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A SYSTEMS APPROACH UTILIZING SIMULATION MODELING FOR THE MANAGEMENT OF THE LAWN ARMYWORM, SPODOPTERA MAURITIA ACRONYCTOIDES (GUENEE) (LEPIDOPTERA:NOCTUIDAE), WITH ITS NUCLEAR POLYHEDROSIS VIRUS

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A SYSTEMS APPROACH UTILIZING SIMULATION MODELING FOR THE MANAGEMENT OF

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

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by

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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
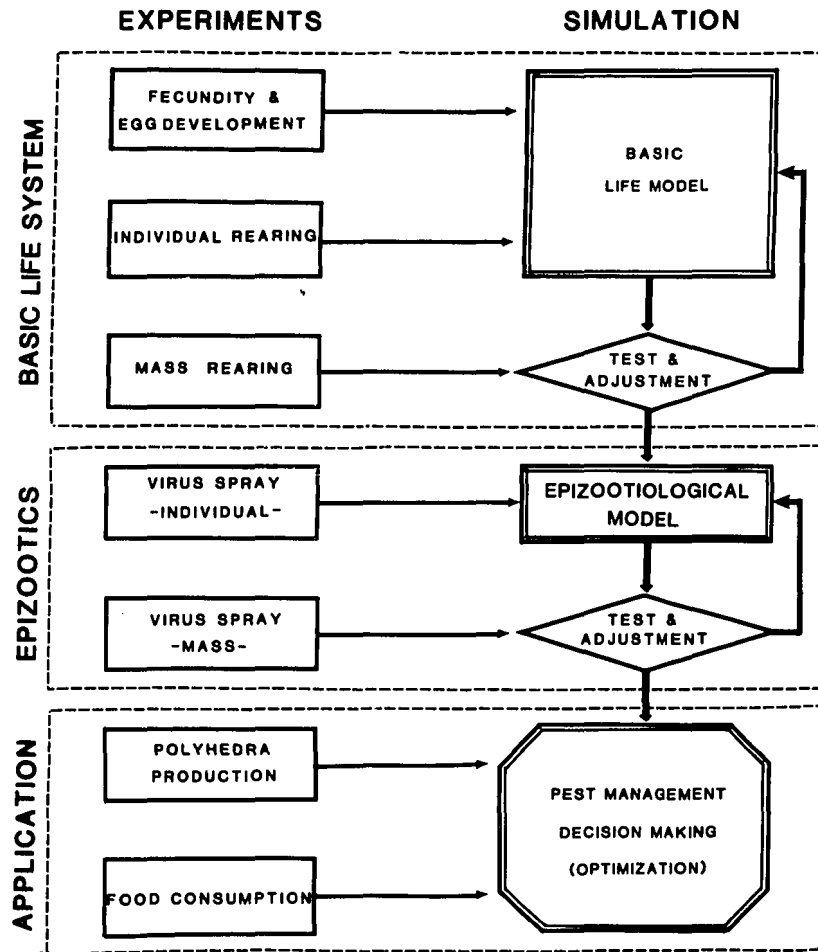
STUDY PROCESS

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 sytem, 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.

LITERATURE REVIEW

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 Pemberton (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 Borrelinavirus. 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 X 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 admininstered 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 LC_{50} of the
larva as 9.29 X 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 sytems 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 Bělerhádek (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:

$$C = Y * (X - A) \text{ --------------------- (1)}$$

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 unlinear 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) Bĕlehrádek'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 Pradhans'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:

$$1/Y = k/(1 + e^{a - b*x}) \text{\textemdash\textemdash\textemdash\textemdash\textemdash\textemdash} (2)$$

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 * 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 spp. 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 $\pm$ 0.266 grams) were sown in the 1 : 1 soil and vermiculite (No. 2) mixture per 800 cm^2 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 cm^3 of the mixture at approximately one month intervals.

Under green house 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 ^{o}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 intar 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 $^{\circ}$ 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 45cm 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 $^{\circ}$ 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 concentration of the stock suspension ranged from 5 X 10^9 to 2 X 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 ± 0.4 ml of the polyhedral suspension for·the first or second instar larvae, and 8.3 ± 0.6 ml for the older larvae. While spraying, the automizer 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 $^\circ$ 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 effect 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
vigrously 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 biolgical 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.

RESULTS, SIMULATION AND DISCUSSION

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
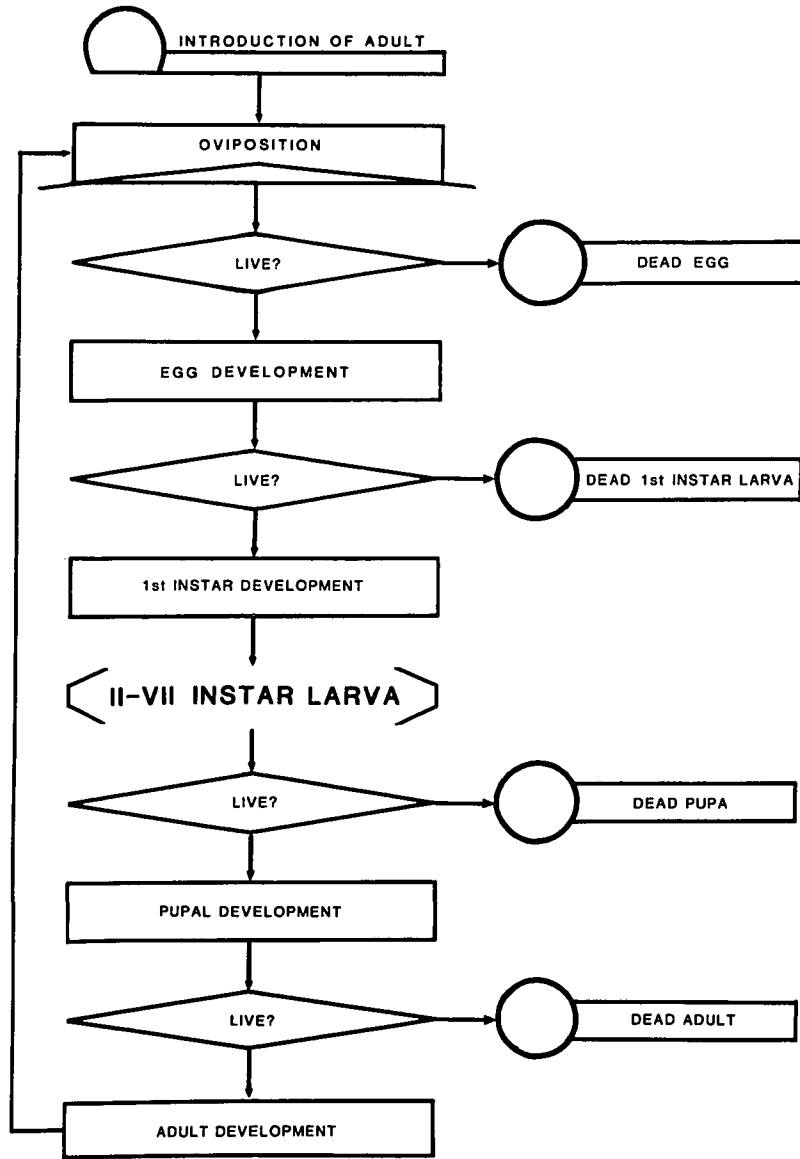
LIFE SYSTEM

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

TABLE 1

DAILY EGG PRODUCTION, UNDER LABORATORY CONDITIONS, BY A LAWN ARMYWORM
FEMALE AFTER EMERGENCE OR FROM INITIAL OVIPOSITION

	AFTER EMERGENCE				FROM INITIAL OVIPOSITION		
D A Y	PERCENT OF FEMALES OVIPOSITING	EGG PRODUCTION INDIVIDUAL (EGGS)	TOTAL* (%)	D A Y	PERCENT OF FEMALES OVIPOSITING	EGG PRODUCTION INDIVIDUAL (EGGS)	TOTAL* (%)
2	1.7	343 ± 249	0.0	1	100.0	486 ± 264	34.1
3	42.5	513 ± 242	15.5	2	94.5	395 ± 175	26.2
4	78.1	450 ± 222	25.0	3	90.4	280 ± 148	17.8
5	91.8	351 ± 218	22.9	4	76.7	180 ± 106	9.7
6	84.9	261 ± 157	15.8	5	63.0	141 ± 88	6.2
7	73.8	174 ± 106	9.2	6	43.8	110 ± 55	3.4
8	57.5	128 ± 84	5.2	7	30.1	86 ± 56	1.8
9	35.6	103 ± 57	2.6	8	11.0	58 ± 39	0.4
10	21.9	85 ± 63	1.3	9	6.9	45 ± 54	0.2
11	11.0	59 ± 55	0.5	10	1.4	13	<0.1
12	4.1	86 ± 44	0.3	11	-	-	-
13	2.7	55	0.1	12	-	-	-

* 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 oviposting 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

DAYS FROM INITIAL OVIPOSITION
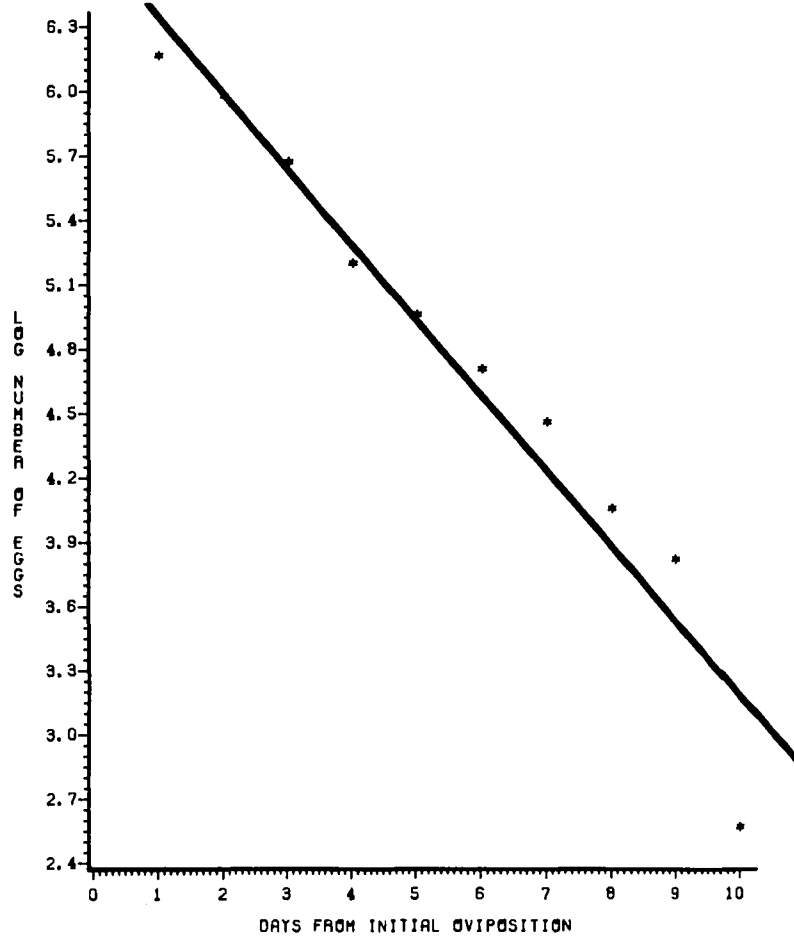
TABLE 2

PERCENT FREQUENCIES OF THE LAWN ARMYWORM FEMALES OVIPOSITING DURING
VARIOUS PREOVIPOSITION AND OVIPOSITION PERIOD COMBINATIONS

PREOVI-POSITION PERIOD		OVIPOSITION PERIOD (IN DAYS)										
		2	3	4	5	6	7	8	9	10	TOTAL	CUMU
	2	0.0	0.0	0.0	0.0	3.4	2.2	2.2	0.0	0.0	7.8	7.8
	3	0.0	2.2	5.6	7.8	7.8	4.4	2.2	2.2	0.0	32.2	40.0
D A Y S	4	3.4	2.2	10.0	7.8	4.4	6.7	2.2	2.2	0.0	38.9	78.9
	5	1.1	2.3	2.2	3.3	1.1	1.1	1.1	1.1	1.1	14.4	93.3
	6	2.2	1.1	0.0	1.1	0.0	1.2	0.0	0.0	0.0	5.6	98.9
	7	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	1.1	100.0
TOTAL		6.7	7.8	17.8	20.0	16.7	15.6	8.8	5.5	1.1	100.0	
CUMU		6.7	14.5	32.3	52.3	69.0	84.6	93.4	98.9	99.9	100.0	

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
preovipostion 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 $\pm$ 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 $\pm$ 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 preovi-
and ovi- position 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 oviositon. 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

DEAD FEMALE
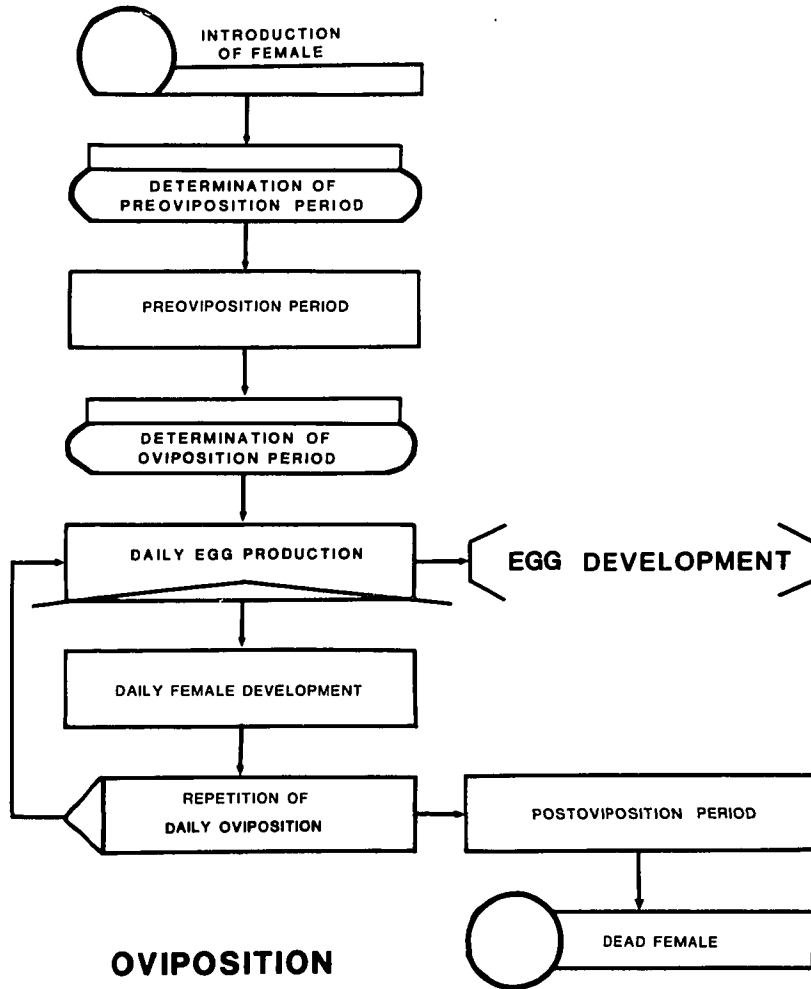
OVIPOSITION

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 preovi- and ovi- position 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 $^{\circ}$ 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 $^{\circ}$ 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

WITHIN LIFE STAGE

| TEMP | | LIFE STAGE | | | | | | | |
| | | | | LARVA | | | | | |
(° C)	EGG	I	II	III	IV	V	VI	VII	PUPA
15	27.8	83.2	86.4	99.9	99.9	97.4	89.2	51.5	-
20	46.0	90.0	99.9	99.9	99.9	92.6	96.0	91.7	86.4
25	89.5	93.3	99.9	92.9	99.9	99.9	96.2	96.0	91.7
30	87.5	93.3	99.9	99.9	92.9	96.2	92.0	95.7	90.9
35	25.8	95.2	98.3	99.9	98.3	98.3	98.3	92.9	71.2

CUMULATIVE

15	-	83.2	71.7	71.7	71.7	69.8	62.3	32.1	-
20	-	90.0	90.0	90.0	90.0	83.3	80.0	73.3	63.3
25	-	93.3	93.3	86.7	86.7	86.7	83.3	80.0	73.3
30	-	93.3	93.3	93.3	86.7	83.3	76.7	73.3	66.7
35	-	95.2	93.7	93.7	92.1	90.5	88.9	82.5	58.7

AVERAGE (20 - 30 ° C)

| WITHIN | 88.5 | 93.3 | 99.9 | 97.6 | 97.6 | 96.3 | 94.7 | 94.4 | 89.7 |
| CUMU | - | 92.2 | 92.2 | 91.1 | 91.1 | 84.4 | 80.0 | 75.5 | 67.8 |

At 20 $^\circ$ C, less than half of the eggs hatched. Because the survival rates at 25 and 30 $^\circ$ 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 $^\circ$ C, the survival rates were generally over 90 %. The survival rates at the first, second and sixth instar larval stages at 15 $^\circ$ C were relatively lower than those at other temperatures.

The lowest survival rate was observed in the last instar at 15 $^\circ$ 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 $^\circ$ C. Only 32.1 % of the test population survived at the end of the larval period at 15 $^\circ$ C, while 73.3, 80.0, 73.3 and 82.5 % survived at temperatures from 20 to 35 $^\circ$ C.

For the pupal stage the emergence was used to establish the survival rate. Aside from the 100 % mortality at 15 $^\circ$ C, the emergence rate was lowest at 35 $^\circ$ C with 71.2 % followed by 86.4 % at 20 $^\circ$ C. The emergence rates at medium temperatures were higher; 91.7 and 90.9 % at 25 and 30 $^\circ$ 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 $^\circ$ C, respectively. From cumulative survival rates, it was observed that the lawn armyworm population has the highest survival during the immature stage around 25 $^\circ$ C, followed by 30 and 20 $^\circ$ C.

In this study for modeling, it was assumed that the temperatures of 20, 25 and 30 $^\circ$ 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 4

DEVELOPMENTAL PERIOD (IN DAYS) OF THE LAWN ARMYWORM AT EACH IMMATURE
LIFE STAGE AT DIFFERENT TEMPERATURES

TEMP (° c)	LIFE STAGE								
	EGG	LARVA							PUPA
		I	II	III	IV	V	VI	VII	
15	15.10	11.00	8.08	9.05	10.00	11.11	11.97	46.94	-
20	6.50	5.07	4.26	4.96	5.19	5.64	5.92	17.23	22.95
25	4.30	3.25	2.46	2.23	2.42	2.77	3.72	6.88	12.23
30	2.93	1.96	1.75	1.32	2.31	2.08	3.09	4.00	6.50
35	2.38	1.93	1.05	1.00	1.12	1.26	1.82	2.52	6.16

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 $1/Y_i$:

$$X_i = A + C * 1/Y_i$$

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: $X_i' = A' + C' * 1/Y_i$. 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:

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

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

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

$$A' + 1/n*\sum_{i=1}^{n}(1/Y_i) * C' = 1/n *\sum_{i=1}^{n}X_i \quad \text{--------} \quad (5)$$

$$\sum_{i=1}^{n}(1/Y_i) * A' + \sum_{i=1}^{n}(1/Y_i^2) * C' = \sum_{i=1}^{n}(X_i/Y_i) \quad \text{--------} \quad (6)$$

In this study the temperatures between 20 - 30 $^\circ$ 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 $^\circ$ 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 $^\circ$ C for the egg, each larval instar and pupal stage, respectively. The egg had the lowest threshold temperature, 10.7 $^\circ$ C, while the last instar had the highest threshold temperature at 17.4 $^\circ$ C.

TABLE 5

MINIMUM THRESHOLD TEMPERATURES (ALPHA VALUES) AND THE TOTAL EFFECTIVE
DAY-DEGREES REQUIRED TO COMPLETE EACH LIFE STAGE OF THE LAWN ARMYWORM
IMMATURES

LIFE STAGE	THRESHOLD ($^\circ$ C)	TOTAL EFFECTIVE DAY-DEGREES
EGG	10.7	59.5 ± 10.0
I	13.7	33.3 ± 4.3
L II	14.4	26.5 ± 4.9
A III	13.5	28.8 ± 5.2
R IV	13.6	32.5 ± 7.0
V V	13.3	34.5 ± 8.4
A VI	12.2	43.9 ± 9.0
VII	17.4	50.8 ± 15.5
PUPA	15.1	110.4 ± 15.6

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:

$$e^{(a - b * X)} = k/y - 1$$

$$\log_e(k/y - 1) = a - b * X \quad \text{------------------} \quad (7)$$

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 $Z(y) = \log_e(k/y -1)$. 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

LIFE STAGE	k**	a	b
EGG	0.44	4.783418	0.202023
I	0.53	6.113860	0.285421
L II	1.00	5.721318	0.226826
A III	1.00	7.251770	0.299121
R IV	1.00	5.320467	0.195736
V V	0.84	5.847562	0.228837
A VI	0.57	5.569131	2.232723
VII	0.42	7.254417	0.271231
PUPA	0.17	6.538893	0.282580

* $y = k/\{1 + e^{(a - b*X)}\}$, 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 varience 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 $^\circ$ C. For both temperatures, the maximum was observed in October (26.6 $^\circ$ C for the average temperature and 26.2 $^\circ$ C for the mean temperature), and the minimum was observed in February (23.3 $^\circ$ C for average temperature and 22.9 $^\circ$ 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 $^\circ$ C, and lowest in March with 25.3 $^\circ$ C. The highest of daily minimum average was shown in September and October with 24.1 $^\circ$ C, while the lowest was in February with 20.3 $^\circ$ C. The ranges of the daily maximum and minimum averages

TABLE 7

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

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

*Mean of temperatures observed at every two hour intervals.

**Mean of maximum and minimum temperatures.

TABLE 8

DAILY AMBIENT TEMPERATURES (^{o} C) ON THE SEASONAL BASIS AT THE MANOA AREA
FROM SEPTEMBER 18, 1979 TO SEPTEMBER 17, 1980

SEASON	MEAN*	MAXIMUM	MINIMUM	AVERAGE**
MAR. - MAY.	23.7 ± 0.97	26.2 ± 1.48	22.1 ± 0.81	24.2 ± 1.02
JUNE. - AUG.	25.6 ± 0.68	28.3 ± 1.16	23.9 ± 0.71	26.1 ± 0.78
SEPT. - NOV.	25.6 ± 1.16	28.5 ± 1.50	23.6 ± 1.31	26.0 ± 1.21
DEC. - FEB.	23.3 ± 1.39	26.3 ± 1.74	21.0 ± 1.59	23.6 ± 1.41
YEAR	24.6 ± 1.50	27.3 ± 1.81	22.6 ± 1.65	25.0 ± 1.57

*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 $^{\circ}$ 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 $^{\circ}$ C and the average temperature of 23.6 - 24.2 $^{\circ}$ C, and 2) the higher "Summer-Fall" type with the mean temperature of 25.6 $^{\circ}$ C and the average temperature of 26.0 - 26.1 $^{\circ}$ 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 $^{\circ}$ C, the difference between different types were more than 2 $^{\circ}$ 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 $^{\circ}$ C respectively, while the maximum and minimum was 27.3 and 22.6 $^{\circ}$ 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
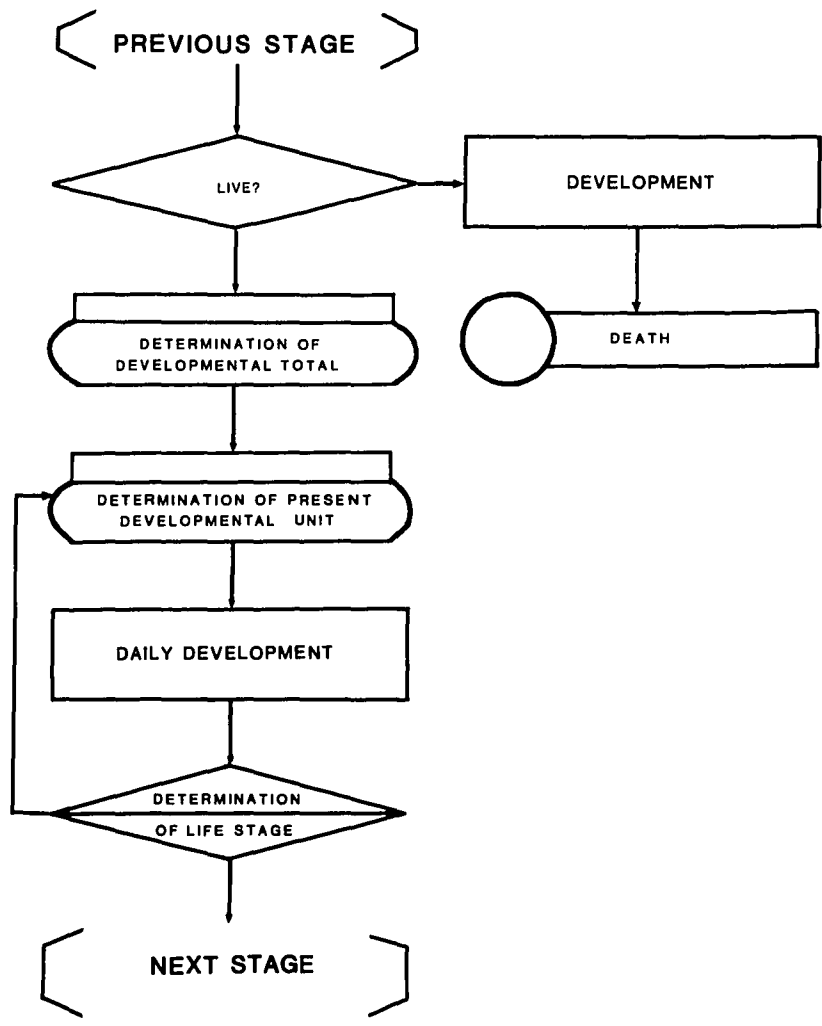
POPULATION DEVELOPMENT

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 developmetal 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:

$$W = (X/Y - 1) * Z$$

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 $^{\circ}$ C) (Table 8), 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
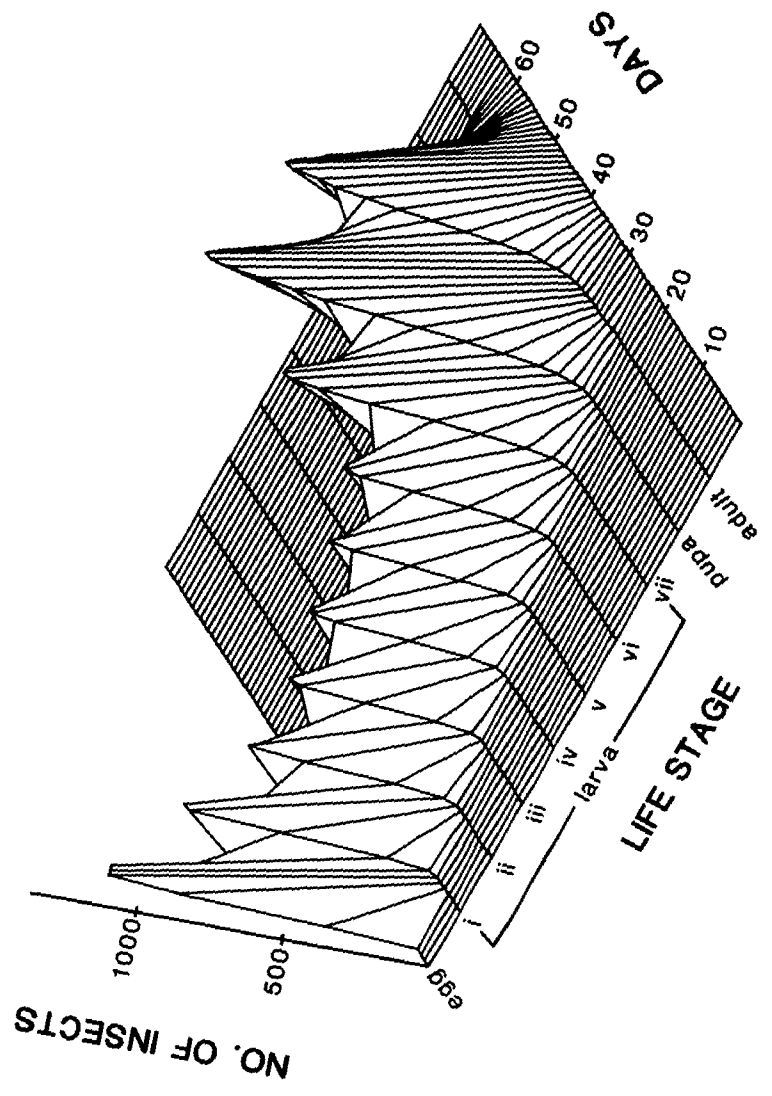
18, 21, 24 and 28 days after introduction of the female respectively for the first to seventh instar. The pupal population peaked on the 38th day, and the adult population peaked on the 47th day. It took approximately 70 days for all of the armyworm to complete development.

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 occured 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 adundance 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

SEPTEMBER 18, 1979

(MODEL)

(ACTUAL)

ABUNDANCE (%)

100

50

DAYS

10

20

30

40

LIFE STAGE

larva
vii
pupa
adult

larva
vii
pupa
adult

- 82 -
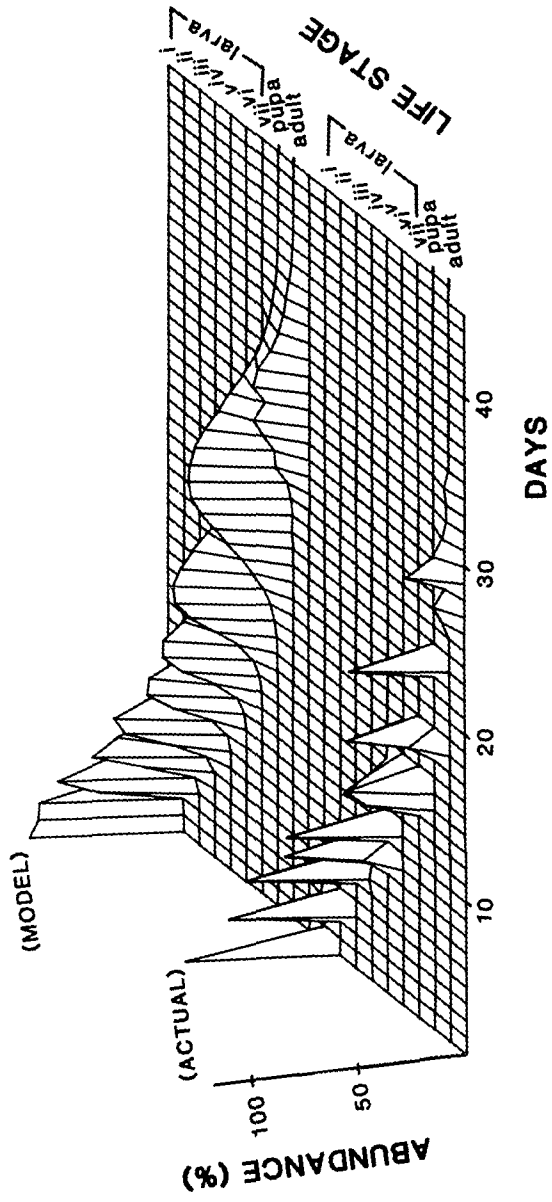
Figure 8. -- Comparison of the actual and calculated data on population development (percent abundance) of the lawn armyworm when the first instar larvae were introduced into a closed and favorable environmental system as the initial population (100 percent) on October 15, 1979

ABUNDANCE (%)

(ACTUAL)

(MODEL)

OCTOBER 15, 1979

DAYS

LIFE STAGE
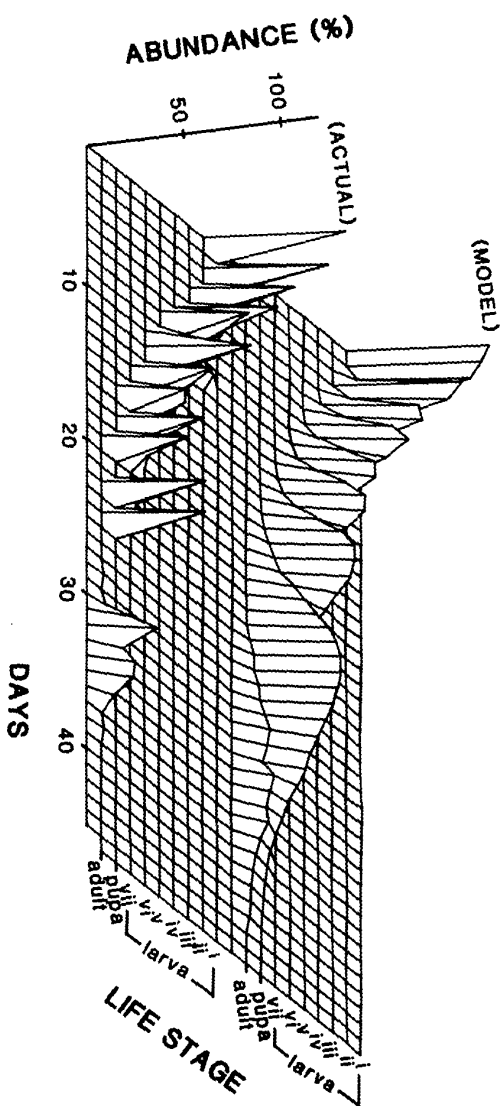
Figure 9. -- Comparison of the actual and calculated data on population
development (percent abundance) of the lawn armyworm when the first
instar larvae were introduced into a closed and favorable environmental
system as the initial population (100 percent) on December 22, 1979

DECEMBER 22, 1979
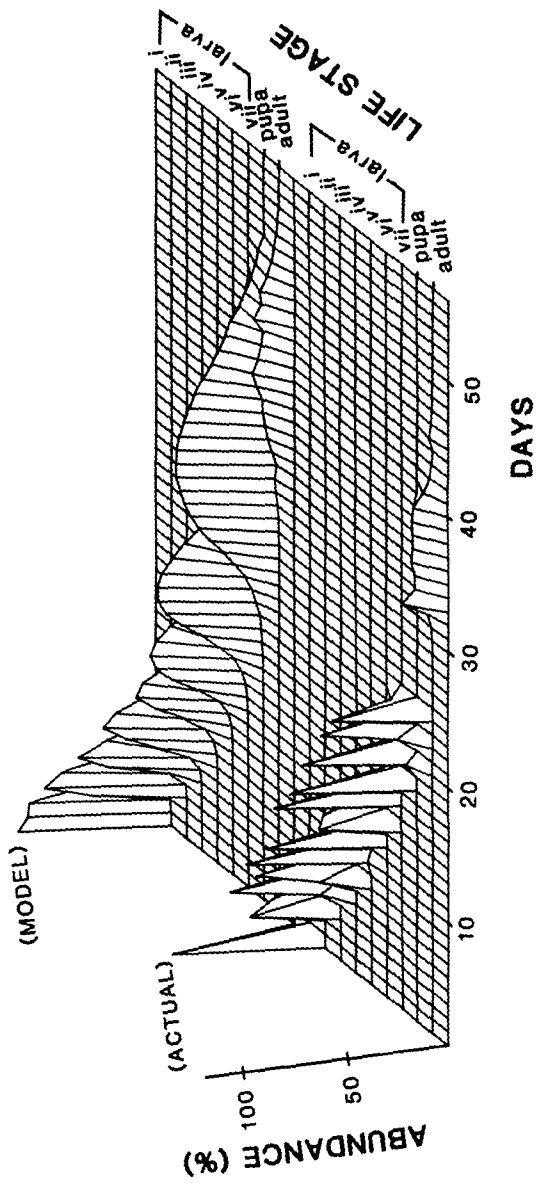
TABLE 9

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)

DAYS AFTER INFESTATION	25	27	29	31	33	35	37	TOTAL
ACTUAL	3	10	29	5	3	.	.	51
THERMAL	2	3	14	21	23	9	1	73
LOGISTIC	.	17	33	18	3	.	.	71

(INFESTED ON OCTOBER 15, 1979)

DAYS AFTER INFESTATION	26	28	30	32	34	36	38	TOTAL
ACTUAL	.	1	12	27	22	4	1	67
THERMAL	3	5	12	18	16	13	4	71
LOGISTIC	2	18	26	14	6	1	.	67

(INFESTED ON DECEMBER 22, 1979)

DAYS AFTER INFESTATION	30	32	34	36	38	40	42	44	>46	TOTAL
ACTUAL	.	12	12	14	14	10	2	1	.	63
THERMAL	1	1	2	3	10	14	18	11	11	71
LOGISTIC	.	.	1	10	14	23	8	10	4	70

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

STATISTICAL ANALYSIS SYSTEM
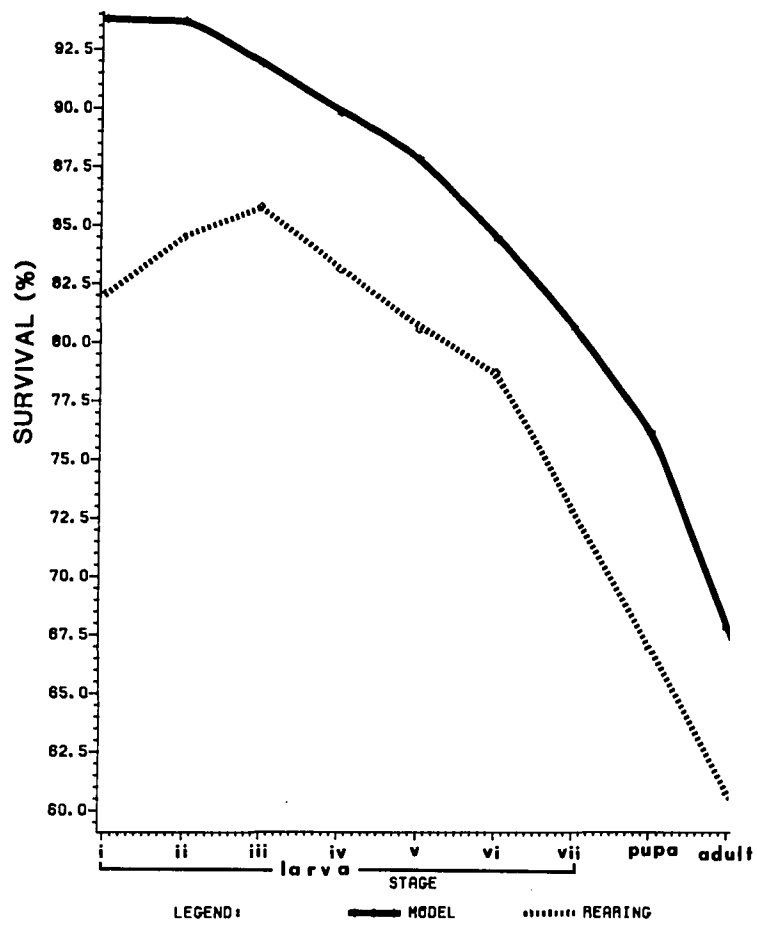
B. Epizootics

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 $2.3 \times 10^3 - 5.2 \times 10^7$, $3.3 \times 10^3 - 8.1 \times 10^7$, $1.3 \times 10^3 - 9.1 \times 10^8$, $4.3 \times 10^3 - 6.3 \times 10^9$, $2.3 \times 10^5 - 7.8 \times 10^9$ 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 (LC_{50}; NUMBER OF POLYHEDRA/100 CM^2) OF NPV
IN THE LAWN ARMYWORM LARVAE FROM THE FIRST TO SIXTH INSTAR

INSTAR	LC_{50}	LOWER LIMIT	UPPER LIMIT	RATE OF INCREASE	
				FROM FIRST INSTAR	BETWEEN STAGE
I	3.47×10^5	2.01×10^5	5.78×10^5	1.00	1.00
II	5.13×10^5	3.24×10^5	8.03×10^5	1.48	1.48
III	1.11×10^6	5.09×10^5	1.99×10^6	3.20	2.26
IV	5.20×10^6	2.89×10^6	9.72×10^6	14.99	4.68
V	4.25×10^7	2.03×10^7	7.60×10^7	122.48	8.17
VI	5.95×10^8	3.62×10^8	8.83×10^8	1714.70	14.00

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 X 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 cm^2) were sprayed on each instar of the lawn armyworm larvae (younger instars). A. First instar, B. Second instar, C. Third instar

STAGE-SPECIFIC MORTALITY
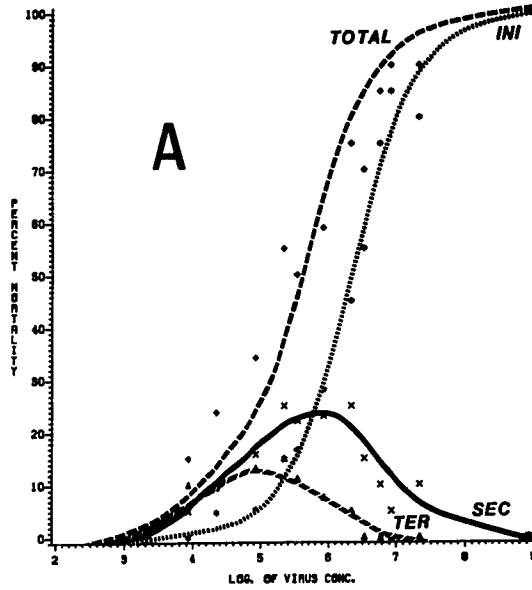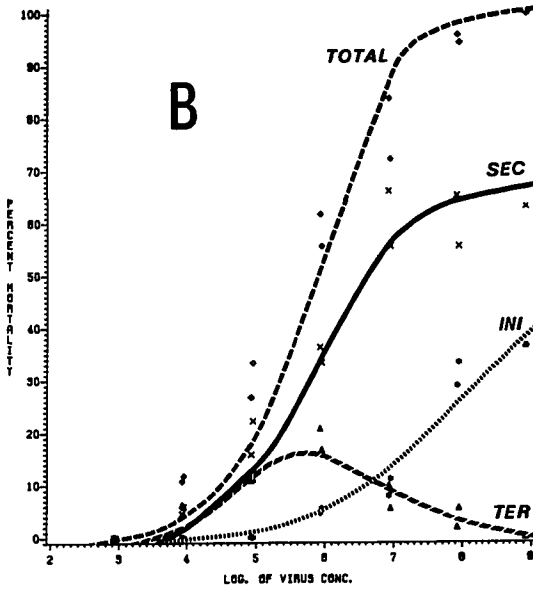
STAGE-SPECIFIC MORTALITY

STAGE-SPECIFIC MORTALITY
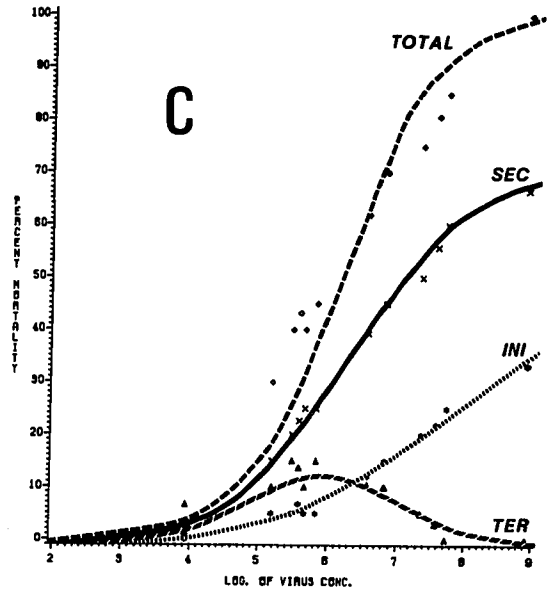
Figure 11 (continued). -- The total and stage-specific mortalities when different virus concentrations (common logarithm of number of polyhedra/ 100 cm^2) were sprayed on each instar of the lawn armyworm larvae (older instars). D. Fourth instar, E. Fifth instar, F. Sixth instar

STAGE–SPECIFIC MORTALITY
INSTAR=4
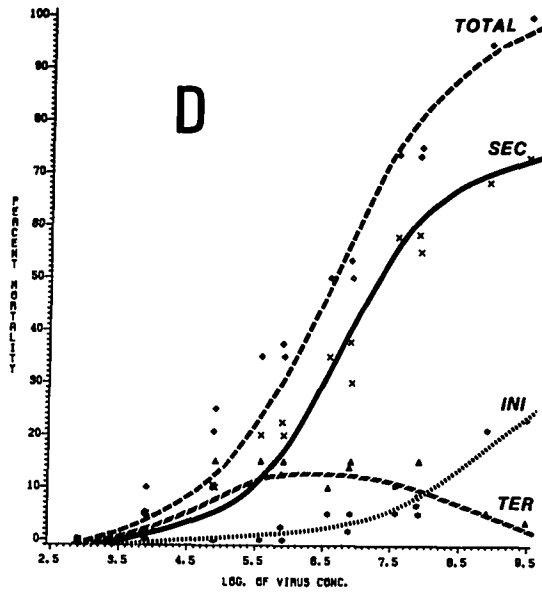
STAGE–SPECIFIC MORTALITY
INSTAR=5
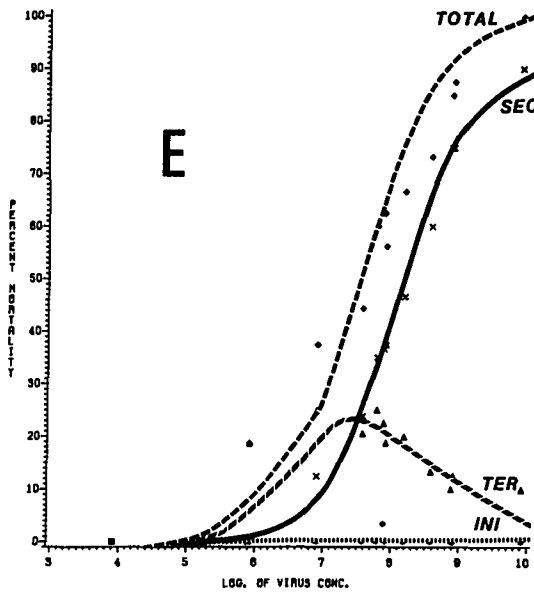
STAGE–SPECIFIC MORTALITY
INSTAR=6
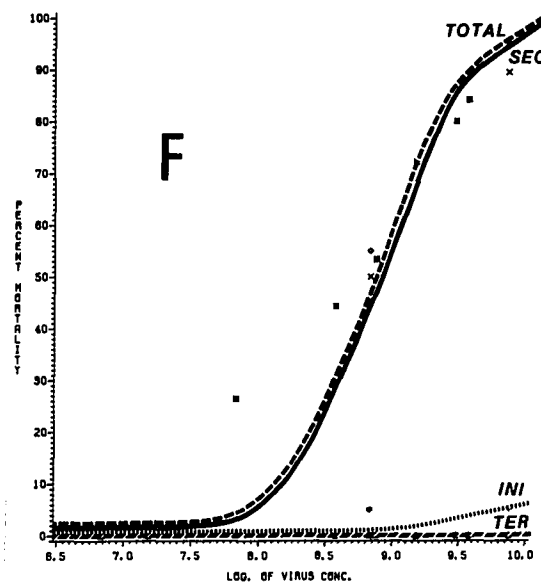
Figure 12. -- The proportion of the stage-specific mortality to the total mortality at each infection stage when different virus concentrations (common logarithm of number of polyhedra/100 cm^2) were sprayed on each instar of the lawn armyworm larvae (younger instars).
A. First instar, B. Second instar, C. Third instar

MORTALITY PROPORTION
INSTAR=1

A

MORTALITY PROPORTION
INSTAR=2

B

MORTALITY PROPORTION
INSTAR=3

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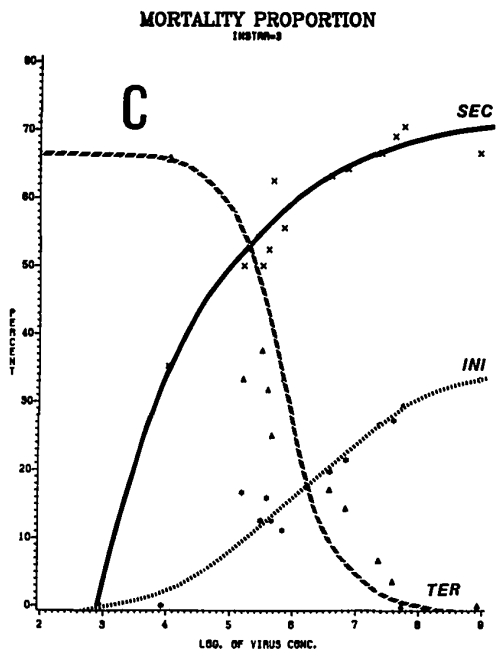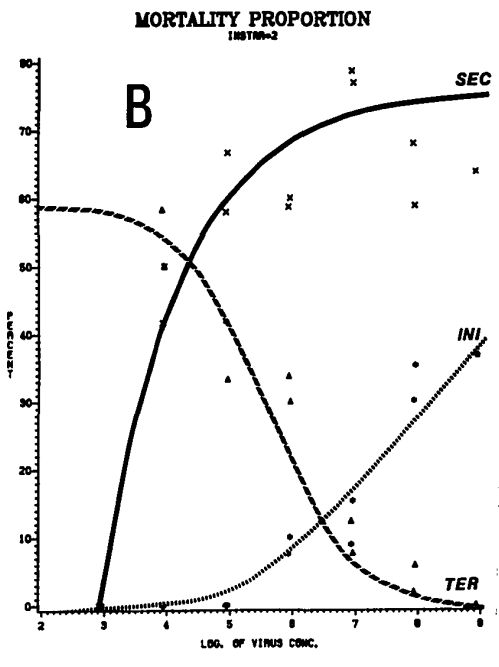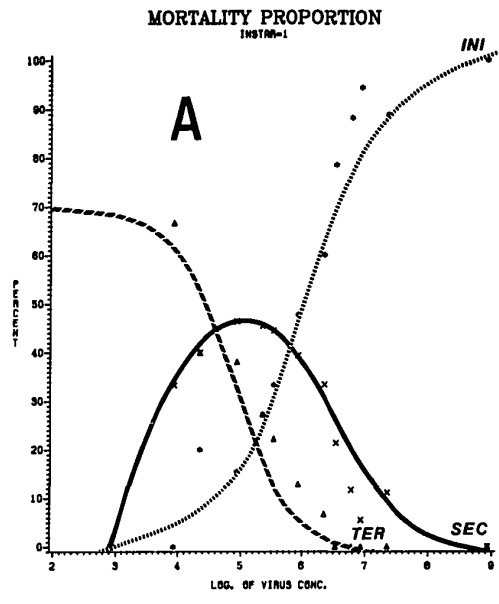
Figure 12 (continued). -- The proportion of the stage-specific mortality to the total mortality at each infection stage when different virus concentrations (common logarithm of number of polyhedra/100 cm^2) were sprayed on each instar of the lawn armyworm larvae (older instars).
           D. Fourth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

MORTALITY PROPORTION
INSTAR-4
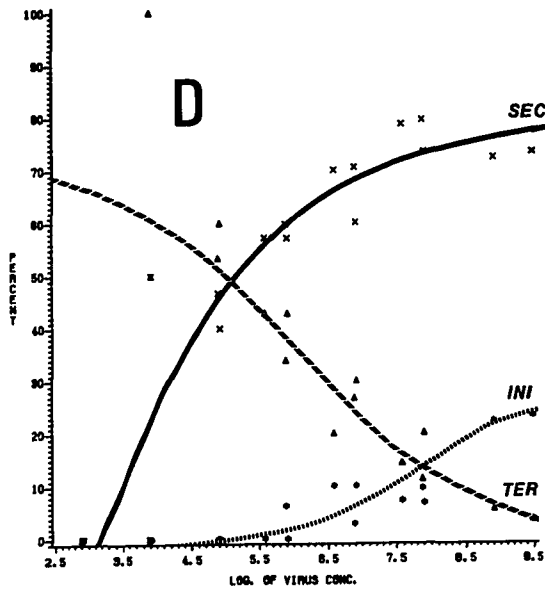
MORTALITY PROPORTION
INSTAR-5
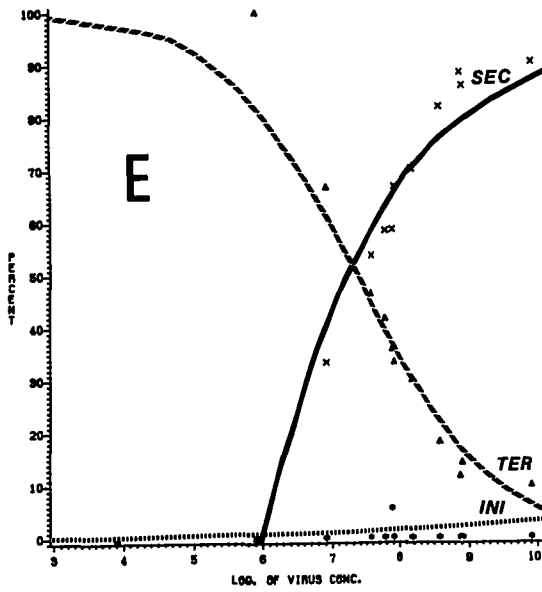
MORTALITY PROPORTION
INSTAR-6
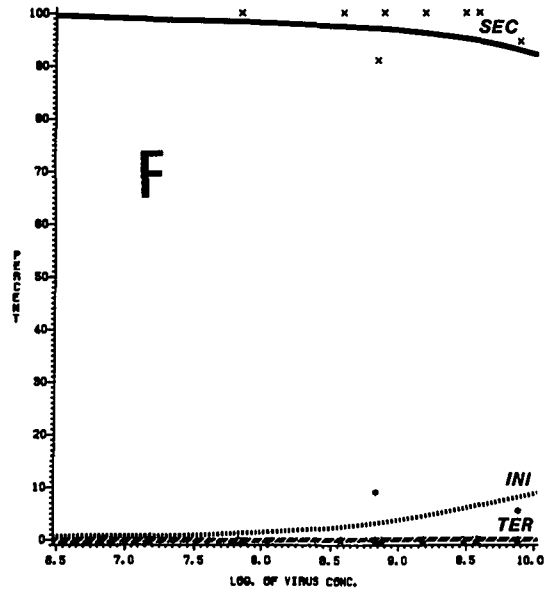
termed, initial, secondary or tertiary mortality. For the sixth instar

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 X 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 X 10^4 and 5.65 X 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 {relative mortality; (stage-specific mortality)/(total mortality) X 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 11

ESTIMATED PARAMETERS IN THE ASYMPTOTIC EQUATION* TO DETERMINE THE
MORTALITY PROPORTION OF THE SECONDARY INFECTION STAGE OF THE LAWN
ARMYWORM LARVAE SPRAYED WITH DIFFERENT NPV CONCENTRATIONS (NUMBER OF
POLYHEDRA/100 CM^2)

INSTARS	A	B	C
II	0.756	7.3160	0.7784
III	0.731	3.4669	0.5344
IV	0.802	4.2605	0.5176
V	0.941	38.1337	0.6181

* $y' = A - B * e^{-C*x}$, where y' is mortality proportion, x is
logarithm (common) of virus concentration (number of polyhedra/100 cm^2),
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, $y' = k'/\{1 + e^{(a' - b'*x')}\}$, 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 CM^2)

(YOUNGER LARVAE)

(FIRST INSTAR)

STAGE	M/P**	k'***	a'	b'	r^2
TOTAL	M	1.000	10.220100	-1.824072	.903
INTITIAL	M	1.000	13.318398	-2.095524	.955
TERTIARY	P	0.694	-11.139353	2.283949	.792

(SECOND INSTAR)

TOTAL	M	1.00	10.184272	1.764551	.854
SECONDARY	M	0.669	9.545506	1.615561	.876
TERTIARY	P	0.591	-8.318631	-1.498302	.744

(THIRD INSTAR)

TOTAL	M	1.000	10.193414	1.639333	.865
SECONDARY	M	0.712	7.449209	1.170588	.770
TERTIARY	P	0.666	-13.650186	-2.338851	.783

* $y' = k'/\{1 + e^{(a' - b'*x')}\}$, 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 cm^2),
k' is aymptote of the logistic curve, and a' and b' are constants.

** M represents that the calcualted 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 CM^2)

(OLDER LARVAE)

(FOURTH INSTAR)

STAGE	M/P	k'	a'	b'	r^2
TOTAL	M	1.000	7.593563	1.146190	.850
SECONDARY	M	0.743	7.449209	1.170588	.864
TERTIARY	P	0.730	-4.679671	0.783778	.783

(FIFTH INSTAR)

STAGE	M/P	k'	a'	b'	r^2
TOTAL	M	1.000	13.621614	1.805412	.912
SECONDARY	M	0.894	16.340271	2.030765	.914
TERTIARY	P	1.000	-15.894713	-2.020251	.742

(SIXTH INSTAR)

STAGE	M/P	k'	a'	b'	r^2
TOTAL	M	1.000	27.901957	3.151054	.910
SECONDARY	P	1.000	27.177353	3.058661	.898

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 occurr. 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 CM^2)

VIRUS CONCENTRATION	INSTAR					
	I	II	III	IV	V	VI
$> 10^5$	8.57	7.90	-	10.63	-	-
$10^5 - 10^6$	6.98	7.29	9.64	9.69	13.33	-
$10^6 - 10^7$	6.34	6.81	8.35	8.92	11.00	-
$10^7 - 10^8$	4.39	6.16	7.20	8.26	10.07	9.80
$10^8 - 10^9$	5.40	-	-	6.89	8.12	9.18
$10^9 - 10^{10}$	-	-	-	-	-	8.61

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

PREVIOUS STAGE

LIVE?

DEATH

DETERMINATION OF SPRAY TIME

DETERMINATION OF VIRUS CONCENTRATION

DEATH

LARVAL DEVELOPMENT

INFECTED?

DISEASE DEVELOPMENT

NEXT STAGE

KILLED?

DISEASE DEVELOPMENT

DEATH

KILLED?

DEATH

DISEASE DEVELOPMENT

NPV SPRAY
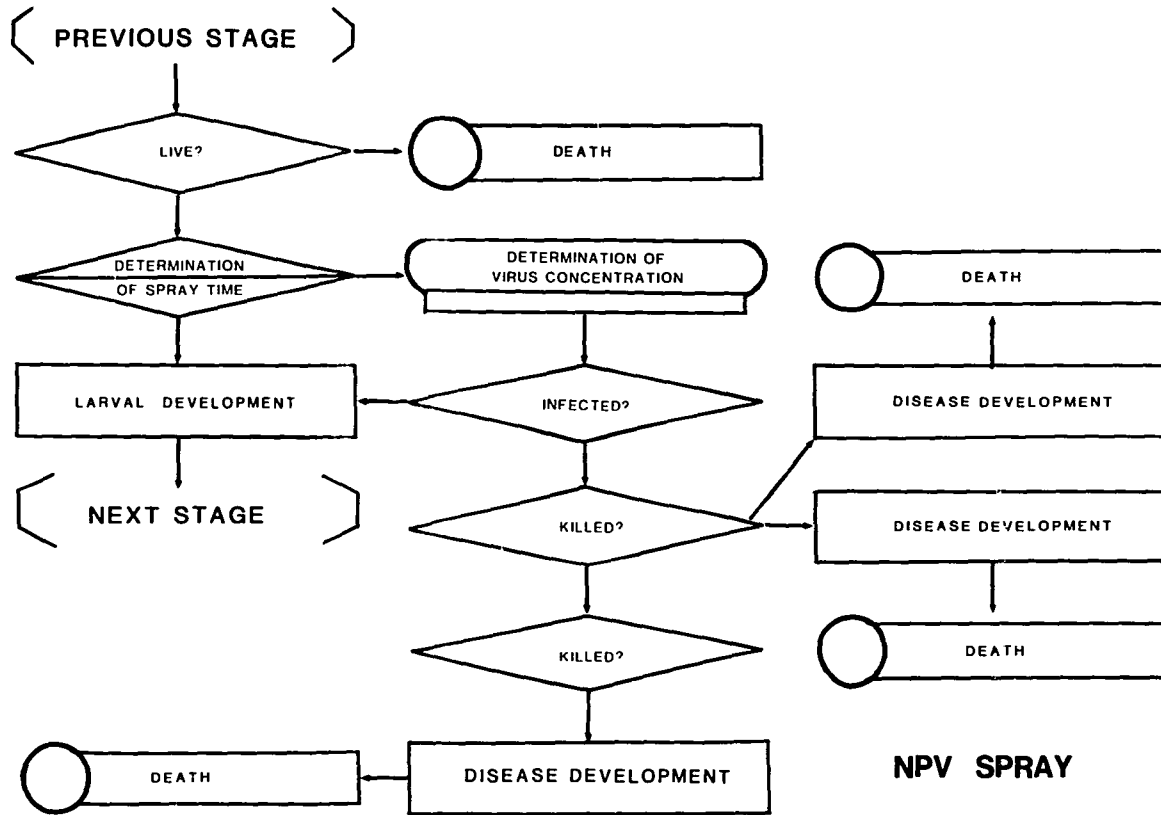
whether the virus will be sprayed or not--is made at the next "test" and "savevalue" blocks. Spray time was determined by certain decision criteria in the "test" block, e. g., host density, control schedule, etc.. If the entering transaction was sprayed, a level of virus concentration was assigned by 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 criteron. 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

September 10, 1980

Virus Concentration
(POLY/100 cm²)

ABUNDANCE (%)

DAYS

INSTARS

(MODEL)
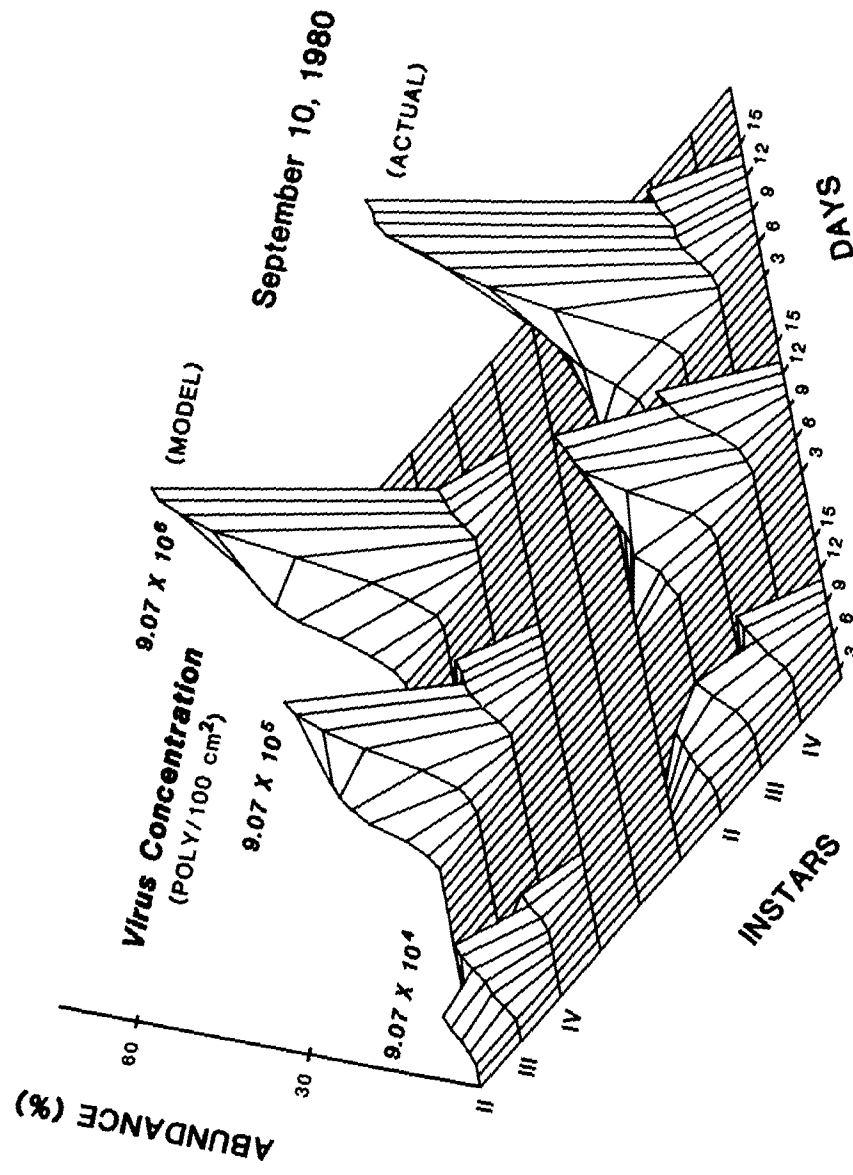
(ACTUAL)

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
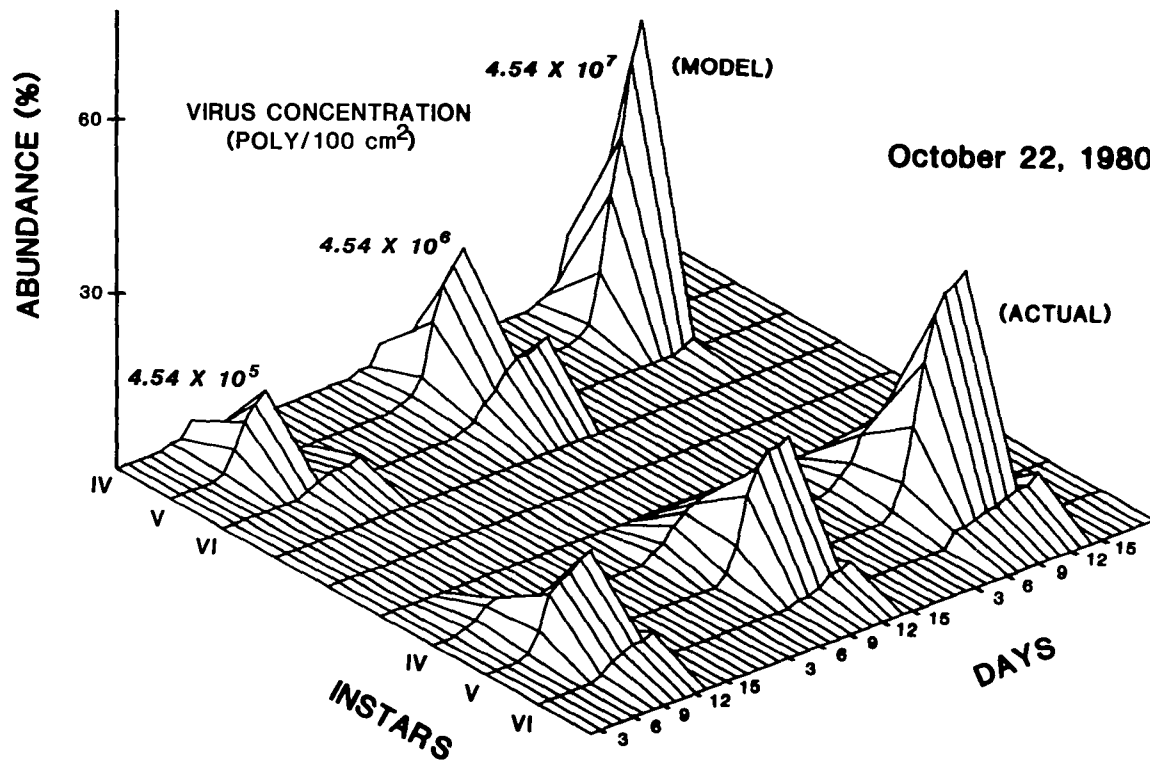
Figure 16. — Comparison of the actual and calculated data on cadaver
abundance (in percent) when different virus concentrations were sprayed
on the fifth instar larvae on December 30, 1980

ABUNDANCE (%)

90

60

30

Virus Concentration
(POLY/100 cm)

8.16 X 10⁸   (MODEL)

December 30, 1980

8.16 X 10⁷

8.16 X 10⁶

(ACTUAL)

V
VI
VII

INSTARS

V
VI
VII

3 6 9 12 15

3 6 9 12 15

3 6 9 12 15

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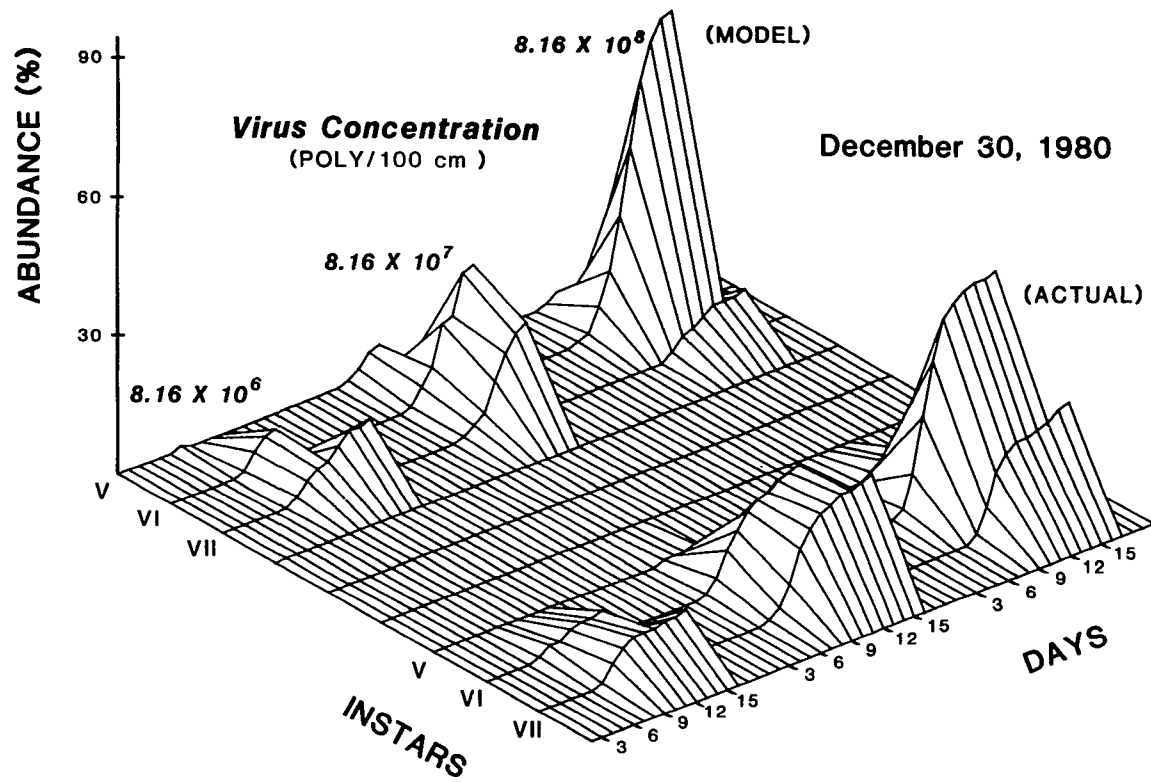
infection stage--seventh instar--occupied the largest proportion of the
total mortality for both actual and calculated data. At the
concentration of 8.16 X 10^7 polyhedra/100 cm^2 for the same instar, both
the secondary and tertiary infection stages appeared important to the
total mortality.

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

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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

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

* 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

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Figure 17. -- Daily feeding amount (fresh weight of Bermuda grass in grams) of the lawn armyworm progenies produced by a single female

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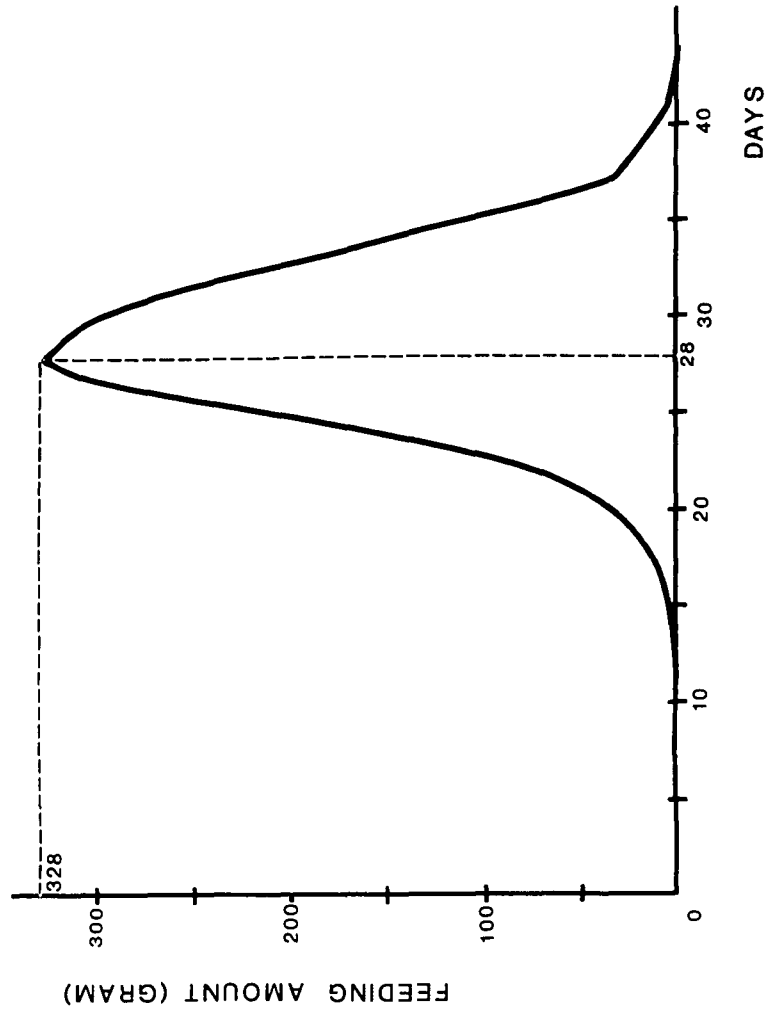
7 X 7 X 7 cm^3 was 4.2 mg, 3.4 kg represented a lawn about 400 m^2 area with grass 7 cm tall.

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 10^7, and 8.16 X 10^8 polyhedra per 100 cm^2 of lawn surface was similar. This may be because, even though the total mortality was higher at the 8.16 X 10^8 polyhedra

TABLE 15

NUMBER OF POLYHEDRA RECOVERED FROM A CADAVER OF A LAWN ARMYWORM LARVA
KILLED BY NPV

LARVAL STAGES	NUMBER OF POLYHEDRA PER CADAVER
I	$1.11 \times 10^6 \pm 5.62 \times 10^5$
II	$6.40 \times 10^6 \pm 2.92 \times 10^6$
III	$2.30 \times 10^7 \pm 1.75 \times 10^6$
IV	$1.12 \times 10^8 \pm 6.05 \times 10^7$
V	$5.15 \times 10^8 \pm 2.65 \times 10^8$
VI	$1.55 \times 10^9 \pm 8.37 \times 10^8$
VII	$4.61 \times 10^9 \pm 1.98 \times 10^9$

Figure 18. -- Cumulative virus production (number of polyhedra, x 10^9) from the lawn armyworm population when different virus concentrations were sprayed on the second and fifth instar larvae
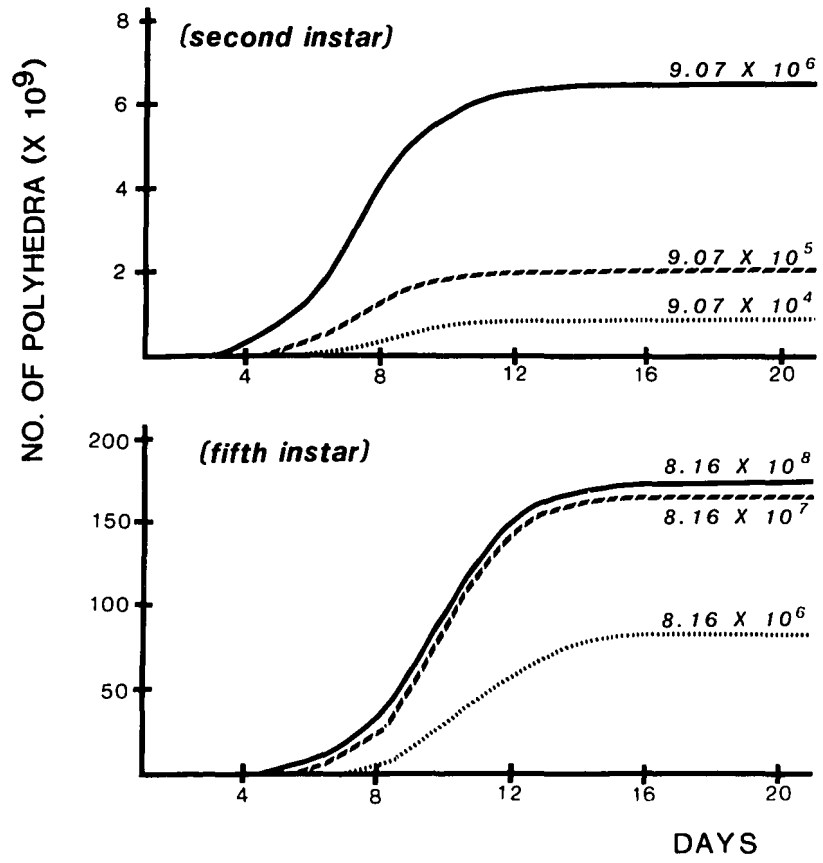
per 100 cm^2, a large proportion of the infected larval population died
at the secondary infection stage; while, for 8.16 X 10^7 per 100 cm^2, a
large number of larvae died at the tertiary infection stage--which has
more polyhedra recovery per cadaver.

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 10^7, 4.54 X 10^6 and 4.54 X 10^5
polyhedra per 100 cm^2 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
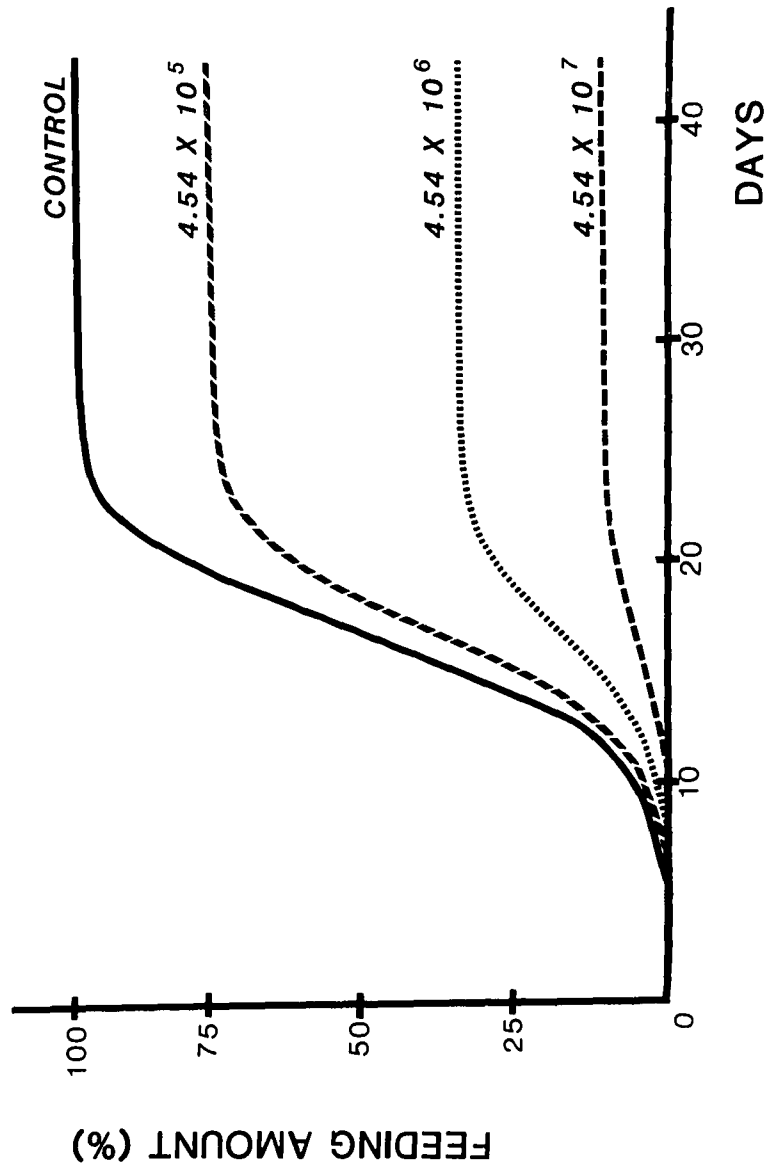
time and virus concentrations to maximize host plant protection and virus production. Since the model can be used to calculate total food consumption or the amount of virus production on the daily basis for any given set of variables, optimization is possible through the contour mapping method. This 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

DAYS	UNIFORM	BINOMIAL(p = 0.5)	BINOMIAL(p = 0.1)
0	0.0714	0.0001	0.2542
1	0.0714	0.0016	0.3672
2	0.0714	0.0095	0.2448
3	0.0714 •	0.0349	0.0998
4	0.0714	0.0873	0.0277
5	0.0714	0.1571	0.0051
6	0.0714	0.2095	0.0008
7	0.0714	0.2095	0.0001
8	0.0714	0.1571	<0.0001
9	0.0714	0.0873	<0.0001
10	0.0714	0.0349	<0.0001
11	0.0714	0.0095	<0.0001
12	0.0714	0.0016	<0.0001
13	0.0714	0.0001	<0.0001

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
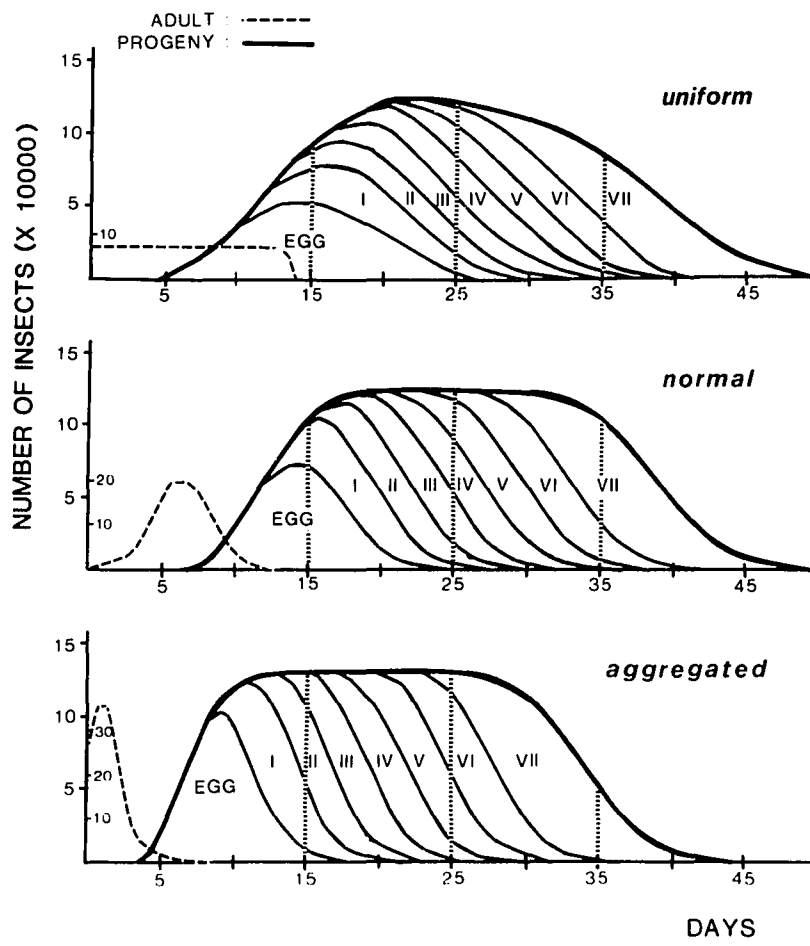
females.   The   pattern   of   adult   introduction--input   time   and

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

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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
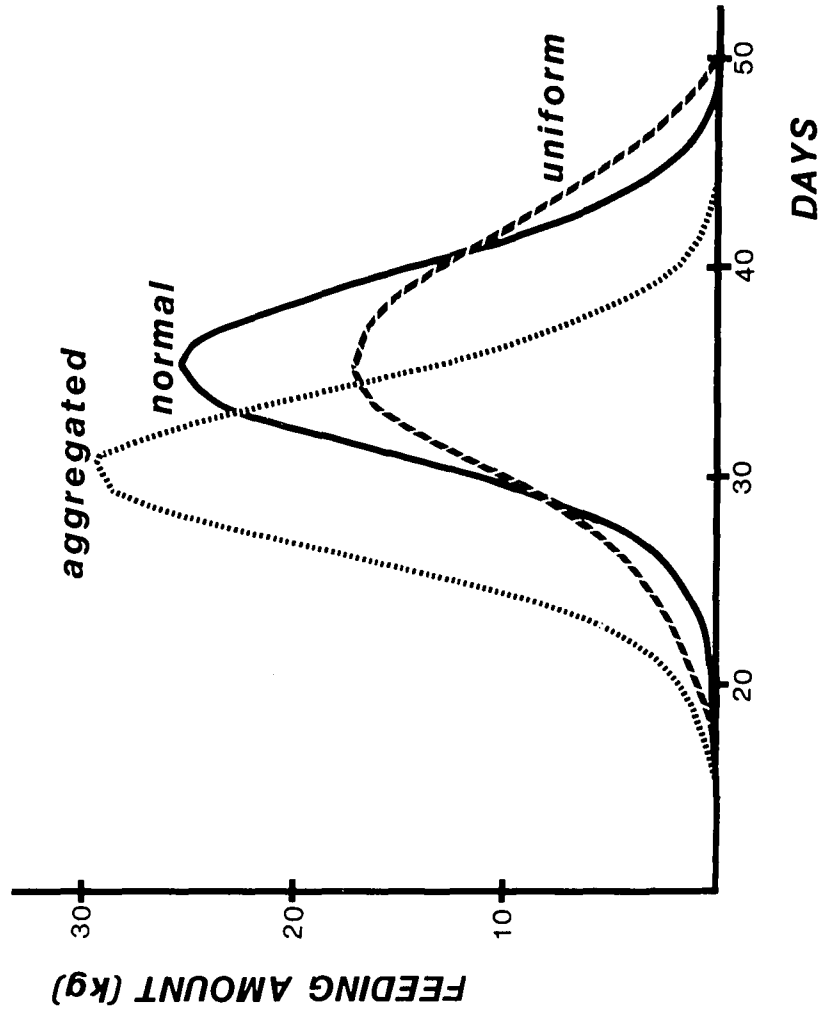
of 21.4 kg of grass while the normal introduction showed a peak consumption of 25.5 kg. This difference in the occurrence of damage caused by different patterns of adult introductions indicated that a lawn would be more severely affected if the adults appeared over a short period. A lawn may be able 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 cm^2 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

(UNIFORM INTRODUCTION)

LOG OF VIRUS CONC.

Grass Weight (X 100 gr)

DAYS
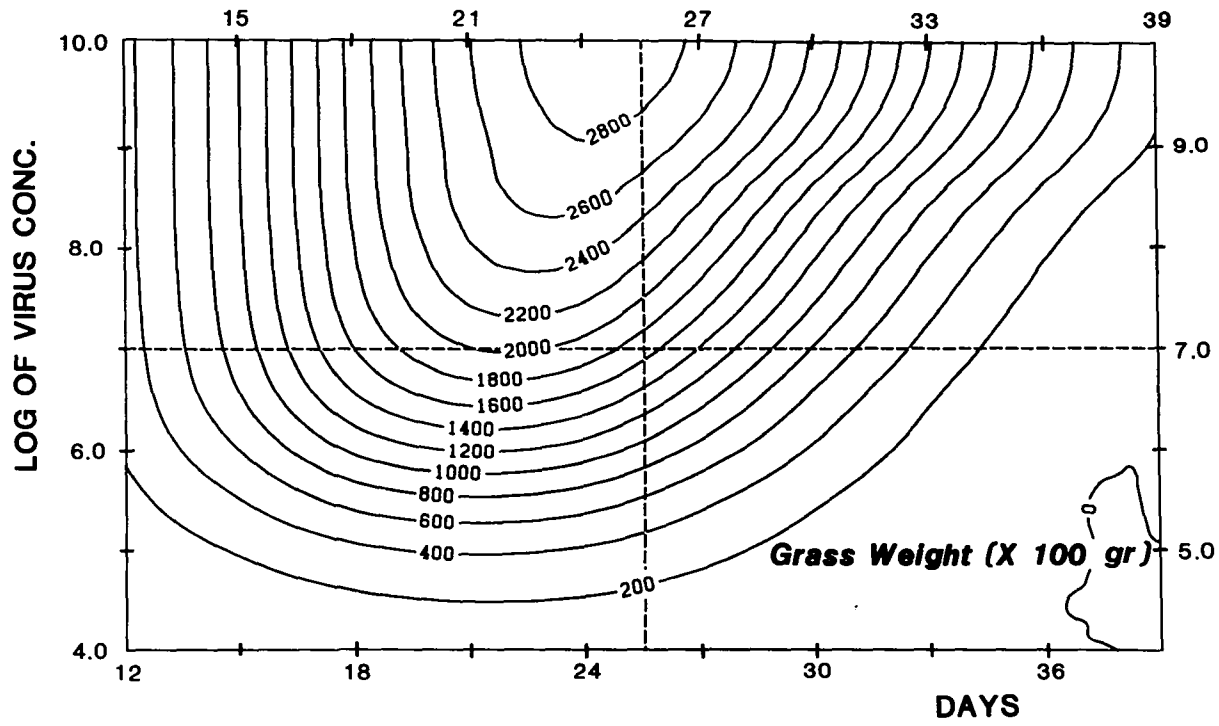
Figure 23. -- Changes in yield of grass (fresh weight of Bermuda grass in 100 grams) at different combinations of virus concentration and spray time when 100 mated females were introduced into a closed environmental system in a binomial distribution pattern with p = 0.5 (normal introduction) over a 14 day period

(NORMAL INTRODUCTION)

Grass Weight
(X 100 gr)

LOG. OF VIRUS CONC.

DAYS

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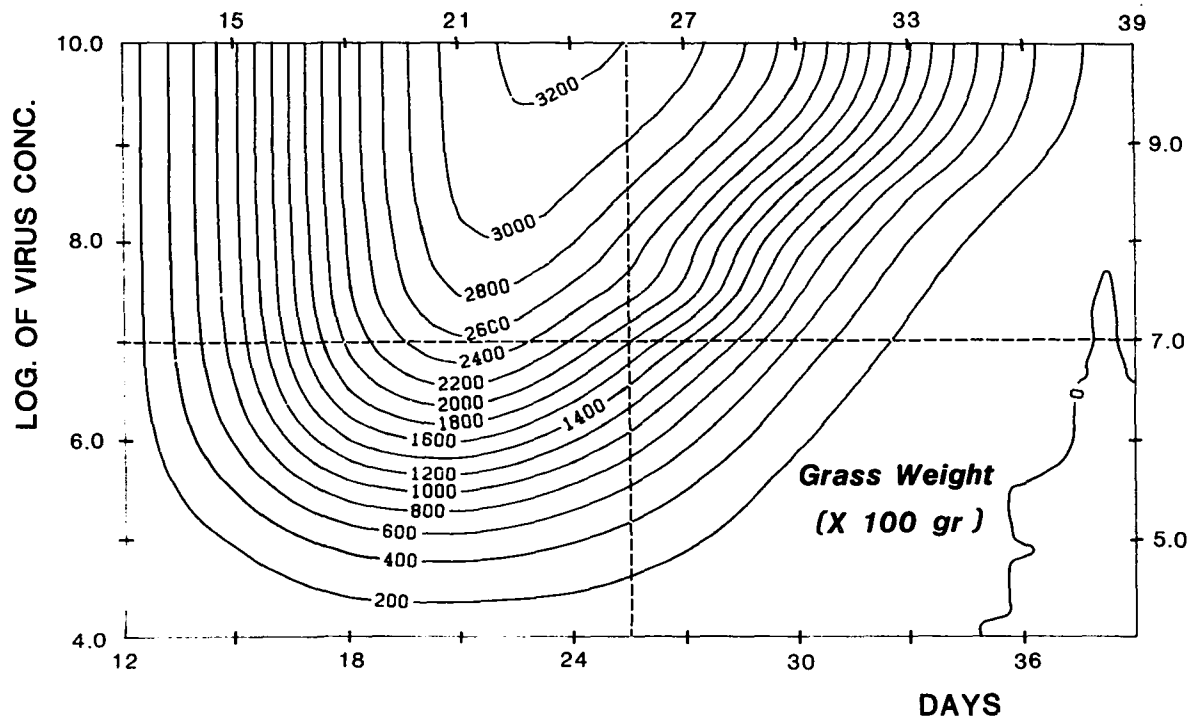
Figure 24. -- Changes in yield of grass (fresh weight of Bermuda grass in 100 grams) at different combinations of virus concentration and spray time when 100 mated females were introduced into a closed environmental system in a bionmial distribution pattern with p = 0.1 (aggregated introduction) over a 14 day period

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(AGGREGATED INTRODUCTION)
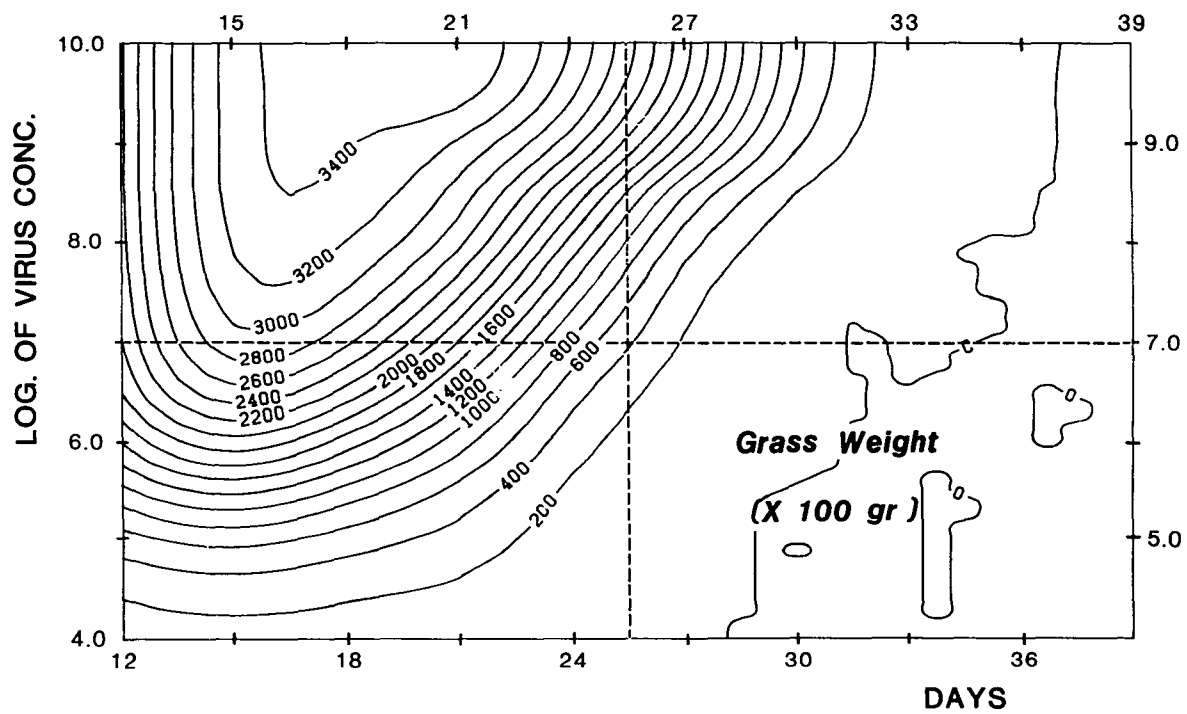
surface) at intervals of 0.5 in the logarithmic scale. The normally-generated fall temperature was used. These contour graphs were made for each of the three adult introduction patterns.

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, "L⁄" 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 appearence 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 "L⁄" 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, X 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

(UNIFORM INTRODUCTION)

No. of Polyhedra(X 10^{11})

LOG. OF VIRUS CONC.

DAYS
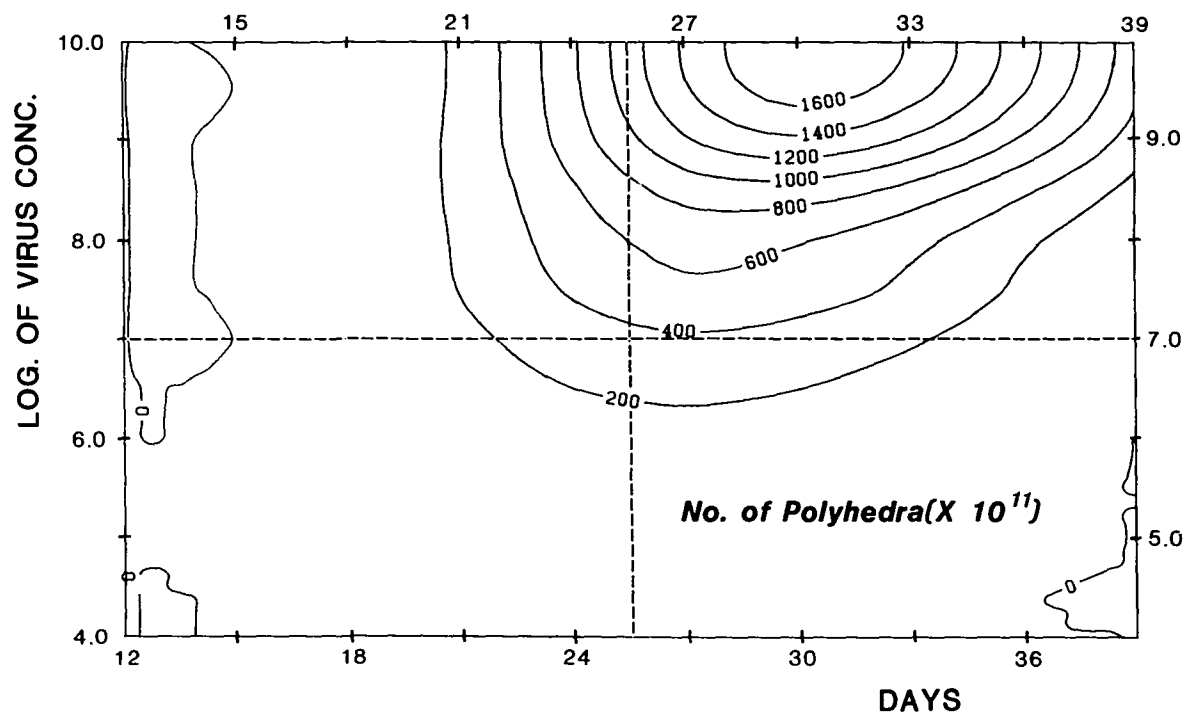
Figure 26. -- NPV production (number of polyhedra, X 10^{11}) at different combinations of virus concentration and spray time when 100 mated females were introduced into a closed environmental system in a binomial distribution pattern with p = 0.5 (normal introduction) over a 14 day period

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(NORMAL INTRODUCTION)

No. of Polyhedra)X 10^11)

LOG. OF VIRUS CONC.

DAYS
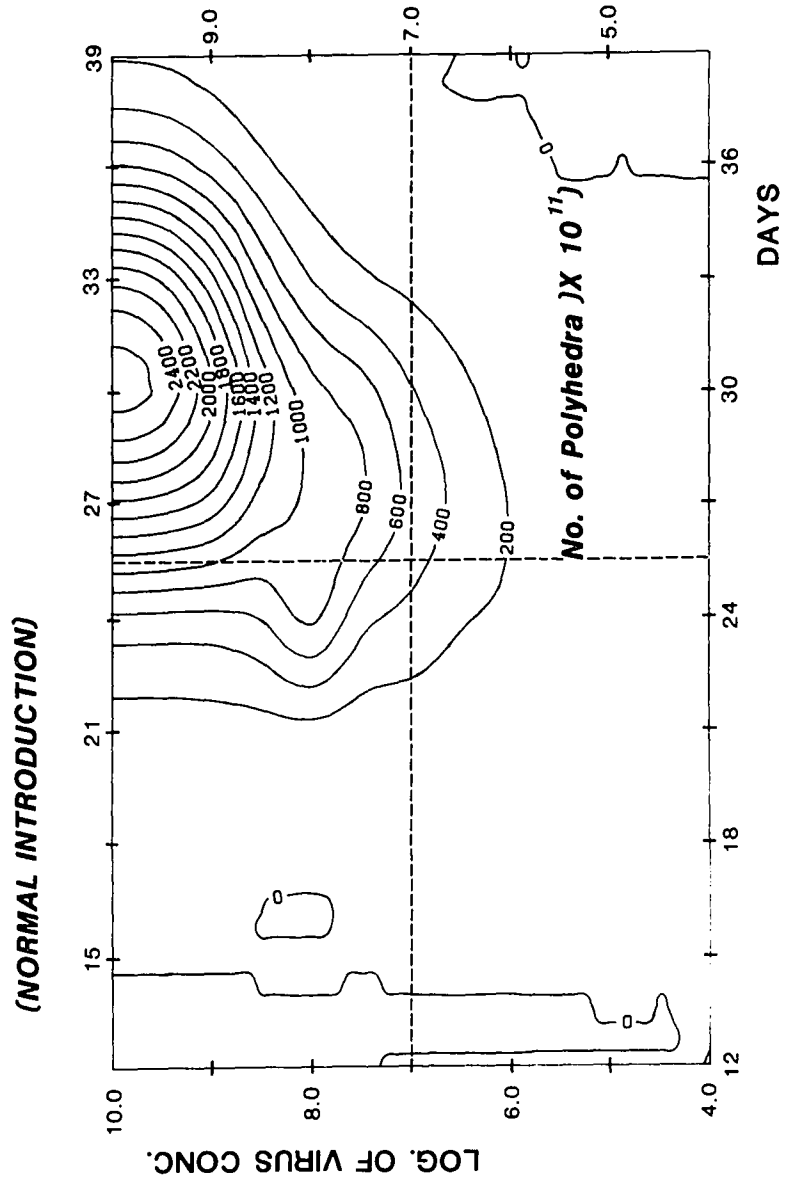
Figure 27. -- NPV production (number of polyhedra, X 10^{11}) at different combinations of virus concentration and spray time when 100 mated females were introduced into a closed environmental system in a binomial distribution pattern with p = 0.1 (aggregated introduction) over a 14 day period

(AGGREGATED INTRODUCTION)

No. of Polyhedra (X 10^{11})
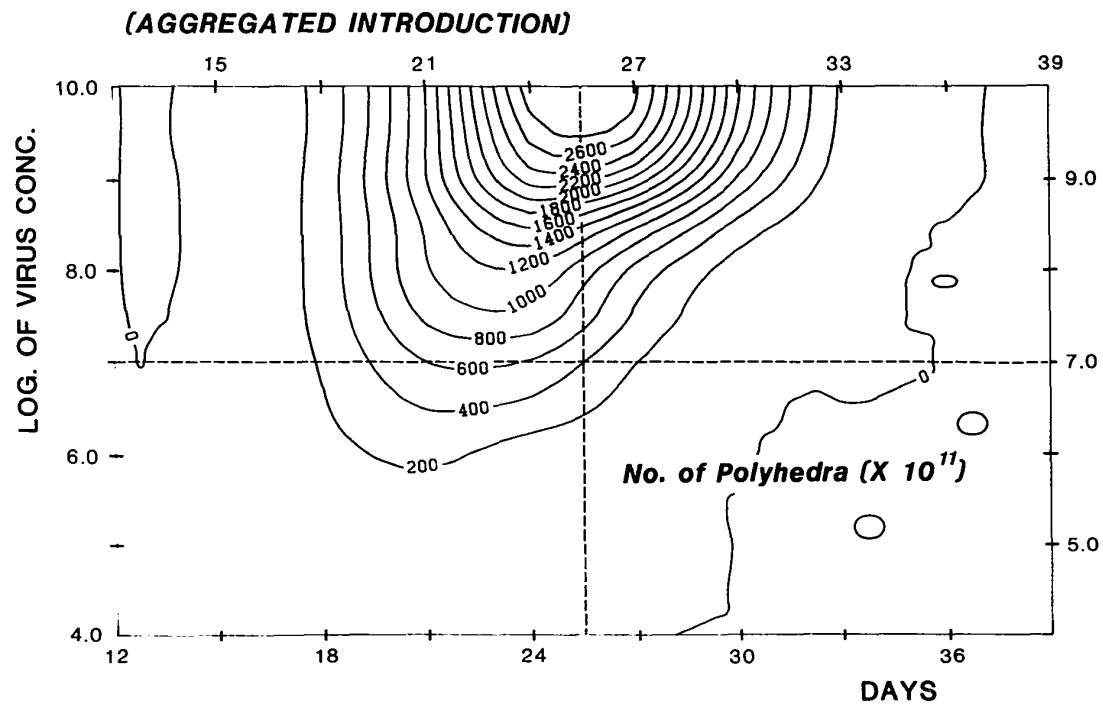
peak of polyhedra production appeared about a week later than the peak
for grass yield when the females were introduced uniformly or in a
normal distribution. For the aggregated introduction the peak was on
the 26th day, which was about five days later than the peak for grass
yield.

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 3.2×10^{14} polyhedra in total while the normal introduction
produced 2.9×10^{14} polyhedra. The most widely dispersed uniform
introduction produced the lowest amount of virus with 1.7×10^{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 sytem 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 preovipostion 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 3.47×10^5, 5.13×10^5, 1.11×10^6, 5.20×10^6, 4.25×10^7, and 5.95×10^8 polyhedra per $100 \ cm^2$ 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 appearence 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 m^2 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)

DAYS AFTER INFESTATION		3	5	8	10	13	14	17	22
L	I	3	.	.	.	.	.	.	.
A	II	76	2	.	.	.	.	.	.
R	III	.	79	4	.	.	.	.	.
V	IV	.	2	62	1	.	.	.	.
A	V	.	.	17	72	1	.	.	.
	VI	.	.	.	7	43	24	.	.
	VII	.	.	.	.	38	52	51	.
	PUPA	.	.	.	.	.	.	19	61
	TOTAL	79	83	83	80	82	76	70	61

(THERMAL SUMMATION MODEL)

		3	5	8	10	13	14	17	22
L	I	14	.	.	.	.	.	.	.
A	II	79	2	.	.	.	.	.	.
R	III	.	86	9	.	.	.	.	.
V	IV	.	4	79	38	.	.	.	.
A	V	.	.	1	49	31	.	.	.
	VI	.	.	.	2	55	69	16	.
	VII	.	.	.	.	.	10	60	28
	PUPA	.	.	.	.	.	.	3	50
	TOTAL	93	92	89	89	86	79	79	78

(LOGISTIC MODEL)

		3	5	8	10	13	14	17	22
L	I	.	.	.	.	.	.	.	.
A	II	92	.	.	.	.	.	.	.
R	III	.	66	9	1	.	.	.	.
V	IV	.	21	64	18	1	1	.	.
A	V	.	.	11	60	15	3	.	.
	VI	.	.	.	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 %)

(ACTUAL)

DAYS AFTER INFESTATION		2	4	6	7	9	10	12	14	16	18	21	23
L	I	82	13	.	.	.	.	.	.	.	.	.	.
A	II	.	71	18	2	8	.	.	.	.	.	.	.
R	III	.	.	69	29	7	.	.	.	.	.	.	.
V	IV	.	.	.	58	40	9	.	.	.	.	.	.
A	V	.	.	.	.	27	71	24	.	.	.	.	.
	VI	.	.	.	.	.	.	51	31	16	.	.	.
	VII	.	.	.	.	.	.	.	42	56	13	5	.
	PUPA	.	.	.	.	.	.	.	.	.	56	69	69
	TOTAL	82	84	87	89	82	80	75	73	72	69	74	69

(THERMAL SUMMATION MODEL)

		2	4	6	7	9	10	12	14	16	18	21	23
L	I	83	.	.	.	.	.	.	.	.	.	.	.
A	II	10	73	1	.	.	.	.	.	.	.	.	.
R	III	.	20	78	26	.	.	.	.	.	.	.	.
V	IV	.	.	13	65	50	16	.	.	.	.	.	.
A	V	.	.	.	.	37	65	38	5	.	.	.	.
	VI	.	.	.	.	.	6	45	56	19	2	.	.
	VII	.	.	.	.	.	.	2	18	56	67	30	7
	PUPA	.	.	.	.	.	.	.	1	3	8	46	66
	TOTAL	93	93	92	91	87	87	85	80	78	77	76	73

(LOGISTIC MODEL)

		2	4	6	7	9	10	12	14	16	18	21	23
L	I	88	.	.	.	.	.	.	.	.	.	.	.
A	II	4	73	.	.	.	.	.	.	.	.	.	.
R	III	.	19	57	18	1	.	.	.	.	.	.	.
V	IV	.	.	33	67	30	12	1	.	.	.	.	.
A	V	.	.	.	2	51	59	17	2	.	.	.	.
	VI	.	.	.	.	3	13	59	32	8	.	.	.
	VII	.	.	.	.	.	.	3	44	68	65	10	.
	PUPA	.	.	.	.	.	.	.	.	.	11	61	70
	TOTAL	92	92	90	87	85	84	80	78	76	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 %)

(ACTUAL)

DAYS AFTER INFESTATION	3	5	7	9	11	13	15	17	19	21	23
I	27	.	.	.	.	.	.	.	.	.	.
L II	53	69	.	.	.	.	.	.	.	.	.
A III	.	15	61	1	.	.	.	.	.	.	.
R IV	.	.	27	78	7	.	.	.	.	.	.
V V	.	.	.	2	76	35	1	.	.	.	.
A VI	.	.	.	.	.	49	79	1	.	.	.
VII	.	.	.	.	.	.	.	82	72	59	8
PUPA	.	.	.	.	.	.	.	.	8	15	63
TOTAL	80	84	88	81	83	84	80	83	80	74	71

(THERMAL SUMMATION MODEL)

	3	5	7	9	11	13	15	17	19	21	23
I	32	.	.	.	.	.	.	.	.	.	.
L II	61	74	.	.	.	.	.	.	.	.	.
A III	.	19	87	32	.	.	.	.	.	.	.
R IV	.	.	5	58	67	13	.	.	.	.	.
V V	.	.	.	1	21	68.	35	9	.	.	.
A VI	.	.	.	.	.	6	50	63	38.	11	.
VII	.	.	.	.	.	.	.	9	39	63	71
PUPA	.	.	.	.	.	.	.	.	1	4	6
TOTAL	93	93	92	91	88	87	85	81	78	78	77

(LOGISTIC MODEL)

	3	5	7	9	11	13	15	17	19	21	23
I	26	.	.	.	.	.	.	.	.	.	.
L II	66	64	3	.	.	.	.	.	.	.	.
A III	.	28	68	28	8	.	.	.	.	.	.
R IV	.	.	20	59	52	18	4	.	.	.	.
V V	.	.	.	4	30	56	37	16	5	.	.
A VI	.	.	.	.	.	14	44	52	35	14	2
VII	.	.	.	.	.	.	.	16	39	63	73
PUPA	.	.	.	.	.	.	.	.	.	1	3
TOTAL	92	92	91	91	90	88	85	84	79	78	78

TABLE 18

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

VIRUS CONCENTRATION (POLY/100CM^2)	MORTALITY				MORTALITY PROPORTION			LETHAL INFECTION PERIOD			
	TOTAL	INI	SEC	TER	INI	SEC	TER	TOTAL	INI	SEC	TER
8.50 X 103	15.0	0.0	5.0	10.0	0.0	33.3	66.7	12.33	–	9.00	14.00
6.40 X 104	30.7	5.1	13.7	12.0	17.0	44.3	38.7	7.84	5.67	6.78	10.17
5.65 X 105	55.7	22.0	23.4	10.3	39.0	42.2	18.8	7.00	5.89	6.86	10.13
5.02 X 106	80.0	65.0	13.8	1.3	80.3	18.0	1.7	6.34	6.18	6.70	8.00
2.21 X 107	90.0	80.0	10.0	0.0	88.9	11.1	0.0	4.39	4.25	5.50	--
8.50 X 108	99.9	99.9	0.0	0.0	99.9	0.0	0.0	5.40	5.40	–	–

APPENDIX B - 2.

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

VIRUS CONCENTRATION $(POLY/100CM^2)$	MORTALITY				MORTALITY PROPORTION			LETHAL INFECTION PERIOD			
	TOTAL	INI	SEC	TER	INI	SEC	TER	TOTAL	INI	SEC	TER
8.67×10^3	11.1	0.0	5.0	6.1	0.0	44.5	55.6	7.89	–	7.33	8.33
8.63×10^4	28.4	0.0	17.4	11.0	0.0	60.1	39.9	8.18	.	7.56	8.96
8.63×10^5	60.1	4.9	35.6	19.7	8.2	59.0	32.8	7.37	5.75	6.91	8.54
8.63×10^6	80.9	8.7	63.4	8.8	10.6	78.2	11.2	6.77	5.81	6.68	8.40
8.64×10^7	95.6	30.0	62.8	2.8	31.4	65.7	2.9	6.08	5.20	6.37	8.00

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

VIRUS CONCENTRATION (POLY/100CM^2)	MORTALITY				MORTALITY PROPORTION			LETHAL INFECTION PERIOD			
	TOTAL	INI	SEC	TER	INI	SEC	TER	TOTAL	INI	SEC	TER
1.51 X 10^4	11.5	0.0	3.7	7.8	0.0	32.1	67.8	11.25	–	10.05	12.78
1.51 X 105	30.0	5.0	15.0	10.0	16.7	50.0	33.3	10.33	9.00	9.33	12.50
4.28 X 105	42.4	5.9	23.0	13.5	14.0	54.2	31.9	9.47	7.17	8.88	11.45
4.28 X 106	63.3	12.6	40.3	10.4	20.0	63.4	16.6	8.35	7.03	8.06	11.11
3.48 X 107	79.6	21.5	54.6	3.4	27.2	68.7	4.2	7.33	5.61	7.76	11.40
5.29 X 107	85.0	25.0	60.0	0.0	29.4	70.6	0.0	6.76	5.20	7.42	·

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

VIRUS CONCENTRATION (POLY/100CM^2)	MORTALITY				MORTALITY PROPORTION			LETHAL INFECTION PERIOD			
	TOTAL	INI	SEC	TER	INI	SEC	TER	TOTAL	INI	SEC	TER
7.78×10^3	7.6	0.0	2.5	5.1	0.0	25.0	75.0	11.75	–	10.00	12.50
7.71×10^4	22.1	0.0	10.3	11.8	0.0	44.5	55.6	10.25	–	8.50	11.72
6.73×10^5	36.3	1.3	21.3	13.8	3.1	58.5	38.4	9.73	7.00	8.69	11.46
6.89×10^6	52.0	3.0	35.7	13.3	5.7	68.3	32.5	8.91	7.80	8.33	10.77
6.89×10^7	73.7	6.1	57.6	10.1	8.42	78.0	13.6	8.27	7.10	8.08	10.27
8.01×10^8	94.7	21.1	68.4	5.3	22.2	72.2	5.6	6.89	5.75	6.92	11.00

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

VIRUS CONCENTRATION (POLY/100CM^2)	MORTALITY				MORTALITY PROPORTION			LETHAL INFECTION PERIOD			
	TOTAL	INI	SEC	TER	INI	SEC	TER	TOTAL	INI	SEC	TER
8.15 X 10^5	18.8	0.0	0.0	18.8	0.0	0.0	99.9	13.33	-	-	13.33
8.16 X 10^6	37.5	0.0	12.5	25.0	0.0	33.3	66.7	11.00	-	9.50	11.75
6.15 X 10^7	55.0	1.1	32.3	21.6	1.9	58.2	39.9	10.04	5.00	9.91	10.43
2.65 X 10^8	70.0	0.0	53.3	16.7	0.0	75.9	24.1	8.49	-	8.34	8.92
7.86 X 10^8	86.3	0.0	75.0	11.3	0.0	87.0	13.0	7.79	-	7.60	9.00

APPENDIX B - 6.

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

VIRUS CONCENTRATION (POLY/100CM^2)	MORTALITY				MORTALITY PROPORTION			LETHAL INFECTION PERIOD			
	TOTAL	INI	SEC	TER	INI	SEC	TER	TOTAL	INI	SEC	TER
6.80 X 10^7	26.3	0.0	26.3	0.0	0.0	99.9	0.0	9.80	-	9.80	-
3.78 X 10^8	44.4	0.0	44.4	0.0	0.0	99.9	0.0	9.49	-	9.49	-
7.18 X 10^8	54.2	2.5	51.7	0.0.	4.6	95.5	0.0	9.24	7.00	9.28	-
1.51 X 10^9	72.2	0.0	72.2	0.0	0.0	99.9	0.0	8.89	-	8.89	-
3.40 X 10^9	82.1	0.0	82.1	0.0	0.0	99.9	0.0	8.99	-	8.99	-
7.56 X 10^9	94.7	5.26	89.5	0.0	5.6	94.4	0.0	7.94	7.00	8.00	-

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

9.07×10^4 POLYHEDRA/100 CM^2

DAYS AFTER SPRAY INSTARS	5	7	9	11	13	15	TOTAL
A II	1	3	2	0	0	0	6
C III	0	3	7	0	0	0	10
T IV	0	1	5	3	0	0	9
TOTAL	1	7	14	3	0	0	25
C II	1	4	0	0	0	0	5
A III	2	3	4	1	0	0	10
L IV	0	0	1	3	0	0	4
TOTAL	3	7	5	4	0	0	19

9.07×10^5 POLYHEDRA/100 CM^2

	5	7	9	11	13	15	TOTAL
A II	2	6	1	1	0	0	10
C III	0	4	21	3	2	0	30
T IV	0	0	2	11	5	0	17
TOTAL	2	10	24 ·	15	7	0	57
C II	2	9	6	3	0	0	20
A III	0	3	18	13	2	0	36
L IV	0	0	2	5	1	1	9
TOTAL	1	12	26	21	3	1	65

9.07×10^6 POLYHEDRA/100 CM^2

	5	7	9	11	13	15	TOTAL
A II	5	9	3	1	0	0	18
C III	4	34	12	9	1	0	60
T IV	0	1	5	1	3	1	11
TOTAL	9	44	20	11	4	1	89
C II	6	14	6	1	0	0	27
A III	1	12	31	10	1	0	55
L IV	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

4.54×10^5 POLYHEDRA/100 CM^2

DAYS AFTER SPRAY INSTARS		5	7	9	11	13	15	TOTAL
A	IV	1	3	1	0	0	0	5
C	V	0	5	9	3	1	0	18
T	VI	0	0	3	2	1	0	6
	TOTAL	1	8	13	5	2	0	29
C	IV	0	1	3	0	0	0	4
A	V	0	1	9	5	0	0	15
L	VI	0	0	0	2	1	1	4
	TOTAL	0	2	12	7	1	1	23

4.54×10^6 POLYHEDRA/100 CM^2

		5	7	9	11	13	15	TOTAL
A	IV	2	4	3	1	0	0	10
C	V	0	2	15	8	1	0	27
T	VI	0	0	1	1	3	1	5
	TOTAL	2	6	19	10	4	1	42
C	IV	0	1	3	1	0	0	5
A	V	0	2	14	10	3	0	29
L	VI	0	1	4	5	2	2	14
	TOTAL	0	4	21	16	5	2	48

4.54×10^7 POLYHEDRA/100 CM^2

		5	7	9	11	13	15	TOTAL
A	IV	3	7	3	0	0	0	13
C	V	2	16	22	5	2	0	47
T	VI	0	3	2	1	1	2	9
	TOTAL	5	26	27	6	3	2	69
C	IV	0	2	7	4	0	0	13
A	V	1	12	27	26	8	0	63
L	VI	0	0	0	2	0	0	2
	TOTAL	1	14	34	32	8	0	78

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

8.16×10^6 POLYHEDRA/100 CM^2

DAYS AFTER SPRAY INSTARS		6	8	10	12	14	>16	TOTAL
A	V	0	0	0	0	0	0	0
C	VI	0	3	2	1	1	0	7
T	VII	0	1	7	2	1	1	12
	TOTAL	0	4	9	3	2	1	19
C	V	0	1	0	0	0	0	1
A	VI	0	0	5	4	0	0	9
L	VII	0	0	5	3	6	1	15
	TOTAL	0	1	10	7	6	1	25

8.16×10^7 POLYHEDRA/100 CM^2

		6	8	10	12	14	>16	TOTAL
A	V	1	0	1	0	0	0	2
C	VI	4	10	7	3	2	0	25
T	VII	1	7	12	4	2	2	28
	TOTAL	6	17	20	7	4	2	55
C	V	3	4	0	0	0	0	7
A	VI	0	5	14	11	1	0	31
L	VII	0	3	9	10	2	0	24
	TOTAL	3	12	23	21	3	0	62

8.16×10^8 POLYHEDRA/100 CM^2

		6	8	10	12	14	>16	TOTAL
A	V	1	2	2	1	0	0	6
C	VI	3	22	23	5	1	1	55
T	VII	0	2	14	6	1	4	27
	TOTAL	4	26	39	12	2	5	88
C	V	0	3	0	0	0	0	3
A	VI	2	14	30	25	6	0	77
L	VII	0	0	5	3	2	1	11
	TOTAL	2	17	35	28	8	1	91

```
        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           COMMENTS
        SIMULATE
BAMO    STARTMACRO    DETER" 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$MORT1,999,#D  SELEC" BASIC MORT" OVER 999
        TRANSFER   ,#E  CONNECT TO DEV MACRO
#D      SAVEVALUE  3,V$MORT1,XH  SAVEVALUE PROB" CRITERIA FOR SURV"
        TRANSFER   .XH3,,#E  CONNECT TO DEV MACRO
        ENTER      #F  BEGINNING OF A LIFE STAGE
        ADVANCE    #G DEVELOPMENT OF NATU" DYING INDI"
        LEAVE      #F  END OF A LIFE STAGE
        TERMINATE      TERMINATE NATURALLY DYING INDI"
        ENDMACRO
*
DEV     STARTMACRO    DETER" 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-ESIMATED THERMAL CONSTANT
        ASSIGN     3,#E,PL  ASSGIN PRE-ESTIMATED STD" OF THERMAL CON"
        ASSIGN     4,V3,PL  ASSGIN THERMAL CON" IN A NORMAL DIST"
#F      ASSIGN     5+,V2,PL  ACCUMUL" DAILY EFFECTIVE DD"
        ADVANCE    1  DAILY DEVELOPMENT
        ASSIGN     4+,1,PB  ASSIGN DEVELOPMENTAL PERIOD
        TEST GE    PL5,PL4,#F  DETER" 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" DD" FOR NEXT STAGE
        ENDMACRO
*
        LOAD       DAG06,EGGPRC
*
*
*********************************************************************
*
*       COMMENTS
*
*********************************************************************
*
* A GPSS MODEL FOR DETERMINING LAWN ARMYWORM DEVELCPMENT
* BY THE THERMAL SUMMATION METHOD.
*
* THE HYPERBCLIC 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 ECG, 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,C27 GEN* NORMAL DISTRIBUTION
0,-3.5/.0013,-3.0/.0035,-2.75/.0062,-2.5/.0122,-2.25/.0228,-2.0
.0401,-1.75/.0668,-1.5/.1056,-1.25/.1587,-1.00/.2266,-.75/.3085,-.5
.4013,-.25/.5,0/.5987,.25/.6915,.50/.7734,.75/.8413,1/.8944,1.25
.9332,1.5/.9599,1.75/.9772,2/.9878,2.25/.9938,2.5/.9965,2.75
.9987,3.0/1,3.5
*
*
 PREOV FUNCTION   RN1,D7  DETER* OF PRE-OVIPOSTION PERIOD
.0111,1/.0888,2/.4110,3/.7998,4/.9330,5/.9885,6/.9999,7
*
 OVIPE FUNCTION   RN1,D10 DETER* OF OVI-POSITION PERIOD
.0111,1/.0667,2/.1443,3/.3221,4/.5221,5/.6887,6/.8442,7/.9330,8
.9885,9/.9995,10
*
 EGSTA FUNCTION   XF1,L18 STD* OF DAILY EGG PRODUCTION
,264/,175/,148/,106/,83/,55/,56/,39/,54/,1/,1/,1/,1/,1/,1/,1/,1
*
*      **********************************************
```

```
*
*       VARIABLES
*
*       ******************************************
1       VARIABLE    AC1-1   DAYS AFTER INFESTATION
2       FVARIABLE   1.16*FN$NORM+25.6-PL1   DAILY TEMP'' IN FALL AT MANOA
3       FVARIABLE   PL3*FN$NORM+PL2  TOTAL EFFECTIVE TEMPERATURE
4       FVARIABLE   1.54*FN$NORM+9.32  LONGEVITY OF AN ADULT
5       FVARIABLE   RN2*2/1000  LONGI'' OF NATU'' DYING II TO IV LARVA
6       FVARIABLE   RN2*3/1000   LONGI" OF NAT" DYING I, V, VI & POST-OVI
7       FVARIABLE   RN2*4/1000  LONGEI" OF NAT'' DYING EGG
8       FVARIABLE   RN2*7/1000 LONGI'' OF NATU'' DYING VII LARVA
9       FVARIABLE   RN2*12/1000 LONGI'' OF NATU'' DYING PUPA
10      FVARIABLE   RN2*9/1000  LONGI'' OF NATU'' DYING ADULT
11      FVARIABLE   (PL5/PL4-1)*XL$NEXT  CUM" EFF" DO" FOR NEXT STAGE
12      FVARIABLE   2*FN$NORM+8  LONGI'' OF ADULT MOTH (MINUS 1 DAY )
13      FVARIABLE   (FN$EGSTA*FN$NORM+XL16)/40   DAILY EGG PRODUC"
*
MORT1   FVARIABLE   XH2*FN$NORM+XH1  BASIC MORTALITY IN 1000 UNIT
PROV    VARIABLE    FN$PREOV-1  INTO" OF FEMALE (PREOC" MINUS ONE DAY)
*
25      FVARIABLE   (0.5*S1+1.1*S2+3.0*S3+9.2*S4)/1000  DAM'' AT YOUNG
26      FVARIABLE   (27.4*S5+83.0*S6+316.7*S7)/1000  DAM'' AT OLD STAGE
FOOD    FVARIABLE   V25+V26  DAILY FOOD DAMAGE
*
************************************************************************
*
*       BASIC LIFE MODEL
*
************************************************************************
*
*       ***********************************************
*
*       INTRODUCTION OF A FEMALE
*
*       ***********************************************
        GENERATE    1,,,1,,1PH,4PB,7PL  INTRO'' OF ORI" TRANSACTION
        ENTER       10  ENTER ADULT STAGE
        ENTER       9  ENTER THE FIRST DAY OF DEVELOPMENT
        ADVANCE     1  FIRST DAY OF INTRO" OF FEMALE
        LEAVE       9  LEAVE THE FIRST DAY OF DEVELOPMENT
*
*       ***********************************************
*
*       OVIPOSITION
*
*       ***********************************************
RPT     ADVANCE     V$PROV  PREOVI" PERIOD (MINUS ONE DAY)
        ASSIGN      2,FN$OVIPE,PB  DETER'' OVIPOSTION PERIOD
OPI3    ADVANCE     1  DAILY DEVELOPMENT OF A FEMALE DURING OVIPO''
        ASSIGN      3+,1,PB  ASSIGN OVIPOSITION DAY
        SAVEVALUE   1,PB3,XF  SAVEVALUE FOR OVIPOSITION DAY
        SAVEVALUE   16,0,XL  SET EGG PRO" TO ZERO BEFORE HELPB
        HELPB       #EGGPRO,1XF,16XL  EGG PRODUCTION (LOG MEAN)
        ASSIGN      1,V13,PH  ASSIGN DAILY EGG PRODUCTION
```

```
        TEST LE      PH1,0,OPI1   SCREEN POSI" EGG PRO"
        TRANSFER     ,OPI2   CONNECTION
OPI1    SPLIT        PH1,INSO   DAILY OVIPOSITION
OPI2    LOOP         2PB,OPI3   REPEAT OVIPOSITION
        ASSIGN       3,0,PB   ASSIGN OVIPOSITION DAY AS ZERO
        ADVANCE      V6    POST-OVIPOSITION PERIOD
        LEAVE        10   LEAVE ADULT STAGE
        TERMINATE         FEMALE IS TERMINATED
*
*
*       ******************************************
*
*       EGG DEVELOPMENT
*
*       ******************************************
*
BAMU    MACRO        INSO,933,10,WWWO,DUMO,60,V7
INSO    SAVEVALUE    1,933,XH
        SAVEVALUE    2,10,XH
        TEST GE      V$MORT1,999,WWWO
        TRANSFER     ,DUMO
WWWO    SAVEVALUE    3,V$MORT1,XH
        TRANSFER     .XH3,,DUMO
        ENTER        60
        ADVANCE      V7
        LEAVE        60
        TERMINATE
DEV     MACRO        DUMO,60,10.7,59.46,10.05,ZZZ,33.33
DUMO    ENTER        60
        ASSIGN       1,10.7,PL
        ASSIGN       2,59.46,PL
        ASSIGN       3,10.05,PL
        ASSIGN       4,V3,PL
ZZZ     ASSIGN       5+,V2,PL
        ADVANCE      1
        ASSIGN       4+,1,PB
        TEST GE      PL5,PL4,ZZZ
        LEAVE        60
        SAVEVALUE    NEXT,33.33,XL
        ASSIGN       5,V11,PL
*
*       FIRST INSTAR LARVA
*       ******************************************
BAMO    MACRO        INS1,933,38,WWW1,DUM1,1,V6
INS1    SAVEVALUE    1,933,XH
        SAVEVALUE    2,38,XH
        TEST GE      V$MORT1,999,WWW1
        TRANSFER     ,DUM1
WWW1    SAVEVALUE    3,V$MORT1,XH
        TRANSFER     .XH3,,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,V3,PL
   AAA     ASSIGN      5+,V2,PL
    .      ADVANCE     1
          ASSIGN      4+,1,PB
          TEST GE     PL5,PL4,AAA
          LEAVE       1
          SAVEVALUE   NEXT,26.52,XL
          ASSIGN      5,V11,PL
*
*         ******************************************
*
*         SECOND INSTAR LARVA
*
*         ******************************************
*
   BAMO    MACRO       INS2,999,38,WWW2,DUM2,2,V5
   INS2    SAVEVALUE   1,999,XH
          SAVEVALUE   2,38,XH
          TEST GE     V$MORT1,999,WWW2
          TRANSFER    ,DUM2
   WWW2    SAVEVALUE   3,V$MORT1,XH
          TRANSFER    .XH3,,DUM2
          ENTER       2
          ADVANCE     V5
          LEAVE       2
          TERMINATE
   DEV     MACRO       DUM2,2,14.4,26.52,4.86,BBB,28,83
   DUM2    ENTER       2
          ASSIGN      1,14.4,PL
          ASSIGN      2,26.52,PL
          ASSIGN      3,4.86,PL
          ASSIGN      4,V3,PL
   BBB     ASSIGN      5+,V2,PL
          ADVANCE     1
          ASSIGN      4+,1,PB
          TEST GE     PL5,PL4,BBB
          LEAVE       2
          SAVEVALUE   NEXT,28,XL
          ASSIGN      5,V11,PL
*
*         ******************************************
*
*         THIRD INSTAR LARVA
*
*         ******************************************
*
   BAMO    MACRC       INS3,967,24,WWW3,DUM3,3,V5
   INS3    SAVEVALUE   1,967,XH
          SAVEVALUE   2,24,XH
          TEST GE     V$MORT1,999,WWW3
          TRANSFER    ,DUM3
   WWW3    SAVEVALUE   3,V$MORT1,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,V3,PL
CCC       ASSIGN       5+,V2,PL
          ADVANCE      1
          ASSIGN       4+,1,PB
          TEST GE      PL5,PL4,CCC
          LEAVE        3
          SAVEVALUE    NEXT,32.50,XL
          ASSIGN       5,V11,PL
*
*         ****************************************
*
*         FOURTH INSTAR LARVA
*
*         ****************************************
*
BAMO      MACRO        INS4,968,32,WWW4,DUM4,4,V5
INS4      SAVEVALUE    1,968,XH
          SAVEVALUE    2,32,XH
          TEST GE      V$MORT1,999,WWW4
          TRANSFER     ,DUM4
WWW4      SAVEVALUE    3,V$MORT1,XH
          TRANSFER     .XH3,,DUM4
          ENTER        4
          ADVANCE      V5
          LEAVE        4
          TERMINATE
DEV       MACRO        DUM4,4,13.6,32.50,7.01,DDD,34.49
DUM4      ENTER        4
          ASSIGN       1,13.6,PL
          ASSIGN       2,32.50,PL
          ASSIGN       3,7.01,PL
          ASSIGN       4,V3,PL
DDD       ASSIGN       5+,V2,PL
          ADVANCE      1
          ASSIGN       4+,1,PB
          TEST GE      PL5,PL4,DDD
          LEAVE        4
          SAVEVALUE    NEXT,34.49,XL
          ASSIGN       5,V11,PL
*
*         ****************************************
*
*         FIFTH INSTAR LARVA
*
*         ****************************************
*
BAMO      MACRO        INS5,978,31,WWW5,DUM5,5,V6
INS5      SAVEVALUE    1,978,XH
          SAVEVALUE    2,31,XH
          TEST GE      V$MORT1,999,WWW5
          TRANSFER     ,DUM5
```

```
WWW5    SAVEVALUE   3,V$MORT1,XH
        TRANSFER    .XH3,,DUM5
        ENTER       5
        ADVANCE     V6
        LEAVE       5
        TERMINATE
DEV     MACRO       DUM5,5,13.3,34.49,8.35,EEE,43.91
DUM5    ENTER       5
        ASSIGN      1,13.3,PL
        ASSIGN      2,34.49,PL
        ASSIGN      3,8.35,PL
        ASSIGN      4,V3,PL
EEE     ASSIGN      5+,V2,PL
        ADVANCE     1
        ASSIGN      4+,1,PB
        TEST GE     PL5,PL4,EEE
        LEAVE       5
        SAVEVALUE   NEXT,43.91,XL
        ASSIGN      5,V11,PL
*
*       ***********************************************
*
*       SIXTH INSTAR LARVA
*
*       ***********************************************
*
BAMO    MACRO       INS6,946,14,WWW6,DUM6,6,V6
INS6    SAVEVALUE   1,946,XH
        SAVEVALUE   2,14,XH
        TEST GE     V$MORT1,999,WWW6
        TRANSFER    ,DUM6
WWW6    SAVEVALUE   3,V$MORT1,XH
        TRANSFER    .XH3,,DUM6
        ENTER       6
        ADVANCE     V6
        LEAVE       6
        TERMINATE
DEV     MACRO       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,V3,PL
FFF     ASSIGN      5+,V2,PL
        ADVANCE     1
        ASSIGN      4+,1,PB
        TEST GE     PL5,PL4,FFF
        LEAVE       6
        SAVEVALUE   NEXT,50.81,XL
        ASSIGN      5,V11,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
        TERMINATE
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,PB
        TEST GE     PL5,PL4,GGG
        LEAVE       7
        SAVEVALUE   NEXT,110.42,XL
        ASSIGN      5,V11,PL
*
*
*       ****************************************************
*
*       PUPAL STAGE
*
*       ****************************************************
*
BAMO    MACRO       INS8,906,55,WWW8,DUM8,8,V9
INS8    SAVEVALUE   1,906,XH
        SAVEVALUE   2,55,XH
        TEST GE     V$MORT1,999,WWW8
        TRANSFER    ,DUM9
WWW8    SAVEVALUE   3,V$MORT1,XH
        TRANSFER    .XH3,,DUM8
        ENTER       8
        ADVANCE     V9
        LEAVE       8
        TERMINATE
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,PB
        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  LONGI'' OF ADULT MOTH (MINUS 1 DAY)
      . LEAVE       10   LEAVE ADULT STAGE
        TERMINATE        PRODUCED ADULTS ARE TERMINATED
*
*
*
********************************************************************************
*
*       CONTROL CARDS
*
********************************************************************************
*
*       *********************************
*
*       TIME CONTROL
*
*       *********************************
*
        GENERATE     1   TIMER ARRIVES EVERYDAY
        SAVEVALUE   DAY,V1,XH   DAYS COUTING FROM INTRO 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       45,,1
*
*       ******************************************
*       OUTPUT CONTROL
*
*       ******************************************
*
        REPORT
        TEXT        #XH$DAY,2/XX#   DAY(S) AFTER INITAL INTRODUCTION
 STO    TITLE       ,AGE COMPOSITION  (NO. OF INDIVIDUALS)
 LSV    TITLE       ,FOOD CONSUMTION 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
 8AMO   STARTMACRO
 #A     TRANSFER   #B,,#C  DETERMINATION OF NATURAL MORTALITY
        ENTER      #D   BEGINNING OF A LIFE STAGE
        ADVANCE    #E   LETHAL DEVELOPMENTAL PERICD FOR NAT'' DYING INDI''
        LEAVE      #D   END OF A LIFE STAGE
        TERMINATE       NAT'' DYING INDIVIDUAL IS TERMINATED
        ENDMACRO
 DEV    STARTMACRO
 #A     ENTER      #B   BEGINNING OF A LIFE STAGE
 #D     SAVEVALUE  1,V2,XL   DAILY TEMPERATURE
        SAVEVALUE  1,#C,XF   SAVEVALUE FOR ADD" OF REL" DEV"
        SAVEVALUE  2,0,XL   SAVEVALUE FOR RELATIVE DEVELCPMENT
        SAVEVALUE  3,0,XL   SAVEVALUE FCR STD'' OF RELATIVE DEVELCPMENT
        HELPB      #LOGDEV,1XF,1XL,2XL,3XL    DET" OF REL" DEV"
        SAVEVALUE  1+,1,XF   SAVEVALUE FOR STD" OF RELDEV"
        HELPB      #LOGDEV,1XF,1XL,2XL,3XL    DET"" STD" FOR REL" DEV"
        TEST LE    V3,0,#E   TEST WHETHER GEN'' REL'' DEV'' IS BELOW ZERO
        SAVEVALUE  1,0,XH   SAVEVALUE 0 FOR MINUS OR 0 RELDEV
        TRANSFER   ,#F   CONNECT TO MAIN BRANCH
 #E     SAVEVALUE  1,V3,XH    SAVE GEN'' REL'' DEV''
 #F     ASSIGN     1+,XH1,PH  ACCUMULATE GEN'' REL''
        ADVANCE    1    DAILY DEVELOPMENT
        TEST GE    PH1,999,#D   DETERMINATION OF A LIFE STAGE
        LEAVE      #B   END OF A LIFE STAGE
        SAVEVALUE  1+,1,XF   SAVEVALUE FOR ADDRESS OF REL" DEV"
        HELPB      #LOGDEV,1XF,2XL,3XL,4XL   RELDEV" FOR NEXT STAGE
        SAVEVALUE  1+,1,XF   SAVEVALUE FOR STD" OF RELDEV"
        HELPB      #LOGDEV,1XF,2XL,3XL,4XL   STD" OF RELDEV FOR NEXT
        TEST LE    V3,0,#G   TEST WHETHER GEN'' REL'' DEV'' IS BELOW ZERO
        SAVEVALUE  1,0,XH   SAVEVALUE 0 FOR MINUS OR 0 RELDEV
        TRANSFER   ,#H   CCNNECT TO MAIN BRANCH
 #G     SAVEVALUE  1,V3,XH   SAVEVALUE FOR REL DEV"
 #H     SAVEVALUE  DELA,XH1,XH   CUMULATED DEVELOPMENT
        ASSIGN     1,V14,PH   ASSIGN CUMULATIVE DEVELOPMENT BET" STAGE
        ENDMACRO
 *
        LOAD       DAG06,LOGDEV
 *
 ****************************************************************************
 *
 *      COMMENTS
 *
 ****************************************************************************
 *
 * A GPSS MODEL FOR DETERMINING LAWN ARMYWORM DEVELCPMENT
 * 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 INTIAL
* POPULATION OF THE FIRST INSAR LARVAE.
*
* THE FIRST MACRO, BAMO, DETERMINED NATURAL MORTALITY WITHIN A
* LIFE STAGE UNDER FAVORALBE ENVIRONMENTAL CONDITIONS.
*
* THE SECOND MACRO, DEV, DETERMINED THE DEVELOPMENTAL PERIOD
* WITHIN A LIFE STAGE.
*
* AFTER COMPLETING THE FIRST GENRATION, 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 ADULTS CN THE FIRST CAY 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.
*
*   ***
*
*   FUNCTICNS
*
*   ***
*
 NORM   FUNCTICN   RN1,C27 GEN* NORMAL DISTRIBUTION PATT*
0,-3.5/.0013,-3.0/.0035,-2.75/.0062,-2.5/.0122,-2.25/.0228,-2.0
.0401,-1.75/.0668,-1.5/.1056,-1.25/.1587,-1.00/.2266,-.75/.3085,-.5
.4013,-.25/.5,0/.5987,.25/.6915,.50/.7734,.75/.8413,1/.8944,1.25
.9332,1.5/.9599,1.75/.9772,2/.9878,2.25/.9938,2.5/.9965,2.75
.9987,3.0/1,3.5
*
 ATE   FUNCTICN   AC1,L43 DAILY AVERAGE TEMP** FROM 790917
,240/,263/,262/,262/,264/,259/,257/   7909:
,253/,258/,263/,250/,258/,265/,266/,249/,255/,265/,265/,262/,265/,261/   7909:
,270/,261/,270/,278/,272/,280/,275/,275/,279/,261/,272/,270/,267/,262/   7910(

```
,263/,255/,270/,263/,268/,259/,265/,272/,268/,251/,241/,268/,267/,266/   79102.
,268/,272/,268/,243/,235/,242/,240/,260/,238/,220/,238/,245/,243/,243/   79110!
*
*      *****************************************
*
*      VARIABLES
*
*      *****************************************
*
1      VARIABLE     AC1-2  DAY(S) AFTER INFESTATION
2      FVARIABLE    FN$ATE/10   DAILY AVERAGE TEMPERATURE (ACTUAL)
3      FVARIABLE    1000*(XL3*FN$NORM+XL2)  GEN'' RELATIVE DEVELCPMENT
4      FVARIAILE    1.90*FN$NORM+9.01   LONGEVITY OF AN ADULT
5      FVARIAILE    RN2*2/1000  LONGI'' OF NATU'' DYING II TO IV LARVA
6      FVARIABLE    RN2*3/1000 LONGI'' OF NATU'' DYING I, V & VI LARVA
8      FVARIABLE    RN2*7/1000 LONGI'' OF NATU'' DYING VII LARVA
9      FVARIABLE    RN2*12/1000 LONGI'' OF NATU'' DYING PUPA
10     FVARIABLE    RN2*9/1000  LONGI'' OF NATU'' DYING ADULT
12     FVARIABLE    V4-1  LONGEI'' OF ADULT MOTH (MINUS 1 DAY)
14     FVARIABLE    (PH1-1000)*XH$DELA/1000   CUMU* DEV* BET* STAGE
*
*      FOOD CCNSUMPTICN
25     FVARIABLE    (0.5*S1+1.1*S2+3.0*S3+9.2*S4)/1000   DAM'' AT YOUNG
26     FVARIABLE    (27.4*S5+83.0*S6+316.7*S7)/1000  DAM'' AT OLD STAGE
FOOD   FVARIABLE    V25+V26  DAILY TOTAL FOOD DAMAGE
*
*******************************************************************************
*
*      BASIC LIFE MODEL
*
*******************************************************************************
*
       GENERATE     1,,,1,,1PH  GENERATION OF ORIGINAL TRANSACTION
       SPLIT        100,INS1  INITIAL PGP'' OF 1ST INSTAR LARVAE
       TERMINATE         TERMINATION CF ORIGINAL TRANSACTION
*
*      ***************************************
*
*      FIRST INSTAR LARVA
*
*      ***************************************
*
BAMO   MACRO        INS1,.933,DUM1,1,V6
INS1   TRANSFER     .933,,DUM1
       ENTER        1
       ADVANCE      V6
       LEAVE        1
       TERMINATE
DEV    MACRO        DUM1,1,1,AAA,XXX11,XXX12,XXX13,XXX14
DUM1   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,XH
        TRANSFER    ,XXX12
XXX11   SAVEVALUE   1,V3,XH
XXX12   ASSIGN      1+,XH1,PH
        ADVANCE     1
        TEST GE     PH1,999,AAA
        LEAVE       1
        SAVEVALUE   1+,1,XF
        HELPB       #LOGDEV,1XF,2XL,3XL,4XL
        SAVEVALUE   1+,1,XF
        HELPB       #LOGDEV,1XF,2XL,3XL,4XL
        TEST LE     V3,0,XXX13
        SAVEVALUE   1,0,XH
        TRANSFER    ,XXX14
XXX13   SAVEVALUE   1,V3,XH
XXX14   SAVEVALUE   DELA,XH1,XH
        ASSIGN      1,V14,PH
*
*       **************************************************
*
*       SECOND INSTAR LARVA
*
*       **************************************************
*
BAMO    MACRO       INS2,.999,DUM2,2,V5
INS2    TRANSFER    .999,,DUM2
        ENTER       2
        ADVANCE     V5
        LEAVE       2
        TERMINATE
DEV     MACRO       DUM2,2,3,BBB,XXX21,XXX22,XXX23,XXX24
DUM2    ENTER       2
BBB     SAVEVALUE   1,V2,XL
        SAVEVALUE   1,3,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,XXX21
        SAVEVALUE   1,0,XH
        TRANSFER    ,XXX22
XXX21   SAVEVALUE   1,V3,XH
XXX22   ASSIGN      1+,XH1,PH
        ADVANCE     1
        TEST GE     PH1,999,BBB
        LEAVE       2
        SAVEVALUE   1+,1,XF
        HELPB       #LOGDEV,1XF,2XL,3XL,4XL
        SAVEVALUE   1+,1,XF
        HELPB       #LOGDEV,1XF,2XL,3XL,4XL
        TEST LE     V3,0,XXX23
        SAVEVALUE   1,0,XH
        TRANSFER    ,XXX24
XXX23   SAVEVALUE   1,V3,XH
XXX24   SAVEVALUE   DELA,XH1,XH
```

```
        ASSIGN      1,V14,PH
*
*       ***********************************************
*
*       THIRD  INSTAR LARVA
*
*       ***********************************************
*
BAMO    MACRC       INS3,.976,DUM3,3,V5
INS3    TRANSFER    .976,,DUM3
        ENTER       3
        ADVANCE     V5
        LEAVE       3
        TERMINATE
DEV     MACRO       DUM3,3,5,CCC,XXX31,XXX32,XXX33,XXX34
DUM3    ENTER       3
CCC     SAVEVALUE   1,V2,XL
        SAVEVALUE   1,5,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,XXX31
        SAVEVALUE   1,0,XH
        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,1XF,2XL,3XL,4XL
        SAVEVALUE   1+,1,XF
        HELPB       #LOGDEV,1XF,2XL,3XL,4XL
        TEST LE     V3,0,XXX33
        SAVEVALUE   1,0,XH
        TRANSFER    ,XXX34
XXX33   SAVEVALUE   1,V3,XH
XXX34   SAVEVALUE   DELA,XH1,XH
        ASSIGN      1,V14,PH
*
*       ***********************************************
*
*       FOURTH INSTAR LARVA
*
*       ***********************************************
*
BAMO    MACRC       INS4,.976,DUM4,4,V5
INS4    TRANSFER    .976,,DUM4
        ENTER       4
        ADVANCE     V5
        LEAVE       4
        TERMINATE
DEV     MACRO       DUM4,4,7,DDD,XXX41,XXX42,XXX43,XXX44
DUM4    ENTER       4
DDD     SAVEVALUE   1,V2,XL
```

```
        SAVEVALUE    1,7,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,XXX41
        SAVEVALUE    1,0,XH
        TRANSFER     ,XXX42
XXX41   SAVEVALUE    1,V3,XH
XXX42   ASSIGN       1+,XH1,PH
        ADVANCE      1
        TEST GE      PH1,999,DDD
        LEAVE        4
        SAVEVALUE    1+,1,XF
        HELPB        #LOGDEV,1XF,2XL,3XL,4XL
        SAVEVALUE    1+,1,XF
        HELPB        #LOGDEV,1XF,2XL,3XL,4XL
        TEST LE      V3,0,XXX43
        SAVEVALUE    1,0,XH
        TRANSFER     ,XXX44
XXX43   SAVEVALUE    1,V3,XH
XXX44   SAVEVALUE    DELA,XH1,XH
        ASSIGN       1,V14,PH
*
*
*        **************************************************
*
*        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
        HELPB        #LOGDEV,1XF,1XL,2XL,3XL
        SAVEVALUE    1+,1,XF
        HELPB        #LOGDEV,1XF,1XL,2XL,3XL
        TEST LE      V3,0,XXX51
        SAVEVALUE    1,0,XH
        TRANSFER     ,XXX52
XXX51   SAVEVALUE    1,V3,XH
XXX52   ASSIGN       1+,XH1,PH
        ADVANCE      1
        TEST GE      PH1,999,EEE
        LEAVE        5
        SAVEVALUE    1+,1,XF
        HELPB        #LOGDEV,1XF,2XL,3XL,4XL
```

```
        SAVEVALUE    1+,1,XF
        HELPB        #LOGDEV,1XF,2XL,3XL,4XL
        TEST LE      V3,0,XXX53
        SAVEVALUE    1,0,XH
        TRANSFER     ,XXX54
XXX53   SAVEVALUE    1,V3,XH
XXX54   SAVEVALUE    DELA,XH1,XH
        ASSIGN       1,V14,PH
*
*       ************************************************
*
*       SIXTH INSTAR LARVA
*
*       ************************************************
*
BAMO    MACRO        INS6,,947,DUM6,6,V6
INS6    TRANSFER     .947,,DUM6
        ENTER        6
        ADVANCE      V6
        LEAVE        6
        TERMINATE
DEV     MACRO        DUM6,6,11,FFF,XXX61,XXX62,XXX63,XXX64
DUM6    ENTER        6
FFF     SAVEVALUE    1,V2,XL
        SAVEVALUE    1,11,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,XXX61
        SAVEVALUE    1,0,XH
        TRANSFER     ,XXX62
XXX61   SAVEVALUE    1,V3,XH
XXX62   ASSIGN       1+,XH1,PH
        ADVANCE      1
        TEST GE      PH1,999,FFF
        LEAVE        6
        SAVEVALUE    1+,1,XF
        HELPB        #LOGDEV,1XF,2XL,3XL,4XL
        SAVEVALUE    1+,1,XF
        HELPB        #LOGDEV,1XF,2XL,3XL,4XL
        TEST LE      V3,0,XXX63
        SAVEVALUE    1,0,XH
        TRANSFER     ,XXX64
XXX63   SAVEVALUE    1,V3,XH
XXX64   SAVEVALUE    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     MACRC       DUM7,7,13,GGG,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+,XH1,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,HHH,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
        SAVEVAL''E  1+,1,XF
        HELPB       #LOGDEV,1XF,1XL,2XL,3XL
        TEST LE     V3,0,XXX81
        SAVEVALUE   1,0,XH
        TRANSFER    ,XXX82
```

```
XXX81 SAVEVALUE   1,V3,XH
XXX82 ASSIGN      1+,XH1,PH
      ADVANCE     1
      TEST GE     PH1,999,HHH
      LEAVE       8
      SAVEVALUE   1+,1,XF
      HELPB       #LOGDEV,1XF,2XL,3XL,4XL
      SAVEVALUE   1+,1,XF
      HELPB       #LOGDEV,1XF,2XL,3XL,4XL
      TEST LE     V3,0,XXX83
      SAVEVALUE   1,0,XH
      TRANSFER    ,XXX84
XXX83 SAVEVALUE   1,V3,XH
XXX84 SAVEVALUE   DELA,XH1,XH
      ASSIGN      1,V14,PH
*
*
*     ***********************************************
*
*     ADULT STAGE
*
*     ***********************************************
*
INS9  ENTER       10  BEGINNING OF ADULT STAGE
      ENTER       9   BEGINNING OF THE FIRST DAY OF EMERGENCE
      ADVANCE     1   DAILY DEVELOPMENT
      LEAVE       9   END OF THE FIRST DAY OF EMERGENCE
      ADVANCE     V12 LOGEIVITY OF ADULT MINUS ONE DAY
      LEAVE       10  END OF ADULT STAGE
      TERMINATE       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   DADAM,VSFOOD,XL   DAILY FOODAM" BY ARMYWORM LARVAE
      SAVEVALUE   CUDA+,XL$DACAM,XL  CUMULATIVE DAILY FOOD DAMAGE
      TERMINATE   1   TIMER COUNTING
      START       55,,1
*
*     ***********************************************
*
*     OUTPUT CONTROL
*
*     ***********************************************
*
      REPORT
      TEXT        #XH2,2/XX# DAY(S) AFTER INITIAL INFESTATION
STO   TITLE       ,AGE COMPOSITION  (NO. OF INDIVIDUALS PER 100  UNIT)
LSV   TITLE       ,FOOD CONSUMPTION AND POLYHEDRA PRODUCTION
      END
```

```
C.... SUBROUTINE LOGDEV CALCULATES DEVELOPMENTAL UNIT
C     (RELATIVE) BY THE LOGISTIC EQUATION.
      SUBROUTINE LOGDEV(IX1,FX2,FX3,FX4)
      GO TO (1,11,2,12,3,13,4,14,5,15,6,16,7,17,8,18),IX1
    1 FX3=0.530/(1+ EXP(6.111386-0.285421*FX2))
      RETURN
   11 FX4=FX3*ABS(FX3-0.530)/0.530*SQRT(0.382990*(1.2+(FX2-25.0)**2
     1/250))
      RETURN
    2 FX3=1.000/(1+ EXP(5.721318-0.226826*FX2))
      RETURN
   12 FX4=FX3*ABS(FX3-1.000)*SQRT(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)*SQRT(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)*SQRT(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*SQRT(0.347708*(1.2+(FX2-25.0)**2
     1/250))
      RETURN
    6 FX3=0.570/(1+ EXP(5.523347-0.233768*FX2))
      RETURN
   16 FX4=FX3*ABS(FX3-0.570)/0.570*SQRT(0.321369*(1.2+(FX2-25.0)**2
     1/250))
      RETURN
    7 FX3=0.420/(1+ EXP(7.342200-0.275901*FX2))
      RETURN
   17 FX4=FX3*ABS(FX3-0.420)/0.420*SQRT(0.235684*(1.2+(FX2-25.0)**2
     1/250))
      RETURN
    8 FX3=0.168/(1+ EXP(6.538893-0.282580*FX2))
      RETURN
   18 FX4=FX3*ABS(FX3-0.168)/0.168*SQRT(0.216730*(1.2+(FX2-25.0)**2
     1/250))
      RETURN
      END
```

```
        APPENDIX F.  A SIMULATION PROGRAM FOR THE EPIZOOTIOLOGICAL MODEL


R  *LOC     OPERATION   A,B,C,D,E,F,G,H,I          COMMENTS
           SIMULATE
   BAMO    .STARTMACRO     DETER" 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     VSMORT1,999,#D   SELEC" BASIC MORT" OVER 999
            TRANSFER    ,#E  CONNECT TC DEV MACRO
   #D       SAVEVALUE   3,VSMORT1,XH   SAVEVALUE PROB" CRITERIA FOR SURV"
            TRANSFER    .XH3,,#E  CONNECT TO DEV MACRO
            ENTER       #F  BEGINNING OF A LIFE STAGE
            ADVANCE     #G  DEVELOPMENT OF NATU" DYING INDI"
            LEAVE       #F  END OF A LIFE STAGE
            ENDMACRO
   *
   DEV     STARTMACRO      DETER'' OF PHYSIOLOGICAL DEVEL'' 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   AVER'' TOTAL EFFEC'' DAY-DEGREES FOR STAGE
            ASSIGN      3,#E,PL   STD'' OF TOTAL EFFEC'' DAY-DEGREES
            ASSIGN      4,V3,PL   NORM'' GENER'' TOT'' EFFE'' DD'' FOR INDI''
   #F       ASSIGN      5+,V2,PL   ACCUMUL'' DAILY EFFEC'' DAY-DEGREES
            ADVANCE     1   DAILY DEVELOPMENT
            TEST GE     PL5,PL4,#F  'DETER'' OF 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   DELAYED EFFEC'' DD'' FOR NEXT STAGE
            ENDMACRO
   *
   SPRAY   STARTMACRO       VIRUS SPRAY TO THE ARMYWORM POPULATION
   #A       TEST E      AC1,1,#B  DETER'' VIRUS SPRAY TIME
            SAVEVALUE   4,9.0000,XL   DETER" VIRUS CONCENTRATION
            TRANSFER    ,#C  CONNECT TO VIRUS-INFECTED STAGE
            ENDMACRO
   *
   NOMA    STARTMACRO       DETER" MORT" IN A NORMAL DISTRI" PATTERN
   #A       SAVEVALUE   1,#B,XF   ADDRESS FOR MORT" IN VIMORT
            SAVEVALUE   #C,0,XL   SAVEVALUE FOR MORT''
            SAVEVALUE   #D,0,XL   SAVEVALUE FOR STD'' OF MORT''
            HELPB       #VIMORT,1XF,4XL,#E,#F   DETER" MORT"
            SAVEVALUE   1+,1,XF   ADDRESS FOR STD" OF MORT" IN VIMORT
            HELPB       #VIMORT,1XF,4XL,#E,#F   CAL STD" OF MORT"
            ENDMACRO
   *
   CHOO    STARTMACRO       ADJUST CAL" MORT" IN 0 - 100 % RNAGE
            TEST LE     #A,0,#B   SELECT NEGATIVE MORT"
            SAVEVALUE   1,1,XH   SAVE VALUE FOR NEGATIVE VALUES
            TRANSFER    ,#C  CONNECT TO NEXT STAGE
   #B       TEST GE     #A,#D,#E   SELECT VALUES MORE THAN 100 % RANGE
            SAVEVALUE   1,#D,XH   SAVEVALUE FOR VALUES MORE THAN 100 % RANGE
            TRANSFER    ,#F  CONNECT TO NEXT STAGE
   #E       SAVEVALUE   1,#A,XH   SAVEVALUE FOR MORT'' IN EFFEC" RANGE
   #F       SAVEVALUE   2,XH1,XH   SAVEVALUE FOR EFFEC" MORT"
            ENDMACRO
   *
   TRAN    STARTMACRO       DETER'' MORTALITY
            TRANSFER    .XH2,,#A   DETER" VIRUS-KILLED INDI"
```

```
          TRANSFER    ,#B   CONNECT TO NEXT STAGE
          ENDMACRO
*
  VDEV    STARTMACRO        CEVELOPMENT OF VIRUS-YIELDED INDIVIDUALS
  #A      ENTER       #B   BEGINNING OF VIRUS-YIELDED LIFE STAGE
          ASSIGN      4,0,PB  ASSIGN DEV'' PERIOD AS ZERO
  DEV     MACRO       #C,#D,#E,#F,#G,#H,#I   DEV" PER" FOR INDI"
          LEAVE       #B   END OF VIRUS-YIELDED LIFE STAGE
          ENDMACRO
*
  VDED    STARTMACRO        LETHAL PERIOD OF VIRUS-KILLED INDIVIDUALS
  #A      ENTER       #B   BEGINNING OF VIRUS-YIELDED LIFE STAGE
          ENTER       #C   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 TRANFO
          SAVEVALUE   13,#F,XL   SAVEVALUE MEAN (LOG) OF POLYHEDRA PER CAD"
          SAVEVALUE   14,#G,XL   SAVEVALUE STD" FOR MEAN POLYHEDRA (LOG)
          SAVEVALUE   15,VSPOL,XL   SAVEVALUE FOR LOG OF POL" PRODUCTION
          SAVEVALUE   16,0,XL   SET O FOR POL" PRODUCTION
          HELPB       #TRANFO,1XF,15XL,16XL   TRANS"" FOR POL" PRODUC"
          SAVEVALUE   17+,XL16,XL   SAVEVALUE FOR DAILY POLYHEDRA
          SAVEVALUE   CUPOL+,XL16,XL   CUMUL" DAILY POL" PRODUCTION
          SAVEVALUE   DAPOL,XL17,XL   DAILY PRODU" POLYHEDRA
          SAVEVALUE   17,0,XL   SET DAILY POL" 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        DAG06,TRANFO,VIMORT
*
*****************************************************************
*
*
* A GPSS MODEL TO DETERMINE THE DEVELOPMENT OF NPV EPIZOOTICS IN
* THE LAWN ARMYWORM.
*
* 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 HAS ASSUMED THAT 10**9 POLYHEDRA PER 100 SQUARE
* CM OF LAWN SURFACE WAS SPRAYED ON THE INTIAL DAY.
*
* THE NEWLY EMERGED ADULTS WERE TERMINATED WITHOUT STARTING NEW
* LIFE CYCLE.
*
* THE FIRST MACRO, BAMO, DETERMINED NATURAL MORTALITY WITHIN A
* LIFE STAGE UNDER FAVORALBE 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, WOMA, 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, VDEV, DETERMINED THE DEVELOPMENTAL PERIOD OF
* THE INFECTED LARVAE AT THE STAGES BEFORE DEATH.
*
* THE LAST MACRO, VDED, 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 TWO DIGIT STORATE CONTENT NO. 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 MENAS 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**9 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,-3.5/.0013,-3.0/.0035,-2.75/.0062,-2.5/.0122,-2.25/.0228,-2.0
.0401,-1.75/.0668,-1.5/.1056,-1.25/.1587,-1.00/.2266,-.75/.3085,-.5
.4013,-.25/.5,0/.5987,.25/.6915,.50/.7734,.75/.8413,1/.8944,1.25
.9332,1.5/.9599,1.75/.9772,2/.9878,2.25/.9938,2.5/.9965,2.75
.9987,3.0/1,3.5
 *        INTRODUCTION PATTERN OF ADULTS
 MOC1   FUNCTION    RN1,C2   UNIFORM INTRODUCTION OF FEMALES
0,1/.999,14
 *        OVIPOSITION
 PREOV  FUNCTION    RN1,C7   DETER'' OF PRE-OVIPOSTION PERIOD
.0111,1/.0888,2/,4110,3/.7998,4/.9330,5/.9885,6/.9999,7
 *
 OVIPE  FUNCTION    RN1,D10  DETER'' OF OVI-POSITION PERIOD
.0111,1/.0667,2/.1443,3/.3221,4/.5221,5/.6887,6/.8442,7/.9330,8
.9885,9/.9999,10
 *
 EGSTA  FUNCTION    XF1,L18  STD'' OF DAILY EGG PRODUCTION
,272/,173/,161/,106/,89/,55/,56/,39/,54/,10/,1/,1/,1/,1/,1/,1/,1/,1
 *
 ATE    FUNCTION    AC1,L40  DAILY AVERAGE TEM" FROM 800102
,246/,242/,242/,232/,222/,228/,230/,241/,229/,238/,237/,243          3001
,244/,242/,260/,243/,245/,235/,239/,230/,210/,223/,226/,221/,227/,239/  3001
,233/,237/,223/,212/,215/,227/,229/,241/,246/,245/,254/,244/,256/,241/  3001
 *
 *        FUNCTIONS FOR LETHAL INFECTION (STAGE-SPECIFIC) PERIOD
 LIP11  FUNCTION    RN1,D5
0.017,4/0.068,5/0.305,6/0.983,7/0.999,8
 LIP12  FUNCTION    RN1,D6
0.063,1/0.250,2/0.438,3/0.688,4/0.875,5/0.999,6
 LIP13  FUNCTION    RN1,D3
0.250,3/0.500,6/0.999,7
 LIP21  FUNCTION    RN1,D5
```

```
0.125,3/0.261,4/0.438,5/0.969,6/0.999,7
  LIP22 FUNCTION    RN1,06
0.054,2/0.174,3/0.523,4/0.832,5/0.946,6/0.999,7
  LIP23 FUNCTION    RN1,07
0.059,1/0.118,2/0.471,3/0.892,4/0.912,5/0.971,7/0.999,9
  LIP31 FUNCTION    RN1,07
0.028,2/0.083,3/0.250,5/0.444,6/0.833,7/0.917,8/0.999,9
  LIP32 FUNCTION    RN1,08
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    RN1,07
0.043,1/0.217,2/0.478,3/0.652,4/0.739,5/0.870,6/0.999,7
  LIP41 FUNCTION    RN1,04
0.083,6/0.333,7/0.583,8/0.999,9
  LIP42 FUNCTION    RN1,09
0.010,2/0.061,3/0.273,4/0.495,5/0.788,6/0.927,7/0.980,8/0.990,9
0.999,11
  LIP43 FUNCTION    RN1,08
0.152,1/0.333,2/0.545,3/0.667,4/0.818,5/0.879,6/0.970,7/0.999,10
  LIP51 FUNCTION    RN1,02
0.500,6/0.999,7
  LIP52 FUNCTION    RN1,07
0.027,3/0.081,4/0.284,5/0.563,6/0.784,7/0.932,8/0.999,9
  LIP53 FUNCTION    RN1,06
0.250,1/0.542,2/0.750,3/0.917,4/0.958,5/0.999,7
  LIP61 FUNCTION    RN1,02
0.333,4/0.999,7
  LIP62 FUNCTION    RN1,07
0.103,1/0.526,2/0.722,3/0.804,4/0.866,5/0.969,6/0.999,7
*
**********************************************************************
*
*     VARIABLES
*
**********************************************************************
*
 1     VARIABLE    AC1-2  DAYS AFTER INTRODUCTION OF ORIGINAL INDI"
 2     FVARIABLE   FN$ATE/10-PL1   EFFECTIVE TEMPERATURE (DAY-DEGREES)
 3     FVARIABLE   PL3*FN$NORM+PL2  TOTAL EFFECTIVE TEMPERATURE
 4     FVARIABLE   1.54*FN$NORM+9.32   LONGEVITY OF AN ADULT
 5     FVARIABLE   RN2*2/1000  LONGI'' OF NATU'' DYING II TO IV LARVA
 6     FVARIABLE   RN2*3/1000  LONGI'' OF NATU'' DYING I, V & VI LARVA
 7     FVARIABLE   RN2*4/1000   LONGI'' OF NAT" DYING EGG
 8     FVARIABLE   RN2*7/1000  LONGI'' OF NATU'' DYING VII LARVA
 9     FVARIABLE   RN2*12/1000  LONGI'' OF NATU'' DYING PUPA
10     FVARIABLE   RN2*9/1000  LONGI'' OF NATU'' DYING ADULT
11     FVARIABLE   (PL5/PL4-1)*XL$NEXT  CUM" EFF" DD" FOR NEXT STAGE
12     FVARIABLE   2*FN$NORM+8  LONGI'' OF ADULT MOTH (MINUS 1 DAY )
13     FVARIABLE   (FN$EGSTA*FN$NORM+XL18)/50   DAILY EGG PRODUC"
*
MORT1 FVARIABLE   XH2*FN$NORM+XH1  BASIC MORTALITY IN 1000 UNIT
PROV  VARIABLE    FN$PREOV-1  INTC" OF FEMALE (PREOC" MINUS ONE DAY)
*
15     FVARIABLE   1000*(XL6*FN$NORM+XL5)  TOTAL MORTALITY
16     FVARIABLE   1000*(XL6*FN$NORM+XL7)  FIRST STAGE-SPECIFIC MORT''
17     FVARIABLE   1000*(XL10*FN$NORM+XL9)  SECOND STAGE-SPECIFIC MORT''
18     FVARIABLE   1000*(V16/XH2)  MORT'' PRO'' FOR FIRST INF'' STAGE
19     FVARIABLE   1000*(V17/(1000-XH2))  RCPU'' FOR SECOND INF'' STAGE
```

```
*        FOOD DAMAGE
 25      FVARIABLE   (0.5*S1+1.1*S2+3.0*S3+9.2*S4)/1000   DAM** AT YOUNG
 26      FVARIABLE   (27.4*S5+83.0*S6+316.7*S7)/1000   DAM** AT OLD STAGE
 27      FVARIABLE   0.9*(0.5*S11+1.1*S12+3.0*S13+9.2*S14)/1000 DAMIN*
 28      FVARIAVLE   0.9*(27.4*S15+83.0*S16)/1000 DAM* AT SNI INF** STA*
 29      FVARIABLE   0.5*(0.5*S21+1.1*S22+3.0*S23+9.2*S24)/1000 DA** SEC**
 30      FVARIABLE   0.5*(27.4*S25+83.0*S26)/1000 DAM** AT SEC** INF** STA
 31      FVARIABLE   0.1*(0.5*S31+1.1*S32+3.0*S33+9.2*S34)/1000 DA** TER**
 32      FVARIABLE   0.1*(27.4*S35+83.0*S36)/1000   DAM** AT SEC** STA
 FOOD    FVARIABLE   V25+V26+V27+V28+V29+V30+V31+V32       FOOD DAMAGE
*        POLYHEDRA PRODUCTION FROM CADAVER
 POL     FVARIABLE   XL14*FNSNORM+XL13  GEN* POLY* NO. (COMMON LOG)
*
************************************************************************
*
*        BASIC LIFE MODEL
*
************************************************************************
*
*        ***********************************************
*
*        GENERATION OF INITIAL TRANSACTIONS
*
*        ***********************************************
*
         GENERATE    1,,,1,,1PH,4PB,7PL   INTRO** OF ORI* TRANSACTION
         SPLIT       100,SPA50  INITAL POPUALTION OF  V INSTAR
         TERMINATE        TERMINATE ORIGINAL TRANSACTION
*
*        INTRODUCTION OF ADULTS
*        ***********************************************
*
 FEM     ADVANCE     FNSMOC1  INTRODUCTION OF FEMALE
         ENTER       10  ENTER ADULT STAGE
         ENTER       9   ENTER THE FIRST DAY OF INTRODUCTION
         ADVANCE     1   FIRST DAY OF INTRO* OF FEMALE
         LEAVE       9   LEAVE THE FIRST DAY OF INTRODUCTION
*
*        OVIPOSITION
*        ***********************************************
*
 RPT     ADVANCE     VSPROV  PREOVI* PERIOD (MINUS ONE DAY)
         ASSIGN      2,FNSOVIPE,PB  DETER** OVIPUSTION PERIOD
 OPI3    ADVANCE     1  DAILY DEVELCPMENT OF A FEMALE DURING OVIPO**
         ASSIGN      3+,1,PB  ASSIGN OVIPOSITION DAY
         SAVEVALUE   1,1,XF  ADDRESS FOR EGG PRODUCTION (TRANFO)
         SAVEVALUE   15,PB3,XL  SAVEVALUE FOR OVIPOSITION DAY
         SAVEVALUE   16,0,XL  SET 0 FOR EGG PRODUCTION
         HELPB       *TRANFO,1XF,15XL,16XL  DET* EGG PRODUCTION
         ASSIGN      1,V13,PH  ASSIGN DAILY EGG PRODUCTION
         TEST LE     PH1,0,OPI1  SELEC* EFFEC* OVIPO*
         TRANSFER    ,OPI2  CONNECTION
 OPI1    SPLIT       PH1,INSO  DAILY OVIPOSITION
 OPI2    LOOP        2PB,OPI3  REPEAT OVIPOSITION
         ASSIGN      3,0,PB  ASSIGN OVIPOSITION DAY AS ZERO
         ADVANCE     V6  POST-OVIPOSITION PERIOD
         LEAVE       10  LEAVE ADULT STAGE
```

```
        TERMINATE      FEMALE IS TERMINATED
*
*       EGG DEVELOPMENT
*       *****************************************
*
 BAMO   MACRO          INS0,933,10,hWh0,DUMO,60,V7
 INS0   SAVEVALUE      1,933,XH
        SAVEVAL I      2,10,XH
        TEST GE        V$MORT1,999,hWh0
        TRANSFER       ,DUMO
 hWh0   SAVEVALUE      3,V$MORT1,XH
        TRANSFER       .XH3,,DUMO
        ENTER          60
        ADVANCE        V7
        LEAVE          60
 DEV    MACRO          DUMO,60,10.7,59.46,10.05,ZZZ,33.33
 DUMO   ENTER          60
        ASSIGN         1,10.7,PL
        ASSIGN         2,59.46,PL
        ASSIGN         3,10.05,PL
        ASSIGN         4,V3,PL
 ZZZ    ASSIGN         5+,V2,PL
        ADVANCE        1
        TEST GE        PL5,PL4,ZZZ
        LEAVE          60
        SAVEVALUE      NEXT,33.33,XL
        ASSIGN         5,V11,PL
*
*       FIRST INSTAR LARVA
*       *****************************************
*
 SPRAY  MACRO          SPA10,INS1,VIM11
 SPA10  TEST E         AC1,1,INS1
        SAVEVALUE      4,9.0000,XL
        TRANSFER       ,VIM11
 BAMC   MACRO          INS1,933,38,hWh1,DUM1,1,V6
 INS1   SAVEVALUE      1,933,XH
        SAVEVALUE      2,38,XH
        TEST GE        V$MORT1,999,hWh1
        TRANSFER       ,DUM1
 hWh1   SAVEVALUE      3,V$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
        SAVEVALUE   4,9.0000,XL
        TRANSFER    ,VIM21
 3AMO   MACRO      INS2,999,38,hhh2,DUM2,2,V5
 INS2   SAVEVALUE   1,999,XH
        SAVEVALUE   2,38,XH
        TEST GE     V$MORT1,999,hhh2
        TRANSFER    ,DUM2
 hhh2   SAVEVALUE   3,V$MORT1,XH
        TRANSFER    .XH3,,DUM2
        ENTER       2
        ADVANCE     V5
        LEAVE       2
 DEV    MACRO      DUM2,2,14.4,26.52,4.36,BBB,28,83
 DUM2   ENTER       2
        ASSIGN      1,14.4,PL
        ASSIGN      2,26.52,PL
        ASSIGN      3,4.86,PL
        ASSIGN      4,V3,PL
 BBB    ASSIGN      5+,V2,PL
        ADVANCE     1
        TEST GE     PL5,PL4,BBB
        LEAVE       2
        SAVEVALUE   NEXT,28,XL
        ASSIGN      5,V11,PL
*
*         THIRD INSTAR LARVA
*         *********************************************
*
 SPRAY  MACRO      SPA30,INS3,VIM31
 SPA30  TEST E      AC1,1,INS3
        SAVEVALUE   4,9.0000,XL
        TRANSFER    ,VIM31
 BAMO   MACRO      INS3,967,24,hhh3,DUM3,3,V5
 INS3   SAVEVALUE   1,967,XH
        SAVEVALUE   2,24,XH
        TEST GE     V$MORT1,999,hhh3
        TRANSFER    ,DUM3
 hhh3   SAVEVALUE   3,V$MORT1,XH
        TRANSFER    .XH3,,DUM3
        ENTER       3
        ADVANCE     V5
        LEAVE       3
 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,V3,PL
 CCC    ASSIGN      5+,V2,PL
        ADVANCE     1
        TEST GE     PL5,PL4,CCC
```

```
        LEAVE      3
        SAVEVALUE  NEXT,32.50,XL
        ASSIGN     5,V11,PL
*
*       FOURTH INSTAR LARVA
*       *******************************************
*
 SPRAY  MACRO      SPA40,INS4,VIM41
 SPA40  TEST E     AC1,1,INS4
        SAVEVALUE  4,9.0000,XL
        TRANSFER   ,VIM41
 BAMO   MACRO      INS4,968,32,hWh4,DUM4,4,V5
 INS4   SAVEVALUE  1,968,XH
        SAVEVALUE  2,32,XH
        TEST GE    VSMORT1,999,hWh4
        TRANSFER   ,DUM4
 hWh4   SAVEVALUE  3,VSMORT1,XH
        TRANSFER   .XH3,,DUM4
        ENTER      4
        ADVANCE    V5
        LEAVE      4
 DEV    MACRO      DUM4,4,13.6,32.50,7.01,DDD,34.49
 DUM4   ENTER      4
        ASSIGN     1,13.6,PL
        ASSIGN     2,32.50,PL
        ASSIGN     3,7.01,PL
        ASSIGN     4,V3,PL
 DDD    ASSIGN     5+,V2,PL
        ADVANCE    1
        TEST GE    PL5,PL4,DDD
        LEAVE      4
        SAVEVALUE  NEXT,34.49,XL
        ASSIGN     5,V11,PL
*
*       FIFTH INSTAR LARVA
*       *******************************************
*
 SPRAY  MACRO      SPA50,INS5,VIM51
 SPA50  TEST E     AC1,1,INS5
        SAVEVALUE  4,9.0000,XL
        TRANSFER   ,VIM51
 BAMO   MACRO      INS5,978,31,hWh5,DUM5,5,V6
 INS5   SAVEVALUE  1,978,XH
        SAVEVALUE  2,31,XH
        TEST GE    VSMOPT1,999,hWh5
        TRANSFER   ,DUM5
 hWh5   SAVEVALUE  3,VSMORT1,XH
        TRANSFER   .XH3,,DUM5
        ENTER      5
        ADVANCE    V6
        LEAVE      5
 DEV    MACRO      DUM5,5,13.3,34.49,8.35,EEE,43.91
 DUM5   ENTER      5
        ASSIGN     1,13.3,PL
        ASSIGN     2,34.49,PL
        ASSIGN     3,8.35,PL
        ASSIGN     4,V3,PL
```

```
EEE     ASSIGN      5+,V2,PL
        ADVANCE     1
        TEST GE     PL5,PL4,EEE
        LEAVE       5
        SAVEVALUE   NEXT,43.91,XL
        ASSIGN      5,V11,PL
*
*       SIXTH INSTAR LARVA
*       ************************************************
*
SPRAY   MACRO       SPA60,INS6,VIM61
SPA60   TEST E      AC1,1,INS6
        SAVEVALUE   4,9.0000,XL
        TRANSFER    ,VIM61
BAMO    MACRO       INS6,946,14,wwh6,DU46,6,V6
INS6    SAVEVALUE   1,946,XH
        SAVEVALUE   2,14,XH
        TEST GE     VSMORT1,999,hwh6
        TRANSFER    ,DUM6
WWW6    SAVEVALUE   3,VSMURT1,XH
        TRANSFER    .XH3,,DUM6
        ENTER       6
        ADVANCE     V6
        LEAVE       6
DEV     MACRO       DUM6,6,12.2,43.91,8.98,FFF,50.31
DUM6    ENTER       6
        ASSIGN      1,12.2,PL
        ASSIGN      2,43.91,PL
        ASSIGN      3,8.98,PL
        ASSIGN      4,V3,PL
FFF     ASSIGN      5+,V2,PL
        ADVANCE     1
        TEST GE     PL5,PL4,FFF
        LEAVE       6
        SAVEVALUE   NEXT,50.81,XL
        ASSIGN      5,V11,PL
*
*       LAST INSTAR LARVA
*       ************************************************
*
BAMU    MACRO       INS7,900,78,wwh7,DUM7,7,V8
INS7    SAVEVALUE   1,900,XH
        SAVEVALUE   2,78,XH
        TEST GE     VSMORT1,999,wwh7
        TRANSFER    ,DUM7
wwh7    SAVEVALUE   3,VSMORT1,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
        TEST GE     PL5,PL4,GGG
        LEAVE       7
        SAVEVALUE   NEXT,110.42,XL
        ASSIGN      5,V11,PL
*
*       PUPAL STAGE
*       ***********************************************
*
BAMU    MACRO       INS8,906,55,hwh8,DUM8,8,V9
INS8    SAVEVALUE   1,906,XH
        SAVEVALUE   2,55,XH
        TEST GE     V$MORT1,999,hwh8
        TRANSFER    ,DUM8
hwh8    SAVEVALUE   3,V$MURT1,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
        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'' OF ADULT MOTH (MINUS 1 DAY)
        LEAVE       10   END OF ADULT STAGE;
        TERMINATE        PRODUCED ADULTS ARE TERMINATED
*
***********************************************************************
*
*       EPIZOOTIC MODEL
*
***********************************************************************
*
*       VIRUS SPRAY TO FIRST INSTAR
*       *****************************************
*
NOMA    MACRO       VIM11,1,5,6,5XL,6XL   TOT'' MORT'' FOR I
VIM11   SAVEVALUE   1,1,XF
        SAVEVALUE   5,0,XL
        SAVEVALUE   6,0,XL
        HELPB       #VIMORT,1XF,4XL,5XL,6XL
```

```
        SAVEVALUE    1+,1,XF
        HELPB        #VIMORT,1XF,4XL,5XL,6XL
CHOO    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,V15,XH
SPA14   SAVEVALUE    2,XH1,XH
TRAN    MACRO        AGE11,INS1
        TRANSFER     .XH2,,AGE11
        TRANSFER     ,INS1
*
*       AGE-SPECIFIC MORTALITY AT INITIAL STAGE OF THE FIRST INSTAR
*
NOMA    MACRO        AGE11,13,7,8,7XL,8XL   INTIAL STAGE-SPECIFIC MORT''
AGE11   SAVEVALUE    1,13,XF
        SAVEVALUE    7,0,XL
        SAVEVALUE    8,0,XL
        HELPB        #VIMORT,1XF,4XL,7XL,3XL
        SAVEVALUE    1+,1,XF
        HELPB        #VIMORT,1XF,4XL,7XL,3XL
CHOO    MACRO        V18,VIM12,AGE16,999,VIM13,VIM14
        TEST LE      V18,0,VIM12
        SAVEVALUE    1,1,XH
        TRANSFER     ,AGE16
VIM12   TEST GE      V18,999,VIM13
        SAVEVALUE    1,999,XH
        TRANSFER     ,VIM14
VIM13   SAVEVALUE    1,V18,XH
VIM14   SAVEVALUE    2,XH1,XH
TRAN    MACRO        FRV31,AGE16
        TRANSFER     .XH2,,FRV31
        TRANSFER     ,AGE16
VOED    MACRO        FRV31,31,41,FNSLIP11,51,6.2026,0.3452
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,V$PUL,XL
        SAVEVALUE    16,0,XL
        HELPB        #TRANFO,1XF,15XL,16XL
        SAVEVALUE    17+,XL16,XL
        SAVEVALUE    CUPCL+,XL16,XL
        SAVEVALUE    DAPCL,XL17,XL
        SAVEVALUE    17,0,XL
        ADVANCE      1
        LEAVE        51
        TERMINATE
*
```

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*       MORTALITY PROPORTICN AT TERTIARY STAGE OF THE FIRST INSTAR
*
NOMA   MACRO       AGE16,15,9,10,9XL,10XL    MORT** PROPOR** AT TER** STA
AGE16  SAVEVALUE   1,15,XF
       SAVEVALUE   9,0,XL
       SAVEVALUE   10,0,XL
       HELPB       #VIMORT,1XF,4XL,9XL,10XL
       SAVEVALUE   1+,1,XF
       HELPB       #VIMORT,1XF,4XL,9XL,10XL
CHOO   MACRO       V19,VIM15,AGE18,999,VIM16,VIM17
       TEST LE     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,XH1,XH
TRAN   MACRO       FRV11,AGE18
       TRANSFER    .XH2,,FRV11
       TRANSFER    ,AGE18
VDEV   MACRO       FRV11,11,ILA11,41,13.7,33.33,4.34,FRA11,26.52
FRV11  ENTER       11
       ASSIGN      4,0,PB
DEV    MACRO       ILA11,41,13.7,33.33,4.34,FRA11,26.52
ILA11  ENTER       41
       ASSIGN      1,13.7,PL
       ASSIGN      2,33.33,PL
       ASSIGN      3,4.34,PL
       ASSIGN      4,V3,PL
FRA11  ASSIGN      5+,V2,PL
       ADVANCE     1
       TEST GE     PL5,PL4,FRA11
       LEAVE       41
       SAVEVALUE   NEXT,26.52,XL
       ASSIGN      5,V11,PL
       LEAVE       11
VDEV   MACRO       FRV22,22,ILB22,42,14.4,26.52,4.86,FRB22,28.83
FRV22  ENTER       22
       ASSIGN      4,0,PB
DEV    MACRO       ILB22,42,14.4,26.52,4.86,FRB22,28.83
ILB22  ENTER       42
       ASSIGN      1,14.4,PL
       ASSIGN      2,26.52,PL
       ASSIGN      3,4.86,PL
       ASSIGN      4,V3,PL
FRB22  ASSIGN      5+,V2,PL
       ADVANCE     1
       TEST GE     PL5,PL4,FRB22
       LEAVE       42
       SAVEVALUE   NEXT,28.83,XL
       ASSIGN      5,V11,PL
       LEAVE       22
VDFD   MACRO       CAD13,33,43,FN$LIP13,53,7.2564,0.3243
CAD13  ENTER       33
       ENTER       43
       ADVANCE     FN$LIP13
```

```
              LEAVE        33
              LEAVE        43
              ENTER        53
              SAVEVALUE    1,2,XF
              SAVEVALUE    13,7.2564,XL
              SAVEVALUE    14,0.3243,XL
              SAVEVALUE    15,VSPUL,XL
              SAVEVALUE    16,0,XL
              HELPB        #TRANFU,1XF,15XL,16XL
              SAVEVALUE    17+,XL16,XL
              SAVEVALUE    CUPOL+,XL16,XL
              SAVEVALUE    OAPOL,XL17,XL
              SAVEVALUE    17,0,XL
              ADVANCE      1
              LEAVE        53
              TERMINATE
       VDEV   MACRO        AGE18,21,ILA21,41,13.7,33.33,4.34,FRA21,26.52
       AGE18  ENTER        21
              ASSIGN       4,0,PB
       OEV    MACRO        ILA21,41,13.7,33.33,4.34,FRA21,26.52
       ILA21  ENTER        41
              ASSIGN       1,13.7,PL
              ASSIGN       2,33.33,PL
              ASSIGN       3,4.34,PL
              ASSIGN       4,V3,PL
       FRA21  ASSIGN       5+,V2,PL
              ADVANCE      1
              TEST GE      PL5,PL4,FRA21
              LEAVE        41
              SAVEVALUE    NEXT,26.52,XL
              ASSIGN       5,V11,PL
              LEAVE        21
       VOEO   MACRO        CAO12,32,42,FNSLIP12,52,6.7602,0.2198
       CAO12  ENTER        32
              ENTER        42
              ADVANCE      FNSLIP12
              LEAVE        32
              LEAVE        42
              ENTER        52
              SAVEVALUE    1,2,XF
              SAVEVALUE    13,6.7602,XL
              SAVEVALUE    14,0.2198,XL
              SAVEVALUE    15,VSPUL,XL
              SAVEVALUE    16,0,XL
              HELPB        #TRANFO,1XF,15XL,16XL
              SAVEVALUE    17+,XL16,XL
              SAVEVALUE    CUPOL+,XL16,XL
              SAVEVALUE    OAPOL,XL17,XL
              SAVEVALUE    17,0,XL
              ADVANCE      1
              LEAVE        52
              TERMINATE
       *
       *      VIRUS SPRAY TO SECOND INSTAR
       *      *********************************************
       *
       NCMA   MACRO        VI421,3,5,6,5XL,6XL   TUMU** FOR II
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```
VIM21 SAVEVALUE   1,3,XF
      SAVEVALUE   5,0,XL
      SAVEVALUE   6,0,XL
      HELPB       #VIMORT,1XF,4XL,5XL,6XL
      SAVEVALUE   1+,1,XF
      HELPB       #VIMORT,1XF,4XL,5XL,6XL
CHOU  MACRO       V15,SPA22,INS2,999,SPA23,SPA24
      TEST LE     V15,0,SPA22
      SAVEVALUE   1,1,XH
      TRANSFER    ,INS2
SPA22 TEST GE     V15,999,SPA23
      SAVEVALUE   1,999,XH
      TRANSFER    ,SPA24
SPA23 SAVEVALUE   1,V15,XH
SPA24 SAVEVALUE   2,XH1,XH
TRAN  MACRO       AGE22,INS2
      TRANSFER    .XH2,,AGE22
      TRANSFER    ,INS2
*
*     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   7,0,XL
      SAVEVALUE   8,0,XL
      HELPB       #VIMORT,1XF,4XL,7XL,8XL
      SAVEVALUE   1+,1,XF
      HELPB       #VIMORT,1XF,4XL,7XL,8XL
CHOU  MACRO       V18,VIM22,AGE26,999,VIM23,VIM24
      TEST LE     V18,0,VIM22
      SAVEVALUE   1,1,XH
      TRANSFER    ,AGE26
VIM22 TEST GE     V18,999,VIM23
      SAVEVALUE   1,999,XH
      TRANSFER    ,VIM24
VIM23 SAVEVALUE   1,V18,XH
VIM24 SAVEVALUE   2,XH1,XH
TRAN  MACRO       SEV22,AGE26
      TRANSFER    .XH2,,SEV22
      TRANSFER    ,AGE26
VDEV  MACRO       SEV22,22,YIB22,42,14.4,26.52,4.86,SEB22,28.83
SEV22 ENTER       22
      ASSIGN      4,0,PB
DEV   MACRO       YIB22,42,14.4,26.52,4.86,SEB22,28.83
YIB22 ENTER       42
      ASSIGN      1,14.4,PL
      ASSIGN      2,26.52,PL
      ASSIGN      3,4.86,PL
      ASSIGN      4,V3,PL
SEB22 ASSIGN      5+,V2,PL
      ADVANCE     1
      TEST GE     PL5,PL4,SEB22
      LEAVE       42
      SAVEVALUE   NEXT,28.83,XL
      ASSIGN      5,V11,PL
      LEAVE       22
VDED  MACRO       CAD22,33,43,FNSLIP22,53,7.2564,0.3243
```

```
CAD22 ENTER        33
      ENTER        43
      ADVANCE      FN$LIP22
      LEAVE        33
      LEAVE        43
      ENTER        53
      SAVEVALUE    1,2,XF
      SAVEVALUE    13,7.2564,XL
      SAVEVALUE    14,0.3243,XL
      SAVEVALUE    15,V$POL,XL
      SAVEVALUE    16,0,XL
      HELPB        #TRANFO,1XF,15XL,16XL
      SAVEVALUE    17+,XL16,XL
      SAVEVALUE    CUPOL+,XL16,XL
      SAVEVALUE    OAPOL,XL17,XL
      SAVEVALUE    17,0,XL
      ADVANCE      1
      LEAVE        53
      TERMINATE
*
*     MORTALITY PROPORTION AT TERTIARY STAGE OF THE SECOND INSTAR
*
NOMA  MACRO        AGE26,19,9,10,9XL,10XL    MORT'' PROPOR'' AT TER'' STA
AGE26 SAVEVALUE    1,19,XF
      SAVEVALUE    9,0,XL
      SAVEVALUE    10,0,XL
      HELPB        #VIMORT,1XF,4XL,9XL,10XL
      SAVEVALUE    1+,1,XF
      HELPB        #VIMORT,1XF,4XL,9XL,10XL
CHCO  MACRO        V19,VIM25,AGE27,999,VIM26,VIM27
      TEST LE      V19,0,VIM25
      SAVEVALUE    1,1,XH
      TRANSFER     ,AGE27
VIM25 TEST GE      V19,999,VIM26
      SAVEVALUE    1,999,XH
      TRANSFER     ,VIM27
VIM26 SAVEVALUE    1,V19,XH
VIM27 SAVEVALUE    2,XH1,XH
TRAN  MACRO        SEV12,AGE27
      TRANSFER     .XH2,,SEV12
      TRANSFER     ,AGE27
VDEV  MACRO        SEV12,12,YIB12,42,14.4,26.52,4.96,SEB12,25.33
SEV12 ENTER        12
      ASSIGN       4,0,PB
DEV   MACRO        YIB12,42,14.4,26.52,4.86,SEB12,23.33
YIB12 ENTER        42
      ASSIGN       1,14.4,PL
      ASSIGN       2,26.52,PL
      ASSIGN       3,4.86,PL
      ASSIGN       4,V3,PL
SEB12 ASSIGN       5+,V2,PL
      ADVANCE      1
      TEST GE      PL5,PL4,SEB12
      LEAVE        42
      SAVEVALUE    NEXT,23.83,XL
      ASSIGN       5,V11,PL
      LEAVE        12
```

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VDEV    MACRO       SEV23,23,YIC23,43,13.5,28.83,5.17,SEC23,32.50
SEV23   ENTER       23
        ASSIGN      4,0,PB
DEV     MACRC       YIC23,43,13.5,28.83,5.17,SEC23,32.50
YIC23   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
VDED    MACRO       CAD24,34,44,FN$LIP23,54,8.3010,0.2342
CAD24   ENTER       34
        ENTER       44
        ADVANCE     FN$LIP23
        LEAVE       34
        LEAVE       44
        ENTER       54
        SAVEVALUE   1,2,XF
        SAVEVALUE   13,8.3010,XL
        SAVEVALUE   14,0.2342,XL
        SAVEVALUE   15,V$POL,XL
        SAVEVALUE   16,0,XL
        HELPB       #TRANFU,1XF,15XL,16XL
        SAVEVALUE   17+,XL16,XL
        SAVEVALUE   CUPOL+,XL16,XL
        SAVEVALUE   OAPOL,XL17,XL
        SAVEVALUE   17,0,XL
        ADVANCE     1
        LEAVE       54
        TERMINATE
VDED    MACRC       AGE27,32,42,FN$LIP21,52,6.7602,0.2198
AGE27   ENTER       32
        ENTER       42
        ADVANCE     FN$LIP21
        LEAVE       32
        LEAVE       42
        ENTER       52
        SAVEVALUE   1,2,XF
        SAVEVALUE   13,6.7602,XL
        SAVEVALUE   14,0.2198,XL
        SAVEVALUE   15,V$POL,XL
        SAVEVALUE   16,0,XL
        HELPB       #TRANFU,1XF,15XL,16XL
        SAVEVALUE   17+,XL16,XL
        SAVEVALUE   CUPOL+,XL16,XL
        SAVEVALUE   OAPOL,XL17,XL
        SAVEVALUE   17,0,XL
        ADVANCE     1
        LEAVE       52
        TERMINATE
*
```

```
*       VIRUS SPRAY TO THIRD INSTAR
*       ************************************************
*
 NOMA  MACRO      VIM31,5,5,6,5XL,6XL  TOMU'' FOR III
 VIM31 SAVEVALUE  1,5,XF
       SAVEVALUE  5,0,XL
       SAVEVALUE  6,0,XL
       HELPB      #VIMORT,1XF,4XL,5XL,6XL
       SAVEVALUE  1+,1,XF
       HELPB      #VIMORT,1XF,4XL,5XL,6XL
 CHOO  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,V15,XH
 SPA34 SAVEVALUE  2,XH1,XH
 TRAN  MACRO      AGE32,INS3
       TRANSFER   .XH2,,AGE32
       TRANSFER   ,INS3
*
*       AGE-SPECIFIC MORTALITY AT SECONDARY STAGE AT THE THIRD INSTAR
*
 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      #VIMORT,1XF,4XL,7XL,8XL
       SAVEVALUE  1+,1,XF
       HELPB      #VIMORT,1XF,4XL,7XL,8XL
 CHOO  MACRO      V18,VIM32,AGE36,999,VIM33,VIM34
       TEST LE    V18,0,VIM32
       SAVEVALUE  1,1,XH
       TRANSFER   ,AGE36
 VIM32 TEST GE    V18,999,VIM33
       SAVEVALUE  1,999,XH
       TRANSFER   ,VIM34
 VIM33 SAVEVALUE  1,V18,XH
 VIM34 SAVEVALUE  2,XH1,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
 DEV   MACRC      SMC23,43,13.5,28.83,5.17,TIC23,32.50
 SMC23 ENTER      43
       ASSIGN     1,13.5,PL
       ASSIGN     2,28.83,PL
       ASSIGN     3,5.17,PL
       ASSIGN     4,V3,PL
 TIC23 ASSIGN     5+,V2,PL
       ADVANCE    1
       TEST GE    PL5,PL4,TIC23
       LEAVE      43
```

```
        SAVEVALUE   NEXT,32.5C,XL
        ASSIGN      5,V11,PL
        LEAVE       23
VOED    MACRO       CAD32,34,44,FN$LIP32,54,8.3010,0.2342
CAD32   ENTER       34
        ENTER       44
        ADVANCE     FN$LIP32
        LEAVE       34
        LEAVE       44
        ENTER       54
        SAVEVALUE   1,2,XF
        SAVEVALUE   13,8.3010,XL
        SAVEVALUE   14,0.2342,XL
        SAVEVALUE   15,V$POL,XL
        SAVEVALUE   16,0,XL
        HELPB       #TRANFO,1XF,15XL,16XL
        SAVEVALUE   17+,XL16,XL
        SAVEVALUE   CUPOL+,XL16,XL
        SAVEVALUE   OAPOL,XL17,XL
        SAVEVALUE   17,0,XL
        ADVANCE     1
        LEAVE       54
        TERMINATE
*
*       MORTALITY PROPORTION AT TERTIARY STAGE OF THE THIRD INSTAR
*
NGMA    MACRO       AGE36,23,9,1C,9XL,10XL    MORT** PRUPOR** AT TER** STA
AGE36   SAVEVALUE   1,23,XF
        SAVEVALUE   9,0,XL
        SAVEVALUE   10,0,XL
        HELPB       #VIMORT,1XF,4XL,9XL,10XL
        SAVEVALUE   1+,1,XF
        HELPB       #VIMORT,1XF,4XL,9XL,10XL
CHOO    MACRO       V19,VIM35,AGE37,999,VIM36,VIM37
        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,XH1,XH
TRAN    MACRO       TIV13,AGE37
        TRANSFER    .XH2,,TIV13
        TRANSFER    ,AGE37
VDEV    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      5+,V2,PL
        ADVANCE     1
        TEST GE     PL5,PL4,TIC13
```

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        LEAVE       43
        SAVEVALUE   NEXT,32.50,XL
        ASSIGN      5,V11,PL
        LEAVE       13
VDEV    MACRO       TIV24,24,SMD24,44,13.6,32.50,7.01,TID24,34.49
TIV24   ENTER       24
        ASSIGN      4,0,PB
DEV     MACRO       SMD24,44,13.6,32.50,7.01,TID24,34.49
SMD24   ENTER       44
        ASSIGN      1,13.6,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   NEXT,34.49,XL
        ASSIGN      5,V11,PL
        LEAVE       24
VDED    MACRO       CAD33,35,45,FN$LIP33,55,8.7068,0.2338
CAD33   ENTER       35
        ENTER       45
        ADVANCE     FN$LIP33
        LEAVE       35
        LEAVE       45
        ENTER       55
        SAVEVALUE   1,2,XF
        SAVEVALUE   13,8.7068,XL
        SAVEVALUE   14,0.2338,XL
        SAVEVALUE   15,V$POL,XL
        SAVEVALUE   16,0,XL
        HELPB       #TRANFO,1XF,15XL,16XL
        SAVEVALUE   17+,XL16,XL
        SAVEVALUE   CUPOL+,XL16,XL
        SAVEVALUE   DAPOL,XL17,XL
        SAVEVALUE   17,0,XL
        ADVANCE     1
        LEAVE       55
        TERMINATE
VDED    MACRO       AGE37,33,43,FN$LIP31,53,7.2564,0.3243
AGE37   ENTER       33
        ENTER       43
        ADVANCE     FN$LIP31
        LEAVE       33
        LEAVE       43
        ENTER       53
        SAVEVALUE   1,2,XF
        SAVEVALUE   13,7.2564,XL
        SAVEVALUE   14,0.3243,XL
        SAVEVALUE   15,V$POL,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
```

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          ADVANCE     1
          LEAVE       53
          TERMINATE
*
*         VIRUS SPRAY TO FOURTH INSTAR
*         **************************************************
*
NOMA      MACRO       VIM41,7,5,6,5XL,6XL   TOMO'' FOR IV
VIM41     SAVEVALUE   1,7,XF
          SAVEVALUE   5,0,XL
          SAVEVALUE   6,0,XL
          HELPB       #VIMORT,1XF,4XL,5XL,6XL
          SAVEVALUE   1+,1,XF
          HELPB       #VIMORT,1XF,4XL,5XL,6XL
CHOO      MACRO       V15,SPA42,INS4,999,SPA43,SPA44
          TEST LE     V15,0,SPA42
          SAVEVALUE   1,1,XH
          TRANSFER    ,INS4
SPA42     TEST GE     V15,999,SPA43
          SAVEVALUE   1,999,XH
          TRANSFER    ,SPA44
SPA43     SAVEVALUE   1,V15,XH
SPA44     SAVEVALUE   2,XH1,XH
TRAN      MACRO       AGE42,INS4
          TRANSFER    .XH2,,AGE42
          TRANSFER    ,INS4
*
*         AGE-SPECIFIC MORTALITY AT SECONDARY STAGE AT THE FOURTH INSTAR
*
NOMA      MACRO       AGE42,25,7,8,7XL,8XL   SECONDARY STAGE-SPECIFIC MORT''
AGE42     SAVEVALUE   1,25,XF
          SAVEVALUE   7,0,XL
          SAVEVALUE   8,0,XL
          HELPB       #VIMORT,1XF,4XL,7XL,8XL
          SAVEVALUE   1+,1,XF
          HELPB       #VIMORT,1XF,4XL,7XL,8XL
CHOO      MACRO       V18,VIM42,AGE46,999,VIM43,VIM44
          TEST LE     V18,0,VIM42
          SAVEVALUE   1,1,XH
          TRANSFER    ,AGE46
VIM42     TEST GE     V18,999,VIM43
          SAVEVALUE   1,999,XH
          TRANSFER    ,VIM44
VIM43     SAVEVALUE   1,V18,XH
VIM44     SAVEVALUE   2,XH1,XH
TRAN      MACRO       FOV24,AGE46
          TRANSFER    .XH2,,FOV24
          TRANSFER    ,AGE46
VDEV      MACRO       FOV24,24,SAD24,44,13.6,32.50,7.01,FOD24,34.49
FOV24     ENTER       24
          ASSIGN      4,0,PB
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
```

```
FOD24 ASSIGN      5+,V2,PL
      ADVANCE     1
      TEST GE     PL5,PL4,FCD24
      LEAVE       44
      SAVEVALUE   NEXT,34.49,XL
      ASSIGN      5,V11,PL
      LEAVE       24
VDED  MACRO       CAD42,35,45,FNSLIP42,55,8.7068,0.2338
CAD42 ENTER       35
      ENTER       45
      ADVANCE     FNSLIP42
      LEAVE       35
      LEAVE       45
      ENTER       55
      SAVEVALUE   1,2,XF
      SAVEVALUE   13,8.7068,XL
      SAVEVALUE   14,0.2338,XL
      SAVEVALUE   15,V$POL,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       55
      TERMINATE
*
*     MORTALITY PROPORTION AT TERTIARY STAGE OF THE FOURTH INSTAR
*
NOMA  MACRO       AGE46,27,9,10,9XL,10XL    MORT'' PROPOR'' AT TER'' STA
AGE46 SAVEVALUE   1,27,XF
      SAVEVALUE   9,0,XL
      SAVEVALUE   10,0,XL
      HELPB       #VIMORT,1XF,4XL,9XL,10XL
      SAVEVALUE   1+,1,XF
      HELPB       #VIMORT,1XF,4XL,9XL,10XL
CHOD  MACRO       V19,VIM45,AGE47,999,VIM46,VIM47
      TEST LE     V19,0,VIM45
      SAVEVALUE   1,1,XH
      TRANSFER    ,AGE47
VIM45 TEST GE     V19,999,VIM46
      SAVEVALUE   1,999,XH
      TRANSFER    ,VIM47
VIM46 SAVEVALUE   1,V19,XH
VIM47 SAVEVALUE   2,XH1,XH
TRAN  MACRO       FOV14,AGE47
      TRANSFER    .XH2,,FOV14
      TRANSFER    ,AGE47
VDEV  MACRO       FOV14,14,SAD14,44,13.6,32.50,7.01,FOD14,34.49
FOV14 ENTER       14
      ASSIGN      4,0,PB
DEV   MACRO       SAD14,44,13.6,32.50,7.01,FOD14,34.49
SAD14 ENTER       44
      ASSIGN      1,13.6,PL
      ASSIGN      2,32.50,PL
      ASSIGN      3,7.01,PL
```

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        ASSIGN      4,V3,PL
FOD14   ASSIGN      5+,V2,PL
        ADVANCE     1
        TEST GE     PL5,PL4,FCD14
        LEAVE       44
        SAVEVALUE   NEXT,34.49,XL
        ASSIGN      5,V11,PL
        LEAVE       14
VDEV    MACRO       FOV25,25,SAE25,45,13.3,34.49,8.35,FOE25,43.91
FOV25   ENTER       25
        ASSIGN      4,0,PB
DEV     MACRO       SAE25,45,13.3,34.49,8.35,FOE25,43.91
SAE25   ENTER       45
        ASSIGN      1,13.3,PL
        ASSIGN      2,34.49,PL
        ASSIGN      3,8.35,PL
        ASSIGN      4,V3,PL
FOE25   ASSIGN      5+,V2,PL
        ADVANCE     1
        TEST GE     PL5,PL4,FCE25
        LEAVE       45
        SAVEVALUE   NEXT,43.91,XL
        ASSIGN      5,V11,PL
        LEAVE       25
VDED    MACRO       CAO43,36,46,FNSLIP43,56,9.1903,0.2967
CAO43   ENTER       36
        ENTER       46
        ADVANCE     FNSLIP43
        LEAVE       36
        LEAVE       46
        ENTER       56
        SAVEVALUE   1,2,XF
        SAVEVALUE   13,9.1903,XL
        SAVEVALUE   14,0.2967,XL
        SAVEVALUE   15,VSPOL,XL
        SAVEVALUE   16,0,XL
        HELPB       #TRANFO,1XF,15XL,16XL
        SAVEVALUE   17+,XL16,XL
        SAVEVALUE   CUPOL+,XL16,XL
        SAVEVALUE   OAPOL,XL17,XL
        SAVEVALUE   17,0,XL
        ADVANCE     1
        LEAVE       56
        TERMINATE
VDED    MACRO       AGE47,34,44,FNSLIP41,54,8.3010,0.2342
AGE47   ENTER       34
        ENTER       44
        ADVANCE     FNSLIP41
        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   16,0,XL
        HELPB       #TRANFO,1XF,15XL,16XL
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          SAVEVALUE   17+,XL16,XL
          SAVEVALUE   CUPOL+,XL16,XL
          SAVEVALUE   OAPOL,XL17,XL
          SAVEVALUE   17,0,XL
          ADVANCE     1
          LEAVE       54
          TERMINATE
*
*         VIRUS SPRAY TO FIFTH INSTAR
*         ******************************************
*
 NOMA  MACRO       VIM51,9,5,6,5XL,6XL   TUMO'' FOR V
 VIM51 SAVEVALUE   1,9,XF
          SAVEVALUE   5,0,XL
          SAVEVALUE   6,0,XL
          HELPB       #VIMORT,1XF,4XL,5XL,6XL
          SAVEVALUE   1+,1,XF
          HELPB       #VIMORT,1XF,4XL,5XL,6XL
 CHOO  MACRO       V15,SPA52,INS5,999,SPA53,SPA54
          TEST LE     V15,0,SPA52
          SAVEVALUE   1,1,XH
          TRANSFER    ,INS5
 SPA52 TEST GE     V15,999,SPA53
          SAVEVALUE   1,999,XH
          TRANSFER    ,SPA54
 SPA53 SAVEVALUE   1,V15,XH
 SPA54 SAVEVALUE   2,XH1,XH
 TRAN  MACRO       AGE52,INS5
          TRANSFER    .XH2,,AGE52
          TRANSFER    ,INS5
*
*         AGE-SPECIFIC MORTALITY AT SECONDARY STAGE AT THE FIFTH INSTAR
*
 NOMA  MACRO       AGE52,29,7,8,7XL,8XL   SECONDARY STAGE-SPECIFIC MORT''
 AGE52 SAVEVALUE   1,29,XF
          SAVEVALUE   7,0,XL
          SAVEVALUE   8,0,XL
          HELPB       #VIMORT,1XF,4XL,7XL,8XL
          SAVEVALUE   1+,1,XF
          HELPB       #VIMORT,1XF,4XL,7XL,8XL
 CHOO  MACRO       V18,VIM52,AGE56,999,VIM53,VIM54
          TEST LE     V18,0,VIM52
          SAVEVALUE   1,1,XH
          TRANSFER    ,AGE56
 VIM52 TEST GE     V18,999,VIM53
          SAVEVALUE   1,999,XH
          TRANSFER    ,VIM54
 VIM53 SAVEVALUE   1,V18,XH
 VIM54 SAVEVALUE   2,XH1,XH
 TRAN  MACRO       FIV25,AGE56
          TRANSFER    .XH2,,FIV25
          TRANSFER    ,AGE56
 VDEV  MACRO       FIV25,25,OHE25,45,13.3,34.49,8.35,FIE25,43.91
 FIV25 ENTER       25
          ASSIGN      4,0,PB
 DEV   MACRO       OHE25,45,13.3,34.49,8.35,FIE25,43.91
 OHE25 ENTER       45
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          ASSIGN      1,13.3,PL
          ASSIGN      2,34.49,PL
          ASSIGN      3,8.35,PL
          ASSIGN      4,V3,PL
FIE25     ASSIGN      5+,V2,PL
          ADVANCE     1
          TEST GE     PL5,PL4,FIE25
          LEAVE       45
          SAVEVALUE   NEXT,43.91,XL
          ASSIGN      5,V11,PL
          LEAVE       25
VDED      MACRO       CAD52,36,46,FN$LIP52,56,9.1903,0.2967
CAD52     ENTER       36
          ENTER       46
          ADVANCE     FN$LIP52
          LEAVE       36
          LEAVE       46
          ENTER       56
          SAVEVALUE   1,2,XF
          SAVEVALUE   13,9.1903,XL
          SAVEVALUE   14,0.2967,XL
          SAVEVALUE   15,V$PUL,XL
          SAVEVALUE   16,0,XL
          HELPB       #TRANFU,1XF,15XL,16XL
          SAVEVALUE   17+,XL16,XL
          SAVEVALUE   CUPUL+,XL16,XL
          SAVEVALUE   DAPUL,XL17,XL
          SAVEVALUE   17,0,XL
          ADVANCE     1
          LEAVE       56
          TERMINATE
*
*         MORTALITY PROPORTION AT TERTIARY STAGE OF THE FIFTH INSTAR
*
NGMA      MACRO       AGE56,31,9,10,9XL,10XL    MORT** PROPOR** AT TER** STA
AGE56     SAVEVALUE   1,31,XF
          SAVEVALUE   9,0,XL
          SAVEVALUE   10,0,XL
          HELPB       #VIMORT,1XF,4XL,9XL,10XL
          SAVEVALUE   1+,1,XF
          HELPB       #VIMORT,1XF,4XL,9XL,10XL
CHOG      MACRO       V19,VIM55,AGE57,999,VIM56,VIM57
          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,V19,XH
VIM57     SAVEVALUE   2,XH1,XH
TRAN      MACRO       FIV15,AGE57
          TRANSFER    .XH2,,FIV15
          TRANSFER    ,AGE57
VDEV      MACRO       FIV15,15,CHE15,45,13.3,34.49,8.35,FIE15,43.91
FIV15     ENTER       15
          ASSIGN      4,0,PB
DEV       MACRO       CHE15,45,13.3,34.49,8.35,FIE15,43.91
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OHE15 ENTER      45
      ASSIGN     1,13.3,PL
      ASSIGN     2,34.49,PL
      ASSIGN     3,8.35,PL
      ASSIGN     4,V3,PL
FIE15 ASSIGN     5+,V2,PL
      ADVANCE    1
      TEST GE    PL5,PL4,FIE15
      LEAVE      45
      SAVEVALUE  NEXT,43.91,XL
      ASSIGN     5,V11,PL
      LEAVE      15
VDEV  MACKO      FIV26,26,OHF26,46,14.7,38.11,8.98,FIF26,50.31
FIV26 ENTER      26
      ASSIGN     4,0,PB
DEV   MACRO      OHF26,46,14.7,38.11,8.98,FIF26,50.81
OHF26 ENTER      46
      ASSIGN     1,14.7,PL
      ASSIGN     2,38.11,PL
      ASSIGN     3,8.98,PL
      ASSIGN     4,V3,PL
FIF26 ASSIGN     5+,V2,PL
      ADVANCE    1
      TEST GE    PL5,PL4,FIF26
      LEAVE      46
      SAVEVALUE  NEXT,50.81,XL
      ASSIGN     5,V11,PL
      LEAVE      26
VDED  MACRU      CAD53,37,47,FN$LIP53,57,9.6252,0.1878
CAD53 ENTER      37
      ENTER      47
      ADVANCE    FN$LIP53
      LEAVE      37
      LEAVE      47
      ENTER      57
      SAVEVALUE  1,2,XF
      SAVEVALUE  13,9.6252,XL
      SAVEVALUE  14,0.1878,XL
      SAVEVALUE  15,V$POL,XL
      SAVEVALUE  16,0,XL
      HELPB      #TRANFO,1XF,15XL,16XL
      SAVEVALUE  17+,XL16,XL
      SAVEVALUE  CUPOL+,XL16,XL
      SAVEVALUE  OAPOL,XL17,XL
      SAVEVALUE  17,0,XL
      ADVANCE    1
      LEAVE      57
      TERMINATE
VDED  MACRG      AGE57,35,45,FN$LIP51,55,8.7068,0.2333
AGE57 ENTER      35
      ENTER      45
      ADVANCE    FN$LIP51
      LEAVE      35
      LEAVE      45
      ENTER      55
      SAVEVALUE  1,2,XF
      SAVEVALUE  13,8.7068,XL
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          SAVEVALUE    14,0.2338,XL
          SAVEVALUE    15,V$POL,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        55
          TERMINATE
*
*         VIRUS SPRAY TO SIXTH INSTAR
*         *******************************************
*
 NOMA    MACRO        VIM61,11,5,6,5XL,6XL   TOMO'' FOR VI
 VIM61   SAVEVALUE    1,11,XF
          SAVEVALUE    5,0,XL
          SAVEVALUE    6,0,XL
          HELPB        #VIMORT,1XF,4XL,5XL,6XL
          SAVEVALUE    1+,1,XF
          HELPB        #VIMORT,1XF,4XL,5XL,6XL
 CHOO    MACRO        V15,SPA62,INS6,999,SPA63,SPA64
          TEST LE      V15,0,SPA62
          SAVEVALUE    1,1,XH
          TRANSFER     ,INS6
 SPA62   TEST GE      V15,999,SPA63
          SAVEVALUE    1,999,XH
          TRANSFER     ,SPA64
 SPA63   SAVEVALUE    1,V15,XH
 SPA64   SAVEVALUE    2,XH1,XH
 TRAN    MACRO        AGE62,INS6
          TRANSFER     .XH2,,AGE62
          TRANSFER     ,INS6
*
*         AGE-SPECIFIC MORTALITY AT SECONDARY STAGE AT THE SIXTH INSTAR
*
 NOMA    MACRO        AGE62,33,7,8,7XL,8XL   SECONDARY STAGE-SPECIFIC MORT''
 AGE62   SAVEVALUE    1,33,XF
          SAVEVALUE    7,0,XL
          SAVEVALUE    8,0,XL
          HELPB        #VIMORT,1XF,4XL,7XL,8XL
          SAVEVALUE    1+,1,XF
          HELPB        #VIMORT,1XF,4XL,7XL,8XL
 CHOO    MACRO        V18,VIM62,AGE61,999,VIM63,VIM64
          TEST LE      V18,0,VIM62
          SAVEVALUE    1,1,XH
          TRANSFER     ,AGE61
 VIM62   TEST GE      V18,999,VIM63
          SAVEVALUE    1,999,XH
          TRANSFER     ,VIM64
 VIM63   SAVEVALUE    1,V18,XH
 VIM64   SAVEVALUE    2,XH1,XH
 TRAN    MACRO        SIV26,AGE61
          TRANSFER     .XH2,,SIV26
          TRANSFER     ,AGE61
 VDEV    MACRO        SIV26,26,YUF26,46,14.7,38.11,8.98,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,V3,PL
SIF26 ASSIGN      5+,V2,PL
      ADVANCE     1
      TEST GE     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,VSPOL,XL
      SAVEVALUE   16,0,XL
      HELPB       #TRANFO,1XF,15XL,16XL
      SAVEVALUE   17+,XL16,XL
      SAVEVALUE   CUPOL+,XL16,XL
      SAVEVALUE   OAPOL,XL17,XL
      SAVEVALUE   17,0,XL
      ADVANCE     1
      LEAVE       57
      TERMINATE
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,VSPOL,XL
      SAVEVALUE   16,0,XL
      HELPB       #TRANFO,1XF,15XL,16XL
      SAVEVALUE   17+,XL16,XL
      SAVEVALUE   CUPOL+,XL16,XL
      SAVEVALUE   OAPOL,XL17,XL
      SAVEVALUE   17,0,XL
      ADVANCE     1
      LEAVE       56
      TERMINATE
********************************************************************
*
```

```
*       CONTROL CARDS
*
***********************************************************************
*
*       TIME CONTROL
*
        GENERATE    1   TIMER ARRIVES EVERYDAY
        SAVEVALUE   DAY,V1,XH   DAYS COUTING FROM INTRO OF FEMALE
        SAVEVALUE   DADAM,VSFCCD,XL   DAILY FOOD DAMAGE BY THE LARVAE
        SAVEVALUE   CUDA+,XLSDADAM,XL   CUMULATIVE DAILY FOOD DAMAGE
        TERMINATE   1   TIMER COUNTING
        START       35,,1
*
*       OUTPUT CONTROL
*
        REPORT
        TEXT        #XHSDAY,2/XX#   DAY(S) AFTER INITAL INTRODUCTION
STO     TITLE       ,AGE COMPOSITION  (NO. OF INDIVIDUALS)
LSV     TITLE       ,FOOD CONSUMTICN AND VIRUS PRODUCTION
        END
```

```
C.... SUBROUTINE VIMORT DETERMINES THE TOTAL AND STAGE-SPECIFIC
C     MORTALITIES AND THEIR STANDARD DEVIATION.
C.... MORTALITIES WERE DETERMINED BY LOGISTIC EQUATIONS.
C.... PARAMETER K IN LOGISTIC EQUATION WAS DETERMINED EMPIRICALLY
C     BY GRAPHIC METHOD WHILE PARAMETERS A AND B WERE DETERMINED BY
C     LINEAR TRANSFORMATION UF LOGISTIC EQUATION.
C
      SUBROUTINE VIMORT(IX1,FX2,FX3,FX4)
C
      GO TO (21,31,22,32,23,33,24,34,25,35,26,36,
     1111,211,116,216,122,222,126,226,132,232,136,236,142,242,146,246,
     1152,252,156,256,162,262),IX1
   21 FX3=1.0/(1.0+ EXP(10.220100-1.824072*FX2))
      RETURN
   31 FX4=FX3*ABS(FX3-1.0)*SQRT(0.853193*(1.066667+(FX2-5.776724)**2
     1/30.914063))
      RETURN
   22 FX3=1.0/(1.0+ EXP(10.184272-1.764551*FX2))
      RETURN
   32 FX4=FX3*ABS(FX3-1.0)*SQRT(1.483684*(1.047619+(FX2-5.746116)**2
     1/53.203998))
      RETURN
   23 FX3=1.0/(1.0+ EXP(10.193414-1.639333*FX2))
      RETURN
   33 FX4=FX3*ABS(FX3-1.0)*SQRT(0.709833*(1.047617+(FX2-6.469012)**2
     1/32.139757))
      RETURN
   24 FX3=1.0/(1.0+ EXP(7.593563-1.146190*FX2))
      RETURN
   34 FX4=FX3*ABS(FX3-1.0)*SQRT(0.610504*(1.047619+(FX2-6.224838)**2
     1/49.951374))
      RETURN
   25 FX3=1.0/(1.0+ EXP(13.621614-1.805412*FX2))
      RETURN
   35 FX4=FX3*ABS(FX3-1.0)*SQRT(0.712668*(1.071429+(FX2-7.099921)**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)*SQRT(0.966383*(1.033333+(FX2-8.666998)**2
     1/9.846137))
      RETURN
  111 FX3=1.000/(1.0+ EXP(13.318398-2.095524*FX2))
      RETURN
  211 FX4=FX3*ABS(FX3-1.000)/1.000*SQRT(0.495442*(1.071429
     1+(FX2-5.551497)**2/20.264052))
      RETURN
  116 FX3=0.694/(1.0+ EXP(-11.139353+2.283949*FX2))
      RETURN
  216 FX4=FX3*ABS(FX3-0.694)/0.694*SQRT(2.533197*(1.071429
     1+(FX2-5.960071)**2/22.227996))
      RETURN
  122 FX3=0.669/(1.0+ EXP(9.545506-1.815561*FX2))
      RETURN
  222 FX4=FX3*ABS(FX3-0.669)/0.669*SQRT(1.032056*(1.047617
     1+(FX2-5.746172)**2/53.146767))
      RETURN
  126 FX3=0.592/(1.0+ EXP(-8.318631+1.498302*FX2))
```

```
1  RELEASE 2.0            VIMORT          DATE = 82107          14/58/39

           RETURN
       226 FX4=FX3*ABS(FX3-0.591)/0.591*SQRT(1.629182*(1.052632
           1+(FX2-6.041342)**2/35.765037))
           RETURN
       132 FX3=0.712/(1.0+ EXP(7.449209-1.170588*FX2))
           RETURN
       232 FX4=FX3*ABS(FX3-0.712)/0.712*SQRT(0.783259*(1.045455
           1+(FX2-6.353580)**2/38.296083))
           RETURN
       136 FX3=0.666/(1.0+ EXP(-13.650186+2.339852*FX2))
           RETURN
       236 FX4=FX3*ABS(FX3-0.666)/0.666*SQRT(2.073403*(1.047619
           1+(FX2-6.516632)**2/26.012885))
           RETURN
       142 FX3=0.743/(1.0+ EXP(9.460840-1.391128*FX2))
           RETURN
       242 FX4=FX3*ABS(FX3-0.743)/0.743*SQRT(0.799291*(1.047619
           1+(FX2-6.224839)**2/49.951822))
           RETURN
       146 FX3=0.730/(1.0+ EXP(-4.678404+0.783601*FX2))
           RETURN
       246 FX4=FX3*ABS(FX3-0.730)/0.730*SQRT(0.363180*(1.050000
           1+(FX2-6.390898)**2/38.369445))
           RETURN
       152 FX3=0.894/(1.0+ EXP(16.340271-2.030765*FX2))
           RETURN
       252 FX4=FX3*ABS(FX3-0.894)/0.894*SQRT(0.880673*(1.071429
           1+(FX2-7.699922)**2/27.064162))
           RETURN
       156 FX3=1.000/(1.0+ EXP(-7.798048+1.058737*FX2))
           RETURN
       256 FX4=FX3*ABS(FX3-1.000)/1.000*SQRT(0.063255*(1.093333
           1+(FX2-8.164626)**2/6.9242052))
           RETURN
       162 FX3=1.000/(1.0+ EXP(27.177353-3.058661*FX2))
           RETURN
       262 FX4=FX3*ABS(FX3-1.000)/1.000*SQRT(0.063255*(1.083333
           1+(FX2-8.666998)**2/9.8461092))
           RETURN
           END



   RELEASE 2.0            MAIN            DATE = 82107          14/58/28

       C....  SUBROUTINE TRANFO CALCULATES NO. OF EGG PRODUCTION (600,
       C      COMMON LOG.) AND NO. OF POLYHEDRA PRODUCED (599).
              SUBROUTINE TRANFO (IX1,FX2,FX3)
              GO TO (600,599),IX1
          600 FX3=EXP(6.6962-0.3525*FX2)
              RETURN
          599 FX3=(10**FX2)/1000000000
              RETURN
              END
```

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