A DISCRETE MODEL SIMULATING THE INTERFIELD MOVEMENT
OF A MULTHOST PHYTOPHAGOUS BEETLE

LOTHAR ALBRECHT DOHSE

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A DISCRETE MODEL SIMULATING THE INTERFIELD MOVEMENT
OF A MULTIHOST PHYTOPHAGOUS BEETLE

by

LOTHAR ALBRECHT DOHSE

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[Signatures]

[Chairman of Advisory Committee]
ABSTRACT

DOHSE, LOTHAR ALBRECHT. A Discrete Model Simulating the Interfield Movement of a Multihost Phytophagous Beetle. (Under the supervision of H. ROBERT VAN DER VAART.)

A system of distinct resource fields is considered between which a beetle of limited flight migrates. It is assumed that these fields are points on a plane surrounded by circular regions of attractivity. A beetle is assumed to migrate into a field if it enters one of these circular regions. A computer algorithm which uses this framework to simulate the interfield beetle movement is developed, and its sensitivity to the different parameters is analyzed. It allows for a maximum of 50 fields, each one of which can be of six different host crop varieties.

Two population models are developed which use the previously discussed interfield movement algorithm. Both models simulate the fluctuations of adult female beetle populations over one season for all the fields under consideration. The first is a Markovian model, which considers each age/migration state. The second uses Monte Carlo techniques to follow each individual beetle (the maximum allowable is 100,000 beetles). This model simulates the life history of each beetle with the help of a linear congruential random number generator. These two models are designed in such a way that the first model gives the expected value of the second. Both of these models are used to study the effect of the spatio-temporal structure of the fields in an agro-ecosystem on the population sizes of a herbivorous beetle species.
The values of the parameters used in these models were inferred from observations of experiments on the Mexican bean beetle (*Epilachna varivestis*, Mulsant) on soy and lima beans (*Glycine maximus* and *Phaseolus vulgaris*).
Lothar Albrecht Dohse was born in Schoettmar, Germany on July 20, 1954. His early childhood was spent with his grandparents in Cologne, Germany. On September 19, 1961 he immigrated to the United States to live with his parents in New Orleans.

The author graduated from John F. Kennedy Senior High School in May of 1972. He entered the University of New Orleans in New Orleans, Louisiana and received a Bachelor of Science degree with a major in mathematics in December of 1975.

In August, 1976, the author entered the applied mathematics program at the North Carolina State University in Raleigh. He earned his Master of Science in mathematics in May of 1978. During these two years he supported himself by teaching freshman mathematics courses.

After completing the requirements for the master's degree, the author changed his curricula, and entered the biomathematics program of the statistics department at North Carolina State University. He continued to teach in the mathematics department until December, 1979. In January, 1980 he became associated with an integrated pest management research program under the direction of Dr. R. E. Stinner and Dr. R. L. Rabb. Interactions with Dr. Stinner and Dr. W. S. Blau, an ecologist of this group, led to the research presented in this dissertation.
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CHAPTER 1:  
INTRODUCTION

In the past, most of the effort in arthropod population modeling has been spent on birth and death processes (Varley et al, 1973; Price, 1975; Ruesink, 1975). Relatively little attention has been given to migration into or out of a region or a system. This thesis will develop some approaches to incorporate migration (or movement) into a population model.

Part of the problem has been that migration, unlike birth or death, is not easily defined. Depending on the arthropod species whose population is being modeled, migration may mean anything from movement from one leaf to the next, as in the case of aphid species (Bryant, 1969); or, as in the case of the monarch butterfly, movement across an entire continent (Baker, 1978). This variability makes it impossible, from a modeling perspective, to approach this phenomenon in a generalized way. Before one can model the effect of migration on the population size of a given species, the term "migration" must be defined. Defining migration in a utilitarian way is only possible if one considers the behavioral attributes of a specific arthropod group and specific patterns of resources.

This paper will concern itself with an insect that lives in a patchy environment. From a zoocentric viewpoint each patch of this environment is distinct. That is, the distance between any two such patches is so large that an individual living in one patch will not be
able to recognize the other patch. Any movement between two patches is now defined as migration. An attempt will be made to simulate this type of interpatch movement for a herbivore of limited mobility (flight potential \( \leq 10 \) kilometers).

The following key definitions should be noted. A field or patch is a single agricultural unit consisting of one crop. The individual plants of a given field will be considered of identical quality (age, growth stage and size). These fields are allowed to range in size from 0.1 are to 10 hectares. The beetle population, unless stated otherwise, will be the number of adult female beetles in a given field on a given day.

Previous attempts to model movement/migration have usually been in a continuous time, homogeneous environment framework (Skellam, 1951; Okubo, 1980; Levin, 1978). This type of approach involves extensive use of diffusion equations. These diffusion models have provided some interesting mathematics but due to the complexity involved in working with non-isotropic diffusion equations, this approach has had limited applicability.

Experimental systems have been set up (Kariveva and Shigesunda, 1981) to validate some simple diffusion models, but these were in a highly artificial design such as to reduce their complexity.

Another approach has been to divide an entire region into cells (Sawyer, 1978), and calculate the probability of moving into adjacent cells. Such a modeling method was used to simulate movement of the cereal leaf beetle between cereal fields in Michigan (Sawyer, 1978), and the interleaf movement of aphids (Bryant, 1969). Here each cell is
likely to be homogeneous and the herbivore tends to move only to an adjacent cell. This approach was also rejected since the fields in the southeastern United States tend to be rather small and the crop mixture diverse. For any larger region, such as a county, the percentage of ground cover of any one field crop is quite small (< 10%). With this resource patchiness, the grid method tends to be inefficient if the insect under consideration has some degree of flight mobility.

Both of the aforementioned modeling approaches assume that each individual of a population has an equal chance of moving from one unit to an adjacent one. This type of behavior can be described as a random walk, and more likely describes the foraging type behavior referred to in the literature as "trivial flight". Also, no account has been made for a possible "migration-prone" phase in the insect's life cycle.

An entirely different approach frequently encountered in the literature simulates the path of an individual organism moving through its "lebensraum" (Siniff and Jesson, 1969; Jones, 1977; Kaiser, 1976). Most of the emphasis in such an approach has been toward the behavioral aspect of migration. The emphasis is placed on the location of one individual and how it responds to given environmental conditions. Actual population sizes are not considered.

Kitching (1971) extended the model used by Siniff and Jesson to encompass a larger number of individuals. His model simulated movement of Tribolium confusum (Linnaeus) from a fixed starting point over a large area which contained several resource patches. These patches were inside hypothetical circular regions. It was assumed that a beetle recognized a resource patch only if it entered one of these
circles. Once a beetle found a food supply, it ceased moving (migrating). This same framework is used to model the Mexican bean beetle/bean field system.

The model to be described hereafter considers not only the fields and their relative locations, but also the age and life stages of the beetles living in those fields. It is discrete both spatially and temporally. Similar models using this approach have already been devised for systems ranging from humans moving between states (Rogers, 1975) to beetles moving between dung patches (Hanski, 1980). These models were empirical (in nature) and utilized the observations of the population fluctuations between the designated resource patches. Unfortunately, there were few data available for the modeling efforts of this paper.

For this model, the beetle populations of each field are divided into various age/development classes. These classes are defined such that the proportion of beetles developing or "moving" from one class to the next is constant with respect to their past history. Thus we have a Markovian model, since it is assumed that the past history of the beetles in each class has no effect on their present behavior.

The two problems which will be addressed in this work are: 1) the possible processes involved in interfield movement and 2) the possible reasons for the high degree of variation between the population sizes in similar fields. Several models with different underlying assumptions (both behavioral and mathematical) are developed in order to test the effects of these various assumptions on model behavior.
CHAPTER 2:
THE BIOLOGICAL SYSTEM

The Insect Herbivore

The Mexican bean beetle, *Epilachna varivestis* (Mulsant), is not a native species to North Carolina. It has extended its range through agricultural practices and established itself as far north as southern Canada (Auclair, 1959). It seems to be limited both by the extent of its hosts (*Phaseolus* spp. and soybeans, *Glycine max*imus) and climatic conditions. Although it feeds on most legumes, it thrives only on the above-mentioned crops and, of those, it prefers *Phaseolus* spp. (lima or snap beans). This beetle is of some importance as a pest on lima beans and occasionally on soybean fields in North Carolina. Its populations may reach high enough densities to cause economic damage if the fields are not managed properly (Auclair, 1959).

*E. varivestis* emerges in early to mid May as an adult from its overwintering site, usually a forest edge near the previous year's host. From there it moves/migrates to a suitable host habitat to reproduce (Eddy and McAlister, 1927; Berndardt and Shepard, 1978).

The beetle's flight ability is limited, as is the case for most Coleoptera. Direct observations of flying beetles in their natural environment show that they rarely fly more than 3 or 4 kilometers a day (Auclair, 1959). There have, however, been records of flights that extended over 10 kilometers.
Evidence of three types of flight behavior has been recorded for the Coccinellid beetles: (1) an upward flight that reaches heights of over 10 meters, (2) a more directional flight of about 3 meters in elevation, and (3) a series of short "hops" (with each individual hop about 10 meters). These types of behaviors have been documented in a study done on another species of the same family, *Coleomegilla maculata* (Solbreck, 1975). These types of behaviors have also been observed in Mexican bean beetles (Blau, 1982).

Mating continues throughout the adult beetle's life. In the case of multiple matings, the sperm of the last male that mated the female fertilize the eggs (Mathews and Mathews, 1978). For most insects, including the Mexican bean beetle, a female can be expected to be fertilized before she is ready to oviposit. In the model, it is assumed that all females will have been fertilized by the time the eggs are matured and the beetle is ready to oviposit.

The eggs are laid on the leaf of a host plant in masses of about 30-50 eggs (Kitayama et al., 1979; Sprenkel and Rabb, 1981). The Mexican bean beetle can lay several of such egg masses in its lifetime. If a female lives until "old age", ca. 40 days, she may lay as many as 12 egg masses (List, 1921).

Although development rates vary with temperature, for North Carolina summers it takes about 5 days for eggs to hatch (Campbell, 1958). The development times for the four larval instars are roughly 4 to 5 days for each, with the latter larval stages taking slightly longer to develop (Campbell, 1958; Wilson et al., 1982). The final immature stage, the pupal stage, takes about 7 days, after which the beetle emerges as an imago.
This imago usually remains in a "preadult" stage for some time. During this "preadult" stage, the beetle will exhibit neither oviposition (Pfarnder et al., 1981) nor flight behavior (Blau and Stinner, 1981). This process can take 6 to 7 days. With the preadult the development time depends not only on temperature but possibly also on the host plant (Blau, 1982). The transition from preadult to adult cannot be observed directly and therefore cannot be measured. Since only mature adults can migrate or oviposit (two phenomena easily observed in the lab), observations on the minimum age of adult beetles exhibiting these phenomenon can be used to estimate the date of maturation.

From mid August through September the beetles will begin to search for overwintering sites. This is usually the F2 generation, but individuals of the F1 and F3 generation may also successfully overwinter (Eddy and McAllister, 1927).

**The Hosts**

Only two host plant types are considered in this simulation attempt: soybeans and *Phaseolus* spp. These two crops are found quite frequently in the Carolinas. The total acreage of soybeans in North Carolina is approximately 600,000 hectares, while the area covered by lima and snap bean fields is only 2,000 hectares (USDC, 1978). The majority of lima beans are planted in small private gardens (on the order of 0.04 hectares). Soybeans, on the other hand, the less preferred host plant, are grown in much larger plots (0.5 - 15 hectares). These statistics differ depending on the region. In North Carolina's counties in the coastal plain, soybeans cover as much as 20% of the counties' area.
In this region the ratio between total soybean acreage and total *Phaseolus* spp. acreage is approximately 800:1 (USDC, 1978). (Note: the U.S. Department of Commerce's survey does not include private gardens, so the ratio is biased in favor of soybeans.)

Although the bean fields are relatively sparse, and this beetle is seldom found in large numbers, occasionally entire fields are destroyed because of massive population buildups. The high degree of patchiness in the local populations of the beetle is possibly due, in part, to the high heterogeneity of the environment. The phenomenon of patchy distribution is another aspect that this modeling effort will explore.
CHAPTER 3:
A DETERMINISTIC INTERFIELD MOVEMENT MODEL

Description of the Model

The purpose of this model is to simulate interpatch movement of an insect with limited mobility. The model itself has been kept flexible enough to encompass a more general system of discrete host patches with one herbivore species moving between these patches. The parameter values used in this simulation were inferred from data taken from experiments on a system of Mexican bean beetle-soy/lima bean fields.

The computer program was designed to be a subcomponent of a population model. This "supermodel", to be discussed in a later section, simulates the population size of a specified insect species living in a system consisting of discrete resource fields or patches. The maximum number of fields presently allowable is 50. If more space is needed, appropriate alterations in the storage allocation statements is all that is necessary. It is possible to have a system with over 100 fields, but the computing cost might be too high with respect to the benefits derived from such a large simulation run. (The execution time is approximately proportional to the square of the number of fields.)

Since this beetle is active only during the daytime, this simulation model is in a discrete time framework. It is only during the day that the insect will fly. Thus, the time increments used are one day in length. To test the effect of the time increments, two simulation
runs (using 1 day and 1/2 day time intervals, respectively) were made. The resulting difference between these runs was negligibly small. For the 1 day increments, the total number of beetles that survived after a 15 day period was 3% higher than in the comparable 1/2 day interval simulation run. (Note: for these two simulations the parameter values used in the first run for the probability of daily survival and the probability of staying in the field were the square of the corresponding parameters used in the latter simulation run.)

The first major step of this program is an initialization routine. This algorithm calculates the conditional probability of reaching field \( i \) from another field \( j \) (PR), given that the beetle will migrate from field \( j \). (Fields \( i \) and \( j \) are any two fields in the system.) This probability will be the product of two probability functions of two (assumed) independent random variables. The first of these (Pr) governs the beetle's flight direction and orientation, the second (Pd) governs the maximum distance a beetle can fly.

\[
PR (\text{from } j \text{ to } i) = Pr (\text{orientation}) \times Pd (\text{distance}) \quad (3.1)
\]

The problem of calculating the above-mentioned conditional probability has been broken into two parts. The first of these probability functions is assumed to be uniform over the interval 0 to \( 2 \times \pi \). The second is assumed to be a shifted negative exponential (see Equation 3.2).

The uniform distribution was chosen because no evidence for directionality was found. Siniff and Jesson (1969) suggested a polar coordinate normal distribution defined over the unit circle but this
would be applicable only if the beetles seemed to have a preferred
direction. The major phenomena which could be expected to influence the
directionality of the flight are light and wind direction. Field
observations, however, are presently too few and have too large a
variance to assume directionality (Blau, 1982). If future observations
should prove that there is a preferred direction, the program is con­
structed in such a way that only one equation needs to be replaced and
one input statement added.

The probability density function governing the maximum time
duration a beetle can fly was taken from the literature. Freeman (1977)
and Jones (1977) suggested a negative exponential function for the
distance of one flight. Tethered flight experiments, though inconclusive,
also suggest this type of curve for the duration of flight (Blau, 1982).

The function which is used in the model to calculate the chance of
a beetle reaching a specified distance \( x \) is:

\[
P_d(x) = \begin{cases} 
1 & \text{for } x \leq d_m \\
\exp \left[ -u \times (c \times x - d_m) \right] & \text{for } x > d_m .
\end{cases}
\]

(3.2)

where

\( P_d(x) = \) the probability that beetle can fly at least \( x \) kilometers,
\( u = \) relative death rate per kilometer,
\( c = \) adjustment constant (discussed later),
\( d_m = \) minimum distance before death rate is considered.
To simplify the calculations and reduce the number of input parameters, the fields are viewed in this program as points in a plane. The entire beetle population is viewed as being in the center of the field, i.e., on that point. Each field is surrounded by a circular "aura" of a specified radius. A beetle is assumed to immigrate into a field if it encounters this aura, i.e., if its flight path intersects this circular region. (See Appendix A.) The equation for the probability of going in the direction of field \( j \) is given by Equation 3.3.

\[
Pr(x, r_j) = \frac{[\arcsin(r_j/x)]}{\pi}
\]  

(3.3)

where:

\( r_j \) = the radius of field \( j \) (includes the "aura"),
\( x \) = distance between point of origin and center of field \( j \).

A parameter "c" was later incorporated into the algorithm to give the program user flexibility in allowing some degree of searching behavior for the beetle. This parameter is not identifiable, and it can be eliminated by appropriate adjustment of \( u, d_m \) and \( r_j \). Its purpose is to allow the program user who wishes to consider beetle searching behavior to conveniently vary all appropriate parameters by just changing \( c \). Let a migrating beetle with minimal searching behavior (beetle flies in a straight line) spend 1 unit of time in a given distance interval from its point of origin. The amount of time spent in that same distance interval is then 1 (\( c = 1 \)). If, on the other hand, the beetle exhibits searching behavior, then \( c > 1 \). For a more specific explanation for the calculation of \( c \), see Appendix A. The value of \( c \)
will affect the probability of reaching a given field from some point of origin in two ways, as c increases: 1) close fields will have a higher chance of being found and 2) more distant fields will have a lower chance of being reached. With the inclusion of c, Equation 3.3 becomes:

\[
Pr(x,r_j) = \begin{cases} 
\frac{\arcsin(cxr_j/x)}{\pi} & r_j < \frac{w}{2x(c-1)} \\
\frac{\arcsin((w/2+r_j)/x)}{\pi} & r_j \geq \frac{w}{2x(c-1)}
\end{cases}
\]  

(3.4)

The parameter, w, might be needed in conjunction with c to prevent the increase of \( r_j \) from becoming too large. \( 2 \times \frac{w}{\pi} \) is described as the maximum width of the corridor in which the beetle is searching or flying. (See Appendix A, Figure 8.3.)

The above functions are strictly dependent on the geographic parameters, field size and location. The probabilities of migrations, on the other hand, depend on the organisms (beetles and crops) of the model. Fortunately, with respect to the probability of migration initiation there are some data available. Several experiments were set up to test parameters such as the propensity to fly at various ages and the youngest age of first flight (Dingle, 1980).

Blau and Stinner (1982) observed this earliest age of migration for the Mexican bean beetle. Their results showed the same characteristic skewed curve seen in Dingle's data. Most of the newly emerged beetles were observed to leave the field within 4 to 9 days after eclosion. After comparing the results of two different hosts (soy and lima), the indication was that beetles will stay longer in a lima bean field than in a soybean field, i.e., the expected time until departure is longer in limas. This difference can be simulated with appropriate values for the probabilities of migration from a given field type.
In this model it is assumed that an adult beetle can be in one of
four migratory states. The first of these is a preadult (premigratory)
state, $s_0$, where no flight behavior is possible. This is followed by a
"ready to migrate state", $s_1$. (See Figure 3.1.)

The beetle leaves state $s_1$ only if it has migrated. Since a beetle
could be in a different physiological state during migration, the
probability of migration could depend on whether a beetle has or has not
migrated on a given previous day. The model is flexible enough to
incorporate this dependency (memory). However, in order to keep the
Markovian assumption, two other migration states are needed. A beetle
is in the migrating state, $s_2$, if it migrated on the previous day.
(Probability for flight in this state is high.) A beetle is in the
"colonizing" state, $s_3$, if it has migrated, but did not migrate on the
previous day. Probability of migration in this state is assumed low.

Since the insect is initially in a flightless state ($s_1$) followed
by a state in which flight is likely ($s_2$), there should be an underlying
probability density function which governs the chance of maturing
(going from $s_1$ to $s_2$) at a given age. This random variable, age of
beetle at first flight, is assumed to be distributed by a shifted
binomial distribution (Equation 3.5).

$$f(\text{age}) = \begin{cases} 
0 & \text{if } \text{age} < m \\
M-m \times p^{(\text{age}-m)} \times (1-p)^{\text{M-\text{age}}} & \text{if } m \leq \text{age} \leq \text{M} \\
0 & \text{if } \text{M} < \text{age}.
\end{cases}$$ (3.5)
Figure 3.1: Digraph of transition probability matrix between the different beetle states. The daily survival rate is assumed to be 1.

\[ f(a) = \text{prob. of maturing at age, } a. \text{ (See eq. 3.5)} \]

\[ \gamma = \gamma(j) = \text{prob. of finding another field.} \]

\[ (\gamma \text{ depends on location of starting point, field } j.) \]

\[ p_i = \text{prob. of migration if in state, } S_i. \]
where:

\[ f(\text{age}) = \text{probability of maturing (dependent on the age of the beetle)}, \]
\[ m = \text{minimum age for maturation}, \]
\[ M = \text{maximum age for maturation}, \]
\[ q = \text{estimated mean age for maturation}/(M-m) \text{ (age is measured in number of days)}. \]

This distribution was chosen for its simplicity in calculation and its goodness of fit. (See Figure 3.2.) The only parameters needed are the earliest, latest and expected age of maturation. These parameters depend on the type and condition of the field. Together with the probability of leaving, the above distribution, \( f(\text{age}) \), is flexible enough to fit most unimodal distributions that could be expected for this process.

Data for the number of days after eclosion at which first flight occurs are available (Blau and Stinner, 1982). (See Figure 3.2.) By simple graphic estimate of the parameters, the simulated curve gave a reasonable fit to the data. Note that the resulting simulated curve is actually the product of \( f(\text{age}) \) and the probability of migrating, given that the adult is in the state, \( s_1 \).

Once a beetle has matured into a migratory state, the probability of migration on any given day will depend on the state of the beetle, the field's condition and the crop type. The more "preferred" the field, the less likely a beetle is to emigrate from that field. (The maximum number of field types this program can accommodate is six, but this also can be easily modified to increase the complexity of the system.) Note,
Figure 3.2: Histogram of percentage of beetles from one cohort flying at given adult beetle age (number of days after eclosion). The simulated results are compared to actual observations on Mexican bean beetles leaving lima bean plants (Blau and Stinner 1982). (The parameter values used for the simulation are: m=3, M=10, q=.58, and p_1=.27.)
it is assumed that, for each migration state, the probabilities of migrating are constant. (Field development is considered only in the extended version of this model discussed in Chapter 4.)

Thus, the probability of leaving a field depends on the type of field and the state of the beetle. There is no density dependent behavior assumed, with one exception: if the population reaches a specified maximum, the field will be destroyed and all the beetles will leave. On the other hand, the probability of reaching any given field is dependent on the location-distribution of emigrating beetles and the size of the given field. Thus, the chance of leaving a given habitat is dependent on biological parameters and the chance of reaching a given habitat is dependent on the geometry (spatial structure) of the system.

Analysis

Since the previous migration model is just a subcomponent of a population model, no birth rates are considered. Thus it is not possible to do any analysis involving the stability of the system, since any nonzero death rate will cause the entire population to reach the ultimate absorbing state, extinction. A sensitivity analysis can, however, be used to determine the effect of key parameters on specific attributes of the population dynamics of the system. Since migration in this simulation model, as in reality, is a costly enterprise (in terms of survival), the migration parameters will be considered, and their effect on the survival rates of the individual beetles discussed.

Let us consider a simple system of several fields, all of which are the same type. This section will test the sensitivities of the model to the relative position of the fields, as well as their relative sizes. All of the probability parameters for migration will be fixed.

Throughout this section, the simulation will run for 15 days. For simplicity's sake, all beetles will have the same age initially, the earliest age of migration will be day 3 and the last day to enter the "ready to migrate" states, $S_1$, will be day 4.

Inter-field Distances

In order to keep the system simple, only a two-field system will be discussed at present. These two fields will be designated as fields 1 and 2. The following is a discussion on the sensitivity of the conditional probability of reaching field 2, $\text{PR}(d_{1,2}, r_2)$ to the interfield distance, $d_{1,2}$. The size of field 2 will remain fixed, and the units for the distance will be measured in terms of $r_2$.

The probability of reaching field 2, if the beetle emigrated from field 1 is given by Equation 3.1. We now have:

$$\text{PR}(d_{1,2}, r_2) = \text{Pr}(d_{1,2}, r_2) \times \text{Pd}(d_{1,2})$$

(3.6)

where:
\( r_2 \) = radius of field 2,
\( d_{1,2} \) = distance between centers of the two fields,
\( \text{PR}(d_{1,2}, r_2) \) = the probability of reaching a field of radius
\( r_2 \), \( d_{1,2} \) units away.

Setting \( r_2 = 1 \), adjusting the scales of the other parameters and using
 equations 3.2 and 3.3, we get:

\[
\text{PR}(x,1) = \frac{\arcsin(1/x)}{\pi} \times \exp[-u \times \max(0,x-d_m)]
\]  
(3.7)

where:
\( x = \) scaled distance between the two fields.

(Recall that \( c \) in Equation 3.2 was used only as a convenient tool to
allow for searching behavior. Since \( u, d_m \) and \( r_2 \) can be adjusted to
compensate for any value of \( c \), it is not necessary to include this
parameter in the sensitivity analysis.) Thus, there are now two parame-
ters to consider, \( u, d_m \). Since it is difficult to estimate \( u, \) a more easily approximated parameter was chosen.

Consider \( D_e \), the expected maximum distance a beetle is able to fly.

\[
D_e = \int_{0}^{\infty} (\exp[-u \times \max(0,x-d_m)])dx,
\]  
(3.8)

which simplifies to

\[
D_e = d_m + 1/u.
\]  
(3.9)
Now combining Equations 3.7 and 3.9 we get

\[ PR(x,l) = \arcsin(1/x)/\pi \times \exp[-\max(0, (x-d_m)/D_{e-d_m})] \]  \hspace{1cm} (3.10)

Note that for the Mexican bean beetle, \( D \) can vary from 1 to 10 kilometers (Auclair, 1959).

The effects of \( d_m \) and \( d_e \) on the function \( PR(x,l) \) are shown graphically. (See Figure 3.3.) Note, for small values of \( x \), \( Pr(x,r_2) \times Pd(x) \), i.e., the chance of not finding a field outweighs the chance of not being able to fly the entire distance \( x \).

**Field Size**

This section will again use the two field system. In this case, the interfield distance, \( d \), as well as the total area covered by the two fields, will be fixed. Migration between the two fields is now considered in both directions. The fields will be identical in all respects except size. Without loss of generality, field 1 will be designated as the larger field.

Let \( A \) be the total acreage of the system, and let \( d \) be the interfield distance. We now have:

\[ r_2 = \sqrt{A/\pi - r_2^2} \]  \hspace{1cm} (3.11)

To keep the system simple, the probability for migration is, at the present, assumed constant (\( p_1 = p_2 = p_3 = p \)). It is now possible to express the beetle interchange between the two fields in matrix form using a \( 2 \times 2 \) matrix. Equation 3.12 will give the populations of the fields at time \( t + 1 \), if the populations at time \( t \) are known.
Figure 3.3: Sensitivity of $\text{PR}(x, l)$, the probability of reaching a field $x$ units away of radius 1, to $D_e$ and $d_m$. (The interfield distance, $r_2$, is scaled so that $r_2 = 1$.)
\[ r_1 \times \arcsin(r_1/d) > r_2 \times \arcsin(r_2/d) \quad \text{for } r_1 > r_2 \]

\[ + \quad r_1/r_2 > \frac{\arcsin(r_2/d)}{\arcsin(r_1/d)} > 1 \]

\[ + \quad \sqrt{r_1/r_2} > \sqrt{\phi_1/\phi_2} > 1 \]

\[ + \quad (r_1/r_2)^2 > (\phi_1/\phi_2)^2 > \sqrt{\phi_1/\phi_2} \]

\[ + \quad \sqrt{\phi_2/r_2}^2 > \sqrt{\phi_1/r_1}^2 \]

Therefore, the expected beetle density, \( (\text{number of beetles})/(\text{field area}) \), of the smaller field will be much greater than that of the larger one.

Note, for small values of the \( \phi_i \)'s, the eigenvalues will not differ much. Thus, their ratio will be close to one, which implies that the rate of convergence is slow. (In these cases, for a 15 day period, the results depend on the initial population sizes.)

The total population size of this two-field system after a "t" day migration period can be expressed as a function of \( r_1 \). Let \( H(r_1) \) be the total beetle population of the system at day \( t \), then:

\[ H(r_1) = (1,1) \times \begin{bmatrix} 1 - p & p \times PR(r_1,d) \\ p \times PR(r_2,d) & 1 - p \end{bmatrix} \times \begin{bmatrix} B_1(\phi) \\ B_2(\phi) \end{bmatrix}^t \quad (3.13) \]

Let \( t = 1 \) and \( B_1(\phi) = B_2(\phi) = B \), then by differentiating with respect to \( r_1 \) one gets:

\[ \frac{dH(r_1)}{dr_1} = p \times \left[ \frac{dPR(r_1,d)}{dr_1} + \frac{dPR(r_2,d)}{dr_2} \times \frac{dr_2}{dr_1} \right] \times B \]

Substituting for \( PR(r_1,d) \) in Equation 3.7, one has:
Let:

\[ B_i(t) = \text{the number of beetles in field } i \text{ at time } t, \]
\[ \phi_1 = PR(d,r_2) = \frac{[\arcsin(r_2/d)]/\pi \times Pd(d)}{/}, \]
\[ \phi_2 = PR(d,r_1) = \frac{[\arcsin(r_1/d)]/\pi \times Pd(d)}{/}. \]

The beetle distribution at time \( t + 1 \) is now given by:

\[
\begin{bmatrix}
B_1(t+1) \\
B_2(t+1)
\end{bmatrix} = \begin{bmatrix}
1 - p & p \times \phi_1 \\
p \times \phi_2 & 1 - p
\end{bmatrix} \times \begin{bmatrix}
B_1(t) \\
B_2(t)
\end{bmatrix}
\] (3.12)

The eigenvalues of the above matrix are:

\[ 1 - p + p \times \sqrt{\phi_1 \times \phi_2} \]

where \( 1 - p + p \times \sqrt{\phi_1 \times \phi_2} \) is the dominant eigenvalue.

Note, if the two fields are far enough apart, \( (d \geq 3 \times r_{\text{max}}) \), the parameters \( \phi_i \) can be approximated by \( (r_i/d) \times (1/\pi) \times Pd(d) \)
\( (|\arcsin(x) - x| < 0.0062, \text{ if } x \leq 1/3) \). This implies that the stable ratio of \( B_1/B_2 \) (i.e., the ratio of the elements of the dominant eigenvector) is:

\[ \sqrt{r_1/r_2} \]

If, on the other hand, the fields are closer together such that the above approximation is not valid, then \( r_1/r_2 \) can be used to find a bound on this stable ratio.

\( x \times \arcsin(x) \) is an increasing function on the interval, \( (0,1) \).

This means that:
\[
\frac{dH(r_1)}{dr_1} = p \times B \times \exp[-u \times \max(0,d-d_m)] \times \\
[(1/\sqrt{d^2-r_1^2}) - (1/\sqrt{d^2-r_2^2}) \times (r_1/r_2)]
\]

\[
\frac{dH(r_1)}{dr_1} = \begin{cases} 
> 0 & \text{if } r_1 < r_2 \\
= 0 & \text{if } r_1 = r_2 \\
< 0 & \text{if } r_1 > r_2
\end{cases}
\]

Thus, \(H(r_1)\) will reach a maximum at \(r_1 = r_2\). This same result will hold true for any initial population size, if \(t\) is "large enough", i.e., large enough so that \(B(t-l)\) can be approximated by the dominant eigenvector of the above matrix in Equation 3.12. (See Figure 3.4 for values \(H(r_1)\) after a 15 day simulation with different initial population distributions.)

These results will change, however, if we imbed the two-field system in a "heat bath" of several fields. The ratio of the number of beetles trapped by field 1 vs. field 2 will be approximately proportional to the ratio of the respective field radii. (This follows directly in the case of the two fields equidistant from some source point, then \(PR(r_1,d)/PR(r_2,d)\) is approximately \(r_1/r_2\).) Since the fields are temporary habitats, a colonization period must occur for a population to exist in any field. In simulation runs where two fields were submerged in a "heat bath" of similar fields, the ratio between their two populations was approximately the ratio of the lengths of their respective radii.

**Effect of Field Distribution**

The evaluation of the effect of clumping vs. uniformity is made difficult by the lack of a good measure for aggregation. In a 3 field,
Figure 3.4: The effect of relative field sizes on the total population size of a two-field system after a 15 day migration period. The total area of the two-field system remained fixed, as well as, the location of the two fields.
one-dimensional system of a specified size, this problem is avoided since there is only one degree of freedom. The location of the inner field is varied, while the two outer fields remain in a fixed location. Again, all fields are assumed to be of equal size and type. The results show that under these assumptions the more uniform the pattern, the more beetles die during migration. (See Figure 3.5.)

A similar study was done on a 10 field, one-dimensional system with similar results. In this case, however, the degree of aggregation was not as well defined as in the 3 field case. Two different "clumping" schemes were used in the analysis of the relation between beetle population at day 15 and a given aggregation measure. The measure of aggregation chosen for this analysis was suggested by Pielou (Ch. 10, 1977). (See Figure 3.6.) Although the curves differ, the general trend is consistent with the previous conclusion, "the more uniform the distribution of fields, the lower the final population densities of the beetles".

For the two-dimensional case, a 4 field system was used to test whether the results from the one-dimensional case could be extended to the more realistic two-dimensional case. This 4 field unit was duplicated eight more times, such that the resulting system had a total of 36 fields. The four fields in each unit were grouped in a specified configuration (see Figure 3.7), while the nine units were distributed uniformly over the entire system. All of these fields were identical with respect to size, type and initial population size. Here, too, the uniform distribution resulted in the minimum beetle survival.
Number of surviving beetles

---

distance of middle field to its nearest neighbor
distance between the two end fields

Figure 3.5: The effect of relative field location on the total population size of a 3 field system after a 15 day migration period. The centers of these fields are colinear and the total distance between the end fields is fixed.
Number of surviving beetles

1000+

800+ B

600+

400+ A

200+

0+----+----+----+----+----+----+----+----+----+--

50 100 150 200

Average distance to nearest neighbor, (x)

Schemes used: (Map of fields)

A: B-x-B--y--B-x-B--y--B-x-B--y--B-x-B--y--B-x-B

B: B-x-B-x-B-x-B-x-B----9*y----B-x-B-x-B-x-B-x-B

Key: $B =$ field location

$x =$ distance to nearest neighbor

Figure 3.5: The effect of field distributions of a one-dimensional system on the total population size after a 15 day migration period. The graph relates the average distance to nearest neighboring field to the total population size. Two schemes of clumping the fields were used to generate the curves.
<table>
<thead>
<tr>
<th>Field configuration for each unit</th>
<th>Total population of the 32 field (inner 4 field) system after a 15 day migration period</th>
</tr>
</thead>
<tbody>
<tr>
<td>*      *</td>
<td>687 (95)</td>
</tr>
<tr>
<td>*      *</td>
<td>704 (96)</td>
</tr>
<tr>
<td>**     **</td>
<td>773 (104)</td>
</tr>
<tr>
<td>**     **</td>
<td>791 (101)</td>
</tr>
<tr>
<td>**     **</td>
<td>1,000 (127)</td>
</tr>
</tbody>
</table>

**Figure 3.7:** Effect of clumping on the total population size of a 4 field system after a 15 day migration period. The configuration given above was represented 9 times in a 36 field system. The 4 field units formed a 3 X 3 square.
Effect of Wind on the Total Population Size

The wind velocity, as well as the beetle flight velocity, is assumed to be constant. Since Mexican bean beetles tend not to fly in winds greater than 5 km/h (Blau, 1982), but their speed of flight can exceed 10 kph (personal observations, August 1982), the program assumes that the ratio of wind speed to speed of flight cannot exceed 1. If the wind speed is higher, it is assumed that the beetle will not fly.

Consider the two-field system with a beetle in field 1 ready to migrate. The probability of finding field 2, PR(\(r_2, d'\)), is now also dependent on the wind velocity. It now becomes necessary to calculate the apparent distance a beetle must fly to reach field 2 (see Figure 8.3 of the Appendix). Let \(d' = d'(W, \alpha)\) = the apparent distance between the fields, 1 and 2, for beetles flying from 1 to 2, and \(d\) = actual distance between the two fields. (See Figure 3.8.) Then:

\[
d'(W, \alpha) = d_{i,j} \times \left[ \frac{\sqrt{1-W^2 \times \sin^2 \alpha} - W \times \cos(\alpha)}{1-W^2} \right] (3.14)
\]

where \(\alpha\) is the angle between the wind direction and the line connecting the center of field 1 to the center of field 2, and \(W\) is the wind speed divided by the beetle's flight speed.

The relation between the probability of reaching the field 2 is now given by \(PR(\(r_2, d'\))\), where \(d'\) is a function of \(W\) and \(\alpha\). (See Figure 3.9 for the graph of PR.)

Assuming the wind speed is known but the wind direction is a uniformly distributed random variable, one can calculate the expected value of \(PR(\(r_2, d'\))\). Let \(E[PR]\) be the expected value of the probability of reaching field 2, then:
d' = d/(cos θ)

Figure 3.8: Graphical representation of the effect of wind on the apparent interfield distance.

- $d_{1,2}$ = actual interfield distance
- $d'_{1,2}$ = apparent interfield distance
- $W$ = wind direction
- $W'$ = wind speed
- $d'$ = $d'_{(W', W)}$
- $\theta$ = angle between wind direction and line connecting field 1 to field 2

(1) (W', W)
Figure 3.9: The effect of the wind direction, $w$, and apparent wind speed, $W$, on the probability of reaching a given field. This field is of size, $r_2$, and $d_{1,2}$ units from point of beetle's flight initiation.

$W = \frac{\text{wind speed}}{\text{beetle flight speed}}$
Using Equation 3.7, and assuming $d_m < d'(W,\alpha)$, one gets:

$$E[PR] = \frac{1}{2\pi} \int_{-\pi}^{\pi} (PR(r_2,d'(W,\alpha))/\pi \times \exp(u \times (d'(W,\alpha)-d_m))d\alpha .$$

The above expression was calculated for different parameter values using numerical integration (Atkinson, 1978). The numerical results show that $E[PR]$ decreases as $W$ gets larger. (See Figure 3.10.) The function $E[PR]/PR(r_2,d)$, does not depend on the values of $d_m$ and $r_2$ (if one approximates the $\arcsin(r/d)$ by $r/d$). Furthermore, simulation runs indicate that this trend remains consistent under different values for $u$ and $d$.

Effects of the Migration Strategies of the Beetles on the Population Structure of the System

This final section of the analysis will discuss the model’s sensitivity to the migration parameters. These parameters, as it turns out, are those to which the model is most sensitive. Unfortunately, observations needed in order to estimate these parameters are very difficult to obtain.

The total population of the system after a 15 day migration period is discussed, as well as the total number of days a beetle is expected to stay in any one of the three migratory states in which migration is possible. The amount of time spent in each state will become important for the population model considered in the next chapter. The expected total number of offspring of each beetle in this population model will
Figure 3.10: Effect of wind speed on the expected probability of reaching the field for different parameter values for $d$, the actual distance. $PR(r,d)$ = the probability of reaching a field with radius $r$, $d$ units away. $E[PR]$ = the expected value of the probability of reaching a specified field, given the wind speed but not the wind direction. The wind direction is assumed uniformly distributed.
be the sum of the expected time spent in each migration state times the fertility rate of beetles in that state.

Effect of Age at First Migration

The adult beetle in the immature state will neither fly nor oviposit, and the chance of survival is assumed to be 1 or close to 1 in this life stage of the beetle. (The simulation runs in this section assume survival rate equals 1.) Thus, the effect of the age at which a beetle matures will only shift the population curve to the right, i.e., lengthen the generation time.

Similarly, the effect of the parameter, $p_1$, the probability of migrating given that the beetle has never migrated before, will not have a significant effect on the total population size of the first generation considered in the system. (Recall that this algorithm does not consider oviposition.) In the population model, however, where oviposition is possible if the beetle is in state $s_1$, the population size of the next generation size depends on $p_1$. The expected time duration a beetle will stay in state $s_1$ is $1/p_1$. If the chance of finding another field is low, a population model will be highly sensitive to the value of $p_1$. (See Equation 3.19.)

Effects of the Probabilities of Migration

The greatest impact on this model is made by the parameters $p_2$ and $p_3$, the probabilities of migration for beetles that have migrated at some time in the past. The first is for the beetle that migrated on the previous day, the second is for one that did not. Unfortunately, these are the least measurable of all the parameters. Their values could range from .1 to .8. The only additional constraint is $p_3 \leq p_2$. 
(Colonizing beetles are less likely to migrate than beetles that have just migrated and are still in the migrating state.)

In a 10 field simulated system in which all the fields were of equal type, the increase in the probabilities for migration decreased the number of surviving beetles. (See Figure 3.11.) Also, larger values for \( p_2 \) (or \( p_3 \)) had the additional effect of increasing the sensitivity of the model to the geometry of the field system.

Aside from simulation runs, another approach can be used to get an approximation to the effect of the migration parameters on the population structure of the system. Consider only the migration states. Let \( \Psi \) be the probability of surviving one migration. Assume that \( \Psi \) is constant. (This assumption is possible if the system of fields is infinitely large with fields distributed uniformly throughout.) Only if the condition, \( \Psi \) constant, is satisfied can the fields be lumped into one group, and the resulting model still be Markovian. The resulting matrix model will now just consider the migration states. This approach allows one to determine the amount of the time spent in each migration state. Using the digraph of the system (Figure 3.1), one can construct a transition matrix for the three migration states. Let \( Q \) be that matrix, then:

\[
Q = \begin{bmatrix}
1 - p_1 & 0 & 0 \\
\Psi \times p_1 & \Psi \times p_2 & \Psi \times p_3 \\
0 & 1 - p_2 & 1 - p_3
\end{bmatrix}.
\] (3.16)
Figure 3.11: Sensitivity of the total population size after a 15-day migration period to the probabilities of migration, $p_2$ and $p_3$.

Initial populations uniformly distributed.

Initial population all in one field.
Let $\Psi$, $p_i$ ($i = 1, 2, 3$) be in the interval $(0, 1)$, and assume $p_2 \neq p_3$, then the matrix, $Q$, is invertible and has a dominant eigenvalue less than 1.

The total expected time spent in each migration class ($Z_i$) can now be determined by the following sum.

$$
\begin{align*}
\begin{pmatrix}
Z_1 \\
Z_2 \\
Z_3
\end{pmatrix} &= \sum_{t=0}^{\infty} Q^t \times \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix} = I - Q \times \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}.
\end{align*}
$$

(3.17)

Since the 3 values of $Q$ are less than one, $(I - Q)^{-1}$ exists. Thus:

$$
\begin{align*}
\begin{pmatrix}
Z_1 \\
Z_2 \\
Z_3
\end{pmatrix} &= (I - Q)^{-1} \times \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}.
\end{align*}
$$

(3.18)

This expression can be evaluated to give:

$$
\begin{align*}
\begin{pmatrix}
Z_1 \\
Z_2 \\
Z_3
\end{pmatrix} &= \begin{pmatrix} 1/p_1 \\ \Psi/(1-\Psi) \\ \Psi/(1-\Psi) \times [(1-p_2)/p_3] \end{pmatrix}.
\end{align*}
$$

(3.19)

Note that although the system is sensitive to $\Psi$, $\Psi$ is a function of the geometry of the system and not just a parameter to be estimated. Its value comes out of simulations conducted for any given geometry. It depends highly on the field density and distribution, as well as average field size. These parameters have already been discussed in the previous section. Field density is discussed further in Chapter 5.
At this stage of the modeling effort it becomes necessary to refer to the actual system. More observations are needed to get a more precise idea of the parameter values.
CHAPTER 4:
A DETERMINISTIC POPULATION MODEL WITH INTERFIELD MOVEMENT

Description of the Model

The previous model was designed as a subcomponent of a larger, more extensive population model. The following proposed model is a simple exploratory simulation that will be used as a population generator for the migration model. In its present form it is not meant to be used for prediction in any pest management programs. Its intent is to further test the performance of the previously discussed movement model.

With one minor exception, all the assumptions of the previous interfield movement model apply to this population model as well. A small modification is needed to economize on computer storage space. In the previous model a beetle is assumed to be in state $s_1$ until it migrates. In the case of the deterministic population model (henceforth referred to as DEPOMD) a beetle will remain in state $s_1$ until it either migrates or reaches a specified age. This age was arbitrarily set to 20 days. (Using the estimated parameters for beetles in soy or lima bean fields, over 98% will have left state $s_1$ after a 20 day simulation.)

Mortality for adults is assumed to be constant within any given field type, and is considered on a daily basis. The mortality for preadults is assumed to depend on the field type and the stage of the beetle. This mortality is only considered at the end of each development stage. (The justifications for the discrepancy between the model and
Reality in the calculation of the mortality are: 1) most data will give survival from one instar to the next, and 2) computing is more efficient.

Development rates will vary from one instar (life stage) to the next. They are assumed to be dependent on the field type and the season of the year. In colder seasons the time to develop from one instar to the next will be longer. An external function is used to determine the magnitude of this increase in the development rate. (See Appendix B, Figure 8.5.)

The daily rate of oviposition also varies from one field type to the next. Although no documentation has been found relating the rates of oviposition to the rates of migration of this specific insect, there is a general tendency among many insects in this direction (Johnson, 1969). The model does allow for different fertility rates for the different migration states.

The size of the egg mass is assumed to be constant. Only the generation number will affect the number of eggs per mass. List (1921) observed a difference between the number of eggs laid by an overwhelming wintering adult and by a later generation adult. Since there is only a slight overlap between the FO and F1 generations, it is possible in the model to increase the fertility by letting the number of eggs/mass be dependent on the time of year. The number of eggs/mass will be increased after a specified day. An FO female is not expected to live more than 35 days, and the earliest an F1 female will oviposit is approximately 45 days into the season. (< .1% of the FO generation will survive into the oviposition period of the next generation.) Whereas the oviposition rate actually may depend on the generation of the
female, the model assigns different fecundity rates according to the calendar date. This discrepancy is too small to cause any problems in final resulting population size.

Fields, too, are allowed to develop in this simulation. Any given field crop can have a number (< 5) of stages in succession. These field crop stages will be considered as separate field types. That is, a beetle's behavior in a field may change if that field develops into another stage. (The parameter values for migration, oviposition, etc., will differ for successive field stages.)

This model does not allow for any species interactions. No predation, density-dependence, or inter-species competition is considered. As in the previous model, weather conditions (with the exception of the effect of seasonal trends on the larval development time) were not incorporated. This simulation is only for one season. The processes of overwintering and the mortalities associated with it are left for later work.

For a more detailed discussion of a similar model, see Appendix B. The stochastic population model, STPOMD, discussed in Appendix B has the same assumptions, and uses the same parameters as the one discussed in this section. The difference between the two is that STPOMD considers each individual beetle. Each beetle's life history is generated with the help of a random number generator. The deterministic model, on the other hand, considers each age/migration class for each field. This model uses the formulae given in Table 8.2 to calculate the population sizes for the next day. Note: since all these formulae are first order, these can also be used to calculate the expected population sizes of the next day in the stochastic model.
Analysis

With this population model it is now possible to consider those parameters not included in the movement subcomponent. Note that the lengthening of the time duration of the simulation increases the sensitivity of the model to the parameters.

Stable age distributions will not be discussed since these are not possible under natural conditions. The time domain of interest in this discussion is too small (3-4 generations at most) for the population to reach a stable age distribution. After four generations (at the highest) winter will set in, and only adults survive the winter. Also, several of the parameters will change during a season as the fields develop.

Effect of Field Density on the Total Population Size

In this study a 32 field system was used. Sixteen of these fields (all of which were identical) were arranged in a 4 x 4 block. (These fields are still separated from each other). The remaining 16 (which were also identical) surrounded this block, four on each side. These latter fields were different from the ones in the block in that they could not support a population. The simulation was run for a 60 day period (long enough to span one generation), and all parameters except field density were kept constant. The field density of the inner fields was varied in two ways: 1) the number of fields remained fixed but the individual field size varied, and 2) the individual field sizes were fixed but the number of fields varied. In both cases the total initial population for the entire system was of constant size and uniformly distributed over the inner fields.
The effect of the field density was similar for the two approaches. As the field density decreased, the total population of the system (after one generation) decreased. (See Figure 4.1.) The system with a few large fields supported a lower beetle density than the system with the same crop acreage with many small fields. (Recall that no density dependence was considered, and no intra-field migration was allowed.)

Effects of Survival Rates on the Population Size

The main purpose of this population model is to give (or be able to give) a reasonable approximation of the number of adult female beetles in any given field. It does not provide an approximation of the (larval) age distribution. Thus, the survival rates for the different instars are pooled. This limits the discussion of survival to two parameters: 1) the survival from egg to adult, and 2) the daily adult survival rate.

The proportion surviving to adulthood, $s_L$, affects only the total population size of a field. Consider one field in a "heat bath" system (one field surrounded by four fields of identical type and size), and simulated for a 120 day period. The relation between $s_L$ and the maximum population size for the F1 generation, $F_{1\text{max}}$, is linear. (See Figure 4.2.) The relation between $s_L$ and $F_{2\text{max}}$, on the other hand, is quadratic. Note that in the simulation results the dates on which these maxima fall are constant; $F_{1\text{max}}$ falls on day 50 and $F_{2\text{max}}$ on day 100.

The daily survival rate for adults, $s_a$, affects both the population size and the apparent generation time (the time between two population size maxima of successive generations). As the adult survival increases
Number of adult beetles in inner fields

Total Bean field acreage inside a region of 184 units in size.

Figure 4.1: Total adult beetle population size vs. field crop density.

Histograms = Field size fixed, number of fields varied.

= Number of fields fixed, field size varied.
Figure 4.2: The maximum beetle population of the F1 and F2 generations vs. survival of the immature from the egg to adult eclosion. (Note: daily adult survival $s_a = .95$) The initial population size was 100 adult beetles in each field.
so does this "generation time". The graphs of $s_a$ vs. $F_{\text{1max}}$ ($F_{\text{2max}}$) can be approximated by an exponential curve. (See Figure 4.3.)

**Effect of Oviposition Rate on the Population Size**

Two oviposition parameters were considered for this analysis:
1) the daily rate of oviposition for colonizing beetles, $P_{\text{0}3}$, and
2) the daily rate of oviposition for migration prone beetles, $P_{\text{0}1}$ and $P_{\text{0}2}$ (assume $P_{\text{0}1} = P_{\text{0}2}$). The system used to test the model's sensitivity was the one field in a heat bath system used in the previous section.

The sensitivity of the model to $P_{\text{0}3}$ was low compared to the sensitivity to $P_{\text{0}1}$. (See Figure 4.4.) This difference in their respective sensitivities is partly due to the low survival rate of migrating adults. The value of the number of the beetle days for the colonizing state (number of beetles in state $S_3$, times number of days in that state) is apparently much lower than that value for the other states under consideration.

Note that both of these parameters tend to affect the "generation time" of the population. An increase in $P_{\text{0}1}$ tends to shorten the time between $F_{\text{1max}}$ and $F_{\text{2max}}$, whereas an increase in $P_{\text{0}3}$ tends to lengthen this time interval. Here too, the model is more sensitive to the former parameter.

**Discussion**

**A Simulation Run**

Using the parameters estimated from data of various experiments (Blau et al., 1981; Kitayama et al., 1979; Wilson et al., 1982), and constructing a field system of 40 fields, an actual simulation run was attempted. The soybean fields covered 10% of the total area and
Figure 4.3: The maximum beetle population of the F1 and F2 generations vs. daily adult survival rate. (Note: survival to adult, $s_L = .5$) The initial population size was 100 adult beetles in each field.
Figure 4.4: Population size of center field at Flmax (day 50 unless specified otherwise) vs. oviposition rate. (Initial population size of center field was 100 adult beetles.)

Initial populations of fields equal.

All beetles in center field initially.
the lima bean fields 0.1%. This field system simulates a nonspecified region on the North Carolina coastal plain. For each field a development history was inputted much like one that would be reasonable in the above mentioned geographic region. A table of input values is given together with the resulting population sizes. (See Table 4.1.) Note that from a beetle's point of view, all parameters associated with lima bean fields are "better" in terms of fitness than those associated with soybeans.

Comparison with Rogers' Type Model

In view of the above discussion one might be tempted to simplify DEPOMD. Rogers (1975) models movement of human populations between two regions. Considering mortality, fertility, and probability of moving between the two regions as functions strictly of age, he was able to estimate all the parameters with a life table study. Although the two models differ, and the data on beetles is not as easily collected as that for humans, their respective approaches are much alike. The only major difference is that DEPOMD has memory of the beetle's recent migratory history. Due to this similarity between the Leslie type model and DEPOMD, a short comparative study was done.

In Rogers' type model, the migration states are age dependent. These are now limited to three separate states: 1) pre-migration, 2) migration, and 3) colonizing. Oviposition is still dependent on the migration state except that an additional parameter was added: earliest date of ovipositing.

This type model also assumes that the organism has no memory of the past, i.e., migration does not affect the probability of migrating the
Table 4.1. Results of a simulation run of a 8.64 sq. km. region containing soybean and lima bean fields. The initial beetle population started to migrate on Julian date 130 from overwintering sites situated around the perimeter of this region. (Note: parameter values for the vegetative and reproductive stages of soybean plants may differ.)

<table>
<thead>
<tr>
<th>Description of Parameters</th>
<th>Values of Parameters for:</th>
<th>Soybeans</th>
<th>Limabean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of fields</td>
<td></td>
<td>25</td>
<td>15</td>
</tr>
<tr>
<td>Dev. time from egg to adult</td>
<td></td>
<td>22 days</td>
<td>19 days</td>
</tr>
<tr>
<td>Survival from 1st instar to pupa</td>
<td></td>
<td>0.50 (veg)</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.60 (rep)</td>
<td></td>
</tr>
<tr>
<td>Survival from pupa to adult</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily oviposition rate</td>
<td></td>
<td>0.02 (veg)</td>
<td>0.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.10 (rep)</td>
<td></td>
</tr>
<tr>
<td>Daily adult survival</td>
<td></td>
<td>0.98</td>
<td>0.98</td>
</tr>
<tr>
<td>Probability of Migration</td>
<td>(veg)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(rep)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P1</td>
<td></td>
<td>0.33</td>
<td>0.26</td>
</tr>
<tr>
<td>P2</td>
<td></td>
<td>0.5</td>
<td>0.4</td>
</tr>
<tr>
<td>P3</td>
<td></td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Total number of adults (larvae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Total field acreage)</td>
<td></td>
<td>80.9 Ha</td>
<td>0.8 Ha</td>
</tr>
<tr>
<td>Julian date 200</td>
<td></td>
<td>206 (627)</td>
<td>301 (6480)</td>
</tr>
<tr>
<td>Julian date 230</td>
<td></td>
<td>1231 (9164)</td>
<td>1726 (17341)</td>
</tr>
<tr>
<td>(Total field acreage)</td>
<td></td>
<td>80.9 Ha</td>
<td>0.2 Ha</td>
</tr>
<tr>
<td>Julian date 200</td>
<td></td>
<td>114 (361)</td>
<td>144 (3227)</td>
</tr>
<tr>
<td>Julian date 230</td>
<td></td>
<td>608 (4780)</td>
<td>799 (8442)</td>
</tr>
</tbody>
</table>
next day. This additional constraint on the model is its major drawback. It alone would be a reason for rejection.

An attempt was made to synchronize the two models such that the overall mortality, fertility and migration probabilities are about the same. This was achieved by fixing those parameters which the two models had in common. The only parameters that needed to be adjusted were oviposition and migration rates. The results indicated that Rogers' type model does not have the flexibility range of DEPOMD. Thus the large contrast between the two types of bean fields seen in the simulation run of the previous section is not possible. This difference is mainly due to the lack of the migration state, $S_2$.

The sensitivities, as before, depend on the probability of migration. Although this model is less flexible, it is just as costly to run as DEPOMD. Its only advantage is that it can be expressed more readily mathematically.
CHAPTER 5:
A STOCHASTIC POPULATION MODEL WITH INTERFIELD MOVEMENT

Description of the Model

In the past, Monte Carlo methods have been used to approximate solutions to equations which were either too complex to solve analytically, or too costly to be solved exactly on the computer. Although these Monte Carlo approximation techniques have generally been used in this type of framework, few attempts have been made to model systems directly with this stochastically oriented approach. Greenspan (1980) showed that a physical system can be approximated by just following a "few" molecules (ca. 1,000). He simulated systems in which individual molecules governed by the simple laws of motion were observed. Then using the observations from this model, he showed that these models were "... more consistent with both the molecular theory of matter and the capabilities of the modern digital computers than are classical continuous models."

In an ecosystem with a high beetle population (ca. $10^6$), a similar approach should be feasible. The number of beetles in one region of interest will not be as numerous as the number of molecules in any given physical system, but the laws governing the behavior of individuals will be much less rigorous. The less defined the processes governing the system, the less predictable the results will be. Thus, if the results of simulation runs are to be predictable, the required number of beetles that need to be "followed" might be large. If the
"following individuals" approach is to be feasible, the computer simulation program needs to accommodate these large numbers of individuals.

The "laws" that are referred to here are the probabilities of oviposition, migration and survival, as well as of intraspecific interactions such as mating, cannibalism, etc. By keeping track of the location, age and life stage of the individual beetles (ca. 10,000), one should be able to get some handle on these demographic phenomena.

It can be argued that this approach is a step closer to reality than working with a deterministic model dealing with averages of entire populations. The results from a model which follows individuals will not only give some indication of the magnitude of the population sizes, but several runs will give an indication of the stability of the system. Calculations of confidence intervals around predicted outcomes are now feasible.

The following proposed model is a Monte Carlo version of the deterministic population model of the previous chapter. Its individual units are female beetles with fertilization assumed to be certain if the beetle reaches maturity (ready to oviposit). This model is designed to make economic use of computer storage space such that it is capable of following 100,000 individual beetles if 270,000 storage bytes are available. (These limits obviously depend on the size of the computer available.) The program is efficient enough to simulate a system whose number of beetle days (number of beetles times number of days) in the simulation is less than 200,000, in fewer than 10 seconds execution time on the available computer (IBM 3081).
Models such as these have been devised before (Kitching, 1971; Kaiser, 1976; Jones, 1977) but their complexity was too great and the amount of storage space needed too large to follow the life histories of any larger number of insects. The order of magnitude of the populations considered in these models did not exceed 100. Furthermore, none of these models simulated the entire life cycle of the insect under consideration. A model devised by Wellington, et al. (1975) could accommodate approximately 60,000 insects. The ecological system this model was simulating was the western tent caterpillars on Vancouver Island. In this particular case, however, the units considered were colonies rather than insects (each colony had several hundred members). Thus, their model was inappropriate for the system considered in this work.

The Random Number Generator

In any Monte Carlo method it is imperative that the values of the "random" numbers generated are nearly independently and identically distributed. In most cases, as in this program, the deviates needed should be uniformly distributed on the interval from zero to one. The present section is a brief discussion of the theory behind random number generators, and the justifications for using the "random" number generating algorithm found in this model.

The terms "random" and "independent", associated with a generator that calculates each deviate from the previous one, are misnomers. A more descriptive set of terms, "pseudo random" and "apparent independence", would be more accurate. Throughout this section the
latter terms are implied when the words "random" and "independence" are used.

Another important aspect of a "random" number generator is its computing efficiency. Most Monte Carlo methods require a large number of random deviates. For the purpose of this program, up to and possibly more than a million numbers might be needed. The "random" number generating algorithm should, therefore, have as few computing steps as possible to minimize computing cost.

The most common type of algorithm used is the linear congruential generator,

\[ U_{i+1} = \left\lfloor U_i \times a + c \right\rfloor \mod m \quad (5.1) \]

\[ U_i = \frac{N_i}{m} \quad (5.2) \]

where \( U_i \) is the ith uniform deviate, and "a", "c" and "m" are integers. The generator used in our simulation model uses this type of algorithm to calculate its uniform deviates, as do most packaged programs (SSP's RANDU (IBM, 1968) and IMSL's GGUBFS (IMSL, 1980) for example).

**Uniformity**

Since the congruential generator is based on integer arithmetic, the maximum number of elements the resulting sequence of U's can possibly have is "m", the modulus used in Equation 5.1. Note that once a value is repeated (i.e., \( U_i = U_{i+n} \); for some \( i \)) all successive values will be repeats, and the sequence of deviates will have a cycle of length "n". Ideally we wish this algorithm to generate a sequence whose periodicity is equal to "m" regardless of the initial seed.
Knuth (1981, p. 10) gives the conditions on "a", "c" and "m" to guarantee that the period of the generator is maximal, namely "m", for each seed.

Theorem. "The linear congruential sequence defined by m, a and c and \( N_0 \) has period length m if and only if,

i) \( c \) is relatively prime to \( m \);

ii) \( b = a - 1 \) is a multiple of \( p \), for every prime \( p \) dividing \( m \);

iii) \( b \) is a multiple of 4, if \( m \) is a multiple of 5."

The values for "a", "c" and "m" chosen in the generator used in my simulation model were 14,343,725, 7 and 2,147,483,348, respectively. The values were chosen so as to comply with the guidelines set by the above theorem. "m" is the largest number that can be stored in an integer address. "c", a shift parameter, has little effect on the distribution of the numbers generated. The value for "a" will be discussed later. Since conditions i, ii and iii hold for these parameter values, the above theorem dictates that every possible integer value between 0 and \( m - 1 \) inclusively will be represented in the sequence, \( \{N_i\} \) (for \( i = 1, 2, 3, \ldots, m'; m' \geq m \) ). Therefore, one is assured that the deviates will be uniformly distributed. The problem remains of having "independence" between any two of these deviates.

Note that there is a slight bias (mean = \( .5 - .5/m \)) in this random number generator, since 0 is a possible value for \( U_i \) (see Eq. 5.2), whereas 1 is not. This bias is insignificant for the purpose of the model used in this thesis. Furthermore, since the deviates are only used in Bernoulli trials, it is possible to eliminate the effect of this bias by appropriate use of the inequalities. For example: \( \text{Prob}(U < 0.5) \) is theoretically equal to \( \text{Prob}(U \leq 0.5) \), if \( U \) is
distributed according to a continuous distribution function. Since a
digital computer does not operate with continuous functions, appropriate
use of these inequalities can adjust for the bias.

We have shown that uniformity is ensured if certain conditions are
met by the parameters of the linear congruential generator, but the
above theorem does not deal with independence. Several statistical
tests were run on the 1000 generated "uniform" deviates to check for
deviations from the expected distribution. Both the Kolmogorov-Smirnov
test, as well as the chi-square test, showed no significant difference
at the 10% level. The mean and the variance also showed no significant
difference from the expected (10% significant level).

Independence

Knuth (1981) developed tests which have been used to measure the
independence of uniform deviates calculated with a given linear con-
gruential generator. His results indicate that the routines found in
many programming packages, especially SSP's RANDU, have a poor choice
for the multiplier "a". These subroutines tend to generate deviates
with a greater autocorrelation than necessary.

The value for "a" used in my random number generator was approxi-
mately 1% of the modulus "m". To test whether the numbers generated
from this formula did have a reasonable degree of independence, the
"poker test" (Knuth, 1981) was used. This test partitions the range
of the function generating the random numbers into 10 sections of equal
length. After generating five consecutive deviates, the number of
deviates from this group of five that fall into each section are
counted. After "n" such groups have been processed, the frequency of
the various "hands" is compared to the expected. (A "hand" refers to
the pattern of the deviates, whether all five fall into different sections, whether there exists exactly one section with two deviates and four sections with only one, etc.) The chi-square test is used to determine if there is any significant deviation from the expected. (Expected, here, refers to the frequency of the "hands" under the null hypothesis that there is no dependence among the five consecutive numbers.) The results of this test did not show any significant deviation from the expected.

In addition to the above test, the autocorrelations were also calculated to 20 lags. Here too, no indication for dependence between deviates was observed.

Efficiency

In any programming effort there is usually a trade-off between computing accuracy and computing efficiency. Since many of the packaged routines available to the FORTRAN programmer are (according to Knuth) unacceptable, writing one's own generator would seem advisable. In a test run comparing my generator to GGUBFS, the IMSL generator, the programmed one was 5% more efficient than the packaged program. (I.e., GGUBFS generated 117,000 deviates in 5 seconds execution time, whereas my program generated 122,000 deviates.)

The efficiency of my own generator is partly due to the use of the IBM machine's methods of doing integer arithmetic. On IBM computers the integer storage space consists of 4 bytes, or 32 bits. Since the first bit is used to store the sign of an integer value, the largest value that can be stored at any one address is $2^{31} - 1$. If during an arithmetic operation the resulting integer is larger than the above
stated maximum, the leading digits are truncated. Thus, the two equations, 5.3 and 5.4, are identical to an IBM computer:

\[ Y = (x \times a + c) \text{Mod}(2^{31}) \]  

\[ Y = |x \times a + c| . \]  

There are, however, several drawbacks to my own random number generating algorithm. This algorithm was written strictly for the use of a specific simulation program; it lacks the flexibility of a prepackaged routine. For a different problem, i.e., several hundred random numbers are needed at one time, a packaged program like GGUBFS could be more efficient. This IMSL routine has a large number of options not mentioned in this text. Furthermore, my routine might have to be rewritten if it is to be used on another machine. The hardware of computers will differ, thus it is possible that this algorithm is incompatible with a non-IBM computer. However, for the present program on an IBM computer, it is superior to any of the packaged programs available in all respects.

**Analysis of the Stochastic Population Model**

The previous deterministic population model was actually developed after this stochastic version. The purpose of the deterministic model was to calculate the expected results (population sizes) of the stochastic model. Sensitivity analyses are only feasible if the model has "predictive" results. The stochastic population model, STPOMD, is very much dependent on the seed which initializes the random number generator. The results from this simulation model may be unpredictable,
depending on the parameter values. The sensitivity analysis was thus done on the deterministic version, and the only analysis that will be discussed in this section is the effect of the parameters on the variance of the output results of the stochastic version.

**Variance**

A population with a high mortality rate and a high fertility rate may yield the same growth rate as a population with a low mortality and a low fertility rate. In the first case, however, the predictability will be much lower. That is, if a stochastic model is used, the variance associated with the outcome will be high.

Consider a semelparous, parthenogenic insect which has a 1% chance of survival until reproduction. At reproduction, this hypothetical insect will produce 100 offspring. Assuming these parameters are the only ones acting on the insect, the expected number of offspring per individual is 1. A similar result will be obtained if the survival rate is 50% and the reproductive capacity is 2.

In the first case, the probability for extinction after one generation is approximately 1/3, whereas in the second case this probability is essentially 0. In this simplified example, the variance associated with the prediction of the population of the next generation is:

\[(\text{No. of offspring})^2 \times N \times p \times (1-p), \tag{5.5}\]

where \( N = \) initial number of adults, and \( p = \) survival probability.

Using equation 5.5 we can now calculate this variance to be 9900 in the first case and 100 in the second.
Although the complexity of the model STPOMD is much greater, the same principle works on the variance associated with the values of the population sizes in the simulation results. This model is much more erratic if the probabilities of death and/or migration and oviposition are high, and more predictable if these probabilities are low. The actual calculation of this variance in a model like STPOMD would be a tedious and formidable task. In this case it is much more feasible to do the next best thing, to estimate the variance. This is easily done by running the program n times with a different seed each time.

**Deviations from the Deterministic Model.**

Let us consider the population curves of the number of beetles in given fields vs. time (one season). The curves associated with the stochastic model are much more peaked, and are shifted farther to the right than those associated with the deterministic model. (See Figure 5.1.)

This shift in the curves of the stochastic model could be due to a series of low probabilities which lead to a high growth rate. Migration and survival at an early age will lead to a high reproductive potential. Even if the probability of this occurrence is small (.001 say), it is still reflected in the expected value curve but would not be likely to occur in any simulation run of the stochastic model.

Simulation runs indicate that if one specifies the age at which a beetle matures, this discrepancy between the two models will diminish. In this case, the curves generated by the deterministic model will be more peaked.
Figure 5.1: Field population size vs. time. Initially (J. date 130), all beetles were in overwintering sites.

Solid line ———— Stochastic model
Broken line ———— Deterministic model
Distribution of Results

The normal distribution function is symmetric and defined over the entire real number domain. Letting the value of the total population size be a random variable, it is immediately apparent that it is a discrete random variable. Furthermore, for low initial population numbers, its probability density function will be skewed to the left. (The population size is always greater than or equal to 0, and for low initial populations the probability of extinction could be large.) This skewness makes the normal approximation unfeasible. An empirical distribution could be estimated with multiple runs of this model.

For large populations, however, the central limit theorem will be applicable. Although this algorithm can handle over 100,000 beetles, it might be too costly to do so. The cost of running a program cannot be justified if there is another (e.g., the deterministic version) which will provide similar results at a much smaller cost. Furthermore, the beetle populations in North Carolina may get very high (> 100,000) but will usually not reach any substantial numbers (< 10,000 per hectare).

Discussion

Assuming that we know something of the economic threshold and the economic injury level and assuming that the parameters in these models are estimated with reasonable accuracy, both population models could be used to test the effect of given planting strategies. The deterministic version would only give one "prediction" of the population size of a given field. This "prediction" might be below the economic
threshold but the chance of economic injury could still be high. The probability of a high infestation cannot be determined with this type of model.

The stochastic model, on the other hand, could be used to get some indication of the underlying distribution. In conjunction with the first model, one would be able to calculate (or at least estimate) the probability of an economically damaging infestation. This could be done for any number of possible planting strategies.

This program also simulates the patchiness characteristic of the real system. A few beetles which happen to migrate to the same field early in the season could thereby cause a major outbreak a generation later. Given a uniform system (see Table 5.1), equal sized fields can have differing populations. The parameters could be chosen in such a way to simulate any degree of patchiness one might wish. Note that in this system the "inner" fields have a higher probability of being infested than the fields near the edge.
Table 5.1. Examples of the interfield variations in two simulation runs using the stochastic population model. The total number of fields = 36.

<table>
<thead>
<tr>
<th>Description of Parameters</th>
<th>Values of Parameters for:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probability of Migration</td>
<td></td>
</tr>
<tr>
<td>( p_1 )</td>
<td>0.500</td>
</tr>
<tr>
<td>( p_2 )</td>
<td>0.500</td>
</tr>
<tr>
<td>( p_3 )</td>
<td>0.025</td>
</tr>
<tr>
<td>Probability of Oviposition</td>
<td></td>
</tr>
<tr>
<td>( p_{o1} )</td>
<td>0.0</td>
</tr>
<tr>
<td>( p_{o2} )</td>
<td>0.0</td>
</tr>
<tr>
<td>( p_{o3} )</td>
<td>0.6</td>
</tr>
<tr>
<td>All other parameters were identical.</td>
<td></td>
</tr>
</tbody>
</table>

Output results: (larval population in parentheses)

**Day 50**

<table>
<thead>
<tr>
<th></th>
<th>Number of fields without beetles</th>
<th>Maximum adult population of a field</th>
<th>Mean number of adults per field</th>
<th>Variance of interfield populations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>18 (33)</td>
<td>36 (44)</td>
<td>4.4 (1.9)</td>
<td>9.2 (61.0)</td>
</tr>
</tbody>
</table>

**Day 170**

<table>
<thead>
<tr>
<th></th>
<th>Number of fields without beetles</th>
<th>Maximum adult population of a field</th>
<th>Mean number of adults per field</th>
<th>Variance of interfield populations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5 (7)</td>
<td>43 (225)</td>
<td>9.4 (64.3)</td>
<td>11.9 (65.2)</td>
</tr>
</tbody>
</table>
CHAPTER 6:
CONCLUSIONS

Further Considerations

Man's Input into this System

Aside from planting dates and harvest dates, the effects of man's interactions with the system have not been considered. Since chemical pesticides are "convenient" and relatively inexpensive, most garden crops in the southeastern United States are treated regularly. These treated crops are unsuitable as a beetle's habitat (at least temporarily), and could be considered from a modeling perspective as temporary death sinks or non-host crops. (For larvae the term "death sink" would be the more appropriate, while non-host might be more descriptive from the adult insect's point of view.) In a system of both treated and untreated crops the untreated crops will have a much higher chance of being infested.

Although pesticide treatment is popular in small gardens, crops are only treated before harvest. After harvest many plots are then neglected. Since the beetle is a foliage feeder, these plots can still support a large population at that time. The program needs to differentiate between a field that is plowed after the harvest and one that is neglected.
Density Dependence

A further possibility that might have a significant effect on the population sizes of the insect is its interactions with members of its own species. The effect of pheromones, for example, was not considered. For some species in the Coccinellidae family, aggregation due to pheromones is known (Mathews and Mathews, 1978). Similar processes could also help bring about the high degree of clumping observed in Mexican bean beetles.

It would not be difficult to amend the model in such a way as to allow for density dependence. Such parameters as survival, propensity to migrate or attractivity of fields could easily be modified to vary with respect to the density of that species or any other species (e.g., predator or pathogen densities).

In any modeling effort, however, it is important to limit oneself to what one assumes to be the essentials. Any model will quickly become extremely complex and unverifiable if all possible influencing factors are considered.

Environmental Factors

One of the most important environmental factors to consider in a migration model of a flying insect is wind. Although the Mexican bean beetle avoids flying in higher winds, low wind speeds (<5 kph) will have an effect on the eventual destination of the beetle. The wind's velocity can be incorporated into the movement submodel. (See Appendix A.) However, for the population model, the assumption of constant wind velocity cannot be made (the winds will change from one day to the next). Thus, the effect of the wind must be calculated for
each time the wind's velocity (direction or magnitude) changes. This means that (preferably) for each day, the wind velocity should be considered in the model. The probabilities of reaching a given field must now be recalculated at the beginning of each day on which the wind velocity changes.

Similarly, the effects of precipitation and humidity on the key life parameters of the beetle (mortality, fecundity, rate of development and probability of migration) need to be considered for a predictive simulation model. Moisture, in conjunction with temperature, has been shown to significantly affect both the fecundity and the development rate of the beetle. Beetles in warm, humid conditions have a higher fecundity (Kitayama et al., 1979) as well as a higher development rate (Wilson et al., 1982) than those living under drier conditions. It has also been shown that extremely dry environmental conditions will result in a high mortality for the beetles (Wilson et al., 1982).

Rainfall has been shown to affect the probability of migration (Bernhardt and Shepard, 1978; Douglass, 1933). They observed most overwintering beetles (> 95%) fly from their overwintering site after a major rain storm.

All of these factors can be treated in the same way as wind speed and wind direction were treated. Daily humidity levels and rainfall data of an entire season would be needed for the input. However, the computing costs of such ventures should be taken into account.

Summary

The framework used in these computer algorithms allows the user to study the effect of an agroecosystem's geometric structure on the
population size of a herbivorous beetle. The following list is an overview of the model's functional response after several iterations to the geometric parameters on the adult beetle population size. Note: no density dependence was considered in these models.

1) Increasing a field's size increases the expected adult beetle population of that field but decreases its expected beetle density.

2) Increasing the average interfield distance decreases the total beetle population size.

3) Uniform field size in a multi-field system maximizes the total population size.

4) Clumping the fields increases the total beetle population.

The effect on the model of these parameters (field sizes, interfield distances and degree of clumpedness) is low.

The parameters affecting the beetle's life history, on the other hand, is high. Aside from estimating mortality, fecundity and development rates, more emphasis is needed toward estimating the probabilities of leaving a field. If this model is to be used as a predictor in pest management studies, more accurate approximations of these last mentioned parameters are needed.

These models were designed as a tool to understand the effect of field location and size on the population of beetles with certain migratory behavior, and to provide additional insight into interfield migration.
REFERENCES CITED


8. APPENDICES
APPENDIX A

The Algorithm For an Interfield Movement Model
(DEMVMD)

Purpose

This model was developed to simulate inter-patch movement of an insect with limited mobility. This movement is assumed to be non-passive (as opposed to passive, drifting with wind currents), in which the species involved is able to make certain key "decisions". These Bernoulli decisions (whether to fly or not to fly, to die or not to die) are made on a daily basis. The values for the parameters were inferred from data of Mexican bean beetle populations on lima and soybean fields (Blau and Stinner, 1982; Wilson, et al., 1982; Kitayama, et al., 1979; Campbell, 1958).

The program itself was designed to be a subcomponent of a population model. The "supermodel" should simulate the population size of a specified insect species living in a system consisting of discrete resource fields or patches. The only restriction on the model, due to the limited amount of computer storage space available, is the number of patches (fields). Presently, the maximum allowable number is 50. If more space is needed, appropriate alterations in the storage allocation statements is all that is necessary.

The Model

The program comes in four parts:

1) The initialization of environmental parameters.

2) An algorithm to display a graphical representation of the system.
3) An algorithm to simulate interfield movement.

4) An algorithm to graph simulated results.

Parts (2) and (4) are optional output routines. Part (2) gives the graphical representation of the fields in the assumed geometry during the simulation runs, and part (4) graphs the final results of each field.

Part (1) is an initialization routine which needs to be repeated only once a season. Parameters such as: number, position, size and type of fields, as well as the maximum distance from which a field can be recognized by a beetle, are read into the program at this point.

One of the major assumptions of this program is: given two fields, i and j, the probability of reaching field j if the beetle has just left field i is strictly related to the size of field j and its relative position to field i. In other words, it is assumed that one can calculate the conditional probability, the chance of reaching a specific field (given a beetle flies from another, specified field), from just the two fields' respective sizes and locations.

Several assumptions need to be made when calculating these probabilities. First, the probability density function which dictates the direction of flight is the uniform distribution. Second, the two random variables, one associated with the beetle's flight direction and the other with the maximum distance a beetle is capable of flying, are assumed to be independently distributed. Third, the probability density function of the latter random variable has a negative exponential distribution function. (See Eq. 8.5.) Calculating the effect of the interfield distance is done in the beginning of part (3) of this program.
In this program, the fields are represented by circular disks on a plane. The entire beetle population is viewed as being in the center of the disk. A beetle is assumed to immigrate into a field if it encounters the disk, i.e., its flight path intersects this circular region. (See Figure 8.1.) Furthermore, the beetle enters the first field it encounters.

Two additional options allow the user a greater degree of flexibility. The first of these is a consideration for beetle behavior. This modification takes into account the amount of searching effort a beetle exhibits during a migratory flight. Consider the distance interval (200 m., 210 m.), and assume that the beetle flies 2 meter/sec. A beetle showing no searching behavior \( c = 1 \) will cover this distance in 5 seconds, a beetle with searching behavior will take \( 5 \times c \) seconds \( (c > 1) \). This results in causing a field within this distance interval to have an increased chance of encounter by the searching beetle. The increase in the probability for a field being encountered is manifested in an increase in the radius of the "attractiveness" range of the field. This increase in the radius is directly proportional to the increase in the amount of time spent in a certain distance interval away from the field of origin. Note this increase may not, however, exceed a given maximum, \( w \). (See Figure 8.2.)

The second option is a consideration for wind velocity. This parameter is assumed constant throughout a simulation run. Here, as in the previous case, the beetle is assumed to fly at a constant speed. Once a beetle begins to migrate its direction of flight is assumed to remain constant. Combining these two velocities one can now calculate the actual beetle's relative flight velocity with respect to the
Figure 8.1: Graphical representation of a 3 field system for which \( Q_r(d_{i,j}, r_j) \) is being calculated.

\[
e_{i,j} = 2\arcsin(r_j/d_{i,j}) - FO
\]

\( FO \) = extent of field overlap (measured in radians)

\[
Q_r(d_{i,j}, r_j) = e_{i,j}/\pi
\]
Case: $c=1$

Figure 8.2: Effects of $c$, searching behavior constant, on the apparent field size,

$$h = \max [w, (c-1) \times r_j],$$

where $w$ is the maximum allowable increase for a field radius.
ground. Using simple vector addition it is possible to calculate the apparent distance and direction a beetle needs to travel in order to reach a specified destination. For the wind velocity considerations it now becomes necessary to recalculate for each possible starting point the apparent interfield distances, and relative field locations. These apparent locations (locations as "viewed" by a beetle flying in a moving airmass) are now used to calculate the probabilities, \( \text{PR}(d'_{i,j}, r_j) \). (See Figure 8.3.) Let \( d'_{i,j} \) be the apparent distance between fields \( i \) and \( j \) for beetles flying from \( i \) to \( j \). Then:

\[
d'_{i,j} = d_{i,j} \times \sqrt{1 - W^2 \sin^2 \alpha - W \cos(\alpha)} / (1-W^2) \tag{8.1}
\]

Note, \( d'_{ij} = d_{ij} = W = 0 \).

A very general version of the model is given by the following formula:

\[
B_i(t+1) = s \times V(i) \times B_i(t) + \sum_{j=1}^{n} \left[ s \times a_{i,j} \times P(j) \times V(j) \times B_j(t) \right]
\]

Note: The variable names used in the program are given with the description of the above formula. The arrays used in the program are not quite identical to these matrices. Most of the elements of these matrices are zero, and to economize on storage space the arrays in the program may differ. For a program listing see Table 8.1.
Table 8.1. The program listing of DEMVMD, the interfield movement model.

### Initialization of the constant parameters

<table>
<thead>
<tr>
<th>DECLARATION OF VARIABLES</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTEGER TYP(50), POP(4, 30, 50), TOPP(4), OUTP(4, 50), AGE, MXCP(50)</td>
</tr>
<tr>
<td>REAL D(50, 50), E (50, 50), LOC(2, 50), ALPHA(50, 50)</td>
</tr>
<tr>
<td>REAL RET, D(50, 50), R(50, 50), I : JC(2, 50)</td>
</tr>
<tr>
<td>ALPH(50, 50), READ, R(4, 10, 50), R(20, 9)</td>
</tr>
<tr>
<td>DIMENS(9, 0), IRMT(4), GRPH(127), CHRCHR(22)</td>
</tr>
</tbody>
</table>

FOR THE DESCRIPTION OF THE DIFFERENT VARIABLES USED SEE SEPARATE PROGRAM DOCUMENTATION.

### Initialization output arrays.

DATA BLANK, GRPH /177/;
DATA CHCHR /'&', '(', ')', ',', '.', '/', +1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 'x', '_'/;
GRPH = CHARACTER STRING USED TO DRAW DIAGRAM.
BLANK = ADDRESS STORING CHARACTER FOR A BLANK.
CHRCHR = STOYES THE DIFFERENT SYMBOLS USED IN GRAPH.

SPACE SAVING STEP. VARIABLES TO BE EXPLAINED LATER.
EQUIVALENCE (D(1, 1), PLT(1, 1)), (D(1, 1), ADP(1, 1))

READ(1, 10) I, J, K, M, N, W
IF = NUMBER OF FIELDS USED IN THIS SIMULATION. (MAXIMUM IS 50)
ND = TIME DURATION OF THIS SIMULATION.
NP = NUMBER OF DIFFERENT FIELD TYPES USED IN THIS SIMULATION.

INPUT PARAMETERS TO ADJUST FOR SEARCHING BEHAVIOR AND FOR WIND.
READ(11, 11) H, COFA, ID, ROH
W = WIDTH OF FIELD'S SEARCHING CORRIDOR.
COFA = ADJUSTS ACTUAL DISTANCE MOVED WITH SEARCHING BEHAVIOR.
WD = WIND DIRECTION IN RADIANS.
WS = RELATIVE WIND SPEED. MAX = 10.
INITIALIZE PARAMETERS USED FOR SEARCHING BEHAVIOR.
W = w/2
Table 8.1 (Continued)

C Loop 200 calculates distances between fields as well as the "arc size" i.e. the angle in radians of the projection of field J onto the unit circle around the center of field I.

DO 200 I=1, NF
  READ(1,11) (FTP(NW,1),NW=1,6),TYP(I),AR,LOC(1,I),LOC(2,I)
C FTP = stores phenological information on each field.
C TYP = index used to specify type of crop planted in each field.
C AR = average radius of "attractability" range of field I.
C LOC(*,I) = respective coordinates of center of field I.
C
C Add to field radius to adjust for zig-zagging movement.
R2 = COFA*AR - AR
C For small fields change in attractability proportional to radius.
C For large fields add width of searching corridor to radius.
D(I,I) = AR + MIN(R2,W)
D(I,I) = average radius of "findability" range of field I.

1 = 1 - I
IF (I.EQ.0) GOTO 200
DO 201 J=1, I
DF1 = LOC(1,J) - LOC(1,I)
DF2 = LOC(2,J) - LOC(2,I)
C The next three lines calculate the distance between fields I & J.
DIST = SQRT((DF1*DF1+DF2*DF2))
DIS(I,J) = DIST
C DIS(J,I) = DIST = actual distance between fields I & J.
DIS(J,I) = DIST
C Next the apparent interfield distance is calculated.
IF (DF1.GE.0) RAL=WD-ARSIN(DF2/DIST)
IF (DF1.LT.0) RAL=WD+ARSIN(DF2/DIST)-3.1416
SMD = RWS * SIN(RAL)
C SMD = temporary storage address.
D(I,J) = DIST*SQR((1-SMD*SMID) - RWS*COS(RAL))/(1-RWS*RWS)
C D(I,J) = the apparent distance from field I to field J.
C Repeat process for the opposite direction.
D(J,I) = D(I,J) + 2*DIST*RWS*COS(RAL)/(1-RWS*RWS)
C D(J,I) = The apparent distance from field J to field I.
C (Note: The apparent distances depend on the direction.
C These two steps calculate the arc size of field I w.r.t. field J.
RAT = D(J,I)/D(I,J)
IF (RAT.GT.1) RAT=1
ALPHA(I,J) = ARSV(RAT)
C These two steps calculate the arc size of field J w.r.t. field I.
RAT = D(I,J)/D(J,I)
IF (RAT.GT.1) RAT=1
ALPHA(J,I) = ARSV(RAT)
C Note: At this point in program ALPHA is half of actual arc size.
201 CONTINUE
200 CONTINUE
Table 8.1 (Continued)

C LOOP 311 CALIBRATES THE EXTENT OF OVERLAP BETWEEN FIELD PROJECTIONS
C ONTO THE UNIT CIRCLE ABOUT FIELD I, AND THE EFFECT OF SUCH ON THE
C RELATIVE "REACHABILITY" OF FIELD J FROM FIELD I.
DO 300 I=1, NF
C
C LOOP 311 CALCULATES THE RELATIVE ANGLE (RA) BY DETERMINING THE ANGLE
C BETWEEN THE LINE CONNECTING THE CENTERS OF FIELDS I & J AND THE
C HORIZONTAL.
DO 311 J=1, NF
IF (I.EQ.J) GOTO 311
RAT = (LOC(I,J)-LOC(I,J))/DIS(I,J)
RA(J) = ARCCOS(RAT)
IF ((LOC(2,J)-LOC(2,J),LT.0) RA(J)=RA(J)
ALPHA(I,J) = ALPHA(I,J)
311 CONTINUE
C
C LOOP 321 DETERMINES THE EXTENT OF THE OVERLAP BETWEEN "ARCS".
C NOTE: ALPHA(I,J)+ALPHA(J,J) = THE ACTUAL ARC SIZE.
DO 321 J=1, NF
IF (I.EQ.J) GOTO 321
J1 = J - 1
IF (J1.EQ.0) GOTO 321
DO 322 K=1, J1
IF (K.EQ.I) GOTO 322
DO NEXT 5 LINES DETERMINE WHICH FIELD (I OR K) IS CLOSER. (KD=CLOSER)
IF (DIS(I,J),LT.DIS(I,K)) GOTO 3221
LD = J
KD = K
GOTO 3222
3221 LD = K
KD = J
GOTO 3222
3222 CONTINUE
RAL = RA(LD)
RACK = RA(KD)
C RACK & RAL USED FOR GREATER CALCULATING EFFICIENCY.
C
C ADJUST RELATIVE ANGLES FOR COMPARISONS.
IF ((RAL-RACK).GT.3.1416) RACK=RACK+.2832
IF ((RAL-RACK).LT.-3.1416) RACK=RACK-.2832
IF (RAL.GT.RACK) GOTO 3224
OL = (RAL-ALPHA(KD,KD)) - (RAL-ALPHA(LD,LD))
IF (OL.LT.(-2*ALPHA(KD,KD))) OL=(-2)*ALPHA(KD,KD)
IF (OL.LT.0) ALPHA(KD,KD)=ALPHA(KD,KD)+OL
GOTO 3225
3224 OL = (RAL-ALPHA(LD,LD)) - (RAL-ALPHA(KD,KD))
IF (OL.LT.(-2*ALPHA(KD,KD))) OL=(-2)*ALPHA(KD,KD)
IF (OL.LT.0) ALPHA(LD,LD)=ALPHA(LD,LD)+OL
3225 CONTINUE
321 CONTINUE
C
C LOOP 331 COMBINES THE EXTENT OF THE OVERLAP AND THE ARC SIZE, AND
C CALCULATES THE ACTUAL PROJECTION OF FIELD I ONTO THE UNIT CIRCLE
C AROUND THE CENTER OF FIELD I.
DO 331 J=1, NF
IF (I.EQ.J) GOTO 331
ALPHA(I,J) = (ALPHA(I,J)+ALPHA(J,I))/6.2832
IF (ALPHA(I,J).LT.0) ALPHA(I,J)=0
331 CONTINUE
C
300 CONTINUE
C PRINT HEADING
WRITE(1,30)
C
Table 8.1 (Continued)

```
+---------------------------------------------------+
| ALGORITHM FOR GRAPHICAL DISPLAY OF SYSTEM          |
+---------------------------------------------------+

PRINT HEADING FOR OUTPUT OF CONSTANT PARAMETERS.
WRITE(1,25)

LOOP 410 PRINTS DESCRIPTION OF EACH FIELD.
WRITE(3,30)
DO 410 I=1, NP
C
CALCULATE AREA OF EACH FIELD.
R2 = D(I,1)
AR = R2*R2,0314
410 WRITE(I,11) I,FPP(NW,1,NW=1,6),LOC(1,I),LOC(2,I),R2,AR
WRITE(1,32)
C
CHECK WHETHER SYSTEM SHOULD BE GRAPHICALLY DISPLAYED.
READ(1,10) IND
IND = INDICATES IF SYSTEM TO BE GRAHPED. (IND=1 => GRAPH SYSTEM)
IF (IND.EQ.0) GOTO 5000
C
NEXT LINES DETERMINE SCALE OF GRAPH.
XMIN = LOC(I,1) - D(I,1)
XMIN WILL BE THE SMALLEST POSSIBLE VALUE FOR X.
XMAX = LOC(I,1) + D(I,1)
XMAX WILL BE THE LARGEST POSSIBLE VALUE FOR X.
C
LOOP 430 DETERMINES EXTREME X VALUES.
DO 430 I=2, NF
R2 = LXC(I,1) - D(I,1)
IF (XMIN.GT.R2) XMIN=R2
R2 = R2 + 2*9D(I,1)
IF (XMAX.GT.R2) XMAX=R2
430 CONTINUE
LENGTH = XMAX - XMIN + 1
C
NEXT LINES DETERMINE THE CONVERSION FACTOR FOR GRAPH.
INC = 2
INC = NUMBER OF SPACES PLUS ONE EQUIVALENT TO 100 METERS.
MPL = 6400
MPL = MAXIMUM PERMISSIBLE LENGTH IN METERS FOR A GIVEN SCALE.
4300 IF (LENGTH.GT.MPL) GOTO 4301
INC = INC + 1
MPL = 12800/INC
GOTO 4300
4301 INC = INC - 1
CONV = 100.0/INC
CONV = CONVERSION FACTOR.
C
YMAX = LOC(2,1)
YMAX = LARGEST POSSIBLE Y VALUE TO BE PLOTTED.
YMIN = YMAX
YMIN = SMALLEST POSSIBLE Y VALUE TO BE PLOTTED.
C
LOOP 440 SCANS DATA DESCRIBING FIELDS, AND FINDS Y EXTREMA.
DO 440 I=1, HF
R2 = LOC(I,3) + D(I,1)
IF (R2.GT.YMAX) YMAX=R2
R2 = R2 - 2*D(I,1)
IF (R2.LT.YMIN) YMIN=R2
```

85
Table 8.1 (Continued)

```
SCALE FIELD DATA INTO DISPLAY UNITS USING A 128 UNIT SPACE.
OUTP(I,1) = (LOC(I,1) - MIN)/CONV + 1.5
OUTP(2,1) = LOC(2,1) + .5/CONV + .5
OUTP(3,1) = (LOC(I,1) + .5)/CONV + .5

440 CONTINUE

C WRITE(3,12)
C PRINTS TITLE OF GRAPHIC DISPLAY.
LINE = VMAX*YR/CONV + .5
MINY = VMIN*YR/CONV + .5
C LOOP 450 OUTPUTS EACH LINE OF DISPLAY FROM THE TOP.
4500 IF (LINE .LT. MINY) GOTO 450
C LOOP 451 FINDS ALL FIELDS LYING ACROSS Y-LINE.
DO 451 I = 1, NF
IND = OUTP(I,1)*.8
IF (FIELD I DOES NOT CROSS LINE GO TO NEXT FIELD.)
IF (LINE .GT. OUTP(I,1) + IND) GOTO 451
IF (LINE .LT. OUTP(I,1) - IND) GOTO 451
C IF FIELD I DOES CROSS LINE INITIALIZE GRPH ARRAY.
K = TYP(I)
IC = OUTP(I,1)
INST = X COORDINATE OF THE CENTER OF FIELD.
INST = THE DISTANCE TO LINE FROM CENTER OF FIELD.
C STORE IN ARRAY GRPH THE CHARACTERS TO BE PRINTED ON GIVEN LINE.
IF (INST) 4512, 4511, 4512
C IF INST IS 0, THEN:
C ONLY THE FIRST TEN FIELDS WILL BE NUMBERED.
4511 IF (I .LE. 10) J = 22
IF (I .LE. 10) J = I + 10
IF (IC .GT. 0 .AND. IC .LT. 127) GRPH(IC) = CHRTR(J)
IS = 2
C IS = USED TO MAKE FIELD I.D. NUMBER MORE READABLE.
IND = IND*.8 + .5
GOTO 4513
C IF INST IS NOT 0, THEN:
C STORE MID FIELD CHARACTERS.
4512 IF (GRPH(IC).NE.BLANK) GRPH(IC) = CHRTR(21)
IF (GRPH(IC).EQ.BLANK) GRPH(IC) = CHRTR(K)
R2 = IND*IND - INST*INST
IND = SQRT(R2)/.8 + .5
C ONLY IF IND IS NOT ZERO DO WE CHANGE CHARACTERS IN GRPH.
IF (IND.EQ.0) GOTO 451
IS = 1
IF ((IND*IND).EQ.1) GRPH(IC) = BLANK
IF ((IND*IND).EQ.1) IS = 2
C NEXT LINES SET OUTPUT ARRAY, GRPH, FOR PRINTING.
4513 IF (INC .EQ. 0) GOTO 451
DO 452 L = IS, IND
C NOTE: DUE TO SYMMETRY ABOUT CENTER WE CAN GO IN BOTH DIRECTION.
IF (IN.GE.127) GOTO 4514
IF (GRPH(IR).NE.BLANK) GRPH(IR) = CHRTR(21)
IF (GRPH(IR).EQ.BLANK) GRPH(IR) = CHRTR(K)
4514 IF (IL .LE. 0) GOTO 452
IF (GRPH(IL).NE.BLANK) GRPH(IL) = CHRTR(21)
IF (GRPH(IL).EQ.BLANK) GRPH(IL) = CHRTR(K)
452 CONTINUE
451 CONTINUE
```
Table 8.1 (Continued)

C LABES FOR YTH LINE
   IF ((LINE*.1*5 - LINE) 4612, 4611, 4612
   REAL = LINE*CONV/A00.0
C REAL = LABEL ON Y AXIS OF DISPLAY.
   WRITE(1,11) REAL, (GRAPH(L),L=1,124)
   GOTO 4611
4612 WRITE(1,15) (GRAPH(L),L=1,124)
4613 CONTINUE
C
C LOOP 471 RESETS THE GRAPH ARRAY TO PRINT NEXT LINE.
   DO 471 L=1, 124
471 IF (GRAPH(L).NE.BLANK) GRAPH(L)=BLANK
C
C GO TO NEXT LINE AND REPEAT PROCESS.
   LINE = LINE - 1
   GOTO 4500
450 CONTINUE
C
C LOOP 480 DETERMINES THE LABELS FOR THE X-AXIS.
   DO 480 L=1, 12
480 LBL(L) = (XMIN + (10*L-5)*CONV)/1000
   WRITE(3,37) LBL
C
C OUTPUT KEY
   WRITE(3,38) INC
   K = -1
4901 K = K + 1
   I = 0
4902 I = I + 1
   IF (TYP(I).NE.K.AND.I.LT.UP.AND.K.LE.NT) GOTO 4902
   IF (TYP(I).NE.K.MID.I.EQ.UP.AND.K.LE.NT) GOTO 4901
   IF (TYP(I).EQ.K) WRITE(3,39) CHRCTM(K), (FTP(M,I),M=1,6)
   IF (K.LT.9) GOTO 4901
Table 8.1 (Continued)

<table>
<thead>
<tr>
<th>Algorithm Simulating Interfield Migration</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRINT HEADING FOR OUTPUT OF SIMULATED RESULTS.</td>
</tr>
<tr>
<td>WRITE(3,25)</td>
</tr>
<tr>
<td>READ(1,13) MAG,GRRATE,SURV,CMO,DR</td>
</tr>
<tr>
<td>GRRATE = GROWTH RATE INDICATOR. (GRRATE=1 -&gt; EMERGENCE EACH DAY)</td>
</tr>
<tr>
<td>SURV = PROPAGATION OF BEETLES SURVIVING TO NEXT DAY.</td>
</tr>
<tr>
<td>DR = DEATH RATE (DUE TO EXHAUSTION) WHILE FLYING.</td>
</tr>
<tr>
<td>READ(1,14) (PM(M,K),M=1,K),K=1,NT)</td>
</tr>
<tr>
<td>PM(1,K) = MINIMUM AGE FOR BEETLE TO MATURE. (MAX. =10)</td>
</tr>
<tr>
<td>PM(2,K) = MAXIMUM AGE FOR BEETLE TO MATURE. (MAX. =20)</td>
</tr>
<tr>
<td>PM(3,K) = MEAN AGE FOR BEETLE TO MATURE.</td>
</tr>
<tr>
<td>PM(4,K) = PROPORTION OF BEETLES MIGRATING BEFORE OVIPOSITING.</td>
</tr>
<tr>
<td>PM(5,K) = PROBABILITY OF BEETLE IN MIGRATORY STATE MIGRATING.</td>
</tr>
<tr>
<td>PM(6,K) = PROBABILITY OF BEETLE IN REPRODUCTIVE STATE MIGRATING.</td>
</tr>
</tbody>
</table>

INITIALIZE "PROBABILITY OF MATURING" ARRAY AND MIGRATION PARAMETERS.

DO 510 K=1, NT
| IL = PM(1,K) |
| IR = PM(2,K) |
| RAL = IR - IL |
| IF (RAL.GT.0) P=(PM(3,K)-IL)/RAL |
| RAT=P/(1-P) |
| INITIALIZE "PROBABILITY OF MATURING" ARRAY. |
| MAT(N,K) = PROBABILITY OF PRE-ADULT MATURING TO NEXT STAGE, |
| AT DAY N IF IN FIELD OF TYPE IT. |
| DO 511 N=1, IL |
| 511 MAT(N,K) = 0 |
| DO 512 N=IR, 20 |
| 512 MAT(N,K) = 1 |
| IF (IL+1.GE.IR) GOTO 510 |
| CDY = 1 - (1-P)**RAL * SURV |
| CDF1 = 1 |
| LOIP 513 CALCULATES ENTRIES FOR MATURATION ARRAY. |
| DO 511 N=IL, IR |

...
Table 8.1 (Continued)

MDF1 = MDF1 + LAT(N,K) * RAY(I,1) * CDF1
CDF1 = CDF1
CDF = CDF1*(1-MAT(N,K))
ND = ND - 1
513 CONTINUE C
510 CONTINUE C
PRINT TABLE OF INPUT PARAMETERS.
WRITE(3,63) K = -1
5201 K = K + 1
I = 0
5202 I = I + 1
IF (TYP(I).NE.K.AND.I.LT.NF.AND.K.LE.NY) GOTO 5202
IF (TYP(I).NE.K.AND.I.EQ.NF.AND.K.LT.NY) GOTO 5201
IF (TYP(I).EQ.K) WRITE(3,64) (FTP(M,I),M=1,6), (PM(M,K),M=1,6)
IF (K.LT.9) GOTO 5201
I = I + 1
5202 CONTINUE
530 CONTINUE
LOOP 530 FINDS PROBABILITIES OF REACHING FIELD J, IF LEAVING FIELD I.
DO 530 1=1, NF
READ(I,16) MCPI(I)
MCPI(I) = MAXIMUM POPULATION FIELD I CAN SUSTAIN.
DO 531 J=1, NF
IF (I.EQ.J) GOTO 531
PDMD = PROB. THAT A BEETLE WILL REACH A GIVEN DISTANCE.
IF (D(I,J).GT.SMD) PDFMD = EXP(DR*(SMD-COFA*DI,I,J))/1000
ALPHA(I,J) = PDFMD*ALPHA(I,J)
C ALPHA(I,J) = PROB. OF REACHING FIELD J, IF LEAVING FIELD I.
531 CONTINUE
530 CONTINUE
J TOP(I) = YOUNGEST POSSIBLE AGE.
TOP(I) = 0
C TOP(I) = POPULATION SIZE OF SYSTEM BEFORE REDISTRIBUTION.
LOOP 540 IS USED TO INPUT THE INITIAL POPULATION SIZES.
DO 540 1=1, NF
RA(I) = 0
C RA(I) = ACCUMULATOR: TOTAL NUMBER OF EMIGRANTS FROM FIELD I.
INTAC = 0
C INTAC = INTEGER ACCUMULATOR (USED FOR GREATER EFFICIENCY)
DO 540 AGE=JA, JAG
READ(I,16) POP(I,AGE,I)
POP(M,AGE,I) = NUMBER OF BEETLES IN FIELD I, OF A GIVEN AGE,
C IN MIGRATORY STATE M.
INTAC = INTAC + POP(I,AGE,I)
DO 542 M=2, 4
NOTE:
M=1 --- PREMIGRATORY BEETLES. (MIGRATION NOT POSSIBLE)
M=2 --- BEETLES IN A MIGRATORY STATE.
M=3 --- BEETLES MIGRATING. (MIGRATED ON PREVIOUS DAY)
M=4 --- BEETLES IN A NON-MIGRATORY STATE.
POP(M,AGE,I) = 0
542 CONTINUE
Table C.1 (Continued)

Table C.1 (Continued)

<table>
<thead>
<tr>
<th>Line</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>541</td>
<td>( \text{OUTPUT}(1,1) = \text{INTAC} )</td>
</tr>
<tr>
<td>542</td>
<td>( \text{OUTPUT}(1,1) = \text{NUMBER OF BEETLES IN FIELD 1 BEFORE MIGRATION}. )</td>
</tr>
<tr>
<td>543</td>
<td>( \text{TOP}(1) = \text{INTAC} )</td>
</tr>
<tr>
<td>544</td>
<td>( \text{TOP}(1) = \text{TOTAL INITIAL POPULATION SIZE OF FIELD 1}. )</td>
</tr>
<tr>
<td>545</td>
<td>( \text{TOP}(1) = \text{TOP}(1) + \text{INTAC} )</td>
</tr>
<tr>
<td>546</td>
<td>( \text{IF (INTAC.EQ.0) P(T(4,10,1)) = 1} )</td>
</tr>
<tr>
<td>547</td>
<td>( \text{IF (INTAC.NE.0) P(T(4,10,1)) = 1} )</td>
</tr>
<tr>
<td>548</td>
<td>( \text{PLT}(4,10,1) = \text{INDICATOR WHETHER FIELD 1 HAD INITIAL POPULATION}. )</td>
</tr>
<tr>
<td>549</td>
<td>( \text{CONTINUE} )</td>
</tr>
<tr>
<td>550</td>
<td>( \text{DO } 30 \text{ I} = 1, \text{NF} )</td>
</tr>
<tr>
<td>551</td>
<td>( \text{APOP(AGE,1) = 0.5} )</td>
</tr>
<tr>
<td>552</td>
<td>( \text{APOP(AGE,1) = NUMBER OF BEETLES ARRIVING AT FIELD 1,} )</td>
</tr>
<tr>
<td>553</td>
<td>( \text{OF A GIVEN AGE, IN MIGRATORY STATE } )</td>
</tr>
<tr>
<td>554</td>
<td>( \text{CONTINUE} )</td>
</tr>
<tr>
<td>555</td>
<td>( \text{PRINT HEADING FOR OUTPUT OF DAILY BEETLE POPULATIONS.} )</td>
</tr>
<tr>
<td>556</td>
<td>( \text{WRITE}(3,4) )</td>
</tr>
<tr>
<td>557</td>
<td>( \text{LOOP 600 REDISTRIBUTES THE POPULATIONS OF THIS SYSTEM.} )</td>
</tr>
<tr>
<td>558</td>
<td>( \text{DO } 600 \text{ N} = 1, \text{ND} )</td>
</tr>
<tr>
<td>559</td>
<td>( \text{JA} = \text{JA} + 1 )</td>
</tr>
<tr>
<td>560</td>
<td>( \text{PRINT } = 0 )</td>
</tr>
<tr>
<td>561</td>
<td>( \text{IF (N.EQ.1).OR.(N.EQ.5).OR.(N.EQ.10)) PRINT = 0} )</td>
</tr>
<tr>
<td>562</td>
<td>( \text{PRINT IS ONLY EQUAL TO ONE IF N IS DIVISIBLE BY 5.} )</td>
</tr>
<tr>
<td>563</td>
<td>( \text{TOP}(2) = 0 )</td>
</tr>
<tr>
<td>564</td>
<td>( \text{TOP}(2) = \text{NUMBER OF MIGRATING BEETLES IN SYSTEM ON GIVEN DAY.} )</td>
</tr>
<tr>
<td>565</td>
<td>( \text{LOOP 61} ) ( \text{CALCULATES NUMBER OF MIGRATING BEETLES ON DAY } )</td>
</tr>
<tr>
<td>566</td>
<td>( \text{DO } 61 \text{ I} = 1, \text{NF} )</td>
</tr>
<tr>
<td>567</td>
<td>( \text{IND} = \text{TYP}(1) )</td>
</tr>
<tr>
<td>568</td>
<td>( \text{INTAC} = 0 )</td>
</tr>
<tr>
<td>569</td>
<td>( \text{INTAC = INTEGER ACCUMULATOR (USED FOR GREATER EFFICIENCY)} )</td>
</tr>
<tr>
<td>570</td>
<td>( \text{LOOP 612 CONSIDERS EACH AGE GROUP.} )</td>
</tr>
<tr>
<td>571</td>
<td>( \text{DO } 612 \text{ AGE} = \text{JA}, \text{MAG} )</td>
</tr>
<tr>
<td>572</td>
<td>( \text{IF ( \text{AGE} ) IN PREMIGRATION STAGE MIGRATION NOT POSSIBLE.} )</td>
</tr>
<tr>
<td>573</td>
<td>( \text{FOR } \text{AGE} = 1, \text{ONLY DEVELOPMENT TO NEXT AGE CLASS POSSIBLE.} )</td>
</tr>
<tr>
<td>574</td>
<td>( \text{IF (AGE.LE.PM(1,IND)) GOTO 612} )</td>
</tr>
<tr>
<td>575</td>
<td>( \text{IF (AGE.GT.PM(1,IND)) GOTO 6130} )</td>
</tr>
<tr>
<td>576</td>
<td>( \text{INST = POP(1,AGE,1) \times \text{MAT(AGE,IND)}} )</td>
</tr>
<tr>
<td>577</td>
<td>( \text{POP(1,AGE,1) = POP(1,AGE,1) - \text{INST}} )</td>
</tr>
<tr>
<td>578</td>
<td>( \text{POP(2,AGE,1) = POP(2,AGE,1) + \text{INST}} )</td>
</tr>
<tr>
<td>579</td>
<td>( \text{CONTINUE} )</td>
</tr>
<tr>
<td>580</td>
<td>( \text{LOOP 613 CONSIDERS EACH DEVELOPMENT STAGE, (MIGRATION MODE).} )</td>
</tr>
<tr>
<td>581</td>
<td>( \text{DO } 613 \text{ M} = 2, 4 )</td>
</tr>
<tr>
<td>582</td>
<td>( \text{IF (POP(M,AGE,1).EQ.0) GOTO 613} )</td>
</tr>
<tr>
<td>583</td>
<td>( \text{PDPL = PM(M+2,IND)} )</td>
</tr>
<tr>
<td>584</td>
<td>( \text{PDPL = PROB. OF MIGRATION. (CONSTANT R.T. AGE &amp; FIELD TYPE)} )</td>
</tr>
<tr>
<td>585</td>
<td>( \text{PDPL IS DEPENDENT ON MIGRATORY STAGE.} )</td>
</tr>
<tr>
<td>586</td>
<td>( \text{CALCULATE THE NUMBER OF MIGRATING BEETLES FROM EACH FIELD. (EMIG)} )</td>
</tr>
<tr>
<td>587</td>
<td>( \text{EMIG = POP(M,AGE,1) \times \text{PDPL}} )</td>
</tr>
<tr>
<td>588</td>
<td>( \text{EMIG = TEMORARY STORAGE FOR NUMBER OF MIGRATING BEETLES.} )</td>
</tr>
<tr>
<td>589</td>
<td>( \text{INTAC = INTAC + EMIG + 0.5} )</td>
</tr>
<tr>
<td>590</td>
<td>( \text{POP(M,AGE,1) = POP(M,AGE,1) - EMIG + 0.5} )</td>
</tr>
<tr>
<td>591</td>
<td>( \text{PRINT } = \text{PRINT + 1} )</td>
</tr>
</tbody>
</table>
Table 8.1 (Continued)

C END MIGRATING BEETLES. MIGRANTS END UP.
DO 614 J = 1, N
IF (AGE .GT. 30) GOTO 614
APOP(M, AGE, J) = TSNED*ALPHA(I, J)*ENIG + APOP(AGE, J)
614 CONTINUE
613 CONTINUE
C IF BEETLE THAT HAS MIGRATED DID NOT MIGRATE THIS DAY, M = 3.
IF (POP(1, AGE, I).NE. 0) POP(4, AGE, I) = POP(3, AGE, I) + POP(4, AGE, I)
POP(1, AGE, I) = 0
612 CONTINUE
C OUTP(2, I) = INTAC
C OUTP(2, I) = NUMBER OF BEETLES MIGRATING FROM FIELD I.
RA(I) = RA(I) + INTAC
C RA(I) = TOTAL NUMBER OF EMIGRANTS FROM FIELD I SINCE DAY 1.
C IF(1 .LE. 10) PLT(2, I, M) = INTAC
C PLT(K, I, DAY) = SAME AS OUTP(K, I) BUT IS USED IN PLOT ROUTINE.
C TPOP(2) = TPOP(2) + INTAC
C TPOP(2) = 0
C TPOP(3) = NUMBER OF MIGRATING BEETLES STAYING WITHIN SYSTEM.
IF (MAG .LT. 30) INST = MAG + 1
C INST = INTEGER STORAGE USED TO DETERMINE TOMORROW'S POPULATIONS.
C LOOP 621 DETERMINES THE POPULATION SIZES OF THE DIFFERENT FIELDS.
DO 621 I = 1, NF
INTAC = 0
C LOOP 622 DETERMINES NUMBER OF EMIGRATING BEETLES FROM FIELD I.
DO 622 AGE = JA, MAG
IF (APOP(AGE, I).LE. 0.5) GOTO 622
POP(3, AGE, I) = POP(3, AGE, I) + APOP(AGE, I)
INTAC = INTAC + APOP(AGE, I)
APOP(AGE, I) = 0.5
622 CONTINUE
C LOOP 632 & 633 SHIFT VECTOR, POP(M, AGE, I), INTO POP(M, AGE+1, I).
DO 632 M = 1, 4
NSTR2 = POP(M, JA, I)
INST = MAG + 1
DO 633 AGE = JA, INST
IF (AGE .GT. 30) GOTO 633
IF (AGE .LE. MAG) NSTR1 = POP(M, AGE, I)
C + - - - - - - - - +
C + - - - - - - - - - 4
IF (AGE .LE. MAG) NSTR2 = NSTR1
633 CONTINUE
632 CONTINUE
C OUTP(3, I) = INTAC
C OUTP(3, I) = NUMBER OF IMMIGRATING BEETLES INTO FIELD I.
C TIP(I) = TIP(I) + INTAC
C ADD TOTAL NUMBER OF IMMIGRANTS TO INITIAL POPULATION SIZE.
IF (1 .LE. 10) PLT(1, I, M) = INTAC
C PLT(K, I, DAY) = SAME AS OUTP(K, I) BUT IS USED IN PLOT ROUTINE.
C OUTP(1, I) = OUTP(1, I) - OUTP(2, I) + INTAC*SURV
C OUTP(4, I) = FINAL POPULATION SIZE OF BEETLES IN FIELD I.
C TPOP(1) = TPOP(1) + INTAC
621 CONTINUE
Table 8.1 (Continued)

SUM = TPOP(4)
WRITE(3,41)
C LOOP 641 DETERMINES THE PERCENTAGE OF BEEFUS LIVING IN FIELD I.
DO 641 I=1, NF
PCT = 0
IF (OUTP(4,1).NE.0) PCT=100.0*OUTP(4,1)/SUM
WRITE(3,42)
WRITE(3,44) I,(FTP(NW,1),NW=1,6),(OUTP(K,1),K=1,4),PCT
CONTINUE
C WRITE(3,45)
WRITE(3,42)
WRITE(3,46) (TPOP(K),K=1,4)
C INCREASE MAXIMUM AGE BY ONE (IF MAG < 31).
C IF (MAG.LT.30) MAG=INST
C INTAC = 0
C LOOP 651 EVALUATES CHANGES IN POPULATION DUE TO BIRTHS.
DO 651 I=1, NF
C AT THE PRESENT STAGE OF THIS MODEL WE ARE NOT CONSIDERING BIRTH
C AND DEATH RATES. WE WILL LET POP(1,1,1) BE ZERO FOR EACH FIELD I.
INST = 0
IF (GRRATE.NE.0) READ(1,16) INST
POP(1,1,1) = INST
OUTP(1,1,1) = OUTP(4,1) + INST
C IF POPULATION REACHES A MAXIMUM CAPACITY FIELD IS DESTROYED.
IF (OUTP(1,1).GT.MXCP(I)) TYP(I)=1
C MXCP(I) = MAXIMUM POPULATION FIELD I CAN SUSTAIN.
C TYP(I)=1 --> FIELD IS NO LONGER AVAILABLE TO BEETLES.
IF (I.LE.10) PLT(1,1,1)=OUTP(1,1)
IF (I.LT.10) PLT(1,1,1)=OUTP(1,1)
C PLT(K,1,DAY) = SAME AS OUTP(K,1) BUT IS USED IN PLOT ROUTINE.
INTAC = INTAC + INST
CONTINUE
C TPOP(I) = TPOP(4) + INTAC
IF (GRRATE.EQ.0) JA=JA1
C C 600 CONTINUE
ALGORITHM GRAPHING SIMULATION RESULTS

ONLY POPULATION OF FIRST 10 FIELDS FOR AT MOST 30 DAYS IS GRAPHED.
IF (NF.GT.10) NF=10
IF (ND.GT.30) ND=30

DETERMINE SCALE OF X AXIS.
INC = 2
INC = NUMBER OF SPACES EQUIVALENT TO ONE DAY.
IF (ND.LE.15) INC=4

LOOP 710 Initializes data array to zero.
DO 710 I=1, 6
PLT(4,I,1) = -1
PLT(4,1,1) = : WILL BE POSITIVE ONLY IF THERE IS DATA AVAILABLE.
PLT(4,9,1) = -1
PLT(4,9,1) = INDICATOR FOR DATA AVAILABILITY FOR FIELD OF TYPE 1.
DO 711 N=2,30
711 PLT(4,I,N) = 0
710 CONTINUE

INPUT DATA ON BEETLE MIGRATION TO COMPARE TO SIMULATION.
READ(1,10) NF,D,ND
C NF = NUMBER OF DIFFERENT FIELD TYPES FOR WHICH THERE IS DATA.
C ND = NUMBER OF DAYS FOR WHICH WE HAVE DATA.
IF (NF.GT.10) GOTO 7200

LOOP 720 Inputs data for each field type.
DO 720 I=1, NF
READ(1,IS) NT,FRMT
NT = FIELD TYPE OF INPUTTED FIELD DATA.
FRMT = STORAGE FORMAT STATEMENT FOR NEXT INPUT LINE.
READ(1,FRMT) (POP(4,NT,N), N=1, NDD)
PLT(4,9,NT) = EMIGRATION DATA FROM FIELD OF TYPE NT ON DAY N.
PLT(4,9,NT) STORES THE PROPORTION OF BEETLES THAT Migrated FROM
FIELD OF TYPE NT. (PLT(4,9,NT)=-1 IMPLIES NO DATA AVAILABLE.)
C
INTAC = 0
C LOOP 721 Sums numbers of emigrating beetles.
DO 721 N=1, NDD
721 INTAC = INTAC + POP(4,NT,N)
C YMAX = 0
C YMAX = LARGEST VALUE OF DATA ARRAY FOR GIVEN FIELD TYPE.
C LOOP 731 Scale data for comparison with simulation results.
DO 731 N=1, NDD
REAL = POP(4,NT,N)
IF (REAL.GT.YMAX) YMAX = REAL
PLT(4,NT,N) = REAL/INTAC
C PLT(4,XT,N) = SCALED EMIGRATION DATA FROM FIELD TYPE XT OF DAY N.
731 CONTINUE
PLT(4,8,NT) = YMAX/INTAC
C PLT(4,8,NT) STORES MAXIMUM SCALED VALUE FOR FIELD OF TYPE NT.
720 CONTINUE
C PRINT HEADING OF GRAPHICAL DISPLAY OUTPUT.
7200 WRITE(3,50)
Table 8.1 (Continued)

<table>
<thead>
<tr>
<th>C</th>
<th>LOOPS WILL RUN FOR EACH OF THE FIELD TYPES OVER THE TIME</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>DURATION OF THIS SIMULATION:</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>1) THE CHANGES IN THE TOTAL POPULATION OF EACH FIELD.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>2) TOTAL NUMBER OF BEETLES IMMIGRATING TO EACH FIELD.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>3) TOTAL NUMBER OF BEETLES LEAVING EACH FIELD.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>4) DATA FOR TOTAL NUMBER OF BEETLES LEAVING A GIVEN FIELD TYPE.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>DO 800 I=1, NF</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>INTAC = IP(I)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>INTAC = INITIAL BEETLE POPULATION SIZE OF FIELD I.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>XMAX = 0</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>XMAX = LARGEST VALUE OF LOG OF POPULATION SIZE.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>YMAX = 0</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>YMAX = LARGEST VALUE OF EMIGRATING POPULATION SIZE.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>DO 811 N=1, NF</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C FIND THE MAXIMUM VALUE OF TOTAL POPULATION SIZE ARRAY.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>REAL = PLT(1,1,N)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IF (REAL.GT.XMAX) XMAX=REAL</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IF (REAL.GT.0) PLT(1,1,N)=ALOG10(REAL)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C FIND THE MAXIMUM VALUE OF TOTAL NUMBER OF EMIGRANTS ARRAY.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IF (RA(1).NE.0) REAL = PLT(2,1,N)/RA(I)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IF (REAL.GT.YMAX) YMAX=REAL</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>PLT(2,1,N) = REAL</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>MAKE A LOG TRANSFORMATION FOR VALUES OF POPULATION SIZE ARRAY.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>if (REAL.GT.YMAX)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>CONTINUE</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C IF THERE IS NO HISTORY OF BEETLE ACTIVITY GO TO NEXT FIELD.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IF (XMAX.EQ.0) GOTO 800</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C DETERMINE THE ORDER OF MAGNITUDE OF THE POPULATION SIZE.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>XMAX = ALOG10(XMAX)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C CALCULATE THE TWO CONVERSION FACTORS TO GRAPH RESULTS.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>CONV = 40/XMAX</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>CONV = CONVERSION FACTOR FOR GRAPHING POPULATION SIZES.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>K = TYP(I)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>F = FIELD TYPE OF FIELD I.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IND = PLT(4,K,1)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IND = INDICATES WHETHER DATA OF THIS FIELD TYPE IS AVAILABLE.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IF (IND.EQ.-1) GOTO 801</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C IF THERE IS DATA RESULTS ARE COMPARED TO IT.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>REAL = PLT(4,8,K)</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IF (REAL.GT.YMAX) YMAX=REAL</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>801 COPA = 40/YMAX</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>COPA = CONVERSION FACTOR FOR GRAPHING EMIGRATING POPULATIONS.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>COPA</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>LOOP 821 PRIMES ARRAYS FOR PLOTTING.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>DO 821 N=1, ND</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>SCALE ARRAYS</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>PLOT(1,1,N) = PLT(1,1,N)*CONV + 0.5</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>PLOT(2,1,N) = PLT(2,1,N)*COPA + 0.5</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>PLOT(3,1,N) = PLT(1,1,N)*CONV + 0.5</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>IF (IND.NE.-1.AND.INTAC.NE.0) PLOT(4,7,N)=PLOT(4,K,N)<em>COPA</em>0.5</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>821 CONTINUE</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C PRINT GRAPH HEADING.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>WRITE(3,52) I</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>C LOOP 831 INITIALIZES AND PRINTS EACH LINE OF GRAPH.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>DO 831 L=1, 42</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>LINE = 41 - L</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>LINE = THE LINE NUMBER OF LINE TO BE OUTPUTED ON GRAPH.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>LOOP 832 INITIALIZES OUTPUT CHARACTERS FOR GRAPH.</td>
<td>C</td>
</tr>
<tr>
<td>C</td>
<td>DO 832 II=1, 62</td>
<td>C</td>
</tr>
</tbody>
</table>
Table 8.1 (Continued)

C* DEPENDING ON THE SCALE OF THE GRAPH, OUTPUT WILL DIFFER.
IF (INC=7) 8312,8312,8311
C
C IF THERE ARE LESS THAN 16 DAYS OF RESULTS, HISTOGRAMS WITH SPACING.
8311 N = IL/4
IF (N.EQ.0) GOTO 832
IF (LINE.EQ.INT(PLT(1,1,N))) GRAPH(IL)=CHRCTR(21)
IF (LINE.EQ.INT(PLT(3,1,N))) GRAPH(IL)=CHRCTR(7)
IF ((IL/4)*4.EQ.IL) GOTO 832
IR = IL + 51
IF (LINE.LE.PL(2,1,N)) GRAPH(IR)=CHRCTR(9)
IF (IR.EQ.123) GRAPH(124)=GRAPH(123)
IF (IR.EQ.1:3) GRAPH(124)=GRAPH(123)
IF (IR.EQ.1:3) GRPH(124)=GRAPH(123)
GOTO 832
C
C IF THERE ARE MORE THAN 15 DAYS OF RESULTS, NO SPACING IN HISTOGRAM.
8312 N = ((L1-1)/7
IF (LINE.EQ.INT(PLT(1,1,N))) GRAPH(IL)=CHRCTR(21)
IF (LINE.EQ.INT(PLT(3,1,N))) GRAPH(IL)=CHRCTR(7)
IR = IL + 51
IF (LINE.LE.PL(2,1,N)) GRAPH(IR)=CHRCTR(8)
IF (IR.EQ.123) GRAPH(124)=GRAPH(123)
IF (IR.EQ.1:3) GRAPH(124)=GRAPH(123)
IF (IR.EQ.1:3) GRPH(124)=GRAPH(123)
GOTO 832
C
C PRINT ARRAY (LABELING Y AXIS ON EVERY FIFTH LINE).
8421 N = LINE/5
IF (LINE.GT.100) GOTO 8422
8422 PRINT Y AXIS LABEL.
8422 REAL = LINE/CONV
C CALCULATE LABEL FOR OTHER GRAPH.
CALCULATE LABEL (J)
8423 WRITE(3,53) REAL,(GRPH(J),J=3,63),(BMG),(BMG(J),J=4,124)
GOTO 8423
C
C PRINT UNLABELED LINE.
8422 WRITE(3,54) (GRPH(J),J=1,63),(GRPH(J),J=64,124)
C
C CLEAR GRPH ARRAY
8423 DO 852 N=1,124
852 GRPH(N) = BLANK
831 CONTINUE
C
C PRINT X AXIS AND DETERMINE THE LABELING BELOW GRAPH.
INST = 8/INC
C DO 861 N=1,6
861 J = N*INST - 1
OUTP(I,J) = J
OUTP(I,4) = J
C OUTP(I,4) IS USED TO STORE THE LABELS FOR GRAPH X.
C
C PRINT X AXIS.
861 WRITE(3,55) (OUTP(N),N=1,6),(CHRCTR(21),CHRCTR(7))
Table 8.1 (Continued)

```plaintext
PRINT 800
IF (IND.ER,-1) WRITE(1,56) CHCTR(1),CHCTR(9)
IF (IND.EQ.-1) WRITE(3,57) CHCTR(7)
RA(I) = RA(I)/TFT(I)
EMIG = PLT(4,9,I)
IF (EMIG.NE.-1) WRITE(1,58) RA(I),EMIG
IF (EMIG.EQ.-1) WRITE(3,59) RA(I)
CONTINUE
```

<table>
<thead>
<tr>
<th>INPUT/OUTPUT FORMAT STATEMENTS</th>
</tr>
</thead>
<tbody>
<tr>
<td>-------------------------------</td>
</tr>
</tbody>
</table>

### INPUT FORMATS

10 FORMAT (3I7)
11 FORMAT (6A4,12,F7.2,2(F8.1))
13 FORMAT (I3,2F6.3,F8.1,F6.3)
14 FORMAT (4(F8.3))
16 FORMAT (19)
18 FORMAT (13,4A4)

### OUTPUT FORMATS

20 FORMAT (1H1,132('**')/)
  2 36X,'**',58('**'),'+**'/
  3 2(36X,'**',58X,'**')/
  4 36X,'**',19X,'D E M V M D (VI-**'),19X,'**'/
  5 36X,'**',58X,'**'/
  6 36X,'**',9X,'A MODEL SIMULATING INTERFIELD MIGRATION' +
    9X,'**'/
  7 2(36X,'**',58X,'**')/
  8 36X,'**',58('**'),'+**'/
  9 36X,62('**')/11
23 FORMAT (1H1,132('**')/)
  2 49X,36('**')/
  3 49X,'**',34X,'**'/
  4 49X,'**',7X,'CONSTANT PARAMETERS',7X,'**'/
  5 49X,'**',34X,'**'/
  6 49X,36('**')/13
  7 2X,130('**')/15
25 FORMAT (1H1,132('**')/)
  2 49X,36('**')/
  3 49X,'**',34X,'**'/
  4 49X,'**',8X,'SIMULATED RESULTS',8X,'**'/
  5 49X,'**',34X,'**'/
  6 49X,36('**')/17
  7 2X,130('**')/19
29 FORMAT (1H1,132('**')/1X,132('**'))
10 FORMAT (1H1,42X,'TABLE I'/)
  2 11*(5X,'**'
  3 56X,'(CONSTANT PARAMETERS')/
  4 24X,'**',344(',**'/
  5 '*','**',344('
```
Table 8.1 (Continued)

<table>
<thead>
<tr>
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<td>&quot;IN METERS&quot; (IN AREA)</td>
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<td>12X, &quot;PERCENTAGE OF EMIGRATING BEETLES&quot;</td>
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<tr>
<td>62</td>
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</tr>
</tbody>
</table>

[Note: The table continues with more columns and rows, but they are not visible in the provided excerpt.]
Table 8.1 (Continued)

59 FORMAT (77X,'PROPORTION OF TOTAL POPULATION THAT EMIGRATED:'//
  2 86X,'IN SIMULATION - - - ','F5.3//'  
  3 86X,'IN ACTUALLY - - - ????''//
  4 40X,64('!' */)//
63 FORMAT (////63X,'TABLE II//'  
  2 1H+,62X,'  
  3 43X,'INPUT VALUES OF PARAMETERS USED IN SIMULATION''//
  4 18X,'!',97('!'),'+!/  
  5 19X,'!',97X,'!'//
  6 18X,'!',30X,'AGE (IN DAYS) OF BEETLE AT: PROBABILITY ','  
  + 'OF MIGRATION IF BEETLE IS IN ''/  
  7 18X,'!' DESCRIPTION OF FIELD TYPE START END''6X,
  + 'MEAN MIGRATORY NON-SEDENTARY NON-MIGRATORY''//
  8 18X,'!',30X,'OF "MATURING" PERIOD.'3(9X,'STACK'),4X,'!''/  
  + '!'//
  9 18X,'!',97('!'),'+!/  
  X 18X,'!',28X,'!',3(8X,'!'),2(13X,'!'),13X,'!'//
64 FORMAT (18X,'!',6A4,2(3X,'!'3,5.0),3X,'!',F5.1,2X,
  + 3('!',4X,F5.3,4X)')'/
  2 18X,'!',28X,'!',3,8X,'!',2(13X,'!'),13X,'!'//
65 FORMAT (18X,'!',97('!'),'+!/  
  2 2X,130('!')///)
C  CCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCC
C  C
C  C
C  C
C WRITE(3,29)
C RETURN
C END
C  CCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCC
**Figure 8.3:** Effects of a constant wind speed, W, from a specified direction on the apparent field locations.

W = 0.5 (1/2 the speed of flying beetle)

Key: Solid circle - actual field location  
Dotted circle - apparent field location
$B_i(t) = \text{Beetle population size for field } i \text{ at start of day } t.$

$P(i) = \text{Probability of migrating from field } i \text{ during a single day.}$

This matrix is dependent on the age and crop type of field $i$.

$V(i) = \text{Stochastic matrix that reclassifies the migration state of the individual beetle. \ This matrix depends on the age and the crop type of field } i.$

$a_{i,j} = \text{Probability of reaching field } j, \text{ given that beetle left field } i. \ (i = j)$

(Note: $a_{i,j} = PR(d_{i,j}, r_j) - \text{Field overlap} * Pd(d_{i,j})$)

$s = \text{Survival rate.}$

$n = \text{Number of fields.}$

$B_i(t)$ (equivalent to program's array $POP(c,i)$ at day $t$), has elements whose values for each field $i$ give the number of beetles in the different age-migration classes, $(k)$. Note, it is assumed that the maximum number of days a beetle can remain a preadult is 20. For $b_{i,j}$ an element of $B_i$, we have:

$k \leq 20 \rightarrow \text{beetles in the pre-migration state, } S_0.$

$k = 21 \rightarrow \text{beetles ready to migrate, but have never migrated before, state } S_1.$

$k = 22 \rightarrow \text{beetles migrated on the previous day. That is, beetles are in the migrating state, } S_2.$

$k = 23 \rightarrow \text{beetles in the colonizing state, } S_3.$
P(i) (equivalent to array PM(type i, k-17) in the program) is a 23 × 23 matrix which depends on the field type of field i. It can be represented by the multiplication of the following two vectors:

\[(0,0,...,0,1,0) \times (0,0,...,0,p_1(i),p_2(i),p_3(i))\]  

(8.3)

\[p_1(i) = \text{probability of leaving, given that the beetle is in the ready to migrate state, } S_1.\]

\[p_2(i) = \text{probability of leaving, given beetle migrated on the previous day. (Beetle is in state } S_2).\]

\[p_3(i) = \text{probability of leaving, given beetle migrated, but not on previous day. (Beetle is in state } S_3).\]

\[a_{i,j} \text{ (equivalent to ALPHA}(i,j) \text{ in the program) is the product of two independent probabilities:}\]

\[a_{i,j} = Qr(d_{i,j},r_j) \times Pd(d_{i,j})\]  

(8.4)

Qr(d_{i,j},r_j), probability of flying in the direction of field j, and Pd(x), the probability of flying the entire distance (x) of the flight. The first of these was calculated in part (1) of the program. (See Figure 8.4.) Pd(x) is assumed to be the following:

\[Pd(x) = \begin{cases} 
1 & \text{for } x \leq d_m \\
\exp \left[-ux(cxx-d_m)\right] & \text{for } x > d_m.
\end{cases}\]  

(8.5)
where

\[ Pd(x) = \text{the probability that the maximum distance a beetle can fly is } x, \]

\[ u = \text{relative death rate per kilometer}, \]

\[ c = \text{adjustment constant, (calculated in part (1)),} \]

\[ d_m = \text{minimum distance before death rate is considered.} \]

(Note: \( x = D(i,j), u = DR, d = SMD, \) and \( c = COFA \) in the program.)

\( V(i) \) (corresponding to \( \text{MAR}(c, \text{type } i) \) in the program) is a \( 23 \times 23 \) matrix which is only dependent on the field type. The entries of the matrix \( V \) will have the values given below. (Note: Only the first 20 columns are dependent on the field type. (See Figure 8.4.).)

\[
\begin{align*}
V_{k,j} & = 1 - z_j & \quad (k \leq 20, j=i-1) \\
V_{21,j} & = z_j & \quad (j \leq 20) \\
V_{21,21} & = V_{22,22} = V_{23,23} = 1 \\
V_{k,j} & = 0 & \quad \text{elsewhere}.
\end{align*}
\]

\( z_j = \text{probability of maturing at age } j, \) given that the beetle was in pre-migratory state, \( S_0, \) at age \( j-1. \)

\[
\begin{cases}
0 & \text{for } j < m, \ (m = \text{minimum age for maturation}) \\
g(j) & \text{for } m \leq j < M. \\
1 & \text{for } M \leq j, \ (M = \text{maximum age for maturation})
\end{cases}
\]

\( g(j) = \text{is an increasing function whose values range from 0 to 1.} \)

The underlying distribution used for this function is the cumulative binomial distribution function.
Figure 8.4: Digraph of the matrix $(I-P)^*V$.

Note, all the parameters in this figure depend on the crop type of field $j$. States $1-M$, 21, 22 & 23 correspond to migration states, $S_0 - S_3$, respectively.
For $J = j - m$, $n = M - m$, $q = \text{empirical probability constant}$ then:

$$q(j) = f(J)/(1-F(J-1))$$

$F(J) = \text{Binomial} (q,n)$. 
APPENDIX B

THE ALGORITHM FOR THE STOCHASTIC POPULATION MODEL
(STPOMD)

Purpose

This model was developed to simulate the sizes of beetle populations in a system of distinct resource fields. Movement (migration) between these fields is assumed possible. Emigration from the system is also allowed, but no accommodation is made for immigration into the system. This model should be used as a tool to test the effect of certain key parameters and assumptions. At its present stage it should not be used as a predictive tool for pest management. Further validation studies and more precise estimations of the parameters are needed if the model is to be used for such purposes.

The model is discrete in both the temporal and spatial framework. Each beetle is considered individually, each simulation day. One simulation run can be up to a year long. As in the previous model, decisions such as whether or not to die, to migrate or to oviposit are made on a daily basis. These Bernoulli trials are decided with the help of (theoretically) uniformly distributed random numbers. (If the random number is less than a given probability parameter, then the decision will fall one way, otherwise, the other way.) A "random" deviate is generated for each trial on each day for each beetle. Since an initial seed is needed to start the random generator, two runs with identical parameter values but different seeds will have different output values. Thus, it could be said that the results from a simulation run depend on the initial seed value given.
The "random" numbers used in this simulation are calculated with the linear congruential generator discussed in Chapter 4. Assuming that these "random" numbers are indeed uniformly distributed, one can now consider such parameters as the variability of the model. Several simulation runs can be used to determine the variance associated with the model's population sizes. With this simulation output, it is now possible to calculate such parameters as the probability of infestation and the probability of economic damage.

The Model

This model (STPOMD) is an extension of the movement model, DEMVMD, discussed previously. The first two parts of both models are identical. The last part in both are output routines which, due to the greater time domain in the population model, are different. This last algorithm will graph the total adult population size, as well as the total preadult population size for specific fields over the last 126 days.

The model starts with the beetles in the overwintering sites. At this point all the fields are assumed to be in existence. (The program allows for a series of stages for each field. An existing field need not necessarily have plants on it at the start of the simulation.) Their radii of attractivity are assumed to be constant throughout the simulation run. All emerging adults are considered to have age zero.

Each beetle and each field will have an information number. In case of the beetle a two byte (maximum value 32,767) is used to store its age, life stage, immediate migration history and location. (See Table 8.2.)
Table 8.2. Explanation of code used in the 5 digit beetle information number.

<table>
<thead>
<tr>
<th>Beetle Information Number</th>
<th>Possible Values</th>
<th>Decoded Information Number (for each stage)</th>
</tr>
</thead>
<tbody>
<tr>
<td>*----</td>
<td>0,1,2,3 (stages)</td>
<td>0 → Larvae or pupal stage</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1 → Adult (S₀, S₁ or S₃)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2 → Adult (S₃ or S₂)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3 → Egg stage</td>
</tr>
<tr>
<td>Q***</td>
<td>0,...,99</td>
<td>(Instar # - 1)*20 + (# days in instar)</td>
</tr>
<tr>
<td>1***</td>
<td>0,...,19</td>
<td>Age of adult in state S₀</td>
</tr>
<tr>
<td></td>
<td>20,...,39</td>
<td>Age + 20 of adult in state S₁</td>
</tr>
<tr>
<td></td>
<td>40,...,99</td>
<td>Age + 40 of adult in state S₃</td>
</tr>
<tr>
<td>2***</td>
<td>0,...,19</td>
<td>Age - 60 of adult in state S₃</td>
</tr>
<tr>
<td></td>
<td>20,...,99</td>
<td>Age + 20 of adult in state S₁</td>
</tr>
<tr>
<td>3***</td>
<td>0,...,26</td>
<td>Age of egg.</td>
</tr>
<tr>
<td>-----</td>
<td>1,...,99</td>
<td>Field no. in which beetle is located</td>
</tr>
<tr>
<td>000000</td>
<td></td>
<td>Dead beetle</td>
</tr>
</tbody>
</table>
A field's information number has an 8 digit number associated with it. These digits are grouped into pairs, and each of these pairs give the day a field develops into the next stage. The two leftmost digits are multiplied by two and compared to the day number of the simulation. If these two numbers are equal, the field develops into the next stage and the leftmost two digits are truncated from the field information number.

The population of a field can be determined at any time by summing all beetles that are in a given field. The formulae describing the day-by-day population change can only give the expected population sizes. The equations used in calculating these expected population sizes are given in Tables 8.3 and 8.4. These formulae are also used in the deterministic version of this model, DEPOMD. (See Chapter 4.)

Let us now follow a beetle's life cycle in terms of this algorithm. Initially, all beetles are in the pre-migration state. The only processes acting on the individuals in this state are mortality and maturation into the next state.

All the initializations needed in the DEMVMD program are also used in this program. Only a few extra parameters are needed to specify fertility and development rates. The major difference between the two is in the "daily" iterative runs. The following is a description of a beetle "day" of this algorithm.

At the start of each day a boolean migration parameter is set to 0 or 1. (0 implies "good" weather such that migration is feasible.) The frequency of "good" weather is considered a constant and is inputted initially into the program. The type of weather a day will have depends on the value of a generated uniform deviate.
Table 8.3. Formulae used to determine the population size in the deterministic version of the model STPOMD. For description of parameters, see Table 8.4 on the next page.

<table>
<thead>
<tr>
<th>Number of:</th>
<th>Iterative equation used</th>
</tr>
</thead>
<tbody>
<tr>
<td>egg masses</td>
<td>( N_{0,j}(i,t+1) = \sum_{j=0}^{M} \left{ \text{PS}(i) \times \sum_{k=0}^{9} [\text{PS}(i,k) \times N_{j,k}(i,t)] \right} )</td>
</tr>
<tr>
<td>(k=0)</td>
<td></td>
</tr>
<tr>
<td>(j&lt;J(i,0))</td>
<td>( N_{j+1,0}(i,t+1) = N_{j,0}(i,t) )</td>
</tr>
<tr>
<td>Larvae:</td>
<td></td>
</tr>
<tr>
<td>hatchlings</td>
<td>( N_{0,1}(i,t+1) = \text{PS}(i,k) \times \text{Fec}(\text{gen}) \times N_{j,0}(i,0),0(i,t) )</td>
</tr>
<tr>
<td>(k=1)</td>
<td></td>
</tr>
<tr>
<td>(j&lt;J(i,0))</td>
<td>( N_{j+1,k}(i,t+1) = N_{j,k}(i,t) )</td>
</tr>
<tr>
<td>molting</td>
<td>( N_{0,k+1}(i,t+1) = \text{PS}(i,k) \times N_{j,k}(i,k),k(i,t) )</td>
</tr>
<tr>
<td>Pupae</td>
<td>Same as for larvae</td>
</tr>
<tr>
<td>(k=5)</td>
<td></td>
</tr>
<tr>
<td>Adults:</td>
<td></td>
</tr>
<tr>
<td>State ( S_0 )</td>
<td>( N_{j+1,6}(i,t+1) = \text{PS}(i) \times [1-\text{Pa}(i,j)] \times N_{j,6}(i,t) )</td>
</tr>
<tr>
<td>(k=6)</td>
<td></td>
</tr>
<tr>
<td>State ( S_1 )</td>
<td>( N_{j+1,7}(i,t+1) = \text{PS}(i) \times [1-\text{Pm}(i,7)] \times N_{j,7}(i,t) + )</td>
</tr>
<tr>
<td>(k=7, j&lt;K)</td>
<td>( \text{PS}(i) \times \text{Pa}(i,j) \times N_{j,6}(i,t) )</td>
</tr>
<tr>
<td>State ( S_2 )</td>
<td>( N_{j+1,8}(i,t+1) = \text{PS}(i) \times \sum_{L=1}^{n} \left{ \Sigma \text{a}(i,L) \times \Sigma \text{Pm}(L,k) \right} \times N_{j,k}(i,t) )</td>
</tr>
<tr>
<td>(k=8)</td>
<td>( \text{PS}(i) \times \text{Pm}(i,8) \times N_{j,8}(i,t) + )</td>
</tr>
<tr>
<td></td>
<td>( \text{PS}(i) \times \text{Pm}(i,k) \times N_{j,9}(i,t) + )</td>
</tr>
<tr>
<td></td>
<td>( \text{PS}(i) \times N_{j,7}(i,t) )</td>
</tr>
</tbody>
</table>
Table 8.4. Description of parameters used in previous table.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_{j,k}(i,t)$</td>
<td># beetles of age $j$, in stage $k$, on field $i$, at time $t$.</td>
</tr>
<tr>
<td>$k$</td>
<td>development stage</td>
</tr>
<tr>
<td>$j$</td>
<td>number of days in stage $k$</td>
</tr>
<tr>
<td>$m_o$</td>
<td>min. age for oviposition</td>
</tr>
<tr>
<td>$K$</td>
<td>maximum age of beetle in state $S_7$ (stage $k=7$)</td>
</tr>
<tr>
<td>$M$</td>
<td>maximum age of the beetle</td>
</tr>
</tbody>
</table>

The following parameters are dependent on the field type of field $i$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_s(i,k)$</td>
<td>prop. of preadults in stage $k$ surviving to next stage.</td>
</tr>
<tr>
<td>$P_o(i,k)$</td>
<td>prop. of adults in migration state $k$ ovipositing.</td>
</tr>
<tr>
<td>$P_m(i,k)$</td>
<td>prop. of adults in migration state $k$ migrating.</td>
</tr>
<tr>
<td>$P_a(i,j)$</td>
<td>prop. of adults of age $j$ that will mature into state $S_1$.</td>
</tr>
<tr>
<td>$P_S(i)$</td>
<td>daily adult survival rate.</td>
</tr>
<tr>
<td>$a(i,L)$</td>
<td>prob. of reaching field $i$ if leaving field $L$.</td>
</tr>
<tr>
<td>$F_{ec}(gen)$</td>
<td>number of female eggs per egg batch. Its value depends on the generation ($gen$) of the mother.</td>
</tr>
<tr>
<td>$J(i,k)$</td>
<td>max. number of days in instar $k$ before molting. Note: if $J(i,k)$ is not an integer but is between $x$ and $x+1$ (where $x$ is an integer), then the fractional part of $J(i,k)$ as the proportion of beetles developing into the next stage at age $x+1$.</td>
</tr>
</tbody>
</table>
The second environmental parameter is an external function dictating the increase in the development time (from the optimal) due to temperature. It, too, is calculated at the start of a simulation day. Presently, this function assumes that the development time to the next stage (egg, instar or pupa) will be largest in the spring, decrease until July and remain unchanged thereafter. (See Figure 8.5.) This option was added into the model since the beetle's development rate is a function of temperature. The actual function used was not verified. This external function should be replaced with a more specific algorithm, once one is available.

As in the previous model an adult will be in one of four states. With the exception of the pre-migratory state, \( S_1 \), all the states are treated in the same manner as in the model DEMVMD. (See Appendix A.) In the case of state, \( S_1 \), a beetle will exit this state if: 1) it migrates, or 2) it reaches a specified age. This specified age is part of the input, and its value may not exceed 20.

The first Bernoulli trial for each adult beetle tests for survival. If the value of the uniform deviant is larger than the probability of survival, the beetle is considered dead. Under this circumstance, the beetle's information number is set to zero and the next beetle is considered. If the beetle survives, its information number is decoded. (Note, this decoding will take only two steps, 1) truncation of last two digits, and 2) storing these truncated digits.)

The next two decisions, oviposition and migration, are made in that order. These two probabilities depend on the field type and the migration state of the beetle. The destination of the beetle in case of migration is also "decided" with the help of a uniform deviate.
Increase in the development time between instars

$\# \text{ of days}$

1.5+

1.0+

0.5+

0.0+

120 180 240 300

Julian Date

Dev$(t) = \max\left(3-t/60, 0\right)$

$t = \text{julian date.}$

Figure 8.5. Graph of the function used to increase the rate of development during the cooler days early in the season. Its value is added on to the parameter $J(k,i)$ (see Table 8.3) to give the number of days needed to reach next instar.
To determine the destination of the beetle in the case of migration, an array was initialized prior to the daily simulation iterations. It, unlike the previous problem, does not store the conditional probabilities of reaching one field from another (given migration is certain), but stores the "cumulative" probabilities. The array, ALPHA\((i,j)\), stores the probability of reaching any field whose identification number is less than or equal to \(j\), given beetle started in field \(i\). Thus, the destination of a migrating beetle can be determined by a random number, \(RN\). The beetle is assumed to land in field \(j\) if

\[
\text{ALPHA}(i,j-1) \leq RN \leq \text{ALPHA}(i,j),
\]

where: \(\text{ALPHA}(i,0) = 0\) and \(\text{ALPHA}(i,i) = \text{ALPHA}(i,i-1)\).

Ovipositing beetles will lay, at most, one egg mass in one day (according to the model). Since it has been reported that the FO generation has a lower fertility rate than the later generations, the size of the egg mass depends on the data. (There is little or no overlap between the overwintering generation and ovipositing females of the F1 generation. The resulting error by letting the number of eggs per egg mass depend on the date, rather than the generation is assumed negligible.) After each egg mass is laid, the "beetle information array" is increased by one more element.

The time for an egg mass to mature can take up to 20 days. If the program calls for 7.4 days development time for an egg mass, then there is a 60% chance that the beetles hatch on day 7, and a 40% chance that they hatch on day 8. It is at this point in time that mortality (or infertility of the eggs) is considered. Until now, the new generation of beetles have been considered only as one mass. After hatching,
a new storage space is allocated for each living beetle, and each beetle is considered separately. Note that the number of eggs in an egg mass is fixed.

Larval and pupal development is treated in a way similar to egg development. There is no migration in these stages, and mortality is considered only during the molting period, i.e., only at the end of each life stage. (Note, there are four instars and one pupal stage.) In the case of death, the beetle's information number is set to zero. As in the previous case, the development time need not be an integer. The procedure for accommodating any non-integer has already been discussed.

At the end of each simulated day the beetle information array is compacted. The entire array is searched, and for each 0 (dead beetle) encountered, the last element is substituted in that location. The array will thus be shortened by the number of beetles that were lost to the system in the course of one simulation day. An integer variable is used to keep track of the array's length.

Also at the end of each day, field development is considered. If the number of adults plus the number of fourth instars reaches a prespecified maximum, the field will be considered destroyed. The field can also develop into the next stage if the last two digits of the field information number times two equal the day of the simulation run. Once two digits have been used they are truncated from the field information number.
Intermediate outputs as to the population of the different fields are optional. The output routine will print a table giving the number of beetles in the different life stages. The final graphs of the population dynamics of the first few fields are also optional (this number is specified by the user).

Any simulation run should be repeated several times with different seeds on each run. The expected outcome of this simulation can be determined by using proportions of the number of beetles in each age/migration state rather than probabilities acting on an individual. (See Table 8.5 for the program listing.) The deterministic version of this program is also available.
Table 8.5. The program listing of STPOMD, the stochastic population model.

```
!------------------------------------------------------------------!
! STPOMD (V)                                                      !
!------------------------------------------------------------------!

THIS PROGRAM IS A MODEL SIMULATING BEETLE MOVEMENT               !
BETWEEN DIFFERENT BEAN FIELDS. EACH BEETLE IS CONSID-             !
ERED SEPARATELY, AND WITH THE USE OF A RANDOM NUMBER GENERATOR,   !
IT'S LIFE HISTORY IS SIMULATED. THIS MODEL IN IT'S PRESENT STAGE   !
ASSUMES DENSITY INDEPENDENCE.                                     !

DESERLARATION OF VARIABLES                                       
INTEGER*2 TYP(50), POP(8, 50), MXP(50), PLT(2, 126, 10), MAX(10) 
INTEGER*2 MBR(101000)                                           
INTEGER*4 TPOP(5), NFD(50)                                      
REAL*4 D(50, 50), LOC(2, 50), ALPHA(50, 50), RA(50), LBL(12)    
REAL*4 RBD(4, 9), PMIG(3, 9), POVI(3, 9)                         
REAL*4 BNM(4, 9), MAT(20, 9), SUR(7, 9)                         
REAL*4 RANU, NW                                                  
DIMENSION FTP(5, 9), GRPH(125), CHRCTR(22)                       
COMMON NSFD                                                     
FOR THE DESCRIPTION OF THE DIFFERENT VARIABLES USED SEE SEPARATE  
PROGRAM DOCUMENTATION.                                            

INITIALIZE OUTPUT ARRAYS.                                        
DATA BLANK, GRPH /127*1/                                         
DATA CHRCTR /'1', '2', '3', '4', '5', '6', '7', '8', '9', 'X',    
+ ' ', '1', '2', '3', '4', '5', '6', '7', '8', '9', '0', '+', '-', 
/ GRPH = CHARACTER STRING USED TO DRAW DIAGRAM.                  
BLANK = ADDRESS STORING CHARACTER FOR A BLANK.                    
CHRCTR = STORES THE DIFFERENT SYMBOLS USED IN GRAPH.              
SPACE SAVING STEP: VARIABLES TO BE EXPLAINED LATER.              
EQUIVALENCE /RA(1), LBL(1)), (D(1, 1), MAT(1, 1)), (D(1, 5), POVI(1, 1)), 
+ (D(1, 6), SUR(1, 1)), (D(1, 8), BNM(1, 1)), (D(1, 9), PMIG(1, 1)) 

REAL(1, 10) NF, NP, NT                                           
NF = NUMBER OF FIELDS USED IN THIS SIMULATION. (MAXIMUM IS 40)    
NP = TIME DURATION OF THIS SIMULATION. (MAX 15)                   
NT = NUMBER OF FIELD TYPES USED IN THIS SIMULATION. (MAX IS 9)    

INPUT PARAMETERS TO ADJUST FOR BEETLE'S SEARCHING BEHAVIOR.       
REAL(1, 15) W, COPA                                              
W = WIDTH OF BEETLE'S SEARCHING CORRIDOR.                        
COPA = ADJUSTS FOR SEARCHING BEHAVIOR. (1 < COPA < 2)            
W = W/2                                                         
```

Table 8.5 (Continued)

C INPUT DESCRIPTION OF FIELD TYPES.
DO 100 IT=1, NT
100 READ(1,11) (FTP(NW,IT),NW=1,6)
C FTP = STORES PHENOLOGICAL INFORMATION OF EACH FIELD TYPE.
C
C
C LOOP 200 CALCULATES DISTANCES BETWEEN FIELDS AS WELL AS THE "ARC
C SIZE" I.E. THE ANGLE IN RADIANS OF THE PROJECTION OF FIELD J ONTO
C THE UNIT CIRCLE AROUND THE CENTER OF FIELD I.
DO 200 I=1, NF
READ(1,12) TYP(I),AR,LOC(1,I),LOC(2,I)
C TYP = INDEX USED TO SPECIFY TYPE OF CROP PLANTED IN EACH FIELD.
C AR = AVERAGE RADIUS OF "ATTRACTIVITY" RANGE OF FIELD I.
C LOC(*,I) = RESPECTIVE COORDINATES OF CENTER OF FIELD I.
C
C ADD TO FIELD RADIUS TO ADJUST FOR SEARCHING BEHAVIOR.
R2 = COFA*AR - AR
C R2 = INCREASE IN FIELD "FINDABILITY" DUE TO SEARCHING BEHAVIOR.
C FOR SMALL FIELDS CHANGE IN ATTRACTABILITY PROPORTIONAL TO RADIUS.
C FOR LARGE FIELDS ADD WIDTH OF SEARCHING CORRIDOR TO RADIUS.
D(I,I) = AR + AMIN(R2,W)
C D(I,I) = AVERAGE RADIUS OF "FINDABILITY" RANGE OF FIELD I.

C 101 I = I - 1
IF (I.EQ.0) GOTO 200
DO 201 J=1, I
DF1 = LOC(1,J) - LOC(1,I)
DF2 = LOC(2,J) - LOC(2,I)
C DF1 & DF2 = TEMPORARY STORAGE ADDRESSES.
C THE NEXT THREE LINES CALCULATE THE DISTANCE BETWEEN FIELDS I & J.
R2 = DF1*DF1 + DF2*DF2
C R2 = SQUARE OF THE DISTANCE BETWEEN CENTERS.
D(I,J) = SQRT(R2)
D(J,I) = D(I,J)
C D(I,J) = DISTANCE BETWEEN CENTER OF FIELDS I & J. (I.NE.J)
C THESE TWO STEPS CALCULATE THE ARC SIZE OF FIELD I W.R.T. FIELD J.
RAT = D(J,I)/D(I,J)
C RAT = RATIO BETWEEN FIELD RADIUS AND INTERFIELD DISTANCE.
IF (RAT.LT.1.0) ALPHA(I,J) = ARSIN(RAT)
IF (RAT.GE.1.0) ALPHA(I,J) = 1.5708
C THESE TWO STEPS CALCULATE THE ARC SIZE OF FIELD J W.R.T. FIELD I.
RAT = D(I,J)/D(J,I)
IF (RAT.LT.1.0) ALPHA(J,I) = ARSIN(RAT)
IF (RAT.GE.1.0) ALPHA(J,I) = 1.5708
C ALPHA(I,J) = 1/2 OF THE SIZE OF THE PROJECTION OF FIELD J ONTO
C THE UNIT CIRCLE AROUND FIELD I'S CENTER. (ARC SIZE)
201 CONTINUE
200 CONTINUE
C
C LOOP 300 DETERMINES THE AMOUNT OF OVERLAP BETWEEN FIELD PROJECTIONS
C ONTO THE UNIT CIRCLE ABOUT FIELD I, AND THE EFFECT OF SUCH ON THE
C RELATIVE "REACHABILITY" OF FIELD J FROM FIELD I.
DO 300 I=1, NF

Table 8.5 (Continued)

C DO 311 J=1, NF
C IF (I.EQ.J) GOTO 311
C RAT = (LOC(1,J)-LOC(1,I))/D(I,J)
C RAT = RATIO BETWEEN DIFFERENCE IN X VALUES AND INTERFIELD DIST.
C RA(J) = ARCS(RAT)
C RA(J) = ANGLE BETWEEN FIELDS I & J AND THE HORIZONTAL.
C IF ((LOC(2,J)-LOC(2,I)).LT.0) RA(J)=RA(J)
C IF (LOC(2,J)-LOC(2,I)).GT.0 RA(J)=2*PI-RA(J)
C ALPH(A(I,J)) = ALPHA(I,J)
C ALPH(A(J,J)) = ALPHA(I,J)
C ALPH(A(J,J)) TEMPORARY STORAGE FOR ALPH(A(I,J)).
C 311 CONTINUE

C LOOP 321 DETERMINES THE EXTENT OF THE OVERLAP BETWEEN "ARCS".
C DO 321 J=1, NF
C IF (I.EQ.J) GOTO 321
C J1 = J - 1
C IF (J1.EQ.0) GOTO 321
C DO 322 K=1, J1
C IF (K.EQ.I) GOTO 322
C NEXT 5 LINES DETERMINE WHICH FIELD (I OR K) IS CLOSER. (KD=CLOSER)
C IF (D(I,J).LT.D(I,K)) GOTO 3221
C LD = J
C KD = K
C GOTO 3222
C 3221 LD = K
C KD = J
C 3222 CONTINUE
C RAL = RA(LD)
C RAK = RA(KD)
C RAK & RAL USED FOR GREATER CALCULATING EFFICIENCY.
C ADJUST RELATIVE ANGLES FOR COMPARISONS.
C IF ((RAL-RAK).GT.3.1416) RAK=RAK+6.2832
C IF ((RAL=RAK).GT.3.1416) RAL=RAL+6.2832
C IF (RAL.RT.RAK) GOTO 3224
C OL = (RAL-ALPHA(KD,KD)) - (RAL+ALPHA(I,LD))
C IF (OL.LT.0) ALPHA(I,LD)=ALPHA(I,LD)+OL
C GOTO 3225
C 3224 OL = (RAL-ALPHA(LD,LD)) - (RAL+ALPHA(I,KD))
C OL = OVERLAP BETWEEN TWO PROJECTIONS ONTO ONE UNIT CIRCLE.
C IF (OL.LT.0) ALPHA(LD,LD)=ALPHA(LD,LD)+OL
C 3225 CONTINUE
C 322 CONTINUE
C 321 CONTINUE
C LOOP 331 COMBINES THE EXTENT OF THE OVERLAP AND THE ARC SIZE, AND CALCULATES THE ACTUAL PROJECTION OF FIELD 4 ONTO THE UNIT CIRCLE.
C DO 331 J=1, NF
C IF (I.EQ.J) GOTO 331
C ALPH(A(I,J)) = (ALPHA(I,J)+ALPHA(J,J))/6.2832
C ALPH(A(I,J)) = PROB. OF REACHING FIELD J, IF LEAVING FIELD I.
C IF (ALPHA(I,J).LT.0) ALPHA(I,J)=0
C 331 CONTINUE
C 300 CONTINUE
C PRINT HEADING
C WRITE(3,20)
C
Table 3.5 (Continued)

<table>
<thead>
<tr>
<th>Algorithm for Graphical Display of System</th>
</tr>
</thead>
</table>

**PRINT HEADING FOR OUTPUT OF CONSTANT PARAMETERS.**

```plaintext
WRITE(3,23)
```

**LOOP 410 PRINTS DESCRIPTION OF EACH FIELD.**

```plaintext
WRITE(3,30)
DO 410 I=1, NF
```

**CALCULATE AREA OF EACH FIELD.**

```plaintext
R2 = D(I,1)
AR = R2*R2*0.031415
```

**AR = AREA COVERED BY THE FIELD'S ATTRACTABILITY "AURA".**

```plaintext
WRITE(3,31) 1,(FTP(NW,FTP(I)),NW=1,6),LOC(1,I),LOC(2,I),R2,AR
```

**CHECK IF GRAPHICAL DISPLAY OF SYSTEM IS WANTED.**

```plaintext
READ(1,10) MIG
```

**MIG = "IF GRAPH WANTED" INDICATOR. (MIG=1 => DISPLAY GRAPH)**

```plaintext
IF (MIG.EQ.0) GOTO 5000
```

**XMIN WILL BE THE SMALLEST POSSIBLE VALUE FOR X.**

```plaintext
XMIN = LOC(1,1) - D(1,1)
```

**XMIN WILL BE THE LARGEST POSSIBLE VALUE FOR X.**

```plaintext
XMAX = LOC(1,1) + D(1,1)
```

**LOOP 430 DETERMINES EXTREM X VALUES.**

```plaintext
DO 430 I=2, NF
R2 = LOC(1,I) - D(I,1)
```

**R2 = TEMP. STORAGE FOR POINT FURTHEST TO LEFT (FOR EACHFIELD).**

```plaintext
IF (XMIN.GT.R2) XMIN=R2
R2 = R2 + 2*D(I,1)
```

**CONTINUE**

```plaintext
CONTINUE
```

**LENGTH = XMAX - XMIN**

```plaintext
LENGTH = SIZE OF THE DOMAIN OF THE GRAPH.
```

**NEXT LINES DETERMINE THE CONVERSION FACTOR FOR GRAPH.**

```plaintext
INC = 2
INC = NUMBER OF SPACES PLUS ONE EQUIVALENT TO 100 METERS.
MPL = 6400
MPL = MAXIMUM PERMISSIBLE LENGTH IN METERS FOR A GIVEN SCALE.
```

**4300 IF (LENGTH.GT.MPL) GOTO 4301**

```plaintext
INC = INC + 1
MPL = 12800/INC
GOTO 4300
```

**4301 INC = INC - 1**

```plaintext
CONV = 100.0/INC
```

**CONV = CONVERSION FACTOR.**

```plaintext
```

**YMAX = LOC(1,1)**

**YMAX = LARGEST POSSIBLE Y VALUE TO BE PLOTTED.**

```plaintext
YMAX = YMAX
```

**YMIN = SMALLEST POSSIBLE Y VALUE TO BE PLOTTED.**
Table 8.5 (Continued)

C LOOP 440 SCALES DATA DESCRIBING FIELDS, AND FINDS Y EXTREMA.
DO 440 I=1,NF
R2 = LOC(2,I) + D(I,1)
C R2 = TEMP. STORAGE FOR HIGHEST POINT, LARGEST Y VALUE OF GRAPH.
IF (R2.GT.YMAX) YMAX=R2
R2 = R2 - 2*D(I,1)
IF (R2.LT.YMIN) YMIN=R2
C SCALE FIELD DATA INTO INTEGER UNITS SPANNING A 128 UNIT SPACE.
POP(1,I) = (LOC(1,I)-XMIN)/CONV + 0.5
C POP(1,I) = TRANSFORMED X-COORDINATE OF FIELD I'S CENTER.
POP(2,I) = LOC(3,I)*0.8/CONV + 0.5
C POP(2,I) = SCALED Y-COORDINATE OF FIELD I'S CENTER.
POP(3,I) = D(I,1)/CONV + 0.5
C POP(3,I) = SCALED RADIUS OF FIELD I.
440 CONTINUE
C
WRITE(3,33)
C PRINTS TITLE OF GRAPHIC DISPLAY.
C
LINE = YMAX*0.8/CONV + 0.5
C LINE = LARGEST INTEGER VALUE OF THE ORDI NATE.
MINY = YMIN*0.8/CONV + 0.5
C MINY = FIRST COLUMN TO CUT THROUGH FIELD I.
C LOOP 450 OUTPUTS EACH LINE OF DISPLAY FROM THE TOP.
4500 IF (LINE.LT.MINY) GOTO 450
C
C LOOP 451 FINDS ALL FIELDS LYING ACROSS Y=LINE.
DO 451 I=1,NF
IND = POP(3,I)*0.8
C IND = SCALED VERTICAL RADIUS. (CHARACTERS ARE NOT SQUARE.)
C IF FIELD I DOES NOT CROSS LINE GO TO NEXT FIELD.
IF (LINE.GT.POP(2,I)+IND) GOTO 451
IF (LINE.LT.POP(2,I)-IND) GOTO 451
C IF FIELD I DOES CROSS LINE INITIALIZE GRAPH ARRAY.
K = TYP(I) + 10
K = INDICATOR USED TO FIND CHARACTERS NEEDED IN GRAPH.
IC = POP(1,I)
C IC = X COORDINATE OF THE CENTER OF FIELD.
INST = POP(2,I) - LINE
C INST = THE DISTANCE TO LINE FROM CENTER OF FIELD.
C STORE IN ARRAY GRAPH THE CHARACTERS TO BE PRINTED ON GIVEN LINE.
IF (INST) 4512,4511,4512
C IF INST IS 0, THEN:
4511 IF (I.GT.10.AND.IC.LT.127) GRAPH(IC) = CHRCTR(I)
IF (I.GT.10.AND.IC.LT.127) GRAPH(IC) = CHRCTR(22)
NE = 2
C NE = USED TO MAKE FIELD I.D. NUMBER MORE READABLE.
IND = IND/0.8 + 0.5
GOTO 4513
C IF INST IS NOT 0, THEN:
4512 IF (GRAPH(IC).NE.BLANK) GRAPH(IC) = CHRCTR(21)
IF (GRAPH(IC).EQ.BLANK) GRAPH(IC) = CHRCTR(K)
R2 = IND*IND-INST*INST
C R2 = INTERMEDIATE TO EVALUATE NEXT STEP.
IND = COT(R2)/0.8 + 0.5
C IND = 1/2*SIZE OF INTERSECTION BETWEEN FIELD AND LINE, Y=LINE.
C ONLY IF IND IS NOT ZERO DO WE CHANGE CHARACTERS IN GRAPH.
IF (IND.EQ.0) GOTO 451
NE = 1
IF (((INST*IND).EQ.1)) GRAPH(IC)=BLANK
IF (((INST*IND).EQ.1)) NE = 2

Table 8.5 (Continued)

<table>
<thead>
<tr>
<th>Line</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>4513</td>
<td><code>IF (IND.EQ.0) GOTO 451</code></td>
</tr>
<tr>
<td>4514</td>
<td><code>DO 452  L=NE, IND</code></td>
</tr>
<tr>
<td>4515</td>
<td><code>C NOTE: DUE TO SYMMETRY ABOUT CENTER WE CAN GO IN BOTH DIRECTION.</code></td>
</tr>
<tr>
<td>4516</td>
<td><code>IR = IC + L</code></td>
</tr>
<tr>
<td>4517</td>
<td><code>IL = IC - L</code></td>
</tr>
<tr>
<td>4518</td>
<td><code>IN A IL ARE USED FOR GREATER COMPUTING EFFICIENCY.</code></td>
</tr>
<tr>
<td>4519</td>
<td><code>IF (IR.GT.127) GOTO 4514</code></td>
</tr>
<tr>
<td>4520</td>
<td><code>IF (IR.EQ.BLANK) GRPH(IR) = CHCTR(10)</code></td>
</tr>
<tr>
<td>4521</td>
<td><code>IF (GRPH(IR).EQ.BLANK) GRPH(IR) = CHCTR(K)</code></td>
</tr>
<tr>
<td>4522</td>
<td><code>GOTO 453</code></td>
</tr>
<tr>
<td>4523</td>
<td><code>IF (IL.LE.0) GOTO 453</code></td>
</tr>
<tr>
<td>4524</td>
<td><code>IF (GRPH(IL).NE.BLANK) GRPH(IL) = CHCTR(10)</code></td>
</tr>
<tr>
<td>4525</td>
<td><code>IF (GRPH(IL).EQ.BLANK) GRPH(IL) = CHCTR(K)</code></td>
</tr>
<tr>
<td>4526</td>
<td><code>452 CONTINUE</code></td>
</tr>
<tr>
<td>4527</td>
<td><code>451 CONTINUE</code></td>
</tr>
<tr>
<td>4528</td>
<td><code>C LABEL EVERY FIFTH LINE</code></td>
</tr>
<tr>
<td>4529</td>
<td><code>IF (((LINE/5)*5 - LINE) .EQ. 4512, 4511, 4513)</code></td>
</tr>
<tr>
<td>4530</td>
<td><code>REAL = LINE*CONV/300.0</code></td>
</tr>
<tr>
<td>4531</td>
<td><code>WRITE(1,34) REAL, (GRPH(I), I=1,126)</code></td>
</tr>
<tr>
<td>4532</td>
<td><code>GOTO 461</code></td>
</tr>
<tr>
<td>4533</td>
<td><code>DO 452  L=1, 126</code></td>
</tr>
<tr>
<td>4534</td>
<td><code>C LOOP 471 RESETS THE GRPH ARRAY TO PRINT NEXT LINE.</code></td>
</tr>
<tr>
<td>4535</td>
<td><code>LINE = LINE + 1</code></td>
</tr>
<tr>
<td>4536</td>
<td><code>GOTO 4500</code></td>
</tr>
<tr>
<td>4537</td>
<td><code>450 CONTINUE</code></td>
</tr>
<tr>
<td>4538</td>
<td><code>C C C LOOP 480 DETERMINES THE LABELS FOR THE X-AXIS.</code></td>
</tr>
<tr>
<td>4539</td>
<td><code>DO 480  L=1, 12</code></td>
</tr>
<tr>
<td>4540</td>
<td><code>LB(L) = (XMIN + (10*L-5)*CONV)/1000</code></td>
</tr>
<tr>
<td>4541</td>
<td><code>WRITE(3,37) LBL</code></td>
</tr>
<tr>
<td>4542</td>
<td><code>OUTPUT LBL</code></td>
</tr>
<tr>
<td>4543</td>
<td><code>WRITE(1,38) INC</code></td>
</tr>
<tr>
<td>4544</td>
<td><code>DO 490 IT=1, NT</code></td>
</tr>
<tr>
<td>4545</td>
<td><code>WRITE(3,39) CHCTR(10+IT), (FTP(NW,IT), NW=1, 9)</code></td>
</tr>
<tr>
<td>4546</td>
<td><code>C C C</code></td>
</tr>
</tbody>
</table>
Table 8.5 (Continued)

```
+----------------------------------------------------+
| ALGORITHM SIMULATING INTERFIELD MIGRATION |
+----------------------------------------------------+

PRINT HEADING FOR OUTPUT OF SIMULATED RESULTS.
5000 WRITE(3,25)

INPUT INFORMATION ON BEETLE POPULATION.
READ(1,10) KD,MAKAG,LD
KD = THE EARLIEST DATE FOR OVPOSITION OF THE F1 GEN.
MAKAG = MAXIMUM AGE OF AN ADULT BEETLE. (MAKAG<31)
LD = LAST DAY AT WHICH BEETLE WILL OVPOSIT.
READ(1,15) EGDPV,PUPD,ERP,FRT,SR,DR,AR
EGDPV = AVERAGE NUMBER OF DAYS IT TAKES FOR EGGS TO DEVELOP.
PUPD = AVERAGE NUMBER OF DAYS IT TAKES FOR PUP; TO DEVELOP.
FRT = AVERAGE NUMBER OF EGGS LAID BY FEMALE OF PREVIOUS GENERATION.
SR = AVERAGE NUMBER OF EGGS LAID IN FEMALE OF F1 GENERATION.
SMD = SHORTEST MAXIMUM DISTANCE A BEETLE WILL FLY BEFORE DEATH.
DR = DEATH RATE FOR FLYING BEETLES (MEASURED IN BEETLES PER DAY).
AR = CHANCE OF MIGRATION PREVENTING WEATHER. (AIRY OR RAINY)

INITIALIZE THE PROBABILITY OF IMMIGRATION MATRIX.
DO 510 I=1, NF
CDF = 0
CDF = C.D.F. OF REACHING ANOTHER FIELD DURING MIGRATION.
DO 511 J=1, NF
PDFMD = PROBABILITY THAT BEETLE WILL REACH A GIVEN DISTANCE.
IF (D(I,J).GT.SW) PDFMD=EXP(DR*(SMD-CDF*A(I,J)/1000))
CDF = CDF + ALPHA(I,J)*PDFMD
511 CONTINUE
ALPHA(I,I) = 1 - CDF
ALPHA(I,I) = PROBABILITY OF LEAVING THE SYSTEM.
510 CONTINUE

INPUT THE REST OF THE INFORMATION NEEDED FOR THE SIMULATION.
READ(1,14) (POP(I),MAXP(I),NFD(I),I=1,NF)
POP(I) = NUMBER OF BEETLES OF LIFE STAGE K IN FIELD I.
MAXP(I) = ARRAY USED TO STORE GROWTH HISTORY OF EACH FIELD.
NFD(I) = MAXIMUM POPULATION SUSTAINABLE IN FIELD I. (MAX=32767)
HRD(I) = (RBD(K,IT),K=1,4), (P4IG(K,IT),K=1,3), IT=1,NT)
ALL OF THE FOLLOWING PARAMETERS DEPEND ON FIELD TYPE, IT.
RBD(K,IT) = NUMBER OF DAYS BEETLE IN INSTAR K.
P4IG(K,IT) = PROBABILITIES OF MIGRATION FROM FIELD OF TYPE IT.
K=1 => BEETLE IN MIGRATORY STAGE.
K=2 => BEETLE MIGRATED ON PREVIOUS DAY.
K=3 => BEETLE IN NON-MIGRATORY STAGE.
K=4 => IMMATURE BEETLE SURVIVING ECOLOGICAL TRANSITION INTO KTH INSTAR.
K=5 => IMMATURE BEETLE SURVIVING TO PUPA.
K=6 => PUPA SURVIVING TO IMAGINARY.
K=7 => DAILY ADULT SURVIVAL RATE.
```

122
Table 8.5 (Continued)

```plaintext
READ(1,15) ((BNM(K,IT),K=1,4),(POVI(K,IT),K=1,3),IT=1,NT)
C ALL OF THE FOLLOWING PARAMETERS DEPEND ON FIELD TYPE, IT.
C
C BNM(1,IT) = MINIMUM AGE FOR MIGRATION.  (MIN=2)
C BNM(2,IT) = MAXIMUM AGE OF PREADULT (1-AGO).  (MAX=20)
C BNM(3,IT) = MEAN AGE FOR PREADULT.  (BNM(1,) < BNM(3,)< BNM(2,))
C BNM(4,IT) = MAX. PREMIGRATORY AGE.  (BNM(2,)< BNM(4,)< 21)
C POVI(K,IT) = PROB. FOR BEETLE IN FIELD OF TYPE IT TO OVIPosit.
C
K=1 => PRE-MIGRATION.  (USUALLY POVI(1,IT)< POVI(2,IT))
K=2 => DURING-MIGRATION.  (USUALLY POVI(2,IT)< POVI(3,IT))
K=3 => POST-MIGRATION.
C
READ(1,13) NSERF
C NSERF = SEED INTEGER WHICH STARTS GENERATOR.
C
READ(1,10) JDATE, NRNPt, NFP
C
C JDATE = JULIAN DATE OF FIRST DAY OF THIS SIMULATION.
C NRNPt = NUMBER OF THE FIRST DAY OF OUTPUT.
C NFP = NUMBER OF FIELDS WHOSE POPULATION TO BE GRAPHED.  (MAX=10)
C
C INITIALIZE FIELD POPULATION ARRAY.
DO 520 1=1, NF
DO 521 K=1, 4
  POP(K,1) = 0
C POP(K,1) = NUMBER OF BEETLES OF LIFE STAGE K, IN FIELD 1.
520 CONTINUE
C
C INITIALIZE "PROBABILITY OF MATURING" ARRAY AND MIGRATION PARAMETERS.
C LOOP 530 Initializes parameters and array for each field type, IT.
DO 530 IT=1, NT
  IL = BNM(1,IT)- 1
  IR = BNM(4,IT)- 1
C IL & IR ARE USED FOR COMPUTING EFFICIENCY.
C
C RAL = IR - IL
C RAL = DURATION OF MATURATION PERIOD.
C IF (RAL.GT.0)  P=(BNM(3,IT)-BNM(1,IT))/RAL
C P = PROBABILITY PARAMETER FOR A BINOMIAL DISTRIBUTION.
C
C IF (RAL.GT.0) RAT=P/(1-P)
C RAT = USED IN THE ITERATIVE CALCULATIONS.

C INITIALIZE "PROBABILITY OF MATURING" ARRAY.
C MAT(N,IT) = PROBABILITY OF PRE-ADULT MATURING TO NEXT STAGE,
C AT DAY N, IF IN FIELD OF TYPE IT.
DO 531 N=1, IL
  MAT(N,IT) = 0
531 CONTINUE
C
DO 532 N=NR, 20
  MAT(N,IT) = 1
C
IF (IL+1.GE.IR)  GOTO 536
C
MAT(IL,IT) = (1-P)**RAL * SUR(7,IT)
CDF = 1
C CDF = 1 - (CUM. DIST. FUNC. OF THE BINOMIAL DISTRIBUTION).
CDF1 = 1 - MAT(IL,IT)
LL = 0
KD = RAL
C LL & KD = TEMPORARY STORAGE SPACES USED IN CALCULATIONS.
C
IL = [IL + 1]
IR = IR - 1
C
C LOOP 533 Calculates entries for maturation array.
DO 533 N=IL, IR
  LL = LL + 1
  MAT(N,IT) = MAT(N-1,IT) + RAT * KD/LL * CDF/CDF1
C CDF = CDF1
C CDF1 = CDF1*(1-MAT(N,IT))
KD = KD - 1
533 CONTINUE
C
C 530 CONTINUE
```

---

**Note:** The above text is a snippet of a computer program, which includes mathematical and logical operations related to population dynamics, specifically focusing on beetle life stages and migration parameters. The program uses arrays and loops to simulate the life cycle and migration of beetles across different fields. The code is designed to initialize parameters, calculate probabilities, and simulate the progression of beetle populations through various stages.
Table 8.5 (Continued)

C PRINT TABLES OF INPUT PARAMETERS.
WRITE(3,40)
DO 540 IT=1, NT
540 WRITE(3,42) (FTP(NW,IT),NW=1,6),
      + (SUR(L,IT),L=1,7), (RBD(L,IT),L=1,4), (POVI(L,IT),L=1,3)
C WRITE(3,44)
WRITE(3,45)
WRITE(3,45)
WRITE(3,46)
WRITE(3,47)
WRITE(3,52)
WRITE(3,53)
DO 550 IT=1, NT
550 WRITE(3,54) (FTP(NW,IT),NW=1,6),
      + (BNM(L,IT),L=1,4), (PMIG(L,IT),L=1,3)
WRITE(3,55)
C
C MNBI = 1
C MMB = POINTER USED IN STORING VALUES INTO ARRAY MBB.
C
C STORE NECESSARY INFORMATION ON EACH BEETLE.
DO 560 I=1, NF
INST = POP7(7,1)
IF (INST.EQ.0) GOTO 560
MNB = MNB1 + INST - 1
C MNB = NUMBER OF LIVING BEETLES AND EGG MASSES AT START OF DAY.
C CHECK FOR AVAILABILITY OF STORAGE SPACE IN BEETLE INFO ARRAY.
MNB = MIN(MNB,101000)
DO 561 I=MNB1, MNB
561 MBB(I) = 10000 + I
C MBB = ARRAY THAT STORES INFORMATION ON EACH BEETLE OR EGGMASS.
C FOR MORE INFORMATION CONSULT SEPARATE PROGRAM DOCUMENTATION.
MNB1 = MNB + 1
560 CONTINUE
C
C TRANSFORM MAXAG INTO MORE EFFICIENT FORM.
MAXAG = MAXAG + 139
C MPL = MAXIMUM POSSIBLE AGE MIGRATION ID NUMBER.
C
C TRANSFORM FERT & FER2 INTO MORE EFFICIENT FORM.
FERT = (FERT1/F2)
FER2 = (FER2/F2)
C
C TRANSFORM KDATE INTO MORE EFFICIENT FORM.
KDATE = KDATE + EGGDV
C
C TRANSFORM PUPDV INTO USABLE FORM.
PUPDV = PUPDV + 80
C
C TRANSFORM EGGDV INTO MORE EFFICIENT FORM.
EGGDV = EGGDV - 1
C
C TRANSFORM POVI(K,IT), BNM(4,IT) & RBD(K,IT) INTO USABLE FORMS.
DO 570 IT=1, NT
DO 571 K=1, 3
RBD(K+1,IT) = RBD(K+1,IT) + 20*K
POVI(K,IT) = SUR7(7,IT) * POVI(K,IT)
571 CONTINUE
BNM4(4,IT) = BNM4(4,IT) + 119
570 CONTINUE
C
C PRINT HEADING FOR THE SIMULATION OUTPUT.
WRITE(3,60)
C
Table 8.5 (Continued)

| C | INITIALIZE MAX ARRAY. (USED IN PLOTTING ROUTINE) |
| C | IF NO CHROMSOF FIELD'S POPULATION SIZES ARE WANTED SKIP NEXT STEP. |
| C | IF (NFP.ES.0) GOTO 5000 |
| C | DO 580 I=1, NFP |
| C | 580 MAX(I) = 0 |
| C | MAX(I) = MAXIMUM VALUE POPULATION PLOT OF FIELD I. |
| C | C |
| C | C |
| C | LOOP 600 SIMULATES BEETLE MIGRATION BETWEEN FIELDS FOR EACH DAY N. |
| C | 5000 DO 600 M=1, ND |
| C | IF (MNB1.NE.1) GOTO 5010 |
| C | INC = N + JDATE |
| C | INC = ACTUAL JULIAN DATE OF SIMULATION RUN. |
| C | DEV = WF(INC) |
| C | DEV = SEASONAL FACTOR CAUSING DECREASE IN DEVELOPMENT RATE. |
| C | MIG = 0 |
| C | MIG = INDICATOR WHETHER MIGRATION IS POSSIBLE. (MIG=1 =+ YES) |
| C | MIG = MIG \\ 1 |
| C | MIG = INDICATOR WHETHER MIGRATION IS POSSIBLE. (MIG=1 =+ YES) |
| C | IF (RANU(NSEED).GT.AR) MIG=1 |
| C | FERT = PRESENT FERTILITY RATE. I.E. # FEMALE EGGS PER EGGMASS |
| C | C |
| C | C |
| C | LOOP 601 DETERMINES THE LIFE STAGE OF EACH BEETLE FOR NEW DAY. |
| C | DO 601 M=1, MNB |
| C | MB = MBB(M) |
| C | MB = TEMPORARY STORAGE OF BEETLE I.D. NUMBER. |
| C | IF MB<10000, THEN BEETLE IS IN THE LARVAL OR PUPAL STAGE. |
| C | IF (MB.LT.10000) GOTO 5012 |
| C | IF 10000<MB<30000, THEN BEETLE IS IN THE ADULT STAGE. |
| C | IF (MB.LT.30000) GOTO 5023 |
| C | C ANOTHER MB IS STORING INFORMATION ON AN EGG MASS. |
| C | K = 1 |
| C | K = INDICATOR FOR THE LIFE STAGE OF BEETLE M. |
| C | INST = (MB-10000)/100 |
| C | INST = STORES AGE OF EGG MASS. |
| C | IF EGGS REACHED MATURITY THEN NEW STORAGE SPACE IS NEEDED. |
| C | IF (INST.LE.(EGGS+DEV)) GOTO 6034 |
| C | MBB(M) = MB + 100 |
| C | GOTO 601 |
| C | C THESE NEXT FEW LINES STORE INFORMATION ON NEWLY HATCHED BEETLES. |
| C | 6034 I = MB - 100*100 |
| C | I = NUMBER OF FIELD IN WHICH BEETLE IS LOCATED. |
| C | NE = FERT + RANU(NSEED) |
| C | NE = NUMBER OF EGGS. |
| C | INST = MB1 |
| C | INST = NUMBER OF NEWLY HATCHED BEETLES. |
| C | LOOP 614 DETERMINES THE NUMBER OF Viable EGGS. |
| C | DO 614 L=1, NE |
| C | C CHECK FOR AVAILABILITY OF STORAGE SPACE IN BEETLE INFO ARRAY. |
| C | IF (MBB1.GT.101000) WRITE(1,93) INC |
| C | IF (RANU(MNB1).GT.SUR(I,IT).OR.MNB1.GT.101000) GOTO 614 |
| C | STORE INFORMATION ON EACH NEWLY HATCHED BEETLE. |
| C | MBB(MNB1) = I |
| C | MNB1 = MNB1 + 1 |
| C | 614 CONTINUE |
Table 8.5 (Continued)

C DETERMINE TOTAL NUMBER OF FIRST INSTARS.
   POP(2,1) = POP(2,1) + MNBl - INST
   GOTO 6021
C
C GIVEN BEETLE IS AN ADULT, IT CAN (DEPENDING ON ITS STAGE OF DEVELOPMENT):
C 1) MIGRATE  2) OVIPOSIT  3) DIE        4) DO NONE OF THESE.
C
6023  RN = RANU(MNSEED)
C   RN = RANDOM NUMBER.
C   INST = MB/100
C   I = MB - INST*100
C   IT = TYP(I)
C   IT = FIELD TYPE IN WHICH BEETLE IS LOCATED.
C   IF (IT.EQ.0) IT =4
C   FIELD TYPES 0 AND 4 ARE ASSUMED TO BE THE SAME.
C   K = 7
C   K = LIFE STAGE OF BEETLE. (K=7 => BEETLE IS AN ADULT.)
C   BEETLE MIGHT GET TOO OLD OR DIE. (MAX. AGE FOR ADULT IS 30 DAYS.)
C   IF (INST.EQ.MAXAG.OR.INS.EQ.EMPL.OR.RN.GE.SUM(7,IT)) GOTO 4021
C
C   ADD ONE DAY TO BEETLE'S AGE.
C   MBB(M) = MBB + 100
C   NE = MB/2000 - 4
C   NE = INDICATOR FOR THE MIGRATION CLASS ADULT BEETLE IS IN.
C   IF (NE.GT.2) NE = NE/7 + 3
C   DECISION OF BEETLE DEPENDS ON THE LIFE STAGE, NE, OF ADULT.
C   GOTO (60230,60232,60236,60234), NE
C
C   FOR PREFLIGHT ADULTS, DEVELOPMENT AS WITH LARVAE.
C   IF BEETLE OLD ENOUGH IT MIGHT MATURE TO NEXT AGE CLASS.
60230 IF (RN.LT.MAT(INST-99,IT)) MBB(M) = MB+2100
   GOTO 401
C
C   FOR PREMIGRATION BEETLES, OVIPOSITION POSSIBLE BUT NOT LIKELY.
C   A GIVEN BEETLE MIGHT OVIPOSIT.
60232 IF (POVI(1,IT).LT.RN.OR.INC.GT.LD) GOTO 6032
C   CHECK FOR AVAILABILITY OF STORAGE SPACE IN BEETLE INFO ARRAY.
C   IF (MNBl.GT.101000) WRITE(3,92) INC
C   IF (MNBl.GT.101000) GOTO 6032
C   MB(MNBl) = 10000 + I
C   POP(I,1) = POP(I,1) + 1
C   MNBl = MNBl + 1
C   A GIVEN BEETLE MIGHT MIGRATE.
6032 IF (MIG.EQ.0.OR.PHIG(I,IT).LE.RANU(MNSEED)) GOTO 6033
C   (CHANGE BEETLE'S CLASSIFICATION NUMBER.)
C   MB = (INST+100)*100 + I
   GOTO 6043
C
C   A GIVEN BEETLE MIGHT MATURE INTO NEXT AGE CLASS.
6033 IF (INST.GE.BMM(4,IT)) MBB(M) = MB+2100+MB
   GOTO 401
Table 8.5 (Continued)

C FOR RECENTLY MIGRATED BEETLES, OVIPosition POSSIBLE BUT UNLIKELY.
C A GIVEN BEETLE MIGHT OVIPosIT.
60234 IF (POVI(2,IT).LT.RN.OR.INC.GT.LD) GOTO 60334
C CHECK FOR AVAILABILITY OF STORAGE SPACE IN BEETLE INFO ARRAY.
IF (MMB1.GT.10100) WRITE(3,92) INC
IF (MMB3.GT.101000) GOTO 60334
MBB(MMB1) = 30000 + I
POP(1, I) = POP(1, I) + 1
NMB1 = NMB1 + I
C C A GIVEN BEETLE MIGHT MIGRATE.
60334 IF (MIG.EQ.0.OR.PMIG(2,IT).GT.RANU(NSEED)) GOTO 6043
C A GIVEN BEETLE MIGHT DO NOTHING AT ALL.
(CHANGE BEETLE'S CLASSIFICATION NUMBER.)
MBB(M) = (INST-79)*100 + I
GOTO 601
C FOR COLONIZED BEETLES, MIGRATION POSSIBLE BUT NOT LIKELY.
C A GIVEN BEETLE MIGHT OVIPosit.
60236 IF (POVI(3,IT).LT.RN.OR.INC.GT.LD) GOTO 60336
C CHECK FOR AVAILABILITY OF STORAGE SPACE IN BEETLE INFO ARRAY.
IF (MMB3.GT.10100) WRITE(3,92) INC
IF (MMB3.GT.101000) GOTO 60336
MBB(MMB1) = 30000 + I
POP(1, I) = POP(1, I) + 1
NMB1 = NMB1 + I
C A GIVEN BEETLE MIGHT MIGRATE.
60336 IF (MIG.EQ.0.OR.PMIG(3,IT).GT.RANU(NSEED)) GOTO 601
C (CHANGE BEETLE'S CLASSIFICATION NUMBER.)
MB = (INST+80)*100 + I
GOTO 6043
C FOR MIGRATING BEETLES DETERMINE DESTINATION.
6043 RN = RANU(NSEED)
J = 1
6052 IF (I.NE.J.AND.J.NE.ALPHA(I,J)) GOTO 6051
J = J + 1
C IF NO FIELD IN BEETLE'S FLIGHT PATH, THEN BEETLE LOST TO SYSTEM.
IF (J.GT.NF) GOTO 6021
GOTO 6052
C IF FIELD IS COLONIZED BY BEETLE, MAKE NECESSARY CHANGES.
5051 MBB(M) = MB - I + J + 100
POP(7, I) = POP(7, I) - 1
POP(7, J) = POP(7, J) + 1
GOTO 601
C FOR PREADULTS DETERMINE DEVELOPMENT AND CONSIDER MORTALITY.
6022 IF (MR.EQ.0) GOTO 601
I = MB - MB/100*100
C I = NUMBER OF FIELD IN WHICH BEETLE IS LOCATED.
IT = TYP(I)
C IT = FIELD TYPE IN WHICH BEETLE IS LOCATED.
K = MB/1000 + 1
C K = INSTAR NUMBER OF BEETLE.
KD = MB/100
C KD = TIME IN DAYS BEETLE HAS BEEN IN INSTAR K.
C
Table 8.5 (Continued)

C IF BEETLE STILL IN PREADULT STAGE MORTALITY ONLY DETERMINED AT C THE END OF EACH LIFE STAGE.
C INCREASE BEETLES AGE BY ONE DAY.
   MBB(M) = MB + 100
C CHECK IF BEETLE CLOSED. (I.E. MATUR ED INTO NEXT INSTAR).
   IF (KD.GT.80) R2=MBD(K,IT)+DEV
   IF (KD.GE.80) R2=PUPDV+DEV
C R2 = USED TO STORE SIZE OF INCREMENT IN BEETLE'S DEVELOPMENT.
   IF (KD.LT.(R2-1)) GOTO 401
   IF (KD.GT.R2) GOTO 50221
   IF (RANU(NSEED).LT.(R2-INT(R2)) GOTO 501
C DETERMINE NEW BETTLE ID NUMBER.
   50221 MBB(M) = K*2005 + I
   K = K + 1
C DETERMINE IF BEETLE SURVIVES.
   IF (RANU(NSEED).GT.SUR(K,IT)) GOTO 6021
   POP(K,I) = POP(K,I) - 1
C IF BEETLE DIES, SET ARRAY ELEMENT TO ZERO.
   6021 MBB(M) = 0
   POP(K,I) = POP(K,I) - 1
C CONTINUE
C COMPACT BETTLE ARRAY, MB5, IF POSSIBLE.
   MNB = MNB1 - 1
   DO 611 M=1, MNB
   IF (M.GE.MNB1 OR MBB(M).GT.0) GOTO 611
   MBB(M) = MBB(MNB1)
   611 CONTINUE
   MNB = MNB1 - 1
C STORE RESULTS OF LAST 125 DAYS OF SIMULATION FOR GRAPHING ROUTINE.
   6010 L = N
   IF (ND.GT.126) L=N+125-ND
C L = USED IN STORING RESULTS INTO OUTPUT ARRAY "PLT".
C LOOP 621 STORES RESULTS IN OUTPUT ARRAY.
   621 CONTINUE
Table 8.5 (Continued)

C DETERMINE WHETHER FIELDS ARE DEVELOPING INTO ANOTHER STAGE.
DO 631 I=1, NF
   IF ((POP(4,I)+POP(7,I)) LE. MXP(I)) GOTO 631
   WRITE(3,90) I, MXP(I), NF
C CHANGE MXP(I) TO AVOID DUPLICATION OF MESSAGE.
   MXP(I) = 32767
   TYP(I) = IT
   GOTO 631
IF (N.NE.(NF0(I)*2/1000000).OR.IT.GE.NT) GOTO 531
   NF0(I) = 100*(NF0(I) - N/2*1000000)
   IT = IT + 1
   TYP(I) = IT
   CONTINUE
C DETERMINE WHETHER OUTPUT SHOULD BE PRINTED.(PRINT IF N=NPRT.)
   IF (N.NE.NPRT) GOTO 600
C IF OUTPUT WANTED PRINT INFORMATION ON EACH FIELD.
   WRITE(3,61) N
C INITIALISES ARRAY STORING TOTAL POPULATION SIZES.
DO 641 K=1, A
   TPOP(K) = TOTAL NUMBER OF BEETLES IN LIFE STAGE K AT DAY N.
C LOOP 651 TOTALS POPS OF SYSTEM, AND OUTPUTS INFO ON EACH FIELD.
   DO 651 I=1, NF
      POP(8,I) = POP(2,I)+POP(3,I)+POP(4,I)+POP(5,I)+POP(6,I)+POP(7,I)
   C TPOP(8,I) = TOTAL NUMBER OF BEETLES AT DAY N IN FIELD I.
   DO 652 K=1, A
      TPOP(K) = TPOP(K) + POP(K,I)
   IF (POP(1,I)+POP(8,I) GT. 0) WRITE(3,64) I, (POP(NN,TYP(I)),NN=1,6),(POP(K,I),K=1,8)
   CONTINUE
   WRITE(3,64) TPOP
   IF (ND.GT.NPRT) READ(1,10) NPRT
C CONTINUE
C CHECK IF ANY FIELD'S POPULATION SHOULD BE GRAPHED.
   IF (NPF.LE.0) GOTO 9000
C
Table 8.5 (Continued)

<table>
<thead>
<tr>
<th>Algorithm for Graphing Simulation Results</th>
</tr>
</thead>
</table>

PRINT THE HEADING OF FINAL RESULTS.
WRITE(1,80) NFP

INITIALIZE VARIABLES NEEDED FOR THIS OUTPUT.
IF (NO.I.E.126) GOTO 7100
JDATE = JDATE + ND - 126
ND = 126
7100 DO 710 L=1, 13
710 NFD(L) = JDATE - 10 + 10*L
NFD IS USED TO STORE THE X-LABLES NEEDED IN THIS GRAPH.

LOOP 800 GRAPHS POPULATION SIZES W.R.T. TIME FOR FIRST FEW FIELDS.
DO 800 I=1, NFP

MPL = MAX(I)
MPL = LARGEST VALUE OF THE ORDIATE.
IF (MPL.EQ.0) GOTO 800
WRITE(1,82) I

LOOP 801 PRINTS EACH LINE OF GRAPH.
DO 971 L=1, 50
LINE = 51 - L
LINE = NUMBER OF NEXT LINE TO BEGRAPHED.

LOOP 802 LOOKS AT EACH DAY TO DETERMINE IF POP. TO BE GRAPHED.
DO 802 N=1, ND
GRPH(N) = BLANK
IF (LINE.LE.(PLT(2,N,I)*50/MPL)) GRPH(N)=CHRCTR(13)
IF (LINE.GT.(PLT(2,N,I)*50/MPL)) GOTO 802
IF (GRPH(N).NE.BLANK) GRPH(N)=CHRCTR(12)
IF (GRPH(N).EQ.BLANK) GRPH(N)=CHRCTR(13)

802 CONTINUE

PRINT NEXT LINE OF GRAPH.
Determine if line should be labeled.
IF (LINE.LE.(LINE/5)) GOTO 801
LINE = LINE*MPL/50

PRINT LINE WITH LABEL.
WRITE(3,84) LINE,GRPH
GOTO 801

PRINT LINE WITHOUT LABEL.
9011 WRITE(3,85) GRPH
801 CONTINUE

PRINT X-AXIS AND ITS LABELING.
WRITE(3,86) (NFD(L),L=1,13)

PRINT KEY
WRITE(3,87)
800 CONTINUE

C

Table 8.5 (Continued)

INPU_T/OUTPUT FORMAT STATEMENTS

INPUT FORMATS

10 FORMAT (315)
11 FORMAT (5A4)
12 FORMAT (12,F7.2,2(F8.1))
13 FORMAT (I11)
14 FORMAT (215,19)
15 FORMAT (7F10.4)

OUTPUT FORMATS

20 FORMAT (1//1,1//34X,62('*')/)
2 36X,)'**',58X,' (*)',/'
3 2(36X,' *,58X,')**'/
4 36X,'**',20X,'S P O T - D (V)',20X,'(*)'
5 36X,'**',38X,'(*)'/
6 36X,)'**',9X,'A MODEL SIMULATING INTERFIELD MIGRATION',
7 9X,'(*)'/
8 2(36X,)'**',58X,' (*)'/
9 36X,'**',58X,' (*)'/
23 FORMAT (140,132('**')///)
2 49X,36('**')/
3 49X,)'**',34X,')*/
4 49X,)'**',7X,'CONSTANT PARAMETERS',7X,'(*)'/
5 49X,)'**',34X,')*/
6 49X,36('**')///
7 3X,130(' ',/)///
25 FORMAT (140,132('**')///)
2 49X,36('**')/
3 49X,)'**',34X,')*/
4 49X,)'**',8X,'SIMULATED RESULTS',8X,'(*)'/
5 49X,)'**',34X,')*/
6 49X,36('**')///
7 2X,130(' ',/)///
29 FORMAT (1//1,132(' ',/)1X,132('**')
30 FORMAT ('/',1asuring',132(' ',/)1X,132('**'))
2 1H+,62X,'/'
3 56X,'(CONSTANT PARAMETERS)'///
4 24X,'+',84(' ',/')/'
5 52X,'/',4X,')//''
6 24X,)'FIELD',13X,'FIELD',13X,'COORDINATES OF CENTER',12X,
' (IN METERS)'///
7 24X,)'NUMBER',19X,'DESCRIPTION',12X,'(UNITS IN METERS) ',
8 73X,'(IN AREA) '///'
9 24X,)'/',84(' ',/')/'
31 FORMAT (24X,' ',15,3X,' ',84,3X,' (',',',9X,')',',12X,')/'
5 2X,F5.1,' ',2X,F7.1,3X,')//''
2 24X,)' ',8X,' ',28X,)' ',9X,')',',12X,')/'
32 FORMAT (24X,)'+',84(' ',/')/'
2 2X,130(' ',/)///
3 3 FORMAT (130,5X,'(GRAPHICAL DISPLAY OF SYSTEM)'///
2 1H+,51X,'/'
3 5X,'(CONTRAST '///
4 7X,'(KILOMETERS)'///
Table 8.5 (Continued)

<table>
<thead>
<tr>
<th>Format</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>34 FORMAT</td>
<td>(1X,P5.2,'+',126A1)</td>
</tr>
<tr>
<td>35 FORMAT</td>
<td>(1X,'+',126A1)</td>
</tr>
<tr>
<td>36 FORMAT</td>
<td>(1X,')',25('</td>
</tr><tr>
<td>')----+(</td>
<td></td>
</tr><tr>
<td>'),'-'/</td>
<td></td>
</tr>
<tr>
<td>37 FORMAT</td>
<td>7X,'12(2X,P5.2,3X)/</td>
</tr>
<tr>
<td>38 FORMAT</td>
<td>(1L0,5X,'KEY/UNIT=5X','/'</td>
</tr>
<tr>
<td>39 FORMAT</td>
<td>34X,'SCALE:100 METERS /12 SPACES'</td>
</tr>
<tr>
<td>40 FORMAT</td>
<td>34X,'NUMBER IN FIELD CENTER - FIELD NUMBER OF FIELD','</td>
</tr>
<tr>
<td></td>
<td>'WHOSE POPULATION WILL BE PLOTTED')</td>
</tr>
<tr>
<td>41 FORMAT</td>
<td>(47X,AL,1X,6('+-'),6A4)</td>
</tr>
<tr>
<td>42 FORMAT</td>
<td>(1H+62X,','/</td>
</tr>
<tr>
<td>43 FORMAT</td>
<td>35X,('INPUT VALUES OF DEMOGRAPHIC PARAMETERS USED IN ','</td>
</tr>
<tr>
<td></td>
<td>'IN THIS SIMULATION')</td>
</tr>
<tr>
<td>44 FORMAT</td>
<td>2X,'+',128('-'),'+'/</td>
</tr>
<tr>
<td>45 FORMAT</td>
<td>2X,'+',128X,'!'</td>
</tr>
<tr>
<td>46 FORMAT</td>
<td>2X,'+',41X,'PROBABILITY OF SURVIVAL',19X,</td>
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<td>'AVERAGE LENGTH OF',6X,'PROB. OF OVIPOSITION' /</td>
</tr>
<tr>
<td>47 FORMAT</td>
<td>2X,'DESCRIPTION OF FIELD TYPE',20X,'THROUGH STAGE:',25X,</td>
</tr>
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<td>'TIME IN INSTAR:',9X,'W.R.T. MIGRATION' /</td>
</tr>
<tr>
<td>48 FORMAT</td>
<td>1X,'31X',E0G IN.1 IN.2 IN.3 IN.4 PUPA</td>
</tr>
<tr>
<td>49 FORMAT</td>
<td>2X,'+',28('-'),'+1',26('-'),'+1',22('-'),'!+1'</td>
</tr>
<tr>
<td>50 FORMAT</td>
<td>2X,'+',28X,'!',1X,4X,1!,2X,1!,2X,1!'/</td>
</tr>
<tr>
<td>51 FORMAT</td>
<td>2X,+',28X,11',1X,4X,11',2X,11',2X,11!'/</td>
</tr>
<tr>
<td>52 FORMAT</td>
<td>34X,'+',66('-'),'!+1'</td>
</tr>
<tr>
<td>53 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>54 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>55 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>56 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>57 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>58 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>59 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>60 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>61 FORMAT</td>
<td>34X,'+',66X,'!'</td>
</tr>
<tr>
<td>62 FORMAT</td>
<td>34X,'+',66X,'!'</td>
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<tr>
<td>63 FORMAT</td>
<td>34X,'+',66X,'!'</td>
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Table 8.6 (Continued)

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<td>64 FORMAT</td>
<td>(1X,'+',6A4,3X,11',2(5S,0,3X),11',5X,1X,'!',5S,0,3X, +</td>
</tr>
<tr>
<td></td>
<td>'4X,P5.3,4X,2X,',4X,5,P5.1,4X)'</td>
</tr>
<tr>
<td>65 FORMAT</td>
<td>(1X,'+',29('-'),'+1',37('-'),'+1',41('-'),'+1'</td>
</tr>
<tr>
<td>66 FORMAT</td>
<td>1X,'+',20X,'!',12(2X,1X,1X,2X,1X,9X,11,2(13X,11,1X,11,11)</td>
</tr>
<tr>
<td>67 FORMAT</td>
<td>(13X,'+',11',5A4,3X,11',2(5S,0,3X),11',5X,1X,'!',5S,0,3X, +</td>
</tr>
<tr>
<td></td>
<td>'11',4X,P5.3,4X,2X,',4X,5,P5.1,4X)'</td>
</tr>
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</table>
Table 8.5 (Continued)

<table>
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<tr>
<th>Column 1</th>
<th>Column 2</th>
<th>Column 3</th>
<th>Column 4</th>
<th>Column 5</th>
<th>Column 6</th>
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<tr>
<td>133</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>EGG MATES IN TR</td>
<td>PUPAE ADULT</td>
<td>TOTALS</td>
<td></td>
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</tr>
</tbody>
</table>

For any given day, the population dynamics of first, second, and third instars are recorded. The population size at the start of the day is calculated, and the maximum sustainable population size is determined. The population in the field is compared to the maximum sustainable population size, and a warning is issued if the population exceeds this limit.

The initial total population size is truncated to a maximum of 10,000 individuals.

The maximum permissible size is also determined, and the total population size on any given day is checked against this limit.

END OF MAIN PROGRAM

9000 WRITE(3,29)
RETURN
END
Table 8.5 (Continued)

USER DEFINED FUNCTIONS

RANU - A RANDOM NUMBER GENERATOR, WHICH GENERATES VALUES FROM A UNIFORM DISTRIBUTION (DEFINED FROM ZERO TO ONE).

REAL FUNCTION RANU(NSEED)
  NSEED = SEED INTEGER WHICH STARTS GENERATOR.
  \[
  NSEED = NSEED \times 149204525 + 7
  \]
  NSEED = IABS(NSEED)
  RANU = NSEED/2147483648.0
  RETURN
END

WF - (WEATHER FUNCTION) SEASONAL FACTOR THAT INFLUENCES THE DEVELOPMENT RATE OF IMMATURE SEEDLES.

REAL FUNCTION WF(N)
  N = JULIAN DATE OF YEAR.
  WF = 0
  THE DEVELOPMENT RATE DECREASES TILL JULY FIRST AT WHICH POINT IT WILL REMAIN CONSTANT.
  IF (N.LT.180) WF = (180-N)/60.0
  THE EXTENT OF DECREASE IS AN EMPIRICALLY DECREASING FUNCTION.
  RETURN
END