar{X}$	0.60	0.17	0.33	0.03	0.00	0.00	1.13	0.00
	SD	1.22	0.59	0.66	0.18	0.00	0.00	1.59	0.00
	SE	0.22	0.11	0.12	0.03	0.00	0.00	0.29	0.00
05 Jun	$\bar{X}$	0.57	0.27	0.13	0.00	0.00	0.00	0.97	0.00
	SD	1.10	0.64	0.35	0.00	0.00	0.00	1.65	0.00
	SE	0.20	0.12	0.06	0.00	0.00	0.00	0.30	0.00
08 Jun	$\bar{X}$	0.60	0.00	0.13	0.20	0.07	0.00	1.00	0.00
	SD	0.89	0.00	0.43	0.68	0.25	0.00	1.14	0.00
	SE	0.16	0.00	0.08	0.09	0.05	0.00	0.21	0.00
11 Jun	$\bar{X}$	0.60	0.17	0.10	0.37	0.37	0.00	1.60	0.00
	SD	2.92	0.46	0.31	0.89	0.72	0.00	3.50	0.00
	SE	0.53	0.08	0.06	0.16	0.13	0.00	0.64	0.00
14 Jun	$\bar{X}$	1.67	0.00	0.06	0.06	0.06	0.00	1.83	0.00
	SD	2.79	0.00	0.24	0.24	0.24	0.00	2.87	0.00
	SE	0.66	0.00	0.06	0.06	0.06	0.00	0.68	0.00
28 Jun	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	0.42	0.42	0.00
	SD	0.00	0.00	0.00	0.00	0.00	0.87	0.47	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.14	0.14	0.00
Total Incidence		47.42	6.27	3.29	2.03	1.41	--	--	3.60

oats

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
07 May	$\bar{X}$	14.53	0.00	0.00	0.00	0.00	0.00	14.53	23.70
	SD	6.43	0.00	0.00	0.00	0.00	0.00	5.43	10.83
	SE	1.17	0.00	0.00	0.00	0.00	0.00	1.67	3.43
14 May	$\bar{X}$	39.90	0.20	0.00	0.00	0.00	0.00	40.10	26.50
	SD	16.58	0.76	0.00	0.00	0.00	0.00	16.74	8.91
	SE	3.03	0.14	0.00	0.00	0.00	0.00	3.06	2.82
17 May	$\bar{X}$	43.20	0.33	0.00	0.00	0.00	0.00	43.53	11.90
	SD	19.84	0.84	0.00	0.00	0.00	0.00	28.04	6.42
	SE	3,62	0.15	0.00	0.00	0.00	0.00	3.66	2.03
22 May	$\bar{X}$	60.70	2.13	0.23	0.00	0.00	0.00	63.07	27.70
	SD	21.75	1.93	0.57	0.00	0.00	0.00	22.91	15.66
	SE	3.97	0.35	0.10	0.00	0.00	0.00	4.18	4.95
24 May	$\bar{X}$	56.97	5.53	0.73	0.00	0.00	0.00	63.23	10.30
	SD	17.23	3.58	1.08	0.00	0.00	0.00	19.01	5.78
	SE	3.14	0.64	0.19	0.00	0.00	0.00	3.47	1.82
27-May	$\bar{X}$	45.87	5.37	2.33	0.00	0.00	0.00	53.27	13.80
	SD	16.26	4.09	1,79	0.00	0.00	0.00	17.77	5.85
	SE	2.97	0.75	0.33	0.00	0.00	0.00	3.28	1.85
30 May	$\bar{X}$	49.00	8.60	3.97	0.07	0.00	0.00	61.63	12.00
	SD	18.72	4.69	2.37	0.25	0.00	0.00	21.32	6.43
	SE	3.42	0.86	0143	0.05	0.00	0.00	3.89	2.03
02 Jun	$\bar{X}$	37.50	7.80	6.87	0.07	0.00	0.00	52.87	16.40
	SD	12.48	3.47	3.23	1.09	0.00	0.00	15.65	11.12
	SE	2.28	0.63	0.59	0.20	0.00	0.00	2.86	3.52
05 Jun	$\bar{X}$	42.30	17.27	8.80	2.10	0.00	0.00	70.47	12.40
	SD	19.05	9.64	4.43	2.47	0.00	0.00	25.82	7.12
	SE	3.48	1.76	0.81	0.45	0.00	0.00	4.71	2.25
08 Jun	$\bar{X}$	13.33	10.07	12.40	7.40	3.37	0.00	46.57	0.00
	SD	11.48	5.31	5.33	4.12	2.44	0.00	18.78	0.00
	SE	2.10	0.97	0.97	0.75	0.45	0.00	3.43	0.00
11 Jun	$\bar{X}$	2.50	6.47	18.23	19.47	13.53	0.00	60.20	3.40
	SD	4.21	4.73	7.20	8.87	8.92	0.00	19.28	2.80
	SE	0.77	0.86	1.31	1.62	1.63	0.00	3.52	0.88
14 Jun	$\bar{X}$	2.37	3.53	10.70	19.20	14.23	0.00	50.03	1.70
	SD	3.51	5.35	6.50	9.76	8.99	0.00	18.05	1.16
	SE	0.64	0.98	1.19	1.78	1.57	0.00	3.30	0.37
17 Jun	$\bar{X}$	1.20	1.63	8.40	15.50	10.53	0.00	37.27	0.00
	SD	1.99	2.49	5.13	6.89	6.80	0.00	16.07	0.00
	SE	0.36	0.45	0.94	1.26	1.24	0.00	2.93	0.00
20 Jun	$\bar{X}$	0.67	0.87	4.00	9.57	8.13	0.00	23.23	0.00
	SD	1.86	1.17	31.2	4.90	5.10	0.00	9.90	0.00
	SE	0.34	0.21	0.57	0.89	0.93	0.00	1.81	0.00
24 Jun	$\bar{X}$	0.17	0.13	0.67	2.27	4.07	0.00	7.30	0.00
	SD	0.46	0.35	0.84	2.60	3.54	0.00	5.52	0.00
	SE	0.08	0.06	0.15	0.47	0.65	0.00	1.01	0.00
28 Jun	$\bar{X}$	0.53	0.07	0.10	0.43	0.53	0.00	1.73	0.00
	SD	1.20	0.37	0.40	0.68	0.86	0.00	1.95	0.00
	SE	0.22	0.07	0.07	0.12	0.16	0.00	0.28	0.00
02 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	51.13	51 13	0.00
	SD	0.00	0.00	0.00	0.00	0.00	17.92	17.92	0.00
	SE	0.00	0.00	0.00	0.00	0.00	5.66	5.66	0.00
Total Incidence		1365	210	238	172	102	--	--	160

TABLE 16.

1968 EAST LANSING FIELD STUDY

oats

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
17 May	$\bar{X}$	4.13	0.00	0.00	0.00	0.00	0.00	4.13	3.40
	SD	3.40	0.00	0.00	0.00	0.00	0.00	3.40	2.22
	SE	0.62	0.00	0.00	0.00	0.00	0.00	0.62	0.70
21 May	$\bar{X}$	8.30	0.00	0.00	0.00	0.00	0.00	8.30	2.70
	SD	3.53	0.00	0.00	0.00	0.00	0.00	3.53	3.13
	SE	0.65	0.00	0.00	0.00	0.00	0.00	0.65	0.99
24 May	$\bar{X}$	8.90	0.07	0.00	0.00	0.00	0.00	8.97	3.10
	SD	3.90	0.25	0.00	0.00	0.00	0.00	3.92	1.85
	SE	0.71	0.05	0.00	0.00	0.00	0.00	0.72	0.59
31 May	$\bar{X}$	5.97	0.53	0.03	0.00	0.00	0.00	6.53	1.90
	SD	3.91	1.01	0.18	0.00	0.00	0.00	3.97	1.79
	SE	0.71	0.18	0.03	0.00	0.00	0.00	0.73	0.57
04 Jun	$\bar{X}$	4.37	2.07	0.20	0.00	0.00	0.00	6.63	1.10
	SD	2.91	2.03	0.48	0.00	0.00	0.00	4.05	1.20
	SE	0.58	0.37	0.09	0.00	0.00	0.00	0.74	0.38
07 Jun	$\bar{X}$	2.60	2.67	0.63	0.00	0.00	0.00	5.90	1.00
	SD	2.61	1.73	1.07	0.00	0.00	0.00	3.96	1.05
	SE	0.48	0.32	0.19	0.00	0.00	0.00	0.72	0.33
10 Jun	$\bar{X}$	1.30	1.60	2.13	0.80	0.13	0.00	5.97	1.10
	SD	1.53	1.50	1.83	1.10	0.43	0.00	3.88	1.37
	SE	0.28	0.27	0.33	0.20	0.08	0.00	0.71	0.43
13 Jun	$\bar{X}$	0.77	1.07	3.23	3.93	0.60	0.00	9.60	0.60
	SD	1.50	1.46	2.70	3.91	1.13	0.00	6.87	0.97
	SE	0.27	0.27	0.49	0.71	0.21	0.00	1.25	0.31
19 Jun	$\bar{X}$	1.03	0.77	1.23	1.77	2.27	0.00	7.07	0.00
	SD	1.90	1.22	1.65	1.19	2.02	0.00	3.76	0.00
	SE	0.35	0.22	0.30	0.22	0.37	0.00	0.69	0.00
08 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	4.00	4.00	0.00
	SD	0.00	0.00	0.00	0.00	0.00	1.64	1.64	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.52	0.52	0.00
Total Incidence		148.68	30.78	28.05	26.28	11.03	--	--	15

wheat

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total
24 Apr	$\bar{X}$	0.37	0.00	0.00	0.00	0.00	0.00	0.37
	SD	0.61	0.00	0.00	0.00	0.00	0.00	0.61
	SE	0.11	0.00	0.00	0.00	0.00	0.00	0.11
2 May	$\bar{X}$	1.50	0.00	0.00	0.00	0.00	0.00	1.50
	SD	1.76	0.00	0.00	0.00	0.00	0.00	1.76
	SE	0.32	0.00	0.00	0.00	0.00	0.00	0.32
9 May	$\bar{X}$	1.27	0.00	0.00	0.00	0.00	0.00	1.27
	SD	1.44	0.00	0.00	0.00	0.00	0.00	1.44
	SE	0.26	0.00	0.00	0.00	0.00	0.00	0.26
17 May	$\bar{X}$	0.77	0.00	0.00	0.00	0.00	0.00	0.77
	SD	1.10	0.00	0.00	0.00	0.00	0.00	1.10
	SE	0.20	0.00	0.00	0.00	0.00	0.00	0.20
21 May	$\bar{X}$	0.43	0.00	0.00	0.00	0.00	0.00	0.43
	SD	0.82	0.00	0.00	0.00	0.00	0.00	0.82
	SE	0.15	0.00	0.00	0.00	0.00	0.00	0.15
24 May	$\bar{X}$	2.50	0.70	0.00	0.00	0.00	0.00	3.20
	SD	2.24	1.18	0.00	0.00	0.00	0.00	3.04
	SE	0.41	0.22	0.00	0.00	0.00	0.00	0.56
27 May	$\bar{X}$	0.80	0.50	0.07	0.00	0.00	0.00	1.37
	SD	1.00	0.68	0.25	0.00	0.00	0.00	1.27
	SE	0.18	0.12	0.05	0.00	0.00	0.00	0.23
4 Jun	$\bar{X}$	0.80	0.63	0.13	0.00	0.00	0.00	1.57
	SD	1.42	0.93	0.43	0.00	0.00	0.00	1.76
	SE	0.26	0.17	0.08	0.00	0.00	0.00	0.32
10 Jun	$\bar{X}$	0.67	0.13	0.40	0.53	0.17	0.00	1.90
	SD	1.12	0.35	0.81	0.90	0.38	0.00	1.77
	SE	0.21	0.06	0.15	0.16	0.07	0.00	0.32
3 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	0.93	0.93
	SD	0.00	0.00	0.00	0.00	0.00	0.70	0.70
	SE	0.00	0.00	0.00	0.00	0.00	0.22	0.22
Total Incidence		48.50	9.82	2.90	2.13	0.67	--	--

TABLE 17.

1969 GALIEN FIELD STUDY

GALIEN OATS 1969

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
16 May	$\bar{X}$	240.05	0.05	0.00	0.00	0.00	0.00	240.10	0.00
	SD	78.01	0.22	0.00	0.00	0.00	0.00	78.09	0.00
	SE	17.44	0.05	0.00	0.00	0.00	0.00	17.46	0.00
19 May	$\bar{X}$	293.30	22.70	0.90	0.00	0.00	0.00	316.90	325.60
	SD	90.11	15.23	1.59	0.00	0.00	0.00	96.82	99.24
	SE	20.15	3.41	0.35	0.00	0.00	0.00	21.65	31.38
26 May	$\bar{X}$	427.95	45.45	15.10	0.45	0.00	0.00	488.95	178.70
	SD	121.43	28.10	8.14	0.60	0.00	0.00	145.90	45.06
	SE	27.15	6.28	1.82	0.14	0.00	0.00	32.62	14.25
2 Jun	$\bar{X}$	363.80	91.35	72.75	29.95	0.75	0.00	558.60	317.50
	SD	120.44	35.78	29.75	15.56	1.74	0.00	123.47	78.15
	SE	26.93	8.00	6.65	3.48	0.39	0.00	27.61	24.71
9 Jun	$\bar{X}$	220.30	75.95	59.45	36.75	21.55	0.00	414.00	136.10
	SD	82.95	49.71	32.84	15.72	18.10	0.00	143.52	41.14
	SE	18.55	11.12	7.34	3.52	4.05	0.00	32.09	13.01
16 Jun	$\bar{X}$	27.00	13.60	45.05	31.90	25.05	0.00	142.60	37.70
	SD	13.05	13.43	26.33	17.58	15.29	0.00	48.24	12.97
	SE	2.92	3.00	5.89	3.93	3.42	0.00	10.79	4.10
23 Jun	$\bar{X}$	31.60	3.25	12.40	18.30	30.30	0.00	95.85	9.90
	SD	29.21	3.48	11.45	9.27	14.41	0.00	48.84	6.06
	SE	6.53	0.78	2.56	2.07	3.22	0.00	10.92	1.92
29 Jun	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	83.36	83.36	0.00
	SD	0.00	0.00	0.00	0.00	0.00	30.24	30.24	0.00
	SE	0.00	0.00	0.00	0.00	0.00	9.56	9.56	0.00
Total Incidence		9377	1719	1432	812	528	--	--	1005

GALIEN WHEAT 1969

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
16 May	$\bar{X}$	52.50	3.40	0.60	0.00	0.00	0.00	56.50	0.00
	SD	11.32	2.01	0.70	0.00	0.00	0.00	12.62	0.00
	SE	3.58	0.64	0.22	0.00	0.00	0.00	3.99	0.00
19 May	$\bar{X}$	51.25	4.90	2.95	0.60	0.00	0.00	59.70	66.60
	SD	26.50	3.08	1.67	0.82	0.00	0.00	28.05	22.22
	SE	5.93	0.69	0.37	0.18	0.00	0.00	6.27	7.33
26 May	$\bar{X}$	41.10	5.10	3.25	1.45	0.10	0.00	51.00	30.70
	SD	23.78	4.13	3.02	1.70	0.31	0.00	28.18	9.63
	SE	5.32	0.92	0.68	0.38	0.07	0.00	6.30	3.04
2 Jun	$\bar{X}$	19.55	7.75	14.20	8.55	3.65	0.00	53.70	38.10
	SD	13.33	3.68	7.80	4.89	3.15	0.00	23.55	9.12
	SE	2.98	0.82	1.75	1.09	0.70	0.00	5.27	2.88
9 Jun	$\bar{X}$	12.70	4.65	8.90	0.05	6.30	0.00	41.60	9.50
	SD	10.14	4.12	5.41	4.63	4.53	0.00	14.11	3.41
	SE	2.27	0.92	1.21	1.03	1.01	0.00	3.16	1.08
16 Jun	$\bar{X}$	3.35	3.15	5.40	6.95	5.45	0.00	24.30	0.00
	SD	3.80	3.33	4.22	3.59	3.12	0.00	9.63	0.00
	SE	0.85	0.74	0.94	0.80	0.70	0.00	2.15	0.00
23 Jun	$\bar{X}$	1.69	0.31	0.63	0.63	0.63	0.00	3.88	0.00
	SD	3.00	0.48	0.89	0.72	0.89	0.00	3.18	0.00
	SE	0.75	0.12	0.22	0.18	0.22	0.00	0.80	0.00
29 Jun	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	4.80	4.80	0.00
	SD	0.00	0.00	0.00	0.00	0.00	2.87	2.87	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.91	0.91	0.00
Total Incidence		906	176	242	189	113	--	--	150

TABLE 18.

1969 GULL LAKE FIELD STUDY

wheat

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
20 May	$\bar{X}$	183.55	10.20	1.00	0.00	0.00	0.00	194.75	424.90
	SD	42.51	6.31	1.81	0.00	0.00	0.00	44.27	130.70
	SE	9.51	1.41	0.40	0.00	0.00	0.00	9.90	41.33
23 May	$\bar{X}$	205.45	4.90	1.70	0.10	0.00	0.00	212.15	36.70
	SD	51.82	3.39	1.49	0.45	0.00	0.00	51.15	15.69
	SE	11.59	0.76	0.33	0.10	0.00	0.00	11.44	4.96
26 May	$\bar{X}$	245.60	13.25	4.45	0.95	0.00	0.00	264.25	47.10
	SD	71.75	7.52	3.39	2.35	0.00	0.00	70.44	21.68
	SE	16.04	1.68	0.76	0.53	0.00	0.00	15.75	6.86
29 May	$\bar{X}$	136.45	36.15	11.95	1.80	0.05	0.00	186.40	0.00
	SD	39.15	26.56	9.01	2.44	0.22	0.00	53.00	0.00
	SE	8.75	5.94	2.02	0.55	0.05	0.00	11.85	0.00
2 Jun	$\bar{X}$	40.75	32.95	32.40	10.70	2.30	0.00	119.10	23.20
	SD	20.56	14.05	17.34	4.89	1.75	0.00	36.26	12.93
	SE	4.60	3.14	3.88	1.09	0.39	0.00	8.11	4.09
5 Jun	$\bar{X}$	44.85	36.45	29.60	13.35	5.05	0.00	129.30	0.00
	SD	26.06	16.55	10.48	7.86	4.47	0.00	30.29	0.00
	SE	5.83	3.70	2.34	1.76	1.00	0.00	6.77	0.00
9 Jun	$\bar{X}$	32.70	29.85	42.60	24.90	8.95	0.00	139.00	0.00
	SD	17.91	18.11	20.06	12.39	8.16	0.00	40.30	0.00
	SE	4.01	4.05	4.49	2.77	1.82	0.00	9.01	0.00
12 Jun	$\bar{X}$	2.70	5.15	29.95	34.35	17.00	0.00	89.15	0.00
	SD	3.67	3.90	16.23	13.64	10.94	0.00	27.75	0.00
	SE	0.82	0.87	3.63	3.05	2.45	0.00	6.20	0.00
16 Jun	$\bar{X}$	4.22	7.06	17.89	32.17	32.33	0.00	93.67	0.00
	SD	3.87	9.85	10.12	18.07	14.87	0.00	31.23	0.00
	SE	0.91	2.32	2.38	4.26	3.50	0.00	7.36	0.00
19 Jun	$\bar{X}$	1.60	1.25	5.60	16.30	28.45	0.00	53.20	0.00
	SD	2.64	1.48	3.25	8.80	10.06	0.00	20.43	0.00
	SE	0.59	0.33	0.73	1.97	2.25	0.00	4.57	0.00
23 Jun	$\bar{X}$	1.65	0.40	1.85	7.05	14.65	0.00	25.60	0.00
	SD	3.41	1.35	1.57	5.17	8.02	0.00	10.57	0.00
	SE	0.76	0.30	0.35	1.16	1.79	0.00	2.36	0.00
26 Jun	$\bar{X}$	0.00	1.50	3.30	3.00	6.50	0.00	14.30	0.00
	SD	0.00	4.74	9v04	7.76	10.78	0.00	32.28	0.00
	SE	0.00	1.50	2.86	2.45	3.41	0.00	10.21	0.00
2 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	32.82	32.82	0.00
	SD	0.00	0.00	0.00	0.00	0.00	12.79	12.79	0.00
	SE	0.00	0.00	0.00	0.00	0.00	4.04	4.04	0.00
Total Incidence		2897	703	703	528	414	--	--	545

oats

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
20 May	$\bar{X}$	112.40	0.00	0.05	0.00	0.00	0.00	112.45	150.50
	SD	38.41	0.00	0.22	0.00	0.00	0.00	36.17	56.92
	SE	8.53	0.00	0.05	0.00	0.00	0.00	8.53	18.00
23 May	$\bar{X}$	104.55	3.05	0.00	0.00	0.00	0.00	107.60	17.10
	SD	38.94	8.04	0.00	0.00	0.00	0.00	39.86	8.02
	SE	8.61	1.80	0.00	0.00	0.00	0.00	8.91	2.54
26 May	$\bar{X}$	122.15	0.00	0.00	0.00	0.00	0.00	122.15	40.80
	SD	38.94	0.00	0.00	0.00	0.00	0.00	38.94	17.96
	SE	8.71	0.00	0.00	0.00	0.00	0.00	8.71	5.68
29 May	$\bar{X}$	185.75	7.35	1.50	0.00	0.00	0.00	194.60	0.00
	SD	55.58	4.91	2.33	0.00	0.00	0.00	58.95	0.00
	SE	12.43	1.10	0.52	0.00	0.00	0.00	13.18	0.00
2 Jun	$\bar{X}$	138.29	26.79	14.71	1.71	0.00	0.00	181.50	213.20
	SD	43.26	12.36	12.86	1.98	0.00	0.00	55.09	35.87
	SE	11.56	3.30	3.44	0.53	0.00	0.00	14.72	11.34
5 Jun	$\bar{X}$	144.20	31.25	21.65	2.10	0.10	0.00	199.30	21.50
	SD	46.84	18.17	14.54	2.90	0.45	0.00	60.27	6.45
	SE	10.47	4.06	3.25	0.65	0.10	0.00	13.48	2.04
9 Jun	$\bar{X}$	121.35	39.70	27.05	8.65	0.90	0.00	197.65	52.30
	SD	35.51	19.34	18.37	8.09	1.77	0.00	54.23	13.01
	SE	7.94	4.32	4.11	1.81	0.40	0.00	12.13	4.12
12 Jun	$\bar{X}$	76.35	17.50	42.25	20.95	15.60	0.00	172.65	40.50
	SD	40.14	13.85	22.94	10.91	11.97	0.00	48.91	16.11
	SE	8.98	3.10	5.13	2.44	2.68	0.00	10.94	5.10
16 Jun	$\bar{X}$	51.95	33.75	52.15	35.20	30.85	0.00	203.90	25.10
	SD	29.46	27.08	25.32	12.91	17.91	0.00	63.03	12.49
	SE	6.59	6.06	5.66	2.89	4.01	0.00	14.09	3.95
19 Jun	$\bar{X}$	49.60	11.70	27.50	37.55	37.85	0.00	164.20	18.70
	SD	36.49	6.26	13.11	14.76	13.56	0.00	62.90	10.46
	SE	8.16	1.40	2.93	3.30	3.03	0.00	14.06	3.31
23 Jun	$\bar{X}$	32.75	6.35	22.80	42.45	39.40	0.00	143.75	7.20
	SD	19.40	4.45	10.52	20.73	17.14	0.00	50.52	4.05
	SE	4.34	1.00	2.35	4.64	3.83	0.00	11.30	1.28
26 Jun	$\bar{X}$	13.75	5.10	11.05	17.40	28.90	0.00	76.20	4.60
	SD	8.87	5.30	6.89	7.49	11.91	0.00	24.61	4.01
	SE	1.98	1.19	1.54	1.68	2.66	0.00	5.50	1.27
2 Jul	$\bar{X}$	2.95	0.35	2.35	3.90	12.15	0.00	21.70	0.00
	SD	2.61	0.81	3.20	3.78	7.08	0.00	13.54	0.00
	SE	0.58	0.18	0.72	0.85	1.58	0.00	3.03	0.00
7 Jul	$\bar{X}$	0.20	0.00	0.30	1.10	2.50	34.31	38.41	0.00
	SD	0.63	0.00	0.67	1.60	2.84	11.28	13.80	0.00
	SE	0.20	0.00	0.21	0.50	0.90	3.57	4.36	0.00
Total Incidence		3728	644	797	623	640	--	--	591

TABLE 19.

1969 EAST LANSING FIELD STUDY

wheat

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total
20 May	$\bar{X}$	36.10	0.05	0.00	0.00	0.00	0.00	36.15
	SD	13.41	0.22	0.00	0.00	0.00	0.00	13.36
	SE	3.00	0.05	0.00	0.00	0.00	0.00	2.99
23 May	$\bar{X}$	19.10	0.00	0.05	0.00	0.00	0.00	19.15
	SD	9.16	0.00	0.22	0.00	0.00	0.00	9.22
	SE	2.05	0.00	0.05	0.00	0.00	0.00	2.06
26 May	$\bar{X}$	16.16	0.68	0.05	0.00	0.00	0.00	16.89
	SD	11.50	0.89	0.23	0.00	0.00	0.00	11.78
	SE	2.64	0.20	0.05	0.00	0.00	0.00	2.70
29 May	$\bar{X}$	10.20	2.35	0.60	0.00	0.00	0.00	13.15
	SD	7.30	2.66	0.88	0.00	0.00	0.00	8.76
	SE	1.63	0.60	0.20	0.00	0.00	0.00	1.96
5 Jun	$\bar{X}$	9.05	5.30	2.95	0.45	0.00	0.00	17.15
	SD	4.26	2.62	2.33	0.60	0.00	0.00	6.58
	SE	0.95	0.59	0.52	0.14	0.00	0.00	1.47
12 Jun	$\bar{X}$	3.70	1.45	5.25	3.50	1.40	0.00	15.30
	SD	3.08	1.90	6.57	4.16	1.82	0.00	12.38
	SE	0.69	0.43	1.47	0.93	0.41	0.00	2.77
19 Jun	$\bar{X}$	1.15	1.00	3.10	5.00	5.70	0.00	15.95
	SD	1.73	2.41	2.53	3.67	4.58	0.00	7.27
	SE	0.39	0.54	0.57	0.82	1.02	0.00	1.63
23 Jun	$\bar{X}$	0.95	0.16	1.58	3.16	3.26	0.00	9.11
	SD	1.61	0.50	1.92	2.97	4.01	0.00	5.71
	SE	0.37	0.12	0.44	0.68	0.92	0.00	1.31
26 Jun	$\bar{X}$	0.06	0.17	1.17	1.11	2.00	0.00	4.50
	SD	0.24	0.38	1.89	1.02	1.68	0.00	3.00
	SE	0.06	0.09	0.44	0.24	0.40	0.00	0.71
7 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	6.18	6.18
	SD	0.00	0.00	0.00	0.00	0.00	3.28	3.28
	SE	0.00	0.00	0.00	0.00	0.00	1.04	1.04
Total Incidence		321	68	86	68	57	--	--

oats

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
26 May	$\bar{X}$	3.90	0.10	0.00	0.00	0.00	0.00	4.00	2.40
	SD	3.07	0.32	0.00	0.00	0.00	0.00	3.20	2.80
	SE	0.97	0.10	0.00	0.00	0.00	0.00	1.01	0.88
29 May	$\bar{X}$	9.05	0.00	0.00	0.00	0.00	0.00	9.05	0.00
	SD	4.95	0.00	0.00	0.00	0.00	0.00	4.95	0.00
	SE	1.14	0.00	0.00	0.00	0.00	0.00	1.14	0.00
5 Jun	$\bar{X}$	27.50	2.45	0.50	0.00	0.00	0.00	30.45	9.00
	SD	13.24	2.06	0.69	0.00	0.00	0.00	12.56	5.23
	SE	2.96	0.46	0.15	0.00	0.00	0.00	2.81	1.65
9 Jun	$\bar{X}$	21.60	2.05	0.50	0.00	0.00	0.00	24.15	4.90
	SD	10.03	1.93	0.83	0.00	0.00	0.00	10.60	3.00
	SE	2.24	0.43	0.18	0.00	0.00	0.00	2.37	0.95
12 Jun	$\bar{X}$	26.05	3.45	2.45	0.05	0.00	0.00	32.00	3.50
	SD	17.85	2.16	3.30	0.22	0.00	0.00	17.73	2.42
	SE	3.99	0.48	0.74	0.05	0.00	0.00	3.96	0.76
16 Jun	$\bar{X}$	15.40	6.25	5.70	0.85	0.05	0.00	28.25	12.40
	SD	7.07	5.09	3.64	1.14	0.22	0.00	9.84	2.67
	SE	1.58	1.14	0.81	0.25	0.05	0.00	2.20	0.85
19 Jun	$\bar{X}$	12.95	3.85	6.60	2.80	0.20	0.00	26.40	3.40
	SD	8.36	2.37	4.47	1.88	0.52	0.00	9.36	2.22
	SE	1.87	0.53	1.00	0.42	0.12	0.00	2.09	0.70
23 Jun	$\bar{X}$	13.70	3.80	6.55	3.05	1.45	0.00	28.55	2.90
	SD	9.03	4.11	5.20	3.05	1.96	0.00	17.02	2.23
	SE	2.02	0.92	1.16	0.68	0.44	0.00	3.80	0.71
26 Jun	$\bar{X}$	6.05	2.80	4.65	6.35	5.75	0.00	25.60	2.50
	SD	4.02	2.14	2.80	3.42	3.89	0.00	8.82	1.43
	SE	0.90	0.48	0.63	0.77	0.87	0.00	1.97	0.45
2 Jul	$\bar{X}$	1.40	0.35	1.85	2.55	6.75	0.00	12.90	1.30
	SD	2.09	0.67	1.60	1.39	2.61	0.00	4.10	1.49
	SE	0.47	0.15	0.36	0.31	0.58	0.00	0.92	0.47
7 Jul	$\bar{X}$	0.10	0.05	0.50	1.70	2.95	0.00	5.30	0.40
	SD	0.31	0.22	0.69	1.78	2.24	0.00	3.51	0.52
	SE	0.07	0.05	0.15	0.40	0.50	0.00	0.79	0.16
10 Jul	$\bar{X}$	0.13	0.00	0.00	0.38	1.81	0.00	2.31	0.00
	SD	0.31	0.00	0.00	0.31	1.52	0.00	1.58	0.00
	SE	0.08	0.00	0.00	0.08	0.38	0.00	0.39	0.00
14 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	14.71	14.71	0.00
	SD	0.00	0.00	0.00	0.00	0.00	6.17	6.17	0.00
	SE	0.00	0.00	0.00	0.00	0.00	1.95	1.95	0.00
Total Incidence		553	96	112	74	87	--	--	43

TABLE 20.

1969 CAGE STUDY

H1 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
9 Jun	X̄	136.73	18.33	2.27	0.07	0.00	0.00	157.40	69.67
	SD	27.29	8.26	2.34	0.26	0.00	0.00	30.14	15.28
	SE	7.05	2.13	0.61	0.07	0.00	0.00	7.78	8.82
18 Jun	X̄	35.00	14.73	31.20	10.33	5.13	0.00	96.40	42.00
	SD	17.26	8.24	11.48	5.15	4.44	0.00	30.21	5.57
	SE	4.46	2.13	2.96	1.33	1.15	0.00	7.80	3.21
20 Jun	X̄	18.13	3.40	8.60	7.80	4.20	0.00	42.13	12.00
	SD	8.92	2.87	3.72	3.34	3.17	0.00	12.22	6.24
	SE	2.30	0.74	0.96	0.86	0.82	0.00	3.15	3.61
24 Jun	X̄	15.73	1.58	5.33	11.33	8.60	0.00	42.53	10.33
	SD	9.60	1.25	2.92	4.50	3.72	0.00	12.05	9.45
	SE	2.48	0.32	0.75	1.16	0.96	0.00	3.11	5.46
27 Jun	X̄	8.27	0.60	3.93	6.27	7.53	0.00	26.60	2.00
	SD	7.86	0.91	3.90	3.17	3.44	0.00	7.97	1.73
	SE	2.03	0.24	1.01	0.82	0.89	0.00	2.06	1.00
1 Jul	X̄	2.07	0.27	2.20	4.27	3.80	0.00	12.60	0.33
	SD	1.67	0.46	1.93	3.17	1.37	0.00	5.50	0.58
	SE	0.43	0.12	0.50	0.82	0.35	0.00	1.42	0.33
7 Jul	X̄	1.07	0.00	0.40	0.93	1.80	0.00	4.20	1.00
	SD	2.12	0.00	0.91	1.49	1.47	0.00	4.18	1.73
	SE	0.55	0.00	0.24	0.38	0.38	0.00	1.08	1.00
10 Jul	X̄	0.47	0.00	0.07	0.67	2.27	0.00	3.47	0.00
	SD	1.13	0.00	0.26	0.82	1.87	0.00	2.90	0.00
	SE	0.29	0.00	0.07	0.21	0.48	0.00	0.75	0.00
15 Jul	X̄	0.00	0.00	0.00	0.00	0.00	6.60	6.60	0.00
	SD	0.00	0.00	0.00	0.00	0.00	5.28	5.28	0.00
	SE	0.00	0.00	0.00	0.00	0.00	1.36	1.36	0.00
Total Incidence		1198	183	253	170	133	--	--	162

H2 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
10 Jun	X̄	119.27	24.93	6.47	0.00	0.00	0.00	150.67	111.00
	SD	43.64	10.97	4.10	0.00	0.00	0.00	54.67	44.17
	SE	11.27	2.83	1.06	0.00	0.00	0.00	14.12	25.50
17 Jun	X̄	29.13	18.07	33.60	9.80	4.13	0.00	94.73	26.67
	SD	18.60	7.69	11.73	4.60	3.23	0.00	40.28	12.86
	SE	4.80	1.99	3.03	1.19	0.83	0.00	10.40	7.42
20 Jun	X̄	14.40	2.93	12.67	17.13	7.20	0.00	54.40	11.00
	SD	8.12	1.91	4.05	10.80	4.02	0.00	20.16	6.24
	SE	2.10	0.49	1.05	2.79	1.04	0.00	5.20	3.61
24 Jun	X̄	9.87	1.13	5.20	16.73	11.87	0.00	44.00	5.33
	SD	6.22	1.55	2.40	5.02	6.13	0.00	16.01	2.08
	SE	1.61	0.40	0.62	1.30	1.58	0.00	4.13	1.20
27 Jun	X̄	2.53	0.27	2.07	8.40	15.87	0.00	29.13	1.33
	SD	2.07	0.46	1.22	4.42	12.43	0.00	16.79	2.31
	SE	0.53	0.12	0.32	1.14	3.21	0.00	4.33	1.33
1 Jul	X̄	0.93	0.20	1.27	5.80	9.73	0.00	17.93	0.33
	SD	1.10	0.41	1.16	4.66	6.43	0.00	10.07	0.58
	SE	0.28	0.11	0.30	1.20	1.66	0.00	2.60	0.33
7 Jul	X̄	0.40	0.00	0.20	0.87	2.80	0.00	4.27	0.67
	SD	0.91	0.00	0.41	1.13	2.27	0.00	3.24	1.15
	SE	0.24	0.00	0.11	0.29	0.59	0.00	0.84	0.67
10 Jul	X̄	0.00	0.00	0.00	0.47	1.87	0.00	2.33	0.00
	SD	0.00	0.00	0.00	0.83	1.81	0.00	2.29	0.00
	SE	0.00	0.00	0.00	0.22	0.47	0.00	0.59	0.00
15 Jul	X̄	0.00	0.00	0.00	0.00	0.00	4.53	4.53	0.00
	SD	0.00	0.00	0.00	0.00	0.00	2.77	2.77	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.72	0.72	0.00
Total Incidence		879	194	268	232	212	--	--	194

H3 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
11 Jun	X̄	42.67	11.80	10.27	0.87	0.00	0.00	65.60	44.67
	SD	16.54	5.70	4.91	1.19	0.00	0.00	22.36	14.98
	SE	4.27	1.47	1.27	0.31	0.00	0.00	5.77	8.65
18 Jun	X̄	19.13	14.93	16.20	7.40	1.53	0.00	59.20	21.67
	SD	8.14	6.98	6.12	5.94	1.41	0.00	21.07	11.93
	SE	2.10	1.80	1.58	1.53	0.36	0.00	5.44	6.89
20 Jun	X̄	12.73	3.33	8.60	13.47	14.87	0.00	53.00	6.67
	SD	7.68	2.02	4.42	8.24	9.93	0.00	25.93	3.79
	SE	1.98	0.52	1.14	2.13	2.56	0.00	6.70	2.19
24 Jun	X̄	4.40	1.07	3.60	11.08	15.13	0.00	35.27	1.67
	SD	3.04	1.16	2.85	6.69	9.29	0.00	17.39	0.58
	SE	0.79	0.30	0.74	1.73	2.40	0.00	4.49	0.33
27 Jun	X̄	1.00	0.07	0.87	5.53	11.07	0.00	18.53	1.67
	SD	1.51	0.26	1.36	5.40	5.98	0.00	11.53	1.53
	SE	0.39	0.07	0.35	1.39	1.54	0.00	2.98	0.88
1 Jul	X̄	0.53	0.07	0.20	1.13	3.73	0.00	5.67	2.67
	SD	0.99	0.26	0.41	0.99	2.76	0.00	3.75	3.79
	SE	0.26	0.07	0.11	0.26	0.71	0.00	0.97	2.19
7 Jul	X̄	0.00	0.00	0.00	0.00	0.07	0.00	0.07	0.00
	SD	0.00	0.00	0.00	0.00	0.26	0.00	0.26	0.00
	SE	0.00	0.00	0.00	0.00	0.07	0.00	0.07	0.00
10 Jul	X̄	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	SD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15 Jul	X̄	0.00	0.00	0.00	0.00	0.00	8.13	8.13	0.00
	SD	0.00	0.00	0.00	0.00	0.00	6.37	6.37	0.00
	SE	0.00	0.00	0.00	0.00	0.00	1.64	1.64	0.00
Total Incidence		421	123	151	141	162	--	--	107

K1 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
10 Jun	X̄	47.33	9.53	5.40	0.73	0.00	0.00	63.00	46.00
	SD	11.12	3.81	3.09	1.16	0.00	0.00	10.98	17.06
	SE	2.87	0.98	0.80	0.30	0.00	0.00	2.84	9.85
18 Jun	X̄	20.00	12.67	27.53	13.87	7.67	0.00	81.73	25.33
	SD	6.86	6.74	10.05	4.73	5.09	0.00	28.25	8.02
	SE	1.77	1.74	2.59	1.22	1.32	0.00	7.29	4.63
20 Jun	X̄	13.73	3.67	12.73	18.20	12.67	0.00	61.00	11.67
	SD	7.50	2.92	6.17	8.09	4.69	0.00	19.13	7.09
	SE	1.94	0.75	1.59	2.09	1.21	0.00	4.94	4.10
24 Jun	X̄	8.13	1.40	6.40	14.20	20.33	0.00	50.47	4.33
	SD	3.44	1.84	2.53	3.67	8.53	0.00	16.23	2.08
	SE	0.89	0.48	0.65	0.95	2.20	0.00	4.19	1.20
27 Jun	X̄	4.27	0.80	4.67	14.67	22.60	0.00	47.00	6.67
	SD	1.87	1.15	2.85	4.45	7.80	0.00	15.44	4.73
	SE	0.48	0.30	0.73	1.15	2.03	0.00	3.99	2.73
1 Jul	X̄	0.87	0.07	1.33	10.07	11.60	0.00	23..3	0.33
	SD	1.13	0.26	1.50	7.72	3.92	0.00	11.60	0.58
	SE	0.29	0.07	0.39	1.99	1.01	0.00	3.00	0.33
7 Jul	X̄	0.00	0.00	0.07	1.33	4.00	0.00	5.40	0.33
	SD	0.00	0.00	0.26	1.11	2.36	0.00	3.18	0.58
	SE	0.00	0.00	0.07	0.29	0.61	0.00	0.82	0.33
10 Jul	X̄	0.00	0.00	0.00	0.20	1.87	0.00	2.07	0.00
	SD	0.00	0.00	0.00	0.41	1.41	0.00	1.67	0.00
	SE	0.00	0.00	0.00	0.11	0.36	0.00	0.43	0.00
15 Jul	X̄	0.00	0.00	0.00	0.00	0.00	49.67	49.67	0.00
	SD	0.00	0.00	0.00	0.00	0.00	15.88	15.88	0.00
	SE	0.00	0.00	0.00	0.00	0.00	4.10	4.10	0.00
Total Incidence		491	121	243	285	309	--	--	114

K2 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
10 Jun	X̄	56.80	6.60	5.80	1.07	0.00	0.00	70.27	42.67
	SD	19.14	2.59	3.76	1.16	0.00	0.00	21.66	12.66
	SE	4.94	0.67	0.97	0.30	0.00	0.00	5.59	7.31
18 Jun	X̄	22.87	13.33	39.40	19.27	10.33	0.00	105.20	19.00
	SD	9.09	8.33	21.68	10.31	4.86	0.00	47.68	4.58
	SE	2.35	2.15	5.60	2.66	1.26	0.00	12.31	2.65
20 Jun	X̄	15.60	4.20	13.33	24.20	18.47	0.00	75.80	7.67
	SD	7.66	3.12	5.26	10.19	9.37	0.00	26.73	1.53
	SE	1.98	0.81	1.36	2.63	2.42	0.00	6.90	0.88
24 Jun	X̄	8.60	1.07	8.53	21.33	26.73	0.00	66.27	6.67
	SD	3.38	1.49	3.50	7.22	11.17	0.00	21.90	2.52
	SE	0.87	0.38	0.90	1.86	2.88	0.00	5.65	1.45
27 Jun	X̄	2.27	0.40	2.80	15.67	29.20	0.00	50.33	1.33
	SD	1.79	0.63	2.31	5.70	16.74	0.00	20.84	1.53
	SE	0.46	0.16	0.60	1.47	4.32	0.00	5.38	0.88
1 Jul	X̄	0.53	0.07	0.87	6.47	9.73	0.00	17.67	0.33
	SD	0.74	0.26	1.06	3.87	3.99	0.00	7.75	0.58
	SE	0.19	0.07	0.27	1.00	1.03	0.00	2.00	0.33
7 Jul	X̄	0.00	0.00	0.00	0.67	2.13	0.00	2.80	0.00
	SD	0.00	0.00	0.00	1.18	2.03	0.00	3.08	0.00
	SE	0.00	0.00	0.00	0.30	0.52	0.00	0.79	0.00
10 Jul	X̄	0.00	0.00	0.00	0.40	0.80	0.00	1.20	0.00
	SD	0.00	0.00	0.00	0.74	1.15	0.00	1.74	0.00
	SE	0.00	0.00	0.00	0.19	0.30	0.00	0.45	0.00
15 Jul	X̄	0.00	0.00	0.00	0.00	0.00	41.33	41.33	0.00
	SD	0.00	0.00	0.00	0.00	0.00	13.95	13.95	0.00
	SE	0.00	0.00	0.00	0.00	0.00	3.60	3.60	0.00
Total Incidence		339	111	304	339	364	--	--	118

K3 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
11 Jun	X̄	51.73	6.27	8.93	4.67	0.00	0.00	71.60	42.33
	SD	19.65	3.20	4.30	3.66	0.00	0.00	23.57	15.04
	SE	5.07	0.83	1.11	0.94	0.00	0.00	6.08	8.69
18 Jun	X̄	19.00	8.67	18.47	12.60	4.80	0.00	63.53	15.67
	SD	12.06	3.87	7.48	4.88	3.10	0.00	22.65	9.02
	SE	3.11	1.00	1.93	1.26	0.80	0.00	5.85	5.21
20 Jun	X̄	11.07	3.20	6.40	16.87	14.60	0.00	52.13	11.33
	SD	4.48	2.27	4.61	6.60	4.88	0.00	12.33	1.53
	SE	1.16	0.59	1.19	1.70	1.26	0.00	3.18	0.88
24 Jun	X̄	6.53	1.07	5.00	15.13	16.13	0.00	43.87	2.67
	SD	3.58	1.16	2.24	6.82	8.19	0.00	16.14	1.53
	SE	0.93	0.30	0.58	1.76	2.12	0.00	4.17	0.88
27 Jun	X̄	1.67	0.07	1.13	6.87	15.40	0.00	25.13	2.33
	SD	1.68	0.26	1.41	3.11	5.08	0.00	8.05	3.21
	SE	0.43	0.07	0.36	0.80	1.31	0.00	2.08	1.86
1 Jul	X̄	0.53	0.13	1.13	5.27	8.73	0.00	15.80	0.33
	SD	0.83	0.52	1.88	3.47	4.03	0.00	8.56	0.58
	SE	0.22	0.13	0.49	0.90	1.04	0.00	2.21	0.33
7 Jul	X̄	0.00	0.00	0.00	0.80	1.40	0.00	2.20	0.00
	SD	0.00	0.00	0.00	1.08	1.88	0.00	2.43	0.00
	SE	0.00	0.00	0.00	0.28	0.49	0.00	0.63	0.00
10 Jul	X̄	0.00	0.00	0.00	0.33	0.73	0.00	1.07	0.00
	SD	0.00	0.00	0.00	0.82	1.28	0.00	1.98	0.00
	SE	0.00	0.00	0.00	0.21	0.33	0.00	0.51	0.00
15 Jul	X̄	0.00	0.00	0.00	0.00	0.00	9.93	9.93	0.00
	SD	0.00	0.00	0.00	0.00	0.00	7.16	7.16	0.00
	SE	0.00	0.00	0.00	0.00	0.00	1.85	1.85	0.00
Total Incidence		451	75	161	232	229	--	--	99

TABLE 21.

1969 CAGE STUDY

M1 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
9 Jun	$\bar{X}$	14.87	3.33	0.87	0.00	0.00	0.00	19.07	8.67
	SD	6.17	2.35	1.13	0.00	0.00	0.00	6.76	3.21
	SE	1.59	0.61	0.29	0.00	0.00	0.00	1.74	1.86
17 Jun	$\bar{X}$	10.07	4.53	9.67	4.67	0.80	0.00	29.78	13.67
	SD	4.37	1.73	4.17	3.04	1.78	0.00	12.29	6.66
	SE	1.13	0.45	1.08	0.78	0.46	0.00	3.17	3.84
20 Jun	$\bar{X}$	6.60	0.47	3.67	5.93	4.87	0.00	21.53	5.33
	SD	4.37	0.83	2.47	1.83	1.68	0.00	6.16	0.58
	SE	1.13	0.22	0.64	0.47	0.43	0.00	1.59	0.33
24 Jun	$\bar{X}$	8.00	0.67	2.33	13.47	9.93	0.00	34.40	5.67
	SD	4.16	0.90	1.76	4.49	3.10	0.00	8.76	1.53
	SE	1.07	0.23	0.45	1.16	0.80	0.00	2.26	0.88
27 Jun	$\bar{X}$	3.27	0.53	2.47	8.67	14.93	0.00	29.87	0.67
	SD	3.31	0.92	1.96	4.20	4.67	0.00	8.66	0.58
	SE	0.85	0.24	0.51	1.09	1.21	0.00	2.24	0.33
1 Jul	$\bar{X}$	0.80	0.20	1.07	5.20	6.53	0.00	13.80	0.33
	SD	0.86	0.56	0.88	3.30	2.53	0.00	5.44	0.58
	SE	0.22	0.14	0.23	0.85	0.65	0.00	1.40	0.33
7 Jul	$\bar{X}$	0.60	0.00	0.13	1.67	4.27	0.00	6.67	0.67
	SD	0.74	0.00	0.35	0.82	1.33	0.00	2.32	1.15
	SE	0.19	0.00	0.09	0.21	0.34	0.00	0.60	0.67
10 Jul	$\bar{X}$	0.00	0.00	0.00	0.40	2.33	0.00	2.73	0.00
	SD	0.00	0.00	0.00	0.74	1.23	0.00	1.53	0.00
	SE	0.00	0.00	0.00	0.19	0.32	0.00	0.40	0.00
15 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	17.13	17.13	0.00
	SD	0.00	0.00	0.00	0.00	0.00	4.87	4.87	0.00
	SE	0.00	0.00	0.00	0.00	0.00	1.26	1.26	0.00
Total Incidence		216	45	92	159	170	--	--	40

L1 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
10 Jun	$\bar{X}$	5.20	0.73	0.20	0.00	0.00	0.00	6.13	5.33
	SD	2.93	0.88	0.56	0.00	0.00	0.00	3.11	3.51
	SE	0.76	0.23	0.14	0.00	0.00	0.00	0.80	2.03
17 Jun	$\bar{X}$	5.67	3.80	4.33	0.80	0.00	0.00	14.60	6.00
	SD	3.75	2.76	2.06	0.94	0.00	0.00	6.74	4.00
	SE	0.97	0.71	0.53	0.24	0.00	0.00	1.74	2.31
20 Jun	$\bar{X}$	3.27	1.20	3.67	2.33	2.13	0.00	12.60	1.33
	SD	1.98	1.15	2.06	1.68	1.55	0.00	4.66	1.15
	SE	0.51	0.30	0.53	0.43	0.40	0.00	1.20	0.67
24 Jun	$\bar{X}$	3.00	0.20	0.80	5.40	5.20	0.00	14.60	0.33
	SD	2.30	0.41	1.08	3.68	2.88	0.00	6.61	0.58
	SE	0.59	0.11	0.28	0.95	0.74	0.00	1.71	0.33
27 Jun	$\bar{X}$	0.80	0.20	0.67	3.13	6.60	0.00	11.40	1.33
	SD	0.77	0.41	0.72	2.90	2.72	0.00	5.38	1.53
	SE	0.20	0.11	0.19	0.75	0.70	0.00	1.39	0.88
1 Jul	$\bar{X}$	0.67	0.07	0.47	3.20	4.13	0.00	8.53	2.67
	SD	0.98	0.26	0.74	2.18	2.59	0.00	5.30	4.62
	SE	0.25	0.07	0.19	0.56	0.67	0.00	1.37	2.67
7 Jul	$\bar{X}$	0.00	0.00	0.00	1.00	1.47	0.00	2.47	0.00
	SD	0.00	0.00	0.00	1.13	1.30	0.00	2.10	0.00
	SE	0.00	0.00	0.00	0.29	0.34	0.00	0.54	0.00
10 Jul	$\bar{X}$	0.00	0.00	0.00	0.27	1.53	0.00	1.80	0.00
	SD	0.00	0.00	0.00	0.46	1.06	0.00	1.21	0.00
	SE	0.00	0.00	0.00	0.12	0.27	0.00	0.31	0.00
15 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	9.33	9.33	0.00
	SD	0.00	0.00	0.00	0.00	0.00	3.56	3.56	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.92	0.92	0.00
Total Incidence		82	28	43	64	82	--	--	18

M2 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
10 Jun	$\bar{X}$	10.86	1.93	1.21	0.00	0.00	0.00	14.00	13.33
	SD	5.08	1.54	1.05	0.00	0.00	0.00	4.96	10.60
	SE	1.36	0.41	0.28	0.00	0.00	0.00	1.33	6.12
18 Jun	$\bar{X}$	7.27	2.87	4.47	3.20	1.07	0.00	18.87	8.67
	SD	2.37	1.81	3.29	2.31	1.28	0.00	7.46	2.31
	SE	0.61	0.47	0.85	0.60	0.33	0.00	1.93	1.33
20 Jun	$\bar{X}$	6.73	0.87	2.67	4.13	3.80	0.00	18.20	3.33
	SD	2.91	1.13	2.23	2.92	2.21	0.00	6.43	0.58
	SE	0.75	0.29	0.57	0.76	0.57	0.00	1.66	0.33
24 Jun	$\bar{X}$	4.20	0.53	1.67	4.73	4.13	0.00	15.27	1.33
	SD	1.82	0.92	1.23	2.94	1.85	0.00	3.92	0.58
	SE	0.47	0.24	0.32	0.76	0.48	0.00	1.01	0.33
27 Jun	$\bar{X}$	2.53	0.53	1.07	6.07	7.33	0.00	17.53	0.33
	SD	2.07	0.64	1.16	3.15	3.62	0.00	5.88	0.58
	SE	0.53	0.17	0.30	0.81	0.93	0.00	1.52	0.33
1 Jul	$\bar{X}$	1.40	0.13	1.07	5.47	5.67	0.00	13.73	0.67
	SD	2.10	0.35	1.03	2.20	2.26	0.00	4.23	0.58
	SE	0.54	0.09	0.27	0.57	0.58	0.00	1.09	0.33
7 Jul	$\bar{X}$	0.33	0.00	0.00	1.40	4.00	0.00	5.73	0.33
	SD	0.49	0.00	0.00	1.45	2.73	0.00	3.58	0.58
	SE	0.13	0.00	0.00	0.38	0.70	0.00	0.92	0.33
10 Jul	$\bar{X}$	0.00	0.00	0.13	1.33	3.60	0.00	5.07	0.00
	SD	0.00	0.00	0.35	0.72	1.64	0.00	2.34	0.00
	SE	0.00	0.00	0.09	0.19	0.42	0.00	0.61	0.00
15 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	16.67	16.67	0.00
	SD	0.00	0.00	0.00	0.00	0.00	9.76	9.76	0.00
	SE	0.00	0.00	0.00	0.00	0.00	2.52	2.52	0.00
Total Incidence		156	29	57	105	118	--	--	32

L2 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
10 Jun	$\bar{X}$	3.33	0.80	0.13	0.00	0.00	0.00	4.27	2.33
	SD	2.61	0.94	0.35	0.00	0.00	0.00	2.94	1.53
	SE	0.67	0.24	0.09	0.00	0.00	0.00	0.76	0.88
18 Jun	$\bar{X}$	3.07	2.27	2.53	1.47	0.73	0.00	10.07	1.67
	SD	2.89	1.79	2.00	1.19	0.70	0.00	5.12	0.58
	SE	0.75	0.46	0.52	0.31	0.18	0.00	1.32	0.33
20 Jun	$\bar{X}$	2.00	1.00	0.80	1.33	2.33	0.00	7.47	0.67
	SD	2.24	1.20	1.08	1.11	2.35	0.00	4.24	1.15
	SE	0.58	0.31	0.28	0.29	0.61	0.00	1.09	0.67
24 Jun	$\bar{X}$	1.53	0.27	0.80	2.87	2.33	0.00	7.80	0.00
	SD	1.41	0.59	0.94	1.60	0.98	0.00	3.30	0.00
	SE	0.36	0.15	0.24	0.41	0.25	0.00	0.85	0.00
27 Jun	$\bar{X}$	1.27	0.00	0.20	2.67	3.40	0.00	7.53	0.00
	SD	0.96	0.00	0.41	1.88	2.44	0.00	3.16	0.00
	SE	0.25	0.00	0.11	0.48	0.63	0.00	0.82	0.00
1 Jul	$\bar{X}$	0.53	0.07	0.13	1.67	1.93	0.00	4.33	0.00
	SD	0.74	0.26	0.35	1.84	1.49	0.00	2.92	0.00
	SE	0.19	0.07	0.09	0.47	0.38	0.00	0.75	0.00
7 Jul	$\bar{X}$	0.13	0.00	0.07	0.60	1.00	0.00	1.80	0.00
	SD	0.35	0.00	0.26	0.74	0.62	0.00	1.37	0.00
	SE	0.09	0.00	0.07	0.19	0.16	0.00	0.35	0.00
10 Jul	$\bar{X}$	0.07	0.00	0.07	0.13	1.47	0.00	1.73	0.00
	SD	0.26	0.00	0.26	0.35	1.25	0.00	1.44	0.00
	SE	0.07	0.00	0.07	0.09	0.32	0.00	0.37	0.00
15 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	2.93	2.93	0.00
	SD	0.00	0.00	0.00	0.00	0.00	2.02	2.02	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.52	0.52	0.00
Total Incidence		55	19	20	42	51	--	--	7.5

M3 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
11 Jun	$\bar{X}$	22.27	4.33	3.60	1.13	0.00	0.00	31.33	18.00
	SD	8.63	2.61	1.30	1.25	0.00	0.00	9.90	6.00
	SE	2.23	0.67	0.34	0.32	0.00	0.00	2.56	3.46
18 Jun	$\bar{X}$	9.33	4.40	9.67	3.33	1.67	0.00	28.40	10.67
	SD	2.69	1.92	4.45	1.72	1.18	0.00	8.13	1.15
	SE	0.69	0.50	1.15	0.44	0.30	0.00	2.20	0.67
20 Jun	$\bar{X}$	7.53	1.00	3.87	9.20	5.93	0.00	27.53	5.33
	SD	5.66	0.85	2.29	3.67	2.63	0.00	7.38	3.21
	SE	1.46	0.22	0.59	0.95	0.68	0.00	1.90	1.86
24 Jun	$\bar{X}$	4.60	0.53	2.40	8.73	10.13	0.00	26.40	2.00
	SD	2.41	1.13	1.40	3.35	3.07	0.00	7.31	0.62
	SE	0.62	0.29	0.36	0.86	0.79	0.00	1.89	0.36
27 Jun	$\bar{X}$	1.87	0.20	0.87	7.73	13.60	0.00	24.27	0.67
	SD	1.73	0.56	1.36	3.08	5.12	0.00	9.60	1.15
	SE	0.45	0.14	0.35	0.80	1.32	0.00	2.48	0.67
1 Jul	$\bar{X}$	1.00	0.07	0.67	6.47	10.27	0.00	18.47	0.67
	SD	1.25	0.26	1.18	2.39	2.81	0.00	6.06	0.58
	SE	0.32	0.07	0.30	0.62	0.73	0.00	1.56	0.33
7 Jul	$\bar{X}$	0.00	0.00	0.00	1.53	3.93	0.00	5.47	0.00
	SD	0.00	0.00	0.00	1.51	2.37	0.00	3.52	0.00
	SE	0.00	0.00	0.00	0.30	0.61	0.00	0.91	0.00
10 Jul	$\bar{X}$	0.00	0.00	0.00	0.73	1.80	0.00	2.53	0.00
	SD	0.00	0.00	0.00	1.28	1.78	0.00	2.88	0.00
	SE	0.00	0.00	0.00	0.33	0.46	0.00	0.74	0.00
15 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	19.13	19.31	0.00
	SD	0.00	0.00	0.00	0.00	0.00	6.55	6.55	0.00
	SE	0.00	0.00	0.00	0.00	0.00	1.69	1.69	0.00
Total Incidence		224	41	83	146	185	--	--	48

L3 CAGE

Date	Stat	Eggs	Instar 1	Instar 2	Instar 3	Instar 4	Pupae	Total	Egg Input
10 Jun	$\bar{X}$	3.75	0.25	0.75	0.00	0.00	0.00	4.75	1.33
	SD	2.60	0.45	1.06	0.00	0.00	0.00	2.99	0.58
	SE	0.75	0.13	0.30	0.00	0.00	0.00	0.86	0.33
18 Jun	$\bar{X}$	2.07	2.20	2.40	1.47	0.40	0.00	8.53	2.33
	SD	1.44	1.70	1.45	1.30	0.74	0.00	3.80	0.58
	SE	0.37	0.44	0.38	0.34	0.19	0.00	0.98	0.33
20 Jun	$\bar{X}$	3.07	0.53	2.07	1.93	2.13	0.00	9.73	0.00
	SD	2.60	0.92	1.53	1.33	2.10	0.00	4.76	0.00
	SE	0.67	0.24	0.40	0.34	0.54	0.00	1.23	0.00
24 Jun	$\bar{X}$	1.67	0.20	0.80	3.67	2.27	0.00	8.60	1.00
	SD	1.40	0.56	1.15	2.32	1.98	0.00	4.87	0.00
	SE	0.36	0.14	0.30	0.60	0.51	0.00	1.26	0.00
27 Jun	$\bar{X}$	1.00	0.07	0.33	3.33	3.60	0.00	8.33	0.33
	SD	0.93	0.26	0.72	2.53	1.92	0.00	4.17	0.58
	SE	0.24	0.07	0.19	0.65	0.50	0.00	1.08	0.33
1 Jul	$\bar{X}$	0.67	0.00	0.27	3.00	3.73	0.00	7.67	0.33
	SD	0.90	0.00	0.70	1.36	1.71	0.00	2.41	0.58
	SE	0.23	0.00	0.18	0.35	0.44	0.00	0.62	0.33
7 Jul	$\bar{X}$	0.00	0.00	0.13	0.60	1.73	0.00	2.47	0.00
	SD	0.00	0.00	0.52	0.99	1.75	0.00	2.88	0.00
	SE	0.00	0.00	0.13	0.25	0.45	0.00	0.74	0.00
10 Jul	$\bar{X}$	0.00	0.00	0.00	0.73	2.07	0.00	2.80	0.00
	SD	0.00	0.00	0.00	0.96	1.33	0.00	2.04	0.00
	SE	0.00	0.00	0.00	0.25	0.34	0.00	0.53	0.00
15 Jul	$\bar{X}$	0.00	0.00	0.00	0.00	0.00	7.13	7.13	0.00
	SD	0.00	0.00	0.00	0.00	0.00	5.10	5.10	0.00
	SE	0.00	0.00	0.00	0.00	0.00	1.32	1.32	0.00
Total Incidence		55	15	27	58	64	--	--	95