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THE LAWN ARMYWORM, Spodoptera mauritia acronyctoides (Guenée)
(LEPIDOPTERA: NOCTUIDAE), WITH ITS NUCLEAR POLYHEDROSIS VIRUS

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS OF THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN ENTOMOLOGY

May 1982

by

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ACKNOWLEDGEMENTS

I have much gratitude to the East-West Center for sponsoring my study in Hawaii.

Special acknowledgement is due to my advisor, Dr. Minoru Tamashiro, from the Department of Entomology, who made my Ph.D. program possible, and who encouraged and supported me throughout my study. I would like to express sincere appreciation to Dr. Tung Liang, from Department of Agricultural Engineering, for his guidance and criticism in carrying out the systems study. I am also indebted to Dr. Blair M. Bennett, from the School of Public Health, who assisted me with the statistical analysis. I especially would like to thank Dr. Devindar Singh, from the Department of Agricultural Engineering, who kindly instructed me in the use of the simulation language.

Grateful acknowledgement is also due to the members of the Insect Pathology and Termite Laboratories, particularly Mr. Richard H. Ebesu, Mr. Abdul Rahman Rashid and Mr. Julian R. Yates III.

I am especially grateful to my wife, Adela (Kum Sook), for her patience, understanding and support that made this undertaking so meaningful.
ABSTRACT

Simulation modeling was employed in a systems technique to represent epizootics of nuclear polyhedrosis virus (NPV) in the lawn armyworm.

An analytic approach which consisted of three research phases was utilized. First, the basic life system of the insect was simulated by developing data on the life history of the armyworm and integrating the data into a proposed algorithm on temperature-development relationships. Secondly, NPV epizootics were simulated by obtaining data on the susceptibility of the armyworm to NPV and this was combined with the basic life system to construct an epizootiological model. Thirdly, the developed models were optimized so that the results could be used to make appropriate pest management decisions. The computer simulation language, GPSS (General Purpose Simulation Systems) was used to represent the life system of the lawn armyworm.

Generally the data obtained from the model were in good agreement with the actual data representing the quantitative and chronological development of armyworm populations and their NPV epizootics. The ability of the computer simulation language to predict and/or accommodate epizootiological phenomena was demonstrated in this study.
The optimization of host plant protection and virus production through the contour mapping indicated that the pattern of adult introduction affected the characteristics of the progeny population. In general, the earlier and the more aggregatedly the females were introduced, the earlier was the optimized spray time for the host plant protection. The more aggregatedly the females were introduced, the more effective was the virus treatment. In addition the yield was greatly increased when the treatment was applied early in the infestation but virus production was greatly increased when the treatment was made after the population was more mature.

Although more tests are required to quantitatively substantiate the reliability of the model, the simulation and optimization processes developed in this study indicated that the systems technique and modeling can be used as a practical strategic tool in pest management. This can be accomplished by integrating the model with empirical knowledge of crop protection or combining it with other optimization models.
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INTRODUCTION

The rapid development of chemical pesticides since the 1940's has produced epoch-making progress in the history of crop protection. The chemicals were fast in effect, economical and applicable to a wide variety of insects, including agricultural pests, urban pests and medically important insects. The ease at which these pesticides could be applied and the early efficiency of these materials have led to a contemporary pest control pattern which is heavily dependent on chemical insecticides.

The long-term indiscriminate use of chemicals resulted in some serious side-effects, such as the development of resistance by pests, abrupt abundance of minor pests, toxicity to man and animals, pollution of the environment by chemical residues, etc..

To cope with these problems resulting from one-sided chemical control, the concept of pest management has been introduced for crop protection. By selecting the most appropriate control practices and integrating them in the manner that the control methods caused least adverse effects, pest management has produced maximum crop protection with a minimum of environmental disruption.

Since pest management is an integrated science that covers all related factors in plant protection, its development has been especially accelerated by the recent advancement of three affiliated fields: 1)
population ecology, 2) re-evaluation of alternative control practices--biological, physical, cultural, etc.--, and 3) modeling and systems technique.

While the development of principles in population ecology supports understanding the complex of interrelationships between pest populations and environmental factors, re-evaluation of importance of alternative control agents provides a more and wide variety of control methods on the practical basis. Regarding various harmful side effects have been produced on the pest status and the ecosystem by the excessive use of chemicals, these two biology-related affiliated fields have been playing a very important role in guiding the future of pest control.

However, the introduction of the biology-affiliated fields to pest management has produced complicated problems in the plant protection system. Not only has the simple aspect of pest regulation by control practices been an important concern, but all the interrelated effects among pest populations, various control agents, environments and other economically important factors have to be considered within the context of the whole food production system.

This complex of pest control problems naturally requires an integrated, and systematic methodology for problem solving so that it can cover all the relational effects of variables in quantitative terms to make it possible to maximize agricultural productivity with minimum of pest damage.
Systems approach, an organized attempt to consider all the interactions among all components in pest management and agro-ecosystems, serves as the best strategic tool for solving the complicated situation of pest problems. With the help of quantitative analysis and mathematical modeling, one may be able to predict the future occurrence of pest and make right decisions for the development of control strategies.

While population ecology and systems technique support the theoretical or methodological development in control strategy, re-evaluation and improvement of alternative control agents have contributed to advancing practical control practices to regulate pest populations. One of the alternative control measures being extensively investigated for use in pest management programs is insect disease.

Insect pathogens can be used either as microbial insecticides or as introductions leading to establishment in pest populations (Burges and Hussey 1971). When properly used, microbial control agents have various advantages such as specificity, relative safety to man and environment, no resistance problems, etc. Among the insect pathogens, the baculoviruses have been considered as one of the more promising pest control agents due to their virulence to their hosts, safety to nontarget organisms and ease of production and handling.

However, because these insect pathogens are organisms, a more complicated control situation would be produced when they are used as
the key control agent in a pest management program. In addition to all the complex relationships between the pest population and environment, the pathogen itself has its own complex relationships to the environmental factors.

To cope with this complex of "pest-pathogen-environment" relationships, the previously-mentioned modeling and systems technique could be most appropriately used. The technique can quantitatively analyze the partial impact of all the control components in the pest management system, and synthesize them again in a manner to provide the basic information on utilizing the control agent as a part of system-based control practices within the whole framework of a pest management program.

Although numerous reports have been published on systems and modeling studies regarding general pest management tactics and other control methods--especially biological and chemical control--very few studies have been made on modeling in insect disease systems. Considering the importance of insect pathogens as one of the most promising alternative control agents as well as their complexity in relationships with pest populations and environments, a more systems-oriented study is desired in the field of microbial control.

Since there has been a considerable history of study on the epizootics of the nuclear polyhedrosis virus (NPV) in the lawn armyworm population in Hawaii, the NPV-armyworm relationship was chosen as the
target disease system in this study. By using this pathogen-host relationship as a subject of quantitative analysis and simulation modeling, it was possible to formulate an epizootiological system of the virus disease to predict the trend of the healthy and infected host population.

Considering that NPV is one of the promising control agents that regulate the armyworm population, the simulation of disease development under the systems concept would be given as a good example on how modeling can be appropriately used as a practical tool in pest management. With the same principle applied to simulation modeling in microbial control in this study, it can be applicable to other control factors, such as chemical control, biological control, etc.

Even though the study was to formulate an epizootiological system of NPV in association with the host insect life system, another important point had to be considered in simulation modeling. Because the ultimate goal of systems study lies in finding the "total optimum" status among all components, numerous factors in the insect management system have to be related from various aspects: agricultural productivity, conservation of system resources, economics, safety to man and animal, etc. However it is practically impossible to integrate all of these components to construct a model without first breaking them down into a more amenable form.
A more realistic and convenient way is an analytic process: to consider all these factors separately and study the system by adding important component one by one to the simplest form of the life system. The simplest life system may be defined as a system where the conditions for population growth are ideal, and the biotic potential of the insect would be fully embodied under favorable environmental conditions.

Because it is assumed that the biotic potential of the insect is not affected by other environmental factors in the simplest life system, the individual effect of target component would clearly appear on the life process of the insect. This makes it easy to determine quantitative impact of the individual component on the insect population. Through this step by step approach--adding factors to the host population one by one--, a greater chance to adjust or compare with the empirical (or experimental) results would also be available.

In realistic terms, however, it is very difficult to produce (or simulate) the exact environmental conditions where all the components --or combinations of the components-- are optimal for the growth of the population. Thus, in this study, it was assumed that the population development would represent the simplest life system of the lawn armyworm if the population was grown under the "empirically known" favorable environmental conditions: sufficient food, free from natural enemies, optimal weather conditions, etc..
Although the population growth could also differ depending upon the variation of components, the variation caused within the optimal range was considered negligible. For this study, general rearing methods in the laboratory or in semi-field conditions were assumed to satisfy the empirical criteria for favorable environmental conditions. Only temperature was considered to be a variable factor to regulate the population development. The population development under these favorable environmental conditions was called a basic life system, and the simulation model to represent the basic life system was designated as a basic life model.

To summarize the general scope of this systems study, the objectives of the research are: 1) to test predicting and accommodating ability of a simulation language in representing a biological phenomenon, insect life system, and 2) to check the applicability of the developed model as a practical strategic tool in planning a pest management program; in this case, the use of microbial agent, NPV. For simplicity, the research process was conducted in three phases in this study (Figure 1). They were 1) simulation of a basic life system of the armyworm by the use of life history data under favorable environmental conditions, 2) simulation of epizootic development based on the basic life model and bioassay results, and 3) application of the developed model through an optimization process to make decisions in pest management planning.
Figure 1. -- Study process of systems approach and simulation modeling in the lawn armyworm management with its virus epizootics
EXPERIMENTS SIMULATION

BASIC LIFE SYSTEM

- FECUNDITY & EGG DEVELOPMENT
- INDIVIDUAL REARING
- MASS REARING

TEST & ADJUSTMENT

SIMULATION

BASIC LIFE MODEL

EPIZOOTICS

- VIRUS SPRAY -INDIVIDUAL-
- VIRUS SPRAY -MASS-

TEST & ADJUSTMENT

APPLICATION

- POLYHEDRA PRODUCTION
- FOOD CONSUMPTION

PEST MANAGEMENT DECISION MAKING (OPTIMIZATION)

STUDY PROCESS
As an initial step for obtaining biological data for the basic life system, individual rearing tests were conducted under different temperatures. Fecundity, periods for physiological development, age structure, and survival rates were observed from the rearing at each life stage of the armyworm.

After collecting biological parameters, the basic life model was constructed to predict population development--quantitative and chronological--based on the proposed algorithm on temperature-development relationship. To represent the armyworm life system, a computer simulation language, GPSS (General Purpose Simulation Systems) was used in this study.

Subsequently, suspensions of NPV polyhedra were sprayed at various concentrations on the armyworm larvae to observe stage-specific mortalities and infection periods. Based on these disease development results, regression analyses were made to express the quantitative relationship between virus concentration and mortalities. By adding the bioassay results to the basic life model, an epizootiological model was constructed to predict disease development in the lawn armyworm population with spray time, virus concentration and daily average temperature as the variables.

After finishing the simulation process, an optimization process was conducted to provide the basis for making decisions in pest control strategy. By running the developed simulation model at different
combinations of control practices--spray time and virus concentration--, the contour mapping method was applied to determine the most effective control impact on the host plant protection (i.e., minimizing feeding damage) and virus recovery after the initial epizootic. Also the applicability and problems of the simulation language in representing the insect life system was further discussed in this study.
A. Lawn Armyworm Biology and the Nuclear Polyhedrosis Virus

Because of its economic importance from the 1950's through the early 1970's, the lawn armyworm has been the subject of a series of studies in Hawaii. The insect was first correctly recorded by Pamberton (1955) on Oahu in 1953. Within a year Tanada (1955) observed the first outbreak of the lawn armyworm on Bermuda grass, Cynodon dactylon (L.) Persoon, and soon it became one of the most serious pests of the lawns in the islands.

In 1958 Tanada and Beardsley conducted an extensive biological study of the insect. They reported that the entire life cycle in the laboratory (temperature ranging from 22 °C to 29 °C) required about 42 days. It took approximately 28 days and 11 days respectively for the completion of larval and pupal development. They also observed that most larvae passed through seven larval instars with some exceptions for eight larval instars, and that a female moth laid an average of 8.6 egg masses.

About two years after the recording of the insect in Hawaii, Bianchi (1957) reported the finding of a nuclear polyhedrosis-like virus disease in the lawn armyworm caterpillars in Honolulu which was apparently important in the natural control of this pest. Tanada and
Beardsley (1957) believed that the virus entered Hawaii together with its host and was probably disseminated by female moths through eggs.

Tanada (1960) found that the virus was rod-shaped and occurred within a polyhedral inclusion body which developed in the nucleus of the host cell. The virus-infected larvae showed a "wilt condition", the typical symptoms of nuclear polyhedrosis; their skins became fragile and their internal contents turned to a fluid mass. The histopathology of the virus was also similar to that of most nuclear polyhedroses in other insects. The main sites of infection were the hypodermis, fat bodies and tracheal matrix.

Based on these observations, Tanada concluded that the disease causing organism in the lawn armyworm caterpillars was a nuclear polyhedrosis virus, and named it as a species of Borrelinivirus. To determine the lethal infection period (the period from exposure to the virus until death of the larvae), he conducted bioassay tests by feeding the larvae with grass leaves coated with massive doses of polyhedra.

In 1965 Raheja further explored the susceptibility of the armyworm to the virus. He found that the susceptibility of the larvae decreased with age. When larvae were fed on Napier grass bouquets dipped in polyhedral suspensions at a concentration of $2.5 \times 10^6$ polyhedra/ml, mortalities were 100% for the first and second instar larvae, 81% for the third, 76% for the fourth, 37% for the fifth, 10% for the sixth and 3% for the seventh instar larvae.
This differential susceptibility in relation to age was also reflected in the length of the lethal infection period, showing similar results to those reported by Tanada (1960). The younger the larvae were infected, the shorter the lethal infection period was. It varied from 3 days when the first instar larvae were infected, to 7-11 days when the fourth to seventh instar larvae were infected. By using the "micro-feeding method", Raheja also determined the median lethal dose (LD$_{50}$) of NPV to the fourth instar larva to be 270 polyhedra/larva.

The integrated effects of the virus and the other biological agents on the armyworm population were also studied. Raheja (1965) reported that mortality resulted mainly from the virus infection when the NPV and a Nosema sp. were administered to fourth instar larvae of the insect simultaneously or at different time intervals.

A comparative pathological study of the interactions of NPV, a Nosema sp. and a parasite, Apanteles marginiventris (Cresson), in the host insect was conducted by Laigo and Tamashiro (1966). According to them, mortality of parasite larvae was due primarily to the premature death of the host (mal-nutrition) rather than to the direct effect of the pathogens. In addition they reported that viral infection apparently did not cause sufficient changes to render the host nutritionally inadequate for the development of the parasite, while the nosema infection did. They also observed that parasites allowed to oviposit in diseased hosts successfully transmitted infective doses of the virus at random rather than logical order.
In 1971 Takei made a detailed physio-pathological study of the lawn armyworm disease of NPV and a *Nosema* sp., along with developing an axenic rearing technique of the insect. From bioassay tests he observed that, in the disease development of the armyworm, the dosage-mortality and time-mortality curves were generally of the sigmoid type. By feeding the fourth instar larvae on polyhedral suspensions with an artificial diet ($6.33 \pm 0.14$ gms per vial), he calculated $L_50$ of the larva as $9.29 \times 10^4$ polyhedra per vial.

Takei also reported that, after the recovery from virus dosages, the surviving larvae showed no significant difference from the controlled groups in developmental period or in the emergence of the adults with exceptions for the case of extremely high dosage treatment. From blood analyses it was observed that lethal doses of the virus resulted in a general reduction of hemolymph proteins (hypo-proteinemia) in infected larvae, and that this appeared to involve stress factors, host reactions and the host endocrine system (Takei and Tamashiro, 1975).

So far much research has been conducted on the life history of the lawn armyworm and its NPV epizootics. Most of it dealt with the qualitative aspects of the armyworm life cycle, while a small portion was concerned with the quantitative side of NPV epizootics. There has been no quantitative data to represent the life table of the armyworm population in Hawaii. As for the epizootic development of the virus,
quantified analysis on dosage-mortality relationships was made only for the fourth instar larval stage. As the basis for constructing a model to simulate the basic and epizootiological life system of the armyworm, it is necessary to obtain a quantified data on the life process of the armyworm population and its disease development.

B. Modeling

According to Ruesink's (1976) review, the earliest literature on the systems approach to insect pest management appeared in 1961 (K. E. F. Watt). Since then many scientists have been involved in developing models and systems techniques for various use in agricultural entomology. By integrating the data from population dynamics, environments and control tactics, specifically designed models have been developed for managing many pest species, important crops and natural enemies.

Although many models have been constructed in various fields of pest management, very little research has been done on microbial control and insect epizootiology. Quite recently several workers initiated a study of modeling in fungal and bacterial diseases of pest insects: development of a predictive equation to forecast *Nomuraea rileyi* (Farlow) levels among the velvetbean caterpillar populations under various environmental conditions (Kish and Allen, 1978) and application of a mathematical model to predict persistency of *Bacillus* thuringiensis and its host mortality in the environment after field application (Brand et al, 1975 and 1976, and Pinnock et al, 1978). No publications have been
found on modeling of virus epizootiology of agricultural insects except for some presentations at the meeting of the Society of Invertebrate Pathology (Stimac, 1979 and Stairs, 1979).

Even though modeling and systems study in pest management have a short history, the efforts to find a mathematical expression to predict the speed of physiological development of the insect at different temperature conditions have probably been going on since the end of the last century. There have been many reviews on this subject (Shelford, 1927, Belehradek, 1935, Davidson, 1942 and 1944, Fry, 1947, Andrewartha and Birch, 1967 and 1973, Wigglesworth, 1972 and Stinner et al, 1974a, and b, and 1975).

Among these, an organized study on the historical development of mathematical expressions has been done by Andrewartha and Birch (1967 and 1973). According to them, a number of proposed models were classified into "physiological" or "biological," based on the purpose for which the models were intended (Fry, 1947), or "theoretical" or "empirical," based on ecological applicability of the developed models (Davidson, 1944).

The traditional vant' Hoff (1884) and Arrhenius (1915) equations as well as the Bølerhádek (1935) formula were designated as "physiological". The equation of Janisch (1925) and the well-known "thermal summation" method were called "biological" expressions. The "theoretical" expressions, somewhat analogous to "physiological" models of Fry, consist
of the equations of vant'Hoff and Arrhenius, while the rest of the
developed models were considered as "empirical" by Davidson.

The theoretical or physiological equations of vant'Hoff and
Arrhenius were part of the earliest developed models to illustrate the
relationship between temperature and the acceleration of chemical and
physical reactions. In essence both expressions imply the same idea that
the proportional increase in the speed of the development produced by a
given difference in temperature is constant throughout temperature range
at which an animal may develop (Andrewartha and Birch, 1967).

In practice, however, there have been many examples of the
parameters being far from constant. They remain stable only for a very
restricted part of the tested temperature range, and vary in a systematic
way with the temperature gradient (Davidson, 1944). By pointing out that
the developed parameters were originally designed to describe the
relationship of temperature to a single chemical reaction, Andrewartha
and Birch (1967) argued on the inadequacy of the application of the
theoretical expressions to the situation of animal morphogenesis, an
immensely complex chain of metabolic reaction.

Empirical equations, which seem to better serve the practical
purpose of the developmental ecology of the insects, were initially
developed from the concept of "thermal summation". According to Shelford
(1927), Becquerel (1853) considered Reaumur (1735) to be one of the
earliest investigators who contended that the product of the mean daily
temperature and the number of days was useful for determination of development in the field. But a modern type of thermal summation study—more mathematically-oriented and actually applicable to practical use—began around the latter part of the last century.

Oettingen (1879) was probably the first to use the term "threshold" for the temperature at which development begins, and made thermal sums from this in his study of the Dorpat woody plants. To determine the threshold of development, he assumed a series of threshold values, calculated the product of the developmental period and temperature for each value, and selected the one which gave the most nearly constant products for different mean temperatures.

The thermal summation method basically stems from the concept of a straight line relationship between temperature and speed of development, and can be expressed as a hyperbolic equation:

\[ C = Y \times (X - A) \]  

(1)

where \( Y \) is the developmental period, \( X \) is temperature, \( A \) is the threshold of development, and \( C \) is the thermal constant. On the condition that the relationship between temperature and speed of development is a straight line, and if the developmental period is plotted against temperature, the points would fall on a hyperbola (Andrewartha and Birch, 1973).
Based on the hyperbolic equation, Simpson (1903) first introduced the concept of "day-degrees" in his study of the codling moth. Since then the day-degrees, as a unit of thermal constant, was widely used for the practice of predicting development until some researchers started to find departures from linearity in the temperature-development relationship at the higher or lower ranges of the temperature.

In his study of effects of temperature on fish and frog eggs, Krogh (1914) discovered that the threshold calculated by the thermal summation method was not the real one and the graph representing the velocity of development was flattened out at the lower end of temperature range, falling off at the upper end. As for insect development, Glenn (1922) was one of the earliest researchers to observe the retarding effect of temperature on development of the codling moth at high temperatures, allowing departure from linearity between temperature and development speed.

On the same insect Shelford (1927) recognized the departures from linearity at both ends of the temperature range. He also introduced the term "developmental unit" to represent this unilinear relationship between the developmental speed of the insect and temperature. While the "effective day-degrees" simply means a physical and arithmatic collection of temperatures over a certain threshold value, the developmental unit is an actual representation for the unlinear progress of the physiological development of the insect at different temperature. He defined the developmental unit as the difference between the amount of development
taking place in one hour at a given degree of mean medial variable
temperature and the amount of development taking place in one hour at a
temperature one degree higher.

Based on this concept of the developmental unit, it became possible
to express the absolute velocity of development as the number of
developmental units per time period. Before, only the relative velocity
of development had been expressed as the reciprocal of the time required
to complete a life stage. Another important contribution by Shelford was
his measurement of the developmental unit on an hourly basis, rather than
on a daily basis. This important refinement made it possible to obtain a
more precise prediction of development.

The non-linearity relationship between development speed and
temperature has become more obvious as a result of measurement techniques
being more refined and development data were accumulated. Many workers
have suggested different types of curvilinear expressions to represent
the departures of development speed from linearity on the lower and
higher range of temperature.

Some of the previously developed models are: 1) the catenary curve
by Janisch (1925) where the curve is derived from two exponential
functions describing the accelerative action on the growth by the
increase in temperature and the decelerative action of high temperature
above the point of fast growth, 2) Bělehrádek's (1935) exponential
expression of the developmental period and temperature which became
linear on a logarithmic scale, 3) the sigmoidal curve by Davidson (1942 and 1944) to represent relative velocity of development in relation to temperature, 4) Pradhan's (1946) symmetric bell-shaped curve of growth rates against temperature on the assumption that the accelerative action of increase in temperature decreases uniformly from the lower threshold to the upper developmental unit, and 5) a parabolic curve used for obtaining the coefficient of developmental velocity (Eubank et al, 1973).

Among these the well-known sigmoidal curve seems best fit for the empirical purpose of developmental ecology and has been widely tested. The early Janisch formula has been tested by many researchers, but the use of this formula was not fully justified due to the unreliability of the curve on its fitness to the observed data over the whole range of temperatures. In Davidson's (1944) review, Voûte (1936) considered that the observed points at temperatures above the 'peak' do not fit a catenary curve, while Messenger and Flitters (1958) have shown that the Janisch formula can produce poor estimates particularly at lower temperatures.

The double-log scale of Bělehrádek's exponential expression can greatly minimize the apparent discrepancies from the curve if an appropriate statistical method for parameter estimation is developed (Andrewartha and Birch 1967). However, as Davidson (1944) reported, the Bělehrádek's function also does not fit over a wide range of temperature. The Pradhan's bell-shape curve and a parabola, which were developed later than the sigmoidal curve, have shown a promise of applicability to
practical use by several workers, but still needs more confirmation tests.

The sigmoidal (or logistic) equation, originally derived by Verhulst and rediscovered by Pearl (Andrewartha and Birch, 1967), was first used by Davidson (1942 and 1944) to describe the speed of insect development. In reviewing Davidson's work, Andrewartha and Birch recommended the sigmoidal equation as one of the most useful expressions to represent the curvilinear relationship between temperature and development speed. They said the logistic curve is realistic, easily calculated from empirical data and gives the easiest comprehensive picture of the trend of development speed at different constant temperatures. The logistic equation could be written as:

\[
\frac{1}{Y} = \frac{k}{1 + e^{a - b\times x}}
\]  \hspace{1cm} (2)

where Y is the developmental period, x is the environmental temperature, and a, b and k are constants.

Lately Stinner et al (1974a) modified the equation by replacing x with corrected temperature, \( t' = 2 \times T - t \), where the tested temperature, t, is over T—temperature at which the maximum developmental rate occurs. To construct a temperature-development model, they also suggested the usefulness of Beta distribution that can accurately simulate the cumulative proportion of individuals developed under most variable temperature regimes and could save some core storage requirement in computation (Stinner et al, 1975).
Recently in the seventies—with the development of computer technique in pest management—, these developed mathematical expressions in temperature-development relationship have been used as basic algorithms for the construction of a simulation model to manage or predict population densities of pests. By using the logistic equation, Stinner et al (1974b and 1975) constructed a FORTRAN simulation program to control _Heliothis_. populations in the field.

In 1977, noting the effectiveness of the temperature-development models in the management of agricultural insects, Lee and Lewis applied the thermal summation concept to formulate a linear regression model to predict schistosome cercarial shedding. To determine the parameters of the equation, they used the iterative method, which seems also applicable to the models of insect populations.

As systems science develops, and more data on the temperature-development relationship are collected, it is generally expected that simulation modeling will become a more and more effective strategic tool for monitoring the development of the insect populations as well as other poikilothermic animals.
MATERIALS AND METHODS

A. Rearing

Lawn armyworm egg masses collected in the Manoa Campus area of the University of Hawaii were used as the source for the experimental population. To prevent inbreeding within the population, newly field-collected eggs or first instar larvae were added to the laboratory stock at about six month intervals.

Hatched larvae were reared in pots planted with a common variety of Bermuda grass, *Cynodon dactylon* (L.) Pers. About 7800 seeds (2.759 ± 0.266 grams) were sown in the 1 : 1 soil and vermiculite (No. 2) mixture per 800 cm² of surface area, to which 16 : 4 : 4 granulate fertilizer (Brewer Chemical Cor., Gaviota-brand) was added at the rate of 1 gram of fertilizer per 6,000 cm³ of the mixture at approximately one month intervals.

Under greenhouse conditions it took 4 - 6 weeks for the grass to grow well enough to support young armyworm larvae. After being established, the grass was mowed to 3 - 5 cm in height at 2 - 4 day intervals. In order to keep the caterpillars from escaping, the soil and vermiculite mixture was filled to only about two fifths of the pot height so that a space could be left between top of the grass and the rim of the pots.
Observations of larval development were carried out on both individual and collective specimens. For individual larvae, daily physiological development of each individual was observed. For the larvae observed collectively, their age composition was recorded. For observation of individual specimens, 1 - 3 newly-hatched first instar larvae were reared in a 237 cc (8 ounce) wax paper cup (Maryland Cup Corp., 7.5 cm in diameter and 9.5 cm in height). When the larvae reached the third instar, they were transferred to a larger 10 cm (diameter) X 15 cm plant pot. In these small containers, it was easier to find each larva and record its development individually.

To observe the development speed of the caterpillars at constant and fluctuating temperatures, the pots containing the larvae were placed in temperature monitored growth chambers or outdoors. Computer programmed growth chambers (Calumet Scientific Inc., Envirotrol, Rearing space; 72 cm X 75 cm X 124 cm) were used to monitor 5 levels of constant temperature: 15, 20, 25, 30 and 35 °C. These growth chambers were programmed to provide 13 - 14 hours of light each day.

For outdoor observations, pots were placed on the roof of the Entomology Department building (Gilmore Hall) of the University of Hawaii. To protect the caterpillars on the roof from natural enemies and other undesired environmental effects, the larvae containing pots were placed on top of empty pots that were sitting in a water filled tray. The trays in turn were placed inside wooden crates (40 cm X 60 cm X 25 cm) covered by a 0.65 cm mesh wire screen.
Fifteen replications were made for each temperature. The larval age and metamorphosis for each larva were recorded daily. After the larvae pupated, the containers were covered with saran cloth (White Rose Fabric, Fine combed organdy, 100% cotton) to collect emerging adults.

For observations of specimens reared in groups, 30 larvae were placed in a 33 cm (diameter) X 29.5 cm plastic pot at ambient conditions. For one test about 40 pots were initially infested with the same number of newly-hatched first instar larvae. At 2 - 3 day intervals 3 pots were randomly chosen, and the age composition of the larvae in these pots was recorded. These larvae were discarded, and 3 new pots were selected for the next observation. In the same manner 2 other trials were made on a different time schedule.

To protect the caterpillars from natural enemies, the pots were covered with saran cloth while the larvae were in the first to fourth instars. For the older larvae, a 0.62 cm mesh wire screen was used to cover the pots.

The Bermuda grass in the pots was sufficient food for the younger stage larvae. As the larvae grew older, however, food was consumed faster. At about the fifth or sixth instar, the grass in the pots was all consumed by the larvae. The larvae were transferred to pots already prepared with fresh vegetation. After the larvae pupated, saran cloth was used to collect the newly-emerging adults.
Hygrothermographs (Weather Measure Corp., Model H311) were used to record temperatures. In the growth chambers, the hygrothermographs were located in the middle of the rearing space. For outdoor observations, they were placed in a Stevenson's screen at a 45 cm height from the ground surface. The charts were changed weekly.

B. Oviposition

A pair of newly emerged male and female moths was introduced into a white 474 cc (16 ounce) plastic container (American Can Co., Dixie squat container, TF16-11, 11 cm in diameter and 8 cm in height). About 20 ml of 1 : 3 honey and water mixture was provided for food. Before being placed into the container, two sheets of 12.7 cm X 21.6 cm tissue paper (Kimberly-Clark Corp., Kimwipes disposable wipers, Stock No. 34155) folded 5 times were soaked in the mixture. Another two sheets of tissue paper folded 2 times were placed inside the container to collect the oviposited egg masses.

After the food mixture and tissue paper were provided, the container was covered with a sheet of tissue paper as an inner layer and a transparent plastic cover as an outer layer. The inner layer was used to collect egg masses, since the female moth sometimes laid her eggs on the underside of the cover. Fifteen to twenty holes (3 mm in diameter) were made in the plastic cover to prevent the build up of excess humidity.
The containers were placed in the laboratory at 24 ± 1 °C and 65 ± 5% relative humidity. Oviposited egg masses were collected daily. The oviposited egg masses were individually placed in 26 cc (7 dram) transparent plastic vials (2.7 cm in diameter and 5 cm in height) topped with a cover. After hatching, the larvae were placed on a 25 cm X 45 cm X 2 cm white metal tray for counting under light conditions that enhanced dispersal. Eggs from unfertilized egg masses were counted by separating them individually with a sharp needle under a 10 X stereo-microscope.

C. Bioassay

The source for the virus stock used for this experiment was a purified polyhedra suspension (1.16 X 10^8 polyhedra/ml) from the lawn armyworm larvae which was kept in the refrigerator at 4 °C in the laboratory since 1963.

The source suspension was fed by a "dipping method" to the third or fourth instar larvae with a Napier grass bouquet. Generally the virus-fed larvae died in 7 - 10 days after treatment. The dead larvae were stored in the refrigerator until 100 - 200 fifth to seventh instar cadavers were collected. The polyhedra were separated from the cadaver and purified by differential centrifugation (Laigo 1964).

The concentration of the purified polyhedra suspension was determined by the use of a Hausser and Levy-Hausser corpuscle counting
chamber (Hausser Scientific) under a 500 X phase-microscope. Generally the concentration of the stock suspension ranged from $5 \times 10^9$ to $2 \times 10^{10}$ polyhedra/ml.

For virus treatments, serial dilutions were made from the stock suspension. Concentration ranges for the initial virus spray were $10^2 - 6$ polyhedra/ml for the first instar larva, $10^3 - 7$ polyhedra/ml for the second and third, $10^4 - 8$ polyhedra/ml for the fourth, and $10^5 - 9$ polyhedra/ml for the older instar larva.

Before spraying, 3 parts of Triton B 1956 (Rohm and Haas) were added to 1000 parts of polyhedral suspension as a wetting agent. The suspension was applied with a 250 ml glass atomizer (Pyrex, 24/40) and a vacuum pump at a pressure of about 0.90 kg/cm$^2$. Initially to establish the dosage-mortality curve, individual larvae were treated with $3.5 \pm 0.4$ ml of the polyhedral suspension for the first or second instar larvae, and $8.3 \pm 0.6$ ml for the older larvae. While spraying, the atomizer was kept at an 9 - 12 cm distance from the surface level of the containers. For the population tests, where 30 larvae per container were reared, 25.2 ± 2.4 ml of the polyhedral suspensions were sprayed into the container.

The spray was generally applied in the late afternoon on a clear day. Treated pots were placed outdoors in the same manner as in the rearing experiment. For the test of individual specimens, daily observations were made on physiological and disease development for each larva for 2 - 3 weeks. For the test of collective specimens,
observations were made on the age composition of treated larvae and cadavers at 1 - 3 day intervals for 3 - 4 weeks. After completion of the observations, treated pots were washed and exposed to the sun for 4 - 5 weeks. The ultra violet of the sun efficiently killed all the virus that may have been left in the pots. The dried pots were recycled for the next test.

**D. Food Consumption Test**

The feeding capacity of the lawn armyworm was established by measuring the amount of natural food (fresh weight) consumed by the larvae. Although the fresh weight method was not as precise as measuring biomass or dry weight, it was closer to the natural situation than other methods.

Food consumption by the armyworm larvae was established in the laboratory. Although it would have been desirable to determine food consumption at different temperatures, this was not possible due to limitation of time and space. Fortunately ambient temperatures in Hawaii are mild with relatively small variations around the mean temperature (about 25 °C).

Fresh Bermuda grass was provided to the newly-hatched first instar larvae. The top 3 - 5 cm of the grass was cut, weighed, and formed into a bouquet. The leaves were given to the larvae individually in a petri dish. There were 30 replications.
Each day the uneaten grass was removed and weighed to determine the amount of grass consumed by the larvae. Before measuring the fresh weight for the next day, the wet end of the grass (due to the water-soaked tissue paper) was cleaned with dry tissue paper and air-dried for 2 - 3 minutes. The weight loss in the control grass which had no larvae was less than 1%. The larvae, except for the first instar, were also weighed each time the grass was weighed.

E. Number of Polyhedra Produced per Larva

Since the polyhedra were large enough to be observed under a compound microscope and easily collected from the cadavers, the direct counting of polyhedra was chosen for this study to measure inocula. That there are some variations in the number of virus rods occluded by each polyhedra, is known, but these variations are not large enough to significantly affect the results.

To make the counts, a fresh NPV-killed larva was collected in a small (5 - 10 ml) screw cap vial. Since the skin of the cadaver was very fragile, extreme care was required to transfer the individual to the vial. After adding a small amount of water, the vial was capped and vigorously shaken for 1 - 2 minutes. Usually for the individual with well developed NPV symptoms, the skin and internal contents were easily disintegrated, and suspended uniformly. If the cadaver was not easily liquified because of early harvest, or the polyhedra suspensions were
too contaminated with other organisms due to late harvest, the sample was discarded.

Since the size of the cadaver varied greatly with the larval age, the initial amount of distilled water mixed with the cadaver in the vial was adjusted to the age of cadaver. Generally 1 ml was mixed with the first and second instar cadaver, 5 ml to the third to fifth instar and 8 ml to the sixth and the last instar cadaver. The initial suspension was further diluted for counting polyhedra in a haematocytometer.

E. Data Process

In this study the data treatment was divided into three processes: 1) collection and analysis of biological data from rearing experiments and virus spray results, 2) integration of the obtained biological parameters with a mathematical algorithm to construct a simulation model, and 3) utilization of the results from the simulation model for an optimization process to determine the most effective control practices.

For the process 1), the data were summarized and analyzed with a statistical package, SAS (Statistical Analysis System). Most linear regression and probit analyses were conducted through the statistical methods specified in SAS. To estimate parameters in some non-linear regression tests, a BMDP (Biomedical Data Process) program was also used.
For process 2), a computer simulation language, GPSS (General Purpose Simulation Systems), was used. With assistance of FORTRAN subroutines, the simulation was conducted through two steps. First, based on the results of individual rearing tests and a mathematical relationship between physiological development and temperature, a basic life model was constructed. Subsequently, by adding the virus spray results to the basic life model, an epizootiological model was also formulated to predict disease development in the armyworm population.

For process 3), the contour mapping method was used to connect the same level of feeding damage (or virus recovery) at different spray time (x axis) and virus concentration (y axis). For interpolation and drawing of contour curves a SPlot (Bridges and Becker, 1976) program was applied.
A. Basic Life System

Figure 2 is a modified GPSS flowchart to represent the overall life cycle of the armyworm. Prior to simulating the life system of the insect, it was assumed that a mated healthy female produced eggs in a closed environmental system where oviposition of the female is the only source of the lawn armyworm, i.e., there is no emigration and immigration of the insect from the system. For the time being, it was also assumed that the female always produced fertilized eggs.

The first block of the flowchart represents the generation of a transaction; in this case it simulates the introduction of a mated female to a closed environmental system. After being generated, the original female produces progenies by the use of a "split" block. The reproduced daughter transactions (eggs) proceed to the subsequent population development. At each life stage of the insect, population development was simulated through two phases: 1) quantitative change in population size, and 2) speed of physiological development.

The diamond shaped "transfer" block represents the quantitative change in population size. Dependent upon a probability criterion (survival rate in this case), the block randomly determines the pathway of an individual transaction to lead to survival or death. The
Figure 2. -- A modified GPSS flowchart for simulating the life cycle of the lawn armyworm
INTRODUCTION OF ADULT

OVIPosition

LIVE?

EGG DEVELOPMENT

LIVE?

1st INSTAR DEVELOPMENT

II-VII INSTAR LARVA

LIVE?

PUPAL DEVELOPMENT

LIVE?

ADULT DEVELOPMENT

LIFE SYSTEM
rectangle shaped "advance" block stands for the time process of physiological development of the armyworm to complete each life stage.

Repeating this quantitative and chronological development for each immature life stage—i.e., egg, first to seventh instar larva and pupa—by the use of "transfer" and "advance" blocks, the individual reaches the adult stage. The newly produced adult returns to the "split" block to oviposit, and the whole life cycle starts again.

In a broad sense, this basic life system of the insect can be divided into two main biological aspects: 1) egg production, and, 2) development of the produced eggs to the subsequent life stages. A detailed simulation process for each aspect is discussed in this section.

1. Egg Production

Seventy-three newly mated female moths were used for the oviposition test. Table 1 shows quantitative results on daily egg production of the armyworm: percent of females ovipositing each day (oviposition rate), mean daily number of eggs produced by an ovipositing female (individual egg production) and percent of the total egg production.

A mated female laid an average of 1505 ± 603 eggs in the laboratory 2–13 days after emergence. As shown in Table 1, the
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<td>OVIPOSING</td>
<td>(EGGS)</td>
<td>(%)</td>
<td>Y</td>
<td>OVIPOSING</td>
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</tr>
<tr>
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<td>15.5</td>
<td>2</td>
<td>94.5</td>
</tr>
<tr>
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<td>25.0</td>
<td>3</td>
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<td>22.9</td>
<td>4</td>
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<tr>
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<td>6</td>
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<tr>
<td>8</td>
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</tbody>
</table>

* Percentage of total eggs laid.
percentage of females ovipositing increased rapidly from the third day after emergence (42.5%), to a peak being reached on the fifth day (91.8%). Subsequently, the percentage of females ovipositing continuously decreased until the thirteenth day when only 2.7% of the tested females laid eggs. More than half of the tested females produced eggs between 4 - 8 days after emergence. With few exceptions, once a female started to lay eggs, she oviposited every day until production was permanently terminated.

Generally more eggs were laid per egg mass early in the oviposition period. More than 250 eggs were produced each day per female between 2 - 6 days after emergence, while less than 200 eggs were produced daily in the later period. The largest number of eggs was produced on the third day after emergence. The number of eggs laid decreased from the fourth day until it reached 50 - 90 eggs 10 - 13 days after emergence.

Generally, the first egg mass laid contained the largest number of eggs and the number decreased with each subsequent oviposition. This first egg mass was usually deposited on the third and fourth day after emergence.

About 80% of the total number of eggs were laid between 3 - 6 days after emergence. The maximum egg production, 25 percent, was on the fourth day after emergence, and from the fourth day on, the daily
total egg production decreased until the thirteenth day after emergence when only 0.1% of the total eggs was produced.

The cumulative data on individual egg production from the day of oviposition show that females laid the largest number of eggs on the first day and the number of eggs laid each day decreased with each subsequent day. Starting at 100% from the initial oviposition day, the oviposition rate decreased--slowly in the earlier, and rapidly in the later period--until it reached 1.4% on the tenth day. More than one third of the total eggs were laid on the initial oviposition day, and about 78% of the eggs were produced during the first three days from initial oviposition.

When the values of daily individual egg production were transformed to the natural logarithm, they showed a good negative linear relationship with time--days from the initial oviposition--with $r^2$ of 0.918 (Figure 3). The regression equation was $Y = 6.69 - 0.35 * X$, where $Y$ is the logarithm of number of produced eggs, and $X$ is days counting from the initial oviposition. This linear relationship was used later as a parametric source for determining the quantitative egg production on a daily basis by a female in the oviposition model.

To observe the time pattern in oviposition of the lawn armyworm, the preoviposition and oviposition periods of 91 females were observed under laboratory conditions. In Table 2, the frequency for a combination of specific preoviposition (column) and oviposition (row)
Figure 3. -- Regression of egg production (natural logarithm of number of eggs) by the lawn armyworm female on the days from initial oviposition
STATISTICAL ANALYSIS SYSTEM

[Graph showing a log-log plot with data points and a trend line indicating a decreasing number of eggs as days from initial oviposition increase.]
<table>
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<tr>
<th>PREOVIPOSITION PERIOD (IN DAYS)</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>TOTAL</th>
<th>CUMU</th>
</tr>
</thead>
<tbody>
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<td>2</td>
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<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>3.4</td>
<td>2.2</td>
<td>2.2</td>
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<td>0.0</td>
<td>7.8</td>
<td>7.8</td>
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<td>2.2</td>
<td>5.6</td>
<td>7.8</td>
<td>7.8</td>
<td>4.4</td>
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<td>2.2</td>
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<td>78.9</td>
</tr>
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<td>1.1</td>
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<td>2.2</td>
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<td>1.1</td>
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</tr>
<tr>
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<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
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<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.1</td>
<td>100.0</td>
</tr>
<tr>
<td>TOTAL</td>
<td>6.7</td>
<td>7.8</td>
<td>17.8</td>
<td>20.0</td>
<td>16.7</td>
<td>15.6</td>
<td>8.8</td>
<td>5.5</td>
<td>1.1</td>
<td>100.0</td>
<td></td>
</tr>
<tr>
<td>CUMU</td>
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<td>14.5</td>
<td>32.3</td>
<td>52.3</td>
<td>69.0</td>
<td>84.6</td>
<td>93.4</td>
<td>98.9</td>
<td>99.9</td>
<td>100.0</td>
<td></td>
</tr>
</tbody>
</table>
periods recorded from the tested females was shown as a percent value. Generally the frequencies were higher when the preoviposition period was 3 or 4 days and the oviposition period was between 4 - 7 days. In total about 54.5% of the females tested produced eggs during the combinations of these preoviposition and oviposition periods.

The last two columns of Table 2 show the total and cumulative frequencies of the preoviposition periods. As expected, the preoviposition of 3 and 4 days showed distinctively higher frequencies than those for other periods. About 71.1% of tested females started to produce eggs in these periods. The maximum appeared on the 4th day after emergence with a frequency of 38.9%. The preoviposition period averaged 3.75 ± 1.07 days.

The two bottom rows of Table 2 represent the total and cumulative frequencies for the oviposition periods. Again, as expected, a large number of females produced eggs for 4 - 7 days. About 70.1% of the tested females oviposited for this length of time with maximum of 20.0% for the 5 day oviposition duration. The oviposition duration average was 5.51 ± 1.92 days, which is relatively shorter than generally believed.

With the regression results between egg production and time--days counting from initial oviposition--, the total frequencies of preoviposition and oviposition periods were used as a parametric source for simulating egg production in the oviposition model.
2. Simulation of Oviposition

Figure 4 is a modified flowchart of GPSS to simulate armyworm oviposition. After generation of a mated female, the preoviposition period was determined by the next "assign" block. As mentioned before, the cumulative frequency of the preoviposition period (Table 2) was used as a probability criterion to determine the days before a female started to oviposit.

The actual time process for the preoviposition period (in days) in the system was simulated by the next "advance" block. By passing this block, the transaction becomes as old as its preoviposition period. After the preoviposition development, the transaction enters another "assign" block for determining the oviposition period. Similar to preoviposition period, the cumulative frequency of the total oviposition period (Table 2) was used as a probability criterion to determine the time period for the generated female to oviposit.

After simulation of oviposition time (preovi- and ovi- position period), the transaction enters the phase for quantitative egg production. For daily oviposition, it was assumed that once a female started to oviposit, she continuously produced eggs each day until the assigned oviposition period ended. This repeated daily oviposition was simulated with the use of a "loop" block (the rectangular-shaped block with a triangle at the end).
Figure 4. -- A modified GPSS flowchart for simulating oviposition by the lawn armyworm female
INTRODUCTION OF FEMALE

DETERMINATION OF PREOVIPOSITION PERIOD

PREOVIPOSITION PERIOD

DETERMINATION OF OVIPOSITION PERIOD

DAILY EGG PRODUCTION

EGG DEVELOPMENT

DAILY FEMALE DEVELOPMENT

REPETITION OF DAILY OVIPosition

POSTOVIPOSITION PERIOD

OVIPOSITION

DEAD FEMALE
By assigning the previously determined oviposition period as a counter of the "loop" block, it was possible to repeat the linkage of certain blocks as many times as the value of the counter. After assigning its oviposition period, the transaction enters a linkage of the "split"-"advance"-"loop" blocks, and cycled through these blocks as many times as the value of oviposition period.

As previously mentioned, the "split" block represents the quantitative egg production by a female moth. Upon entering the "split" block, the original transaction reproduces new daughter transactions. The newly produced transactions have the same attributes as the original transaction. Each daughter transaction can represent each individual insect.

As mentioned before, the number of eggs produced daily (daughter transactions) was determined by the regression equation of individual egg production on the days counting from the initial oviposition. For generating a calculated number of produced eggs on each day for the oviposition model, the number obtained from the regression equation was considered as a mean value. The actual numbers were generated to show the normal distribution around the mean value with the empirically-given standard deviation of egg production on each day (Table 1).
Based on this regression equation, initial entrance of the transaction to the "split" block generated the number of eggs produced on the first day of oviposition. After producing eggs, the transaction passes through the "advance" block which simulates daily time process (one day) of oviposition, and enters the "loop" block. From the "loop" block the transaction goes back to the "split" block, producing eggs for the next day according to the regression equation of the quantitative egg production.

After ovipositing for the second day, the original transaction passes through the "advance" and "loop" blocks again, and repeats this cycle as many times as the assigned counter of the "loop" block. This eventually represents the egg production by a female during the generated oviposition period. After completing oviposition, the original transaction enters another "advance" block that represents the time process of the postoviposition period. Postoviposition was assigned as the longevity of adults minus the total of the preoviposition periods. Based on the preliminary test, the adult longevity was 9.32 ± 1.54 days.

After the post-oviposition period, the original transaction reaches the "terminate" block which stands for the death of a female moth. While the mother (original) transaction is terminated after its life span is reached, the daughter transactions proceed to the population development of the subsequent life stages.
3. Population Development at Immature Stages

Population development in the basic life system of the insect was observed in two aspects: 1) quantitatively, i.e., change in population size, and 2) chronologically, i.e., speed of physiological development. In this study the speed of population development was represented by measuring the developmental period for each instar from the individual rearing test, while natural mortality through the life cycle of the insect was used as a basic parameter for determining population size in the basic life system.

Table 3 shows the observed survival rate (in percent) for each immature life stage at different constant temperatures between 15 and 35 °C. At the egg stage 20 - 35 egg masses were tested for each temperature. After the egg stage, the results were obtained from observations of the individual rearing test. For this test, 30 - 60 newly hatched first instar larvae were held until emergence at each temperature.

In the egg stage the hatching rate was considered as the survival rate. As shown in Table 3, the hatching rate was 27.8, 46.0, 89.5, 87.5 and 25.8 percent respectively for each temperature at 15, 20, 25, 30 and 35 °C. At the lowest and highest temperatures, less than one third of the tested egg masses survived.
TABLE 3

SURVIVAL RATE (PERCENT) OF THE LAWN ARMYWORM AT EACH IMMATURE LIFE STAGE AT DIFFERENT TEMPERATURES

<table>
<thead>
<tr>
<th>TEMP (°C)</th>
<th>EGG</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
<th>PUPA</th>
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</thead>
<tbody>
<tr>
<td>15</td>
<td>27.8</td>
<td>83.2</td>
<td>86.4</td>
<td>99.9</td>
<td>99.9</td>
<td>97.4</td>
<td>89.2</td>
<td>51.5</td>
<td>-</td>
</tr>
<tr>
<td>20</td>
<td>46.0</td>
<td>90.0</td>
<td>99.9</td>
<td>99.9</td>
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<td>92.6</td>
<td>96.0</td>
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</tr>
<tr>
<td>25</td>
<td>89.5</td>
<td>93.3</td>
<td>99.9</td>
<td>92.9</td>
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<td>96.7</td>
<td>96.0</td>
<td>91.7</td>
<td>-</td>
</tr>
<tr>
<td>30</td>
<td>87.5</td>
<td>93.3</td>
<td>99.9</td>
<td>99.9</td>
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<td>98.3</td>
<td>98.3</td>
<td>98.3</td>
<td>92.9</td>
<td>71.2</td>
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</table>

<table>
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<th>TEMP (°C)</th>
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<tr>
<td>15</td>
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<td>20</td>
<td>90.0</td>
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<td>25</td>
<td>93.3</td>
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<tr>
<td>30</td>
<td>93.3</td>
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<tr>
<td>35</td>
<td>95.2</td>
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<table>
<thead>
<tr>
<th>TEMP (°C)</th>
<th>AVERAGE (20 - 30 °C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>WITHIN</td>
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</tr>
<tr>
<td>CUMU</td>
<td>92.2</td>
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</table>
At 20 °C, less than half of the eggs hatched. Because the survival rates at 25 and 30 °C were much higher than those at other temperatures, the optimal range for egg hatching was considered to lie within these temperatures. In the basic life model, the average survival rate (88.5 %) at these two temperatures was used as a probability criterion to determine the natural hatching of produced eggs.

During the larval period the observed survival rate of each instar was generally high and similar among different temperatures. With a few exceptions at 15 °C, the survival rates were generally over 90 %. The survival rates at the first, second and sixth instar larval stages at 15 °C were relatively lower than those at other temperatures.

The lowest survival rate was observed in the last instar at 15 °C. As shown in Table 3, 51.5 % of the population of the last instar larvae survived. Furthermore, all of the remaining larvae died during the pupal stage.

The decrease in survival rate (within each life stage) was also reflected in the total cumulative survival at 15 °C. Only 32.1 % of the test population survived at the end of the larval period at 15 °C, while 73.3, 80.0, 73.3 and 82.5 % survived at temperatures from 20 to 35 °C.
For the pupal stage the emergence was used to establish the survival rate. Aside from the 100% mortality at 15°C, the emergence rate was lowest at 35°C with 71.2% followed by 86.4% at 20°C. The emergence rates at medium temperatures were higher; 91.7% and 90.9% at 25 and 30°C, respectively. In terms of cumulative survival rates, 63.3, 73.3, 66.7 and 58.7% of the initial population of the first instar larvae reached adulthood at 20, 25, 30 and 35°C, respectively. From cumulative survival rates, it was observed that the lawn armyworm population has the highest survival during the immature stage around 25°C, followed by 30 and 20°C.

In this study for modeling, it was assumed that the temperatures of 20, 25 and 30°C fall in the optimal range for development of the insect, and the average survival rates at these temperatures were used as the probability criteria for survival of each immature life stage in the basic life model.

The cumulative survival rates of each immature life stage were 92.2, 92.2, 91.1, 91.1, 84.4, 80.0, 75.5 and 67.8% from the first to last instar larva and the pupal stage, respectively. This implies that, if a newly hatched first instar larva is generated in the basic life model where temperature is in the optimal range, the probability of survival for the first instar larva was 75.5% until pupation, and 67.8% until emergence.
Table 4 shows the developmental period average at each immature life stage at different (constant) temperatures from 15 to 35 °C. As expected, the developmental periods became shorter with the increase in temperature. From the highest to the lowest temperature, the developmental period ranged 2.4 - 15.1, 1.9 - 11.0, 1.1 - 8.1, 1.0 - 9.1, 1.1 - 10.0, 1.3 - 11.1, 1.8 - 12.0 and 2.5 - 46.9 days for the egg and the first to last instar larval stage, respectively. The developmental periods for the pupal stage ranged between 6.2 and 23.0 days at higher temperatures from 35 to 20 °C.

Aside from the pupal stage, the longest developmental period was observed at the last instar larva. This may be partly due to the pooling of developmental periods for the seventh and eighth instar larval stages when a larva went through an extra instar. It seemed that the armyworm larvae had a relatively higher chance of molting more than six times at the lower temperatures, but this needs confirmation.

The next longest developmental period for the larval stage was observed at the sixth instar. Besides the two oldest larval stages, the developmental periods for the younger instars were similar for each tested temperature. For completion of the total immature period—from oviposition to emergence—, it required 77.8, 40.3, 25.9 and 19.2 days respectively at 20, 25, 30 and 35 °C.

Since the average daily Hawaiian ambient temperature is relatively close to 25 °C, about forty days would be required from oviposition to
<table>
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<tr>
<th>TEMP (°C)</th>
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<th>LIFE STAGE</th>
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<th>LARVA</th>
<th>LARVA</th>
<th>LARVA</th>
<th>LARVA</th>
<th>LARVA</th>
<th>LARVA</th>
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<td>11.97</td>
<td>46.94</td>
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<td></td>
<td></td>
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<td>5.07</td>
<td>4.26</td>
<td>4.96</td>
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<td>6.50</td>
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</table>
emergence of the lawn armyworm in the Islands. Since the longevity of the adult was found to be 9 - 10 days from the preliminary test, the total life cycle of the insect would take a little more than one and a half months in Hawaii.

These observed developmental periods were used as the bases for determining the mathematical relationship between temperature and physiological development of the insect at each life stage. Among many proposed models, two approaches were chosen for this study: 1) the traditional thermal summation method, and 2) the widely used logistic equation for temperature-development relationships.

To determine threshold temperatures and the total effective day-degrees in the thermal summation method, the previously mentioned hyperbolic equation, (1), was used. If $Y_i$ and $X_i$ respectively represent the (observed) developmental period and tested temperature for each individual, $i$, where $n$ samples were investigated in total, the equation can be transformed as a linear form of $X_i$ on $1/Y_i$:

$$X_i = A + C \times \frac{1}{Y_i}$$

Since $A$ and $C$ can be considered as parameters in the linear regression equation, the least square method can be conducted to determine the values of parameters. If $A'$ and $C'$ respectively stands for the estimated value of $A$ and $C$, the calculated value of $X'_i$ can be expressed as: $X'_i = A' + C' \times \frac{1}{Y_i}$. If $G^2 = \sum_{i=1}^{n} (X_i - X'_i)^2 = \sum_{i=1}^{n} (X_i - A' -$
C'/Y_i)^2$, the following two equations have to be satisfied to obtain $A'$ and $C'$ by the least square method:

$$\frac{\partial^2 G}{\partial A'^2} = \frac{\partial}{\partial A'} \left[ \sum_{i=1}^{n} (X_i - A' - C'/Y_i)^2 \right] = 0 \quad (3)$$

$$\frac{\partial^2 G}{\partial C'^2} = \frac{\partial}{\partial C'} \left[ \sum_{i=1}^{n} (X_i - A' - C'/Y_i)^2 \right] = 0 \quad (4)$$

Equations (3) and (4) were further simplified as:

$$A' + \frac{1}{n} \sum_{i=1}^{n} \left( \frac{1}{Y_i} \right) * C' = \frac{1}{n} \sum_{i=1}^{n} X_i \quad (5)$$

$$\sum_{i=1}^{n} \left( \frac{1}{Y_i} \right) * A' + \sum_{i=1}^{n} \left( \frac{1}{Y_i^2} \right) * C' = \sum_{i=1}^{n} \left( \frac{X_i}{Y_i} \right) \quad (6)$$

In this study the temperatures between 20 - 30 °C were assumed to be in the optimal range for development of the armyworm, and the developmental periods observed at these temperatures—20, 25 and 30 °C—were used to determine the threshold temperature by solving the simultaneous equations, (5) and (6).

As shown in Table 5, the obtained (minimum) threshold temperatures for immature life stages were 10.7, 13.7, 14.4, 13.5, 13.6, 13.3, 12.2, 17.4 and 15.1 °C for the egg, each larval instar and pupal stage, respectively. The egg had the lowest threshold temperature, 10.7 °C, while the last instar had the highest threshold temperature at 17.4 °C.
<table>
<thead>
<tr>
<th>LIFE STAGE</th>
<th>THRESHOLD (°C)</th>
<th>TOTAL EFFECTIVE DAY-DEGREES</th>
</tr>
</thead>
<tbody>
<tr>
<td>EGG</td>
<td>10.7</td>
<td>59.5 ± 10.0</td>
</tr>
<tr>
<td>I</td>
<td>13.7</td>
<td>33.3 ± 4.3</td>
</tr>
<tr>
<td>II</td>
<td>14.4</td>
<td>26.5 ± 4.9</td>
</tr>
<tr>
<td>III</td>
<td>13.5</td>
<td>28.8 ± 5.2</td>
</tr>
<tr>
<td>IV</td>
<td>13.6</td>
<td>32.5 ± 7.0</td>
</tr>
<tr>
<td>V</td>
<td>13.3</td>
<td>34.5 ± 8.4</td>
</tr>
<tr>
<td>VI</td>
<td>12.2</td>
<td>43.9 ± 9.0</td>
</tr>
<tr>
<td>VII</td>
<td>17.4</td>
<td>50.8 ± 15.5</td>
</tr>
<tr>
<td>PUPA</td>
<td>15.1</td>
<td>110.4 ± 15.6</td>
</tr>
</tbody>
</table>
Except for the last two instars, the threshold temperatures during the larval period were around 14 °C. The reason why the threshold temperature was distinctively high at the last instar larval stage may be due to: 1) pooling of the developmental periods of the seventh and eighth instars in some observations in the calculation for temperature threshold, or 2) the physiological instability of older larvae before pupation. These observations need further confirmation.

Even though the threshold temperature can be obtained by calculation, there was a possibility that these obtained values did not reflect the true threshold temperatures for the development of the insect. There have been many cases where insects actually developed below the calculated threshold values. Other researchers also reported that there is variation in threshold temperatures among individual insects. Because of this reasoning, Shelford (1927) and other workers believed that the calculated threshold value has only theoretical meaning, and called it "alpha" value instead of threshold temperature.

Table 5 also shows the calculated total effective day-degrees at each immature life stage. The maximum thermal requirement was observed at the pupal stage with 110.4 day-degrees. The next longest thermal requirement was around 59.5 day-degrees at the egg stage. Similar to threshold values, the total effective day-degrees at the larval stage were relatively stable. Except for the last two instars, they were in the range of 26.5 and 34.5 day-degrees.
While this thermal summation method is mainly effective in the optimal range of temperatures, the logistic equation is generally more applicable to a wide range of temperatures for insect development. Instead of using just 3 levels of temperature for the thermal summation method, all five tested temperatures were used for determining the parameters in the logistic equation.

The previously mentioned logistic equation, (2), can be transformed as follows:

\[ e^{(a - b \times X)} = \frac{k}{y - 1} \]

\[ \log_e(\frac{k}{y - 1}) = a - b \times X \quad (7) \]

where \( y \) is the relative developmental unit (reciprocal of developmental period, \( Y \)).

For simplicity of analysis, the parameter \( k \) was empirically determined by plotting the results from the individual rearings. Once \( k \) is known as a constant, equation (7) can be considered as a linear regression form of \( Z(y) \) on \( X \) if \( Z(y) = \log_e(\frac{k}{y - 1}) \). The unknown parameters, \( a \) and \( b \) could be estimated through the least square method. Table 6 enlists the estimated parameters for \( k \), \( a \) and \( b \) in the logistic equation. Since only one day was required to complete each instar for many individuals from the second to third instar larvae at higher temperatures, the \( k \) value was assumed as 1.0 for those stages.
### TABLE 6

**ESTIMATED PARAMETERS IN THE LOGISTIC EQUATION** for determining the relative developmental unit to complete each life stage of the lawn armyworm immatures

<table>
<thead>
<tr>
<th>LIFE STAGE</th>
<th>$k^{**}$</th>
<th>$a$</th>
<th>$b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>EGG</td>
<td>0.44</td>
<td>4.783418</td>
<td>0.202023</td>
</tr>
<tr>
<td>I</td>
<td>0.53</td>
<td>6.113860</td>
<td>0.285421</td>
</tr>
<tr>
<td>L II</td>
<td>1.00</td>
<td>5.721318</td>
<td>0.226826</td>
</tr>
<tr>
<td>A III</td>
<td>1.00</td>
<td>7.251770</td>
<td>0.299121</td>
</tr>
<tr>
<td>R IV</td>
<td>1.00</td>
<td>5.320467</td>
<td>0.195736</td>
</tr>
<tr>
<td>V V</td>
<td>0.84</td>
<td>5.847562</td>
<td>0.228837</td>
</tr>
<tr>
<td>A VI</td>
<td>0.57</td>
<td>5.569131</td>
<td>2.232723</td>
</tr>
<tr>
<td>VII</td>
<td>0.42</td>
<td>7.254417</td>
<td>0.271231</td>
</tr>
<tr>
<td>PUPA</td>
<td>0.17</td>
<td>6.538893</td>
<td>0.282580</td>
</tr>
</tbody>
</table>

* $y = k/(1 + e^{(a - bX)})$, where $y$ is the relative developmental unit, $X$ is temperature, $k$ is the asymptote of the logistic equation, and $a$ and $b$ are constants.

** $k$ was empirically determined through the graphic method.
Besides parameters, the variance of the relative developmental unit, \( V(y) \), was also needed to give a variation to the generated developmental period in the model. To estimate \( V(y) \), Taylor's theorem was applied (Snedecor and Cochran, 1978). Since;

\[
V(Z) = \{Z'(y)\}^2 V(y) \quad \text{--------------------------------} \quad (8)
\]

where \( V(Z) \) is variance of \( Z \), and \( Z'(y) \) is derivative of \( Z \) on \( y \).

The equation (8) can be re-written as:

\[
V(y) = V(Z) / \{Z'(y)\}^2 \quad \text{--------------------------------} \quad (9)
\]

Because variance of \( Z \) can be obtained from regular regression analysis on the equation (7), only \( Z'(y) \) is required to be known to estimate variance of \( y \). Since \( Z(y) = \log_e(k/y - 1) \),

\[
Z'(y) = dZ/dy = d\{ \log_e(k/y - 1) \}/dy
\]

\[
= k/(y^2 - ky) \quad \text{--------------------------------} \quad (10)
\]

By putting (10) to (9), variance of \( y \) can be obtained as:

\[
V(y) = V(Z) * \{y * (y - k)/k\}^2.
\]
4. Temperature

The daily ambient temperature was chosen as the thermal input source for monitoring armyworm development in the simulation model. Table 7 and 8 show summary of the daily ambient temperatures measured in the Manoa area on the monthly and seasonal basis from September 18, 1979 to September 17, 1980. In the table, the term, mean temperature, is used to represent the mean of temperatures observed at two hour intervals each day, while the term, average temperature, designates the mean of the daily maximum and minimum temperatures.

Generally there were very little differences between the average and mean temperatures. All through the year, differences between two temperatures were small with the average temperature consistently higher than the mean temperature by 0.4 - 0.6 °C. For both temperatures, the maximum was observed in October (26.6 °C for the average temperature and 26.2 °C for the mean temperature), and the minimum was observed in February (23.3 °C for average temperature and 22.9 °C for the mean temperature).

The pattern of the monthly averages of daily maximum and minimum was similar to those for the mean and average temperature. The daily maximum average appeared highest in October with 29.1 °C, and lowest in March with 25.3 °C. The highest of daily minimum average was shown in September and October with 24.1 °C, while the lowest was in February with 20.3 °C. The ranges of the daily maximum and minimum averages
TABLE 7

DAILY AMBIENT TEMPERATURES (°C) ON THE MONTHLY BASIS AT THE MANOA AREA FROM SEPTEMBER 18, 1979 TO SEPTEMBER 17, 1980

<table>
<thead>
<tr>
<th>MONTH</th>
<th>MEAN*</th>
<th>MAXIMUM</th>
<th>MINIMUM</th>
<th>AVERAGE**</th>
</tr>
</thead>
<tbody>
<tr>
<td>JAN.</td>
<td>23.1 ± 1.07</td>
<td>26.0 ± 1.68</td>
<td>20.8 ± 1.37</td>
<td>23.4 ± 1.07</td>
</tr>
<tr>
<td>FEB.</td>
<td>22.9 ± 1.34</td>
<td>26.2 ± 1.48</td>
<td>20.3 ± 1.57</td>
<td>23.3 ± 1.37</td>
</tr>
<tr>
<td>MAR.</td>
<td>23.2 ± 0.45</td>
<td>25.3 ± 0.81</td>
<td>21.8 ± 0.61</td>
<td>23.6 ± 0.57</td>
</tr>
<tr>
<td>APR.</td>
<td>23.3 ± 0.92</td>
<td>25.9 ± 1.46</td>
<td>21.8 ± 0.78</td>
<td>23.8 ± 0.93</td>
</tr>
<tr>
<td>MAY.</td>
<td>24.7 ± 0.67</td>
<td>27.3 ± 1.31</td>
<td>22.8 ± 0.61</td>
<td>25.1 ± 0.84</td>
</tr>
<tr>
<td>JUNE.</td>
<td>25.3 ± 0.66</td>
<td>27.9 ± 1.09</td>
<td>23.8 ± 0.74</td>
<td>25.8 ± 0.77</td>
</tr>
<tr>
<td>JULY.</td>
<td>25.4 ± 0.72</td>
<td>27.9 ± 1.09</td>
<td>23.8 ± 0.74</td>
<td>25.8 ± 0.80</td>
</tr>
<tr>
<td>AUG.</td>
<td>25.9 ± 0.51</td>
<td>29.0 ± 0.95</td>
<td>24.0 ± 0.69</td>
<td>26.5 ± 0.60</td>
</tr>
<tr>
<td>SEPT.</td>
<td>26.0 ± 0.53</td>
<td>28.8 ± 0.92</td>
<td>24.1 ± 0.74</td>
<td>26.5 ± 0.67</td>
</tr>
<tr>
<td>OCT.</td>
<td>26.2 ± 0.75</td>
<td>29.1 ± 1.15</td>
<td>24.1 ± 0.92</td>
<td>26.6 ± 0.78</td>
</tr>
<tr>
<td>NOV.</td>
<td>24.6 ± 1.31</td>
<td>27.4 ± 1.77</td>
<td>22.6 ± 1.51</td>
<td>25.0 ± 1.34</td>
</tr>
<tr>
<td>DEC.</td>
<td>23.9 ± 1.52</td>
<td>26.9 ± 1.93</td>
<td>21.7 ± 1.58</td>
<td>24.3 ± 1.58</td>
</tr>
</tbody>
</table>

*Mean of temperatures observed at every two hour intervals.

**Mean of maximum and minimum temperatures.
<table>
<thead>
<tr>
<th>SEASON</th>
<th>MEAN*</th>
<th>MAXIMUM</th>
<th>MINIMUM</th>
<th>AVERAGE**</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAR. - MAY.</td>
<td>23.7 ± 0.97</td>
<td>26.2 ± 1.48</td>
<td>22.1 ± 0.81</td>
<td>24.2 ± 1.02</td>
</tr>
<tr>
<td>JUNE. - AUG.</td>
<td>25.6 ± 0.68</td>
<td>28.3 ± 1.16</td>
<td>23.9 ± 0.71</td>
<td>26.1 ± 0.78</td>
</tr>
<tr>
<td>SEPT. - NOV.</td>
<td>25.6 ± 1.16</td>
<td>28.5 ± 1.50</td>
<td>23.6 ± 1.31</td>
<td>26.0 ± 1.21</td>
</tr>
<tr>
<td>DEC. - FEB.</td>
<td>23.3 ± 1.39</td>
<td>26.3 ± 1.74</td>
<td>21.0 ± 1.59</td>
<td>23.6 ± 1.41</td>
</tr>
<tr>
<td>YEAR</td>
<td>24.6 ± 1.50</td>
<td>27.3 ± 1.81</td>
<td>22.6 ± 1.65</td>
<td>25.0 ± 1.57</td>
</tr>
</tbody>
</table>

*Mean of temperatures observed at every two hour intervals.

**Mean of maximum and minimum temperatures.
were relatively small. Difference between the highest and the lowest was 3.8 °C for both maximum and minimum temperatures. These results on daily ambient condition confirm that temperatures at the experimental area were mild with little variation.

When the daily temperatures were summarized on the seasonal basis, it appeared largely of two types: 1) the lower "Spring-Winter" type with the mean temperature of 23.3 - 23.7 °C and the average temperature of 23.6 - 24.2 °C, and 2) the higher "Summer-Fall" type with the mean temperature of 25.6 °C and the average temperature of 26.0 - 26.1 °C. While the difference of temperatures between seasons within the same type (i.e., Spring vs. Winter, or Summer vs. Fall) ranged only 0.0 - 0.6 °C, the difference between different types were more than 2 °C. By combining all the seasonal temperatures, the total mean and average of daily ambient temperature for the year was 24.6 and 25.0 °C respectively, while the maximum and minimum was 27.3 and 22.6 °C.

Two methods were chosen to include the daily average temperature in the model: 1) applying the actually-observed temperatures to the model for descriptive purposes, e.g., comparison of actual and calculated data for testing reliability of the developed model, or 2) artificially generating expected temperatures as a function in the model so that it could be used for predictive purposes, e.g., estimation of population development in the future.
A normal distribution was assumed when temperatures were generated. For the statistical parameters, the mean and standard deviation of the average seasonal temperature were used in this study. Because the period of the armyworm life cycle in Hawaii was between one and three months, the seasonal data could fully cover the population development of the insect in one generation without changing the thermal input in the model.

Because the descriptive model was constructed based on the actually measured temperatures from the experimental site, the reliability of the predictive model could be better compared with the descriptive model if its statistical parameters for the thermal input source were obtained from the temperature data measured at the same site.

5. Simulation of Population Development after Oviposition

A population development model was constructed by integrating all the biological, mathematical and environmental information on the life system of the armyworm. Figure 5 is a modified GPSS flowchart simulating population development in the basic life system of the insect after oviposition. The simulation was conducted through two phases: 1) quantitative change in population size, and 2) determination of speed of physiological development.
Figure 5. -- A modified GPSS flowchart for simulating population development of the lawn armyworm immatures at each life stage after oviposition.
DETERMINATION OF DEVELOPMENTAL TOTAL

DETERMINATION OF PRESENT DEVELOPMENTAL UNIT

DAILY DEVELOPMENT

DETERMINATION OF LIFE STAGE

NEXT STAGE

POPULATION DEVELOPMENT
The quantitative change in population size resulted from the mortality occurring at each life stage. At the first "transfer" block, the entering transaction was determined to survive or to be killed depending upon a probability criterion. The obtained survival rates (within a life stage) from the individual rearing test (Table 3) were used as the probability criteria to represent natural survival under favorable environmental conditions in the basic life system.

If the newly generated daughter transactions (eggs) enter the first "transfer" block in the flowchart, and that the survival rate at egg stage, 0.885, was assigned as the probability criterion for the block, about 88.5% of entering transactions were randomly chosen to survive, while the remaining 11.5% were determined to be dead at the egg stage. This determination on survival and death was made for each entering individual.

The transactions leading to death pass through a chain of "advance" and "terminate" blocks. The "advance" block represents the time process for the lethal developmental period of the insect, while the "terminate" block stands for the death of the entering individual. The lethal period was determined by multiplying a randomly generated number between 0.000 - 0.999 by the developmental periods of the armyworm at 25 °C. After termination, the transaction was eliminated from the whole simulated life system of the armyworm.
On completing simulation of quantitative change in population size, transactions entered the phase for determining speed of development. Once chosen to survive, transactions passed through a series of blocks in the main pathway. The mathematical relationship between temperature and developmental period was represented by two methods: thermal summation and logistic equation. To represent the process of physiological development of the armyworm at each life stage, the accumulated effective day-degrees were used in the thermal summation method, while the sum of developmental proportion (cumulative relative developmental units) was employed in the logistic equation.

At the first "assign" block in the main branch of the flowchart, the total developmental unit to complete each life stage of the armyworm was initially determined. For the thermal summation method, the calculated total effective day-degrees (Table 5) were used as the developmental total. In the simulation model, variation was given to the thermal constant by individually generating the obtained total effective day-degrees with a normal distribution.

When the logistic equation was applied, the number, 1, was used to represent the developmental total. The daily accumulation of relative developmental units in the logistic equation represented the proportional development (less than one) of the armyworm at each stage. If relative development exceeded 1, this represented the
completion of a life stage. For simplicity of calculation, the developmental unit in this study was multiplied by 1000.

After the total developmental unit was assigned, the "present" daily developmental unit for each transaction is calculated by the next "assign" block based on the thermal input source given to the basic life system everyday. For the thermal summation method, effective day-degrees--daily temperature minus threshold values--were assigned, while the daily relative developmental unit for each individual was used for applying the logistic equation.

The "assign" block for the daily developmental unit forms a loop by linking with the subsequent "advance" and "test" blocks. The "advance" block in the loop represented the daily time process of the development of each individual in the basic life system. The next "test" block compares the previously-assigned developmental total and the present daily developmental unit; if the present developmental unit is smaller than the total developmental unit, the transaction was sent back to the "assign" block, receiving the next day's effective day-degrees calculated from the newly-generated daily temperature. The next day's developmental unit is then added to the previous developmental unit to form the cumulative developmental unit of the individual for the second day.

After passing the one day "advance" block for simulating daily time process, the cumulative developmental unit for the second day was
compared again with the total developmental unit. This process was repeated until the present cumulative developmental unit was larger than the previously assigned total developmental unit. The difference of the present unit over total developmental unit represented the completion of a life stage.

The transactions that finished a life stage proceeded to the development of the next life stage, which was essentially a repetition of the above mentioned simulation process: quantitative determination by the "transfer" and "termination" blocks and a series of "assign", "advance" and "test" blocks to represent the speed of the physiological development of the armyworm.

Since the developmental units of temperature were assigned in increments, there were instances where the entire increment was not used before the insect molted into the next stage. In these cases, the unused units were converted to the initial developmental units for the next life stage by the use of following correction formula:

\[ W = (X/Y - 1) \times Z \]

where \( W \) is the corrected developmental units on the initial day of the next life stage, \( X \) is the accumulated developmental units for
the previous stage, Y is the total developmental units assigned for
the previous stage, and Z is the total developmental units assigned
for the next stage.

The construction of the basic life model was made possible by
combining this simulation on population development with the
previously mentioned oviposition process. The basic life model could
be used to calculate the future change in age structure of the
population as the time variable (day) proceeded if the initial age
structure of the population and the daily average temperature were
known.

6. Test of the Basic Life Model

If a mated, one-day-old female moth was introduced into a closed
and favorable environmental system, the development of the progenies
(first generation) by the thermal summation method would proceed as
shown in Figure 6. In the model the daily average ambient temperature
measured at the Manoa area in the fall season (26.0 ± 1.21 °C) (Table
9), was used. For the predictive purpose, temperature was individually
generated for each insect on each day in the normal distribution
pattern.

As shown in the figure, the peak of the egg stage appeared on the
sixth day after the introduction of the female. The peaks for the
subsequent life stages in the larval period were shown on 11, 13, 16,
Figure 6. -- A calculated population development (single generation) by
the thermal summation method when a mated lawn armyworm female was
introduced into a closed and favorable environmental system under fall
temperature condition
18, 21, 24 and 28 days after introduction of the female respectively for the first to seventh instar. The pupal population peaked on the 38th day, and the adult population peaked on the 47th day. It took approximately 70 days for all of the armyworm to complete development.

The figure also shows the quantitative change in population size. Starting from one female, the population rapidly increased on the sixth day to show the peak of egg production with ca. 1110 individuals. After the egg stage, the peak abundance decreased continuously until it reached the third instar. Approximately 880, 720 and 640 individuals occurred in the peaks of the first to third instar, respectively. From the fourth to sixth instar, the peaks were relatively stable, about 650 individuals. After the sixth instar, however, the peaks rapidly increased, showing 950 individuals for the seventh instar larva and 1140 individuals for the pupal stage.

The reason why higher peak densities were shown for the last instar larva and the pupal stage was that, these stages took a longer time to complete, so more individuals could be found in those stages. The peak of adult was distinctively lower than that of the previous pupal stage although the adults did live a relatively long time. The abundance of the adult peak was about 930 individuals on the 47th day. Because the developmental period at the pupal stage (12 days) was longer than that of adult stage (9 - 10 days), the input speed from pupa to adult was slower than the output speed of adult to death.
The results from the model—calculated peak time for each life stage and the quantitative trend—seemed to agree with what generally was expected in the fall in Hawaii. However, to check the reliability of the model, the calculated values were compared with the actual data from mass-rearing tests in the descriptive manner. For simplicity of comparison, population development was observed from the first instar larva to adult in a single generation.

The mass-rearing tests were conducted three times—on September 18, October 15, and December 22, 1979. For calculating the developmental period in the descriptive model, the actually-measured daily average temperatures (arithmetic mean of daily maximum and minimum) from the initial day of each rearing test were used.

Figure 7-9 and Table 9 compare the calculated and actual data on the population development (see also Appendix A). The values in the figures and tables were percent abundance of each life stage when the initial population of the first instar larvae was considered as 100%. Since the observations on the rearing tests were made at 2–3 day intervals during the larval period and 1–2 times during the pupal period, the abundance curves for the actual data in the figures appeared discrete. For the adults the number emerging each day was recorded.

The trend of population development between the actual and calculated data was generally quite similar. Quantitatively, however,
Figure 7. -- Comparison of the actual and calculated data on population development (percent abundance) of the lawn armyworm when the first instar larvae were introduced into a closed and favorable environmental system as the initial population (100 percent) on September 18, 1979.
Figure 8. -- Comparison of the actual and calculated data on population development (percent abundance) of the lawn armyworm when the first instar larvae were introduced into a closed and favorable environmental system as the initial population (100 percent) on October 15, 1979.
Figure 9. -- Comparison of the actual and calculated data on population development (percent abundance) of the lawn armyworm when the first instar larvae were introduced into a closed and favorable environmental system as the initial population (100 percent) on December 22, 1979.
TABLE 9

COMPARISON OF THE ACTUAL AND CALCULATED DATA ON THE EMERGENCE (PERCENT ABUNDANCE) OF THE LAWN ARMYWORM MOTH WHEN THE FIRST INSTAR LARVAE WERE INFESTED AS THE INITIAL POPULATION (100 %) UNDER FAVORABLE ENVIRONMENTAL CONDITIONS

(INFESTED ON SEPTEMBER 18, 1979)

<table>
<thead>
<tr>
<th>DAYS AFTER INFESTATION</th>
<th>25</th>
<th>27</th>
<th>29</th>
<th>31</th>
<th>33</th>
<th>35</th>
<th>37</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACTUAL</td>
<td>3</td>
<td>10</td>
<td>29</td>
<td>5</td>
<td>3</td>
<td>.</td>
<td>.</td>
<td>51</td>
</tr>
<tr>
<td>THERMAL</td>
<td>2</td>
<td>3</td>
<td>14</td>
<td>21</td>
<td>23</td>
<td>9</td>
<td>1</td>
<td>73</td>
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<tr>
<td>LOGISTIC</td>
<td>.</td>
<td>17</td>
<td>33</td>
<td>18</td>
<td>3</td>
<td>.</td>
<td>.</td>
<td>71</td>
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</tbody>
</table>

(INFESTED ON OCTOBER 15, 1979)

<table>
<thead>
<tr>
<th>DAYS AFTER INFESTATION</th>
<th>26</th>
<th>28</th>
<th>30</th>
<th>32</th>
<th>34</th>
<th>36</th>
<th>38</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACTUAL</td>
<td>.</td>
<td>1</td>
<td>12</td>
<td>27</td>
<td>22</td>
<td>4</td>
<td>1</td>
<td>67</td>
</tr>
<tr>
<td>THERMAL</td>
<td>3</td>
<td>5</td>
<td>12</td>
<td>18</td>
<td>16</td>
<td>13</td>
<td>4</td>
<td>71</td>
</tr>
<tr>
<td>LOGISTIC</td>
<td>2</td>
<td>18</td>
<td>26</td>
<td>14</td>
<td>6</td>
<td>1</td>
<td>.</td>
<td>67</td>
</tr>
</tbody>
</table>

(INFESTED ON DECEMBER 22, 1979)

<table>
<thead>
<tr>
<th>DAYS AFTER INFESTATION</th>
<th>30</th>
<th>32</th>
<th>34</th>
<th>36</th>
<th>38</th>
<th>40</th>
<th>42</th>
<th>44</th>
<th>&gt;46</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACTUAL</td>
<td>.</td>
<td>12</td>
<td>12</td>
<td>14</td>
<td>14</td>
<td>10</td>
<td>2</td>
<td>1</td>
<td>.</td>
<td>63</td>
</tr>
<tr>
<td>THERMAL</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>10</td>
<td>14</td>
<td>18</td>
<td>11</td>
<td>11</td>
<td>71</td>
</tr>
<tr>
<td>LOGISTIC</td>
<td>.</td>
<td>.</td>
<td>1</td>
<td>10</td>
<td>14</td>
<td>23</td>
<td>8</td>
<td>10</td>
<td>4</td>
<td>70</td>
</tr>
</tbody>
</table>
the total population from actual observations were generally lower than that from the model, especially in the early instars. In addition, beyond the fifth instar, the calculated peak for each life stage appeared slightly later than that from actual observation.

For the rearing test conducted in winter, more time was required to complete the life cycle. However the trend of population development between the actual and calculated data was similar. The difference in peak times for the older life stages beyond the sixth instar larva seemed larger than that from the fall rearing test. This may be due to the requirement of the longer period to complete each life stage in the winter.

The calculated population development by the logistic model was similar to that by the thermal summation model. Generally the logistic model predicted the appearance of the older stages slightly earlier than the thermal summation model. The logistic model is applicable over a wider range of temperatures than the thermal summation method.

Table 9 shows percent emergence of adults in the actual and calculated data. For the September test, the peak emergence from actual observation and the logistic model appeared on the 29th day, while it was shown on the 31st to 33rd day in the thermal summation model. For the October rearing test, the logistic model predicted the peak time on the 30th day, while the actual observation and the thermal summation model showed the highest emergence on the 32nd day. In the winter test
the earliest peak time was shown in the actual observation on the 36th to 38th day after infestation, followed by the 40th day in the logistic model and the 42nd day in the thermal summation model.

It was also observed that the thermal summation model showed a more dispersed emergence of adults on the time scale than the logistic model. In total, the emergence of adults in the two models were similar, averaging around 70 percent, while those from actual observations were 51, 67 and 63 percent for September, October and December, respectively.

As shown from the adult emergence as well as the quantitative development of the immature stages, the estimates of population size by the models were generally higher than those from actual observations. This indicated that the probability criteria used in the model for determining survivability of the armyworm—which was the survival rates obtained from individual rearing tests of each life stage—were higher than those of the actual survival of the armyworm. An adjustment was needed in the model.

Initially, to obtain the natural survival rate under favorable environmental conditions, the quantitative trends of the population sizes in the mass-rearing tests were utilized. For convenience of comparison, it was assumed that a "population age" was represented by the life stage which was most abundant in the population at that time.
Using this technique, it was possible to combine all the results of different mass-rearing tests.

Figure 10 shows the average of percent survival at each life stage of the lawn armyworm when the results from all the mass-rearing tests were combined. In the model the calculated population trend steadily decreased, from 93.8 to 67.8 percent from the first instar to the adult stage. The actual observations, however, showed a peak at the third instar.

The apparent low survival in the first and second instars was probably due to sampling error. The first and second instar larvae were so small that it was very difficult to find all of the larvae in the sampling plot. After the second instar larva, the difference in actual observation and calculation was relatively small and constant ranging from 6 to 11%. With the exception of the first two instars, these newly calculated survival rates from mass-rearing tests were used to replace the previous input obtained from the individual rearings in the basic life model.

Although both models predicted the population development equally well, the thermal summation method was used to develop the epizootiological model in this study; because the ambient temperature in Hawaii is in the optimal range and its variation is relatively small. Also the thermal summation model is relatively simple to run in the simulation program.
Figure 10. -- Comparison of the actual and calculated data on population size (percent survival) when the results of mass-rearing tests were combined on the basis of population age.
B. Epizootics

1. Bioassay

To obtain the basic data for simulating epizootic development, bioassays were made by spraying NPV on the food of the lawn armyworm larvae at various virus concentrations. The seventh instar was not included in the tests since it was highly resistant to the virus.

The effective range of lethal concentrations—which caused 5 to 95% mortality in the population was respectively $2.3 \times 10^3 - 5.2 \times 10^7$, $3.5 \times 10^3 - 8.1 \times 10^7$, $1.3 \times 10^3 - 9.1 \times 10^8$, $4.3 \times 10^3 - 6.3 \times 10^9$, $2.3 \times 10^5 - 7.8 \times 10^9$ and $2.5 \times 10^7 - 1.4 \times 10^{10}$ polyhedra per 100 cm$^2$ of lawn surface at each larval stage from the first instar. The median lethal concentrations ($LC_{50}$) and fiducial limits are shown in Table 10. As expected, $LC_{50}$ rapidly increased with the age of treated larvae.

The rate of increase in susceptibility (virulence index for $LC_{50}$) is also given in Table 10. For the second and third instar, less than 15 times of $LC_{50}$ of the first instar larvae was required to produce the median mortality, but more than 1700 times was required to kill the same proportion of the sixth instar larvae.

When $LC_{50}$'s of two succeeding stages were compared, $LC_{50}$ of the present instar divided by that of the previous instar, the rapid increase in virulence index was more clearly shown. At each succeeding
### TABLE 10

**MEDIAN LETHAL CONCENTRATIONS \( (\text{LC}_{50}; \text{NUMBER OF POLYHEDRA/100 CM}^2) \) OF NPV IN THE LAWN ARMYWORM LARVAE FROM THE FIRST TO SIXTH INSTAR**

<table>
<thead>
<tr>
<th>INSTAR</th>
<th>( \text{LC}_{50} )</th>
<th>LOWER LIMIT</th>
<th>UPPER LIMIT</th>
<th>RATE OF INCREASE FROM FIRST INSTAR</th>
<th>BETWEEN STAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>( 3.47 \times 10^5 )</td>
<td>( 2.01 \times 10^5 )</td>
<td>( 5.78 \times 10^5 )</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>II</td>
<td>( 5.13 \times 10^5 )</td>
<td>( 3.24 \times 10^5 )</td>
<td>( 8.03 \times 10^5 )</td>
<td>1.48</td>
<td>1.48</td>
</tr>
<tr>
<td>III</td>
<td>( 1.11 \times 10^6 )</td>
<td>( 5.09 \times 10^5 )</td>
<td>( 1.99 \times 10^6 )</td>
<td>3.20</td>
<td>2.26</td>
</tr>
<tr>
<td>IV</td>
<td>( 5.20 \times 10^6 )</td>
<td>( 2.89 \times 10^6 )</td>
<td>( 9.72 \times 10^6 )</td>
<td>14.99</td>
<td>4.68</td>
</tr>
<tr>
<td>V</td>
<td>( 4.25 \times 10^7 )</td>
<td>( 2.03 \times 10^7 )</td>
<td>( 7.60 \times 10^7 )</td>
<td>122.48</td>
<td>8.17</td>
</tr>
<tr>
<td>VI</td>
<td>( 5.95 \times 10^8 )</td>
<td>( 3.62 \times 10^8 )</td>
<td>( 8.83 \times 10^8 )</td>
<td>1714.70</td>
<td>14.00</td>
</tr>
</tbody>
</table>
instar, the index increased approximately two times. This geometric increase in virulence index between subsequent stages confirms that there is a strong age immunity in the armyworm larvae, and that the immunity is accelerated with the increase in larval age (Takei, 1971).

The LC$_{50}$'s obtained in this study were generally higher than those reported by previous workers. Takei (1971) obtained an LC$_{50}$ for the fourth instar larvae as $9.29 \times 10^4$ polyhedra per vial where the NPV was included in an artificial diet. Raheja (1965) reported the median lethal dose (LD$_{50}$) of the fourth instar larvae as 270 polyhedra per larva when the NPV was microfed. It was apparent that spraying the NPV, which was the normal way the virus is applied in the field, was a less efficient method to treat the armyworm.

Figures 11 and 12 show the change in the stage-specific and total mortality of the lawn armyworm larvae treated with different virus concentrations (see also Appendix B). With very few exceptions, the larvae treated with NPV were killed in the instar at which they were treated or within the next two larval instars. For simplicity of analysis, it was assumed that the proportion of the larvae killed three instars after treatment was insignificant in the total disease development. The few larvae that did die three instars after treatment were included with those dying two instars after treatment.

The stage-specific mortality, i. e. whether the larva died in the instar in which it was treated or in the subsequent two instars, was
Figure 11. -- The total and stage-specific mortalities when different virus concentrations (common logarithm of number of polyhedra/100 cm²) were sprayed on each instar of the lawn armyworm larvae (younger instars). A. First instar, B. Second instar, C. Third instar
STAGE-SPECIFIC MORTALITY

A

STAGE-SPECIFIC MORTALITY

B

STAGE-SPECIFIC MORTALITY

C
Figure 11 (continued). -- The total and stage-specific mortalities when different virus concentrations (common logarithm of number of polyhedra/100 cm²) were sprayed on each instar of the lawn armyworm larvae (older instars). D. Fourth instar, E. Fifth instar, F. Sixth instar
Figure 12. -- The proportion of the stage-specific mortality to the total mortality at each infection stage when different virus concentrations (common logarithm of number of polyhedra/100 cm$^2$) were sprayed on each instar of the lawn armyworm larvae (younger instars).

A. First instar, B. Second instar, C. Third instar
MORTALITY PROPORTION

A

MORTALITY PROPORTION

B

MORTALITY PROPORTION

C
Figure 12 (continued). -- The proportion of the stage-specific mortality to the total mortality at each infection stage when different virus concentrations (common logarithm of number of polyhedra/100 cm²) were sprayed on each instar of the lawn armyworm larvae (older instars).

D. Fourth instar, E. Fifth instar, F. Sixth instar
termed, initial, secondary or tertiary mortality. For the sixth instar larvae the tertiary infection stage was the pupal stage which was generally refractile to infection. Therefore, for the sixth instar, stage-specific mortality was recorded for just the primary or secondary stages.

Although many studies have been made on the relationship between the total mortality and virus concentration (Tanada, 1960, Raheja, 1965 and Takei, 1971), no reports are available on stage-specific mortality due to NPV treatment. This information was required to form a mathematical relationship between the stage-specific mortality and virus concentration to be able to predict the stage at which the infected larva died. This was then related to determine how much virus was produced in the dead larvae (on the populational basis). The older and larger larvae produced more virus since they had more tissues to be infected. The amount of virus produced determined how much inoculum was released into the environment to infect other larvae.

The stage-specific mortality curves appeared in various patterns depending upon larval age and virus concentration (Figure 11). In the first instar larvae, mortality at the initial infection stage showed the typical sigmoidal shape, reaching to asymptotic (100%) mortality at high concentrations. When the concentration of NPV was over $2.21 \times 10^7$ polyhedra per 100 cm$^2$, more than 90% of the larvae died in the initial stage (see also Appendix B).
At low concentrations, however, there were more individuals dying in the secondary and tertiary infection stages. At the lowest concentration, most larvae were killed at the tertiary stage. At concentrations between $6.40 \times 10^4$ and $5.65 \times 10^5$ polyhedra per 100 cm$^2$, more than 40 percent of the virus-killed larvae were dead at the secondary infection stage.

For the second to sixth instar larvae, most of the mortality occurred in the secondary stage. This phenomenon was more pronounced as the virus concentration was increased. In the second instar, however, there was a slight drop in the mortality for secondary stage at the highest virus concentrations. Larvae treated with high concentrations died more in the initial stage. The data also indicated that the duration of the lethal infection was a function of age of the larva and the concentration of NPV. The younger the larva and the higher the concentration of NPV, the shorter was the lethal infection period.

The stage-specific mortality was better compared when the mortality was transformed to the proportion of the total mortality

\[
\text{relative mortality; } \frac{\text{stage-specific mortality}}{\text{total mortality}} \times 100
\]

As shown in Figure 12, the relative mortality at the tertiary infection stage appeared highest at the lower end of virus concentrations, and decreased as virus concentration increased in each larval stage (see also Appendix B). It was the converse of the initial stage mortality. Even in the third to sixth instars, initial stage
mortality probably would have increased if higher concentration of virus was used.

In general the mortality in the armyworm after NPV treatment could be summarized as follows: 1) The mortality patterns were divided into two types depending on the age of treated larvae: (a) the "first instar type" where the initial mortality was most responsible for the total mortality, and (b) the "older instars type" where most of the larvae died in the secondary stage. 2) The stage-specific mortalities which were the most important component of the total mortality generally had a sigmoidal shape. 3) When stage-specific mortality was transformed into a proportion, tertiary mortality appeared as a negative sigmoidal pattern with the increase in virus concentration, and 4) the mortality proportion of the secondary stage (except for the first and sixth instar) was represented by an asymptotic curve (Table 11).

The mathematical relationship between mortality and virus concentration was investigated by running regression analyses. Generally dosage-mortality curves were calculated by using probit analysis, which is a weighted curvilinear regression on the logistic equation (Finney, 1962). In probit analysis, the variance is weighted to increase the accuracy of the estimated mortality around LC$_{50}$. This was not desirable, so a weighted curvilinear regression on the logistic equation was used for modeling in this study.
<table>
<thead>
<tr>
<th>INSTARS</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>II</td>
<td>0.756</td>
<td>7.3160</td>
<td>0.7784</td>
</tr>
<tr>
<td>III</td>
<td>0.731</td>
<td>3.4669</td>
<td>0.5344</td>
</tr>
<tr>
<td>IV</td>
<td>0.802</td>
<td>4.2605</td>
<td>0.5176</td>
</tr>
<tr>
<td>V</td>
<td>0.941</td>
<td>38.1337</td>
<td>0.6181</td>
</tr>
</tbody>
</table>

*y' = A - B * e^{-C*x}, where y' is mortality proportion, x is logarithm (common) of virus concentration (number of polyhedra/100 cm²), and A, B and C are constants. Constant A was obtained empirically through the graphic method, and B and C were calculated by the least square technique specified in BMDP (1979).
Since three infection stages were considered in modeling, the formulation of mathematical relationship on only two stages was sufficient to determine the third stage. Therefore, the logistic relationships for the secondary (stage-specific mortality) and tertiary (mortality proportion) infection stages were used for simulating disease development. For the first instar larvae, however, the initial mortality was used instead of the secondary mortality because the stage-specific mortality at the initial infection stage was most responsible for the total mortality, and showed the good logistic relationship with virus concentration.

The parameters in the logistic equation for the mortality-concentration relationship were determined by linear transformation. The equation, \( y' = \frac{k'}{1 + e^{(a' - b'x')}} \), where \( y' \) is mortality, \( x' \) is the logarithm (common) of virus concentration, \( k' \) is asymptote of the logistic curve, and \( a' \) and \( b' \) are constants, was used to estimate the values for the parameters as shown in Table 12.

For simplicity of parameter estimation, the asymptote, \( k' \)--the maximum limit of mortality shown at each infection stage--was empirically determined by observing the response curve on the stage-specific mortality (Figure 11 and 12). For the first instar larvae, \( k' \) was close to 1.000, meaning that, if virus concentration increased without limit, virtually all the armyworm larvae would die at the initial stage (first instar in this case). At the second instar, however, the asymptote for the secondary mortality appeared low, showing
TABLE 12

ESTIMATED PARAMETERS IN THE LOGISTIC EQUATION* TO DETERMINE THE TOTAL AND STAGE-SPECIFIC MORTALITIES OF THE LAWN ARMYWORM LARVAE SPRAYED WITH DIFFERENT NPV CONCENTRATIONS (NUMBER OF POLYHEDRA/100 CM²)

(YOUNGER LARVAE)

(FIRST INSTAR)

<table>
<thead>
<tr>
<th>STAGE</th>
<th>M/P**</th>
<th>k' ***</th>
<th>a'</th>
<th>b'</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTAL</td>
<td>M</td>
<td>1.000</td>
<td>10.220100</td>
<td>-1.824072</td>
<td>.903</td>
</tr>
<tr>
<td>INTITIAL</td>
<td>M</td>
<td>1.000</td>
<td>13.318398</td>
<td>-2.095524</td>
<td>.955</td>
</tr>
<tr>
<td>TERTIARY</td>
<td>P</td>
<td>0.694</td>
<td>-11.139353</td>
<td>2.283949</td>
<td>.792</td>
</tr>
</tbody>
</table>

(SECOND INSTAR)

<table>
<thead>
<tr>
<th>STAGE</th>
<th>M/P**</th>
<th>k' ***</th>
<th>a'</th>
<th>b'</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTAL</td>
<td>M</td>
<td>1.000</td>
<td>10.184272</td>
<td>1.764551</td>
<td>.854</td>
</tr>
<tr>
<td>SECONDARY</td>
<td>M</td>
<td>0.669</td>
<td>9.545506</td>
<td>1.615561</td>
<td>.876</td>
</tr>
<tr>
<td>TERTIARY</td>
<td>P</td>
<td>0.591</td>
<td>-8.318631</td>
<td>-1.498302</td>
<td>.744</td>
</tr>
</tbody>
</table>

(THIRD INSTAR)

<table>
<thead>
<tr>
<th>STAGE</th>
<th>M/P**</th>
<th>k' ***</th>
<th>a'</th>
<th>b'</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTAL</td>
<td>M</td>
<td>1.000</td>
<td>10.193414</td>
<td>1.639333</td>
<td>.865</td>
</tr>
<tr>
<td>SECONDARY</td>
<td>M</td>
<td>0.712</td>
<td>7.449209</td>
<td>1.170588</td>
<td>.770</td>
</tr>
<tr>
<td>TERTIARY</td>
<td>P</td>
<td>0.666</td>
<td>-13.650186</td>
<td>-2.338851</td>
<td>.783</td>
</tr>
</tbody>
</table>

* $y' = k'/(1 + e^{a' - b'x'})$, where $y'$ is mortality or mortality proportion (of the stage-specific mortality to total mortality), $x'$ is logarithm (common) of virus concentration (number of polyhedra/100 cm²), $k'$ is asymptote of the logistic curve, and $a'$ and $b'$ are constants.

** M represents that the calculated value for $y'$ is the total or stage-specific mortality, and P represents that the calculated value is mortality proportion.

*** $k'$ was empirically determined through the graphic method.
TABLE 12 (continued).

ESTIMATED PARAMETERS IN THE LOGISTIC EQUATION TO DETERMINE THE TOTAL AND STAGE-SPECIFIC MORTALITIES OF THE LAWN ARMYWORM LARVAE SPRAYED WITH DIFFERENT NPV CONCENTRATIONS (NUMBER OF POLYHEDRA/100 CM²)

(OLDER LARVAE)

(FOURTH INSTAR)

<table>
<thead>
<tr>
<th>STAGE</th>
<th>M/P</th>
<th>k'</th>
<th>a'</th>
<th>b'</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTAL</td>
<td>M</td>
<td>1.000</td>
<td>7.593563</td>
<td>1.146190</td>
<td>.850</td>
</tr>
<tr>
<td>SECONDARY</td>
<td>M</td>
<td>0.743</td>
<td>7.449209</td>
<td>1.170588</td>
<td>.864</td>
</tr>
<tr>
<td>TERTIARY</td>
<td>P</td>
<td>0.730</td>
<td>-4.679671</td>
<td>0.783778</td>
<td>.783</td>
</tr>
</tbody>
</table>

(FIFTH INSTAR)

<table>
<thead>
<tr>
<th>STAGE</th>
<th>M/P</th>
<th>k'</th>
<th>a'</th>
<th>b'</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTAL</td>
<td>M</td>
<td>1.000</td>
<td>13.621614</td>
<td>1.805412</td>
<td>.912</td>
</tr>
<tr>
<td>SECONDARY</td>
<td>M</td>
<td>0.894</td>
<td>16.340271</td>
<td>2.030765</td>
<td>.914</td>
</tr>
<tr>
<td>TERTIARY</td>
<td>P</td>
<td>1.000</td>
<td>-15.894713</td>
<td>-2.020251</td>
<td>.742</td>
</tr>
</tbody>
</table>

(SIXTH INSTAR)

<table>
<thead>
<tr>
<th>STAGE</th>
<th>M/P</th>
<th>k'</th>
<th>a'</th>
<th>b'</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTAL</td>
<td>M</td>
<td>1.000</td>
<td>27.901957</td>
<td>3.151054</td>
<td>.910</td>
</tr>
<tr>
<td>SECONDARY</td>
<td>P</td>
<td>1.000</td>
<td>27.177353</td>
<td>3.058661</td>
<td>.898</td>
</tr>
</tbody>
</table>
k' as 0.669. From the second instar on, the k' increased gradually with each succeeding instar. The observed k' for the secondary mortality was respectively 0.712, 0.743, 0.894 and 1.000 from the third to sixth instar.

The asymptote for the proportion of the mortality occurring tertiary infection stage was also shown in table 12. This proportion increased as virus concentration decreased. However, there was a minimum concentration below which mortality did not occur. This was at virus concentrations below $10^3$ polyhedra/100 cm$^2$. For virus concentrations below this level, k' was empirically determined based on results from the lowest virus concentrations tested. Because of this, the k's for the tertiary infection stage did not reach 100% except for the fifth instar. Therefore, the sum of the mortality proportions for the initial, secondary and tertiary infection stages was less than 100% from the first to fourth instar at the low concentrations (Figure 12). Except for the first instar, the k' increased as treated larvae matured. This implied that, at low virus concentrations, the old larvae took a longer time to be killed. Most of the larvae lasted to the tertiary stage.

The lethal infection period was also an important concern for the construction of the epizootic model. Table 13 shows the observed total lethal infection periods for each instar larvae sprayed with NPV at various concentrations. As expected, the lethal infection periods decreased as the polyhedra concentration increased. The shortest lethal
# Table 13

The lethal infection periods (in days) of the lawn armyworm larvae infected by NPV at different ranges of virus concentrations (number of polyhedra/100 cm²)

<table>
<thead>
<tr>
<th>Virus Concentration</th>
<th>Instar I</th>
<th>Instar II</th>
<th>Instar III</th>
<th>Instar IV</th>
<th>Instar V</th>
<th>Instar VI</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt; 10⁵</td>
<td>8.57</td>
<td>7.90</td>
<td>-</td>
<td>10.63</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>10⁵ - 10⁶</td>
<td>6.98</td>
<td>7.29</td>
<td>9.64</td>
<td>9.69</td>
<td>13.33</td>
<td>-</td>
</tr>
<tr>
<td>10⁶ - 10⁷</td>
<td>6.34</td>
<td>6.81</td>
<td>8.35</td>
<td>8.92</td>
<td>11.00</td>
<td>-</td>
</tr>
<tr>
<td>10⁷ - 10⁸</td>
<td>4.39</td>
<td>6.16</td>
<td>7.20</td>
<td>8.26</td>
<td>10.07</td>
<td>9.80</td>
</tr>
<tr>
<td>10⁸ - 10⁹</td>
<td>5.40</td>
<td>-</td>
<td>-</td>
<td>6.89</td>
<td>8.12</td>
<td>9.18</td>
</tr>
<tr>
<td>10⁹ - 10¹⁰</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>8.61</td>
</tr>
</tbody>
</table>
infection period was 4.4 - 5.4 days which occurred when the first instar larvae were sprayed with high virus concentrations (10^7 to 10^9 polyhedra per 100 cm^2), while the longest lethal infection period, 13.3 days, occurred when the fifth instar larvae were treated at low concentrations (10^5 to 10^6 polyhedra per 100 cm^2) of NPV. The reason why the longest lethal infection period was shown at the fifth instar rather than at the sixth instar was that the latter pupated at the tertiary stage.

The lethal infection periods decreased with the increase in virus concentration in each stage (Table 13). Even within stage-specific mortality, there was a correlation between age of the larva and virus concentration. Within a given stage, where all the larvae were killed in that same stage, there were still correlations with the virus concentration, i.e., the higher the virus concentration, the shorter the lethal periods. This negative relationship between the stage-specific lethal period and virus concentration confirms the fact that the armyworm larvae become less susceptible to infection by NPV as they mature (see also Appendix B).

The effect of virus treatment on the total lethal infection period can be analyzed in two aspects: 1) the change in age structure of cadaver population, and 2) the negative relationship of virus concentrations and lethal infection periods within each infection stage.

In the model the stage-specific lethal infection period was generated through two phases: 1) developmental period after treatment
for the host to reach the stage (initial or secondary) in which it is killed, and 2) the period in the terminal stage before the host died. Since there were no significant differences in the developmental periods of healthy and infected larvae until the terminal stage, the model for the basic life system was used to generate the developmental periods for the pre-terminal stages. To estimate the time that the larva was in the terminal stage before dying, the actually observed lethal periods in spray tests were empirically utilized. These data were arranged in a frequency table according to the day on which the larva died.

2. Simulation of Epizootics

The simulation model for NPV epizootics in the lawn armyworm was constructed from the data obtained in the previous experiments. The developmental process of the epizootiological model was: 1) to transform the biological data on NPV epizootics to simulation language, and 2) to combine this simulation of disease development with the basic life model of the insect.

Figure 13 shows the modified GPSS flowchart for simulating disease development in the insect population after virus spray. At each larval stage, the simulation of epizootics was inserted between the quantitative and chronological phases of the basic life model.

After passing the first "transfer" block in the flowchart for determining natural mortality in the basic life system, a decision--
Figure 13. -- A modified GPSS flowchart for simulating development of epizootics in the lawn armyworm population by NPV spray
NPV SPRAY

DISEASE DEVELOPMENT

DEATH

DETERMINATION OF VIRUS CONCENTRATION

DEATH

LARVAL DEVELOPMENT

DEATH

DEATH

NEXT STAGE

DEATH

DEATH

DEATH

DISEASE DEVELOPMENT

DISEASE DEVELOPMENT

DISEASE DEVELOPMENT

PREVIOUS STAGE

LIVE?

DEATH

DEATH

DEATH

DISEASE DEVELOPMENT

DEATH

NPV SPRAY
whether the virus will be sprayed or not—is made at the next "test" and "savevalue" blocks. Spray time was determined by certain decision criteria in the "test" block, e.g., host density, control schedule, etc. If the entering transaction was sprayed, a level of virus concentration was assigned by the use of the "savevalue" block. If the decision was not to spray, the individual proceeds to the subsequent larval development in the basic life model.

After simulating spray time and virus concentration, the total mortality was determined by using a "transfer" block. The logistic equation of the total mortality for the virus concentrations, was used in this study (Table 12) as the probability criteria for determining mortality for each entering individual. The death or survival for each infected larva was individually determined based on the probability criterion. The variation in mortality at each virus concentration was generated in a normal distribution pattern by the use of the obtained variance from the regression analysis.

While the transactions chosen to survive the virus infection were transferred to the blocks for the subsequent development of healthy insect, the individuals chosen to be killed enter the next "transfer" block to determine the stage-specific mortality. Generally the logistic equation for the secondary stage-specific mortality (initial mortality for the first instar) was used as the first probability criterion, and that for the mortality proportion of the tertiary infection stage was used as the second probability criterion. After the stage-specific
mortality was determined, the individual was transferred to the chain of "advance" and "terminate" blocks for simulating the time process of the lethal period and cadaver production.

3. Test of the Epizootiological Model

To compare the calculated epizootic development from the model with actual observations, bioassays were conducted with NPV in mass-reared populations of the armyworms. On September 10, October 22, and December 30, 1980, different concentrations of virus were sprayed on second, fourth and fifth instar larval populations, respectively. Figure 14 - 16 compare the cumulative occurrence (percent) of cadaver population between the actual and calculated data (see also Appendix C).

As shown in the figures, the general trend of disease development—the total and stage-specific mortalities and the occurrence of cadaver population—appeared similar for both the actual and calculated data. For both estimates, there was a good correlation between total mortality and virus concentration. In general the difference between the actual and calculated total mortalities ranged between 1 and 9 percent.

The stage-specific mortalities, generally showed good agreement between the actual and calculated data. In most cases the secondary infection stage was most important to the total mortality. At the lowest concentration for the fifth instar larvae, however, the tertiary
Figure 14. -- Comparison of the actual and calculated data on cadaver abundance (in percent) when different virus concentrations were sprayed on the second instar larvae on September 10, 1980.
Figure 15. -- Comparison of the actual and calculated data on cadaver abundance (in percent) when different virus concentrations were sprayed on the fourth instar larvae on October 22, 1980
VIRUS CONCENTRATION
(POLY/100 cm²)

October 22, 1980

4.54 × 10⁷
(MODEL)

4.54 × 10⁶

4.54 × 10⁵

ABUNDANCE (%)
Figure 16. -- Comparison of the actual and calculated data on cadaver abundance (in percent) when different virus concentrations were sprayed on the fifth instar larvae on December 30, 1980.
Virus Concentration
(POLY/100 cm)

December 30, 1980

8.16 x 10^6 (MODEL)

8.16 x 10^7

8.16 x 10^6

December 30, 1980

0 3 6 9 12 15

DAYS

VII

VI

V

INSTARS

ABUNDANCE (%)

30

60

90
infection stage—seventh instar—occupied the largest proportion of the total mortality for both actual and calculated data. At the concentration of $8.16 \times 10^7$ polyhedra/100 cm$^2$ for the same instar, both the secondary and tertiary infection stages appeared important to the total mortality.

Although most stage-specific mortalities showed good agreement between the actual and calculated data, the deviations became larger as the virus concentration was increased. This was especially true for the mortality in the second stage which accounted for the highest proportion of the total mortality.

As expected, the difference for the low and medium concentrations was smaller than that for the highest concentration. At the medium concentration the difference ranged 5 - 10, 2 - 6 and 4 - 9 %, respectively for the initial, secondary and tertiary mortality, while the corresponding deviation at the low concentration was respectively 0 - 1, 0 - 3 and 2 - 5 %. In total the differences between the actual and calculated data ranged between 0 - 22 % for the high concentrations, 2 - 10 % for the medium, and 0 - 5 % for the low concentrations.

The time of appearance of cadavers in the environmental system at each infection stage was also similar between the actual and calculated data. In both results, the higher the virus concentrations, the shorter the periods. Another general trend observed on the lethal infection periods was that the older larvae died over a longer span of time (on
the populational basis) than the young larvae. For the second instar larvae, death occurred in 5 - 11, 5 - 14, and 4 - 14 days after treatment at the lowest to the highest virus concentration in the actual observations respectively, while it occurred in 5 - 13, 5 - 15, and 4 - 14 days for the fourth instar and 7 - 16, 5 - 16, and 5 - 17 days for the fifth instar for each concentration from the lowest to the highest level. Between the calculated and actual data, generally 1 - 4 day differences occurred in the time required for the larvae to die.

Peak mortality also occurred at a similar time for the actual and calculated data. In both instances, the peak mortality appeared 6 - 8 days after treatment for the second instar larvae, 7 - 9 days for the fourth instar and 9 - 10 days for the fifth instar larvae. The stage-specific peak mortality also was similar between the actual and calculated data with differences of 0 - 3 days between the two figures.

Although more quantitative data were probably required to severely test the reliability of the epizootiological model, the calculated results in the present study seemed, on the empirical basis, to fall in an acceptable range to represent the general trend of disease development of the armyworm.
C. Application of the Model in Pest Management

1. Feeding Damage and Polyhedra Production

So far it has been shown that the developed simulation model can be used to predict population development of the pest insect. This predictability, alone, would be helpful for pest control—e.g., determining the peak time of pest abundance, estimating current pest density after treatment, etc. But, through an optimization process, the model can be further utilized as a basic strategic tool for making decisions in pest management.

Two important factors were linked to the model in this study. These were, feeding damage (by the armyworm larvae) and virus replication (after initial epizootic). For feeding damage, the relationship between feeding and temperature was investigated because it is known that temperature plays an important role in insect appetite. Although it would have been desirable to conduct feeding tests in the field, this was not possible. As an alternative, the feeding tests were conducted in the laboratory.

Table 14 shows the fresh weight of the average amount of Bermuda grass consumed by an armyworm larva at each instar. In total about 2670 mg of grass was eaten by an individual armyworm before it pupated. Food consumption rapidly increased after the fifth instar stage. Less than one percent of grass was consumed during the period from the first to
TABLE 14

DAILY AND TOTAL FOOD CONSUMPTION (FRESH WEIGHT OF BERMUDA GRASS IN MILLIGRAMS) BY A LAWN ARMYWORM LARVA AT EACH INSTAR UNDER LABORATORY CONDITIONS

<table>
<thead>
<tr>
<th>INSTARS</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
</tr>
</thead>
<tbody>
<tr>
<td>DAILY (mg)</td>
<td>0.5</td>
<td>1.1</td>
<td>2.9</td>
<td>9.7</td>
<td>27.4</td>
<td>83.6</td>
<td>316.7</td>
</tr>
<tr>
<td>S.D.</td>
<td>0.2</td>
<td>0.4</td>
<td>0.7</td>
<td>4.4</td>
<td>10.7</td>
<td>38.7</td>
<td>66.0</td>
</tr>
<tr>
<td>TOTAL (mg)</td>
<td>1.6</td>
<td>2.8</td>
<td>6.6</td>
<td>10.7</td>
<td>76.0</td>
<td>267.5</td>
<td>2308.6</td>
</tr>
<tr>
<td>PERCENT</td>
<td>&lt;0.1</td>
<td>0.1</td>
<td>0.2</td>
<td>0.4</td>
<td>2.8</td>
<td>10.0</td>
<td>85.9</td>
</tr>
<tr>
<td>LARVAL WEIGHT* (mg)</td>
<td>&lt;0.1</td>
<td>0.64</td>
<td>2.34</td>
<td>8.88</td>
<td>37.09</td>
<td>170.31</td>
<td>821.11</td>
</tr>
<tr>
<td>S.D.</td>
<td>-</td>
<td>0.19</td>
<td>0.57</td>
<td>4.13</td>
<td>16.41</td>
<td>80.85</td>
<td>156.25</td>
</tr>
</tbody>
</table>

* Maximum among daily measurements of fresh weight (mg) during the developmental period at each larval stage.
fourth instar. For the fifth and sixth instar larval period, approximately 2.8 and 10.0% were consumed respectively. The largest proportion of the grass, more than 85%, was consumed at the last instar stage. The average daily food consumption for each instar was used to estimate the total grass consumption by the armyworm population in the basic life model.

Table 14 also shows the fresh weight of a larva at each instar. The value in the table was the maximum weight of larva during each instar. Proportionally, in terms of body weight, the young larvae consumed more grass than the older larvae. The first instar consumed more than 50 times its own body weight of grass. For the last instar, about one third of its body weight of grass was consumed daily.

Figure 17 shows the total amount of Bermuda grass consumed by a single generation of armyworms produced by one mated female in the fall. The feeding curve started to increase rapidly two weeks after the introduction of the original female. This was about the time that the peak of the third instar larvae appeared. On the 28th day when the most food was consumed, the last instar larvae occupied the largest proportion of the total population. The fresh weight of Bermuda grass consumed at this time was about 330 mg. From the 28th day on, the feeding amount decreased as the last instar larvae pupated. In total, the armyworms from a single generation consumed approximately 3.4 kilograms of fresh Bermuda grass. Since the weight of Bermuda grass in
Figure 17. -- Daily feeding amount (fresh weight of Bermuda grass in grams) of the lawn armyworm progenies produced by a single female
FEEDING AMOUNT (GRAM)

DAYS

328

0

300 200 100
7 X 7 X 7 cm³ was 4.2 mg, 3.4 kg represented a lawn about 400 m² area with grass 7 cm tall.

In order to utilize the model to determine the total amount of virus produced by an epizootic, information on the amount of virus produced in an armyworm killed by NPV was required. Table 15 shows the number of polyhedra recovered from a single NPV-killed larva. The number increased more than 4,000 times from the first to last instar.

Figure 18 shows the cumulative polyhedra production from the second and fifth instar larvae when sprayed with three different concentrations of NPV. The initial population size was assumed to be 100 individuals for both instars.

Generally, the production curve appeared sigmoidal between 3 - 16 days. This pattern was more clearly shown at the higher virus concentrations. At the highest concentration, the second instar larvae started dying on the third day and the fifth instar on the fifth day.

The total amount of virus produced was dependent upon the concentration of the NPV and the age structure of the population. For the second instar, virus production distinctively increased as the sprayed concentration increased. For the fifth instar larvae, however, the virus production at concentrations of 8.16 X 10⁷, and 8.16 X 10⁸ polyhedra per 100 cm² of lawn surface was similar. This may be because, even though the total mortality was higher at the 8.16 X 10⁸ polyhedra
<table>
<thead>
<tr>
<th>LARVAL STAGES</th>
<th>NUMBER OF POLYHEDRA PER CADAVER</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>$1.11 \times 10^6 \pm 5.62 \times 10^5$</td>
</tr>
<tr>
<td>II</td>
<td>$6.40 \times 10^6 \pm 2.92 \times 10^6$</td>
</tr>
<tr>
<td>III</td>
<td>$2.30 \times 10^7 \pm 1.75 \times 10^6$</td>
</tr>
<tr>
<td>IV</td>
<td>$1.12 \times 10^8 \pm 6.05 \times 10^7$</td>
</tr>
<tr>
<td>V</td>
<td>$5.15 \times 10^8 \pm 2.65 \times 10^8$</td>
</tr>
<tr>
<td>VI</td>
<td>$1.55 \times 10^9 \pm 8.37 \times 10^8$</td>
</tr>
<tr>
<td>VII</td>
<td>$4.61 \times 10^9 \pm 1.98 \times 10^9$</td>
</tr>
</tbody>
</table>
Figure 18. -- Cumulative virus production (number of polyhedra, \( x \times 10^9 \)) from the lawn armyworm population when different virus concentrations were sprayed on the second and fifth instar larvae.
(second instar)

(acceptable) $9.07 \times 10^6$

$9.07 \times 10^5$

$9.07 \times 10^4$

(fifth instar)

$8.16 \times 10^8$

$8.16 \times 10^7$

$8.16 \times 10^6$

Days
per 100 cm², a large proportion of the infected larval population died at the secondary infection stage; while, for 8.16 X 10⁷ per 100 cm², a large number of larvae died at the tertiary infection stage—which has more polyhedra recovery per cadaver.

The epizootiological model was combined with food consumption to estimate the amount of food consumed by an infected population of armyworms. The data for food consumption for healthy larvae were used in this study with the assumption that: 1) the individual does not consume food in the stage (or instar) in which it dies, 2) the infected individual consumes about half as much as untreated healthy individuals in the stage immediately before death, and, 3) the feeding ability of an infected individual in the two stages before death is as same as a healthy one.

Figure 19 shows the food consumption when fourth instar larvae were treated with different concentrations of NPV. As expected, food consumption decreased as the concentration of NPV increased. NPV-treated armyworm consumed about 9, 32, and 75 percent of the grass eaten by untreated populations at 4.54 X 10⁷, 4.54 X 10⁶ and 4.54 X 10⁵ polyhedra per 100 cm² of lawn surface, respectively.

2. Optimization

The epizootiological model can provide the basis for making optimized decisions in pest management such as determination of spray
Figure 19. -- Cumulative food consumption (in percent) by the lawn armyworm population when different virus concentrations were sprayed on the fourth instar larvae
time and virus concentrations to maximize host plant protection and virus production. Since the model can be used to calculate total food consumption or the amount of virus production on the daily basis for any given set of variables, optimization is possible through the contour mapping method. This can be accomplished by connecting similar levels of food consumption and virus production at different combinations of virus concentrations and spray times. For ease of comparison, the amount of food saved by the virus treatment was used instead of the amount of food consumed. This was the difference between the amount of food consumed by an untreated population and one that was treated.

For optimization, it would have been desirable to include actual data on the introduction of armyworm into the environment in the field, but, since this was not possible, some hypothetical patterns were used. For simplicity of modeling, a homogeneous population of newly mated females was used as the original pest source.

Three simple theoretical frequencies were used to introduce the females: 1) the same number of females introduced each day during a certain introduction period, 2) females introduced in a symmetric pattern following the curve for normal distribution, and 3) a large number of females introduced in an aggregated manner early in the introduction period. The patterns 1), 2) and 3) were respectively called as the "uniform", "normal" and "aggregated" introductions in this study.
A hypothetical 100 mated females were introduced according to the selected pattern into a closed and favorable environmental system over a 14-day period. Fourteen days were used as the duration of the introduction period because: 1) this was about the lag period before the food consumption curve rapidly increased (Figure 17), 2) the period was sufficiently short so that there was no overlapping of progenies from the first generation females with those from the second generation females, and 3) the short period was relatively easier to follow in the model.

For simulating the uniform introduction, an equal probability (reciprocal of the introduction period) was given on each day as the frequency of appearance of the females during the introduction period. Since no statistical parameters are known from actual data, the probabilities for the normal and aggregated introduction were calculated by the use of the binomial distribution. For simplicity of data analysis and modeling, the probabilities in the binomial distribution with \( p = 0.5 \) and \( p = 0.1 \) were used to represent the normal and aggregated introductions respectively. The binomial distribution with \( p = 0.5 \) approximated as the normal distribution, while that with \( p = 0.1 \) for the early introduction was fitted to a Poisson distribution. Table 16 shows the probability of female introductions into the environmental system for the three different introduction patterns.

Figure 20 shows population development of the progeny from the egg to the last instar for the three different introduction patterns of
**TABLE 16**

**EXPECTED FREQUENCY OF DAILY FEMALE INTRODUCTION IN THREE DIFFERENT PATTERNS: WITH EQUAL PROBABILITY, OR IN THE BINOMIAL DISTRIBUTIONS WITH P = 0.5 AND P = 0.1**

<table>
<thead>
<tr>
<th>DAYS</th>
<th>UNIFORM</th>
<th>BINOMIAL (p = 0.5)</th>
<th>BINOMIAL (p = 0.1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.0714</td>
<td>0.0001</td>
<td>0.2542</td>
</tr>
<tr>
<td>1</td>
<td>0.0714</td>
<td>0.0016</td>
<td>0.3672</td>
</tr>
<tr>
<td>2</td>
<td>0.0714</td>
<td>0.0095</td>
<td>0.2448</td>
</tr>
<tr>
<td>3</td>
<td>0.0714</td>
<td>0.0349</td>
<td>0.0998</td>
</tr>
<tr>
<td>4</td>
<td>0.0714</td>
<td>0.0873</td>
<td>0.0277</td>
</tr>
<tr>
<td>5</td>
<td>0.0714</td>
<td>0.1571</td>
<td>0.0051</td>
</tr>
<tr>
<td>6</td>
<td>0.0714</td>
<td>0.2095</td>
<td>0.0008</td>
</tr>
<tr>
<td>7</td>
<td>0.0714</td>
<td>0.2095</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>8</td>
<td>0.0714</td>
<td>0.1571</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>9</td>
<td>0.0714</td>
<td>0.0873</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>10</td>
<td>0.0714</td>
<td>0.0349</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>11</td>
<td>0.0714</td>
<td>0.0095</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>12</td>
<td>0.0714</td>
<td>0.0016</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>13</td>
<td>0.0714</td>
<td>0.0001</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
Figure 20. -- Population development and the change in age structure of the lawn armyworm progenies (first generation) when 100 females were introduced into a closed and favorable environmental system with an equal frequency (uniform introduction) or with binomial distribution patterns ($p = 0.5$ for normal introduction and $p = 0.1$ for aggregated introduction) over a 14 day period.
ADULT PROGENY

NUMBER OF INSECTS (x 10000)

DAYS

uniform

normal

aggregated
females. The pattern of adult introduction--input time and compactness--was reflected in the development and age structure of the progeny population. For the uniform introduction, the curve for the total occurrence was relatively smoother and lower than those for the aggregated and normal introductions. Also the total developmental period was the longest, approximately 49 days from the initial day of adult introduction.

Among the three patterns, the early aggregated introduction, where a large number of females were introduced simultaneously in the early period, caused the most compact and fastest population development. Approximately 41 days were required after the initial day of adult introduction to complete population development. The total abundance curve for the normal introduction appeared to be between the other two patterns. Since the females were introduced with a high frequency in the middle period, the outline of population development was relatively smoother than the aggregated introduction, but was more compact than the uniform introduction. The population developmental period for the normal introduction, 48 days, was almost as long as the uniform introduction because the female input was relatively widely dispersed on the time scale.

The difference in population development among different introduction patterns of adults was more clearly shown when the age structure of the population was analyzed on the daily basis. On the 25th day after the initial introduction of the females, for example, the
uniform introduction consisted of all the age classes from the egg to the last instar larval stage.

In contrast, the progenies from the aggregated introduction consisted of only the older larvae from the fourth to last instar, which demonstrated the effect of aggregated introduction of the females to show the homogeneity (in the age structure) and fast development of the progeny population. For the normal introduction, the speed of population development was about the same as the uniform introduction. But the age composition was not as diverse as the uniform introduction consisting of the age classes between the first and sixth instar larvae.

These differences in progeny populations—compactness and developmental speed—were tied into the model with the feeding damage to the host plant population. Figure 21 shows the food consumption curves for the three different introduction patterns of the females.

As expected, the peak in the curve for the aggregated introduction appeared earliest and was the most compact. The peak appeared on the 31st day, and the larvae ate 29.3 kg of grass on the peak day.

The feeding periods for the uniform and normal introduction were similar with peaks appearing on the same 36th day, but the compactness—kurtosis—of the curves appeared differently. The uniform introduction produced a smoother and lower curve with a peak consumption
Figure 21. -- Daily food consumption (fresh weight of Bermuda grass in kilograms) by the lawn armyworm progenies when 100 mated females were introduced into a closed and favorable environmental system with an equal frequency (uniform introduction) or with binomial distribution patterns (p = 0.5 for normal introduction and p = 0.1 for aggregated introduction) over a 14 day period.
of 21.4 kg of grass while the normal introduction showed a peak consumption of 25.5 kg. This difference in the occurrence of damage caused by different patterns of adult introductions indicated that a lawn would be more severely affected if the adults appeared over a short period. A lawn may be able to withstand a higher total population of larvae if the introduction was uniform since there would be time for some regrowth in the lawn.

Since the required data were generated, the subsequent step was to investigate the feasibility of the use of this model in the management of the armyworm. This model was used to estimate feeding damage when the concentrations of NPV and the application times were varied.

To give an overall estimation on the grid values, the contour mapping method (Bridges and Becker, 1976) was applied to the optimization process by connecting the same level of grass yield (or grass saved by virus treatment) through an interpolation (among the obtained grid values). The contour curves then provided a basis for determining the optimum virus concentration and spray time for the armyworm management with NPV. Figures 22, 23 and 24 show the contour graphs of the amount of food saved (fresh weight of Bermuda grass in 100 grams) when the spray time (x axis) and virus concentration (y axis) were combined. For simplicity of optimization, the spray time was set between 12 and 39 days after the initial introduction of females. NPV was sprayed at 3 day intervals at concentrations ranging from 4.0 and 10.0 (common logarithm of the number of polyhedra per 100 cm² of lawn
Figure 22. -- Changes in yield of grass (fresh weight of Bermuda grass in 100 grams) at different combinations of virus concentration and spray time when 100 mated females were uniformly introduced into a closed environmental system over a 14 day period.
Figure 23. -- Changes in yield of grass (fresh weight of Bermuda grass in 100 grams) at different combinations of virus concentration and spray time when 100 mated females were introduced into a closed environmental system in a binomial distribution pattern with $p = 0.5$ (normal introduction) over a 14 day period.
(NORMAL INTRODUCTION)

Grass Weight
(X 100 gr)

LOG. OF VIRUS CONC.

DAYS
Figure 24. -- Changes in yield of grass (fresh weight of Bermuda grass in 100 grams) at different combinations of virus concentration and spray time when 100 mated females were introduced into a closed environmental system in a binomial distribution pattern with \( p = 0.1 \) (aggregated introduction) over a 14 day period.
(AGGREGATED INTRODUCTION)
surface) at intervals of 0.5 in the logarithmic scale. The normally-generated fall temperature was used. These contour graphs were made for each of the three adult introduction patterns.

In general, some common points were observed among the contour graphs. These were: 1) the least amount of damage occurred (or the highest amount of grass was saved) at the highest virus concentration, 2) the contour curves formed a concentric gradient, 3) the curves were close together, and formed a belt zone between 60 and 200 kg, and, 4) the contour curves appeared flat-hook-like, "V" in shape, consisting of three phases--vertical, horizontal, and diagonal.

The specific characteristics of the contour graphs reflected the patterns of adult introductions (input time and compactness). A good example was the time of appearance of the peaks which indicated when the least amount of damage was expected. For the early introduction of females, the peak appeared at about 18 to 21 days after the initial introduction of females, while the peaks for the uniform and normal introductions were shown to be around the 24th day.

The time interval of the introduction of the adults also affected the level of damage. The peak weight of the grass saved was more than 340 kg for the early aggregated introduction. For the normal introduction, about 320 kg, and for the uniform introduction, a total of 290 kg of grass was saved. These results showed that: 1) the earlier the females were introduced, the earlier the optimum control time
appeared, 2) the shorter the time interval for female introduction, the greater the effect of the NPV treatment, and, 3) the earlier and the more aggregated the introduction, the more critical the early spray time.

The optimum spray time changed as the concentration of NPV changed. At a concentration of $10^6$ polyhedra per 100 cm$^2$ for the normal introduction, the most effective date of application was around the 21st day after the first female was introduced. Approximately 160 kg of grass could be saved when treated at this time. For the highest concentration of $10^{10}$ polyhedra per 100 cm$^2$, on the other hand, the optimum spray date was around the 24th day. If the introduction period was set other than 14 days, the optimum spray date would also vary.

The differential impact of control practices on grass protection appeared more clearly in the belt zone. Between 18 - 30 days for the normal introduction (Figure 23), the contour curves were divided into a dense (belt) zone and a sparse zone at a concentration of $10^7$ polyhedra/100 cm$^2$. In the belt zone, an increase in spray concentration from $10^5$ to $10^7$ polyhedra/100 cm$^2$, increased the amount of grass saved by more than four times, while in the sparse zone an increase of $10^7$ to $10^{10}$ polyhedra/100 cm$^2$ increased the amount of grass saved by only 1.5 times. This shows that changes in the NPV concentration in the belt zone had a greater effect than outside the belt zone. If related to the data on the economic threshold and the cost of pathogen production, this
information can be most effectively used to develop a realistic, and
optimized strategy on armyworm management.

Another important characteristic of the contour graphs was the
shape of the curves. As previously mentioned, the three different types
of adult introductions produced generally the same "V" shaped contour
curves, consisting of the "early-vertical", "middle-horizontal" and
"late-diagonal" phases.

Initially, the curves formed almost vertical lines above a low
level of virus concentration in the early period (Figure 22, 23 and 24).
This suggested that above that low level of NPV concentration, spray
time (rather than virus concentration) was the most important variable
in determining how much grass was saved. Spraying the grass too early
resulted in poor control because more eggs were still being laid by the
adult. The spray application had to be made after all of the eggs had
hatched. Spraying too late, of course, did not help.

The duration of the vertical phases was dependent upon the speed
of development of the population. For the early aggregated introduction
of adults, the vertical zone ended before the 15th day after the
introduction of females, while, for the uniform and normal
introductions, it ended around the 20th day. This was about the time
all of the eggs had hatched.
At the time that the vertical phase ended, the population consisted of the first to the fourth instars. This may be the reason why there did not seem to be any concentration-related control effect above a certain level. The young larvae were susceptible at low concentrations of NPV and increasing the concentration could not have any additional effect. Therefore, above the concentration that is required for 100% mortality, spray time was the only factor that had any effect on the amount of damage sustained.

After the vertical phase, the contour curves moved into the horizontal phase. This was shown in the belt zone at the lower levels of virus concentration (generally below $10^7$ polyhedra per 100 cm$^2$). The duration of the horizontal phase was also dependent upon the patterns of adult introductions. With the uniform and normal introductions, it lasted approximately 10 days between the 18th and 27th day after the initial introduction of females, while, for the early aggregated introduction, the horizontal phase lasted only about 5 days between the 14th and 18th day.

In contrast to the vertical phase, virus concentration was more important than spray time in the horizontal phase. Since the virus concentrations, which showed a horizontal phase, were the lower concentrations, the treatment did not minimize in absolute terms. In the relative terms, however, changes in the concentration of NPV had a more significant effect than in the vertical phase.
The last part of the contour curves was generally diagonal, showing that in this phase grass protection was positively related to virus concentration, and negatively related to spray time. If the virus was sprayed early, a lower virus concentration was needed. If the virus was sprayed late, a higher concentration of virus was required to achieve the same results. In the contour graph for the normal introduction (Figure 23), for example, about 60 kilograms of grass were saved when the virus was sprayed at $10^6$ polyhedra per 100 cm$^2$ on the 27th day, but, if the virus was sprayed on the 33rd day, more than $10^8$ polyhedra per 100 cm$^2$ was needed to obtain the same yield of grass.

The duration of the diagonal phase was also dependent upon the introduction pattern of females. It was 32 days for early aggregated introduction, 38 days for the normal introduction, and 42 days for the uniform introduction.

The contour graphs for virus production (Figure 25, 26 and 27) were derived for virus concentration and spray time, using the same techniques as used to determine yield. The results indicated that: 1) the most virus was produced at the highest virus concentration in each introduction pattern, and, 2) the contour curves formed the concentric gradient with the changes in spray time and virus concentration.

Compared to grass yield, however, the peaks for polyhedra production appeared later. This was generally expected because the older and larger larvae produced more polyhedra per individual. The
Figure 25. -- NPV production (number of polyhedra, \( \times 10^{11} \)) at different combinations of virus concentration and spray time when 100 mated females were uniformly introduced into a closed environmental system over a 14 day period.
Figure 26. -- NPV production (number of polyhedra, $X \times 10^{11}$) at different combinations of virus concentration and spray time when 100 mated females were introduced into a closed environmental system in a binomial distribution pattern with $p = 0.5$ (normal introduction) over a 14 day period.
Figure 27. -- NPV production (number of polyhedra, $10^{11}$) at different combinations of virus concentration and spray time when 100 mated females were introduced into a closed environmental system in a binomial distribution pattern with $p = 0.1$ (aggregated introduction) over a 14-day period.
peak of polyhedra production appeared about a week later than the peak for grass yield when the females were introduced uniformly or in a normal distribution. For the aggregated introduction the peak was on the 26th day, which was about five days later than the peak for grass yield.

The effect of aggregation on the introduction of females was also reflected in the amount of virus produced. The more aggregated the introduction, the higher the production of virus. This was in part due to the homogeneity of age structure. The aggregated introduction produced $3.2 \times 10^{14}$ polyhedra in total while the normal introduction produced $2.9 \times 10^{14}$ polyhedra. The most widely dispersed uniform introduction produced the lowest amount of virus with $1.7 \times 10^{14}$ polyhedra. The contour curves reflected this phenomenon.

The patterns of adult introduction were also reflected in forming the specific characteristics of the belt zone. For the aggregated and normal introduction of females, the range of the belt zone was $1.2 - 2.6 \times 10^{14}$ polyhedra, while it was $0.8 - 1.6 \times 10^{14}$ polyhedra for the dispersed uniform introduction.

Overall, the optimization study through the contour mapping method can be summarized as: 1) the pattern of adult introductions determined the characteristics of progeny population--age structure, developmental speed, etc.. 2) the contour curves of the three patterns of adult introductions had some common characteristics such as the peaks at the
highest virus concentration, formulation of the concentric gradients from the peaks, existence of a belt zone, and appearance of the curves as the flat-hook-like shape. 3) the hook form appeared more clearly in the graphs for grass yield and consisted of the early-vertical, middle-horizontal, and late-diagonal phases. 4) within these general categories of common points, the specific characteristics of the contour curves—e.g., the yield of grass, the appearance time of the peaks, the range of the belt zone, etc.—were dependent upon the patterns of adult introductions, and 5) the yield was more significantly affected by early treatment while the population was still young, while virus production was more affected by treatments at a later period when the population was more mature.

This study, therefore, has explained the feasibility of the use of the simulation model in terms of optimizing the two control practices—spray time and virus concentration—for the best protection of the host plant and the maximum virus recovery. There are, however, other components of armyworm management that could be included in the model. Unfortunately, these studies were beyond the scope of this study. The followings are some of the important aspects to be included to the simulation model.

First, it would be desirable to add the concept of "space" to the simulation system. For simplicity of modeling, the abundance of the insect was mainly discussed in terms of "time scale", and not of density. The environmental system was assumed to be capable of
supporting an unlimited number of insects without causing the space-related problems such as crowding, food shortage, etc..

By extending the dimension of "space" into the simulation system, a physical ecosystem which has a spatial boundary, e.g., the lawns of parks, golf courses, etc., can be represented. Also, all the density-related problems such as feeding competition, determination of economic threshold, differences in disease transmission rates, etc., can be studied in the system. However, to successfully transfer these space-oriented effects in the simulation model, more data on spatial distribution of the insect and host plant, vegetation status, effect of feeding damage on the host plant, spatial dispersion and transmission patterns of the pathogen in environment, etc., are needed.

Secondly, it would be desirable to add more climatic data to the system. In this study only temperature was included. But there are numerous other components of weather which affect the life process of the insect, pathogen and host plant such as humidity, rain, wind, sunlight, etc.. Not only the quantitative effect of each component, but also the combinational impact of different components on the insect life system should be determined and added to the system.

Thirdly, it would be desirable to determine persistency and frequency of outbreaks of the disease in the environment. This requires data from the long-term studies of the pathogen-pest-environment relationships.
And fourthly, for a precise estimate of food supply for the insect, a model for the growth of the host plant should be developed and linked to the simulation model. By introducing the plant development model into the system, a more realistic assessment of the feeding damage can be made by monitoring input variables such as environmental factors, insect appetite, spray times, virus concentration, etc..

The model can effectively integrate these additional components relating to the insect disease system. Additionally, the epizootiological model can be effectively linked to the other important key factors in the armyworm management, such as the effect of natural enemies, chemical control, etc.. If the cost factors are also included, the crop protectors can utilize the model to make decisions to maximize the cost benefit ratios in the management of the pest.

The modeling tool, GPSS, used in this study, demonstrated its excellence in the ability of simulation, prediction and accommodation of system components. By considering the individual as a basic unit (transaction) of simulation, it provided a very close representation of the natural phenomena of insect life processes.

Due to its individual approach, however, GPSS required more computer time and the cost to run the program was high. Also, GPSS was originally designed to represent an engineering and marketing system in which there were lines, e. g., customers waiting in line for service,
cars in traffic to pass the toll gate in rush hours, etc.. These conditions generally did not occur in this study.

In this study, therefore, a basic epizootiological model was developed for the lawn armyworm. The model can be used in the management of the armyworm with NPV. However, the utility of the model can be enhanced by developing and including additional biological, ecological and physical data.
SUMMARY AND CONCLUSIONS

The lawn armyworm, one of the most serious lawn pests in Hawaii, was used to develop an epizootiological model.

An analytic approach was applied with the three research steps. First, the basic life system of the insect was simulated by developing data on the armyworm life history and integrating them into a proposed algorithm on the temperature-development relationship. Secondly, the simulation of NPV epizootics was combined with the basic life system to construct an epizootiological model. And thirdly, the developed models of the basic and epizootiological life systems of the armyworm were optimized so that the results could be used to make appropriate pest management decisions.

For the basic life system, the population growth was divided into two biological phases: 1) egg production and 2) development of the eggs to subsequent life stages. In each phase, there were two aspects for simulating the population development, quantitative, i.e., population size, and chronological, i.e., developmental period.

A large proportion of females had a preoviposition period of 3 - 4 days with an average of $3.75 \pm 1.07$ days. The frequent oviposition period was 4 - 7 days with an average of $5.51 \pm 1.92$ days. Observation of egg production showed that a large proportion of eggs was laid in the
early period of oviposition. On the average, 1505 ± 603 eggs were produced by a female under laboratory conditions.

Individual rearing tests were conducted at temperatures between 15 and 35 °C at 5 degree intervals. It required 77.8, 40.3, 25.9 and 19.2 days from oviposition to emergence at temperatures of 20, 25, 30 and 35 °C, respectively. The observed survival rate at each life stage of the armyworm varied from 89.7 to 99.9 percents at temperatures between 20 and 30 °C. About 70 percent of the larvae survived from the first instar to emergence when the rearing was initiated from the first instar.

The developmental period for each life stage of the armyworm was determined using the thermal summation method and the logistic equation. The minimum threshold temperature obtained by the thermal summation method was 10.7, 13.7, 14.4, 13.5, 13.6, 13.3, 12.2, 17.4 and 15.1 °C for the egg, first to seventh instar larva and the pupal stage, respectively.

The computer simulation language, GPSS (General Purpose Simulation Systems), was used to represent the life system of the lawn armyworm in this study. The simulative ability of the model was tested through the predictive and descriptive manner.

When the basic life model was run in the predictive manner, the peak days for abundance of the progeny from the egg to adult were 6, 11,
13, 16, 18, 21, 24, 28, 38 and 47 days after the initial female introduction. Approximately 70 days were required to complete a single generation of the armyworm.

There were approximately 1110 eggs on the peak day. From the egg stage on, the peak abundances gradually decreased in the larval stages until it reached ca. 650 in the sixth instar. For the last instar larval and pupal stages, however, the peak increased to ca. 950 and 1140 individuals. This was due to the longer developmental periods at these stages. Therefore more individuals could be accumulated in these stages. For the adult stage, there were approximately 930 individuals on the day of peak abundance.

There was general agreement in the trend of population development--calculated peak time and population size--between the actual and calculated data. Quantitatively, however, the total populations from actual observations were generally lower than those from the model.

The calculated populations by the logistic model was similar to that by the thermal summation model. The logistic model predicted the appearance of the older stages slightly earlier than the thermal summation model.

The thermal summation method was further used to develop the epizootiological model in this study because the ambient temperature in
Hawaii is in the optimal range and the variation is slight. Also the thermal summation model was relatively simple to run in the simulation program.

To develop epizootiological data, suspensions of NPV were sprayed on armyworm populations.

The calculated median lethal concentration was $3.47 \times 10^5$, $5.13 \times 10^5$, $1.11 \times 10^6$, $5.20 \times 10^6$, $4.25 \times 10^7$, and $5.95 \times 10^8$ polyhedra per $100 \text{ cm}^2$ of lawn surface for the first to sixth instar, respectively. The older the larva, the more resistant it was to infection. The virulence index indicated that the resistance between each succeeding larval stage increased geometrically. This confirmed that the immunity of the armyworm larva against the virus infection increases as the larvae mature.

The observed mortality was further analyzed stage-specifically. The mortality patterns were largely divided into two types depending upon the age of the treated larvae. In the "first instar type", most of the larvae died in the treated instar, and, in the "older instars type", most of the larvae died in the next instar. The stage-specific mortality that was the most important component of the total mortality generally had a sigmoidal shape. When the stage-specific mortality was transformed to the proportion of the total mortality, that for the tertiary mortality appeared as the negative sigmoidal pattern with the increase in virus concentration, while the mortality proportion of the
secondary stage (except for the first and sixth instar) fitted an asymptotic curve.

Besides mortality, the total and stage-specific lethal infection periods were also observed at various virus concentrations at ambient conditions. As expected, the younger the larvae and/or the higher the virus concentration, the shorter the lethal infection period. The shortest lethal infection periods were around 4.4 to 5.4 days when the first instar larvae were sprayed with virus concentrations of $10^7$ and $10^9$ polyhedra per 100 cm$^2$, while the longest infection period was around 13.3 days when the fifth instar larvae were treated at virus concentrations of $10^5$ and $10^6$ polyhedra per 100 cm$^2$.

When the lethal infection periods were further analyzed stage-specifically, generally two kinds of gradients were found, within and between infection stages. Within each infection stage, the stage-specific lethal infection periods decreased as virus concentration increased.

Comparative tests of the developed model and actual epizootiological data showed that the general trends of disease development—the total and stage-specific mortalities and the time occurrence of the cadaver population—appeared similar between the actual and calculated data. In general the difference of the actual and calculated data on the total mortalities ranged between 1 and 9 percent.
The stage-specific mortalities were also similar between the actual and calculated data in quantitative terms, and the secondary infection stage was most responsible for the total mortality in most cases. The total and stage-specific lethal infection periods—the appearance time of cadavers at each infection stage—were also similar between the actual and calculated data.

One of the objectives of the present study was to test the feasibility of using the developed model to maximize control practices. Two important factors in the management of this pest were linked to the epizootiological model. These were, feeding damage and virus replication. The basic data required for determining feeding damage were obtained in the laboratory.

By linking the daily food consumption data to the simulation model, it was possible to predict the total feeding damage by the armyworm population with time. The calculated feeding damage appeared to rapidly increase two weeks after the introduction of the female. Feeding damage reached its peak on the 28th day. Most of the larvae were in the last instar at that time. According to the model, the armyworm larvae from a single female consumed approximately 3.4 kilograms of Bermuda grass (fresh weight). This was equal to a lawn about 400 m² in which the grass was 7 cm tall.

To estimate virus replication, the number of polyhedra produced in a single NPV-killed larva was counted. The number increased more than
4,000 times from the first to the last instar stage. In general the total amount of virus produced was dependent upon the spray concentration and the age structure of the cadaver population.

Since the simulation model can be used to calculate the total feeding damage and the amount of virus production on a daily basis under any given condition, optimization was possible by using a contour mapping method.

Three simple theoretical frequencies were used to introduce the armyworms into the system. In the first introduction a similar number of females were introduced each day over a certain introduction period--uniform introduction. In the second, females were introduced with a relative high frequency in the middle of the introduction period in a symmetric way--normal introduction. In the third method, a large number of females were introduced in an aggregated manner during the early part of the introduction period--aggregated introduction.

The patterns of adult introductions were reflected in the development and age structure of the progeny population. For the uniform introduction where the female input was the most dispersed on the time scale, the curve for the total population was smoother and lower, and encompassed a longer time than those for the normal or aggregated introductions. The population development for the aggregated
introduction was compact and fast. The total abundance curve for the normal introduction appeared to be between the other two patterns.

Contour mapping of these data revealed that the highest virus concentrations produced the highest yields of grass. The contour lines from this peak formed a concentric gradient with the change in virus concentration and spray time. The contour lines were dense, and formed the belt zone at a certain level. The contour lines appeared in a flat-hook-like, "L/" shape, consisting of vertical, horizontal and diagonal phases depending on spray time and virus concentration.

In general these results of optimization showed that, the earlier and the more aggregated were the females introduced, the earlier was the optimized control time for the host plant protection. The more aggregatedly were the females introduced, the more effective were the control practices.

The input time and compactness of adult introduction were also reflected in the amount of virus produced in the epizootic. Because of its high abundance and homogeneity of age structure, the aggregated early introduction produced the largest amount of virus.

Overall, the optimization study through the contour mapping method on the host plant protection and virus production indicated that the pattern of adult introduction affected the characteristics of progeny population--age structure, developmental speed, etc.. In addition, the
yield was greatly affected by measures taken in the treatment during the early period, while that for virus production was more affected by measures taken when the population was more mature.

Although more tests are required to further investigate the reliability of the model on a quantitative basis, the simulation and optimization process developed in this study indicated that the systems technique and modeling can be used as a practical strategic tool in pest management.

Although the simulation modeling with GPSS showed some disadvantages, such as, the cost of computer time and the repeated execution of the model for optimization processes, crop protectors can use the model by integrating it with their empirical knowledge of crop protection or combining it with other optimization models.
### TABLE 17

**COMPARISON OF THE ACTUAL AND CALCULATED POPULATION DEVELOPMENT (PERCENT ABUNDANCE) OF THE LAWN ARMYWORM IMMATURES WHEN THE FIRST INSTAR LARVAE WERE INFESTED ON SEPTEMBER 18, 1979 AS THE INITIAL POPULATION (100%)**

#### (ACTUAL)

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#### (THERMAL SUMMATION MODEL)

| I                      | 14 |   |   |    |    |    |    |    |
| L                      |   | 79| 2 |    |    |    |    |    |
| A                      |   |   | 86| 9  |    |    |    |    |
| R                      |   | 4 | 79| 38 |    |    |    |    |
| V                      |   | 1 | 49| 31 |    |    |    |    |
| A                      |   | 2 | 55| 69 | 16 |    |    |    |
| VII                    |   |   | 10| 60 | 28 |    |    |    |
| PUPA                   |   |   |   | 3  | 50 |    |    |    |
| TOTAL                  | 93| 92| 89| 89 | 86 | 79 | 79 | 78 |

#### (LOGISTIC MODEL)

| I                      |   |   |   |    |    |    |    |    |
| L                      |   | 92|   |    |    |    |    |    |
| A                      |   | 66| 9 | 1  |    |    |    |    |
| R                      |   | 21| 64| 18 | 1  | 1  |    |    |
| V                      |   | 11| 60| 15 | 3  |    |    |    |
| A                      |   | 5 | 59| 58 | 5  |    |    |    |
| VII                    |   |   | 7 | 20 | 74 | 6  |    |    |
| PUPA                   |   |   |   |    |    |    | 67 |
| TOTAL                  | 92| 87| 84| 84 | 82 | 82 | 79 | 73 |
### TABLE 17 (continued)

**COMPARISON OF THE ACTUAL AND CALCULATED POPULATION DEVELOPMENT (PERCENT ABUNDANCE) OF THE LAWN ARMYWORM IMMATURES WHEN THE FIRST INSTAR LARVAE WERE INFESTED ON OCTOBER 15, 1979 AS THE INITIAL POPULATION (100%)**

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| **(THERMAL SUMMATION MODEL)** |   |   |   |   |   |    |    |    |    |    |    |    |
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| L II                   | 10|73 |  1|   |   |    |    |    |    |    |    |    |
| A III                  | 20|78 |26 |   |   |    |    |    |    |    |    |    |
| R IV                   | 13| 65|  5|16 |   |    |    |    |    |    |    |    |
| V V                    | 37| 65| 58 |  5|   |    |    |    |    |    |    |    |
| A VI                   | 6 |45 | 56| 19|  2|    |    |    |    |    |    |    |
| VII                    | 2 |18 | 56| 67|30 |  7|    |    |    |    |    |    |
| **PUPA**               |  1|  3|  8|46 |66 |
| **TOTAL**              | 93| 92| 91| 87|87 |85 |80 |78 |77 |76 |73 |

| **(LOGISTIC MODEL)**  |   |   |   |   |   |    |    |    |    |    |    |    |
| I                      | 88|   |   |   |   |    |    |    |    |    |    |    |
| L II                   |  4|73 |   |   |   |    |    |    |    |    |    |    |
| A III                  | 19|57 |18 |  1|   |    |    |    |    |    |    |    |
| R IV                   | 33| 67| 30| 12|  1|    |    |    |    |    |    |    |
| V V                    |  2|51 | 59| 17|  2|    |    |    |    |    |    |    |
| A VI                   |  3|13 | 59| 32|  8|    |    |    |    |    |    |    |
| VII                    |  3| 44| 68| 65|10 |    |    |    |    |    |    |    |
| **PUPA**               |   |   |   |   |   |    |    |    |    |    |11  | 61|
| **TOTAL**              | 92| 92| 90| 87|85 |84 |80 |78 |76 |71 |70 |
TABLE 17 (continued)

COMPARISON OF THE ACTUAL AND CALCULATED POPULATION DEVELOPMENT (PERCENT ABUNDANCE) OF THE LAWN ARMYWORM IMMATURES WHEN THE FIRST INSTAR LARVAE WERE INFESTED ON DECEMBER 22, 1979 AS THE INITIAL POPULATION (100 %)

<table>
<thead>
<tr>
<th>(ACTUAL)</th>
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<tbody>
<tr>
<td>DAYS AFTER INFESTATION</td>
</tr>
<tr>
<td>--------------------------</td>
</tr>
<tr>
<td>I</td>
</tr>
<tr>
<td>L II</td>
</tr>
<tr>
<td>A III</td>
</tr>
<tr>
<td>R IV</td>
</tr>
<tr>
<td>V V</td>
</tr>
<tr>
<td>A VI</td>
</tr>
<tr>
<td>VII</td>
</tr>
<tr>
<td>PUPA</td>
</tr>
<tr>
<td>TOTAL</td>
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</table>

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<th>(THERMAL SUMMATION MODEL)</th>
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</tr>
<tr>
<td>--------------------------</td>
</tr>
<tr>
<td>I</td>
</tr>
<tr>
<td>L II</td>
</tr>
<tr>
<td>A III</td>
</tr>
<tr>
<td>R IV</td>
</tr>
<tr>
<td>V V</td>
</tr>
<tr>
<td>A VI</td>
</tr>
<tr>
<td>VII</td>
</tr>
<tr>
<td>PUPA</td>
</tr>
<tr>
<td>TOTAL</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(LOGISTIC MODEL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DAYS AFTER INFESTATION</td>
</tr>
<tr>
<td>-----------------------</td>
</tr>
<tr>
<td>I</td>
</tr>
<tr>
<td>L II</td>
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<tr>
<td>A III</td>
</tr>
<tr>
<td>R IV</td>
</tr>
<tr>
<td>V V</td>
</tr>
<tr>
<td>A VI</td>
</tr>
<tr>
<td>VII</td>
</tr>
<tr>
<td>PUPA</td>
</tr>
<tr>
<td>TOTAL</td>
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</table>


APPENDIX B - 1.

TABLE 18
STAGE-SPECIFIC MORTALITY (PERCENT) AND LEthal INFECTION PERIOD (DAY) OF THE LAWN ARMYWORM WHEN THE FIRST INSTAR LARVAE WERE TREATED WITH VARIOUS CONCENTRATIONS OF NPV

<table>
<thead>
<tr>
<th>VIRUS CONCENTRATION (POLY/100CM²)</th>
<th>MORTALITY</th>
<th>MORTALITY PROPORTION</th>
<th>LETHAL INFECTION PERIOD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TOTAL</td>
<td>INI</td>
<td>SEC</td>
</tr>
<tr>
<td>8.50 X 10³</td>
<td>15.0</td>
<td>0.0</td>
<td>5.0</td>
</tr>
<tr>
<td>6.40 X 10⁴</td>
<td>30.7</td>
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<td>13.7</td>
</tr>
<tr>
<td>5.65 X 10⁵</td>
<td>55.7</td>
<td>22.0</td>
<td>23.4</td>
</tr>
<tr>
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<td>65.0</td>
<td>13.8</td>
</tr>
<tr>
<td>2.21 X 10⁷</td>
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<td>80.0</td>
<td>10.0</td>
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<td>8.50 X 10⁸</td>
<td>99.9</td>
<td>99.9</td>
<td>0.0</td>
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</table>
### TABLE 18 (continued)

STAGE SPECIFIC MORTALITY (PERCENT) AND LETHAL INFECTION PERIOD (DAY) OF THE LAWN ARMYWORM WHEN THE SECOND INSTAR LARVAE WERE TREATED WITH VARIOUS CONCENTRATIONS OF NPV

<table>
<thead>
<tr>
<th>VIRUS CONCENTRATION (POLY/100CM²)</th>
<th>TOTAL MORTALITY</th>
<th>MORTALITY PROPORTION</th>
<th>LETHAL INFECTION PERIOD</th>
</tr>
</thead>
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<td>SEC</td>
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<td>80.9</td>
<td>8.7</td>
<td>63.4</td>
</tr>
<tr>
<td>8.64 x 10⁷</td>
<td>95.6</td>
<td>30.0</td>
<td>62.8</td>
</tr>
</tbody>
</table>
APPENDIX B-3.

TABLE 18 (continued)

STAGE-SPECIFIC MORTALITY (PERCENT) AND LETHAL INFECTION PERIOD (DAY) OF THE LAWN ARMYWORM WHEN THE THIRD INSTAR LARVAE WERE TREATED WITH VARIOUS CONCENTRATIONS OF NPV

<table>
<thead>
<tr>
<th>VIRUS CONCENTRATION (POLY/100CM²)</th>
<th>MORTALITY</th>
<th>MORTALITY PROPORTION</th>
<th>LETHAL INFECTION PERIOD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TOTAL</td>
<td>INITI SECONDS TERMINI</td>
<td>TOTAL INITI SECONDS TERMINI</td>
</tr>
<tr>
<td>1.51 X 10⁴</td>
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<td>0.0</td>
<td>3.7 7.8</td>
</tr>
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<td>1.51 X 10⁵</td>
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<td>15.0 10.0</td>
</tr>
<tr>
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<td>23.0 13.5</td>
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<tr>
<td>4.28 X 10⁶</td>
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<td>12.6</td>
<td>40.3 10.4</td>
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<tr>
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<td>54.6 3.4</td>
</tr>
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<td>5.29 X 10⁷</td>
<td>85.0</td>
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<td>60.0 0.0</td>
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</table>
APPENDIX B - 4.

TABLE 18 (continued)

STAGE-SPECIFIC MORTALITY (PERCENT) AND LETHAL INFECTION PERIOD (DAY) OF THE LAWN ARMYWORM WHEN THE FOURTH INSTAR LARVAE WERE TREATED WITH VARIOUS OF CONCENTRATIONS OF NPV

<table>
<thead>
<tr>
<th>VIRUS CONCENTRATION (POLY/1000CM²)</th>
<th>MORTALITY</th>
<th>MORTALITY PROPORTION</th>
<th>LETHAL INFECTION PERIOD</th>
</tr>
</thead>
<tbody>
<tr>
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<td>TOTAL</td>
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<td>SEC</td>
</tr>
<tr>
<td>7.78 x 10³</td>
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</tr>
<tr>
<td>7.71 x 10⁴</td>
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</tr>
<tr>
<td>6.73 x 10⁵</td>
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<td>6.89 x 10⁶</td>
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<td>57.6</td>
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<td>8.01 x 10⁸</td>
<td>94.7</td>
<td>21.1</td>
<td>68.4</td>
</tr>
</tbody>
</table>
APPENDIX B - 5.

TABLE 18 (continued)

STAGE-SPECIFIC MORTALITY (PERCENT) AND LETHAL INFECTION PERIOD (DAY) OF THE LAWN ARMYWORM WHEN THE FIFTH INSTAR LARVAE WERE TREATED WITH VARIOUS CONCENTRATIONS OF NPV

<table>
<thead>
<tr>
<th>VIRUS CONCENTRATION (POLY/100CM²)</th>
<th>MORTALITY</th>
<th>MORTALITY PROPORTION</th>
<th>LETHAL INFECTION PERIOD</th>
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</thead>
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<tr>
<td></td>
<td>TOTAL</td>
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<td>8.16 X 10⁶</td>
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<td>6.15 X 10⁷</td>
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<td>32.3</td>
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<td>7.86 X 10⁸</td>
<td>86.3</td>
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TABLE 18 (continued)

STAGE-SPECIFIC MORTALITY (PERCENT) AND LETHAL INFECTION PERIOD (DAY) OF THE LAWN ARMYWORM WHEN THE SIXTH INSTAR LARVAE TREATED WITH VARIOUS CONCENTRATIONS OF NPV

<table>
<thead>
<tr>
<th>VIRUS CONCENTRATION (POLY/100CM²)</th>
<th>MORTALITY</th>
<th></th>
<th></th>
<th>MORTALITY PROPORTION</th>
<th></th>
<th></th>
<th>LETHAL INFECTION PERIOD</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TOTAL</td>
<td>SEC</td>
<td>TER</td>
<td></td>
<td>TOTAL</td>
<td>SEC</td>
<td>TER</td>
<td></td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.80 X 10⁷</td>
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<td>0.0</td>
<td>99.9</td>
<td>0.0</td>
<td>9.80</td>
</tr>
<tr>
<td>3.78 X 10⁸</td>
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<td>44.4</td>
<td>0.0</td>
<td>0.0</td>
<td>99.9</td>
<td>0.0</td>
<td>9.49</td>
</tr>
<tr>
<td>7.18 X 10⁸</td>
<td>54.2</td>
<td>2.5</td>
<td>51.7</td>
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<td>4.6</td>
<td>95.5</td>
<td>0.0</td>
<td>9.24</td>
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<td>1.51 X 10⁹</td>
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<td>72.2</td>
<td>0.0</td>
<td>0.0</td>
<td>99.9</td>
<td>0.0</td>
<td>8.89</td>
</tr>
<tr>
<td>3.40 X 10⁹</td>
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<td>82.1</td>
<td>0.0</td>
<td>0.0</td>
<td>99.9</td>
<td>0.0</td>
<td>8.99</td>
</tr>
<tr>
<td>7.56 X 10⁹</td>
<td>94.7</td>
<td>5.26</td>
<td>89.5</td>
<td>0.0</td>
<td>5.6</td>
<td>94.4</td>
<td>0.0</td>
<td>7.94</td>
</tr>
</tbody>
</table>
TABLE 19

COMPARISON OF THE ACTUAL AND CALCULATED DATA ON PERCENT ABUNDANCE OF CADAVERS WHEN DIFFERENT CONCENTRATIONS OF NPV WERE SPRAYED ON THE SECOND INSTAR LARVAE ON SEPTEMBER 10, 1980

<table>
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<tr>
<th>DAYS AFTER SPRAY</th>
<th>5</th>
<th>7</th>
<th>9</th>
<th>11</th>
<th>13</th>
<th>15</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9.07 X 10^4 POLYHEDRA/100 CM^2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A II</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>A III</td>
<td>0</td>
<td>3</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>T IV</td>
<td>0</td>
<td>1</td>
<td>5</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>TOTAL</td>
<td>1</td>
<td>7</td>
<td>14</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C II</td>
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<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>A III</td>
<td>2</td>
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<td>0</td>
<td>10</td>
</tr>
<tr>
<td>L IV</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>TOTAL</td>
<td>3</td>
<td>7</td>
<td>5</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>19</td>
</tr>
</tbody>
</table>

9.07 X 10^5 POLYHEDRA/100 CM^2

|                  | 2 | 6 | 1 | 1  | 0  | 0  | 10    |
|                  | 0 | 4 | 21| 3  | 2  | 0  | 30    |
|                  | 0 | 0 | 2 | 11 | 5  | 0  | 17    |
| TOTAL            | 2 | 10| 24| 15 | 7  | 0  | 57    |

9.07 X 10^6 POLYHEDRA/100 CM^2

|                  | 5 | 9 | 3 | 1  | 0  | 0  | 18    |
|                  | 4 | 34| 12| 9  | 1  | 0  | 60    |
|                  | 0 | 1 | 5 | 1  | 3  | 1  | 11    |
| TOTAL            | 9 | 44| 20| 11 | 4  | 1  | 89    |

9.07 X 10^7 POLYHEDRA/100 CM^2

|                  | 6 | 14| 6 | 1  | 0  | 0  | 27    |
|                  | 1 | 12| 31| 10 | 1  | 0  | 55    |
|                  | 0 | 0 | 2 | 3  | 1  | 0  | 6     |
| TOTAL            | 7 | 26| 39| 14 | 2  | 0  | 88    |
TABLE 19 (continued)

COMPARISON OF THE ACTUAL AND CALCULATED DATA ON PERCENT ABUNDANCE OF CADAVERS WHEN DIFFERENT CONCENTRATIONS OF NPV WERE SPRAYED ON THE FOURTH INSTAR LARVAE ON OCTOBER 22, 1980

<table>
<thead>
<tr>
<th>4.54 X 10^5 POLYHEDRA/100 CM^2</th>
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<th>7</th>
<th>9</th>
<th>11</th>
<th>13</th>
<th>15</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>A IV</td>
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<td>3</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>C V</td>
<td>0</td>
<td>5</td>
<td>9</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>18</td>
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</tr>
<tr>
<td>T VI</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>1</td>
<td>8</td>
<td>13</td>
<td>5</td>
<td>2</td>
<td>0</td>
<td>29</td>
<td></td>
</tr>
<tr>
<td>C IV</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>A V</td>
<td>0</td>
<td>1</td>
<td>9</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>L VI</td>
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<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
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</tr>
<tr>
<td>TOTAL</td>
<td>0</td>
<td>2</td>
<td>12</td>
<td>7</td>
<td>1</td>
<td>1</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>4.54 X 10^6 POLYHEDRA/100 CM^2</td>
<td>A IV</td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>C V</td>
<td>0</td>
<td>2</td>
<td>15</td>
<td>8</td>
<td>1</td>
<td>0</td>
<td>27</td>
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</tr>
<tr>
<td>T VI</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>5</td>
<td></td>
</tr>
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<td>TOTAL</td>
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<td>19</td>
<td>10</td>
<td>4</td>
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<td>42</td>
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<td>3</td>
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<td>0</td>
<td>0</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>A V</td>
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<td>2</td>
<td>14</td>
<td>10</td>
<td>3</td>
<td>0</td>
<td>29</td>
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</tr>
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<td>5</td>
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<td>2</td>
<td>14</td>
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</tr>
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### TABLE 19 (continued)

Comparison of the actual and calculated data on percent abundance of cadavers when different concentrations of NPV were sprayed on the fifth instar larvae on December 30, 1980

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APPENDIX D. A SIMULATION PROGRAM FOR THE BASIC LIFE MODEL
BY THE THERMAL SUMMATION METHOD

*LOC OPERATION A,B,C,D,E,F,G,H,I

SIMULATE

BAMO START MACRO DETERMINE OF BASIC MORTALITY

A SAVEVALUE 1,#B,XH SAVEVALUE FOR MEAN OF BASIC MORT
SAVEVALUE 2,#C,XH SAVEVALUE FOR STD OF BASIC MORT
TEST GE V#MORT1,999,#D SELECT BASIC MORT OVER 999
TRANSFER #E CONNECT TO DEV MACRO

#D SAVEVALUE 3,#V#MORT1,XH SAVEVALUE PROB CRITERIA FOR SURV
TRANSFER #X#H,#E CONNECT TO DEV MACRO
ENTER #F BEGINNING OF A LIFE STAGE
ADVANCE #G DEVELOPMENT OF NATURAL DYING INDIVIDUALS
LEAVE #F END OF A LIFE STAGE
TERMINATE TERMINATE NATURALLY DYING INDIVIDUALS
ENDMACRO

DEV START MACRO DETERMINE OF DEVELOPMENTAL PERIOD OF A LIFE STAGE

A ENTER #B BEGINNING OF A LIFE STAGE
ASSIGN 1,#C,PL ALPHA VALUE FOR EACH LIFE STAGE
ASSIGN 2,#D,PL ASSIGN PRE-ESTIMATED THERMAL CONSTANT
ASSIGN 3,#E,PL ASSIGN PRE-ESTIMATED STD OF THERMAL CON
ASSIGN 4,#V3,PL ASSIGN THERMAL CON IN A NORMAL DISTRIBUTION

#F ASSIGN 5,#V2,PL ACCUMULATES DAILY EFFECTIVE DEG
ADVANCE 1 DAILY DEVELOPMENT
ASSIGN 4+1,#P ASSIGN DEVELOPMENTAL PERIOD
TEST GE P#L5,PL4,#F DETERMINE COMPLETION OF A LIFE STAGE
LEAVE #B END OF A LIFE STAGE
SAVEVALUE NEXT,#G,XL TOTAL EFF DEG FOR NEXT STAGE
ASSIGN 5+V11,PL ASSIGN CUM EFF DEG FOR NEXT STAGE
ENDMACRO

LOAD DAG06,EGGPRG

**************************************************************

COMMENTS

**************************************************************

A GPSS MODEL FOR DETERMINING LAWN ARMYWORM DEVELOPMENT
BY THE THERMAL SUMMATION METHOD.

THE HYPERBOLIC EQUATION FOR THE THERMAL SUMMATION METHOD WAS
K = Y * (X - A), WHERE K IS THERMAL CONSTANT, Y IS DEVELOPMENTAL PERIOD, T IS THRESHOLD TEMPERATURE (CENTIGRADE), AND A IS THE TESTED TEMPERATURE (CENTIGRADE).

THIS MODEL WAS USED FOR PREDICTIVE PURPOSE BY GENERATING THE AVERAGE DAILY TEMPERATURES IN A NORMAL DISTRIBUTION.

LIFE CYCLE IN THIS MODEL CONSISTED OF THE EGG, FIRST TO SEVENTH INSTAR LARVA, PUPA AND ADULT.

THE FIRST MACRO DETERMINES NATURAL MORTALITY WITHIN A LIFE STAGE UNDER FAVORABLE ENVIRONMENTAL CONDITIONS.
• THE SECOND MACRO DETERMINES THE DEVELOPMENTAL PERIOD WITHIN
  A LIFE STAGE.

• ONE TRANSACTION WAS GENERATED TO REPRESENT THE INTRODUCTION OF
  A FEMALE INTO THE SIMULATION SYSTEM.

• TO SAVE TRANSACTIONS, THE NUMBER OF EGGS PRODUCED BY THE FEMALE
  WAS DIVIDED BY 40.

• CALCULATION OF FEEDING DAMAGE IS INCLUDED.

• UNIT OF THRESHOLD TEMPERATURE (ALPHA VALUE) IS DEGREE CENTIGRADE
  AND THAT OF THE THERMAL CONSTANT IS DAY-DEGREE.

• UNIT OF FEEDING DAMAGE IS MG (FRESH WEIGHT OF BERMUDA GRASS).

• THE CONTENT OF STORAGE 1 (S1) REPRESENTS THE NUMBER OF FIRST INSTAR
  LARVAE, S2 THE NUMBER OF SECOND INSTAR, S3 THE THIRD
  INSTAR, AND SO FORTH.

• S8 REPRESENTS THE NUMBER OF PUPAE.

• S9 REPRESENTS THE NUMBER OF ADULTS ON THE FIRST DAY OF EMERGENCE.

• S10 REPRESENTS THE NUMBER OF ADULTS.

*********** FUNCTIONS ***********

NORM FUNCTION RN1,27 GENNORMAL DISTRIBUTION
0.35,.0013,.3,.0035,-2.75,.0062,-2.5,.0122,-2.25,.0228,-2.0
.0401,-1.75,.0668,-1.5,.1056,-1.25,.1587,-1.0,.2266,-.75,.3085,.5
.4013,-.25,.5,.5987,.25,.6915,.50,.7734,.75,.8413,.1,.8944,1.25
932,.15,.9599,.15,.9772,.2,.9876,.25,.9938,.25,.9965,.25
9987,.3,.0113.5

PREOV FUNCTION RN1,07 DETERMINE PRE-OVI-POSITION PERIOD
.011,.1,.0888,.2,.4110,.3,.7998,.4,.9330,.5,.9885,.6,.9999,.7

OVIPE FUNCTION RN1,01 DETERMINE OVI-POSITION PERIOD
.011,.1,.0667,.2,.1443,.3,.3221,.4,.5221,.5,.6887,.6,.8442,.7,.9330,.8
9885,.9,.9999,.10

EGSTA FUNCTION XF1,.18 STD OF DAILY EGG PRODUCTION
264,.175,.148,.106,.83,.55,.39,.54,.1,.1,.1,.1,.1,.1,.1,.1,.1,.1,.
### BASIC LIFE MODEL

#### INTRODUCTION OF A FEMALE

#### VARIABLES

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#### RPT

- ADVANCE VS Prov Previou Period (Minus One Day)
- ASSIGN 2*FNS*VIPEP,8 DETER** ViPoseiion Period
- OPI3 ADVANCE 1 DAILY DEVELOPMENT OF A FEMALE DURING OVIPO
- ASSIGN 3+I,TP ASSIGN OviPosition Day
- SAVEVALUE 1*PB*XP SAVEVALUE FOR OVIPOSITION DAY
- HELP9 *EGGRPO,1XF,16XL EGG PRODUCTION (LOG MEAN)
- ASSIGN 1*V13*PH ASSIGN DAILY EGG PRODUCTION
TEST LE  PH1,0,OP11 SCREEN POSI" EGG PRO" TRANSFER ,OP12 CONNECTION
OP11 SPLIT  PH1,INSO DAILY UVIPosition
OP12 LOOP  DPB,OP13 REPEAT UVIPosition
ASSIGN  3,0,73 ASSIGN UVIPosition DAY AS ZERG
ADVANCE  V6 POST-UVIPOSITION PERIOD
LEAVE  10 LEAVE ADULT STAGE
TERMINATE  FEMALE IS TERMINATED

****************************************************

EGG DEVELOPMENT

****************************************************

BAMO MACRO  INSO,933,10,WWW0,DUMO,60,V7
INSO SAVEVALUE  1,933,XH
SAVEVALUE  2,10,XH
TEST GE  VM3MORT1,999,WWW0
TRANSFER ,DUMO
WWW0 SAVEVALUE  3,VM3MORT1,XH
TRANSFER ,XH333,DUMO
ENTER  60
ADVANCE  V7
LEAVE  60
TERMINATE

DEV MACRO  DUMO,60,10,7,59,46,10,05,ZZ,33,33
DUMO ENTER  60
ASSIGN  1,10,7,PL
ASSIGN  2,59,46,PL
ASSIGN  3,10,05,PL
ASSIGN  4,VL,PL
ZZZ ASSIGN  5,VL,PL
ADVANCE  1
ASSIGN  4,1,PB
TEST GE  PL5,PL5,ZZZ
LEAVE  60
SAVEVALUE  NEXT,33,33,VL
ASSIGN  5,VL,PL

FIRST INSTAR LARVA

****************************************************

BAMO MACRO  INSO,933,38,WWW1,DUM1,1,V6
INSO SAVEVALUE  1,933,XH
SAVEVALUE  2,38,XH
TEST GE  VM3MORT1,999,WWW1
TRANSFER ,DUM1
WWW1 SAVEVALUE  3,VM3MORT1,XH
TRANSFER ,XH333,DUM1
ENTER  1
ADVANCE  V6
LEAVE  1
TERMINATE

DEV MACRO  DUM1,1,13,7,33,33,4,34,AAA,26,52
DUM1 ENTER  1
ASSIGN  1,13,7,PL
ASSIGN  2,33,33,PL
ASSIGN 3,4,34,PL
ASSIGN 4,4,V3,PL
ASSIGN 5+,V2,PL
ADVANCE 1
ASSIGN 4+,1,PB
TEST GE PL5,PL4,AAA
LEAVE 1
SAVEVALUE NEXT,26,52,XL
ASSIGN 9,5,V11,PL

***********************************************

SECOND INSTAR LARVA

***********************************************

BAMO MACRO IN52,999,38,WWW2,DUM2,2,V5
IN52 SAVEVALUE 1,999,XH
SAVEVALUE 2,38,XH
TEST GE VSMORT1,999,WWW2
TRANSFER ,DUM2
WWW2 SAVEVALUE 3,VSMORT1,XH
TRANSFER +XH3,DUM2
ENTER 2
ADVANCE V5
LEAVE 2
TERMINATE

DEV MACRO DUM2,2,14,4,26,52,4,86,888,28,83
DUM2 ENTER 2
ASSIGN 1,14,4,PL
ASSIGN 2,26,52,PL
ASSIGN 3,4,86,PL
ASSIGN 4,V3,PL
BAMO ASSIGN 5+,V2,PL
ADVANCE 1
ASSIGN 4+,1,PB
TEST GE PL5,PL4,BBB
LEAVE 2
SAVEVALUE NEXT,28,XL
ASSIGN 9,5,V11,PL

***********************************************

THIRD INSTAR LARVA

***********************************************

BAMO MACRO INS3,967,24,WWW3,DUM3,3,V5
INS3 SAVEVALUE 1,967,XH
SAVEVALUE 2,24,XH
TEST GE VSMORT1,999,WWW3
TRANSFER ,DUM3
WWW3 SAVEVALUE 3,VSMORT1,XH
TRANSFER +XH3,DUM3
ENTER 3
ADVANCE V5
LEAVE 3
TERMINATE

DEV MACRO DUM3,3,13.5,28.83,5.17,CCC,32.50

DUM3 ENTER 3
ASSIGN 1,13.5,PL
ASSIGN 2,28.83,PL
ASSIGN 3,5.17,PL
ASSIGN 4,53,PL

CCC ASSIGN 5,52,PL
ADVANCE 1
ASSIGN 4,1,PL
TEST GE PL9,PL4,CCC
LEAVE 3
SAVEVALUE NEXT,32.50,PL
ASSIGN 5,51,PL

******************************

FOURTH INSTAR LARVA

******************************

BAMQ MACRO INS4,968,32,.WW4,OUM4,5,V5

INS4 SAVEVALUE 1,968,PL
SAVEVALUE 2,32,PL
TEST GE V$MORT1,999,.WW5
TRANSFER .OUM4

WWW4 SAVEVALUE 3,999,WH3,SYM4
TRANSFER .SU3,INS4
ENTER 6
ADVANCE V5
LEAVE 4
TERMITE

DEV MACRO DUM4,4,13.6,32.50,7.01,OUM5,34.49

DUM4 ENTER 4
ASSIGN 1,13.6,PL
ASSIGN 2,32.50,PL
ASSIGN 3,7.01,PL
ASSIGN 4,53,PL

OUM5 ASSIGN 5,52,PL
ADVANCE 1
ASSIGN 4,1,PL
TEST GE PL9,PL4,DDD
LEAVE 4
SAVEVALUE NEXT,34.49,PL
ASSIGN 5,51,PL

******************************

FIFTH INSTAR LARVA

******************************

BAMQ MACRO INS5,978,31,.WW5,OUM5,5,V6

INS5 SAVEVALUE 1,978,PL
SAVEVALUE 2,31,PL
TEST GE V$MORT1,999,.WW5
TRANSFER .OUM5
WW5  SAVEVALUE  3,VSMDRT1,XH
    TRANSFER  .XH3,.DUMS
    ENTER      5
    ADVANCE     V6
    LEAVE      5
    TERMINATE

DEV  MACRG  DUM5,5,13.3,34.49,8.35,EEE,43.91
    DUMS  ENTER      5
    ASSIGN  1,13.3,PL
    ASSIGN  2,34.49,PL
    ASSIGN  3,8.35,PL
    ASSIGN  4,43.91,PL
    ADVANCE  1
    ASSIGN  4,1,PL
    TEST GE  PL5,PL4,EEE
    LEAVE      5
    SAVEVALUE  NEXT,43.91,XL
    ASSIGN  5,11,PL

****************************************************
SIXTH INSTAR LARVA
****************************************************

BAMO  MACRC  INS6,946,14,WWW6,DUM6,6,43.91
    INS6  SAVEVALUE  1,940,XH
    TEST GE  VSMDRT1,999,WWW6
    TRANSFER  .DUM6
    WWW6  SAVEVALUE  3,VSMDRT1,XH
    TRANSFER  .XH3,.DUM6
    ENTER      6
    ADVANCE     V6
    LEAVE      6
    TERMINATE

DEV  MACRG  DUM6,6,12.2,43.91,8.98,FFF,50.81
    DUM6  ENTER      6
    ASSIGN  1,12.2,PL
    ASSIGN  2,43.91,PL
    ASSIGN  3,8.98,PL
    ASSIGN  4,50.81,PL
    FFF  ASSIGN  5,11,PL
    ADVANCE  1
    ASSIGN  4,1,PL
    TEST GE  PL5,PL4,FFF
    LEAVE      6
    SAVEVALUE  NEXT,50.81,XL
    ASSIGN  5,11,PL

****************************************************
LAST INSTAR LARVA
****************************************************
BAMO MACRO
INS7,900,78,WWW7,DUM7,7,V8
INS7 SAVEVALUE 1,900,XH
SAVEVALUE 2,78,XH
TEST GE V$MORT1,999,WWW7
TRANSFER ,DUM7
WWW7 SAVEVALUE 3,V$MORT1,XH
TRANSFER +XH3,DUM7
ENTER 7
ADVANCE V8
LEAVE 7
DEV MACRO
DUM7,7,17,4,50,81,15,54,GGG,110,42
DUM7 ENTER 7
ASSIGN 1,17+4,PL
ASSIGN 2,50+81,PL
ASSIGN 3,15,54,PL
ASSIGN 4,V3,PL
GGG ASSIGN 5+V2,PL
ADVANCE 1
ASSIGN 4+1,PL
TEST GE PL5,PL4,GGG
LEAVE 7
SAVEVALUE NEXT,110,42,XL
ASSIGN 5,V11,PL

***************
PUPL AstrA
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BAMO MACRO
INS8,906,55,WWW8,DUM8,8,V9
INS8 SAVEVALUE 1,906,XH
SAVEVALUE 2,55,XH
TEST GE V$MORT1,999,WWW8
TRANSFER ,DUM8
WWW8 SAVEVALUE 3,V$MORT1,XH
TRANSFER +XH3,DUM8
ENTER 8
ADVANCE V9
LEAVE 8
DEV MACRO
DUM8,8,15,1,110,42,15,62,HHH,0
DUM8 ENTER 8
ASSIGN 1,15+1,PL
ASSIGN 2,110,42,PL
ASSIGN 3,15,62,PL
ASSIGN 4,V3,PL
HHH ASSIGN 5+V2,PL
ADVANCE 1
ASSIGN 4+1,PL
TEST GE PL5,PL4,HHH
LEAVE 8
SAVEVALUE NEXT,0,XL
ASSIGN 5,V11,PL

***************
* ADULT STAGE
*
* INS9
ENTER 10 BEGINNING OF ADULT STAGE
ENTER 9 BEGINNING OF INITIAL DAY OF EMERGENCE
ADVANCE 1 INITIAL DAY OF ADULT STAGE
LEAVE 9 END OF INITIAL DAY OF ADULT STAGE
TRANSFER .500 RPT SELECT FEMALES
ADVANCE V12 LONGEST OF ADULT MOTH (MINUS 1 DAY)
LEAVE 10 LEAVE ADULT STAGE
TERMINATE PRODUCED ADULTS ARE TERMINATED
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* CONTROL CARDS
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* TIME CONTROL
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* GENERATE 1 TIMER ARRIVES EVERYDAY
SAVEVALUE DAY,V1,XH DAYS COUNTING FROM INTRG OF FEMALE
SAVEVALUE XADAM,XFOOD,XL DAILY FOOD DAMAGE BY THE LARVAE
SAVEVALUE XADAM,XFOOD,XL CUMULATIVE DAILY FOOD DAMAGE
TERMINATE 1 TIMER COUNTING
START 45
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* OUTPUT CONTROL
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* REPORT
TEXT #XH$DAY,Z/XX# DAY(S) AFTER INITIAL INTRODUCTION
STO TITLE AGE COMPOSITION (NO. OF INDIVIDUALS)
LSV TITLE FOOD CONSUMPTION AND VIRUS PRODUCTION
END
C.... SUBROUTINE EGGPRO DETERMINES NO. OF DAILY EGG PRODUCTION
SUBROUTINE EGGPRO(IX1,FX2)
FX2=EXP(6.6962-0.3525*IX1)
RETURN
END
APPENDIX E. A SIMULATION PROGRAM FOR THE BASIC LIFE MODEL
BY THE LOGISTIC EQUATION

*LOC  OPERATION  A, B, C, D, E, F, G, H, I  COMMENTS
SIMULATE
BAMO  STARTMACRO
#A  TRANSFER  B, C, D  DETERMINATION OF NATURAL MORTALITY
ENTER  E  BEGINNING OF A LIFE STAGE
ADVANCE  F  LETHAL DEVELOPMENTAL PERIOD FOR NAT** DYING INDIVIDUAL
LEAVE  G  END OF A LIFE STAGE
TERMINATE  H** DYING INDIVIDUAL IS TERMINATED
ENDMACRO

DEV  STARTMACRO
#A  ENTER  B  BEGINNING OF A LIFE STAGE
#D  SAVEVALUE  1.0, 2.0  DAILY TEMPERATURE
SAVEVALUE  1.0, 2.0  SAVEVALUE FOR ADDITIONAL REL** DEV
SAVEVALUE  2.0, 2.0  SAVEVALUE FOR RELATIVE DEVELOPMENT
SAVEVALUE  3.0, 2.0  SAVEVALUE FOR STD** OF RELATIVE DEVELOPMENT
HELPB  #LOGDEV, 1.0, 2.0, 3.0, 2.0  DET** OF REL** DEV
SAVEVALUE  1.0, 1.0  SAVEVALUE FOR STD** OF RELDEV
HELPB  #LOGDEV, 1.0, 2.0, 3.0, 2.0  DET** OF RELDEV
TEST LE  V3, 0  TEST WHETHER GEN** REL** DEV** IS BELOW ZERO
SAVEVALUE  1.0, 0  SAVEVALUE O FOR MINUS OR 0 RELDEV
TRANSFER  #F  CONNECT TO MAIN BRANCH
#E  ASSIGN  1.0, 0  IF CONNECT TO MAIN BRANCH
#F  LAST  1.0, 0  DETERMINATION OF A LIFE STAGE
LEAVE  1.0, 999  END OF A LIFE STAGE
SAVEVALUE  1.0, 1.0  SAVEVALUE FOR ADDRESS OF REL** DEV
HELPB  #LOGDEV, 1.0, 2.0, 3.0, 4.0  RELDEV** FOR NEXT STAGE
SAVEVALUE  1.0, 1.0  SAVEVALUE FOR STD** OF RELDEV
HELPB  #LOGDEV, 1.0, 2.0, 3.0, 4.0  STD** OF RELDEV FOR NEXT
TEST LE  V3, 0  TEST WHETHER GEN** REL** DEV** IS BELOW ZERO
SAVEVALUE  1.0, 0  SAVEVALUE O FOR MINUS OR 0 RELDEV
TRANSFER  #H  CONNECT TO MAIN BRANCH
#G  SAVEVALUE  1.0, 0  IF CONNECT TO MAIN BRANCH
#H  ASSIGN  1.0, 0  CUMULATED DEVELOPMENT
ASSIGN  1.0, 1.0  ASSIGN CUMULATIVE DEVELOPMENT BETWEEN STAGE
ENDMACRO

LOAD  OAG06.LOGDEV

**********************

COMMENTS

**********************

* A GPSS MODEL FOR DETERMINING LAWN ARMYWORM DEVELOPMENT
* BY THE LOGISTIC MODEL.
* THE FORMULA FOR THE LOGISTIC EQUATION WAS:
* W = K/(1 + EXP(A - B*X))
* WHERE W IS RELATIVE DEVELOPMENTAL UNIT (RECIPROCAL OF DEVELOPMENTAL
* PERIOD) AT TEMPERATURE, X, AND K, A AND B ARE CONSTANTS.
* THIS MODEL WAS USED FOR COMPARISON OF THE RESULTS OF VIRUS SPRAYS
* BETWEEN ACTUAL AND SIMULATED DATA.
SIMULATION WAS STARTED FROM SEPTEMBER 18, 1979 AND AVERAGE DAILY TEMPERATURES ACTUALLY MEASURED IN THE MANOA AREA WERE USED AS THE THERMAL INPUT SOURCE.

LIFE CYCLE IN THIS PROGRAM CONSISTED OF THE FIRST TO SEVENTH INSTAR LARVA, PUPA AND ADULT.

ONE HUNDRED TRANSACTIONS WERE GENERATED TO REPRESENT THE INITIAL POPULATION OF THE FIRST INSTAR LARVAE.

THE FIRST MACRO, BAMB, DETERMINED NATURAL MORTALITY WITHIN A LIFE STAGE UNDER FAVORABLE ENVIRONMENTAL CONDITIONS.

THE SECOND MACRO, DEV, DETERMINED THE DEVELOPMENTAL PERIOD WITHIN A LIFE STAGE.

AFTER COMPLETING THE FIRST GENERATION, NEWLY EMERGED ADULTS WERE TERMINATED WITHOUT STARTING NEW LIFE CYCLE.

UNIT OF FEEDING DAMAGE IS MG (FRESH WEIGHT OF BERMUDA GRASS).

THE CONTENT OF STORAGE 1 (S1) REPRESENTS THE NUMBER OF FIRST INSTAR LARVAE, S2 THE NUMBER OF SECOND INSTAR, S3 THE THIRD INSTAR, AND SO FORTH.

S8 REPRESENTS THE NUMBER OF PUPAE.

S9 REPRESENTS THE NUMBER OF PUPAE ON THE FIRST DAY OF EMERGENCE.

S10 REPRESENTS THE NUMBER OF ADULTS.

SINCE THE CREATION OF THE ORIGINAL TRANSACTIONS REQUIRED ONE TIME UNIT, THE SIMULATION FOR THE INSECT LIFE SYSTEM WAS STARTED FROM (AC - 1) DAY.

***************NORM FUNCTION RN1,C27 GEN NORM DISTRIBUTION PATT********

***************ATE FUNCTION AC1,L43 DAILY AVERAGE TEMP** FROM 790917********
7909;
7909;
7910;
7910;
**VARIABLES**

1. VARIABLE AC1-2 DAY(S) AFTER INFESTATION
2. FVARIABLE FN2ATE/10 DAILY AVERAGE TEMPERATURE (ACTUAL)
3. FVARIABLE 1000*(XL3*FN**NORM*XL2) GEN** RELATIVE DEVELOPMENT
4. FVARIABLE 1.9*FN**NORM+9.01 LONGEVITY OF AN ADULT
5. FVARIABLE RN2*2/1000 LONGI** OF NATU** DYING II TO IV LARVA
6. FVARIABLE RN2*3/1000 LONGI** OF NATU** DYING I, V & VI LARVA
7. FVARIABLE RN2*7/1000 LONGI** OF NATU** DYING VII LARVA
8. FVARIABLE RN2*12/1000 LONGI** OF NATU** DYING PUPA
9. FVARIABLE RN2*9/1000 LONGI** OF NATU** DYING ADULT
10. FVARIABLE RN2*(XL3*FN**NORM+9.01) LONGI** OF ADULT MOTH (MINUS 1 DAY)
11. FVARIABLE PH1-1000*XHSDETA/1000 CUMU DEVIATION BETWEEN STAGE
12. FVARIABLE (0.5*31+1.1*52+3.0*53+9.2*54)/1000 DAM** AT YOUNG
13. FVARIABLE (27.4*55+83.0*56+31.6*57+51)/1000 DAM** AT OLD STAGE
14. FVARIABLE V25+V26 DAILY TOTAL FOOD DAMAGE

**BASIC LIFE MODEL**

**GENERATE** 1,1,1,1PM GENERATION OF ORIGINAL TRANSACTION
**SPLIT** 100,INS1 INITIAL POP** OF 1ST INSTAR LARVAE
**TERMINATE** TERMINATION OF ORIGINAL TRANSACTION

**FIRST INSTAR LARVA**

**BAMO MACRO**

INS1,933,DOM1,1,V6
INS1 TRANSFER 933,DOM1
ENTER 1
ADVANCE V6
LEAVE 1
TERMINATE

DEVMacro DOM1,1,l,AAA,XXX11,XXX12,XXX13,XXX14
DOM1 ENTER 1
AAA SAVEVALUE 1,V2,XL
SAVEVALUE 1,1,XF
SAVEVALUE 2,0,XL
SAVEVALUE 3,0,XL
HELPB #LOGDEV,1XF,1XL,2XL,3XL
SAVEVALUE 1,1,XF
HELPB #LOGDEV,1XF,1XL,2XL,3XL
TEST LE V3.0,XXX11
SAVEVALUE 1.0,PH
TRANSFER ,XXX12
XXX11 SAVEVALUE 1.0,PH
TRANSFER ,XXX12
XXX12 ASSIGN 1.0,PH
ADVANCE 1
TEST GE PH1,999,AAA
LEAVE 1
SAVEVALUE 1.0,PH
HELPB #LOGODEV,1XF,2XL,3XL,4XL
SAVEVALUE 1.0,PH
HELPB #LOGODEV,1XF,2XL,3XL,4XL
TEST LE V3.0,XXX13
SAVEVALUE 1.0,PH
TRANSFER ,XXX14
XXX13 SAVEVALUE 1.0,PH
XXX14 SAVEVALUE DELA,XH1,XH
ASSIGN 1.0,PH

SECOND INSTAR LARVA

BAMD MACRO INS2,999,DUM2,2,0V5
INS2 TRANSFER 999,DUM2
ENTER 2
ADVANCE V5
LEAVE 2
TERMINATE DUM2,2,0V5,XXX21,XXX22,XXX23,XXX24
DUM2 ENTER 2
999 SAVEVALUE 1.0,0V5
SAVEVALUE 1.3,0V5
SAVEVALUE 2.0,0V5
SAVEVALUE 3.0,0V5
HELPB #LOGODEV,1XF,1XL,2XL,3XL
SAVEVALUE 1.0,0V5
HELPB #LOGODEV,1XF,1XL,2XL,3XL
TEST LE V3.0,XXX21
SAVEVALUE 1.0,PH
TRANSFER ,XXX22
XXX21 SAVEVALUE 1.0,PH
XXX22 ASSIGN 1.0,PH
ADVANCE 1
TEST GE PH1,999,0V5
LEAVE 2
SAVEVALUE 1.0,PH
HELPB #LOGODEV,1XF,2XL,3XL,4XL
SAVEVALUE 1.0,PH
HELPB #LOGODEV,1XF,2XL,3XL,4XL
TEST LE V3.0,XXX23
SAVEVALUE 1.0,PH
TRANSFER ,XXX24
XXX23 SAVEVALUE 1.0,PH
XXX24 SAVEVALUE DELA,XH1,XH
ASSIGN 1*V14,PH

************************************************************

THIRD INSTAR LARVA

************************************************************

BAM0 MACRO INS3, 976, DUM3, 3, V5
INS3 TRANSFER 976, DUM3
ENTER 3
ADVANCE V5
LEAVE 3
TERMINATE

DEV MACRO DUM3, ENTER 3
CCC SAVEVALUE 1*V2, XL
SAVEVALUE 1*5, XF
SAVEVALUE 2*0, XL
SAVEVALUE 3*0, XL
HELPB #LOGDEV, 1*XF, 1*XL, 2*XL, 3*XL
SAVEVALUE 1*+1, XF
HELPB #LOGDEV, 1*XF, 1*XL, 2*XL, 3*XL
TEST LE V3*0, XXX31
SAVEVALUE 1*0, XM
TRANSFER XXX32

XXX31 SAVEVALUE 1*V3, XH
XXX32 ASSIGN 1*+XH1, PH
ADVANCE 1
TEST GE PH1, 999, CCC
LEAVE 3
SAVEVALUE 1*+1, XF
HELPB #LOGDEV, 1*XF, 2*XL, 3*XL, 4*XL
SAVEVALUE 1*+1, XF
HELPB #LOGDEV, 1*XF, 2*XL, 3*XL, 4*XL
TEST LE V3*0, XXX33
SAVEVALUE 1*0, XM
TRANSFER XXX34

XXX33 SAVEVALUE 1*V3, XM
XXX34 SAVEVALUE DELA, XH1, XH
ASSIGN 1*V14, PH

************************************************************

FOURTH INSTAR LARVA

************************************************************

BAM0 MACRO INS4, 976, DUM4, 4, V5
INS4 TRANSFER 976, DUM4
ENTER 4
ADVANCE V5
LEAVE 4
TERMINATE

DEV MACRO DUM4, ENTER 4
DDD SAVEVALUE 1*V2, XL
<table>
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<tr>
<th>Instruction</th>
<th>Value 1</th>
<th>Value 2</th>
<th>Value 3</th>
<th>Value 4</th>
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<tr>
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<tr>
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<tr>
<td>TEST GE</td>
<td>PH1, 999, DDC</td>
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<tr>
<td>LEAVE</td>
<td>4</td>
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<tr>
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<tr>
<td>HELPB</td>
<td>LOGDEV, 1XF, 2XL, 3XL, 4XL</td>
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<tr>
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</tbody>
</table>

************ FIFTH INSTAR LARVA ************

BAMO MACRO INS5, 963, DUM5, 5, V6
INS5 TRANSFER 963, DUM5
ENTER 5
ADVANCE V6
LEAVE 5
TERMINATE

DEV MACRO DUM5, 5, 9, EEE, XXX51, XXX52, XXX53, XXX54
DUM5 ENTER 5
EEE SAVEVALUE 1, V2, XL
SAVEVALUE 1, 9, XF
SAVEVALUE 2, 0, XL
SAVEVALUE 3, 0, XL
HELBP LOGDEV, 1XF, 1XL, 2XL, 3XL
SAVEVALUE 1*1, 1XF
HELBP LOGDEV, 1XF, 1XL, 2XL, 3XL
TEST LE V3, 0, XXX51
SAVEVALUE 1, 0, XM
TRANSFER XXX52
XXX51 SAVEVALUE 1, V3, XM
XXX52 ASSIGN 1*, XM1, PH
ADVANCE 1
TEST GE PH1, 999, EEE
LEAVE 5
SAVEVALUE 1*1, XF
HELBP LOGDEV, 1XF, 2XL, 3XL, 4XL
SOME1 VALUE 1 + 1, XF
HELPB # LOGDEV, 1XF, 2XL, 3XL, 4XL
TEST LE V3, 0, XXX53
SOME1 VALUE 1 + 0, XH
TRANSFER , XXX54
XXX53 SOME1 VALUE 1 + V3, XH
XXX54 SOME1 VALUE DELA, XH1, XH
ASSIGN 1 + V14, PH

*******************************************
SIXTH INSTAR LARVA
*******************************************

BAMO MACRO INS6, .947, DUM6, 6, V6
INS6 ENTER 6
ADVANCE V6
LEAVE 6
TERMINATE
DEV MACRO DUM6, 6, 11, FFF, XXX61, XXX62, XXX63, XXX64
DUM6 ENTER 6
FFF SOME1 VALUE 1 + V2, XL
SOME1 VALUE 1 + 11, XF
SOME1 VALUE 2 + 0, XL
SOME1 VALUE 3 + 0, XL
HELPB # LOGDEV, 1XF, 1XL, 2XL, 3XL
SOME1 VALUE 1 + 1, XF
HELPB # LOGDEV, 1XF, 1XL, 2XL, 3XL
TEST LE V3, 0, XXX61
SOME1 VALUE 1 + 0, XH
TRANSFER , XXX62
XXX61 SOME1 VALUE 1 + V3, XH
XXX62 ASSIGN 1 +, XH1, PH
ADVANCE 1
TEST GE PH1, 999, FFF
LEAVE 6
SOME1 VALUE 1 + 1, XF
HELPB # LOGDEV, 1XF, 2XL, 3XL, 4XL
SOME1 VALUE 1 + 1, XF
HELPB # LOGDEV, 1XF, 2XL, 3XL, 4XL
TEST LE V3, 0, XXX63
SOME1 VALUE 1 + 0, XH
TRANSFER , XXX64
XXX63 SOME1 VALUE 1 + V3, XH
XXX64 SOME1 VALUE DELA, XH1, XH
ASSIGN 1 + V14, PH

*******************************************
*******************************************
LAST INSTAR LARVA
*******************************************

BAMO MACRO INS7, .944, DUM7, 7, V8
INS7 TRANSFER 944, DUM7
ENTER 7
ADVANCE V8
LEAVE 7
TERMINATE

DEV MACRO DUM7, 7, 13, UC, XXX71, XXX72, XXX73, XXX74
DUM7 ENTER 7
GGG SAVEVALUE 1, V2, XL
SAVEVALUE 1, 13, XF
SAVEVALUE 2, 0, XL
SAVEVALUE 3, 0, XL
HELPB #LOGDEV, 1XF, 1XL, 2XL, 3XL
SAVEVALUE 1+1, XF
HELPB #LOGDEV, 1XF, 1XL, 2XL, 3XL
TEST LE V3, 0, XXX71
SAVEVALUE 1, 0, XH
TRANSFER XXX72
XXX71 SAVEVALUE 1, V3, XH
XXX72 ASSIGN 1+, XM1, PH
ADVANCE 1
TEST GE PH1, 999, GGG
LEAVE 7
SAVEVALUE 1+1, XF
HELPB #LOGDEV, 1XF, 2XL, 3XL, 4XL
SAVEVALUE 1+1, XF
HELPB #LOGDEV, 1XF, 2XL, 3XL, 4XL
TEST LE V3, 0, XXX73
SAVEVALUE 1, 0, XH
TRANSFER XXX74
XXX73 SAVEVALUE 1, V3, XH
XXX74 SAVEVALUE DELA, XH1, XH
ASSIGN 1, V14, PH

*********************************************************************

PUPAL STAGE

*********************************************************************

BAMO MACRO INS8, .897, DUM8, 8, V9
INS8 TRANSFER .897, , DUM8
ENTER 8
ADVANCE V9
LEAVE 3
TERMINATE

DEV MACRO DUM8, 8, 15, HMH, XXX81, XXX82, XXX83, XXX84
DUM8 ENTER 8
HHH SAVEVALUE 1, V2, XL
SAVEVALUE 1, 15, XF
SAVEVALUE 2, 0, XL
SAVEVALUE 3, 0, XL
HELPB #LOGDEV, 1XF, 1XL, 2XL, 3XL
SAVEVALUE 1+1, XF
HELPB #LOGDEV, 1XF, 1XL, 2XL, 3XL
TEST LE V3, 0, XXX81
SAVEVALUE 1, 0, XH
TRANSFER , XXX82
BEGINNING OF THE FIRST DAY OF EMERGENCE

END OF THE FIRST DAY OF EMERGENCE

LOGEOIVITY OF ADULT MINUS ONE DAY

END OF ADULT STAGE

TERMINATION OF THE NEXT GENERATION'S ADULT

CONTROL CARDS

TIME CONTROL

GENERATE 1 TIMER ARRIVES EVERYDAY

SAVEVALUE 2,v1,XH COUNTING THE DAYS AFTER INFESTATION

SAVEVALUE DAMM,v1,FOOD,XL DAILY FOOD DAMM BY ARMYWORM LARVAE

SAVEVALUE CUO**,XL#DACAM,XL CUMULATIVE DAILY FOOD DAMAGE

TERMINATE 1 TIMER COUNTING

START 55++,1

OUTPUT CONTROL

REPORT

TEXT #XM2,2/XX# DAY(S) AFTER INITIAL INFESTATION

STO TITLE #AGE COMPOSITION (NO. OF INDIVIDUALS PER 100 UNIT)

LSV TITLE #FOOD CONSUMPTION AND POLYHEDRA PRODUCTION

END
SUBROUTINE LOGDEV CALCULATES DEVELOPMENTAL UNIT
C (RELATIVE) BY THE LOGISTIC EQUATION.
SUBROUTINE LOGDEV(X1,FX2,FX3,FX4)
GO TO (1,11,2,12,3,13,4,14,5,15,6,16,7,17,8,18,9,19,10,20,11,21)
1 FX3=0.530/(1+ EXP(6.111386-0.285421*FX2))
RETURN
11 FX4=FX3*ABS(FX3-0.530)/0.530*SQR0(0.382990*(1.2+(FX2-25.0)**2/250))
RETURN
2 FX3=1.000/(1+ EXP(5.721318-0.226826*FX2))
RETURN
12 FX4=FX3*ABS(FX3-1.000)*SQR0(0.484389*(1.2+(FX2-25.0)**2/250))
RETURN
3 FX3=1.000/(1+ EXP(7.25177-0.299121*FX2))
RETURN
13 FX4=FX3*ABS(FX3-1.000)*SQR0(1.637547*(1.2+(FX2-25.0)**2/250))
RETURN
4 FX3=1.000/(1+ EXP(5.320467-0.195736*FX2))
RETURN
14 FX4=FX3*ABS(FX3-1.000)*SQR0(0.351586*(1.2+(FX2-25.0)**2/250))
RETURN
5 FX3=0.840/(1+ EXP(5.847562-0.228837*FX2))
RETURN
15 FX4=FX3*ABS(FX3-0.840)/0.840*SQR0(0.347708*(1.2+(FX2-25.0)**2/250))
RETURN
6 FX3=0.570/(1+ EXP(5.523347-0.233768*FX2))
RETURN
16 FX4=FX3*ABS(FX3-0.570)/0.570*SQR0(0.321369*(1.2+(FX2-25.0)**2/250))
RETURN
7 FX3=0.420/(1+ EXP(7.342200-0.275901*FX2))
RETURN
17 FX4=FX3*ABS(FX3-0.420)/0.420*SQR0(0.235684*(1.2+(FX2-25.0)**2/250))
RETURN
8 FX3=0.168/(1+ EXP(6.538893-0.282580*FX2))
RETURN
18 FX4=FX3*ABS(FX3-0.168)/0.168*SQR0(0.216730*(1.2+(FX2-25.0)**2/250))
RETURN
END
TRANSFER "#6 CONNECT TO NEXT STAGE
ENDMACRO

VDEV STARTMACRO DEVELOPMENT OF VIRUS-YIELDED INDIVIDUALS
AA ENTER "#B BEGINNING OF VIRUS-YIELDED LIFE STAGE
ASSIGN 4,0,PD ASSIGN DEV** PERIOD AS ZERO
DEV MACRO "G,D,B,E,*F,*G,*M,*I DEV** PER** FOR INJ**
LEAVE "#B END OF VIRUS-YIELDED LIFE STAGE
ENDMACRO

VODE STARTMACRO LETHAL PERIOD OF VIRUS-KILLED INDIVIDUALS
AA ENTER "#B BEGINNING OF VIRUS-KILLED LIFE STAGE
ADVANCE "D INFECTION PERIOD (LETHAL OR PATHOLOGICAL)
LEAVE "#B END OF VIRUS-YIELDED LIFE STAGE
LEAVE "#C END OF VIRUS-KILLED LIFE STAGE
ENTER "#E BEGINNING OF THE FIRST DAY OF CADAVER
SAVEVALUE 1,2,XF ADDRESS FOR TRANCE
SAVEVALUE 13,4,F,XL SAVEVALUE MEAN (LUG) OF POLYHEDA PER CAD
SAVEVALUE 14,4,F,XL SAVEVALUE SF** FOR MEAN POLYHEMA (LUG)
SAVEVALUE 15,POL,XL SAVEVALUE FOR LUG OF POL** PRODUCTION
SAVEVALUE 16,4,F,XL SET 0 FOR PUL** PRODUCTION
HELPB TRANCE,15XL,15XL TRANS** FOR PUL** PRODUCTION
SAVEVALUE 17,XL15,XL SAVEVALUE FOR DAILY POLYHEMA
SAVEVALUE CUPOL,XL15,XL CUMUL** DAILY PUL** PRODUCTION
SAVEVALUE DPOL,XL17,XL DAILY PRODU** POLYHEMA
SAVEVALUE 17,4,F,XL SET DAILY PUL** TO ZERO
ADVANCE 1 DEVELOPMENT OF CADAVER ON ITS FIRST DAY
LEAVE "#E END OF THE FIRST DAY OF CADAVER
TERMINATE VIRUS-KILLED INDIVIDUALS WERE TERMINATED
ENDMACRO

* LOAD CA06,TRANF,VMORT

**************************************************************************************************

* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
* A GPSS MODEL TO DETERMINE THE DEVELOPMENT OF XPV EPIDEMICS IN *
* THE LAMN ARMYCMN. *
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
* THIS MODEL WAS USED FOR DESCRIPTIVE PURPOSES TO COMPARE *
* THE ACTUAL AND SIMULATED DATA. *
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
* IN THIS PROGRAM, SIMULATION WAS INITIATED FROM JANUARY 2, 1980 *
* BY USING THE ACTUALLY OBSERVED DAILY AVERAGE TEMPERATURES AS *
* THE THERMAL INPUT SOURCE. *
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
* THERMAL SUMMATION METHOD WAS USED FOR DETERMINING DEVELOPMENTAL *
* PERIOD. *
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
* LIFE CYCLE IN THIS PROGRAM CONSISTED OF THE EGG, FIRST TO SEVENTH *
* INSTAR LARVA, PUPA AND ADULT STAGE. *
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
* FOR THE INITIAL POPULATION, ONE HUNDRED FIFTH INSTAR LARVAE WERE *
* GENERATED *
In this program, it was assumed that 10**9 polyhedra per 100 square cm of lawn surface was sprayed on the initial day.

The newly emerged adults were terminated without starting new life cycle.

The first macro, bamdo, determined natural mortality within a life stage under favorable environmental conditions.

The second macro, dev, determined the developmental period within a life stage.

The third macro, spray, determined spray time and virus concentration.

The fourth macro, homa, determined the total and stage-specific mortalities according to the logistic equation.

The fifth and sixth macros, choo and tran, adjusted the calculated mortalities in the range of 1 - 100%, and connected the sprayed larvae to an appropriate healthy or infection stage.

The seventh macro, videv, determined the developmental period of the infected larvae at the stages before death.

The last macro, video, determined the lethal period of NPV-infected larvae at the killing stage.

After completing the first generation, newly emerged adults were terminated without starting new life cycle.

The content of storage 1 (S1) represents the number of first instar larvae, S2 for the number of second instar, S3 for third instar, and so forth. One digit storage content number represents healthy insects.

S8 represents the number of pupae.

S9 represents the number of adults on the first day of emergence.

S10 represents the number of adults.

S60 represents the number of eggs.

Besides S60 and S10, the twodigit storage content number represents virus-infected and killed larvae.

1) 10's represent the infected stage two instars before death.
2) 20's represent the infected stage immediately before death.
3) 30's represent the killing stage.
4) 40's represent the total number of infected and killed larvae.

For example: S15 means the number of infected fifth instar larvae which will be killed two instars later. S25 means the number of infected larvae which will be killed.
• AT THE NEXT INSTAR, S35 MEANS THE NUMBER OF FIFTH
• INSTAR LARVAE AT THE KILLING STAGE. S45 MEANS THE
• TOTAL NUMBER OF INFECTED LARVAE AT THAT TIME.
•
• FEEDING DAMAGE AND POLYHEDRA PRODUCTION WERE ALSO CALCULATED.
• THE UNIT USED FOR CALCULATING FEEDING DAMAGE IS MG (FRESH WEIGHT
• OF BERMUDA GRASS).
•
• THE UNIT OF POLYHEDRA PRODUCTION IS 10**5 POLYHEDRA.
•
• SINCE THE CREATION OF THE ORIGINAL TRANSACTIONS REQUIRED ONE
• TIME UNIT, THE SIMULATION FOR THE INSECT LIFE SYSTEM WAS STARTED
• FROM (AC - 1) DAY.

FUNCTIONS

NORM FUNCTION RN1,C27
0.1/0.003, -3.5/0.035, -2.5/0.062, -2.0/0.122, -1.5/0.228, -1.0/0.413, -0.5/0.894, 0.0
0.5/0.894, 1.0/0.413, 1.5/0.228, 2.0/0.122, 2.5/0.062, 3.0/0.035, 3.5/0.003

MO1 FUNCTION RN1,C2 UNIFORM INTRODUCTION OF FEMALES

INTRODUCTION PATTERN OF ADULTS

CUV1 POSITION FUNCTION RN1,D7 OBTAIN OF PRE-UVIPOSITION PERIOD
0.011, 0.0886, 2.0/0.110, 3.0/0.7998, 4.0/0.9330, 5.0/0.9838, 6.0/0.9999

CUV1E FUNCTION RN1,D10 OBTAIN OF UVI-POSITION PERIOD
0.011, 0.0667, 2.0/0.1443, 3.0/0.5211, 4.0/0.8876, 5.0/0.9442, 6.0/0.9999, 7.0/0.9999

CGSTA FUNCTION RN1,D18 STD OF DAILY EGG PRODUCTION
272/1.731, 1.616/1.086, 0.897/0.556, 0.394/0.11, 0.011/0.1, 0.001/0.1, 0.001/0.1

ATE FUNCTION AC1,L40 DAILY AVERAGE TEM FROM 800102
237/223, 227/227, 227/229, 241/246, 254/256, 247/241

FUNCTIONS FOR LETHAL INFECTION (STAGE-SPECIFIC) PERIOD

LIP11 FUNCTION RN1,D5
0.017/0.083, 0.035/0.083, 0.001/0.999

LIP12 FUNCTION RN1,D6
0.063/0.250, 0.048/0.938, 0.001/0.999

LIP13 FUNCTION RN1,D7
0.025/0.500, 0.001/0.999

LIP21 FUNCTION RN1,D5

- 214 -
- 215 -

0.125, 1/0.261, 1/0.438, 5/0.969, 6/0.999, 7
LIP22 FUNCTION RNL1,06
0.054, 2/0.174, 3/0.523, 4/0.932, 5/0.946, 6/0.999, 7
LIP23 FUNCTION RNL1,07
0.059, 1/0.118, 2/0.471, 3/0.932, 4/0.912, 5/0.971, 7/0.999, 9
LIP31 FUNCTION RNL1,07
0.028, 2/0.333, 3/0.520, 5/0.444, 6/0.833, 7/0.917, 8/0.999, 9
LIP32 FUNCTION RNL1,08
0.008, 2/0.148, 3/0.410, 4/0.770, 5/0.959, 6/0.984, 7/0.992, 8/0.999, 10
LIP33 FUNCTION RNL1,07
0.043, 2/0.217, 2/0.478, 3/0.652, 4/0.735, 5/0.870, 6/0.999, 7
LIP41 FUNCTION RNL1,04
0.083, 6/0.333, 7/0.583, 8/0.999, 9
LIP42 FUNCTION RNL1,09
0.008, 2/0.148, 3/0.410, 4/0.770, 5/0.959, 6/0.984, 7/0.992, 8/0.999, 10
LIP43 FUNCTION RNL1,07
0.027, 3/0.081, 4/0.495, 5/0.788, 6/0.927, 7/0.980, 8/0.999, 9
0.999, 11
LIP51 FUNCTION RNL1,08
0.152, 1/0.333, 2/0.545, 3/0.867, 4/0.818, 5/0.879, 6/0.970, 7/0.999, 10
LIP52 FUNCTION RNL1,06
0.500, 6/0.999, 7
LIP53 FUNCTION RNL1,07
0.027, 3/0.081, 4/0.285, 5/0.568, 6/0.784, 7/0.932, 8/0.999, 9
LIP54 FUNCTION RNL1,06
0.250, 1/0.542, 2/0.750, 3/0.917, 4/0.959, 5/0.999, 7
LIP61 FUNCTION RNL1,02
0.333, 4/0.999, 7
LIP62 FUNCTION RNL1,07
0.103, 1/0.520, 2/0.722, 3/0.834, 4/0.830, 5/0.969, 6/0.999, 7

* **************************************************
*
* VARIABLES
*
* **************************************************
* 1 VARIABLE AC1-2 DAYS AFTER INTRODUCTION OF ORIGINAL INDIVIDUAL
2 VARIABLE FNL4STATE/100 PL1 TOTAL EFFECTIVE TEMPERATURE (DAY=OF INCREASE)
3 VARIABLE PL3 FNSNORM+PL2 TOTAL EFFECTIVE TEMPERATURE
4 VARIABLE L3.5 FNSNORM+L3.3 LONGEVITY OF AN ADULT
5 VARIABLE RN2*2/1000 LNG1** OF N AT** DYING II TO IV LARVA
6 VARIABLE RN2*3/1000 LNG1** OF N AT** DYING I V VI LARVA
7 VARIABLE RN2*4/1000 LNG1** OF N AT** DYING EGG
8 VARIABLE RN2*5/1000 LNG1** OF N AT** DYING VII LARVA
9 VARIABLE RN2*6/1000 LNG1** OF N AT** DYING PUPA
10 VARIABLE RN2*7/1000 LNG1** OF N AT** DYING ADULT
11 VARIABLE (PL5/PL4-1)*XL5 NEXT "GHM" EFF=" 30" FOR NEXT STAGE
12 VARIABLE Z FNSNORM+XL10 LNG1** OF ADULT MOTH (IN US 1 DAY)
13 VARIABLE (FNSNORM+XL10)/50 DAILY EGG PRODUCTION
*
* MORTALITY VARIABLE XM2 FNSNORM+XM1 BASIC MORTALITY IN 1000 UNIT
* PROJ VARIABLE FNSNORM-1 INT== OF FEMALE (PROJ==) IN US ONE DAY
*
15 VARIABLE 1000*(XL6 FNSNORM+XL5) TOTAL MORTALITY
16 VARIABLE 1000*(XL6 FNSNORM+XL5) FIRST STAGE-SPECIFIC MORTALITY
17 VARIABLE 1000*(XL6 FNSNORM+XL5) SECOND STAGE-SPECIFIC MORTALITY
18 VARIABLE 1000*(V16/XM2) AGA*** PCT*** FOR FIRST INF*** STAGE
19 VARIABLE 1000*(V17/1000-XM2) CIP*** FOR SECOND INF*** STAGE
**FOOD DAMAGE**

25 VARIABLE 0.5*S1+1.1*S2+3.0*S3+9.2*S4/1000 OAM** AT YOUW

26 VARIABLE (27.4*S5+8.3*S6+316.7*S7)/1000 OAM** AT OLD STAGE

27 VARIABLE 0.9*(10.5*S11+1.1*S12+3.0*S13+9.2*S14)/1000 OAM**

28 VARIABLE 0.9*(27.4*S15+83.0*S16)/1000 OAM** AT SN1 INF** STA

29 VARIABLE 0.9*(5.9*S21+1.1*S22+3.0*S23+9.2*S24)/1000 OAM** SEC**

30 VARIABLE 0.9*(27.4*S25+83.0*S26)/1000 OAM** AT SEC** INF** STA

31 VARIABLE 0.1*(3.5*S31+1.1*S32+3.0*S33+9.2*S34)/1000 OAM**

32 VARIABLE 0.1*(27.4*S35+83.0*S36)/1000 OAM** AT SEC** STA

**FOOD** VARIABLE V25+V26+V27+V28+V29+V30+V31+V32 FOOD DAMAGE

**POLYHETRA PRODUCTION FROM CADAVER**

**FEMALE** POLY** NO. (COMMON LOG)

*================================================================================================================*}

**BASIC LIFE MODEL**

*================================================================================================================*

**GENERATION OF INITIAL TRANSACTIONS**

*================================================================================================================*

**GENERATE 1,1,1,1PH,4PB,7PL INTRODUCTION OF ORIGINAL TRANSACTION**

**SPLIT 1O,SP65O INITI AL POPULATION OF Y INSTAR**

**TERMINATE TERMINATE ORIGINAL TRANSACTION**

*================================================================================================================*

**INTRODUCTION OF ADULTS**

*================================================================================================================*

**FEMALE** FNS**OCL INTRODUCTION OF FEMALE

**ENTER** 10 ENTER ADULT STAGE

**ENTER** 9 ENTER THE FIRST DAY OF INTRODUCTION

**ADVANCE** 1 FIRST DAY OF INTRODUCTION OF FEMALE

**LEAVE** 9 LEAVE THE FIRST DAY OF INTRODUCTION

*================================================================================================================*

**OVIPPOSITION**

*================================================================================================================*

**RPT ADVANCE V2** PROV** PREVIOUS PERIOD (MINUS ONE DAY)

**ASSIGN 2.** FNS**WIPE,PB** DETER** OVIPPOSITION PERIOD

**OP13 ADVANCE** 1 DAILY DEVELOPMENT OF A FEMALE DURING OVIPUS**

**ASSIGN 3,** 1PB** ASSIGN OVIPPOSITION DAY**

**SAVEVALUE 1,** 1XF** ADDRESS FOR EGG PRODUCTION (TRANSFER)**

**SAVEVALUE 15,** 1P63** XL** SAVEVALUE FOR OVIPPOSITION DAY

**SAVEVALUE 16,** 0** XL** SET 0 FOR EGG PRODUCTION

**HELP** 1** TRANSF** ,1XF,15XL,16XL DET** EGG PRODUCTION

**ASSIGN 1,** 13** PH** ASSIGN DAILY EGG PRODUCTION

**TEST** 1** PH+O** SPILL SELECT** EFFECT** OVIPUS**

**TRANSFER 1** UP12 CONNECTION

**OP11 SPLIT** PH1,**INSO** DAILY OVIPUS

**OP12 LGP** 2PB,**OP13** REPEAT OVIPUS

**ASSIGN 3,** 0** PB** ASSIGN OVIPOSIT ION DAY AS ZERO

**ADVANCE** V6 POST-OVIPUS PERIOD

**LEAVE** 10 LEAVE ADULT STAGE
**TERMINATE**
**FEMALE IS TERMINATED**

**EGG DEVELOPMENT**

-------------------

**BAMO**
MACRO INSQ, 933, 10, mmm, DUMO, 00, V7

**INSQ**
SAVEVALUE 1, 933, XH
SAVEVAL 2, 10, XM
TEST GE VERORT1, 999, mmm0
TRANSFER DUMO

**mmm0**
SAVEVALUE 3, Y MORT1, XH
TRANSFER XH3, DUM0
ENTER 60
ADVANCE V7
LEAVE 60

**DEV**
MACRO DUMO, 00, 10, 7, 59, 40, 10, 05, ZZZ, 33, 33

**DUMO**
ENTER 60
ASSIGN 1, 10, 7, PL
ASSIGN 2, 59, 40, PL
ASSIGN 3, 10, 05, PL
ASSIGN 4, V3, PL

**ZZZ**
ASSIGN 5, V2, PL
ADVANCE 1
TEST GE PL5, PL4, ZZZ
LEAVE 6U
SAVEVALUE NEXT, 33, 33, XL
ASSIGN 5, V11, PL

**FIRST INSTAR LARVA**

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**SPRAY**
MACRO SPAI0, INS1, VIM11

**SPAI0**
TEST E AC1, 1, INS1
SAVEVALUE 4, 9, 0000, XL
TRANSFER VIM11

**RAMC**
MACRO INS1, 933, 38, mmm1, DUM1, 1, V6

**INS1**
SAVEVALUE 1, 933, XH
SAVEVALUE 2, 38, XM
TEST GE VERORT1, 999, mmm1
TRANSFER DUM1

**mmm1**
SAVEVALUE 3, Y MORT1, XH
TRANSFER XH3, DUM1
ENTER 1
ADVANCE V6
LEAVE 1

**DEV**
MACRO DUM1, 1, 13, 7, 33, 33, 4, 34, AAA, 26, 52

**DUM1**
ENTER 1
ASSIGN 1, 13, 7, PL
ASSIGN 2, 33, 33, PL
ASSIGN 3, 4, 34, PL
ASSIGN 4, V3, PL

**AAA**
ASSIGN 5, V2, PL
ADVANCE 1
TEST GE PL5, PL4, AAA
LEAVE 1
SAVEVALUE NEXT, 26, 52, XL
ASSIGN 5, V11, PL
SECOND INSTAR LARVA

SPRAY MACRO SPA20, INS2, VIM21

SPA20 TEST E AC1,1, INS2
SAVE VALUE 4,9,0000, XL
TRANSFER VIM21

BAMO MACRO INS2, 999, 38, DUM2, 2, V5

INS2 SAVE VALUE 1,999, XM
SAVE VALUE 2,38, XM
TEST GE VSMORT1, 999, 38
TRANSFER DUM2

VERMAC SAVE VALUE 3, VSMORT1, XM
TRANSFER XM3, DUM2
ENTER 2
ADVANCE V5

LEAVE 2

DEV MACRO DUM2, 2, 14, 4, 26, 52, 4, 36, 88, 28, 83

DUM2 ENTER 2
ASSIGN 1,14,4, PL
ASSIGN 2,26,52, PL
ASSIGN 3,4,86, PL
ASSIGN 4,38, PL
ASSIGN 5, V2, PL
ADVANCE 1
TEST GE PL5, PL4, DUMD
LEAVE 2
SAVE VALUE NEXT, 28, XL
ASSIGN 5, V11, PL

THIRD INSTAR LARVA

SPRAY MACRO SPA30, INS3, VIM31

SPA30 TEST E AC1,1, INS3
SAVE VALUE 4,9,0000, XL
TRANSFER VIM31

BAMO MACRO INS3, 967, 24, DUM3, 13, 3, V5

INS3 SAVE VALUE 1,967, XM
SAVE VALUE 2,24, XM
TEST GE VSMORT1, 999, 38
TRANSFER DUM3

VERMAC SAVE VALUE 3, VSMORT1, XM
TRANSFER XM3, DUM3
ENTER 3
ADVANCE V5

LEAVE 3

DEV MACRO DUM3, 3, 13, 5, 28, 83, 5, 36, 57, CCC, 32, 50

DUM3 ENTER 3
ASSIGN 1,13,5, PL
ASSIGN 2,28,83, PL
ASSIGN 3,5,17, PL
ASSIGN 4, V3, PL
ASSIGN 5, V2, PL
ADVANCE 1
TEST GE PL5, PL4, CCC
LEAVE 3
SAVEVALUE NEXT,32,5,49,51
ASSIGN 5,v5.1,PL

FIFTH INSTAR LARVA

SPRAY MACRU SPA50,INS5,VLIM51
SPA50 TEST E ACL1.1,INS5
SAVEVALUE 4.9,00000,51
TRANSFER V1M51
BAMU MACRU INS5,978.31,520.99,DU55,5.60,5.60
INS5 SAVEVALUE 1.978,31
TRANSFER v1M51
VMM5 SAVEVALUE 2.31,31
TEST GE v1M51,999,520.99
TRANSFER DuM5
VMM5 SAVEVALUE 3,1978.31
TRANSFER v1M51
ENTER 5
ADVANCE V6
SAVEVALUE NEXT,34.49,51
ASSIGN 5,v5.1,PL

FIFTH INSTAR LARVA

SPRAY MACRU SPA50,INS5,VLIM51
SPA50 TEST E ACL1.1,INS5
SAVEVALUE 4.9,00000,51
TRANSFER V1M51
BAMU MACRU INS5,978.31,520.99,DU55,5.60,5.60
INS5 SAVEVALUE 1.978,31
TRANSFER v1M51
VMM5 SAVEVALUE 2.31,31
TEST GE v1M51,999,520.99
TRANSFER DuM5
VMM5 SAVEVALUE 3,1978.31
TRANSFER v1M51
ENTER 5
ADVANCE V6
SAVEVALUE NEXT,34.49,51
ASSIGN 5,v5.1,PL
### SIXTH INSTAR LARVA

- **SPRAY**
  - **MACR**
  - **SPRAY**
  - **TEST**
  - **SAVEVALUE**
  - **TRANSFER**
  - **SAVEVALUE**
  - **TRANSFER**
  - **TRANSFER**
  - **ENTER**
  - **ADVANCE**
  - **LEAVE**
  - **DEV**
  - **DUM**

### LAST INSTAR LARVA

- **BAM**
- **MACR**
- **INS**
- **SAVEVALUE**
- **TRANSFER**
- **SAVEVALUE**
- **TRANSFER**
- **ENTER**
- **ADVANCE**
- **LEAVE**
- **DEV**
- **DUM**

**GGG**

**ASSIGN**

**ADVANCE**

**TEST**

**LEAVE**

**SAVEVALUE**

**ASSIGN**
**PUPAL STAGE**

- **BAM**
  - **MACRO**
    - INS8, 908, 55, HHH8, DUMB8, 8, v9
  - **SAVEVALUE** 1, 906, v9
  - **SAVEVALUE** 1, 906, v9
  - **TEST GE** VSMORT1, 999, hHH
  - **TRANSFER** DUMB8
  - **SAVEVALUE** 3, VSMUTL, v9
  - **TRANSFER** XM3, DUM8
  - **ENTER** 8
  - **ADVANCE** V9
  - **LEAVE** 8

- **DEV**
  - **MACRO** DUMB8, 8, 15, 1, 110, 42, 15, 62, HHH, 0
  - **ENTER** 8
  - **ASSIGN** 1, 15, 1, PL
  - **ASSIGN** 2, 110, 42, PL
  - **ASSIGN** 3, 15, 62, PL
  - **ASSIGN** 4, v3, PL
  - **ASSIGN** 5, v2, PL
  - **ADVANCE** 1
  - **TEST GE** PL5, PL4, HHH
  - **LEAVE** 8
  - **SAVEVALUE** NEXT, 0, XL
  - **ASSIGN** 5, v11, PL

**ADULT STAGE**

- **INS9**
  - **ENTER** 10 BEGINNING OF ADULT STAGE
  - **ENTER** 9 BEGINNING OF INITIAL DAY OF EMERGENCE
  - **ADVANCE** 1 INITIAL DAY OF ADULT STAGE
  - **LEAVE** 9 END OF INITIAL DAY OF ADULT STAGE
  - **ADVANCE** V12 LONGI** UF ADULT YUTH (MINUS 1 DAY)
  - **LEAVE** 10 END OF ADULT STAGE;
  - **TERMINATE** PRODUCED ADULTS ARE TERMINATED

**EPIDEMIC MODEL**

**VIRUS SPRAY TO FIRST INSTAR**

**NDMA**

- **MACRO** VIM11, 1, 5, 6, 5XL, nXL TOT** HFR** FOR 1
- **VIM11**
  - **SAVEVALUE** 1, 1, v9
  - **SAVEVALUE** 5, v9, XL
  - **SAVEVALUE** 6, v9, XL
  - **HELPB** #VIM11RT, 1, v9, 4XL, 5XL, 6XL
A~E-SPECIFIC MORTALITY AT INITIAL STAGE OF THE FIRST INSTAR

**QMRA MACRO**
AGE11 SAVEVALUE 1,13,XF
HELPB #V11MORT,1XF,4XL,5XL,6XL
CMUO MACRO V15,SPA12,INS1,999,SPA13,SPA14
TEST LE V15,0,SPA12
SAVEVALUE 1,1,XH
TRANSFER .INS1
SPA12 TEST GE V15,999,SPA13
SAVEVALUE 1,999,XH
TRANSFER .SPA14
SPA13 SAVEVALUE 1,15,XH
SPA14 SAVEVALUE 2,1XL,1,XH
TRAN MACRC AGE11,INS1
TRANSFER .XM2,AGE11
TRANSFER .INS1

* * *

**AGE-SPECIFIC MORTALITY AT INITIAL STAGE OF THE FIRST INSTAR**

**QMRA MACRO**
AGE11 SAVEVALUE 1,13,XF
SAVEVALUE 7,0,XL
HELPB #V11MORT,1XF,4XL,7XL,3XL
SAVEVALUE 1,1,XF
HELPB #V11MORT,1XF,4XL,7XL,3XL
CHGU MACRC V15,999,SPA13
TEST LE V15,0,SPA12
SAVEVALUE 1,1,XH
TRANSFER .AGE16
VIM12 TEST GE V15,999,SPA13
SAVEVALUE 1,999,XH
TRANSFER .VIM14
VIM13 SAVEVALUE 1,10,XH
VIM14 SAVEVALUE 2,1H1,1,XH
TRAN MACRC FRV31,AGE16
TRANSFER .XM2,FRV31
TRANSFER .AGE16
VOED MACRO FRV31,31,41,FNSLIP11,51,0.2026,0.3452
FRV31 ENTER 31
ENTER 41
ADVANCE FNSLIP11
LEAVE 31
LEAVE 41
ENTER 51
SAVEVALUE 1,2,XF
SAVEVALUE 13,6,2026,XL
SAVEVALUE 14,0,3452,XL
SAVEVALUE 15,1,SPG1,XL
SAVEVALUE 16,0,XL
HELPB #TRANFO1XF,15XL,16XL
SAVEVALUE 17,0,1XL
ADVANCE 1
LEAVE 51
TERMINATE
* MORTALITY PROPORTION AT TERTIARY STAGE OF THE FIRST INSTAR *

**NOMA MACRO**

AGE16 SAVEVALUE 1.15, XF
SAVEVALUE 9, O, XL
HELPB #VINCR1, 1XF, 4XL, 9XL, 10XL
SAVEVALUE 10, 0, XL
HELPB #VINCR1, 1XF, 4XL, 9XL, 10XL

**CHUG MACRO**

V19, VIM15, AGE18, 999, VIM16, VIM17
TEST GE V19, 0, VIM15
SAVEVALUE 1, 1, XH
TRANSFER *AGE18
VIM15 TEST GE V19, 999, VIM16
SAVEVALUE 1, 999, XH
TRANSFER *VIM17
VIM16 SAVEVALUE 1, V19, XH
VIM17 SAVEVALUE 2, V19, XH

**TRAN MACRO**

FRV11, AGE18
TRANSFER *XH2, FRV11
TRANSFER *AGE18

**VDEV MACRO**

FRV11 ENTER 11
ASSIGN 4, 0, PB

**DEV MACRO**

ILA11 ENTER 41
ASSIGN 1, 13, 7, PL
ASSIGN 2, 33, 33, PL
ASSIGN 3, 8, 34, PL
ASSIGN 4, V3, PL
FR11 ASSIGN 5, V2, PL
ADVANCE 1
TEST GE PL5, PL4, FR11
LEAVE 41
SAVEVALUE NEXT, 26, 52, XL
ASSIGN 5, V11, PL
LEAVE 11

**VDEV MACRO**

FRV22, 22, ILd22, 42, 14, 4, 26, 52, 4, 88, FRQ22, 28, 83
FRV22 ENTER 22
ASSIGN 4, 3, PB

**DEV MACRO**

ILB22 ENTER 42
ASSIGN 1, 14, 4, PL
ASSIGN 2, 26, 52, PL
ASSIGN 3, 5, 86, PL
ASSIGN 4, V3, PL
FRB22 ASSIGN 5, V2, PL
ADVANCE 1
TEST GE PL5, PL4, FRG22
LEAVE 42
SAVEVALUE NEXT, 28, 83, XL
ASSIGN 5, V11, PL
LEAVE 22

**VDO MACRO**

CAD1, 33, 43, FNSLIP, 53, 2504, 0, 32, 3
CAD1 ENTER 33
ENTER 43
ADVANCE FNSLIP, 13
AGE-SPECIFIC MORTALITY AT SECONDARY STAGE AT THE SECOND INSTAR

NOMA MACRO AGE22,17,7,8,7XL,8XL SECONDARY STAGE-SPECIFIC MORT**

AGE22 SAVEVALUE 1,17,XF
SAVEVALUE 7,XL
SAVEVALUE 17,7,8,0,XL
HELPB #VIM2R,1XF,4XL,7XL,8XL
SAVEVALUE 17,1,4,AF
HELPB #VIM2R,1XF,4XL,7XL,8XL
CHOU MACRO V18,VI122,AGE26,999,VI123,VI124
TEST LE VI18,0,VI122
SAVEVALUE 1,1,1,XF
TRANSFER #AGE26
VI122 TEST GE V18,999,VI123
SAVEVALUE 1,999,XH
TRANSFER #VI124
VI123 SAVEVALUE 1,V18,XH
VI124 SAVEVALUE 2,18,0,XH
TRAN MACRO SEV22,AGE26
TRANSFER #XH2,SEV22
TRANSFER #AGE26
VDEV MACRO SEV22,22,Y1D22,42,26.92,48,SE922,26.83
SEV22 ENTER 22
ASSIGN 4,0,PS
DEV MACRO Y1B22,42,144,26,52,48,SE822,28,83
Y1B22 ENTER 42
ASSIGN 1,4,4,PL
ASSIGN 2,26,52,PL
ASSIGN 3,4,86,PL
ASSIGN 4,0,3,PL
SÉB22 ASSIGN 5,42,PL
ADVANCE 1
TEST GE P15,5,PL,SEn22
LEAVE 42
SAVEVALUE NEXT,20,83,XL
ASSIGN 5,VI1,XH
LEAVE 22
VOED MACRO CA022,33,43,FNSL1P22,53,7.2564,0.3243
**CA02Z ENTER** 33  
**ENTER** 43  
**AUVAt.CE**  
**FNSLIP22**  
**LEAVE** 33  
**LEAVE** 43  
**ENTER** 53  
**SAVEVALUE** 1,2,XF  
**SAVEVALUE** 13,7,2564,XL  
**SAVEVALUE** 14,0,3243,XL  
**SAVEVALUE** 15,V7POL,XL  
**SAVEVALUE** 16,0,XL  
**HELPB** 0,TRANFO,IXF,15XL,10XL  
**SAVEVALUE** 17,0,XL16,XL  
**SAVEVALUE** CUPOL+,XL16,XL  
**SAVEVALUE** DAPOL,XL17,XL  
**SAVEVALUE** 17,0,XL  
**ADVANCE** 1  
**LEAVE** 53  
**TERMINATE**

**MORTALITY PROPORION AT TERTIARY STAGE OF THE SECOND INSTAR**  

**NOMA MACRO** AGE26,19,9,10,9XL,10XL MORT** PROPOR** AT TERT** STA

**AGE26**  
**SAVEVALUE** 1,19,XF  
**SAVEVALUE** 9,0,XL  
**SAVEVALUE** 10,0,XL  
**HELPB** 0,TRANFO,IXF,4XL,9XL,10XL  
**SAVEVALUE** 11,1,XF  
**HELPB** 0,TRANFO,IXF,4XL,9XL,10XL  

**CHGO MACRO** V19,VIM25,AGE27,999,VIM26,VIM27  
**TEST LE** V19,0,VIM29  
**SAVEVALUE** 1,1,XH  
**TRANSFER** .AUG27  
**VIM25**  
**TEST GE** V19,999,VIM26  
**SAVEVALUE** 1,999,XH  
**TRANSFER** .VIM27  
**VIM26**  
**SAVEVALUE** 2,19,XH  

**VIM27**  
**SAVEVALUE** 2,XH1,XH  

**TRAN MACRO** SEV12,AGE27  
**TRANSFER** .XH22,SEV12  

**VDEV MACRO** SEV12,12,Y1B12,42,14,4,26.52,4,98,SEB12,23,33  

**SEV12**  
**ENTER** 12  
**ASSIGN** 4,0,PB  

**DEV MACRO** Y1B12,42,14,4,26.52,4,98,SEB12,23,33  

**Y1B12**  
**ENTER** 42  
**ASSIGN** 1,14,4,PL  
**ASSIGN** 2,26,52,PL  
**ASSIGN** 3,4,68,PL  

**SEB12**  
**ASSIGN** 4,3,PL  
**ADVANCE** 1  
**TEST GE** PL5,PL4,SEB12  
**LEAVE** 42  
**SAVEVALUE** .EXT,28.82,XL  
**ASSIGN** 5,SEV1,PL  
**LEAVE** 12
VDEV MACRO
SEV23, Y1C23, 43, 13.5, 28.83, 5.17, SEC23, 32.50

SEV23 ENTER 23
ASSIGN 4, 0, PB

DEV MACRO
Y1C23 ENTER 43
ASSIGN 1, 13.5, PL
ASSIGN 2, 28.83, PL
ASSIGN 3, 5, 17, PL
ASSIGN 4, V3, PL

SEC23 ASSIGN 5, +, V2, PL
ADVANCE 1
TEST GE PL5, PL4, SEC23
LEAVE 43
SAVEVALUE NEXT, 32.50, XL
ASSIGN 5, V11, PL.
LEAVE 23

VDEO MACRO CAD24, 34, 44, FN$LIP23, 54, 8, 3010, 0.2342
CAD24 ENTER 34
ADVANCE FN$LIP23
LEAVE 34
LEAVE 44
ENTER 54
SAVEVALUE 1, 2, XF
SAVEVALUE 13, 8, 3010, XL
SAVEVALUE 14, 0, 2342, XL
SAVEVALUE 15, VSPOL, XL
SAVEVALUE 16, J, XL
HELPb #TRANFU, 1XF, 15XL, 16XL
SAVEVALUE 17, XLI0, XL
SAVEVALUE CUPUL+, XL16, XL
SAVEVALUE DAPUL, XL17, XL
SAVEVALUE 17, O, XL
ADVANCE 1
LEAVE 54
TERMINATE

VDEO MACRO AGE27, 32, 42, FN$LIP21, 52, 6, 7602, 0.2198
AGE27 ENTER 32
ADVANCE FN$LIP21
LEAVE 32
LEAVE 42
ENTER 52
SAVEVALUE 1, 2, XF
SAVEVALUE 13, 6, 7602, XL
SAVEVALUE 14, 0, 2198, XL
SAVEVALUE 15, VSPOL, XL
SAVEVALUE 16, J, XL
HELPb #TRANFU, 1XF, 15XL, 16XL
SAVEVALUE 17, XLI0, XL
SAVEVALUE CUPUL+, XL16, XL
SAVEVALUE DAPUL, XL17, XL
SAVEVALUE 17, O, XL
ADVANCE 1
LEAVE 52
TERMINATE
VIRUS SPRAY TO THIRD INSTAR

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NOMA MACRO V1M31,5,5,6,5XL,6XL TQA** FOR III

V1M31 SAVEVALUE 1,5,XF
SAVEVALUE 5,0,XL
SAVEVALUE 0,0,XL
HELPB #V1M3RT,1XF,4XL,5XL,6XL
SAVEVALUE 1,1,XF
HELPB #V1M3RT,1XF,4XL,5XL,6XL

CH00 MACRO V15,SPA32,INS3,999,SPA33,SPA34
TEST LE V15,0,SPA32
SAVEVALUE 1,1,XH
TRANSFER +INS3

SPA32 TEST GE V15,999,SPA33
SAVEVALUE 1,999,XH
TRANSFER +SPA34

SPA33 SAVEVALUE 1,15,XH

SPA34 SAVEVALUE 2,1XH,XH

TRAN MACRO AGE32,INS3
TRANSFER +XH2,AGE32
TRANSFER +INS3

AGE-SPECIFIC MORTALITY AT SECONDARY STAGE AT THE THIRD INSTAR

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NOMA MACRO AGE32,21,7,8,7XL,8XL SECONDARY STAGE-SPECIFIC MORT**

AGE32 SAVEVALUE 1,21,XF
SAVEVALUE 7,0,XL
SAVEVALUE 8,0,XL
HELPB #V1M3RT,1XF,4XL,7XL,8XL
SAVEVALUE 1,1,XF
HELPB #V1M3RT,1XF,4XL,7XL,8XL

CH00 MACRO V10,V1M32,AGE36,999,V1M33,V1M34
TEST LE V10,0,V1M32
SAVEVALUE 1,1,XH
TRANSFER +AGE36

V1M32 TEST GE V10,999,V1M33
SAVEVALUE 1,999,XH
TRANSFER +V1M34

V1M33 SAVEVALUE 1,10,XH

V1M34 SAVEVALUE 2,1XH,XH

TRAN MACRO TIV23,AGE36
TRANSFER +XH2,TIV23
TRANSFER +AGE36

VDEV MACRO TIV23,23,SMC23,43,13,5,28,83,5,17,TIC23,32,50

TIV23 ENTER 23
ASSIGN 4,0,PB

VDEV MACRO SMC23,43,13,5,28,33,5,17,TIC23,32,50

SMC23 ENTER 43
ASSIGN 1,13,5,PL
ASSIGN 2,28,83,PL
ASSIGN 3,5,17,PL
ASSIGN 4,83,PL

TIC23 ASS=new 5,2,V2,PL
ADVANCE 1
TEST GE PL3,PL4,TIC23
LEAVE 43
SAVEVALUE NEXT, 32, 50, XL
ASSIGN 5, V11, PL
LEAVE 23

VODE macro CAD32, 34, 44, FNSLIP32, 54, 8, 3010, 0, 2342

CAD32 ENTER 34
ENTER 44
ADVANCE FNSLIP32
LEAVE 34
LEAVE 44
ENTER 54
SAVEVALUE 1, 2, XE
SAVEVALUE 13, 0, 3010, XL
SAVEVALUE 14, 0, 2342, XL
SAVEVALUE 15, VSPOL, XL
SAVEVALUE 16, 0, XL
HELPB #TRANFO, 1XF, 15XL, 10XL
SAVEVALUE 17, XL, 10, XL
ADVANCE 1
LEAVE 54
TERMINATE

* MORTALITY PROPORTION AT TERTIARY STAGE OF THE THRIU INSTAR

NGMA macro AGE36, 23, 9, 10, 9XL, 10XL
MORT** PROP** AT TERT** STAGE

AGE36 SAVEVALUE 1, 23, XF
SAVEVALUE 9, 0, XL
SAVEVALUE 10, 0, XL
HELPB #VIMURT, 1XF, 4XL, 9XL, 10XL
SAVEVALUE 1+, 1, XF
HELPB #VIMURT, 1XF, 4XL, 9XL, 10XL

CHOO macro V19, VIM35, AGE37, 999, VIM36, V1M37
TEST LE V19, 0, VIM35
SAVEVALUE 1, 1, XH
TRANSFER +AGE37
VIM35 TEST GE V19, 999, VIM36
SAVEVALUE 1, 999, XH
TRANSFER +VIM37
VIM36 SAVEVALUE 1, V19, XH
VIM37 SAVEVALUE 2, XH, 1, XH
TRAN MACRU TIV13, AGE37
TRANSFER +VIM37
VODE macro TIV13, 13, SMC13, 43, 13, 5, 28, 83, 5, 17, TIC13, 32, 50

TIV13 ENTER 13
ASSIGN 4, 0, PB
DEV macro SMC13, 43, 13, 5, 28, 83, 5, 17, TIC13, 32, 50

SMC13 ENTER 43
ASSIGN 1, 13, 5, PL
ASSIGN 2, 28, 83, PL
ASSIGN 3, 5, 17, PL
ASSIGN 4, V3, PL
TIC13 ASSIGN 54, V2, PL
ADVANCE 1
TEST GE PL5, PL4, TIC13
LEAVE 43
SAVEVALUE NEXT32.50, XL
ASSIGN 5;V11, PL
LEAVE 13

VOEO MACRO TIV44, 24, SMD24, 44, 13.5, 32.50, 7.01, TID24, 34.49
TIV24 ENTER 24
ASSIGN 4;P8
DEV MACRO SMD24, 44, 13.5, 32.50, 7.01, TID24, 34.49
SMD24 ENTER 44
ASSIGN 1;13.5, PL
ASSIGN 2;32.50, PL
ASSIGN 3;7.01, PL
ASSIGN 4;V3, PL
TID24 ASSIGN 5;V2, PL
ADVANCE 1
TEST GE PL5, PL4, TID24
LEAVE 44
SAVEVALUE NEXT34.49, XL
ASSIGN 5;V11, PL
LEAVE 24

VDAT MACRO CAO33, 35, 45, FNSLP33, 35, 8.7068, 0.2338
CAO33 ENTER 35
ADVANCE FNSLP33
LEAVE 35
SAVEVALUE 1;2, XF
SAVEVALUE 13, 8.7068, XL
SAVEVALUE 14, 0.2338, XL
SAVEVALUE 15, VSPOL, XL
SAVEVALUE 16, 0, XL
HELPBE #TRANFO 1XF, 15XL, 16XL
SAVEVALUE 17, 1XL6, XL
SAVEVALUE CUPOL+, XL16, XL
SAVEVALUE DAPOL, XL17, XL
SAVEVALUE 17, 0, XL
ADVANCE 1
LEAVE 55
TERMINATE

VDAT MACRO AGE37, 33, 43, FNSLP31, 53, 7.2564, 0.3243
AGE37 ENTER 33
ADVANCE FNSLP31
LEAVE 33
SAVEVALUE 1;2, XF
SAVEVALUE 13, 7.2564, XL
SAVEVALUE 14, 0.3243, XL
SAVEVALUE 15, VSPOL, XL
SAVEVALUE 16, 0, XL
HELPBE #TRANFO 1XF, 15XL, 16XL
SAVEVALUE 17, 1XL6, XL
SAVEVALUE CUPOL+, XL16, XL
SAVEVALUE DAPOL, XL17, XL
SAVEVALUE 17, 0, XL
• ADVANCE 1
• LEAVE 53
• TERMINATE

• VIRUS SPRAY TO FOURTH INSTAR
•

**NOAA MACRO**

**VIM41**
SAVEVALUE 1,7,XF
SAVEVALUE 5,0, XL
SAVEVALUE 6,0, XL
HELPB #V1MORT,1, XF, 4, XL, 5, XL, 6, XL
SAVEVALUE 1,0, 1, XF
HELPB #V1MORT,1, XF, 4, XL, 5, XL, 6, XL

**CHDQ MACRO**
TEST LE V15,0, SPA42, I NS4, 999, SPA43, SPA44
SAVEVALUE 1,1, XF
TRANSFER, I NS4

**SPA42**
TEST GE V15,999, SPA43
SAVEVALUE 1,999, XH
TRANSFER, SPA44

**SPA43**
SAVEVALUE 1, V15, XH
TRANSFER, SPA44

**TRAN MACRO**
AGE42, I NS4
TRANSFER, XH2, AGE42
TRANSFER, I NS4

• AGE-SPECIFIC MORTALITY AT SECONDARY STAGE AT THE FOURTH INSTAR

**NOAA MACRO**

**AGE42**
SAVEVALUE 1,25, XF
SAVEVALUE 7, 0, XL
SAVEVALUE 8,0,XL
HELPB #V1MORT,1, XF, 4, XL, 7, XL, 8, XL
SAVEVALUE 1,0, 1, XF
HELPB #V1MORT,1, XF, 4, XL, 7, XL, 8, XL

**CHDQ MACRO**
TEST LE V16,0, VIM42
SAVEVALUE 1,1, XH
TRANSFER, AGE46

**VIM42**
TEST GE V16,999, VIM43
SAVEVALUE 1,999, XH
TRANSFER, VIM44

**VIM43**
SAVEVALUE 1, V18, XH

**VIM44**
SAVEVALUE 2, XH1, XH

**TRAN MACRO**
FDV24, AGE46
TRANSFER, XH2, FDV24
TRANSFER, AGE46

**VDEV MACRO**
FDV24, 24, SAD24, 44, 13, 6, 32, 50, 7, 01, FOD24, 34, 49

**FDV24**
ENTER 24
ASSIGN 4,0, P8

**DEV MACRO**
SAD24, 44, 13, 6, 32, 50, 7, 01, FOD24, 34, 49

**SAD24**
ENTER 44
ASSIGN 1,13, 6, PL
ASSIGN 2,32, 50, PL
ASSIGN 3,7, 01, PL
ASSIGN 4, V3, PL
MORTALITY PROPORTION AT TERTIARY STAGE OF THE FOURTH INSTAR

NOMA MACRO AGE4,19,27,9,10,9XL,10XL MORT** PROPOR** AT TER** STA
AGE46 SAVEVALUE 1,27,XF
SAVEVALUE 9,0,XL
SAVEVALUE 10,0,XL
HELPB #VIMUR1,1XF,4XL,9XL,10XL
SAVEVALUE 1,1,1XF
HELPB #VIMUR1,1XF,4XL,9XL,10XL
CHOD MACRO V19,VIM45,AGE47,999,VIM46,VIM47
TEST LE V19,0,VIM45
SAVEVALUE 1,1,XH
TRANSFER 1,AGE47
VIM45 TEST GE V19,999,VIM46
SAVEVALUE 1,999,XH
TRANSFER 1,VIM47
VIM46 SAVEVALUE 1,1,V19,XH
VIM47 SAVEVALUE 2,XH1,XH
TRAN MACRO F0V14,AGE47
TRANSFER 1,XH2,F0V14
TRANSFER 1,AGE47
VDEV MACRO F0V14,14,SAD14,44,13,6,32,50,7,01,F0D14,34,49
FOV14 ENTER 14
ASSIGN 4,0,PB
DEV MACRO SAD14,44,13,6,32,50,7,01,F0D14,34,49
SAD14 ENTER 44
ASSIGN 1,13,6,PL
ASSIGN 2,32,50,PL
ASSIGN 3,7,01,PL
ASSIGN 4, V3, PL
ASSIGN 5, V2, PL
ADVANCE 1
TEST GE PL5, PL4, FOD14
LEAVE 44
SAVE VALUE NEXT, 34, 49, XL
ASSIGN 5, V11, PL
LEAVE 14
VDEV MACRO FOV25, 25, SAE25, 45, 13, 3, 34, 44, 8, 35, FOD25, 43, 91
FOV25 ENTER 25
ASSIGN 4, 3, PB
DEV MACRO SAE25, 45, 13, 3, 34, 44, 8, 35, FOD25, 43, 91
SAE25 ENTER 45
ASSIGN 1, 13, 3, PL
ASSIGN 2, 34, 49, PL
ASSIGN 3, 8, 35, PL
ASSIGN 4, V3, PL
FOD25 ASSIGN 5, V2, PL
ADVANCE 1
TEST GE PL5, PL4, FCE25
LEAVE 45
SAVE VALUE NEXT, 43, 91, XL
ASSIGN 5, V11, PL
LEAVE 25
VDE0 MACRO CA043, 36, 46, FN5LIP43, 35, 9, 1903, 0, 2967
CA043 ENTER 36
ENTER 46
ADVANCE FN5LIP43
LEAVE 36
LEAVE 46
ENTER 56
SAVE VALUE 1, 2, XF
SAVE VALUE 13, 9, 1903, XL
SAVE VALUE 14, 0, 2967, XL
SAVE VALUE 15, VSPOL, XL
SAVE VALUE 16, 0, XL
HELPB #TRANPO, 1XF, 15XL, 16XL
SAVE VALUE 17, XL, 16XL
SAVE VALUE CUPOL, 1, XL, 16XL
SAVE VALUE QAPOL, XL, 17, XL
SAVE VALUE 17, 0, XL
ADVANCE 1
LEAVE 56
TERMINATE
VDE0 MACRO AGE47, 34, 44, FN5LIP41, 54, 8, 3010, 0, 2342
AGE47 ENTER 34
ENTER 44
ADVANCE FN5LIP41
LEAVE 34
LEAVE 44
ENTER 54
SAVE VALUE 1, 2, XF
SAVE VALUE 13, 8, 3010, XL
SAVE VALUE 14, 0, 2342, XL
SAVE VALUE 15, VSPOL, XL
SAVE VALUE 16, 0, XL
HELPB #TRANPO, 1XF, 15XL, 16XL
VIRUS SPRAY TO FIFTH INSTAR

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NOMA MACRO VIM51, 9, 5, 6, 5XL, 6XL TUNO** FOR V
VIM51 SAVE VALUE 1, 9, XF
SAVE VALUE 5, 0, XL
SAVE VALUE 6, 0, XL
HELP 8 #VIMORT, 1, XF, 4XL, 5XL, 6XL
SAVE VALUE 10, L, XF
HELP 8 #VIMORT, 1, XF, 4XL, 5XL, 6XL
CHOQ MACRO V15, SPA52, IN55, 999, SPA53, SPA54
TEST LE V15, 0, SPA52
SAVE VALUE 1, 1, XM
TRANSFER + IN55
SPA52 TEST UE V15, 999, SPA53
SAVE VALUE 1, 999, XM
TRANSFER + SPA54
SPA53 SAVE VALUE 1, 1, 5, XM
TRANSFER + SPA55
SPA54 SAVE VALUE 2, XM1, XM
TRANSFER + SPA55
TRAN MACRO AGE52, IN55
TRANSFER + XM2, + AGE52
TRANSFER + IN55

AGE-SPECIFIC MORTALITY AT SECONDARY STAGE AT THE FIFTH INSTAR

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NOMA MACRO AGE52, 29, 7, 8, 7XL, 8XL SECONDARY STAGE-SPECIFIC MORT**
AGE52 SAVE VALUE 1, 29, XF
SAVE VALUE 7, 0, XL
SAVE VALUE 8, 0, XL
HELP 8 #VIMORT, 1, XF, 4XL, 7XL, 8XL
SAVE VALUE 10, L, XF
HELP 8 #VIMORT, 1, XF, 4XL, 7XL, 8XL
CHOQ MACRO V18, VIM52, AGE52, 999, VIM53, VIM54
TEST LE V18, 0, VIM52
SAVE VALUE 1, 1, XM
TRANSFER + AGE56
VIM52 TEST GE V18, 999, VIM53
SAVE VALUE 1, 999, XM
TRANSFER + VIM56
VIM53 SAVE VALUE 1, V18, XM
VIM54 SAVE VALUE 2, XML, XM
TRAN MACRO FIV25, AGE56
TRANSFER + XM2, + FIV25
TRANSFER + AGE56
VDEV MACRO FIV25, 25, OME25, 45, L3, 3, 34, 49, 3, 35, FIE25, 43, 39
FIV25 ENTER 25
ASSIGN 4, 0, P8
DEV MACRO OME25, 45, L3, 3, 34, 49, 8, 35, FIE25, 43, 39
OME25 ENTER 45

ASSIGN 1,13.3,PL  
ASSIGN 2,34.49,PL  
ASSIGN 3,1,35.9,PL  
ASSIGN 4,3,1,PL  
PFE25 ASSIGN 5,1,2,PL  
ADVANCE 1  
TEST GE PL5,PL4,FIE25  
LEAVE 45  
SAVEVALUE NEXT,43.91,XL  
ASSIGN 5,1,1,PL  
LEAVE 25  
VODE MACRO CAD52,36,46,FSFLIP52,56,9,1903,0.2967  
CADI52 ENTER 36  
ENTER 46  
ADVANCE FSFLIP52  
LEAVE 36  
LEAVE 46  
ENTER 56  
SAVEVALUE 1,2,XF  
SAVEVALUE 13,9,1903,4X,4XL,13XL  
SAVEVALUE 14,0,2967,4XL,13XL  
SAVEVALUE 15,595,1XL  
SAVEVALUE 16,0,4XL  
HELPB #TRANSF,1XF,15XL,16XL  
SAVEVALUE 17,5,1XL,16XL  
SAVEVALUE CUPUL,4XL,17XL  
SAVEVALUE 17,0,4XL  
ADVANCE 1  
LEAVE 56  
TERMINATE  

MORTALITY PROPORTION AT TERTIARY STAGE OF THE FIFTH INSTAR  

NOMA MACRO AGE56,31,910,4XL,10XL  
SAVEVALUE 1,31,XF  
SAVEVALUE 9,0,4XL  
SAVEVALUE 10,0,4XL  
HELPB #VIMGRT,1XF,14XL,9XL,13XL  
SAVEVALUE 1,1,XF  
HELPB #VIMGRT,1XF,4XL,9XL,10XL  
CHGD MACRO V19,VIM55,AGE57,999,VIM56,999  
TEST LE V19,0,VIM55  
SAVEVALUE 1,1,XH  
TRANSFER AGE57  
VIM55 TEST GE V19,999,VIM56  
SAVEVALUE 1,999,XH  
TRANSFER VIM57  
VIM56 SAVEVALUE 1,919,XH  
VIM57 SAVEVALUE 2,919,XH  
TRAN MACRO FIV15,AGE57  
TRANSFER E15,F15  
TRANSFER AGE57  
VDEV MACRO FIV15,15,15,AL15,45,49,8,13,3,49,8,35,F15,43,91  
FIV15 ENTER 15  
ASSIGN 4,0,1PB  
DEV MACRO CHE15,45,13,3,34,49,8,35,F15,43,91
OHE15 ENTER 45
ASSIGN 1,13,3,PL
ASSIGN 2,34,49,PL
ASSIGN 3,8,39,PL
ASSIGN 4,3,PL
FIE15 ASSIGN 5+,V2,PL
ADVANCE 1
TEST GE PL5,PL4,FIE15
LEAVE 45
SAVEVALUE NEXT,4,2,91,PL
ASSIGN 5,VI1,PL
LEAVE 15
VDEV MACRO F1V26,26,GMF26,46,14,7,38,11,8,98,FIF26,50,91
FIV26 ENTER 26
ASSIGN 4,0,PB
DEV MACRO OMF26,46,14,7,38,11,8,98,FIF26,50,91
OMF26 ENTER 46
ASSIGN 1,14,7,PL
ASSIGN 2,38,11,PL
ASSIGN 3,8,98,PL
ASSIGN 4,3,PL
FIF26 ASSIGN 5+,V2,PL
ADVANCE 1
TEST GE PL5,PL4,FIF26
LEAVE 46
SAVEVALUE NEXT,50,91,PL
ASSIGN 5,VI1,PL
LEAVE 26
VDED MACRO CAD53,37,47,FSNLP53,57,9,6252,0,1878
CAD53 ENTER 37
ENTER 47
ADVANCE FSNLP53
LEAVE 37
SAVEVALUE 1,2,XP
SAVEVALUE 13,9,6252,PL
SAVEVALUE 14,0,1878,PL
SAVEVALUE 15,VSPO+,PL
SAVEVALUE 16,0,PL
HELP #TRANPO,1XF,15XL,16XL
SAVEVALUE 17,0,PL
SAVEVALUE CUPOL,1XL10,PL
SAVEVALUE DAPOL,1XL17,PL
SAVEVALUE 17,0,PL
ADVANCE 1
LEAVE 57
TERMINATE
VDED MACRO AG6,57,35,45,FSNLP51,55,0,7068,0,2323
AGE57 ENTER 35
ENTER 45
ADVANCE FSNLP51
LEAVE 35
SAVEVALUE 1,2,PL
SAVEVALUE 13,8,7068,PL
SAVEVALUE 14,0,2338,XL
SAVEVALUE 15,5SPOL,XL
SAVEVALUE 16,0,XL
HELPB #TRANF0,1XF,15XL,16XL
SAVEVALUE 17,0,XL
SAVEVALUE CUPOL+,XL16,XL
SAVEVALUE DAPOL,XL17,XL
SAVEVALUE 17,0,XL
ADVANCE 1
LEAVE 95
TERMINATE

* VIRUS SPRAY TO SIXTH INSTAR *
* *******************************************
* NODA MACRO VIM61,11,5,6,5XL,6XL TOMO** FOR VI
VIM61 SAVEVALUE 1,11,15F
SAVEVALUE 5,0,XL
SAVEVALUE 6,0,XL
HELPB #VIMORT,1XF,4XL,5XL,6XL
SAVEVALUE 1+,1,1XF
HELPB #VIMORT,1XF,4XL,5XL,6XL
CHOO MACRO V15,SPA62,INS6,999,SPA63,SPA64
TEST LE V15,0,SPA62
SAVEVALUE 1,1,1XM
TRANSFER ;INS6
SPA62 TEST GE V15,999,SPA63
SAVEVALUE 1,999,1XM
TRANSFER ;SPA64
SPA63 SAVEVALUE 1,V15,1XM
SPA64 SAVEVALUE 2,XH1,1XM
TRAN MACRO AGE62,1,INS6
TRANSFER ;XH2,AGE62
TRANSFER ;INS6

* AGE-SPECIFIC MUTUALITY AT SECONDARY STAGE AT THE SIXTH INSTAR *
* NODA MACRO AGE62,33,7,8,7XL,8XL SECONDARY STAGE-SPECIFIC MORT**
AGE62 SAVEVALUE 1,33,1XF
SAVEVALUE 7,0,XL
SAVEVALUE 8,0,XL
HELPB #VIMORT,1XF,4XL,7XL,8XL
SAVEVALUE 1+,1,1XF
HELPB #VIMORT,1XF,4XL,7XL,8XL
CHOO MACRO V18,VIM62,AGE61,999,VIM63,VIM64
TEST LE V18,0,VIM62
SAVEVALUE 1,XH1
TRANSFER ;AGE61
VIM62 TEST GE V18,999,VIM63
SAVEVALUE 1,999,1XM
TRANSFER ;VIM64
VIM63 SAVEVALUE 1,V18,1XM
VIM64 SAVEVALUE 2,XH1,1XM
TRAN MACRO SIV26,AGE61
TRANSFER ;XH2,;SIV26
TRANSFER ;AGE61
VDEV MACRO SIV26,26,YUF26,4,14,7,38,11,8,98,SIF26,50,81
SIV26 ENTER 26
ASSIGN 4+0,PB
DEV MACRO YUF26,46,14,7,38,11,8,98,SIF26,50,81
YUF26 ENTER 46
ASSIGN 1,14,7,PL
ASSIGN 2,38,11,PL
ASSIGN 3,8,98,PL
ASSIGN 4,3,PL
SIF26 ASSIGN 5+V2,PL
ADVANCE 1
TEST US PL5,PL4,SIF26
LEAVE 46
SAVEVALUE NEXT,50,81,XL
ASSIGN 5+V11,PL
LEAVE 26
VDED MACRO CAD62,37,47,FNSLIP62,57,9,6252,0,1878
CAD62 ENTER 37
ENTER 47
ADVANCE FNSLIP62
LEAVE 37
LEAVE 47
ENTER 57
SAVEVALUE 1,2,XF
SAVEVALUE 13,9,6252,XL
SAVEVALUE 14,0,1878,XL
SAVEVALUE 15,VPOL,XL
SAVEVALUE 16,0,XL
HELPB "TRANFO,1XF,15XL,16XL"
SAVEVALUE 17+,XL16,XL
SAVEVALUE CUPOL+,XL16,XL
SAVEVALUE DAPOL,XL17,XL
SAVEVALUE 17,0,XL
ADVANCE 1
LEAVE 57
TERM INATE
VDED MACRO AGE61,36,46,FNSLIP61,56,9,1903,0,2967
AGE61 ENTER 36
ENTER 46
ADVANCE FNSLIP61
LEAVE 36
LEAVE 46
ENTER 56
SAVEVALUE 1,2,XF
SAVEVALUE 13,9,1903,XL
SAVEVALUE 14,0,2967,XL
SAVEVALUE 15,VPOL,XL
SAVEVALUE 16,0,XL
HELPB "TRANFO,1XF,15XL,16XL"
SAVEVALUE 17+,XL16,XL
SAVEVALUE CUPOL+,XL16,XL
SAVEVALUE DAPOL,XL17,XL
SAVEVALUE 17,0,XL
ADVANCE 1
LEAVE 56
TERM INATE

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**CONTROL CARDS**

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**TIME CONTROL**

GENERATE 1 TIMER ARRIVES EVERYDAY
SAVEVALUE DAY,V1,XH DAYS COUNTING FROM INITIATION OF FEMALE
SAVEVALUE DADAM,V#FOOD,XL DAILY FOOD DAMAGE BY THE LARVAE
SAVEVALUE CUDA,XL DADAM,XL CUMULATIVE DAILY FOOD DAMAGE
TERMINATE 1 TIMER COUNTING
START 35,1

**OUTPUT CONTROL**

REPORT
TEXT #XH$DAY,2/XX# DAY(S) AFTER INITIAL INTRODUCTION
STO TITLE AGE COMPOSITION (NO. OF INDIVIDUALS)
LSV TITLE FOOD CONSUMPTION AND VIRUS PRODUCTION
END
```
SUBROUTINE VIMORT DETERMINES THE TOTAL AND STAGE-SPECIFIC MORTALITIES AND THEIR STANDARD DEVIATION.

MORTALITIES WERE DETERMINED BY LOGISTIC EQUATIONS.
PARAMETER K IN LOGISTIC EQUATION WAS DETERMINED empirically by GRAPHIC METHOD while parameters A and B were determined by LINEAR TRANSFORMATION OF LOGISTIC EQUATION.

SUBROUTINE VIMORT(I,X1,FX2,FX3,FX4)

GO TO [LIST OF GO TO STATEMENTS]

RETURN

1111 FX3=1.0/(1.0+EXP(10.42000-1.824072*FX2))
RETURN

31 FX4=FX3*ABS(FX3-1.0)*SQR(T(1.066667*FX2-5.776724)**2
1/30.914063))
RETURN

22 FX3=1.0/(1.0+EXP(10.0+272-1.764551*FX2))
RETURN

32 FX4=FX3*ABS(FX3-1.0)*SQR(T(1.43668**((1.047419*FX2-5.74616)**2
1/53.203998))
RETURN

23 FX3=1.0/(1.0+EXP(10.04344-1.639333*FX2))
RETURN

33 FX4=FX3*ABS(FX3-1.0)*SQR(T(1.43668**((1.047419*FX2-5.74616)**2
1/53.203998))
RETURN

24 FX3=1.0/(1.0+EXP(17.593563-1.109000*FX2))
RETURN

34 FX4=FX3*ABS(FX3-1.0)*SQR(T(1.61054**((1.047419*FX2-6.22438)**2
1/4.951374))
RETURN

25 FX3=1.0/(1.0+EXP(13.62194+1.805412*FX2))
RETURN

35 FX4=FX3*ABS(FX3-1.0)*SQR(T(1.71268**((1.071429*FX2-7.09921)**2
1/27.064171))
RETURN

26 FX3=1.0/(1.0+EXP(27.901957+3.151054*FX2))
RETURN

36 FX4=FX3*ABS(FX3-1.0)*SQR(T(1.906383**((1.033333*FX2-9.669981)**2
1/9.846137))
RETURN

111 FX3=1.000/(1.0+EXP(13.1138398+2.095524*FX2))
RETURN

211 FX3=1.000/(1.0+EXP(13.1138398+2.095524*FX2))
RETURN

110 FX3=0.694/(1.0+EXP(-11.139353+2.283949*FX2))
RETURN

210 FX4=FX3*ABS(FX3=0.694*0.694*1.071429*(1.0+FX2-5.551497)**2
28.264822))
RETURN

112 FX3=0.694/(1.0+EXP(-11.139353+2.283949*FX2))
RETURN

212 FX4=FX3*ABS(FX3=0.694*0.694*1.071429*(1.0+FX2-5.551497)**2
28.264822))
RETURN

122 FX3=0.694/(1.0+EXP(9.545506-1.01551*FX2))
RETURN

222 FX4=FX3*ABS(FX3=0.694*0.694*1.071429*(1.0+FX2-5.746172)**2
28.264822))
RETURN

126 FX3=0.592/(1.0+EXP(-8.318831+1.498302*FX2))
RETURN
DECLARE 2.0 VIMORT DATE = 32107

RETURN
226 FX3=ABS(FX3-0.591)/0.591*SQRT(1.629182*0.362632
1+FX2=6.04342)**2/35.76537)
RETURN
132 FX3=0.712/1.0+ EXP(17.49209*1.170548*FX2)
RETURN
232 FX3=ABS(FX3-0.712)/0.712*SQRT(0.783259*0.045455
1+FX2=6.353580)**2/30.496083)
RETURN
136 FX3=0.660/1.0+ EXP(-13.650186*2.39852*FX2)
RETURN
236 FX3=ABS(FX3-0.660)/0.660*SQRT(2.073403*0.476119
1+FX2=6.516632)**2/26.012885)
RETURN
142 FX3=0.743/1.0+ EXP(9.460840-1.391128*FX2)
RETURN
242 FX3=ABS(FX3-0.743)/0.743*SQRT(0.794291*0.047619
1+FX2=6.224839)**2/49.951822)
RETURN
146 FX3=0.730/1.0+ EXP(-4.678404+0.793601*FX2)
RETURN
246 FX3=ABS(FX3-0.730)/0.730*SQRT(0.363110*0.050000
1+FX2=6.390898)**2/30.369443)
RETURN
152 FX3=0.894/1.0+ EXP(16.340271-2.030765*FX2)
RETURN
252 FX3=ABS(FX3-0.894)/0.894*SQRT(0.880673*1.074129
1+FX2=7.099922)**2/27.064162)
RETURN
156 FX3=1.000/1.0+ EXP(-7.798048+1.358737*FX2)
RETURN
260 FX3=ABS(FX3-1.000)/1.000*SQRT(0.083333*0.03255
1+FX2=8.106626)**2/49.920425)
RETURN
162 FX3=1.000/1.0+ EXP(27.177853-3.058031*FX2)
RETURN
262 FX3=ABS(FX3-1.000)/1.000*SQRT(0.083333*0.03255
1+FX2=6.666998)**2/9.801092)
RETURN

END

RELEASE 2.0 MAIN DATE = 32107 14/58/28

C**** SUBROUTINE TRANFG CALCULATES NG. OF EGG PRODUCTION (600,
C COMMON LOG) AND NG. OF POLYHEDRA PRODUCED (599).
SUBROUTINE TRANFG (FX1, FX2, FX3)
GO TO (600, 599), XI1
900 FX3=EXP(6.6962-0.3525*FX2)
RETURN
599 FX3=1.0*FX2/100000000
RETURN
END
LITERATURE CITED


Tanada, Y. and J. W. Beardsley. 1957. Probable origin and dissemination of a polyhedrosis virus of an armyworm in Hawaii. J. Econ. Entomol. 50 (2) : 118 - 120.


