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MODELING A GENETIC CONTROL PROGRAM FOR THE TOBACCO BUDWORM WITH SLAM

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A simulation model is described and used to investigate the potential for controlling the tobacco budworm through hybrid sterilization. The results indicated that high levels of population control appear feasible with relatively large release ratios. However, driving population levels to zero may be ruled out by such factors as different egg laying capabilities between budworm and backcross moths and by in-migration of budworm moths.

A general SLAM insect model is also described and developed which may be of value to other researchers studying population dynamics. The authors were well satisfied with the capabilities of SLAM.

INTRODUCTION

It is the purpose of this paper to describe a simulation model of a hybrid sterilization program for controlling the tobacco budworm. The model was written in SLAM, a relatively recent FORTRAN-based simulation language. In the authors' opinion, SLAM offers the potential for modeling complex insect population dynamics with relative simplicity. Therefore, a general insect population dynamics model will also be described. This will serve two purposes: (1) it will serve as an aid in understanding the complexities of the hybrid sterilization model, and (2) it may be helpful to research in modeling populations of other insects.

The paper will begin with a brief overview of SLAM. A general SLAM insect model formulation will be presented in the following section. This model will then be adapted to the particular situation of genetic control of the tobacco budworm. Conclusions for both budworm control and insect modeling using SLAM will be presented in the final section.

OVERVIEW OF SLAM

SLAM is a recent simulation language developed by Pritsker and Pegden. A detailed description of the language and users manual was published in 1979. In this section, those portions of the language which were used in the present study are briefly described.

SLAM offers capabilities for modeling both discrete-change systems and continuous-change systems. Only the discrete-change options were used here. For discrete-change systems, both a process (network) approach and an event orientation are allowed. The relative simplicity of the network approach and the greater flexibility of the event approach can be combined; this was the approach taken here.

In the network approach, the system is depicted by a series of branches and specialized nodes provided in the language. The nodes typically represent queues, decision points, collection of statistics, etc. Entities flow through the network in accordance with user-specified paths. These entities may each be described by up to 98 attributes.

The event approach requires that the user code FORTRAN subroutines which describe changes in entities, attributes, and/or system variables associated with the occurance of an event. The event subroutine will be called each time an entity flows through an EVENT node in the network. The EVENT node is generally useful when no standard network node will adequately describe a certain system operation.

Entities can be entered into the network through the operation of a CREATE node. They may also be placed in the network through calls to SLAM subroutine ENTER. Thus, entities can be created and described in user-supplied subroutines without sacrificing the relatively simple operational features of the network approach.

In addition to the CREATE and EVENT nodes, only the ASSIGN, GOON, and TERM nodes are required to model insect population dynamics. The ASSIGN node assigns values to entity attributes or global system variables; the GOON ("go on") node is simply a continuation node; and the TERM node removes entities from the network.

In the next section, a combined network-event model using the above described nodes, the ENTER subroutine, user-supplied EVENT subroutines, and user-supplied functions (USERFs) will be described. The model provides a general framework within which insect population dynamics can be modeled. The relative simplicity of the model masks its substantial capabilities in both modeling and output.

A GENERAL SLAM INSECT MODEL

Modeling insect population dynamics is complicated by several factors. For example, the insect being modeled will generally go through several life stages, each with a different daily development rate and mortality. In addition, the population in any particular life stage on a given day will generally be composed of individuals of various ages. The physiological age of each individual is essential in determining when the transition to the next life stage will occur. Finally, adults normally lay eggs over a period of several days, so progeny of a single adult will typically span several days and perhaps even several life stages. For reasons such as these, simulation modeling of insect systems is sufficiently complex to justify consideration of a simulation language.

A hypothetical insect was modeled using SLAM to illustrate the concepts which will be used in modeling the hybrid program in the next section of this paper. It was assumed that the hypothetical insect (like many real insects) had four life stages: egg, larva, pupa, and adult. The length of each life stage was assumed to be five days for eggs, eight days for larva, ten days for pupa, and four days for adults. On each day of its life, an adult female was assumed to lay 150 eggs. Daily mortalities of 30 percent for eggs, 25 percent for larvae, five percent for pupae, and 15 percent for adults were assumed.

The key to using SLAM in modeling insect populations is the definition of an entity. An entity is taken to be a cohort of insects in the model presented here. A cohort is all of the insects of a particular life stage which first enter the model (through pupa emergence or egg lay) on a given day. Each entity (cohort) has three associated attributes. Attribute One is a number one, two, three or four indicating the current life stage of the cohort (one indicates eggs, two indicates larvae, etc.). The second attribute is the percent development of the cohort. When this attribute, which is updated daily, reaches a level of one (100 percent), the cohort passes into the next life stage. Attribute Three is the number of individuals currently in the cohort. It, too, is updated daily.

Daily insect population levels are recorded in four system variables: SS(1) is the total number of eggs from all cohorts on the particular simulation day, SS(2) is similarly defined for larvae, SS(3) for pupae, and SS(4) for adults.[1] As is shown in Figure 1, values for these variables are increased when new cohorts enter the system through either CREATE node EMRG or ENTER node NEGG. Variable values are decreased each day in accord with daily mortality rates in ASSIGN node MORT. In ASSIGN nodes UPDT and CHST, populations are shifted from one SS total to another as their developmental stage changes.

Population levels of each cohort are updated daily in the five nodes which are enclosed by dashed lines in Figure 1. Beginning with GOON node DAY, entities "wait" for one day before proceeding to ASSIGN node MORT. The number of individuals which die that day is calculated according to four USERF functions (one for each life stage) and stored as system variable XX(10). This value is subtracted from both ATRIB(3), the surviving individuals in the cohort, and the appropriate daily total. Four other USERF functions are then used to update the percent development in each cohort in ASSIGN node DEVP. GOON node ACHK routes adults to EVENT node ELAY and non-adults back to GOON node DAY. In EVENT node ELAY a user-supplied subroutine is called in which adults lay their eggs and the adults then return to DAY.

Entities can enter the developmental loop through one of two paths. The first is through CREATE node EMRG which describes new adults emerging from overwintering. By manipulating the parameters of the CREATE node and the immediately following ASSIGN node, various emergence patterns can be simulated. The second entry point is ENTER node NEGG, wherein the eggs laid by adults in the ELAY node are placed into the network as new cohorts.

The only exit from the developmental loop follows ASSIGN node DEVP. Here, fully developed cohorts are routed to ASSIGN node UPDT. Fully developed adults leave the system permanently through TERM node DIE. Otherwise, life stage indices, development values, and daily totals (SS) are updated in ASSIGN node CHST and entities are returned to the developmental loop through GOON node DAY.

The three-node loop at the bottom of Figure 1 is used in conjunction with EVENT node ELAY to enter new eggs into the model. In ELAY, new eggs are added to system variable XX(1). However, they are not immediately entered into the network since several cohorts of adults may lay eggs on a single day and the number of new entities would become unnecessarily large. Instead, once a day CREATE node NCRT initiates a call to an event subroutine which puts all of the eggs stored in XX(1) into the network as a single cohort.

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[1] SS system variables are normally used in continuous models. They are used in place of XX variables in this model to allow for graphics output.
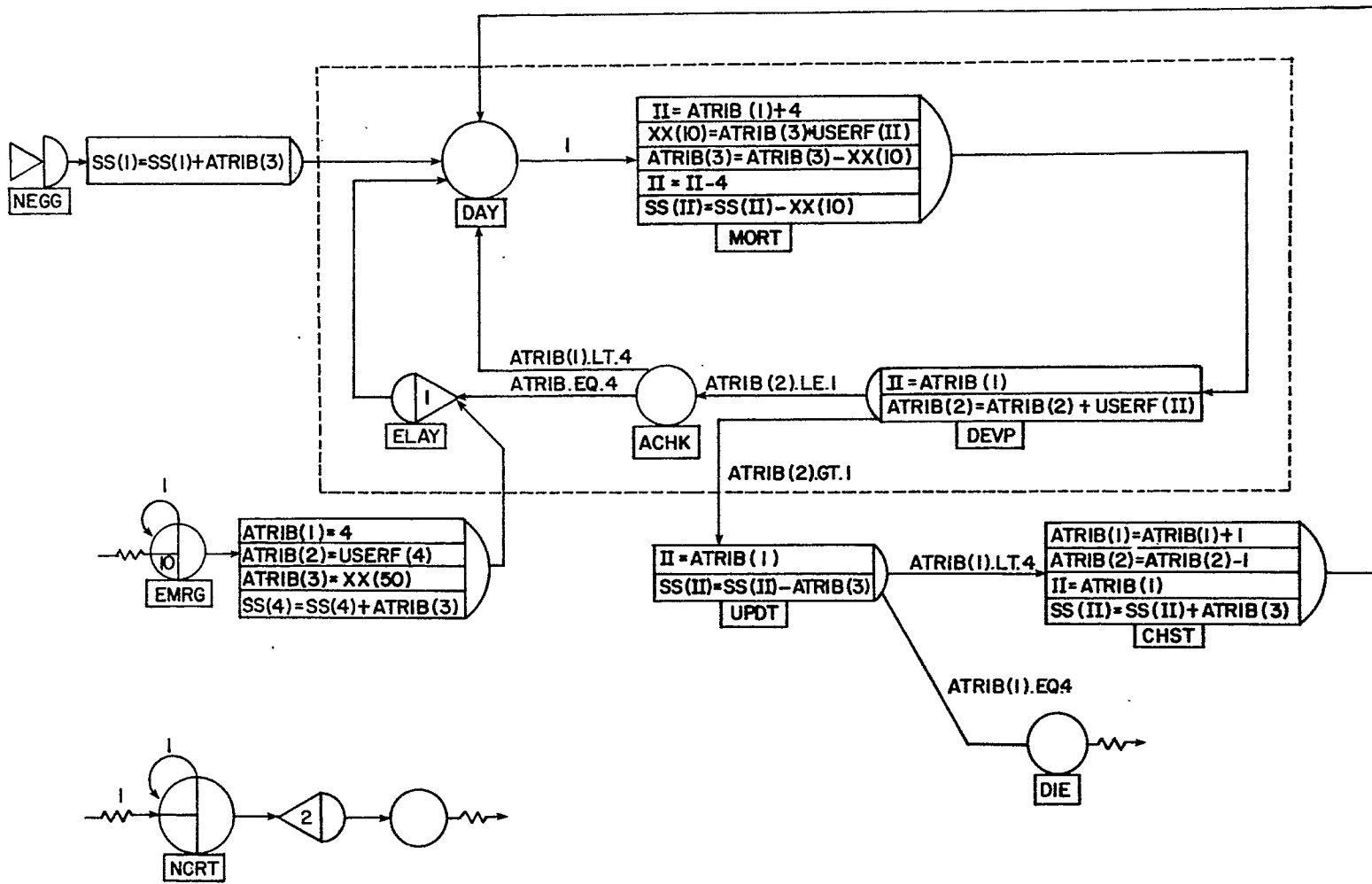
Figure 1. Network diagram of the general insect model.

The USERF functions and EVENT subroutines are coded in Figures 2 and 3, respectively. The functions and subroutines are intentionally simple, but various means of making them more sophisticated are readily apparent. For example, the daily egg lay of adults could be made dependent on the age (daily development) of the adult at the time of egg lay. As a second example, both development and mortality could be made dependent on temperature by reading in daily temperature data through a second small network like that at the bottom of Figure 1.

The network coding is shown in Figure 4. In addition to the network statements, the RECORD and VAR control statements provide for both tabular and graphical output of results. Control statement INITIALIZE indicates the number of days for which the simulation is to be run, and statement INTLC sets the daily emergence rate.

The coding in Figures 2-4, along with a trivial main program which does little more than call the SLAM executive routine, is all that is required to produce both graphical and tabular output showing the total number of insects in each life stage for each simulated day.

```
        FUNCTION USERF(IFN)
        ---(SLAM COMMON)---
        GO TO (10,20,30,40,50,60,70,80) IFN
C       DAILY DEVELOPMENT OF EGGS
     10 USERF=.20
        RETURN
C       DAILY DEVELOPMENT OF LARVAE
     20 USERF=.125
        RETURN
C       DAILY DEVELOPMENT OF PUPAE
     30 USERF=.10
        RETURN
C       DAILY DEVELOPMENT OF ADULTS
     40 USERF=.25
        RETURN
C       DAILY MORTALITY FOR EGGS
     50 USERF=.30
        RETURN
C       DAILY MORTALITY FOR LARVAE
     60 USERF=.25
        RETURN
C       DAILY MORTALITY FOR PUPAE
     70 USERF=.05
        RETURN
C       DAILY MORTALITY FOR ADULTS
     80 USERF=.15
        RETURN
        END
```

Figure 2. USERF function for general
           insect model.

MODEL OF GENETIC CONTROL PROGRAM

The tobacco budworm (Heliothis virenscens) is currently an economic pest of cotton, tomatoes, okra, field peas, sesame, and tobacco. Insecticide resistance in the tobacco budworm has caused the pest to be a limiting factor in crop production in some areas. Neither organochlorine nor organophosphorous insecticides now provide effective control of the budworm. The recent development of synthetic pyrethroid insecticides has eased the situation temporarily, but most researchers feel that the budworm will eventually develop resistance to pyrethroids as well. This, along with environmental concerns of pesticide use, emphasizes the necessity for controlling the tobacco budworm by some means other than conventional insecticides.

```
        SUBROUTINE EVENT(I)
        ---(SLAM COMMON)---
C
        GO TO (10,20) I
C
C       EGG LAY
     10 CONTINUE
C       LAY EGGS, ADD TO XX(1), THE EGG SUM
        XX(1)=XX(1)+(150.*ATRIB(3)*.5)
        RETURN
C
C       START A NEW COHORT WITH TODAY'S EGGS
     20 CONTINUE
        IF(XX(1).LT.1.0) GO TO 25
C       SET EGG ATTRIBUTES
        ATRIB(1)=1.
        ATRIB(2)=0.
        ATRIB(3)=XX(1)
C       PUT EGGS IN NETWORK AS A NEW COHORT
        CALL ENTER(1,ATRIB)
C       RESET EGG COUNT
     25 XX(1)=0.0
        RETURN
        END
```

Figure 3. EVENT subroutine for general
           insect model.

In 1962, Knipling proposed the development and release of insect strains that carry deficient genetic characteristics as one way of using an insect species to destroy its own kind. He suggested that crossing two related species of some insects might produce sterile hybrids without changing their mating behavior or their ability to find females of the natural population. In 1972, Laster demonstrated interspecific hybridization of the budworm and Heliothis subflexa, a closely related species. H. subflexa females mated to budworm males produced progeny in which the males were sterile and the females fertile. These fertile females, when backcrossed to budworm males, also produced sterile male and fertile female progeny. A pilot genetic control program conducted on St. Croix and preliminary modeling studies indicate good potential for controlling the budworm with this method.

The literature contains several reports which describe simulation models of budworm population dynamics. Overviews of simulation methods for insect populations are provided in articles by Berryman and Pienaar and by Barrett and Peart. Hartstack et.al., Parker et.al. and Stinner et.al. model budworm population dynamics, but do not address genetic suppression. Genetic suppression of the budworm is addressed in models by Parvin et.al. and Makela and Huettel.

```
GEN,LEVINS&PARKER,MODEL 2,4/17/81,1;
LIMITS,1,4,1000;
CONT,0,4;
RECORD,TNOW,DAY,0,B,1,1,100,NO;
VAR,SS(1),E,EGGS;
VAR,SS(2),L,LARVAE;
VAR,SS(3),P,PUPAE;
VAR,SS(4),A,ADULTS;
INTLC,XX(50)=100.;
NETWORK;
;
EMRG   CREATE,1,,,10;
       ASSIGN,ATRIB(1)=4,ATRIB(2)=0,ATRIB(3)=XX(50),
              SS(4)=SS(4)+ATRIB(3);
       ACT,,,ELAY;
;
NEGG   ENTER,1;
       ASSIGN,SS(1)=SS(1)+ATRIB(3);
;
DAY    GOON;
       ACT,1.0;
MORT   ASSIGN,II=ATRIB(1)+4,XX(10)=ATRIB(3)*USERF(II),
              ATRIB(3)=ATRIB(3)-XX(10),
              II=II-4,SS(II)=SS(II)-XX(10);
DEVP   ASSIGN,II=ATRIB(1),ATRIB(2)=ATRIB(2)+USERF(II);
       ACT,,ATRIB(2).GT.1,UPDT;
       ACT,,ATRIB(2).LE.1,ACHK;
ACHK   GOON;
       ACT,,ATRIB(1).LT.4,DAY;
       ACT,,ATRIB(1).EQ.4,ELAY;
ELAY   EVENT,1;
;
       ACT,,,DAY;
;
UPDT   ASSIGN,II=ATRIB(1),SS(II)=SS(II)-ATRIB(3);
       ACT,,ATRIB(1).LT.4,CHST;
       ACT,,ATRIB(1).GE.4,DIE;
;
CHST   ASSIGN,ATRIB(1)=ATRIB(1)+1,ATRIB(2)=ATRIB(2)-1,
              II=ATRIB(1),SS(II)=SS(II)+ATRIB(3);
       ACT,,,DAY;
;
DIE    TERM;
;
NCRT   CREATE,1,1;
       EVENT,2;
       TERM;
;
       ENDNETWORK;
INITIALIZE,0,100;
FIN;
```

Figure 4. SLAM data statements for general insect model.

While these studies of budworm population dynamics and genetic control provide general guidance, a more detailed model is necessary to fully evaluate the potential of a genetic control program. Daily releases of backcross moths, daily emergence of budworm moths, and the rather complex mating/fertility interaction of the two moth types should be included. Such a model is described in this section.

There are several aspects of the genetic control program model that were handled exactly as in the general model discussed previously. As before, development rates and mortality factors (assumed identical for the budworm and backcross moths) were entered as USERF statments. The same network

was used with minor modifications. These included the addition of ATRIB(4) to designate the type of insect (budworm or backcross) and separate CREATE nodes to enter the initial populations of each type into the network. Twice as many SS variables were required, and an additional USERF function was added to match entities and SS variables.

The major departure from the logic of the general model is in the rather complex mating interaction of the two insect types. Adult females of either type lay eggs daily. If they have last been mated to a fertile male (budworm), these eggs will be fertile; otherwise, they will not hatch. A female (of either type) mated to a fertile male is thought to not seek another mating during the following two nights. She will, however, lay fertile eggs each night during the inter-mating period. On the other hand, a female mated to a sterile male will lay sterile eggs that night, regardless of any previous fertile matings, but will seek another mating on the following night. A final complicating factor in the mating activity is that females of each type have egg laying patterns which change with the age of the female and differ between the two types.

The egg laying, mating and fertility interaction of the two moth types were handled in the EVENT subroutine without further modification of the network. In EVENT(1), the egg laying functions were coded using SLAM subroutine GTABL, a table look-up. In EVENT(2), the fraction of the adult males which were fertile was determined and used to calculate the fraction of that day's matings which were fertile. The fraction of the adult females receiving fertile matings on the previous two days was then used to determine the fraction of the eggs laid on the current day which were fertile. Only fertile eggs were entered into the network.

Development rates and egg laying patterns published by Smith et.al. for a constant $25 \, ^\circ$C. laboratory environment were chosen. The development rates were: eggs, 4 days; larvae, 17 days; pupae, 17 days; and adults, 15 days. Development rates for both moth types vary with temperature. However, the data used here suggest that the only effect of varying temperatures will be to vary the length (in days) of generations. Conclusions based on generations rather than days concerning suppression potential should therefore not be seriously affected by the assumption of constant temperature.

Daily mortality factors of 20 percent for eggs, 15 percent for larvae, five percent for pupae, and 10 percent for adults were used. These values were chosen in accordance with the generally accepted notion that the natural tobacco budworm population will increase by a factor of five with each generation.

A daily emergence of 100 budworms (50 males and 50 females) for each of the first 10 days of simulation was assumed. On each of these same days, a constant number of backcross moths was also released. Five backcross release rates were simulated: 0 per day; 100 per day; 1,000 per

day; 3,000 per day; and 5,000 per day. The model was run for 200 simulation days.

The results of these simulation runs are shown in Table 1. In addition to results on the adult population, the larvae totals are included since it is this developmental stage which actually damages crops. As expected, the higher backcross release ratios provided the highest degree of population suppression. However the percent fertile males increased with time because of the lower egg laying of the backcross moths. Therefore, even relatively high levels of initial backcross release did not drive the budworm population to zero because of this "recovery factor". Even for a 50:1 ratio, the budworm population was stable between generations three and four and would increase thereafter in the absence of additional backcross releases.

The results in Table 1 reflect the assumption that backcross moths lay fewer eggs than do budworm moths. While this assumption is consistent with the findings of Smith et.al., it was questioned by several scientists who reviewed earlier drafts of this manuscript. Furthermore, previous studies of the potential for genetic control of the budworm have assumed that the two moth types lay equal numbers of eggs. Therefore, a second set of model runs was made in which the backcross egg lay was set equal to that of the budworm. The results of these runs suggested that virtual elimination of the budworm in a single season is theoretically possible if an equal egg lay is assumed. For a 30:1 ratio, only 11 budworms remained in generation 4; for a 50:1 ratio, only 2 budworms remained.

CONCLUDING REMARKS

With respect to the hybrid sterilization model, the results of this study indicate that the relative egg laying capacity is an important variable in determining the success of a backcross release program. Even though such factors as in-migration of budworm moths were ignored, the budworm population was shown to survive relatively high release ratios when different egg lays were assumed. However, the fact remains that population levels were generally much lower in later generations with the backcross releases than without them. This suggests that the program has considerable potential as a population management technique.

As for the general effectiveness of SLAM in modeling insect populations, the authors were well satisfied with its capabilities. One only needs to spend a few hours trying to develop a "straight FORTRAN" model to duplicate the results presented here to gain some appreciation of the authors' conviction. In addition, there may well be value in developing relatively standardized insect models, such as the type developed here, as a means of increasing the degree and ease of communication among modelers.

Table 1. Adult and larva totals (virescens and backcross) for five release ratios.

Release Ratio (BC/V)	Total (BC + V)[a]	Generation				
		0[b]	1	2	3	4
0:1	Adults	651 (100)[c]	2,397 (100)	9,800 (100)	40,448 (100)	167,926 (100)
	Larvae	38,888	156,959	641,009	2,663,832	10,956,843
1:1	Adults	1,303 (50)	2,846 (63)	8,125 (75)	26,813 (83.7)	96,711 (89.7)
	Larvae	46,191	129,717	422,829	1,515,070	5,807,027
10:1	Adults	7,165 (9.1)	3,797 (14.5)	3,279 (22.5)	4,175 (33.2)	7,521 (47.4)
	Larvae	61,364	51,966	65,544	117,309	278,469
30:1	Adults	20,191 (3.2)	4,052 (5.4)	1,411 (8.8)	799 (14.4)	724 (23.5)
	Larvae	65,436	22,339	12,499	11,276	15,555
50:1	Adults	33,217 (2.0	4,114 (3.3)	900 (5.5)	329 (9.2)	202 (15.7)
	Larvae	66,437	14,236	5,150	3,145	3,119

a/ Adult and larvae totals are the maximum values observed for each generation.

b/ Generation 0 is that resulting from initial virescens emergence and backcross release.

c/ Numbers in parenthesis are the percent of the total adults whch are virescens.

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