MATHEMATICAL MODELS FOR A POPULATION OF INSECTS INFESTING STORED CEREAL PRODUCTS (WITH REFERENCE TO WEEVILS IN WHEAT)

by

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APPENDICES

SUMMARY

The example of the grain weevils (*sitophilus granarius*) and the rice weevils (*sitophilus oryzae*) infesting stored wheat is used. The weevils destroy the wheat by (1) ovipositing eggs into the grains and (2) eating the wheat. Models for predicting the damage to the wheat and the size of the population of the weevils are given.

The weevil population comprises of (1) the immature group consisting of the eggs, larvae, pupae and pre-emergence adults and (2) the group of sexually mature adults.

The system is modelled to go through two phases. In phase I the *food ratio* (that is the number of intact grains per weevil) is above a specified critical value and has no influence on the activities of the weevils. In phase II the food ratio has dropped below the critical value. Then the activities of the weevils are influenced by the food ratio. Continuous time deterministic models for both phases are given. Because of the delay in the emergence of adults from eggs the equations for the weevil population are delay differential equations. The method of steps and Laplace transform techniques are used in solving the equations.

The effect of temperature variation on the system is incorporated by formulating the parameters of the system as functions of both the temperature and the food ratio. Two computer programmes, one for constant temperature conditions and the other for variable temperature conditions, are included.

In the stochastic analysis of the system the distribution of the bivariate process of the number of intact grains and the number of adult weevils is discussed. The moments of the other variables such as the size of the immature group and the number of emigrants can be deduced from this distribution. The phase I stochastic model is a reformulation of the phase I deterministic model. For phase II two stochastic models are given. The first one is a reformulation of the phase II deterministic model. The second one incorporates the possibility that under reduced food ratio more than one egg may be oviposited into a single grain. This is achieved by dividing time into developmental periods. During each period a grain (whether already containing eggs or not) is susceptible to attacks by the weevils. Those grains that are attacked are regarded useless at the end of the period.

In the last model equations for the spatial distribution of weevils within wheat stored in a container are derived. The derivation is based on the hypothesis that the probability that a weevil continues to stay at a point of the container is proportional to the food ratio at the point. One of the equations is a delay integro-differential equation. A Laplace transformation technique is used in solving the equation. It is also shown that the method of steps could be used to solve the equation.

DECLARATION

This thesis contains no material which has been used to obtain any other degree or diploma in any University. To the best of my knowledge, this thesis contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

(L.S. Luboobi)

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CHAPTER 1

INTRODUCTION

1.1 DESCRIPTION OF THE ECOLOGICAL SITUATION

In the formulation of the models in this thesis the example of grain weevils (*Sitophilus granarius*, abbreviated to *S.G.*) and the rice weevils (*Sitophilus oryzae*, abbreviated to *S.O.*) infesting stored quantities of wheat is used. In most of the discussions the quantities of wheat are comparable to those used in laboratory experiments. The wheat is supposed to be stored in containers from which the weevils may emigrate.

The weevils damage the wheat by (1) eating the grain and (2) ovipositing eggs into individual grains. The female bores a hole into a grain, oviposits an egg in it and then seals off the hole with secreted material (Richards, 1947). All the stages of the development of the egg, that is the egg, larva, pupa and the pre-emergence adult, take place within the grain. A large proportion of the grain is used up for the development of the egg. The proportion which is left over after an adult has emerged from the egg can only be used for consumption by the adult weevils. If another egg is oviposited in a hollow grain from which an adult has already emerged, the egg does not develop into an adult. The length of the developmental period of an egg depends on the environmental conditions, such as temperature and relative humidity or the moisture content of the grain, through which the egg develops. Row 1 of Table A.1 (in Appendix 1.1) gives a few of the observed lengths under different environmental conditions by different researchers.

The life styles of the two species, *S.G.* and *S.O.* are similar except that the longevity (life span) of *S.O.* is shorter than that of *S.G.* However the progeny for *S.O.* (that is the total number of eggs laid by a *S.O.* female) is greater than that for *S.G.* (see row 6 of Table A.1 in Appendix 1.1). It has been observed in experiments conducted at the Waite Agricultural Research Institute, University of Adelaide, that the *S.O.* is more dispersive than the *S.G.* Other differences and similarities can easily be noticed from Table A.1 in Appendix 1.1.

1.2 THE AIM OF THIS STUDY

The models given in this thesis are for the purpose of predicting the damage to stored cereal products by insects infesting the products. Also the size of the population of the insects is of interest. As mentioned in Section 1.1 the example of weevils infesting wheat stored in a container is used. Though the experimental results referred to in this study are for small quantities of wheat, the mathematical analysis gives an insight into what might happen in systems of large quantities such as in a silo. It is also hoped that, by revising the assumptions made, the models can be modified to apply to other similar infestation situations. Also the prediction by the models may be useful in establishing control on the damage that is caused by the insects.

It should be noted that while in most experimental work it is not possible to determine the total effect of several environmental factors on an ecosystem, mathematical models can be handy in predicting and/or estimating the combined effect of these factors.

1.3 PREVIOUS AND/OR RELATED MATHEMATICAL MODELS

The *Sitophilus* species have been extensively studied experimentally in many parts of the world. However there have not been, to the best of my knowledge, analytical models for the populations of the species that compare with those for the related beetle, *Tribolium*. Unlike the *Sitophilus* the *Tribolium* thrives best on wheat flour. The eggs are laid indiscriminately in the flour and the larvae are capable of moving within the flour. Though the life style of *Tribolium* is different from that of *Sitophilus*, some of the analytical methods for *Tribolium*, for example Bartlett (1960), Mertz and Davis (1968), Neyman, Park and Scott (1956) and Niven (1968), have proved useful in the formulation of some of the models (for *Sitophilus*) discussed in this thesis.

The system of weevils infesting wheat can be modelled as a prey-predator system. However in this case the prey (i.e. the wheat grains) are passive in that they cannot react physically to the attacks from the predators (i.e. the weevils). For example they cannot run away! The prey-predator models that have proved useful are referred to in Sections 2.0 and 2.2.1.

Also the grain-weevil system can be regarded as a carrier-borne epidemic in which the wheat grains are the susceptibles and the weevils the carriers. In fact, for the stochastic models in Chapter 5, techniques for carrier-borne epidemics (for example Henderson, 1979 and Bailey, 1975) are used in solving some of the equations.

1.4 THE SCOPE AND METHODS OF THE STUDY

The population of the weevils is taken to comprise two age groups. Since all the developmental stages of an egg take place within a single grain, it is reasonable to consider the eggs, larvae, pupae and pre-emergence adults as one group. The second group consists of mature adults capable of laying eggs and moving. The movements may result in emigration. Tognetti and Mazanov (1970) and Tognetti (1975) discussed similar two-stage population models in which the egg-group is supposed to give "births" to the adult-group and vice-versa. The giving of births by the eggs is the emergence of adults from the eggs. In the stochastic models (Chapters 4,5) the emergence process is treated as an immigration process into the second group. It should be noted that the Tognetti and Mazanov models do not include explicit equations for the food medium as done in this thesis.

The system (that is, the wheat grains and the two-age population of the weevils) is modelled to go through two phases. In phase I the number of intact grains available per adult weevil (to be referred to as the *food ratio*) is above a specified value (to be referred to as the *critical food ratio*). In this phase the food ratio has no influence on the activities of the weevils. In phase II the food ratio has dropped to and below the critical value. Then the activities of the weevils become influenced by the food ratio.

In Chapter 2 two continuous time deterministic models, one for each of the two phases, are discussed. In the phase I model the parameters such as the oviposition rate, mortality rate and emigration rate are constants. In the phase II model the parameters become functions of the food ratio. In both models other environmental conditions such as the temperature, moisture content of the grain and relative humidity are assumed to be optimal as those that are possible in controlled laboratory experiments. Because of the delay in the emergence of adults from eggs the equations for the population of the weevils are delay differential equations. The method of steps and Laplace transform techniques are used in solving the equations.

In Chapter 3, the effect of temperature variation on the system is incorporated by redefining the parameters as functions of both the temperature and the food ratio. Discrete time equations corresponding to the continuous time equations of the models in Chapter 2 are used in two computer programmes, one of which is for the constant temperature conditions and the other for the variable temperature conditions.

In the stochastic analysis of the system the distribution of the bivariate process of the number of intact grains and the number of adult weevils is discussed. The moments of other variables, for example the size of the immature age group and the number of emigrants, can be deduced from this distribution. The phase I stochastic model, discussed in Chapter 4, is a stochastic reformulation of the phase I deterministic model of Section 2.1. In Chapter 5 two phase II models are given. The first one is a stochastic reformulation of the phase II deterministic model of Section 2.2. The second model incorporates the possibility that, under reduced food ratio, more than one egg may be oviposited into a single grain. This is achieved by dividing the time line into developmental periods. During each developmental period a grain (whether already containing eggs or not) is susceptible to attacks by the weevils. Those grains that are attacked are regarded useless at the end of the period. Agreements as well as differences between the stochastic means and the deterministic values of the variables involved are noted.

In the last model of this thesis equations for the spatial distribution of weevils within wheat stored in a container are derived. The derivation is based on the hypothesis that the probability that a weevil continues to stay at a point inside the container is proportional to the food ratio at the point. The method of separation of variables is applied to the equations. The time factor equation, which results, is a delay integro-differential equation. A Laplace transform technique is used in solving the equation. It is, also, shown that the method of steps could be used to solve such an equation.

1.5 VALUES OF PARAMETERS USED IN THE STUDY

Several parameters are used in the models in this thesis. In establishing properties of the solutions to the models it is essential that the values these parameters could take on are known. Table A.1 in Appendix 1.1 gives a summary of the parameters, their values, the researchers responsible for the values and, where possible or applicable, the conditions under which the values were determined. Though, according to the table, the values of a parameter may differ from researcher to researcher, it is important to appreciate that these values give an idea of the possible range of values for the parameter.

CHAPTER 2

CONTINUOUS TIME DETERMINISTIC MODELS

2.0 INTRODUCTION

Let $S(t)$ be the number of unattacked (intact) grains and $W(t)$, the number of adult weevils in the system at time t. Then the *food ratio* for the system, at time t, is $F(t) \triangleq S(t)/W(t)$. The reciprocal of the food ratio may be interpreted as the *density* in terms of weevils per intact grain. The other variables of interest are $U(t)$, the size of the immature group, and $R(t)$, the total number of emigrants (that is, the number of weevils that have emigrated from the system) by time t.

With C as the *critical food ratio*, the system is in phase I if $F(t) > C$ and in phase II if $F(t) \leqslant C$. The existence of such a critical food ratio in a real ecological system has been discussed by, for example, MacLagan and Dunn (1935), as the number of grains per weevil below which the oviposition rate decreases and the mortality rate increases. According to MacLagan and Dunn $C \simeq 12.5$ grains per weevil. Hardman (1977) used the reciprocal of this value (that is 0.08 weevils per grain) as the threshold density above which there are increased contacts between *Sitophilus oryzae*. Coombs and Woodroffe (1973) gave the critical food ratio as 10 grains per female. Though Richards (1947) observed that a significant drop in oviposition occurs when there were 10 grains per female, he pointed out that there was a significant increase in the rate of oviposition when the food ratio was increased to 20 grains per female. However, above 20 grains per female there was no significant increase in the rate. Thus according to Richards we could take $10 \leqslant C \leqslant 20$ grains per female.

We should note that since the consumption rate for an individual weevil could be as small as $\frac{1}{100}$ of the oviposition rate (see rows 5 and 6(b) of Table A.1 in Appendix 1.1) the female weevil would need about 100 times as many grains as the male weevil. Hence in a system in which the sex ratio is for example 1:1, the need for the intact grains by the female weevils is a good estimate of the need for the grains by the whole population.

In the models we do not differentiate between females and males. We assume that the mortality rate, the consumption rate and the emigration rate are the same for both the female weevil and the male weevil. However in a system of sex ratio 1:1 the oviposition rate per weevil would be ½ the rate per female; for the male does not lay eggs.

It is interesting that Arditi, Abillon and Vieira Da Silva (1977, 1978) used the same idea of "critical food ratio" in their two-phase prey-predator models. In their model the food ratio is defined as the ratio of the number of prey to the number of the predators. This is an example of prey-predator methods that can be applied to our grain-weevil system. However, we should note that Arditi *et al.* investigated stability of their system. In the grain-weevil system the discussion of stability is of little interest

We will refer to "optimal temperature conditions" as those environmental conditions which maximise oviposition and consumption rates. Note that, since emigration and death rates are not necessary maximised or minimised under these conditions, there is no reason to believe that weevil growth, grain depletion or time to certain landmarks, will attain their maximum or minimim values.

because by the time the system becomes stable all the grain will have been destroyed. Therefore, in this chapter, attempts are made to obtain explicit solutions, especially for the earlier stages of the storage, rather than asymptotic solutions.

In each of the Sections 2.1 and 2.2 assumptions, equations based on these assumptions and the solutions to the equations are discussed.

2.1 PHASE I: SUFFICIENT CEREAL AVAILABLE

2.1.1 Basic Assumptions and Equations

For this phase there are enough intact wheat grains and, therefore, the weevils' activities are not influenced in any way by the availability of intact grains. We also assume that other environmental conditions such as the temperature, relative humidity or moisture content of the grains are optimal. ∧ Insert : See opposite page Then under these optimal conditions we have the oviposition rate of λ eggs/day/weevil, the consumption rate of ν grains/weevil/day, the death rate of μ weevils/day/weevil and the emigration rate of ε weevils/day/weevil as constants. Also the time it takes an egg to develop into a mature adult is taken to be $\underset{\sim}{a}$ days, where $\underset{\sim}{a}$ is a constant. Thus, for phase I, the rates of change of the variables $S(t)$, $W(t)$, $U(t)$ and $R(t)$ are given by

$$\frac{dS}{dt} = -(\nu + \lambda)W(t) \tag{2.1.1}$$

$$\frac{dW}{dt} = p\lambda W(t - a) - (\mu + \varepsilon)W(t) \tag{2.1.2}$$

$$\frac{dU}{dt} = - \lambda W(t - a) + \lambda W(t) \qquad (2.1.3)$$

$$\frac{dR}{dt} = \varepsilon W(t) \qquad (2.1.4)$$

where p is the proportion of eggs that develop into adults. The equations are subject to

(1) *initial* conditions: $S(0) = S_0$, $W(0) = W_0$, $U(0) = 0$ and $R(0) = 0$;

(2) *nonnegativity:* $S(t), W(t), U(t), R(t) \geqslant 0$ for $t \geqslant 0$;

and

(3) *boundary* conditions: $S(t), W(t), U(t), R(t) \equiv 0$ for $t < 0$.

According to the equations (2.1.1) - (2.1.4), once $W(\tau)$ is determined for $\tau < t$, the values of the other variables at time t, can be derived.

The term $\lambda W(t)$ in (2.1.1) is the total rate at which the intact grains are attacked because of the oviposition of the eggs. Since ν could be as small as $(0.01)\lambda$ (see rows 5 and 6(b) of Table A.1 in Appendix 1.1), it is, according to (2.1.2), the laying of eggs that is the dominant factor in the destruction of the wheat grains. Equation (2.1.1), also, incorporates the assumption that once a grain has been attacked it cannot be used in future for oviposition purposes. In phase I, that is when $F(t) > C$, the female avoids grains already containing larvae (MacLagan and Dunn, 1935; Coombs and Woodroffe, 1973). The term $\lambda W(t - a)$ in (2.1.3) is the total rate at which the adults are expected to emerge from the eggs laid a days ago. However not all the eggs survive the developmental stages; hence the term $p\lambda W(t - a)$ in (2.1.2) with $p < 1$.

The size of the immature group is implicitly involved in determining $W(t)$ and $S(t)$. The emigrants are of a lesser importance in that once a weevil has left the system it cannot damage the wheat any more. Therefore, we shall not lay much emphasis on equations (2.1.3) and (2.1.4). However, in Chapter 3, we shall compare computed values of the total number of emigrants $R(t)$ with those obtained experimentally at the Waite Agricultural Research Institute, University of Adelaide.

2.1.2 Solution of the Equations

(A) Method of steps

We solve the system of equations (2.1.1) - (2.1.4) (2.1.2 in particular) for $0 \leqslant t < a$ and then we use the solution as an input to the system for $a \leqslant t < 2a$. Then the solution for $a \leqslant t < 2a$ is used in a similar way when solving the equations for $2a \leqslant t < 3a$. This procedure is continued to $3a \leqslant t < 4a$ and the following intervals.

Many authors have tended not to use this rather natural way of solving *delay* differential equations because they are interested in the asymptotic solutions to the equations. We should note that the method is useful if we are interested in earlier solutions rather than in the long run solutions. However, I must admit that the solutions might become untrackable after a few delays have been used. I should mention that El'sgol'ts and Norkin (1973) have indicated the significance of this method by applying it to several examples of equations in the delay differential equations family.

Let $\kappa = \mu + \varepsilon$ (= total rate at which weevils are removed from the system). Then multiplying (2.1.2) by $e^{\kappa t}$ and rearranging the equation we obtain

$$\frac{d}{dt}(e^{\kappa t}W(t)) = p\lambda e^{\kappa t}W(t - a) \ . \qquad (2.1.5)$$

Now define the function

$$J(t) = e^{\kappa t}W(t). \qquad (2.1.6)$$

Then from (2.1.5) we have

$$\frac{dJ}{dt} = p\lambda e^{\kappa a}J(t - a)$$

with $J(0) = W_0$ (since $W(0) = W_0$)

and $J(t) \equiv 0$ for $t < 0$ (from boundary condition $W(t) \equiv 0$ for $t < 0$).

So

$$J(t) = W_0 + p\lambda e^{\kappa a}\int_0^t J(\tau - a)d\tau$$

$$= J(m_t a) + p\lambda e^{\kappa a}\int_{m_t a}^t J(\tau - a)d\tau \qquad (2.1.7)$$

where $m_t = [t/a]$ (i.e., the greatest integer less than or equal to t/a) and $J(m_t a) = \lim_{\tau \uparrow m_t a} J(\tau)$.

Thus for $\underline{0 \leqslant t < a}$ we have

$$J(t) = W_0 \ . \qquad (2.1.8)$$

For $\underline{a \leqslant t < 2a}$ we have

$$\left.\begin{aligned} J(t) &= J(a) + p\lambda e^{\kappa a}\int_0^{t-a} W_0\,d\tau \\ &= J(a) + J(0)p\lambda(t-a)e^{\kappa a} \\ &\doteq W_0[1 + p\lambda(t-a)e^{\kappa a}] \end{aligned}\right\} . \qquad (2.1.9)$$

Similarly for <u>$2a \leqslant t < 3a$</u> we obtain

$$J(t) = J(2a) + J(a)\Omega(t-2a) + J(0)\frac{\Omega^2}{2!}(t-2a)^2$$

where $\Omega = p\lambda e^{\kappa a}$. So substituting for $J(2a)$ from (2.1.9) we obtain

$$J(t) = W_0[1 + \Omega a + \Omega(t-2a) + \frac{\Omega^2}{2!}(t-2a)^2]$$

$$= W_0[1 + \Omega(t-a) + \frac{\Omega^2}{2!}(t-2a)^2] . \qquad (2.1.10)$$

Continuing with this procedure we deduce that, for an arbitrary t,

$$\left.\begin{aligned} J(t) &= \sum_{r=0}^{m_t} J((m_t - r)a)\,\frac{\Omega^r(t-m_t a)^r}{r!} \\ &\doteq W_0 \sum_{r=0}^{m_t} \frac{\Omega^r}{r!}(t-ra)^r . \end{aligned}\right\} \qquad (2.1.11)$$

Then, according to (2.1.6)

$$W(t) = J(t)e^{-\kappa t} . \qquad (2.1.12)$$

<u>(B) Laplace Transform Method</u>

Let us denote the Laplace transform of $W(t)$ by $\hat{W}(z)$; that is

$$\hat{W}(z) = \mathcal{L}(W(t)) \triangleq \int_0^\infty e^{-tz}W(t)\,dt.$$

Then the Laplace transform of (2.1.2) gives us

$$z\hat{W}(z) - W(0^+) = p\lambda e^{-az}\hat{W}(z) - \kappa\hat{W}(z),$$

that is

$$\hat{W}(z) = \frac{W_0}{z+\kappa-p\lambda e^{-az}} \tag{2.1.13}$$

$$= \frac{W_0}{\psi(z)} \quad , \text{ say.}$$

Usually to invert an equation of the form (2.1.13) we need to establish where the zeros of $\psi(z)$ lie. Bellman and Cooke (1963, Chapters 4 and 12) have discussed, in great detail, the curve on which the zeros of $\psi(z)$ lie. However, the locations of these zeros are important only if we are interested in the asymptotic properties of the solution. In this thesis (especially for phase I) we are concerned with solutions for the early stages of storage. We, therefore, try to obtain explicit solutions.

In order to invert (2.1.13) (without first establishing the locations of the zeros of $\psi(z)$) we write

$$\frac{1}{\psi(z)} = \frac{1}{z+\kappa}\left(\frac{1}{1-p\lambda e^{-az}/(z+\kappa)}\right) .$$

Now expanding the second factor in powers of $p\lambda e^{-az}/(z+\kappa)$, we get

$$\frac{1}{\psi(z)} = \sum_{r=0}^{\infty} \psi_r(z) \tag{2.1.14}$$

where

$$\psi_r(z) = \frac{(p\lambda)^r e^{-raz}}{(z+\kappa)^{r+1}} .$$

Now noting that with the Heaviside unit function

$$H(t) \triangleq \begin{cases} 0 & \text{for} \quad t < 0 \\ 1 & \text{for} \quad t \geqslant 0 \end{cases}$$

we have

$$\mathcal{L}(H(t-b)g(t-b)) = e^{-bz}\hat{G}(z) \quad ,$$

the inverse Laplace transform of $\psi_r(z)$ is

$$\psi_r(t) = (p\lambda)^r H(t-ra)g(t-ra)$$

where

$$g(t) = \mathcal{L}^{-1}\left[\frac{1}{(z+\kappa)^{r+1}}\right]$$

$$= \frac{t^r e^{-\kappa t}}{r!} \quad .$$

According to Erdélyi (1962, Section 4.2) the series (2.1.14) is uniformly convergent. Hence, from (2.1.13) and (2.1.14), the inverse Laplace transform of $\hat{W}(z)$ is

$$W(t) = W_0 \sum_{r=0}^{\infty} \frac{(p\lambda)^r}{r!} (t-ra)^r H(t-ra) e^{-\kappa(t-ra)} \quad . \qquad (2.1.15)$$

Also, for a similar application of Erdélyi's results, see Mazanov and Tognetti (1974). Now for $na \leqslant t < (n+1)a$, n an integer, we have $t - ra < 0$ for $r \geqslant n+1$ and therefore $H(t - ar) \equiv 0$ for $r \geqslant (n+1)$. Hence, from (2.1.15), we have

$$W(t) = W_0 \sum_{r=0}^{[t/a]} \frac{(p\lambda)^r (t-ra)^r e^{-\kappa(t-ra)}}{r!} \qquad (2.1.16)$$

which is the same as the solution (2.1.12) by the method of steps.

Expressions for the Variables $S(t)$, $U(t)$ and $R(t)$

Now from (2.1.1) we have the remaining number of intact grains, $S(t)$, at time t given by

$$S(t) = S_0 - \alpha Q(t) \qquad (2.1.17)$$

where

$$Q(t) = \int_0^t W(\tau)d\tau = \left[\sum_{n=0}^{m_t-1} \int_{na}^{(n+1)a} W(\tau)d\tau + \int_{m_t a}^{t} W(\tau)d\tau\right],$$

$$\alpha = \nu + \lambda, \quad m_t = [t/a], \quad S_0 = S(0)$$

and

$$\sum_{n=0}^{-1} \int_0^a W(\tau)d\tau \equiv 0.$$

Now from (2.1.16) we have

$$\int_{m_t a}^{t} W(\tau)d\tau = W_0 \sum_{r=0}^{m_t} \frac{(p\lambda)^r}{r!} \int_{m_t a}^{t} (\tau - ra)^r e^{-\kappa(\tau-ra)} d\tau \quad .$$

Evaluating the integral in the right-hand side by parts or using table of integrals we obtain

$$\int_{m_t a}^{t} W(\tau)d\tau = \frac{W_0}{\kappa} \sum_{r=0}^{m_t} \left(\frac{\Omega}{\kappa}\right)^r \sum_{k=0}^{r} \frac{1}{k!}\left\{\left[\kappa(m_t-r)a\right]^k e^{-\kappa m_t a} - \left[\kappa(t - ra)\right]^k e^{-\kappa t}\right\} \quad , \qquad (2.1.18)$$

where $\Omega = p\lambda e^{\kappa a}$.

Similarly,

$$\int_{na}^{(n+1)a} W(\tau)d\tau = \frac{W_0}{\kappa} \sum_{r=0}^{n} \left(\frac{\Omega}{\kappa}\right)^r \sum_{k=0}^{r} \frac{1}{k!} \left\{\left[\kappa(n-r)a\right]^k e^{-\kappa na} - \left[\kappa(n + 1 - r)a\right]^k e^{-\kappa(n+1)a}\right\}$$

Then, after some manipulation, we get

$$\sum_{n=0}^{m_t-1} \int_{na}^{(n+1)a} W(\tau)\,d\tau = \frac{W_0}{\kappa}\left\{ \sum_{r=0}^{m_t-1} \left(\frac{\Omega}{\kappa}\right)^r e^{-\kappa ra} - \sum_{r=0}^{m_t-1} \left(\frac{\Omega}{\kappa}\right)^r \sum_{k=0}^{r} \frac{[\kappa(m_t-r)a]^k}{k!} e^{-\kappa m_t a} \right\} . \tag{2.1.19}$$

Adding (2.1.18) and (2.1.19) we get

$$Q(t) = \frac{W_0}{\kappa}\left\{ \sum_{r=0}^{m_t} \left(\frac{\Omega}{\kappa}\right)^r e^{-\kappa ra} - e^{-\kappa t} \sum_{r=0}^{m_t} \left(\frac{\Omega}{\kappa}\right)^r \sum_{k=0}^{r} \frac{[\kappa(t-ra)]^k}{k!} \right\} . \tag{2.1.20}$$

From (2.1.3) the size of the immature group, at time t, is given by

$$U(t) = \lambda \int_{t-a}^{t} W(\tau)\,d\tau = \lambda[Q(t) - Q(t-a)]$$

and from (2.1.4) the total number of emigrants by time t is given by

$$R(t) = \varepsilon \int_{0}^{t} W(\tau)\,d\tau = \varepsilon\, Q(t),$$

where $Q(t)$ is given by (2.1.20).

For an arbitrary large t the expressions (2.1.16) for $W(t)$, (2.1.7) (in conjunction with (2.1.20)) for $S(t)$ and similarly for $U(t)$ and $R(t)$, are not simple to handle. However, we should note that the solutions are used only for $t < t^*$; where t^* is the time at which the critical food ratio is reached and then phase I ends. The value of t^* is likely to fall within the first few developmental periods over which the expressions for the solutions would be relatively simple.

2.1.3 The time at which cereal supply becomes critical

Let us denote this time by t^* as in the previous section. Then t^* is the smallest positive root of the equation $F(t) = C$, that is

$$S(t) = C\,W(t)$$

or, according to (2.1.17),

$$S_0 - \alpha\,Q(t) = C\,W(t) .$$

Now substituting for $Q(t)$ from (2.1.20) and for $W(t)$ from (2.1.16) and then doing some simplifying, we obtain

$$\begin{aligned} F_0 - \frac{\alpha}{\kappa}\sum_{r=0}^{m_t}\left(\frac{\Omega}{\kappa}\right)^r e^{-\kappa ra} &= e^{-\kappa t}\left\{\left(C - \frac{\alpha}{\kappa}\right)\sum_{r=0}^{m_t}\left(\frac{\Omega}{\kappa}\right)^r \frac{[\kappa(t-ra)]^r}{r!}\right. \\ &\quad \left. - \frac{\alpha}{\kappa}\sum_{r=0}^{m_t}\left(\frac{\Omega}{\kappa}\right)^r \sum_{k=0}^{r-1}\frac{[\kappa(t-ra)]^k}{k!}\right\} , \qquad (2.1.21) \end{aligned}$$

where $F_0 \triangleq S_0/W_0$ is the initial food ratio.

For $m_t \geqslant 1$, the roots of (2.1.21) (and therefore t^*) cannot be obtained explicitly. However we should note that the value of t^* depends on the initial conditions $S(0) = S_0$ and $W(0) = W_0$ and therefore on the initial food ratio F_0 . So let us determine the conditions on F_0 such that, for example, $0 < t^* < a$, $a < t^* < 2a$, $2a < t^* < 3a$, and so on.

For $\underline{0 \leqslant t < a}$ (2.1.21) reduces to

$$F_0 - \alpha/\kappa = (C - \alpha/\kappa)e^{-\kappa t} \quad . \qquad (2.1.22)$$

Now for $10 \leqslant C \leqslant 20$ (see Section 2.0) and according to the possible values of the parameters ν, λ, μ and ε as given in Table A.1 in Appendix 1.1 $C - \alpha/\kappa < 0$. Hence the right hand side (RHS) of (2.1.22) is an increasing function of t over the interval $[0,a)$. Now at $t = 0$

$$\text{RHS of (2.1.22)} = C - \alpha/\kappa < F_0 - \alpha/\kappa \ ,$$

since $F_0 > C$ for phase I. Therefore $t^* \in (0,a)$ only if

$$F_0 \leqslant \frac{\alpha}{\kappa} + \left(C - \frac{\alpha}{\kappa}\right)e^{-\kappa a} \quad ;$$

and then

$$t^* = \frac{1}{\kappa} \ln \left[\frac{C-\alpha/\kappa}{F_0-\alpha/\kappa}\right] .$$

Otherwise

$$F_0 > \frac{\alpha}{\kappa} + \left(C - \frac{\alpha}{\kappa}\right)e^{-\kappa a} \Rightarrow t^* > a. \qquad (2.1.23)$$

For $\underline{a \leqslant t < 2a}$ (2.1.21) reduces to

$$F_0 - \alpha/\kappa = (C - \alpha/\kappa)[1 + \Omega(t - a)]e^{-\kappa t}$$

$$+ \frac{\alpha\Omega}{\kappa^2}(e^{-\kappa a} - e^{-\kappa t}) \qquad (2.1.24)$$

$$= \phi(t) \ , \text{ say } .$$

Note that $\phi(a) = (C - \alpha/\kappa)e^{-\kappa a}$.

So if $t^* > a$, then according to (2.1.23) we have

$$\phi(a) < F_0 - \alpha/\kappa \quad .$$

It can be shown that, for $C - \alpha/\kappa < 0$, $\phi(t)$ is an increasing function on $(a,2a)$. So (2.1.24) has a real solution for t (i.e., $t^* \in (a,2a)$) only if $\phi(t)$ can increase to and possibly beyond $F_0 - \alpha/\kappa$ over the interval. This is so only if

$$\phi(2a) \geqslant F_0 - \alpha/\kappa \; . \tag{2.1.25}$$

Thus, from (2.1.23) and (2.1.25), we have $t^* \in (a,2a)$ if

$$\frac{\alpha}{\kappa} + \left(C - \frac{\alpha}{\kappa}\right)e^{-\kappa a} < F_0 \leqslant \frac{\alpha}{\kappa} + \phi(2a) \tag{2.1.26}$$

and $t^* > 2a$ if

$$F_0 > \frac{\alpha}{\kappa} + \phi(2a) \; .$$

The conditions on F_0 for $t^* \in (2a,3a)$ and higher developmental intervals may be obtained in a similar way. But for these higher intervals the computation becomes more and more difficult.

Example 2.1 With the values of the parameters as follows:

$$\mu = 0.008333, \; \varepsilon = 0.006436, \; \lambda = 1.0$$
$$\nu = 0.01482 \; , \; p = 0.7 \text{ and } a = 50$$

we can show, from (2.1.26), that $t^* \in (a,2a)$ if

$$40.63 < F_0 < 1140.12 \quad \text{for} \quad C = 10$$

and

$$45.41 < F_0 < 1208.78 \quad \text{for} \quad C = 20.$$

The example above indicates that for small quantities of wheat, for example those used in laboratory experiments, it is very likely that the critical food ratio is reached before the end of the second developmental period. Hardman's (1977) observations agree with this. In Hardman's experiments he had several cells initially containing 100 weevils and an average of 695.6g ($\cong$ 19900 grains) of wheat. He observed that *his* critical food ratio of 12.5 grains to a weevil was reached in several of the cells as early as 84 days after the start of the experiments. According to him the developmental period was 50 days. The initial food ratio, F_0 , was approximately 200 grains per weevil.

Even if we may establish the developmental interval in which t^* lies, the exact value of t^* (for $t^* > a$) is difficult to obtain from (2.1.21). In Chapter 3 estimates of t^* , for different initial conditions, are obtained by solving (2.1.21) numerically on the computer.

2.2 PHASE II: LIMITED CEREAL AVAILABLE

2.2.0 Introduction

Phase II starts at time t^* at which the critical food ratio C is reached for the first time. Note that $t' > t^*$ does not necessarily mean that $F(t') < C$. In other words there is a chance that the food ratio may rise up to and even above C at some time instant $t' > t^*$. But in Section 2.2.2 it is shown that, according to the assumptions made in Section 2.2.1, $F(t) < C$ for $t > t^*$.

2.2.1 Basic Assumptions and Discussions

(A) Oviposition rate

As the food ratio, $F(t)$, drops to and below the critical value C the oviposition rate, $\lambda(t)$, is expected to decrease. When $F(t) = 0$ (that is, when intact grains are finished) $\lambda(t)$, also, should be zero. So a reasonable assumption to make is the following

$$\lambda(t) = (\text{constant}) \times F(t) .$$

We make $\lambda(t)$ continuous at $t = t^*$ by choosing the constant to be λ/C. That is

$$\lambda(t) = \frac{\lambda F(t)}{C} = \frac{\lambda S(t)}{CW(t)} \tag{2.2.1}$$

where the constant λ is the oviposition rate in phase I.

The assumption that the oviposition rate is a function of the food ratio is in accordance with MacLagan's (1932) observations on the effect of density (the reciprocal of $F(t)$) on the oviposition rate. In the mathematical representation of his data MacLagan tried to fit the data with the curve of the form $\lambda = mF^n$ where m and n are constants. He realised that he had to divide the range of the values of $F(t)$ into sub-ranges over which the pair (m,n) took on different values. For example for $0.25 \leqslant F \leqslant 9$ wheat grains per weevil, (m,n) was determined to be $(0.19, 1.66)$; for $9.1 < F < 200$, (m,n) was $(1.38, 0.55)$. He also observed that when there is one grain for every four female weevils, the insects cannot or will not oviposit at all. However, we should note that according to MacLagan's values of m and n, $\lambda = 25.44$ at $F = 200$, 4.65 at $F = 9.1$, 7.29 at $F = 9$ and 0.019 at $F = 0.25$. The value of λ at $F = 200$ is an overestimation of the possible values λ can take on (see row 6(b) of Table A.1 in Appendix 1.1). Also there is some inconsistency in the values of λ at $F = 9.1$ and $F = 9$; these values are not expected to differ that much and the first one should be greater than the second one. However, according to MacLagan's (1932, Fig. 3) it is apparent that for $F < 12.5$ the data points could be fitted by a linear relation of the form $\lambda(t) = (\text{constant}) \times F(t)$. One way of reducing the overestimation of the oviposition rate for $F > 12.5$ would be to take it as a constant over this range. Hence the formulae for $\lambda(t)$ used in the models in this thesis, that is $\lambda(t) = m[F(t)]^n$ with $m = \lambda$ and $n = 0$ for $F > C(= 10)$ and, according to (2.2.1),

$$m = \lambda/C \quad \text{and} \quad n = 1 \quad \text{for} \quad F \leqslant C(= 10),$$

are reasonable.

(B) The consumption rate

The consumption rate, $\nu(t)$, is assumed to obey the same law as the oviposition rate. When intact grains become scarce for ovipositional purposes it is reasonable to assume that it is equally difficult to find intact grains for consumption, So, for phase II, we assume that

$$\nu(t) = \frac{\nu S(t)}{CW(t)} \tag{2.2.2}$$

where the constant ν is the consumption rate in phase I.

(C)

From the wheat viewpoint the intact grains are attacked and damaged by an individual weevil at the rate of

$$\alpha(t) \triangleq \nu(t) + \lambda(t) = \left[\frac{\nu+\lambda}{C}\right] \frac{S(t)}{W(t)} \qquad (2.2.3)$$

grains per day.

In connection with the prey-predator theory as mentioned in Section 1.3 (the wheat grains being the passive prey and the weevils the predators), the assumption (2.2.3) is well supported by Arditi, Abillon and Vieirra Da Silva (1978). They refer to $\alpha(t)$ (or to be more precise $\alpha(S(t),W(t))$) as the functional response between the prey and the predators. They compare their

$$\alpha(S(t),W(t)) \triangleq \begin{cases} a_1 & \text{if } S(t) > dW(t) \\ a_2 S(t)/W(t) & \text{if } S(t) < dW(t), \end{cases}$$

where a_1, a_2 and d are constants, with the Lotka-Voltera functional response $\varphi(S(t),W(t)) = (\text{Constant}) \times S(t)$ (or more generally $\varphi(S(t),W(t)) = \varphi(S(t))$. The weakness of the Lotka-Volterra functional response is that there is no upper limit on the number of prey that a predator can kill in a unit time. The functional response of the form (2.2.3) would prevent a situation in which it would be possible for the whole prey population to be eaten at one time by the predators. Pearce (1970) too preferred the functional response of the form (2.2.3) to the Lotka-Volterra response.

There are, of course, other forms of $\varphi(S(t),W(t))$ that could be used for our grain-weevil system. However we should note that the form for $\alpha(S(t),W(t))$ that would be used depends on (1) the structure of the problem being studied and (2) the form of the solution required from the model. If an analytic solution is required, then, in most cases, the forms of the functions, such as $\alpha(S(t),W(t))$, involved in the model have to be relatively simple. If a numerical solution is considered sufficient, then the functions could be general. However, we should realise that, in some situations, solutions to a rather general model may give the same information as the solution to a relatively simpler model. For our grain-weevil system (2.2.3) seems appropriate for phase II.

(D)

It may be argued that the two fundamental causes for migration of insects are: (1) excessive contact stimulation due to crowded conditions and (2) shortage of food supply in the habitat (MacLagan, 1932). However, we should realise that even in situations where (1) and (2) do not apply there may be some migration. Thus even in phase I during which (1) and (2) do not apply we expect some emigration of the weevils. For phase II during which (1) and (2) apply, we expect the emigration rate $\varepsilon(t)$ to *increase* with the decreasing food ratio $F(t)$. Again here there are many possible forms for the emigration rate $\varepsilon(t)$ as a function of $F(t)$. For our model we assume that

$$\varepsilon(t) = \varepsilon + \varepsilon b(C - S(t)/W(t)) \qquad (2.2.4)$$

where the constant ε in the RHS of (2.2.4) is the emigration rate in phase I and b is another parameter which allows some freedom in adjusting the magnitude of $\varepsilon(t)$. Note that $\varepsilon(t^*) = \varepsilon$. That is $\varepsilon(t)$ is continuous at the common boundary of phase I and phase II.

According to (2.2.4) the maximum rate of emigration is $\varepsilon(1 + bC)$ weevils/day/weevil and this occurs when $F(t) = 0$, that is when the grains are finished. One would expect all the weevils to leave the habitat,at once, when grains are finished. This would imply that $\varepsilon(t) \to \infty$ as $F(t) \to 0$. But this is not the case. Some weevils choose to continue staying in the habitat. In fact it has been observed that when the food ratio is low the weevils feed on frass and husks of the grains from which young ones have emerged (Coombs and Woodroffe, 1964).

(E) The mortality rate

The mortality rate is expected to increase as the food ratio decreases. However, if the weevils are free to emigrate then the pressure of death would be relieved a bit. In other words the increase in the mortality rate would be accounted for through the increased rate of emigration. Thus we may assume that the mortality rate of μ weevils/day/weevil remains constant even in phase II.

(F)

Finally we make the assumption that it still takes a days for a mature adult to emerge from an egg. We should note that because all the developmental stages of an egg take place within a grain the factor of crowding (that is, reduced food ratio) has no effect on the rate of development of the egg. The only factor that could influence the rate is the competition between larvae if more than one egg is oviposited in a single grain (MacLagan and Dunn, 1935). However, under optimal temperature, relative humidity and moisture content of the grain the developmental period may not differ that much from that for phase I; its length can still be approximated by a days. Then the emergence rate of mature adults from the eggs at time t is

$$\eta(t) = p\lambda(t-a)W(t-a) \qquad (2.2.5)$$

where

$$\lambda(t-a) = \begin{cases} \lambda & \text{for } t < t^* + a \\ \dfrac{\lambda S(t-a)}{CW(t-a)} & \text{for } t > t^* + a \,. \end{cases}$$

2.2.2 The Equations

According to assumption (C) in Section 2.2.1 and using (2.2.3) the equation for the number of intact grains, $S(t)$, is

$$\frac{dS}{dt} = -\,\hat{\alpha}\,S(t)\;, \qquad (2.2.6)$$

where now $\hat{\alpha} = (\nu + \lambda)/C$.

Now using assumption (E) and equations (2.2.4) and (2.2.5), the equation for the number of adult weevils, $W(t)$, is

$$\frac{dW(t)}{dt} = p\lambda(t-a)W(t-a) - \rho W(t) + b\varepsilon S(t) \qquad (2.2.7)$$

where $\rho = \mu + \varepsilon(1 + bC)$.

The equation for the size of the immature group, $U(t)$, is

$$\frac{dU(t)}{dt} = -\lambda(t-a)W(t-a) + \lambda(t)W(t). \qquad (2.2.8)$$

The total number of emigrants, $R(t)$, by time t satisfy the equation

$$\begin{aligned}\frac{dR(t)}{dt} &= \varepsilon(t)W(t)\\ &= \varepsilon(1+bC)W(t) - b\varepsilon\, S(t). \qquad (2.2.9)\end{aligned}$$

We require $S(t)$, $W(t)$, $U(t)$ and $R(t) \geqslant 0$.

It should be emphasised, at this point, that the RHS of (2.2.6) is the rate at which *intact grains* are attacked. It does not mean that the already attacked grains, for example, those containing eggs, are not attacked again. We can assume that the total rate of attacks on the grains is still $\nu + \lambda$ but only the fraction $S(t)/[CW(t)]$ of the attacks manage to land on the intact grains. Since at most one adult may emerge from a grain which at one time holds more than one egg (Coombs and Woodroffe, 1973; Hardman, 1977) $S(t)/[CW(t)]$ also represents the fraction of the eggs 100p% of which are expected to develop into adults.

The term $b\varepsilon S(t)$ in (2.2.7) may be interpreted as the rate at which the intact grains attract the weevils to continue staying in the habitat.

Note, from (2.2.8) and (2.2.9), that once $S(t)$ and $W(t)$ have been determined then we can solve for $U(t)$ and $R(t)$. For this reason we shall concentrate on determining solutions to (2.2.6) and (2.2.7).

Let us check whether the food ratio $F(t)$ is likely to rise to and above the critical food ratio C at some time instant $t' > t^*$. If $F(t) > C$, for $t = t' > t^*$, then $\alpha(t')$ would be greater than the rate at which the intact grains are attacked in phase I. This would not be in accordance with the intention that $\alpha(t)$ is smaller in phase II than in phase I. Also if $F(t') > C$ then $\varepsilon(t') < \varepsilon$ and could become negative in which case it would be meaningless to refer to $\varepsilon(t)$ as an emigration rate. Let us consider

$$\frac{dF(t)}{dt} = \frac{d}{dt}(S(t)/W(t)) = \frac{W(t)S'(t)-W'(t)S(t)}{W^2(t)} .$$

Now substituting for $S'(t)$ and $W'(t)$ from (2.2.6) and (2.2.7) we obtain

$$\frac{dF(t)}{dt} = -\left[\hat{\alpha} - \rho + \frac{p\lambda(t-a)W(t-a)}{W(t)}\right]F(t) - b\varepsilon[F(t)]^2. \tag{2.2.10}$$

Thus for $W(t) > 0$ and $F \geqslant 0$, $\hat{\alpha} > \rho$, for example, is a *sufficient condition* that $F'(t) < 0$ (that is $F(t)$ is a decreasing function) for $t \geqslant t^*$.

For the possible ranges of values for the parameters μ, ν, λ, C, ε (see Table A.1, Appendix 1.1), for example with

$\mu = 0.008333$, $\nu = 0.01482$, $\lambda \geqslant 0.5$,
and $\varepsilon = 0.006436$,

$\hat{\alpha} > \rho$ if $b < 0.5703$ for $C = 10$ or if $b < 0.08525$ for $C = 20$.

This also indicates the range of values the dimensionless parameter b (assumption (D), Section 2.2.1) could take on without invalidating the equations (2.2.6) - (2.2.9).

So we can take $F(t) < C$ and decreasing for $t > t^*$.

2.2.3 Solutions of the Equations

Solving (2.2.6) subject to the initial condition $S(t^*) = S^*$ we obtain

$$S(t) = S^* e^{-\hat{\alpha}(t-t^*)} \qquad (2.2.11)$$

for $t \geqslant t^*$.

For $\underline{t^* \leqslant t < t^*+a}$ we have $\lambda(t-a) = \lambda$. Then from (2.2.7) we have

$$\frac{dW}{dt} = p\lambda W(t-a) - \rho W(t) + b\varepsilon\, S(t) \,.$$

Now multiplying this equation by $e^{\rho t}$ and rearranging the equation we get

$$\frac{d}{dt}(We^{\rho t}) = p\lambda W(t-a)e^{\rho t} + b\varepsilon\, S(t)e^{\rho t} \,.$$

Substituting for $S(t)$ from (2.2.11) and then integrating we obtain

$$W(t) = W^* e^{-\rho(t-t^*)} + \frac{b\varepsilon\, S^*}{\hat{\alpha} - \rho}\left[e^{-\rho(t-t^*)} - e^{-\hat{\alpha}(t-t^*)}\right]$$

$$+ p\lambda \int_{t^*}^{t} W(\tau - a)e^{-\rho(t-\tau)}d\tau \,, \qquad (2.2.12)$$

where $W^* = W(t^*)$. The integral in (2.2.12) is evaluated using the phase I solution for $W(\tau)$ from (2.1.16) (or (2.1.11) and (2.1.12)).

For $\underline{t > t^*+a}$ (2.2.7) becomes

$$\frac{dW}{dt} = \frac{p\lambda}{C}\, S(t-a) - \rho W(t) + b\varepsilon\, S(t) \;.$$

Now substituting for $S(t-a)$ and $S(t)$ from (2.2.11) and then integrating we obtain

$$W(t) = W(t^*+a)\, e^{-\rho(t-t^*-a)} + S^*\left[p\lambda/C + b\varepsilon\, e^{-\hat{\alpha}a}\right]\left\{\frac{e^{-\rho(t-t^*-a)} - e^{-\hat{\alpha}(t-t^*-a)}}{\hat{\alpha} - \rho}\right\} \tag{2.2.13}$$

for $t \geqslant t^* + a$.

2.2.4 The time at which the cereal supply is likely to get finished

According to (2.2.11) $S(t)$ decreases exponentially but remains positive for finite t . So theoretically intact grains never get finished. However we should note that although, theoretically, one grain remaining implies that we still have intact grains, practically 1 grain or even 10 or 100 grains remaining, may be regarded as a situation with no "useful" grains left. The remaining intact grains may be useless because either they are inaccessible because of their locations or they are contaminated. For example MacLagan (1932) observed that when less than one grain is available to every four females (that is when $F(t) \leqslant 0.25$) oviposition stops. Depending on the number of weevils at the time when $F(t) = 0.25$, the number of intact grains left in the system may be large. In order to get an idea of how soon useful grains are likely to get finished we could solve for the time at which the number of the remaining intact grains is, for example, 1 or 10.

Example 2.2: With $\lambda = 1.0$, $\nu = 0.01482$, $C = 10$ and $S^* = 8952$, for example, $S(t) = 1$ (that is one intact grain remaining) when $t - t^* \simeq 90$ days.

When $S(t) = 10$, $t - t^* \simeq 67$ days. So if the one (ten) remaining intact grain(s) is (are) regarded useless, then useful grains are finished in about 90 (67) days after the critical food ratio is reached.

CHAPTER 3

DISCRETE TIME EQUATIONS AND INCORPORATION OF TEMPERATURE.

3.0 INTRODUCTION

Having solved the continuous time model for our grain-weevil system one may feel that there is no need to try to solve the corresponding discrete time model. We should have it borne in mind that continuous time equations are an approximate description of the real situation. The events occur in the system at discrete time points. Thus the use of discrete time equations may be justified. However we should note that even when we use the discrete time equations we are still describing the situation approximately. The solution to the discrete time model and the solution to the continuous time model may give the same general picture of the behaviour of the system. The advantage of continuous time equations is that they may be analytically solvable in some cases where the corresponding discrete time equations are not solvable or very difficult to solve analytically. However the advantage of the discrete time equations is that they are easily handled on the computer. In this chapter we do not intend to solve the discrete time equations analytically but numerically on the computer. The discrete time formulation becomes very handy when incorporating the temperature effect on the behaviour of our system (see Section 3.2).

3.1 THE EQUATIONS FOR OPTIMAL TEMPERATURE CONDITIONS

Since the unit of time used when referring to the values of the parameters is a day (see Section 2.1.1), the unit of time for the discrete time formulation will be *one* day. Then the discrete time equations are

$$\begin{aligned} S(t+1) &= S(t) - [\lambda(t)+\nu(t)]W(t) \\ W(t+1) &= W(t) + p\lambda(t-a)W(t-a) - [\varepsilon(t)+\mu(t)]W(t) \\ U(t+1) &= U(t) - \lambda(t-a)W(t-a) + \lambda(t)W(t) \\ R(t+1) &= R(t) + \varepsilon(t)W(t) \end{aligned} \qquad (3.1.1)$$

for $t = 0,1,2,\ldots$ and where the variables S, W, U and R are as defined in Chapter 2. The equations are still subject to

$$S(0)=S_0, \quad W(0)=W_0, \quad U(0)=0=R(0)$$

and $S(t)$, $W(t)$, $U(t)$, $R(t) \geqslant 0$ for $t \geqslant 0$.

The parameters $\lambda(t)$, $\nu(t)$, $\varepsilon(t)$ and $\mu(t)$ are given by:

the oviposition rate, $\lambda(t) = \begin{cases} \lambda & \text{for } S(t) > CW(t) \\ \dfrac{\lambda S(t)}{CW(t)} & \text{for } S(t) \leqslant CW(t); \end{cases}$

the consumption rate, $$\nu(t) = \begin{cases} \nu & \text{for } S(t) > CW(t) \\ \dfrac{\nu S(t)}{CW(t)} & \text{for } S(t) \leqslant CW(t); \end{cases}$$

the emigration rate, $$\varepsilon(t) = \begin{cases} \varepsilon & \text{for } S(t) > CW(t) \\ \varepsilon + b\varepsilon(C - S(t)/W(t)) & \text{for } S(t) \leqslant CW(t); \end{cases}$$

and the mortality rate $\mu(t) = \mu$(a constant),

as in Chapter 2.

3.1.1 Computer Programme I

The FORTRAN programme used to solve the equations (3.1.1) is given in Appendix 3.1.

Input. The values of the parameters used in the programme were as follows:

$\lambda = 1.0$, $\mu = 0.008333$, $\varepsilon = 0.006436$, $a = 50$,
$p = 0.7$, $\nu = 0.021285$, $b = 0.12$ and $C = 10$.

These values were based on the values of the parameters for *Sitophilus Oryzae* as given in Table A.1 in Appendix 1.1. Where several values for a single parameter are given in the Table, the value used in the programme was considered to be a compromise between the values in the Table. In particular the length of the developmental period of 50 days was based on Hardman's

(1977) estimation (see row 1 of Table A.1 in Appendix 1.1).

The initial amount of wheat used was 600 g estimated to be equivalent to 20,000 grains of variety 8156 Olympic wheat. Runs of the programme were made for the initial numbers of 240, 120, 60 and 30 weevils in equal initial quantities of wheat.

Output. The key parts of the numerical output that I choose to look at are the time, t^*, at which the critical food ratio is reached and the times t_{10} and t_1 at which there are 10 grains and 1 grain, respectively, remaining in the system. According to the argument in Section 2.2.4 t_{10} and t_1 gives us an idea of how fast and when the intact grains are likely to get finished. These parts of the output are given in Table 3.1.

TABLE 3.1 The times t^*, t_{10}, t_1 (days) at which the critical food ratio is reached, 10 grains are remaining and 1 grain is remaining, respectively, for the initial number of W_0 weevils.

W_0	t^*	t_{10}	t_1
240	56	119	140
120	64	127	148
60	76	137	158
30	95	152	173

From Table 3.1 we note that for each of the four initial conditions, t^* lies in the second developmental period: 50 - 100 days. This is in agreement with the condition on the initial food ratio F_0 as given in Example 2.1. Also the times $t_{10}-t^*$ and t_1-t^* do not differ much from those obtained from the continuous time solutions. For example for the initial number of 240 weevils $S(t^*) = 8952$ (same value used in Example 2.2) and, according to Table 3.1, $t_{10}-t_1 = 63$ days (compared with the continuous time solution of 67 days in Example 2.2) and $t_1-t^* = 84$ days (compared with 90 days in Example 2.2). This tends to confirm that the discrete time solutions and the continuous time solutions give more or less the same information about the behaviour of the system.

For a more detailed description of the behaviour of the system I feel that it is appropriate to give it in a graphical form. Figures 3.1A,B give a typical graphical output of the computer programme in Appendix 3.1. The curves in Figures 3.1A,B are for the initial number of 120 weevils.

From the graphical output the number of intact grains is decreasing as expected; for the wheat is never renewed. In the first developmental period no young mature weevils come up. So over this period the size of the population of adult weevils decreases due to deaths and emigration. After the first developmental period the population increases well after the time t^* at which the critical food ratio is reached. Then it decreases monotonically. The size of the immature group

FIGURE 3.1A

Curves for (1) the Food Ratio,
(2) Number of intact grains,
(3) Number of adult weevils.

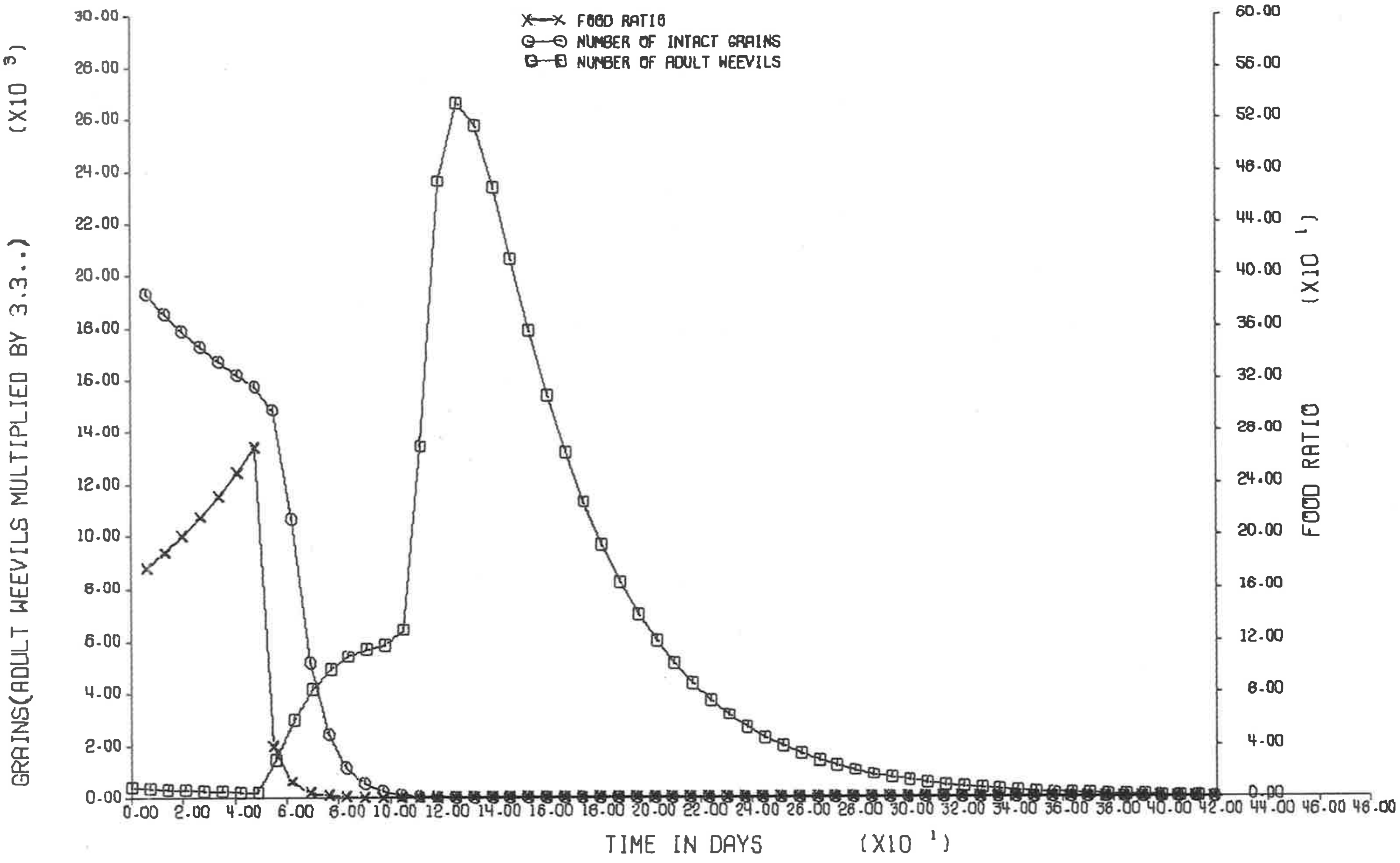
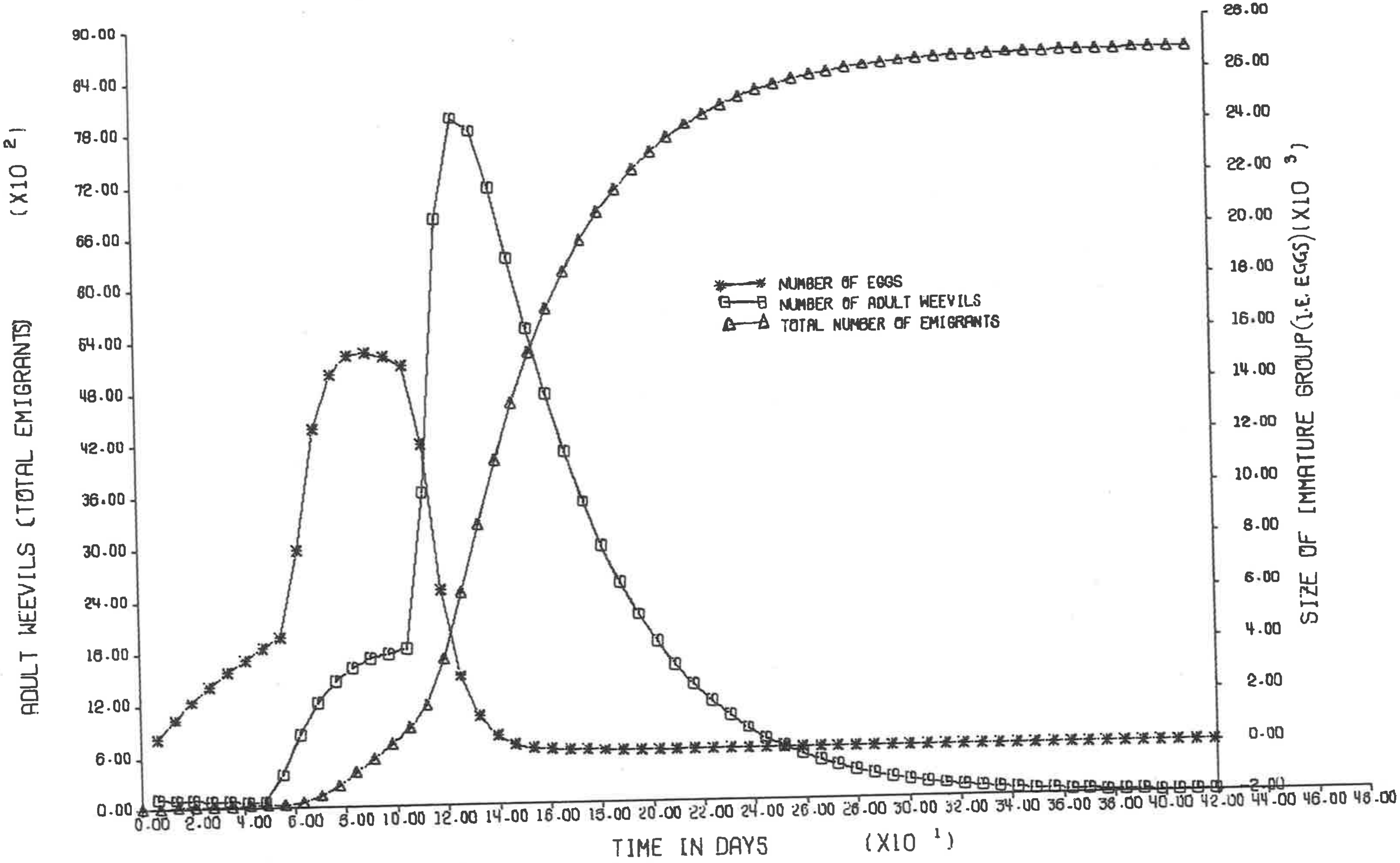

FOOD RATIO
NUMBER OF INTACT GRAINS
NUMBER OF ADULT WEEVILS
GRAINS(ADULT WEEVILS MULTIPLIED BY 3.3..)
(X10 3)
FOOD RATIO
(X10 1)
TIME IN DAYS (X10 1)
0.00
2.00
4.00
6.00
8.00
10.00
12.00
14.00
16.00
18.00
20.00
22.00
24.00
26.00
28.00
30.00
32.00
34.00
36.00
38.00
40.00
42.00
44.00
46.00
48.00
52.00
56.00
60.00

FIGURE 3.1B

Curves for (1) the size of the immature group, $U(t)$,
(2) the number of adult weevils, $W(t)$,
(3) the total number of emigrants, $R(t)$.


90.00
84.00
78.00
72.00
66.00
60.00
54.00
48.00
42.00
36.00
30.00
24.00
18.00
12.00
6.00
0.00
(X10 2)
ADULT WEEVILS (TOTAL EMIGRANTS)
28.00
26.00
24.00
22.00
20.00
18.00
16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
-2.00
SIZE OF IMMATURE GROUP (I.E. EGGS) (X10 3)
NUMBER OF EGGS
NUMBER OF ADULT WEEVILS
TOTAL NUMBER OF EMIGRANTS
0.00
2.00
4.00
6.00
8.00
10.00
12.00
14.00
16.00
18.00
20.00
22.00
24.00
26.00
28.00
30.00
32.00
34.00
36.00
38.00
40.00
42.00
44.00
46.00
48.00
TIME IN DAYS
(X10 1)

increases monotonically from zero to a maximum which occurs after time t^* but before the time at which the population of the adults attains its maximum. Then the size drops rapidly. In other words the rate of emergence of adults increases rapidly. This results in a peak of the population of the adults being reached soon after. The food ratio increases over the first developmental period and then it decreases monotonically and rapidly for the rest of the developmental periods.

3.2 TEMPERATURE VARIATION INCORPORATED

3.2.0 Introduction

For wheat stored in places with fluctuating temperatures there is need to incorporate the temperature effect on the parameters. In large bulks of wheat temperatures take long to change but in small bulks temperature changes are likely to be as fast as the outside temperature changes.

For the weevils, like many insects and animals, there is an interval of temperatures within which the weevils are active. Outside this interval, most of the activities come to a stop and this may result in deaths of the weevils. In the following sections I outline the temperature effects on various activities of the weevils.

3.2.1 Development of the Egg

An egg requires a certain amount of heat energy in order to complete its development into a mature adult.

Thus at low temperatures the rate of development of the egg is small. However the temperatures cannot be increased arbitrarily so as to accelerate the development. In fact there exists an *upper* temperature *threshold,* θ_U , above which a retardation in the development results and even deaths of the immature weevils may occur. Also there exists a *lower* temperature *threshold,* θ_L , below which development stops. In the interval (θ_L, θ_U) there exists a temperature at which the rate of development is maximum. We shall refer to this temperature as the *optimal temperature* (for development) and we shall denote it by θ^*. [For the lower threshold, upper threshold and the optimal temperature in the case of *Sitophilus Oryzae* and *Sitophilus granarius* see row 8 of Table A.1 in Appendix 1.1.]

The curve for the rate of development of an immature weevil is of the form in Figure 3.2. The shape of the development curve in Figure 3.2 is common to many insects and animals. Logan, Wollkind, Hoyt and Tanigoshi (1976) described the rate of development in arthropods in two phases with respect to temperature. For the phase below the optimal temperature θ^* Logal *et al* gave the rate as an increasing exponential function and for the phase above θ^* they gave the rate as a decreasing exponential function of the temperature θ with θ^* and θ_U as parameters. Combining the two functions, Logan *et al* obtained a curve of the shape in Figure 3.2.

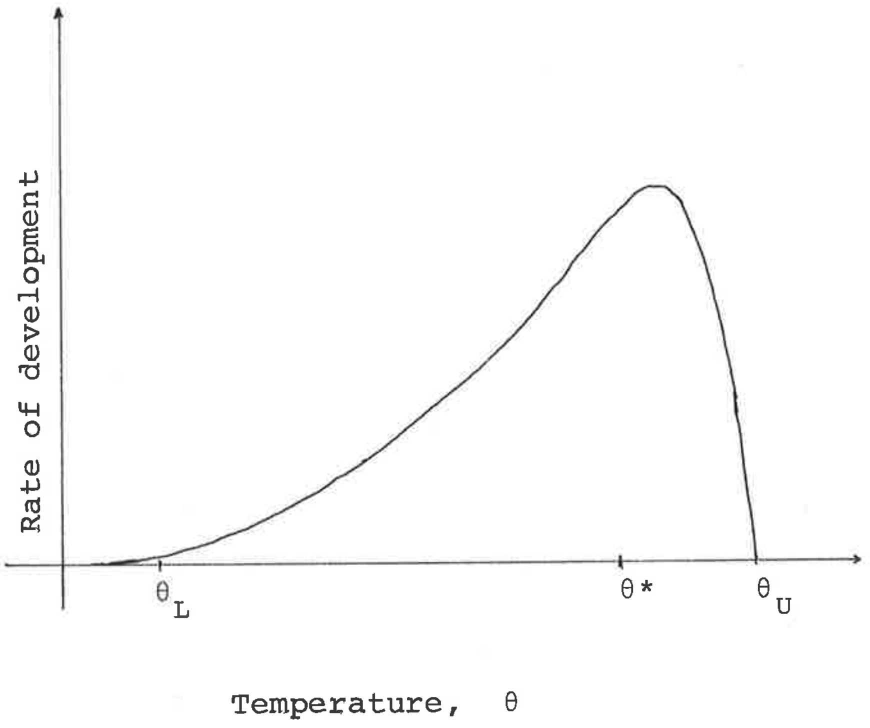


FIGURE 3.2. The curve for the rate of the development of the egg. θ_L, θ^* and θ_U are the lower temperature threshold, the optimal temperature and the upper temperature threshold respectively.

Since in our models we are taking the immature stages of the eggs, larvae, pupal and pre-emergence adults to constitute the immature group, we shall not be concerned with the rates of development of the individual stages but rather with the *accumulative* development. In other words we need to determine the amount of heat energy that has been received by an egg by some point in time. [The effect of temperature on the individual immature stages is well discussed in Birch (1945).]

One of the units used in measuring the heating energy for development is a *day-degree*.

Definition. In simple terms, let us consider the following hypothetical situation. Suppose that on a certain day the temperature remained constant at $\theta_0 (> \theta_L)$, then the amount of heating energy received by an egg (larva, pupa, or even an adult weevil) during that day would be $\theta_0 - \theta_L$ *day-degrees* (D^o). If the temperature remained constant for n days, then the heating energy gained by an individual during those days would be $n(\theta_0 - \theta_L)$ D^o.

For a general situation, the number of day-degrees gained by an individual, in an interval of time, is the area under the temperature curve and between the two temperature thresholds as shown in Figure 3.3. Hardman (1978) estimated the amount of heating energy required by *Sitophilus oryzae* to pass from egg to newly-emerged adult to be 422.7 D^o.

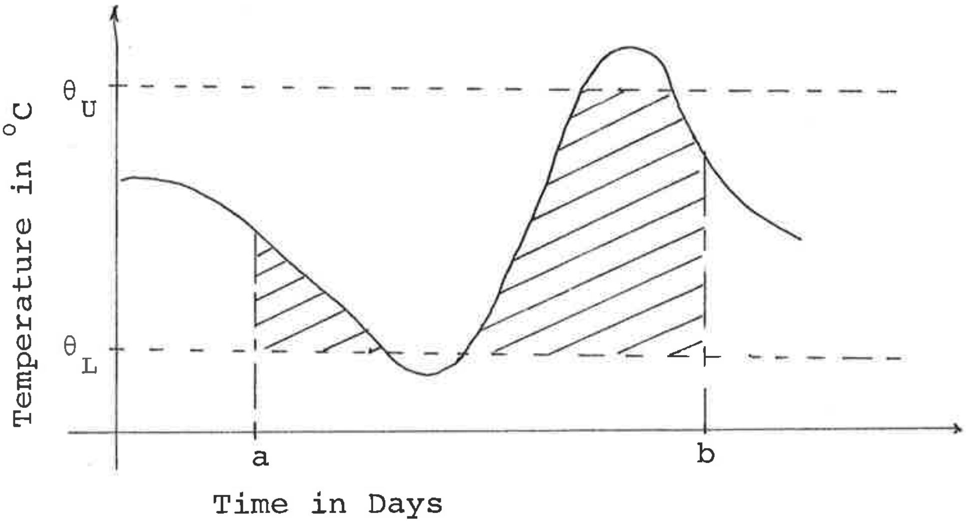


FIGURE 3.3. The shaded area is the number of day-degrees received in the time interval [a,b].

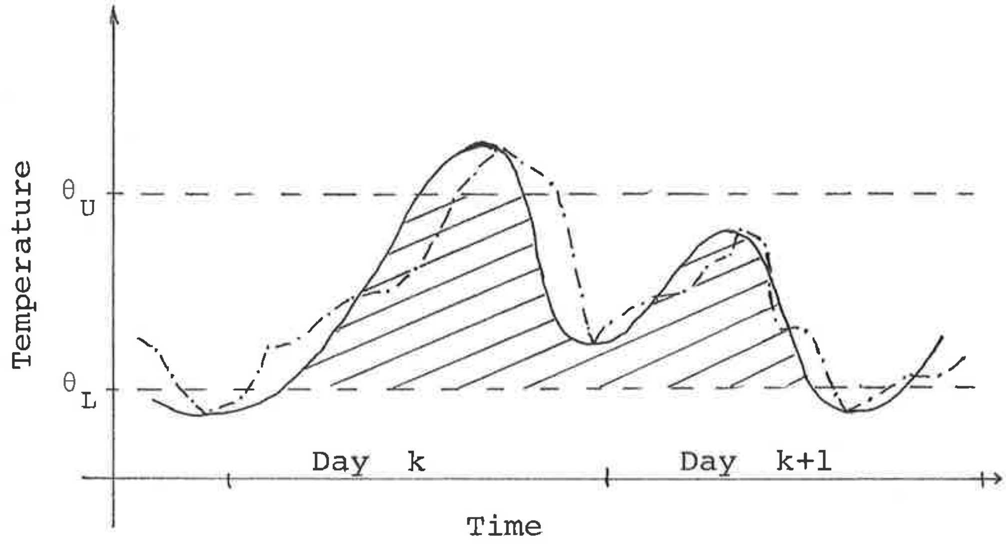


FIGURE 3.4. Observed temperature —·—·—·— is approximated by the smooth modified sine wave ——— .

Note that each insect or egg receives the heating energy independently of the others in the system. In other words individuals who live through the same interval of time receive the same amount of heating energy over the interval.

We should have it borne in mind that temperature is a random function of time. So in order to compute the number of day-degrees accumulated during an interval of time we must have recorded the temperatures over the interval. One way of estimating the number of day-degrees accumulated over the interval is to suppose that the temperature varies according to a *modified sine wave* whose consecutive minima (or maxima) are not necessarily the same, as shown in Figure 3.4. The shaded area in the figure is the accumulated number of day-degrees as estimated by the sine wave.

Allen (1976) used the sine wave approximation technique to derive an algorithm for calculating the number of day-degrees accumulated over a given time interval based on the two temperature thresholds and the daily minima and maxima temperatures recorded over the interval. Allen divided each day into two twelve-hour intervals. Then the minima and maxima temperatures over each of these intervals were the input data into the modified sine wave.

In the Computer Programme II (Appendix 3.2) which incorporates the influence of temperature on the parameters I have adopted Allen's algorithm.

If an adult emerges from an egg at time t then the egg must have been laid at time $\hat{t}$ where $t-\hat{t}$ is the time it took the egg to receive A heating day-degrees required for its full development. Thus the length of the developmental period, $t-\hat{t}$, depends on the seasons through which the egg has developed. According to the output of the Computer Programme II the length of the developmental period could be as short as 31 days for those eggs that develop in summer and as long as 220 days for those which develop through winter.

3.2.2 Effect of Temperature on Mortality Rate

Temperature fluctuations also affect the mortality rate of the immature stages. According to Birch (1945) the larval stage, the longest of the immature stages, is the one which is very susceptible to temperature fluctuations. However since we have combined all the immature stages into a single stage we need only to consider the accumulative effect of temperature on the survival of the eggs. So the proportion, p, of the eggs that survive to mature adults is an accumulative measure of survival of the immature stages. In other words p is a function of each of the temperature points that occur during the development of the egg and its values depend particularly on the extreme temperatures that occur during the development. For this reason it is very difficult to incorporate p as a direct function of instantaneous temperature. However the reduction in p may be indirectly accounted for through the reduced oviposition rate discussed in section 3.2.3.

In adult weevils the mortality rate is expected to increase at extreme temperatures. Between the temperature thresholds θ_L and θ_U the mortality rate is expected to vary according to the curve in Figure 3.5. That is the rate is more or less constant for the temperatures between the lower threshold θ_L and the optimal temperature θ^*. Above θ^* it increases rapidly.

In Chapter 2 it was assumed that, for optimal temperature conditions, the mortality rate remains constant even in phase II. So now by incorporating temperature the mortality rate is

$$\mu(t) = \mu(\theta(t)) \tag{3.2.1}$$

where $\mu(\theta)$ is of the form in Figure 3.5 and $\mu(\theta^*)$ is the constant mortality rate used in Chapter 2.

3.2.3 Effect of Temperature on Oviposition Rate

The oviposition is affected by temperature in the same way as the development of the egg. That is there is an interval of temperatures within which oviposition is possible. At temperatures outside this interval oviposition stops. Also there is an *optimal* temperature at which the oviposition rate is maximum. According to Birch's (1945) observations the lower

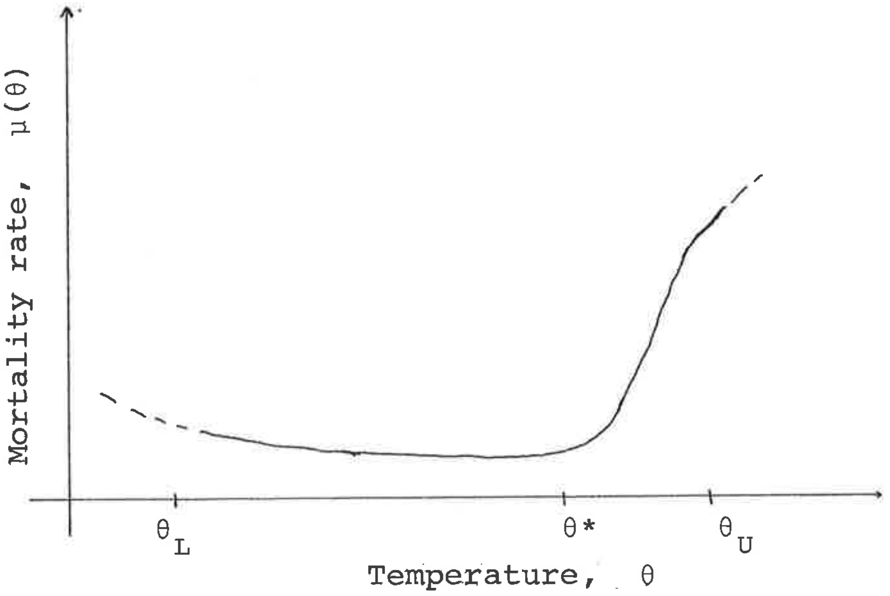


FIGURE 3.5. Effect of temperature on the mortality rate of adult weevils.

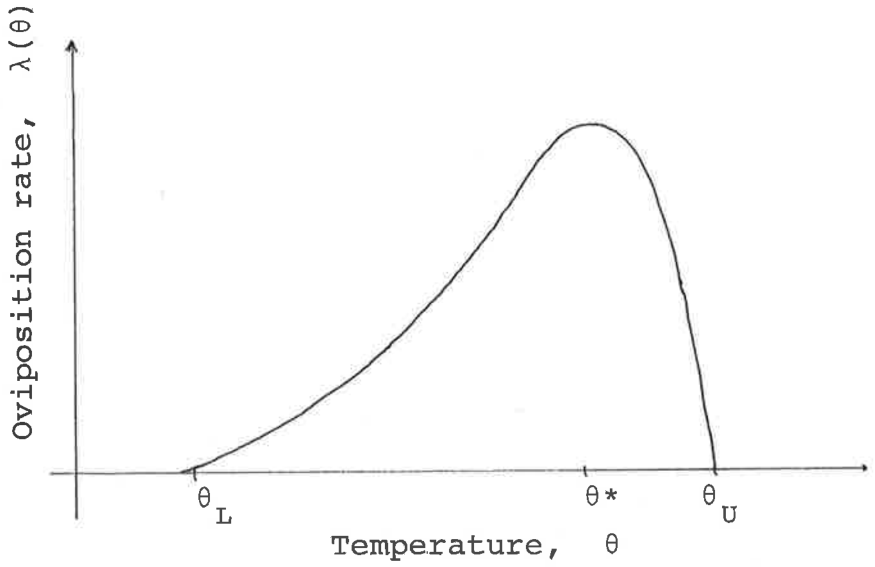


FIGURE 3.6. The oviposition rate as a function of temperature.

temperature threshold, the optimal temperature and the upper threshold, for *Sitophilus oryzae*, are 15.2°C, 29.1°C and 34.6°C respectively. The oviposition rate curve is of the form shown in Figure 3.6.

Now combining the temperature and the food ratio influences the resultant oviposition rate is

$$\lambda(t) = \begin{cases} \lambda(\theta(t)) & \text{for } S(t) > CW(t) \\ \lambda(\theta(t))S(t)/CW(t) & \text{for } S(t) \leqslant CW(t) \end{cases} \tag{3.2.2}$$

where the factor $\lambda(\theta(t))$ is given by the curve in Figure 3.6 and $\lambda(\theta^*)$ is the oviposition rate in phase I under optimal temperature conditions.

3.2.4 The Consumption Rate

The consumption rate, ν, at which adults eat the wheat grain is assumed to remain constant. That is, it is independent of density and temperature.

3.2.5 The Emigration Rate

I have not come across any literature on how the emigration of weevils is influenced by temperature. However the emigration rate is expected to increase with increasing temperature. This is because the weevils become more active as the temperature rises. But there is a limit to how high the temperature can rise before the activeness is drastically reduced. Also

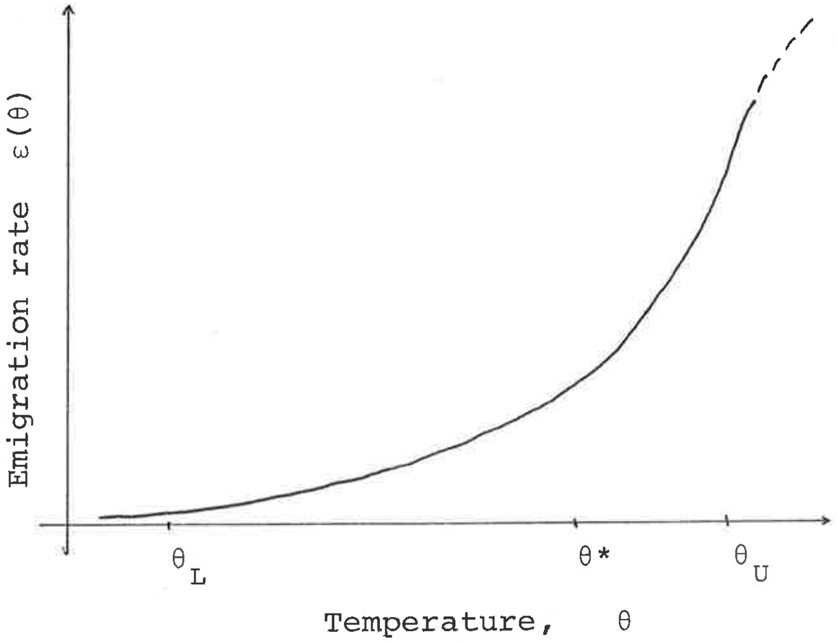


FIGURE 3.7. The emigration rate as a function of temperature.

we assume the existence of a lower temperature threshold below which the weevils are so dormant that they cannot emigrate. In general we expect the emigration rate curve to be of the form in Figure 3.7.

With the food availability factor and the temperature effect combined, the resultant emigration rate is given by

$$\varepsilon(t) = \begin{cases} \varepsilon(\theta(t)) & \text{for } S(t) > CW(t) \\ \varepsilon(\theta(t))\,[1+bC-bS(t)/W(t)] & \text{for } S(t) \leqslant CW(t) \end{cases} \qquad (3.2.3)$$

where $\varepsilon(\theta)$ is of the form in Figure 3.7 and $\varepsilon(\theta^*)$ is the emigration rate at the optimal temperature in phase I.

3.2.6 The Emergence Rate

When the temperature influence on the developmental period is incorporated the rate at which adults emerge from the eggs at t is given by

$$\eta(t) = p'\lambda(\theta(\hat{t}))W(\hat{t}) \qquad (3.2.4)$$

where p' is the new proportion of eggs that are expected to survive the immature stages and $\hat{t}$ is the time at which the eggs, from which adults are emerging at time t, were laid. If the temperatures over the interval $(0,t)$ have been recorded then $\hat{t}$ can be determined by using the requirement that in the $t-\hat{t}$ days the amount of A heating day-degrees must have been received by each of the emerging insects (see Section 3.2.1).

3.2.7 The Equations Incorporating Temperature and Food Ratio

Now the equations which incorporate both the temperature and the food ratio can be deduced from the optimal temperature equations (3.1.1) by replacing the constants $\lambda, \mu, \varepsilon$ and p by $\lambda(\theta(t))$, $\mu(\theta(t))$, $\varepsilon(\theta(t))$ and p' respectively and the new expression for the emergence rate $\eta(t)$ is given by (3.2.4).

In most situations the functions $\lambda(\theta)$, $\mu(\theta)$ and $\varepsilon(\theta)$ are unknown. However if some values of a parameter $\xi(\theta)$ can be determined (experimentally) at a few temperature points, then the values of the parameter at other temperature points may be estimated by linear interpolation. If, for example, we use the values of the parameter ξ at the lower temperature threshold θ_L, the optimal temperature θ^* and the upper temperature threshold θ_U, then the linear interpolation for ξ on (θ_L, θ_U) is given by

$$\xi(\theta) = \begin{cases} \xi_L + (\xi^*-\xi_L)\left(\dfrac{\theta - \theta_L}{\theta^*-\theta_L}\right) & \text{for} \quad \theta < \theta^* \\ \xi^* + (\xi_U-\xi^*)\left(\dfrac{\theta-\theta^*}{\theta_U-\theta^*}\right) & \text{for} \quad \theta > \theta^* \end{cases} \qquad (3.2.5)$$

where $\xi_L = \xi(\theta_L)$, $\xi^* = \xi(\theta^*)$ and $\xi_U = \xi(\theta_U)$.

In the computer programme II I have used the formulae (3.2.5) in computing the values of the parameters $\lambda(\theta)$, $\mu(\theta)$, and $\varepsilon(\theta)$.

3.2.8 The Computer Programme II: Input/Output

Input

The daily minimum and maximum temperatures used as the input for the programme were recorded from December 1, 1977 in one of the experimental sheds at the Waite Agricultural Research Institute, University of Adelaide.

The values of the parameters used in the programme were as follows:

$\theta_L = 13^\circ C$ and $\theta_U = 1000^\circ C$ for development;

$\theta_L = 12^\circ C$, $\theta^* = 22^\circ C$ and $\theta_U = 26^\circ C$ for the other activities such as oviposition and emigration;

$\lambda(\theta^*) = 1.0$, $\mu(\theta^*) = 0.008333$, $\varepsilon(\theta^*) = 0.006436$;

$\lambda(\theta_L) = 0.$, $\mu(\theta_L) = \mu(\theta^*)$, $\varepsilon(\theta_L) = 0.10 \times \varepsilon(\theta^*)$;

$\lambda(\theta_U) = 0.$, $\mu(\theta_U) = 2.0 \times \mu(\theta^*)$, $\varepsilon(\theta_U) = \varepsilon(\theta^*)$;

$p = 0.7$; $C = 10$; $\nu = 0.021285$; and $b = 0.12$.

The initial number of grains $S_0 = 20000$ ($\cong$ 600 g of variety 8156 Olympic wheat). Runs of the programme were done for the initial numbers of 240, 120, 60 and 30 adult weevils.

Note that the temperature thresholds for the development of the egg (that is for the computation of heating day-degrees) are different from those for the other activities such as oviposition and emigration. It is assumed that these activities, other than the development of the eggs, share the same temperature thresholds and the same optimal temperature. In the real situation these temperatures may be different. Note also that the upper temperature threshold for development was set to an arbitrary large value ($1000^{\circ}C$), for theoretically the higher the temperature the greater the number of heating day-degrees accumulated in a unit time.

The data above are for *Sitophilus oryzae*. However I should point out that the values of the temperature thresholds and the optimal temperature are lower than those quoted from the cited literature (see row 8 of Table A.1). The explanation is as follows. The values of the parameters as given in Table A.1 were determined at constant (optimal) temperatures. I would say there is a difference between the optimal temperature for cultures of weevils reared at constant temperatures and the optimal temperature for cultures reared at fluctuating temperatures. In the later case the weevils tend to acclimatize to the variable conditions. So instead of regarding a single temperature as the optimal one we would have an optimal interval of temperatures. This interval could be represented by an average temperature in which case this average temperature would be less than the optimal temperature for cultures reared at constant temperatures. In order to minimise errors in the estimation of the daily average temperatures by using the mean of the daily minimum and maximum temperatures, I used the average of three temperature points: the minimum in the morning (night), the maximum during the day, and the minimum in the evening (night). Then I realised that only one of the average temperatures (of 31.3°C) obtained this way exceeded the optimal temperature of 29.1°C for oviposition as given by Birch (1953) (see row 6(a) of Table A.1). So I had to lower the thresholds and the optimal temperature accordingly to the values given above. I should say that these values may not be the best to use. However, according to the range of the average temperatures obtained by using the three-temperature-points technique, it did not make any significant difference in the computer output when the optimal (average) temperature and/or the upper threshold were increased by ±1 or ±2°C.

Output

According to the output of the programme, as mentioned at the end of Section 3.2.1, the developmental period could be as short as 31 days for the eggs which developed through the summer period of December 1978-January 1979, and as long as 220 days for the eggs which developed through part of Autumn, the winter and spring of 1978. These values compare well with Birch's (1945) observations of 27.7 days at the supposedly optimal temperature of 29.1°C and 230 days at 15.2°C for one egg of *Sitophilus oryzae* per grain.

Figures 3.8 and 3.9 are the graphical output of the programme for the initial numbers of weevils $W_0 = 120$ and 30 respectively. The curves for $S(t)$ and $F(t)$

FIGURE 3.8A

Curves for (1) the Food Ratio
(2) Number of Intact Grains
(3) Number of Adult Weevils
(4) Temperature (December 1, 1977 - February 1, 1979)
for the initial number of $W_0 = 120$ weevils, in 20,000 grains.

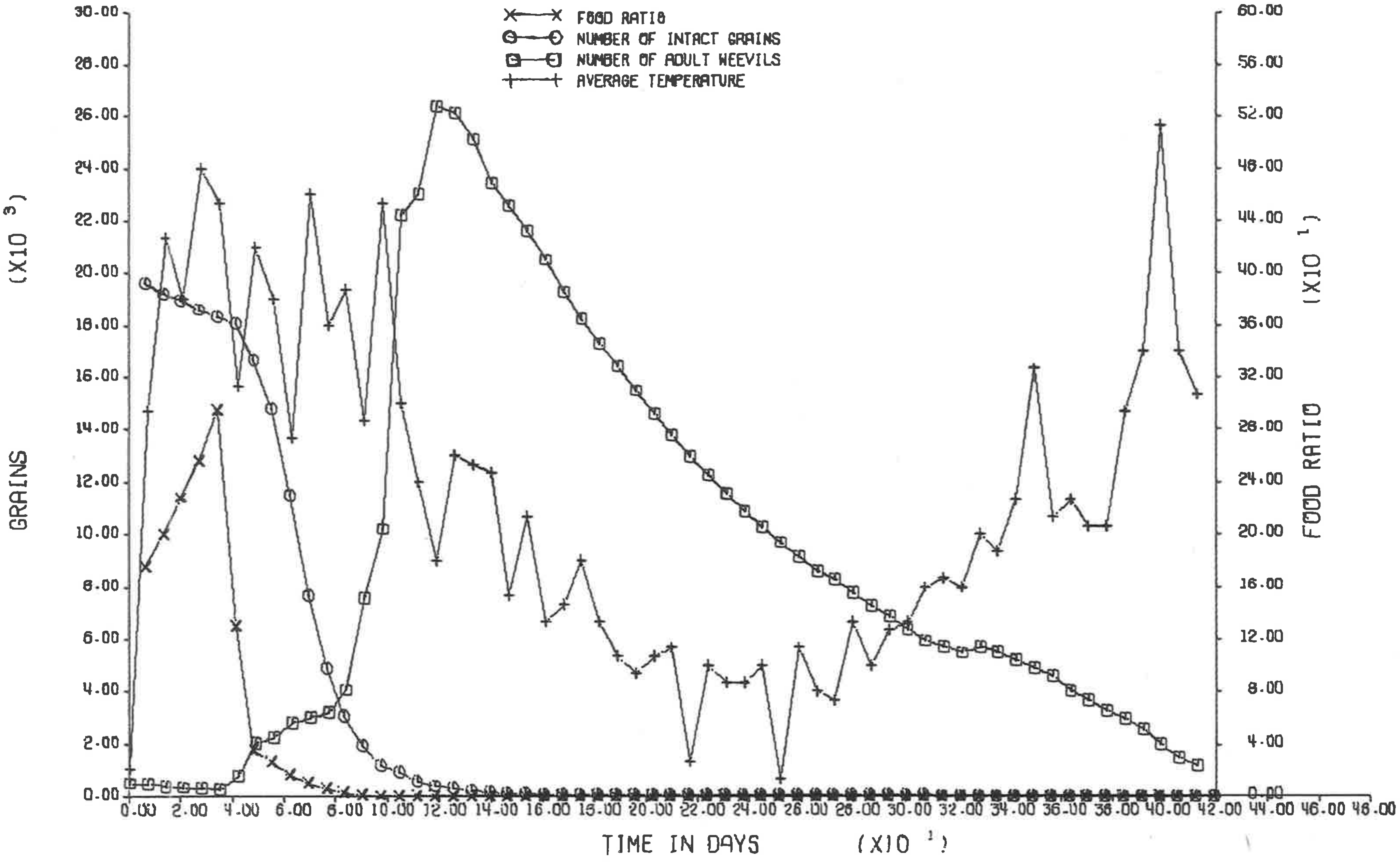

FOOD RATIO
NUMBER OF INTACT GRAINS
NUMBER OF ADULT WEEVILS
AVERAGE TEMPERATURE
GRAINS
(X10 3)
FOOD RATIO
(X10 1)
TIME IN DAYS (X10 1)
0.00
2.00
4.00
6.00
8.00
10.00
12.00
14.00
16.00
18.00
20.00
22.00
24.00
26.00
28.00
30.00
0.00
4.00
8.00
12.00
16.00
20.00
24.00
28.00
32.00
36.00
40.00
44.00
48.00
52.00
56.00
60.00
0.00
2.00
4.00
6.00
8.00
10.00
12.00
14.00
16.00
18.00
20.00
22.00
24.00
26.00
28.00
30.00
32.00
34.00
36.00
38.00
40.00
42.00
44.00
46.00
48.00

FIGURE 3.8B

Curves for (1) Temperature (December 1, 1977-February 1, 1979)
(2) Size of Immature Group
(3) Number of Adult Weevils
(4) Total Number of Emigrants
for the initial number of W_0 = 120 weevils in 20,000 grains.

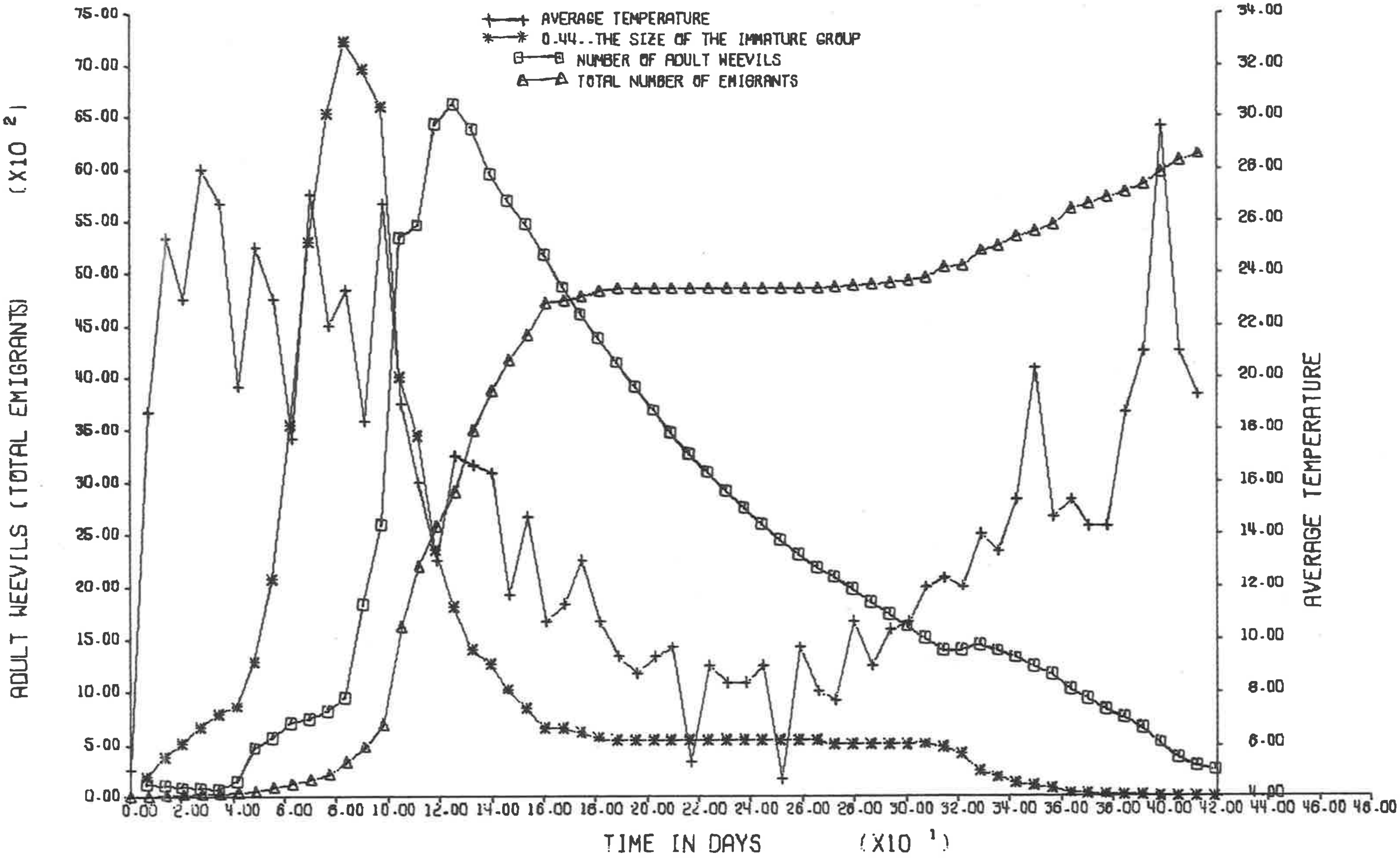

AVERAGE TEMPERATURE
0.44..THE SIZE OF THE IMMATURE GROUP
NUMBER OF ADULT WEEVILS
TOTAL NUMBER OF EMIGRANTS
ADULT WEEVILS (TOTAL EMIGRANTS)
(X10 2)
AVERAGE TEMPERATURE
TIME IN DAYS
(X10 1)
0.00
5.00
10.00
15.00
20.00
25.00
30.00
35.00
40.00
45.00
50.00
55.00
60.00
65.00
70.00
75.00
4.00
6.00
8.00
10.00
12.00
14.00
16.00
18.00
20.00
22.00
24.00
26.00
28.00
30.00
32.00
34.00
0.00
2.00
4.00
6.00
8.00
10.00
12.00
14.00
16.00
18.00
20.00
22.00
24.00
26.00
28.00
30.00
32.00
34.00
36.00
38.00
40.00
42.00
44.00
46.00
48.00

FIGURE 3.9A

Curves for (1) Food Ratio
(2) Number of Intact Grains
(3) Number of Adult Weevils
(4) Temperature (December 1, 1977-February 1, 1979)
for the initial number of W_0 = 30 weevils in 20,000 grains.

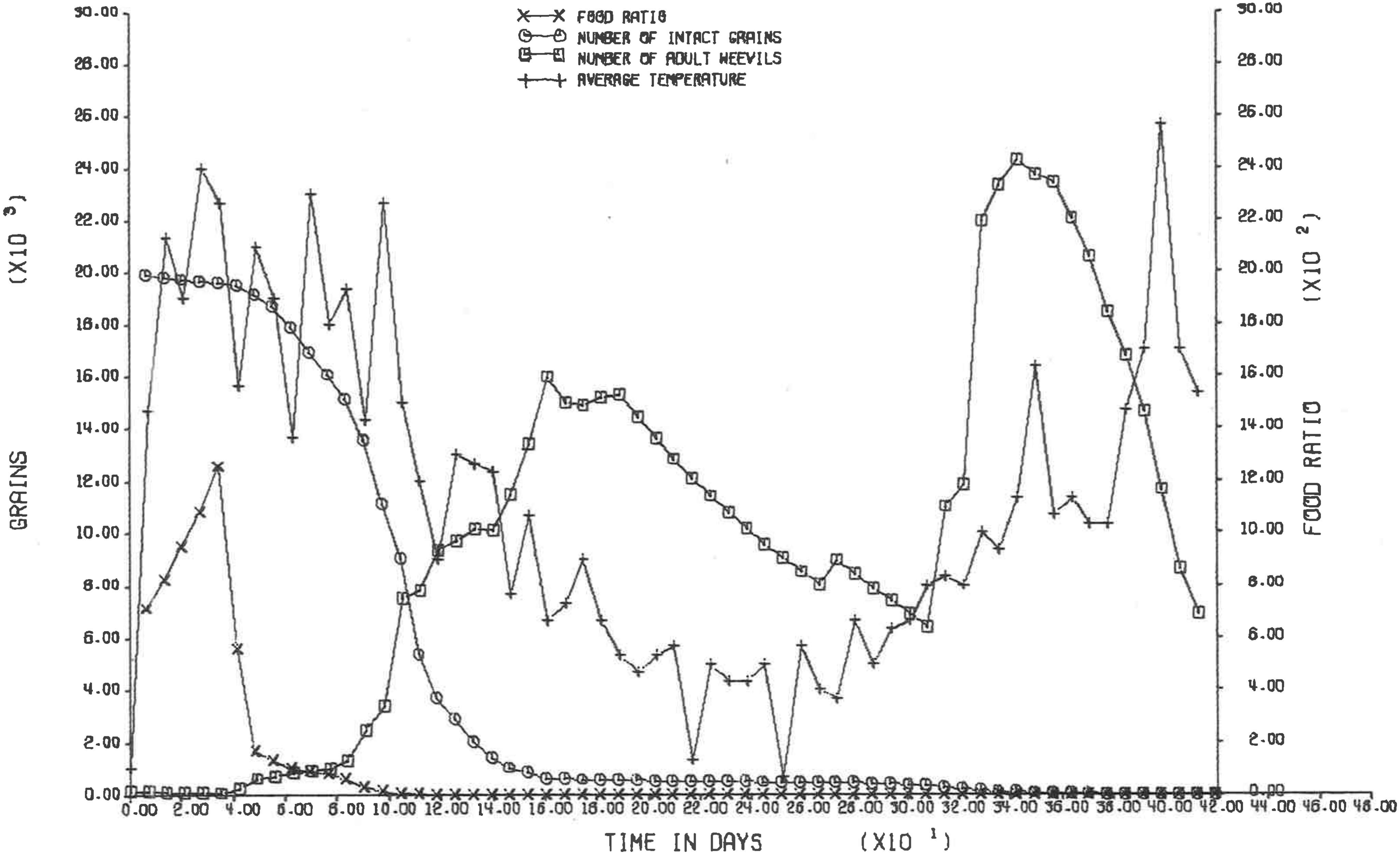
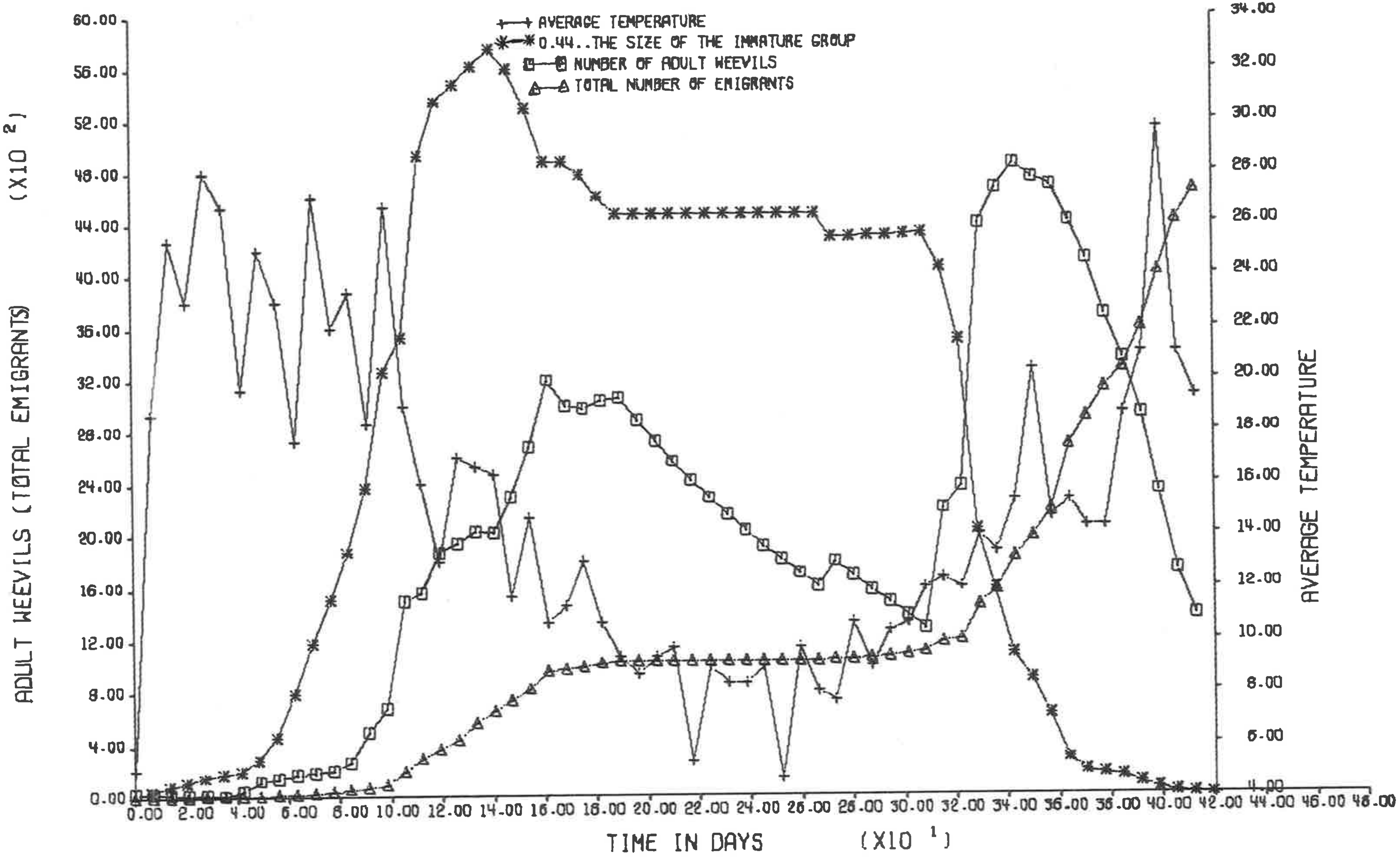

FOOD RATIO
NUMBER OF INTACT GRAINS
NUMBER OF ADULT WEEVILS
AVERAGE TEMPERATURE
GRAINS
(X10 3)
FOOD RATIO
(X10 2)
TIME IN DAYS
(X10 1)
0.00
2.00
4.00
6.00
8.00
10.00
12.00
14.00
16.00
18.00
20.00
22.00
24.00
26.00
28.00
30.00
32.00
34.00
36.00
38.00
40.00
42.00
44.00
46.00
48.00

FIGURE 3.9B

Curves for (1) Temperature (December 1, 1977-February 1, 1979)
(2) Size of Immature Group
(3) Number of Adult Weevils
(4) Total Number of Emigrants
for the initial number of $W_0 = 30$ weevils in 20,000 grains.


AVERAGE TEMPERATURE
0.44..THE SIZE OF THE IMMATURE GROUP
NUMBER OF ADULT WEEVILS
TOTAL NUMBER OF EMIGRANTS
ADULT WEEVILS (TOTAL EMIGRANTS)
(X10 2)
AVERAGE TEMPERATURE
TIME IN DAYS
(X10 1)
0.00
4.00
8.00
12.00
16.00
20.00
24.00
28.00
32.00
36.00
40.00
44.00
48.00
52.00
56.00
60.00
2.00
6.00
10.00
14.00
18.00
22.00
26.00
30.00
34.00
38.00
42.00
46.00
48.00

are similar to the corresponding curves in Figure 3.1A for optimal temperature condition. Though the curve for W(t) is similar to that in Figure 3.1 there is a rise in the curve in Figures 3.8 and 3.9 at the end of Winter. This rise, which is absent in Figure 3.1, is due to the relatively large number of adults emerging from the eggs whose developmental periods had been lengthened by Winter temperatures. The rise is more pronounced in the case of the initial number of 30 weevils. Unlike in the case of optimal temperature (Figure 3.1B) the curves for U(t) and R(t) in Figures 3.8B and 3.9B are rather flat in Winter. The stationary feature of U(t) in Winter is due to the reduced rate of oviposition combined with the reduced rate of emergence; and that for R(t) is due to the reduced rate of emigration.

Also from the output of programme II we have Table 3.2 which shows the times, t*, at which the critical food ratio was reached in the four cases of the initial numbers of 240, 120, 60 and 30 weevils. The times t_{10}, t_1 are the times at which there were 10 intact grains and 1 intact grain, respectively, remaining in the system.

Note that in the case of the initial number of 240 weevils the values of t* in Tables 3.1 and 3.2 are nearly the same (that is t* = 55 days for the

There appears to be a contradiction here between the performance of weevils under real and optimal temperature conditions, in that the weevils have reached t^* earlier under real conditions than under supposedly optimal conditions. However, the problem is overcome by referring to the definition of optimal temperature conditions (p. 10), especially the comment "there is no reason to believe that weevil growth, grain depletion or time to the critical temperature will attain their maximum or minimum values under these conditions".

TABLE 3.2. Times t^*, t_{10}, t_1 (days) at which the critical food ratio was reached, 10 grains were remaining and 1 grain was remaining for the initial number of W_0 weevils when the temperature was incorporated.

W_0	t^*	t_{10}	t_1
240	55	315	372
120	72	341	388
60	88	369	413
30	102	388	427

variable temperature conditions and $t^* = 56$ days for the optimal temperature conditions). This implies that the Summer temperatures correspond to the optimal range of temperatures. Insert : See opposite page ^ For the other initial numbers of weevils phase I was prolonged due to the Autumn and Winter weather which commenced before the critical food ratio had been reached.

Finally I compare the total number of emigrants, $R(t)$, determined experimentally by Mr S. Mlambo at the Waite Agricultural Research Institute, University of Adelaide, with the corresponding output of programme II at several time points as shown in Table 3.3. According to Table 3.3 there is a reasonable agreement between the observed and the computed total number of emigrants for the initial numbers of $W_0 = 240$, 120 and 60 weevils. In

TABLE 3.3. Comparison between the observed and computed total number of emigrants, $R(t)$, from systems which started in December 1, 1977 with W_0 = 240, 120, 60 and 30 weevils in 20,000 grains. In each case the initial ratio of females to males was 1:1.

Day	F/nght Ending	TOTAL NUMBER OF EMIGRANTS							
		Observed	Computed	Observed	Computed	Observed	Computed	Observed	Computed
		For W_0 = 240		For W_0 = 120		For W_0 = 60		For W_0 = 30	
0	1/12/77	0	0	0	0	0	0	0	0
22	22/12/77	-	31	-	16	-	8	-	4
64	2/2/78	329	243	134	99	66	50	11	25
120	30/3/78	2012	3420	940	2084	636	951	24	370
176	25/5/78	3060	4948	1704	3835	1041	2183	33	1001
232	20/7/78	3192	4987	2052	3885	1115	2239	38	1036
288	14/9/78	3805	5007	3025	3914	2638	2275	41	1060
344	9/11/78	4655	5270	4265	4285	3035	2869	59	1860
400	4/1/79	4827	5582	4780	4798	4401	4018	126	4115
427	1/2/79	5493	5703	5071	4975	-	4432	-	4953

the case of $W_0 = 30$ the computed number of emigrants is far greater than the observed ones. The big differences may be due to lack of the weevils to aggregate for the purpose of mating. Individuals wander about the habitat for a long time before they can meet one another. Hence the oviposition rate would be drastically reduced resulting in a very slow growth of the population and hence the small number of emigrants.

The $W_0 = 30$ case tends to suggest that there is an interval for the food ratio within which emigration (as well as other activities) is independent of the food ratio. Outside this interval (that is at low food ratio as well as high food ratio) it is a function of the food ratio. In fact MacLagan (1932) pointed out that his experiments indicated that if the number of wheat grains were increased from 400 per female weevil to 800 or even 600, there followed a reduction in the number of progeny, which meant there was an optimal degree of crowding (or food supply per weevil) in regard to the number of eggs oviposited. So it seems that the food ratio of 800 grains per female weevil (that is 400 grains per weevil if the ratio of females to males is 1:1) is another critical food ratio which is not incorporated in our equations. However we should note that for the initial number of $W_0 = 240$, 120, and 60 weevils in 20,000 grains the food ratio is less than 400 grains per weevil. Hence, for these initial conditions our equations should be alright.

According to the discussion in the previous two paragraphs the two-phase formulation would be applicable to quantities of wheat and initial numbers of weevils used in laboratory experiments in which the initial food ratio is not too high. For large quantities of wheat such as those stored in silos (with small initial numbers of weevils) we would need to consider a three-phase formulation. So this is another approach that could be considered for future models.

CHAPTER 4

A STOCHASTIC MODEL FOR PHASE I

4.1 INTRODUCTION

The model discussed in this chapter is a stochastic version of the deterministic model in Section 2.1. In the present model the parameters are no longer deterministic but probabilistic. That is, for example, with the oviposition rate as λ eggs/day/weevil we mean that the probability that a weevil oviposits an egg in an infinitesimal time interval $(t,t+\delta t)$ is $\lambda\delta t$. So the number of intact grains, $S(t)$; the number of adult weevils, $W(t)$; the size of the immature group, $U(t)$; and the total number of emigrants, $R(t)$, at time t, are random variables. We still define the random variable for the food ratio as $F(t) = S(t)/W(t)$.

In any situation a stochastic version of a deterministic model, if possible, enables us to determine or estimate the variances (and higher moments), in addition to the means, of the variables involved. Also the stochastic mean of a random variable may be used as a check on the accuracy and/or validity of the corresponding deterministic value of the variable. For example for our grain-weevil system it is shown in Section 4.5.1 that the stochastic mean of the number of intact grains is not the same as the deterministic solution obtained in Section 2.1.

In the stochastic version we consider the distribution of the bivariate process $\{S(t), W(t), t \geq 0\}$. Let us recall from Section 2.1.1 that during phase I the weevil population is not influenced by the number of intact grains available but the weevils destroy the grains. So the distribution of $W(t)$ can be derived independently of the distribution of $S(t)$. Then using the conditional distribution of $S(t)$ given a sample path of $\{W(\zeta), \zeta \leq t\}$ the distribution (moments, in particular) of $S(t)$ may be determined.

The differential equations for the conditional probabilities

$$p_s(t|W(\cdot)) = P(S(t) = s|\{W(\zeta), \zeta \leq t\})$$

are derived and solved recursively. However in an attempt to obtain expressions for the conditional moments or the probability generating function (p.g.f.) of $S(t)$, the solutions prove cumbersome to use. In order to reduce the difficulty in handling the p.g.f. of $S(t)$ an artificial variable $\hat{S}(t)$ is introduced to represent $S(t)$. The variable $\hat{S}(t)$ takes on the positive values with the same probabilities as $S(t)$. But, unlike $S(t)$, $\hat{S}(t)$ takes on, also, the artificial values $-1, -2, \ldots, -\infty$. The equations for the means of $\hat{S}(t)$ and $W(t)$ work out to be the same as the ones for $S(t)$ and $W(t)$, respectively, in the deterministic model in Section 2.1. But, since $\hat{S}(t) \neq S(t)$, this implies that the mean of the random variable $S(t)$ does not satisfy the same equation as the deterministic variable $S(t)$. In section 4.7 it is shown that the mean of $\hat{S}(t)$ is a lower bound of the mean of $S(t)$.

The conditional p.g.f. of $\hat{S}(t)$ given $\{W(\zeta), \zeta \leqslant t\}$ is used in the derivation of an approximate joint p.g.f. of $\hat{S}(t)$ and $W(t)$. In the derivation the emergence process $\{\eta(t), t \geqslant 0\}$ is regarded as an immigration process that is independent of the adult weevil population. Two independent methods (one of which is the method of "marks and catastrophe") are used to obtain the approximate expression for the joint p.g.f.

The means of $\hat{S}(t)$ and $W(t)$ are used in determining an estimate of the time t^* at which the food ratio is expected to drop to the critical value C for the first time.

4.2 A REVIEW OF THE ASSUMPTIONS

With the same environmental conditions assumed for phase I in Section 2.1 the oviposition rate of λ eggs/day/weevil, the rates of emigration and mortality of ε and μ, respectively, weevils/day/weevil and the consumption rate of ν grains/weevil/day are constants. Also the proportion, p, of the eggs that are expected to develop into mature adults is a constant. The expected length of the developmental period, from egg to mature adult, is taken to be equal to a fixed number of a days.

As in the deterministic case (section 2.1) phase I corresponds to $F(t) > C$ (or $S(t) > CW(t)$). When the food ratio $F(t)$ drops to and below the critical value C the formulation presented in this chapter will no longer be valid. The models for the phase II (that is, for $F(t) \leqslant C$) are discussed in Chapter 5.

At time $t=0$ there are S_0 intact grains and W_0 mature weevils in the system. The size of the immature age group, at the time, is zero.

Given a sample path of the weevil population, $\{W(t), t \geqslant 0\}$, the wheat grains are destroyed at the rate

$$\tilde{\alpha}(t) = (\lambda+\nu)W(t) \tag{4.2.1}$$

and the rate at which mature adults emerge from the immature age group is

$$\eta(t) = p\lambda W(t-a) \tag{4.2.2}$$

where the parameters in the right hand sides of (4.2.1) and (4.2.2) are as defined in the first paragraph above.

4.3 THE DISTRIBUTION OF THE WEEVILS (INSECTS)

Since there are no young weevils emerging from the eggs over the time interval $0 \leqslant t < a$, $\{W(t), 0 < t \leqslant a\}$ is equivalent to a death process in which the "death" rate, κ, is the sum of the death rate μ and the emigration rate ε. That is $\kappa = \mu+\varepsilon$. Hence with W_0 adult weevils at time $t=0$

$$P(W(t) = w) = \binom{W_0}{w} e^{-w\kappa t}(1-e^{-\kappa t})^{W_0-w}$$

for $0 < t \leqslant a$. Therefore

$$\left.\begin{aligned} E[W(t)] &= W_0 e^{-\kappa t} \\ \mathrm{Var}[W(t)] &= W_0 e^{-\kappa t}(1-e^{-\kappa t}) \end{aligned}\right\} \qquad (4.3.1)$$

for $0 \leqslant t \leqslant a$.

Let us denote the n-th developmental period, that is the time interval $((na,(n+1)a]$, by $\mathcal{D}_n$. Next let us consider the conditional distribution of $W(t)$, $t \in \mathcal{D}_n$ given a sample path of $\{W(\zeta), \zeta \in \mathcal{D}_{n-1}\}$.

For $n \geqslant 1$, $\{W(t), t \in \mathcal{D}_n\}$ is a death-emergence process in which the emergence rate is given by (4.2.2). Then, for $t \in \mathcal{D}_n$, the probabilities

$$p_w(t|\{W(\zeta), \zeta \in \mathcal{D}_{n-1}\}) \triangleq P(W(t) = w|\{W(\zeta), \zeta \in \mathcal{D}_{n-1}\})$$

satisfy the difference-differential equations

$$\frac{dp_w}{dt} = -[\kappa w+\eta(t)]p_w(t) + \kappa(w+1)p_{w+1}(t) + \eta(t)p_{w-1}(t) \qquad (4.3.2)$$

with $p_w \equiv 0$ for $w < 0$.

Multiplying (4.3.2) by y^w and summing over $w \geqslant 0$ we can show that the p.g.f.

$$G_n(t|\{W(\zeta), \zeta \in \mathcal{D}_{n-1}\}) = \sum_w y^w p_w(t|\{W(\zeta), \zeta \in \mathcal{D}_{n-1}\})$$

satisfies the differential equation

$$\frac{\partial G_n}{\partial t} = -\kappa(y-1)\frac{\partial G_n}{\partial y} + (y-1)\eta(t)G_n . \qquad (4.3.3)$$

The auxiliary equations for (4.3.3) are

$$\frac{dt}{1} = \frac{dy}{\kappa(y-1)} = \frac{dG_n}{(y-1)\eta(t)G_n} .$$

Hence we have

$$\frac{dy}{dt} = \kappa(y-1) \Rightarrow (y-1) = Ae^{\kappa t} \qquad (4.3.4)$$

where A is a constant; and

$$d(\ell n\ G_n) = (y-1)\eta(t)dt .$$

Now substituting for $(y-1)$ from (4.3.4) and integrating we obtain

$$G_n \exp\{-\int_{na}^{t} A\eta(\tau)e^{\kappa\tau}d\tau\} = \text{constant}$$

$$= \Phi(A) , \text{ say.} \qquad (4.3.5)$$

Substituting for A from (4.3.4) we have

$$G_n \exp\{-(y-1)\int_{na}^{t} \eta(\tau)e^{-\kappa(t-\tau)}d\tau\}$$

$$= \Phi((y-1)e^{-\kappa t}) . \qquad (4.3.6)$$

Now using the initial condition

$$G_n(na|\{W(\zeta),\ \zeta \in \mathcal{D}_{n-1}\}) = y^{W(na)}$$

we have

$$y^{W(na)} = \Phi((y-1)e^{-\kappa na})$$

which implies that

$$\Phi(\theta) = [\theta e^{\kappa na} + 1]^{W(na)} \quad .$$

Hence from (4.3.6) we have

$$\begin{aligned} G_n(t|\{W(\zeta),\ \zeta \in \mathcal{D}_{n-1}\}) &\\ &= [1 + (y-1)e^{-\kappa(t-na)}]^{W(na)} \times \\ &\quad \exp\{(y-1)\int_{na}^{t} \eta(\tau)e^{-\kappa(t-\tau)}\} \end{aligned} \tag{4.3.7}$$

Then from the p.g.f. (4.3.7) we obtain the conditional expectation of $W(t)$, $t \in \mathcal{D}_n$, to be

$$\begin{aligned} E[W(t)|\{W(\zeta),\ \zeta \in \mathcal{D}_{n-1}\}] &\\ &= W(na)e^{-\kappa(t-na)} + \int_{na}^{t} \eta(\tau)e^{-\kappa(t-\tau)}d\tau \end{aligned} \tag{4.3.8}$$

and the conditional variance

$$\begin{aligned} \mathrm{Var}[W(t)|\{W(\zeta),\ \zeta \in \mathcal{D}_{n-1}\}] &\\ &= W(na)e^{-\kappa(t-na)}(1-e^{-\kappa(t-na)}) \\ &\quad + \int_{na}^{t} \eta(\tau)e^{-\kappa(t-\tau)}d\tau \ . \end{aligned} \tag{4.3.9}$$

<u>Proposition 4.1</u> The stochastic mean, $E(W(t))$, of the number of adult weevils is the same as the deterministic value of $W(t)$ determined in Section 2.1.2.

<u>Proof</u>. From (4.3.8) we have

$$E[W(t)] = E[W(na)]e^{-\kappa(t-na)} + \int_{na}^{t} p\lambda E[W(\tau-a)]e^{-\kappa(t-\tau)}d\tau \qquad (4.3.10)$$

(where $\eta(\tau)$ has been substituted for from (4.2.2)). Now setting $J(t) = E(W(t))e^{\kappa t}$ in (4.3.10) we obtain

$$J(t) = J(na) + p\lambda e^{\kappa a}\int_{na}^{t} J(\tau-a)d\tau$$

which is the same as equation (2.1.7). |||

Hence, according to the proposition, the solution for $E[W(t)]$ from (4.3.10) is given by (2.1.16). That is

$$E[W(t)] = W_0 \sum_{r=0}^{[t/a]} \frac{(p\lambda)^r (t-ra)^r e^{-\kappa(t-ra)}}{r!} . \qquad (4.3.11)$$

It is not possible to come out from (4.3.9) with a neat expression (such as (4.3.11) for $E[W(t)]$) for the unconditional variance $\mathrm{Var}[W(t)]$. However, if the distribution of $W(\zeta)$, $\zeta \in D_{n-1}$ has been determined (for example for $\zeta \in D_0$), (4.3.9) can be useful in estimating the possible range of values $\mathrm{Var}[W(t)]$ can take on for $t \in D_n$.

4.4 THE DISTRIBUTION OF INTACT GRAINS GIVEN A SAMPLE PATH OF THE INSECT POPULATION

Let $p_s(t|W(\cdot)) = P(S(t) = s|\{W(\zeta),\ 0 \leqslant \zeta \leqslant t\})$ (4.4.0)

Since the wheat is not renewed and the grains are continuously being destroyed by the weevils $S(t) \leqslant S_0$ (the initial number of intact grains). Also, obviously, $S(t) \geqslant 0$. Hence

$$p_s(t|W(\cdot)) \equiv 0 \quad \text{for} \quad s < 0 \quad \text{or} \quad s > S_0 . \tag{4.4.1}$$

Now, by considering the transitions of $S(t)$ given $\{W(\zeta),\ 0 \leqslant \zeta \leqslant t\}$ over the time interval $(t,t+\delta t)$ we can easily show that the probabilities (4.4.0) satisfy the differential difference equations

$$\frac{dp_s}{dt} = -\tilde{\alpha}p_s + \tilde{\alpha}p_{s+1} , \tag{4.4.2}$$

for $s = 1,2,\ldots,S_0$, and

$$\frac{dp_0}{dt} = \tilde{\alpha}p_1 \tag{4.4.3}$$

(where $\tilde{\alpha}$ is given by (4.2.1)), subject to the initial conditions

$$p_s(0|W(0)) = \begin{cases} 0 & \text{for} \quad s \neq S_0 \\ 1 & \text{for} \quad s = S_0 \end{cases} \tag{4.4.4}$$

The term $-\tilde{\alpha}p_0$ is absent from the right-hand side of (4.4.3) because once the grains are finished the weevils cannot eat any more!

Let $G_s(t,x|W(\cdot)) = \sum_{s=0}^{S_0} x^s p_s(t|W(\cdot))$.

Then from equations (4.4.2) and (4.4.3) we get

$$\frac{\partial G_s}{\partial t} = \tilde{\alpha}(\frac{1}{x} - 1)G_s - \tilde{\alpha}(\frac{1}{x} - 1)p_0 \qquad (4.4.5)$$

The awkward unknown term $-\tilde{\alpha}(\frac{1}{x} - 1)p_0(t|W(\cdot))$ presents difficulties if we try to solve for the p.g.f. G_s from (4.4.5). If $\tilde{\alpha}$ were a constant then one way of solving (4.4.2) and (4.4.3) would be to apply Bailey's (1964, Chapter 11) Laplace transform technique to these equations to isolate $p_0(t)$. But in this case, where $\alpha = \alpha(t)$ and unspecified as yet, Laplace transforms of the right-hand sides of (4.4.2) and (4.4.3) cannot be worked out explicitly in terms of the transforms of p_s, $s=0,1,\ldots,S_0$.

We now resort to solving (4.4.2) and (4.4.3) recursively. Starting with $s = S_0$, (4.4.1) and (4.4.2) give

$$p_{S_0} = e^{-A(t)} \qquad (4.4.6)$$

where

$$A(t) = \int_0^t \tilde{\alpha}(\tau)d\tau \ . \qquad (4.4.7)$$

Now from (4.4.2) and (4.4.4) we obtain

$$p_s e^{A(t)} = \int_0^t \tilde{\alpha}(\tau)e^{A(\tau)}p_{s+1}(\tau)d\tau \qquad (4.4.8)$$

for $0 < s \leqslant S_0-1$.

So setting $s = S_0-1$ in (4.4.8), then substituting for p_{S_0} from (4.4.6) and integrating we get

$$p_{S_0-1} = A(t)e^{-A(t)} .$$

Similarly, for $s = S_0-2$, we get

$$p_{S_0-2} = \left(\int_0^t \tilde{\alpha}(\tau_2)\int^{\tau_2} \tilde{\alpha}(\tau_1)d\tau_1 d\tau_2\right)e^{-A(t)}$$

$$= \frac{1}{2!}\left(\int_0^t \tilde{\alpha}(\tau)d\tau\right)^2 e^{-A(t)} .$$

Inductively or recursively we obtain

$$p_s = \frac{[A(t)]^{S_0-s}}{(S_0-s)!} e^{-A(t)} , \quad \text{for} \quad s=1,2,\ldots,S_0 . \qquad (4.4.9)$$

Now by either integrating (4.4.3) or using

$$\sum_{s=0}^{S_0} p_s(t|W(\cdot)) = 1$$

we obtain

$$\left.\begin{aligned} p_0(t|W(\cdot)) &= 1 - \sum_{r=0}^{S_0-1} \frac{[A(t)]^r}{r!} e^{-A(t)} \\ &= \sum_{r=S_0}^{\infty} \frac{[A(t)]^r}{r!} e^{-A(t)} \end{aligned}\right\} \qquad (4.4.10)$$

Let us note that with $\tilde{S}(t) \triangleq S_0 - S(t)$, that is $\tilde{S}(t)$ is the number of grains damaged by time t, we have

$$P(\tilde{S}(t) = s|W(\cdot)) = \frac{[A(t)]^s e^{-A(t)}}{s!} \quad \text{for} \quad s=0,1,\ldots,S_0-1 \tag{4.4.11}$$

and

$$P(\tilde{S}(t) = S_0|W(\cdot)) = \sum_{r=S_0}^{\infty} \frac{[A(t)]^r e^{-A(t)}}{r!} \quad .$$

The right-hand side of (4.4.11) is a probability mass function for the Poisson distribution with $A(t)$ as its mean. In other words the grains are destroyed according to a Poisson process but, unlike the usual Poisson process whose source is infinite, the destruction process comes to an end when there are no more intact grains left.

From the probabilities (4.4.9) and (4.4.10) we can get the conditional p.g.f. of $S(t)$ given $\{W(\zeta), \zeta \leqslant t\}$ in a series form. However this form proves cumbersome to use. This difficulty prompted me to introduce a non-physical random variable $\hat{S}(t)$ which is closely related to $S(t)$ and whose conditional p.g.f. given $\{W(\zeta), 0 \leqslant \zeta \leqslant t\}$ can be obtained in a more compact form as shown in the next section. Also working with $\hat{S}(t)$ it is possible to show that the stochastic mean $E(S(t))$ is not the same as the deterministic value of $S(t)$ as determined in Section 2.1.

4.5 AN ARTIFICIAL RANDOM VARIABLE FOR THE INTACT GRAINS

Let the random variable $\hat{S}(t)$ be defined as follows.

(i) $P(\hat{S}(t) = s | \{W(\zeta),\ 0 \leqslant \zeta \leqslant t\}) = P(S(t)=s | \{W(\zeta),\ 0 \leqslant \zeta \leqslant t\})$

for $s=1,2,\ldots,S_0$. (4.5.1)

(ii) The conditional probabilities

$$\hat{p}_s(t|W(\cdot)) = P(\hat{S}(t) = s | \{W(\zeta),\ 0 \leqslant \zeta \leqslant t\})$$

satisfy the equation (4.4.2). That is

$$\left.\begin{aligned} \frac{d\hat{p}_s}{dt} &= -\tilde{\alpha}\hat{p}_s + \tilde{\alpha}\hat{p}_{s+1} \\ &\text{for integers } s \in (-\infty, S_0] , \end{aligned}\right\} \qquad (4.5.2)$$

where

$$\hat{p}_s = 0 \quad \text{for} \quad s > S_0 .$$

Then according to (4.5.1)

$$p_s(t|W(\cdot)) = \hat{p}_s(t|W(\cdot)) \quad \text{for} \quad s \geqslant 1 .$$

Proposition: $p_0(t|W(\cdot)) = \sum_{s=-\infty}^{0} \hat{p}_s(t|W(\cdot))$. (4.5.3)

Proof: Solving (4.5.2) recursively in the same way as when solving (4.4.2) we get

$$\hat{p}_s = \frac{[A(t)]^{S_0-s}}{(S_0-s)!} e^{-A(t)} \qquad (4.5.4)$$

for $s = S_0,\ S_0-1,\ \ldots,1,0,-1,\ldots,-\infty$.

So

$$\sum_{s=-\infty}^{0} \hat{p}_s = \sum_{s=-\infty}^{0} \frac{[A(t)]^{S_0-s}}{(S_0-s)!} e^{-A(t)}$$

$$= \sum_{r=S_0}^{\infty} \frac{[A(t)]^r}{r!} e^{-A(t)}$$

$$= p_0 \qquad \text{(from (4.4.10))} . \qquad |||$$

Thus knowing the probabilities $\hat{p}_s$, integer $s \in (-\infty, S_0]$, we can deduce the probabilities p_s from (4.5.1) and (4.5.3).

Let $\hat{G}(t,x|W(\cdot))$ be the generating function for the probabilities $\hat{p}_s$. That is

$$\hat{G}(t,x|W(\cdot)) = \sum_{s=-\infty}^{S_0} x^s \hat{p}_s , \quad |x| \leqslant 1.$$

Substituting for $\hat{p}_s$ from (4.5.4) we get

$$\hat{G}(t,x|W(\cdot)) = x^{S_0} \exp\{(\tfrac{1}{x}-1)A(t)\} .$$

Now substituting for $A(t)$ from (4.4.7) and using (4.2.1) we obtain

$$\hat{G}(t,x|W(\cdot)) = x^{S_0} \exp\{(\lambda+\nu)(\tfrac{1}{x}-1)\int_0^t W(\tau)d\tau\} . \qquad (4.5.5)$$

Let me point out that we can extend the artificial-variable technique, used above, in determining the conditional probabilities $p_s(t|W(\cdot))$ to deriving (the generating function of) the joint probabilities

$$p_{sw}(t) \triangleq P(S(t) = s, W(t) = w) .$$

An example of this extension is in Chapter 5, Section

5.1.2 in which the number of weevils $W(t)$ (instead of $S(t)$) is the one represented by an artificial variable.

Also it is worth mentioning Cox and Smith's (1961, Chapter III, Section 3.1) example on queues in which, because of the awkwardness of the equations (similar to the one of the equations (4.4.2) and (4.4.3)) satisfied by the probabilities for their system, they extended the domain of the states of the system to $-\infty$. To ensure that their extended system gave the required solutions for the probabilities, they introduced an artificial relation connecting the 0 and -1 states of the system. So, in their case, once the probability for being in the artificial -1 state is determined, the probability for the zero state can be deduced. For our grain-weevil system the probability of the zero-grains state is the sum of the probabilities for the artificial states $0,-1,-2,\ldots,-\infty$.

4.5.1 Mean and Variance of the Artificial Variable

From the conditional p.g.f. (4.5.5) of $\hat{S}(t)$ given $\{W(\zeta),\ \zeta \leqslant t\}$ we have the conditional expectation of $\hat{S}(t)$ given by

$$E[\hat{S}(t)\,|W(\cdot)] = \left.\frac{\partial \hat{G}(t,x|W(\cdot))}{\partial x}\right|_{x=1}$$

$$= S_0 - (\nu+\lambda)\int_0^t W(\tau)\,d\tau \qquad (4.5.6)$$

Therefore the unconditional expectation of $\hat{S}(t)$ is given by

$$E(\hat{S}(t)) = S_0 - (\nu+\lambda)\int_0^t E(W(\tau))d\tau \ . \qquad (4.5.7)$$

Since $E(W(t))$ satisfies the same equation as the deterministic value for $W(t)$ (see Section 4.3), the equations (4.5.7) and (2.1.7) show that $E(\hat{S}(t))$ satisfies the same equation as the deterministic value for the number of intact grains, $S(t)$. But the artificial variable $\hat{S}(t)$ is not the same as $S(t)$. Therefore the *stochastic mean*, $E(S(t))$, and the *deterministic value* for the number of intact grains are *not the same*. In Section 4·7 I show that the deterministic value is a lower bound for the stochastic mean.

The conditional variance of $\hat{S}(t)$ given $\{W(\zeta),\ \zeta < t\}$ is given by

$$\mathrm{Var}[\hat{S}(t)|W(\cdot)] = \left[\frac{\partial^2\hat{G}}{\partial x^2} - \left(\frac{\partial\hat{G}}{\partial x}\right)^2 + \frac{\partial\hat{G}}{\partial x}\right]_{x=1}$$

$$= \left[\frac{\partial}{\partial x}\left(\frac{1}{\hat{G}}\frac{\partial\hat{G}}{\partial x}\right) + \frac{\partial\hat{G}}{\partial x}\right]_{x=1}$$

where $\hat{G} \equiv \hat{G}(t,x|W(\cdot))$ as in (4.5.5). Taking the logarithm of (4.5.5) and then differentiating the result twice with respect to x we have

$$\frac{\partial}{\partial x}\left(\frac{1}{\hat{G}}\frac{\partial\hat{G}}{\partial x}\right)\Bigg|_{x=1} = -S_0 + 2(\nu+\lambda)\int_0^t W(\tau)d\tau \ .$$

So adding $\left.\frac{\partial\hat{G}}{\partial x}\right|_{x=1}$ to both sides we obtain

$$\mathrm{Var}[\hat{S}(t)\,|W(\cdot)] = (\nu+\lambda)\int_0^t W(\tau)d\tau \qquad (4.5.8)$$

Before we determine the unconditional variance of $\hat{S}(t)$ let us note the implication of (4.5.8). According to (4.5.8) the variance of $\hat{S}(t)$ is an increasing function of time for any given sample path of the weevil population.

In the evaluation of $\mathrm{Var}[\hat{S}(t)]$ let us note the identity

$$\mathrm{Var}[\hat{S}(t)] = E[\mathrm{Var}(\hat{S}(t)\,|W(\cdot))] + \mathrm{Var}[E(\hat{S}(t)\,|W(\cdot))]$$

Hence from (4.5.8) and (4.5.6) we have

$$\begin{aligned}\mathrm{Var}[\hat{S}(t)] &= \alpha\int_0^t E[W(\tau)]d\tau \\ &\quad + \alpha^2\int_0^t\int_0^t E[W(\tau)W(\zeta)]d\tau d\zeta \\ &\quad - \alpha^2\int_0^t\int_0^t E[W(\tau)]E[W(\zeta)]d\tau d\zeta \qquad (4.5.9) \\ &= \alpha\int_0^t E[W(\tau)]d\tau \\ &\quad + \alpha^2\int_0^t\int_0^t \mathrm{Cov}(W(\tau),W(\zeta))d\tau d\zeta\ .\end{aligned}$$

While $E[W(t)]$ is given by (4.3.11) we have not determined the joint distribution of $W(\zeta)$ and $W(\tau)$, $\zeta \neq \tau$. Hence the evaluation of $E[W(\zeta)W(\tau)]$ is not possible for all values of ζ,τ. However for $\tau,\zeta \leqslant a$ it is possible as follows. Since $\{W(\tau),\ 0 < \tau \leqslant a\}$ is a pure-death process (see beginning of Section 4.3) the conditional distribution of $W(\tau)$ given $W(\zeta)$, $\zeta < t$, is the binomial distribution $b(W(\zeta),\ e^{-\kappa(\tau-\zeta)})$. Now consider

$$E[W(\zeta)W(\tau)] = E[W(\zeta)E(W(\tau)\,|W(\zeta))]$$

$$= E[W^2(\zeta)e^{-\kappa(\tau-\zeta)}] \qquad (4.5.10)$$

But $W(\zeta)$ is of the binomial distribution, $b(W_0,e^{-\kappa\zeta})$. Hence $E[W(\zeta)W(\tau)]$ can be determined from (4.5.10). Then substituting for the expectations in the R.H.S. of (4.5.9) and integrating it can be shown that, for $0 \leqslant t \leqslant a$,

$$\mathrm{Var}[\hat{S}(t)] = \frac{\alpha W_0}{\kappa}(1-e^{-\kappa t})[1+\alpha t-\frac{\alpha}{\kappa}(1-e^{-\kappa t})] .$$

4.6 APPROXIMATE DERIVATION OF JOINT DISTRIBUTION OF THE ARTIFICIAL VARIABLE AND THE WEEVILS

In this section our grain-weevil system is approximated to one in which the emergence process of young weevils from the eggs is taken as an immigration process independent of the adult weevil population. The original weevils (at time $t=0$) as well as the "immigrants" (that is the offsprings) are assumed to behave independently of each other.

The derivation of the approximate joint p.g.f. of $\hat{S}(t)$ and $W(t)$ gives us an opportunity to look at two alternative methods (see Sections 4.6.1 and 4.6.2) that can be used to derive Puri's (1975, Eqn. 14) result for a time-homogeneous birth-and-death process with possibly time dependent immigration rate. In our case the immigration rate (emergence rate) $\eta(t)$ could be deterministic or stochastic, but it should be independent of the weevil population.

First we look at this joint p.g.f. $\hat{G}(t,x,y)$ of $\hat{S}(t)$ and $W(t)$ given $\hat{S}(0) = S_0$ and $W(0) = W_0$. That is

$$\hat{G}(t,x,y) = E(x^{\hat{S}(t)}y^{W(t)}) \ , \quad |x|,|y| \leq 1$$

with

$$\hat{G}(0,x,y) = x^{S_0}y^{W_0} \ .$$

Now

$$\hat{G}(t,x,y) = E[y^{W(t)}E(x^{\hat{S}(t)}|\{W(\tau),\ 0 \leq \tau \leq t\})]$$

$$= E[y^{W(t)}\hat{G}(t,x|W(\cdot))]$$

Now substituting for $\hat{G}(t,x|W(\cdot))$ from (4.5.5) we have

$$\hat{G}(t,x,y) = E[y^{W(t)}\exp\{(\lambda+\nu)(\frac{1}{x}-1)\int_0^t W(\tau)d\tau\}]$$

$$= x^{S_0}E[y^{W(t)}e^{ZQ(t)}]$$

where

$$Q(t) = \int_0^t W(\tau)d\tau$$

and

$$Z = (\lambda+\nu)(\frac{1}{x} - 1) \ .$$

Let us write

$$E[y^{W(t)}e^{ZQ(t)}] = E(E[y^{W(t)}e^{ZQ(t)}|\{\eta(\tau),\ 0 \leqslant \tau \leqslant t\}]) \ .$$

Then with

$$H(t,y,z) = E[y^{W(t)}e^{ZQ(t)}|\{\eta(\tau),\ 0 \leqslant \tau \leqslant t\}]$$

the joint p.g.f. of $\hat{S}(t)$ and $W(t)$ is

$$\hat{G}(t,x,y) = x^{S_0}E[H(t,y,z)] \qquad (4.6.0)$$

We could use Puri (1975, Eqn. 14) to obtain an expression for $H(t,y,z)$. However (as already mentioned) we shall derive the expression for $H(t,y,z)$ using two alternative methods. Method A (Section 4.6.1) gives us insights into the techniques used to derive Puri's result. The techniques used in the second method (that is the method of "marks and catastrophe", Section 4.6.2) are not only interesting but also give insights into a wide range of problems to which the method could be applied.

4.6.1 Method A

According to this method we make use of the expression for

$$H_1(t,y,z) \triangleq E[y^{W_1(t)}e^{ZQ_1(t)}]$$

where $\{W_1(t),\ t \geqslant 0\}$ is a death process and

$$Q_1(t) = \int_0^t W_1(\tau)d\tau \ .$$

Therefore we need to determine $H_1(t,y,z)$. [In our case we could interpret $W_1(t)$ as the number of the original weevils still in the system at time t.]

Let the death rate in the process $\{W_1(t),\ t \geqslant 0\}$ be $\kappa = \mu+\varepsilon$ and $W_1(0) = W_0$ (the initial number of weevils).

In order to determine $H_1(t,x,y)$ we shall use Puri's (1966) argument by which he derived the characteristic function for the bivariate process $\{(X(t),\ \int_0^t X(\tau)d\tau),\ t \geqslant 0\}$, where $\{X(t),\ t \geqslant 0\}$ is a birth-death process. In our case we are interested in the moment quasi-probability generating function, $H_1(t,y,z)$ of $\{(W_1(t),\ Q_1(t),\ t \geqslant 0\}$.

Let δW_1 and δQ_1 be changes in $W_1(t)$ and $Q_1(t)$, respectively, over the time interval $(t,\ t+\tau)$ where τ is infinitesimal, such that a maximum of one event (death) may occur over the interval.

So, given $W(t) = n$

$\delta W_1 = 0$ and $\delta Q_1 = n\tau$ if no death occurs

and $\delta W_1 = -1$ and $\delta Q_1 = n\theta+(n-1)(\tau-\theta)$

if a death occurs, where $t+\theta$ $(\theta < \tau)$ is the time at which it occurs.

Let $P_{0,n}$ = P(no death occurs in $(t,t+\tau)\,|W_1(t) = n)$

and $P_{1,n}$ = P(a death occurs in $(t,t+\tau)\,|W_1(t) = n)$.

Now with the probabilistic rate of death as $\kappa = \mu+\varepsilon$,

P(an individual does not die by time $\tau) = e^{-\kappa\tau}$.

Therefore

$$\left.\begin{aligned} P_{0,n} &= (e^{-\kappa\tau})^n = e^{-n\kappa\tau} \\ P_{1,n} &= \binom{n}{1}(1-e^{-\kappa\tau})e^{-(n-1)\kappa\tau} \end{aligned}\right\} \qquad (4.6.1)$$

Let Θ be the r.v. which takes on the values θ (where death occurs at $t+\theta$). Then from Puri (1966) the conditional probability density function of Θ given $\Theta < \tau$ is

$$f(\theta) = \frac{\kappa e^{-\kappa\theta}}{1-e^{-\kappa\tau}} \quad . \qquad (4.6.2)$$

Next we consider

$$H_1(t+\tau,y,z) = E(y^{W_1(t)+\delta W_1}e^{z(Q_1(t)+\delta Q_1)})$$

$$= E[y^{W_1(t)}e^{ZQ_1(t)}E(y^{\delta W_1}e^{Z\delta Q_1}\,|W_1(t))]. \qquad (4.6.3)$$

First let us evaluate

$$E(y^{\delta W_1}e^{Z\delta Q_1}\,|W_1(t) = n)$$

$$= P_{0,n}y^0e^{Zn\tau} + P_{1,n}y^{-1}\int_0^\tau e^{Z[n\theta+(n-1)(\tau-\theta)]}f(\theta)d\theta$$

$$+ 0(\tau) \quad .$$

Now substituting for $P_{0,n}$ and $P_{1,n}$ from (4.6.1) and for $f(\theta)$ from (4.6.2) and then evaluating the integral we obtain

$$E(y^{\delta W_1} e^{Z\delta Q_1} | W_1(t) = n)$$

$$= e^{(z-\kappa)n\tau} + \frac{n\kappa}{y} e^{(z-\kappa)(n-1)\tau} [\frac{e^{(z-\kappa)\tau}-1}{z - \kappa}]$$

$$+ 0(\tau) \qquad (4.6.4)$$

So replacing n in (4.6.4) by $W_1(t)$ and then using (4.6.3) we have

$$\frac{H_1(t+\tau),y,z)-H_1(t,y,z)}{\tau}$$

$$= E\{y^{W_1(t)} e^{zQ_1(t)} [(e^{(z-\kappa)\tau W_1(t)}-1)/\tau$$

$$+ \frac{\kappa W_1(t)(e^{(z-\kappa)\tau}-1)e^{(z-\kappa)\tau(W_1(t)-1)}}{y(z-\kappa)\tau}]\}$$

$$+ 0(\tau) \text{ .}$$

Now taking the limits of both sides as $\tau \to 0$ we obtain

$$\frac{\partial H_1}{\partial t} = E\{y^{W_1(t)} e^{ZQ_1(t)} W_1(t)[z-\kappa+\kappa/y]\}$$

$$= [(z-\kappa)y+\kappa]\frac{\partial}{\partial y}E\{y^{W_1(t)} e^{ZQ_1(t)}\}$$

That is $$\frac{\partial H_1}{\partial t} = [(z-\kappa)y+\kappa]\frac{\partial H_1}{\partial y} \text{ .} \qquad (4.6.5)$$

Since $W_1(0) = W(0) = W_0$ and $Q_1(0) \equiv 0$ we have

$$H_1(0,y,z) = y^{W_0} \tag{4.6.6}$$

Solving (4.6.5) subject to the initial condition (4.6.6) we obtain

$$H_1(t,y,z) = [h(t,y,z)]^{W_0} \tag{4.6.7}$$

where $$h(t,y,z) = \frac{[\kappa+y(z-\kappa)]e^{(z-\kappa)t}-\kappa}{z - \kappa} \tag{4.6.8}$$

Note that for $W_0 \equiv 1$

$$\left.\begin{array}{l} \\ H_1(t,y,z) \equiv h(t,y,z) \end{array}\right\} \tag{4.6.9}$$

Now to obtain the full expression for $H(t,y,z)$ we incorporate immigration (that is the emergence of adult weevils from eggs). To do this we shall use Bartlett's (1966, Sec. 3.41) technique for deriving a p.g.f. for a birth-death-and-immigration process as follows.

Let us divide the interval $[0,t]$ into subintervals $[\tau_{r-1},\tau_r]$, $r=1,2,\ldots$. The probability that there is an immigrant (that is, a mature weevil emerging from an egg) during the interval (τ_r,τ_{r+1}) is $\eta(\tau_r)\Delta\tau_r+0(\Delta\tau_r)$, where $\Delta\tau_r = \tau_{r+1} - \tau_r$. Assuming that the weevils behave independently of each other, the immigrant in the time interval (τ_r,τ_{r+1}) would set up an independent death process starting at approximately $t = \tau_r$. Then, according to (4.6.9), the p.g.f. of the component of the bivariate process $\{W(t),Q(t),\ t \geqslant 0\}$ contributed by the immigrant is $h(t-\tau_r,t,z)$. So the contribution to $H(t,y,z)$ by what happens (that is, one immigrant or none) in the interval (τ_r,τ_{r+1}) is

$$
\begin{aligned}
&(1-\eta(\tau_r)\Delta\tau_r)[h(t-\tau_r,y,z)]^0 \\
&\qquad + \eta(\tau_r)\Delta\tau_r h(t-\tau_r,y,z) + 0(\Delta\tau_r) \\
&= 1+\eta(\tau_r)\Delta\tau_r[h(t-\tau_r,y,z)-1] + 0(\Delta\tau_r)
\end{aligned}
$$

Now from the assumption of independence of individuals, we have the contribution to $H(t,y,z)$ by all the immigrants by time t as

$$
H_2(t,y,z) = \lim_{\|\Delta\tau_r\|\to 0} \prod_r \{1+\eta(\tau_r)[h(t-\tau_r,y,z)-1]\Delta\tau_r\} \qquad (4.6.10)
$$

where $\|\Delta\tau_r\| = \max_r\{\Delta\tau_r\}$.

Now taking the natural logarithm of (4.6.10) and taking $\eta(\tau)[h(t-\tau,y,z)-1]$ to be continuous in τ so that we have

$$
\ln \lim \prod_r \{\quad\} = \lim \ln \prod_r \{\quad\} ,
$$

we get

$$
\begin{aligned}
\ln H_2(t,y,z) &= \lim_{\|\Delta\tau_r\|\to 0} \sum_r \ln\{1+\eta(\tau_r)[h(t-\tau_r,y,z)-1]\Delta\tau_r\} \\
&= \lim_{\|\Delta\tau_r\|\to 0} \sum_r \{\eta(\tau_r)[h(t-\tau_r,y,z)-1]\Delta\tau_r + 0(\Delta\tau_r)\} \\
&= \int_0^t \eta(\tau)[h(t-\tau,y,z)-1]d\tau .
\end{aligned}
$$

Hence $H_2(t,y,z) = \exp\int_0^t \eta(\tau)[h(t-\tau,y,z)-1]d\tau$ (4.6.11)

Now using the assumption that the "immigration" process is independent of the weevil population (and therefore independent of the population of the original weevils) we have $H(t,y,z) = H_1(t,y,z)H_2(t,y,z)$. So substituting for $H_1(t,y,z)$ and $H_2(t,y,z)$ from (4.6.7) and (4.6.11), respectively, in (4.6.0) we have the approximation of the joint p.g.f. of $\hat{S}(t)$ and $W(t)$ given by

$$\hat{G}(t,x,y) = x^{S_0}[h(t,y,z)]^{W_0} \times E[\exp\{\int_0^t \eta(\tau)[h(t-\tau,y,z)-1]d\tau\}] \quad (4.6.12)$$

where $h(t,y,z)$ is given by (4.6.8) and

$$z = (\nu+\lambda)(1/x-1) .$$

4.6.2 Method of Marks and Catastrophe

As in Method A we use this method to evaluate

$$H(t,y,z) = E[y^{W(t)}e^{zQ(t)}|\{\eta(\tau),\ 0 \leqslant \tau \leqslant t\}]$$

where $W(t)$ and $Q(t)$ are defined as before. Let us write $H(t,y,z)$ in the form

$$H(t,y,z) = \sum_{r=0}^{\infty}\int_0^{\infty} y^r e^{zq} dF_r(q)$$

where $F_r(q) = P(W(t) = r, \ Q(t) \leqslant q)$.

Now let $\zeta = -z = -(\nu+\lambda)(\frac{1}{x}-1)$ be interpreted as the "catastrophe" rate per weevil. Then

$\zeta W(t)$ = total catastrophe rate to live weevils at time t.

So $\zeta q(t) = \int_0^t \zeta W(u)\,du$ is the catastrophe rate to live weevils over $(0,t)$.

Hence

$$e^{zq} = e^{-\zeta q} = P\begin{bmatrix}\text{no catastrophe occurs to live weevils} \\ \text{over } (0,t) \,|\, Q(t) = q\end{bmatrix}$$

Also let us interpret y as the probability that a weevil is "marked". Then

$$H(t,y,z) = \sum_{r=0}^{\infty} \int_0^{\infty} y^r e^{-\zeta q} dF_r(q)$$

$$\equiv P\begin{bmatrix}\text{no catastrophe has occured to the} \\ \text{weevils alive and marked at time } t \\ \text{and no catastrophe occurred before} \\ \text{death for all those who died in } (0,t).\end{bmatrix} \qquad (4.6.13)$$

Let us define events (or properties) E_1 and E_2 as follows:

$$E_1 = \{\text{a weevil is alive and marked at time } t \text{ and has had no catastrophe}\}$$

$$E_2 = \{\text{a weevil dies in } (0,t) \text{ before a catastrophe occurs to it}\}.$$

Let $E = E_1 \cup E_2$.

Then

$$H(t,y,z) = P\begin{bmatrix}\text{each of the original weevils as} \\ \text{well as the immigrants (offsprings)} \\ \text{in } (0,t) \text{ has property } E\end{bmatrix}$$

But since the immigration process is assumed to be independent of the weevil population we can write

$$H(t,y,z) = H_1(t,y,z)H_2(t,y,z) \tag{4.6.14}$$

where

$$H_1(t,y,z) = P\begin{bmatrix}\text{each of the original weevils} \\ \text{has property } E\end{bmatrix}$$

and

$$H_2(t,y,z) = P\begin{bmatrix}\text{all immigrants in } (0,t) \text{ will} \\ \text{satisfy } E\end{bmatrix}$$

Now with $W(0) = W_0$ (the initial number of weevils) and using independence of individual weevils, we have

$$\begin{aligned} H_1(t,y,z) &= \{P(E_1 \cup E_2)\}^{W_0} \\ &= \{P(E_1) + P(E_2)\}^{W_0} \end{aligned}$$

(since E_1 and E_2 are mutually exclusive).

Now $P(E_1) = e^{-\kappa t}ye^{-\zeta t}$

and

$$P(E_2) = P\begin{bmatrix}\text{first event is death}\,|\,\text{either death or} \\ \text{catastrophe in } (0,t)\end{bmatrix} \times$$

$$P[\text{either death or catastrophe in } (0,t)]$$

$$= \frac{\kappa}{\kappa+\zeta}(1-e^{-\kappa t}e^{-\zeta t}) \quad .$$

Hence $H_1(t,y,z) = [ye^{-(\zeta+\kappa)t} + \frac{\kappa}{\kappa+\zeta}(1-e^{-(\zeta+\kappa)t})]^{W_0}$

So replacing ζ by $-z$ and rearranging the terms we obtain

$$H_1(t,y,z) = [\frac{\kappa+y(z-\kappa)e^{(z-\kappa)t}-\kappa}{z-\kappa}]^{W_0}$$

$$= [h(t,y,z)]^{W_0}$$

which is the same as the result given by (4.6.7) and (4.6.8). From the definition of $h(t,y,z)$ we have the following interpretation:

$$1-h(t,y,z) = P\left[\begin{array}{l}\text{a catastrophe occurs in } (0,t) \text{ to}\\ \text{a weevil alive and marked at } t \text{ or}\\ \text{if the weevil is dead at } t \text{ the}\\ \text{catastrophe occurred before its death}\end{array}\right]$$

$$= P(\bar{E}) \ .$$

Similarly if a weevil emerges at time $\tau < t$ then $1-h(t-\tau,y,z)$ is the probability that the weevil does not satisfy property E. So the rate of immigration (emergence), at time t, of weevils that will not satisfy E

$$= \eta(\tau)[1-h(t-\tau,y,z)] \ .$$

Therefore the total rate of emergence of weevils over $(0,t)$ which will not satisfy E at time t

$$= \int_0^t \eta(\tau)[1-h(t-\tau,y,z)]d\tau \ .$$

Hence

$$H_2(t,y,z) = P(\text{all immigrants in } (0,t) \text{ will satisfy } E)$$
$$= P(\text{no immigrants do not satisfy } E)$$
$$= \exp\{-\int_0^t \eta(\tau)[1-h(t-\tau,y,z)]d\tau\} .$$

So substituting for $H_1(t,y,z)$ and $H_2(t,y,z)$ in (4.6.14) we get

$$H(t,y,z) = [h(t,y,z)]^{W_0}\exp\{\int_0^t \eta(\tau)[h(t-\tau,y,z)-1]d\tau\}$$

as by the first method.

Finally let us note that the interpretation of $E(y^{W(t)}e^{zQ(t)})$ as a probability, such as in (4.6.13), applies to a general class of problems. If the probability of the "event E" (defined according to the situation being investigated) can be determined then the expression for the corresponding generating function such as $H(t,y,z)$ can be obtained.

4.6.3 On the Immigration (Emergence) Rate

Substituting for $H(t,y,z)$ in (4.6.0) we obtain the approximate joint p.g.f. of $\hat{S}(t)$ and $W(t)$ as

$$\hat{G}(t,x,y) = x^{S_0}[h(t,y,z)]^{W_0}E[\exp\{\int_0^t \eta(\tau)[h(t-\tau,y,z)-1]d\tau\}] \qquad (4.6.15)$$

where $h(t,y,z)$ is given by (4.6.8) and $z = (\nu+\lambda)(1/x-1)$.

The choice of the "immigration" process $\{\eta(t),\ t \geqslant 0\}$ could be arbitrary. However the rather natural stochastic form $\eta(t) = p\lambda W(t-a)$, as defined in (4.2.2), cannot be used here because, in the derivation of (4.6.15), we have assumed that the immigration process is independent of the weevil population. If we take $\eta(t)$ as deterministic then one possible value for $\eta(t)$ is its deterministic value $p\lambda W(t-a)$ as given by the solution for $W(t)$ in the phase I deterministic model (Section 2.1).

Using the deterministic value $p\lambda W(t-a)$ for $\eta(t)$ and setting $x=1$ in (4.6.15) we obtain the approximate marginal p.g.f. of $W(t)$ as

$$G(t,y) = [1+(y-1)e^{-\kappa t}]^{W_0}\exp\{(y-1)\int_0^t \eta(\tau)e^{-\kappa(t-\tau)}d\tau\}. \quad (4.6.16)$$

From (4.6.16) we obtain the approximate stochastic mean of $W(t)$ as

$$E[W(t)] = W_0e^{-\kappa t} + \int_0^t \eta(\tau)e^{-\kappa(t-\tau)}d\tau. \qquad (4.6.17)$$

But according to the Proposition 4.1 the deterministic value of $\eta(t)$ is the same as $p\lambda E[W(t-a)]$. Substituting $p\lambda E[W(t-a)]$ for $\eta(t)$ in (4.6.17), it is not difficult to verify that $E(W(t))$, as given by (4.6.17), is the same as the deterministic value of $W(t)$ in Section 2.1. In otherwords the stochastic mean of $W(t)$ by the approximate derivation is the same as the exact stochastic mean derived in Section 4.3. This also, according to (4.5.6), implies that the stochastic mean of $\hat{S}(t)$ is the same as the exact one given by (4.5.7).

From (4.6.16) the approximate variance of $W(t)$ is

$$\mathrm{Var}[W(t)] = W_0 e^{-\kappa t}(1-e^{-\kappa t}) + \int_0^t \eta(\tau) e^{-\kappa(t-\tau)} d\tau$$

which is different from the exact variance that can be obtained from (4.3.8) and (4.3.9). Similarly the approximate variance of $\hat{S}(t)$ would be different from the exact one.

Let me conclude this section by pointing out that the derivation of an exact expression of $E[y^{W(t)} e^{zQ(t)} | \{\eta(\tau), \tau \leqslant t\}]$ where $\{\eta(\tau), \tau \leqslant t\}$ is a function of the process $\{W(t), t \geqslant 0\}$ (as in the case of the weevil population in which $\eta(t) = p\lambda W(t-a))$ is a difficult problem. However I feel that it can be solved. I will look at this problem in my future research work.

4.7 BOUNDS FOR THE MEAN AND VARIANCE OF THE NUMBER OF INTACT GRAINS

Let us recall that $S(t)$, the number of unattacked (intact) grains at time t, is related to the artificial random variable $\hat{S}(t)$ by the relations (4.5.1), (4.5.2) and (4.5.3).

Multiplying equation (4.5.2) by s and summing over the integers $s \in (-\infty, S_0]$ we obtain

$$\frac{d}{dt}(E[\hat{S}(t) | \{W(\zeta), 0 \leqslant \zeta \leqslant t\}])$$

$$= \tilde{\alpha}(t) \sum_{s=-\infty}^{S_0} s(-\hat{p}_s + \hat{p}_{s+1})$$

$$= \tilde{\alpha}(t) \sum_{s=-\infty}^{S_0} (-\hat{p}_{s+1}) = -\tilde{\alpha}(t) . \quad (4.7.1)$$

Similarly using equation (4.4.2) we obtain

$$\frac{d}{dt}(E[S(t) | \{W(\zeta), 0 \leqslant \zeta \leqslant t\}])$$

$$= -\tilde{\alpha}(t)[1 - p_0(t | \{W(\zeta), 0 \leqslant \zeta \leqslant t\})] . \quad (4.7.2)$$

The difference of the equations (4.7.1) and (4.7.2) is

$$\frac{d}{dt}(E[S(t) | \{W(\zeta), 0 \leqslant \zeta \leqslant t\}])$$

$$= \frac{d}{dt}(E[\hat{S}(t) | \{W(\zeta), 0 \leqslant \zeta \leqslant t\}])$$

$$+ \tilde{\alpha}(t) p_0(t | \{W(\zeta), 0 \leqslant \zeta \leqslant t\}) .$$

Now integrating with respect to t and then taking the expectations we obtain

$$E(S(t)) = E[\hat{S}(t)] + \int_0^t E(\tilde{\alpha}(\tau) p_0(\tau | \{W(\zeta), 0 \leqslant \zeta \leqslant \tau\})) d\tau \quad (4.7.3)$$

It is difficult to reduce the second term of the right-hand side of (4.7.3) to a reasonable expression not involving any of the operators of integration and expectation. However, since $\tilde{\alpha}(t) \geqslant 0$ and $p_0 \geqslant 0$, the term is non-negative. Hence

$$E[S(t)] \geqslant E[\hat{S}(t)] \tag{4.7.4}$$

That is, the expected number of intact grains at time t is greater than or equal to the expectation of the artificial variable $\hat{S}(t)$.

Next we consider

$$\mathrm{Var}(\hat{S}(t)) = \sum_{s=-\infty}^{S_0} (s-E(\hat{S}(t)))^2 P(\hat{S}(t) = s)$$

in which $P(\hat{S}(t) = s) = P(S(t) = s)$ for $s > 0$.

So

$$\mathrm{Var}(\hat{S}(t)) = \sum_{s=1}^{S_0} (s-E(\hat{S}))^2 P(S=s) + \sum_{s=-\infty}^{0} (s-E(\hat{S}))^2 P(\hat{S}=s) .$$

At this point let us note that because $E(S(t)) \geqslant 0$ and $E(S(t)) \geqslant E(\hat{S}(t))$, $E(\hat{S}(t)) < 0$ would correspond to the situation when the expected number of intact grains is zero or close to zero. In this case we would expect $\mathrm{Var}(S(t))$ be zero or almost zero.

However if $E(\hat{S}(t)) \geqslant 0$ then, according to (4.7.4), we expect some intact grains still remaining in the system. In this case $(s-E(\hat{S}))^2 \geqslant (E(\hat{S}))^2$ for $s \leqslant 0$ and then

$$\mathrm{Var}(\hat{S}(t)) \geqslant \sum_{s=1}^{0}(s-E(\hat{S}))^2 P(S=s) + (E(\hat{S}(t)))^2 \sum_{s=-\infty}^{0} P(\hat{S}=s) \; .$$

But according to (4.5.3)

$$\sum_{s=-\infty}^{0} P(\hat{S}=s) = P(S=0) \; .$$

Therefore

$$\mathrm{Var}(\hat{S}(t)) \geqslant \sum_{s=0}^{0}(s-E(\hat{S}))^2 P(S=s)$$

The right-hand side would be minimum if $E(\hat{S}(t)) = E(S(t))$. But according to (4.7.3) or (4.7.4) this equality does not necessarily hold. Therefore

$$\mathrm{Var}(S(t)) \leqslant \mathrm{Var}(\hat{S}(t)) \qquad (4.7.5)$$

for $\qquad E(\hat{S}(t)) \geqslant 0$.

4.8 THE TIME AT WHICH NUMBER OF INTACT GRAINS PER WEEVIL BECOMES CRITICAL

Let T^* be the time at which the critical food ratio is first reached. Then T^* is a random variable whose distribution is given by

$$P(T^* > t) = P(S(t) > CW(\tau) \quad \text{for} \quad 0 \leqslant \tau \leqslant t)$$

Its probability distribution function is

$$F_{T^*}(t) = 1-P(S(\tau) > CW(\tau) \quad \text{for} \quad 0 \leqslant \tau \leqslant t).$$

Its expectation is

$$E(T^*) = \int_0^\infty [1-F_{T^*}(t)]dt$$

$$= \int_0^\infty P(S(\tau) > CW(\tau) \quad \text{for} \quad 0 \leqslant \tau \leqslant t)dt \tag{4.8.1}$$

But to obtain explicit expressions for the joint probabilities $p_{sw}(t)$ for the bivariate process $\{(S(t), W(t)), t \geqslant 0\}$ and therefore an expression for the probability in (4.8.1) is very complicated. Thus equation (4.8.1) is not very useful in determining $E(T^*)$. Instead of determining the exact value of $E(T^*)$ as given by (4.8.1), we try to estimate T^* by t^* satisfying the equation

$$E(\hat{S}(t)) = CE(W(t)) \; . \tag{4.8.2}$$

Since $E(\hat{S}(t))$ and $E(W(t))$ are the same as the deterministic values for $S(t)$ and $W(t)$ respectively, equation (4.8.2) is the same as the deterministic one (2.1.21). But, as already pointed out in Section 2.1.3, explicit expressions for t^* and other roots of (4.8.2) cannot be obtained. This is the point at which we would turn to the computer as we did in Section 3.1.1.

Finally we should note that the value of t^* obtained from (4.8.2) is less than or equal to that given by

$$E(S(t)) = CE(W(t)) \; . \tag{4.8.3}$$

This is because $E(S(t))$ and $E(\hat{S}(t))$ are decreasing and $E(S(t)) \geqslant E(\hat{S}(t))$ (during phase I). But since we have not determined $E(S(t))$, we cannot solve for t^* from (4.8.3).

4.9 DISCUSSION

In this Chapter I have discussed the stochastic version of the phase I deterministic model discussed in Chapter 2, Section 2.1. The probability distributions of the number of intact grains, $S(t)$, and the number of adult weevils, $W(t)$, have been considered.

In order to reduce the difficulty in handling the rather untrackable expression for the p.g.f. of $S(t)$, an artificial variable $\hat{S}(t)$ was introduced to represent $S(t)$. The stochastic means of $\hat{S}(t)$ and $W(t)$ worked out to be the same as the deterministic values for $S(t)$ and $W(t)$, respectively, as determined in Section 2.1.1. It has been shown (see Section 4.7) that $E(\hat{S}(t))$ and therefore the deterministic value for $S(t)$ underestimates the stochastic mean of the number of intact grains.

Treating the emergence process of the weevils from the eggs as an immigration process independent of the adult weevil population an approximate expression for the joint p.g.f. of $\hat{S}(t)$ and $W(t)$ has been derived. In this approximate derivation two independent methods (one of which is the method of "marks and catastrophe") with notable techniques have been used (see Sections 4.6.1 and 4.6.2).

Though it has not been possible to determine the exact value of the expected time t^* at which the critical food ratio is reached for the first time, it has been indicated that an estimate of it can be obtained from the equation $E(\hat{S}(t)) = CE(W(t))$. The estimate obtained this way (and therefore the deterministic value of t^*) is less than or equal to that obtained by using the non-artificial mean of $S(t)$ instead of $E(\hat{S}(t))$.

The distributions (or moments) of the size of the immature group, $U(t)$, and the total number of emigrants, $R(t)$, have not been explicitly discussed. However they are implicitly involved through the oviposition and emergence rates and the emigration rate respectively. But if explicit consideration is required, it can be achieved through the *stochastic* equations

$$\frac{dU(t)}{dt} = \lambda(W(t)-W(t-a))$$

and

$$\frac{dR(t)}{dt} = \varepsilon W(t) \quad .$$

Finally let me point out that where the expressions or equations for the means and variances are complicated enough not to reveal the general properties of these moments, computer programmes such as those in Chapter 3 could be helpful in revealing the properties.

CHAPTER 5

STOCHASTIC MODELS FOR PHASE II

5.0 INTRODUCTION

As already noted in Section 2.2.0, phase II starts at time t^* at which the critical food ratio C is reached for the first time. Other than the revision of the assumptions made for phase I, continuity of the parameters involved, at time t^*, is maintained. Unfortunately, as pointed out in Section 4.8, the distribution of the random variable T^* which takes on the values t^* could not be established. For this reason I have used t^*, the estimate of T^* (obtained as in Section 4.8), rather than the random variable T^*, as the starting point in time for phase II. The number of intact grains, S^*, and the number of adult weevils, W^*, at time t^* are determined using the solutions for $S(t)$ and $W(t)$ in the deterministic model of Section 2.1 (or $E(\hat{S}(t))$ and $E(W(t))$ in the corresponding stochastic model; Sections 4.3 and 4.5). However upper bounds for S^* and W^*, given the initial conditions $S(0) = S_0$ and $W(0) = W_0$, can be determined independently of the solutions of Section 2.1 or Sections 4.3 and 4.5 as demonstrated at the end of Section 5.1.0.

In this chapter I present two models. Model A is a stochastic version of the deterministic model discussed in Section 2.2. In Model B the time line is divided into developmental periods $[(n-1)a, na)$ where a is the length of a developmental period as in earlier chapters, $n = n^*, n^* + 1, \ldots$ and $(n^*-1)a \leq t^* < n^*a$; n^* an integer. Model B incorporates the fact that under reduced food ratio more than one egg may be oviposited into a single grain (Hardman, 1978). So rather than removing a grain from the group of grains susceptible to attacks from the weevils, immediately it is attacked, it is kept there until the end of the developmental period during which it is attacked. At the end of the period the grain is considered no longer useful in that the weevils will not use it anymore. Also, by taking the emigration rate as a step function with respect to the developmental periods, the ecological hypothesis that young weevils are more dispersive than the old ones (private communication with Dr. R. Laughlin, Department of Entomology, Waite Agriculatural Research Institute) is incorporated (see Section 5.2.1, assumption 2).

In Model A the joint distribution of $S(t)$ and $W(t)$ is considered. But because of the complicated form of the equation for the joint p.g.f. of $S(t)$ and $W(t)$ an artificial random variable $\hat{W}(t)$ is introduced to represent $W(t)$ to reduce the complication. The stochastic means of $S(t)$ and the artificial variable $\hat{W}(t)$ are compared with the corresponding deterministic values. For Model B in addition to establishing the joint distribution of $S(t)$ and $W(t)$ during a developmental period, recurrence relations for their expected values at the beginnings of consecutive developmental periods are derived. Also the distribution of the number of eggs oviposited in a single grain during a given time interval is determined.

A comparison between the solutions of the two models is made.

5.1 MODEL A

5.1.0 A Review of the assumptions for phase II

As mentioned in Section 5.0 this model is a stochastic version of the deterministic model for phase II discussed in Section 2.2. Briefly let us review the assumptions made in Section 2.2. For the stochastic consideration the parameters are probabilistic as explained in Section 4.1. In this probabilistic context we have the oviposition rate

$$\lambda(t) = \lambda\ S(t)/W(t),$$

the consumption rate

$$\nu(t) = \nu\ S(t)/W(t),$$

the mortality rate μ remains constant and the emigration rate

$$\varepsilon(t) = \varepsilon + b\varepsilon(C-S(t)/W(t)) .$$

The emergence rate

$$\eta(t) = p\ \lambda(t-a)W(t-a)$$

is a random variable as in the phase I stochastic model. The constants λ, ν, ε, b, p and C are the same as those used in the phase I model in Chapter 4.

Combining the oviposition and consumption rates we obtain the rate

$$\alpha(t) = \left(\frac{\nu+\lambda}{C}\right) \frac{S(t)}{W(t)} = \hat{\alpha}\ S(t)/W(t)$$

at which an individual weevil attacks and damages the intact grains.

We make a further assumption that the expressions for the parameters given above will apply at any time $t \geqslant t^*$ even if the food ratio $S(t)/W(t)$ might be greater than C once again. But the rising of the food ratio above C after time t^* is very unlikely since, according to the expression for the emigration rate $\varepsilon(t)$, this would tend to reduce the number of emigrants and therefore increase the number of weevils that decide to stay in the system for a while. This, in turn, implies that the grains are attacked at a greater rate. So $S(t)$ would decrease faster whereas $W(t)$ would be increasing (or decreasing at a reduced rate). Then the food ratio $S(t)/W(t)$ would decrease - which is a contradiction to the supposition that the food ratio might rise above C at some time $t > t^*$. Recall that in Section 2.2.2 it was proved that the deterministic food ratio is decreasing for $t > t^*$.

As in the previous chapter we shall be concerned mainly with the bivariate process $\{(S(t),W(t)),t \geqslant t^*\}$. The initial condition for the process is $S(t^*) = S^*$ and $W(t^*) = W^*$ where S^* and W^* are determined using phase I solutions as mentioned in Section 5.0. However, rough but reasonable upper bounds for S^* and W^* given $S(0) = S_0$ and $W(0) = W_0$ can be determined independently of the solutions of Section 2.1 or Sections 4.3 and 4.5 by using the following argument. Suppose that none of the original weevils and those that have emerged during phase I have died or emigrated by time t^*. Then using the assumption that only one egg is oviposited in a grain during phase I, we have

$$\begin{aligned} W^* &= W_0 + p \times \{(\text{number of grains used up to time } t^*) \\ &\qquad - (\text{number of grains still holding eggs at time } t^*)\} \\ &< W_0 + p \times (\text{number of grains used up to time } t^*) \end{aligned}$$

so

$$W^* < W_0 + p(S_0 - S^*) , \tag{5.1.0}$$

where p is the proportion of eggs that are expected to develop into adults. But $S^* = CW^*$. Therefore from (5.1.0) we have

$$W^* < (W_0 + p\,S_0)/(1 + pC)$$

and hence

$$S^* < C(W_0 + p\,S_0)/(1 + pC) .$$

5.1.1 Equations for the joint distribution of weevils and the intact grains

Let $t_m = t^* + ma$ and denote the time interval $(t_m, \ldots, t_{m+1}]$ by D_m for $m = 0,1,2,\ldots$. We shall consider the conditional bivariate process $\{(S(t),W(t)), t \in D_m\}$ given $\{(S(\zeta),W(\zeta)), \zeta \in D_{m-1}\}$. Given $\{(S(\zeta),W(\zeta)), \zeta \in D_{m-1}\}$ the emergence rate $\eta(t) \triangleq p\lambda(t-a)W(t-a)$ becomes specified at all $t \in D_m$. Then the possible transitions of the bivariate process over a short time interval $(t,t+\delta t) \subset D_m$ are:

$$\left.\begin{array}{ll} \underline{\text{Transition}} & \underline{\text{probability}} \\ (s,w) \to (s-1,w) & \hat{\alpha}s + 0(\delta t) \quad \text{for} \quad w > 0 \\ (s,w) \to (s,w+1) & \eta(t)\delta t + 0(\delta t) \\ (s,w) \to (s,w-1) & \rho w - b\varepsilon s + 0(\delta t) \quad \text{for} \quad w > 0 \\ (s,w) \to (s,w) & 1 - [\eta(t) + (\hat{\alpha} - b\varepsilon)s + \rho w]\delta t \\ & \quad + 0(\delta t) \quad \text{for} \quad w > 0 \\ (s,0) \to (s,0) & 1 - \eta(t)\delta t + 0(\delta t) \\ \text{Others} & 0(\delta t) \end{array}\right\} \quad (5.1.1)$$

where

$$\rho = \mu + \varepsilon + b\varepsilon C \quad \text{and} \quad \hat{\alpha} = (\nu + \lambda)/C.$$

Now with the conditional probabilities

$$p_{sw}(t;m) \triangleq P(S(t)=s, W(t)=w \mid \{(S(\zeta), W(\zeta)), \zeta \in \mathcal{D}_{m-1}\})$$

we have, from (5.1.1),

$$\begin{aligned} \frac{d}{dt}(p_{sw}) = &- [(\hat{\alpha} - b\varepsilon)s + \eta(t) + \rho w]p_{sw} \\ &+ \hat{\alpha}(s+1)p_{s+1,w} + [\rho(w+1) - b\varepsilon s]p_{s,w+1} \\ &+ \eta(t)p_{s,w-1} \end{aligned} \qquad (5.1.2)$$

for $w \geqslant 1$,

and

$$\frac{d}{dt}(p_{s0}) = -\eta(t)p_{s0} + (\rho - b\varepsilon s)p_{s1} \qquad (5.1.3)$$

where

$$p_{sw} \equiv 0 \quad \text{for} \quad sw < 0 .$$

Initially (that is, at time t_m) we have

$$P(S(t_m)=s,\ W(t_m)=w \mid \{(S(\zeta),W(\zeta)),\zeta \in D_{m-1}\}$$

$$= \begin{cases} 1 & \text{for} \quad s = s_m \quad \textit{and} \quad w = w_m \\ 0 & \text{otherwise} , \end{cases}$$

where $s_m = S(t_m)$ and $w_m = W(t_m)$.
Now define the conditional probability generating function

$$G_m(t,x,y) = \sum_{s=0}^{\infty} \sum_{w=0}^{\infty} x^s y^w p_{sw}(t;m) , \quad |x|,|y| \leq 1. \quad (5.1.4)$$

Multiplying (5.1.2) by $x^s y^w$ and (5.1.3) by x^s and then summing with respect to s and w as in (5.1.4) we obtain

$$\frac{\partial G_m}{\partial t} = -\rho(y-1)\frac{\partial G_m}{\partial y} - \{\hat{\alpha}(x-1) - b\varepsilon x(y-1)/y\}\frac{\partial G_m}{\partial x}$$

$$+ \eta(t)(y-1)G_m + \{\hat{\alpha}(x-1) - b\varepsilon x(y-1)/y\} \sum_{s=0}^{\infty} s x^{s-1} p_{s0} \ . \quad (5.1.5)$$

Again, like in phase I (see Section 4.4), we have the awkward term

$$\{\hat{\alpha}(x-1) - b\varepsilon x(y-1)/y\} \sum_{s=0}^{\infty} s x^{s-1} p_{s0}$$

sticking around. This term looks even more awkward than that in equation (4.4.5). Even solving equations (5.1.2) and (5.1.3) recursively, unlike in Section 4.4, is very complicated. So again we shall try to use an artificial random variable to represent the number of adult weevils in a way similar to that used in Section 4.5.

5.1.2 Artificial random variable for weevils

Let us extend the range of the values $W(t)$ could take on to $-\infty$ by defining the artificial random variable $\hat{W}(t)$ to represent $W(t)$ as follows:

$$\left.\begin{array}{ll}
\text{(i)} & \hat{p}_{sw}(t;m) \triangleq P(S(t) = s,\ \hat{W}(t) = w \mid \{(S(\zeta),\ W(\zeta)), \\
& \qquad\qquad \zeta \in \mathcal{D}_{m-1}\}) \\
& \qquad\qquad = p_{sw}(t,m) \quad \text{for} \quad w > 0 \\
\multicolumn{2}{l}{\text{and } \hat{p}_{sw} \text{ satisfy equation (5.1.2), that is}} \\
\text{(ii)} & \frac{d}{dt}(\hat{p}_{sw}) = -[(\hat{\alpha} - b\varepsilon)s + \eta(t) + \rho w]\hat{p}_{sw} \\
& \qquad + \hat{\alpha}(s+1)\hat{p}_{s+1,w} + [\rho(w+1) - b\varepsilon s]\hat{p}_{s,w+1} \\
& \qquad + \eta(t)\hat{p}_{s,w-1}
\end{array}\right\} \quad (5.1.6)$$

for $s \geqslant 0$ and $-\infty < w < \infty$.

Then with $\hat{G}_m(t,x,y)$ as the generating function of the "artificial" probabilities $\hat{p}_{sw}$, that is

$$\hat{G}_m(t,x,y) = \sum_{s=0}^{\infty} \sum_{w=-\infty}^{\infty} x^s y^w \hat{p}_{sw} ,$$

equation (5.1.5) becomes

$$\frac{\partial \hat{G}_m}{\partial t} = -\rho(y-1)\frac{\partial \hat{G}_m}{\partial y} - \{\hat{\alpha}(x-1) - b\varepsilon x(y-1)/y\}\frac{\partial \hat{G}_m}{\partial x}$$

$$+ \eta(y-1)\hat{G}_m \quad . \qquad (5.1.7)$$

The auxiliary equations for (5.1.7) are

$$\frac{dt}{1} = \frac{dy}{\rho(y-1)} = \frac{dx}{\{\hat{\alpha}(x-1) - b\varepsilon x(y-1)/y\}} = \frac{d\hat{G}_m}{\eta(t)(y-1)\hat{G}_m} \quad .$$

Hence we have

$$(1) \quad \frac{1}{y-1}\frac{dy}{dt} = \rho \Rightarrow (y-1)e^{-\rho t} = \text{Constant} = A\,. \qquad (5.1.8)$$

$$(2) \quad \frac{d(\ell n\hat{G}_m)}{dt} = \eta(t)(y-1)\,.$$

Now substituting for y from (5.1.8) and integrating we obtain

$$\hat{G}_m \exp\left\{-\int_{t_m}^{t} \eta(\tau)\, Ae^{\rho\tau} d\tau\right\} = \text{Constant.}$$

Substituting for A from (5.1.8) we get

$$\hat{G}_m \exp\left\{-(y-1)\int_{t_m}^{t} \eta(\tau)\, e^{-\rho(t-\tau)} d\tau\right\}$$

$$= \text{Constant} = B. \qquad (5.1.9)$$

$$(3) \quad \frac{dx}{dt} = \hat{\alpha}(x-1) - b\varepsilon x(y-1)/y\,.$$

Now substituting for y from (5.1.8) and rearranging the terms we obtain

$$\frac{dx}{dt} + \left(\frac{b\varepsilon Ae^{\rho t}}{1+Ae^{\rho t}} - \hat{\alpha}\right)x = -\hat{\alpha}\,.$$

Integrating this equation we get

$$x(1 + Ae^{\rho t})^{b\varepsilon/\rho} e^{-\hat{\alpha}t} = -\hat{\alpha}\int_{t_m}^{t} (1 + Ae^{\rho\tau})^{b\varepsilon/\rho} e^{-\hat{\alpha}\tau} d\tau$$

$$+ \text{Constant.}$$

So substituting for A from (5.1.8) we have

$$xy^{b\varepsilon/\rho} e^{-\hat{\alpha}t} + \hat{\alpha}\int_{t_m}^{t} \left[1 + (y-1)e^{-\rho(t-\tau)}\right]^{b\varepsilon/\rho} e^{-\alpha\tau} d\tau$$

$$= \text{Constant} = D. \qquad (5.1.10)$$

Therefore, according to (5.1.9),

$$\hat{G}_m(t,x,y)\exp\left\{ - (y-1) \int_{t_m}^{t} \eta(\tau)e^{-\rho(t-\tau)}d\tau\right\}$$

$$= \Phi(A,D) \text{ (that is, an arbitrary function of A and D).}$$

Now using the initial condition

$$\hat{G}_m(t_m,x,y) = x^{s_m}y^{w_m} ,$$

we have

$$\Phi((y-1)e^{-\rho t_m}, xy^{b\varepsilon/\rho}e^{-\hat{\alpha}t_m}) = x^{s_m}y^{s_m} .$$

Hence

$$\Phi(A,D) = [1 + Ae^{\rho t_m}]^{w_m}[De^{\hat{\alpha}t_m}(1 + Ae^{\rho t_m})^{-b\varepsilon/\rho}]^{s_m} .$$

So now substituting for A and D from (5.1.8) and (5.1.10) respectively we obtain

$$\begin{aligned}
&\hat{G}_m(t,x,y) \\
&\quad = [1 + (y-1)e^{-\rho(t-t_m)}]^{w_m-b\varepsilon s_m/\rho} \times \\
&\qquad \{xy^{b\varepsilon/\rho}e^{-\hat{\alpha}(t-t_m)} + \hat{\alpha}\int_{t_m}^{t} [1 + (y-1)e^{-\rho(t-\tau)}]^{b\varepsilon/\rho} \times \\
&\qquad e^{-\hat{\alpha}(\tau-t_m)}d\tau\}^{s_m} \times \\
&\qquad \exp\{(y-1)\int_{t_m}^{t} \eta(\tau)e^{-\rho(t-\tau)}d\tau\} . \qquad (5.1.11)
\end{aligned}$$

5.1.3 Distribution of intact grains

Setting $y = 1$ in (5.1.11) we obtain the conditional p.g.f. of $S(t)$, $t \in \mathcal{D}_m$, given $\{(S(\zeta),W(\zeta)),\ \zeta \in \mathcal{D}_{m-1}\}$ as

$$G_m(t,x) = \left[x e^{-\hat{\alpha}(t-t_m)} + \hat{\alpha} \int_{t_m}^{t} e^{-\hat{\alpha}(\tau-t_m)} d\tau \right]^{s_m}$$

$$= \left[1 + (x-1) e^{-\hat{\alpha}(t-t_m)} \right]^{s_m} \qquad (5.1.12)$$

which is the p.g.f. of the binomial distribution $b(s_m, e^{-\hat{\alpha}(t-t_m)})$. Let us note that, of the entire $\{(S(\zeta), W(\zeta)),\ \zeta \in \mathcal{D}_{m-1}\}$, the p.g.f. (5.1.12) depends on only s_m.

Claim. Given $S(t^*) = S^*$ (and $W(t^*) = W^*$), $S(t)$ for $t \geqslant t^*$ is of the binomial distribution $b(S^*, e^{-\hat{\alpha}(t-t^*)})$.

Proof. Let us rewrite

$$G_m(t,x) = G(t,x;s_m) \triangleq G(t,x|S(t_m) = s_m) .$$

Then from (5.1.12) we deduce

$$G(t_m,x;s_{m-1}) = [1 + (x-1)e^{-\hat{\alpha}a}]^{s_{m-1}} . \qquad (5.1.13)$$

Multiplying (5.1.12) by $P(S(t_m) = s_m | S(t_{m-1}) = s_{m-1})$ and summing with respect to s_m we get

$$G(t,x;s_{m-1}) = G(t_m, 1 + (x-1)e^{-\hat{\alpha}(t-t_m)}; s_{m-1})$$

which, using (5.1.13),

$$= [1 + (x-1)e^{-\hat{\alpha}(t-t_{m-1})}]^{s_{m-1}} . \qquad (5.1.14)$$

From (5.1.12) and (5.1.14) it is clear that working recursively backwards we obtain

$$G(t,x;S^*) = [1 + (x-1)e^{-\hat{\alpha}(t-t^*)}]^{S^*}$$

which is the p.g.f. in the Claim. |||

Hence for $t \geqslant t^*$ the mean and the variance of $S(t)$ given $S(t^*) = S^*$ are

$$\left.\begin{aligned} E[S(t)] &= S^* e^{-\hat{\alpha}(t-t^*)} \\ \mathrm{Var}[S(t)] &= S^*(1 - e^{-\hat{\alpha}(t-t^*)})e^{-\hat{\alpha}(t-t^*)} \ . \end{aligned}\right\} \qquad (5.1.15)$$

We should note that the stochastic mean, $E[S(t)]$, of the number of intact grains is the same as the deterministic value $S(t)$ given by (2.2.11). Hence the investigation of how soon intact grains are likely to get finished is the same as in Section 2.2.4.

5.1.4 The mean of the artificial variable

By setting $x = 1$ in (5.1.11) we would obtain conditional p.g.f. of $\hat{W}(t)$. However, because the resulting expression is not simple enough to handle, we shall restrict our discussion to the mean $E[\hat{W}(t)]$.

Differentiating (5.1.11) with respect to y and then setting $x = 1$ and $y = 1$ we obtain

$$\begin{aligned} E[\hat{W}(t) \mid \{(S(\zeta),W(\zeta)),\ \zeta \in \mathcal{D}_{m-1}\}] \\ &= w_m e^{-\rho(t-t_m)} + s_m q(t_m,t) \\ &\quad + \int_{t_m}^{t} \eta(\tau) e^{-\rho(t-\tau)} d\tau \end{aligned} \qquad (5.1.16)$$

where

$$q(t_m,t) = b\varepsilon(e^{-\rho(t-t_m)} - e^{-\hat{\alpha}(t-t_m)})/(\hat{\alpha} - \rho) \ .$$

From (5.1.16) we deduce the unconditional expectation of $\hat{W}(t)$, $t \in \mathcal{D}_m$, to be

$$E[\hat{W}(t)] = E[W(t_m)]e^{-\rho(t-t_m)} + E[S(t_m)]q(t_m,t) + \int_{t_m}^{t} E[\eta(\tau)]e^{-\rho(t-\tau)}d\tau \quad . \qquad (5.1.17)$$

Substituting for $E[S(t_m)]$ from (5.1.15) and then substituting for $E[W(t_n)]$, $n = m, m-1, \ldots, 0$, recursively in the right-hand side of (5.1.17) it can be shown that, given $S(t^*) = S^*$ and $\hat{W}(t^*) = W^*$,

$$E[\hat{W}(t)] = W^* e^{-\rho(t-t^*)} + S^* q(t^*,t) + \int_{t^*}^{t} E[\eta(\tau)]e^{-\rho(t-\tau)}d\tau \ . \qquad (5.1.18)$$

With the appropriate expression for $\eta(\tau)$, it is not difficult to verify that (5.1.18) is equivalent to (2.2.12) for $t^* \leqslant t \leqslant t^*+a$ and to (2.2.13) for $t \geqslant t^*+a$. In other words the stochastic mean of the artificial random variable $\hat{W}(t)$ is the same as the deterministic value of the number of the weevils. But since $\hat{W}(t) \not\equiv W(t)$, this implies that the stochastic mean and the deterministic value of the number of weevils are not the same. Under certain assumptions (see next section) the deterministic value of $W(t)$ (that is $E[\hat{W}(t)]$) is a lower bound for the stochastic mean.

5.1.5 Relationship between the means of the artificial variable and the weevils

$$E[\hat{W}] = \sum_{w=-\infty}^{\infty} w\,\hat{p}_w = \sum_{w=0}^{\infty} w\,\hat{p}_w + \sum_{w<0} w\,\hat{p}_w \ .$$

But according to (5.1.6) $\hat{p}_w = p_w$ for $w > 0$. Hence

$$E[\hat{W}] = E[W] + \sum_{w<0} w\,\hat{p}_w \;. \tag{5.1.19}$$

The complicated form of the generating function of the generating function of the "artificial" probabilities $\hat{p}_w$ makes it difficult to establish whether $\hat{p}_w > 0$ for $w \leqslant 0$. If $\hat{p}_w \geqslant 0$ for all $w < 0$ then

$$\sum_{w<0} w\,\hat{p}_w \leqslant 0 \quad \text{which, from (5.1.19),}$$

implies that

$$E[\hat{W}] \leqslant E[W] \;. \tag{5.1.20}$$

5.1.6 Conclusion

It is interesting to note that according to this model the grain-weevil system is equivalent to one in which the weevils have no influence on a "pure-death" grain process but the availability of the grain influences the weevil population. This is the reverse of the influences in the stochastic model for phase I.

While the stochastic mean and the deterministic value of the number of intact grains work out to be the same, the stochastic mean of the number of weevils is different from the corresponding value which happens to be the same as the mean of the artificial random variable $\hat{W}(t)$.

The distribution of the weevils could not be obtained explicitly. Inferences about the distribution can be made through that of the artificial r.v. $\hat{W}(t)$ (for example, through the relation (5.1.20)). But even then the distribution of $\hat{W}(t)$ is not that easy to handle. These difficulties prompted me to revise some of the assumptions made in Section 5.1.0. This led to Model B which, I should say, is not necessarily easier to handle, but explicitly incorporates two important aspects of the grain-weevil system under critical food ratio conditions: (1) more than one egg may be oviposited into a grain and (2) young weevils are more dispersive than the old ones.

5.2 MODEL B

As in Model A the initial point in time is t^*. We consider the joint distribution of the number of intact grains $S(t)$ and the number of weevils $W(t)$ over each of the developmental periods $[(n-1)a, na)$, $n = n^*, n^*+1, \dots,$ where $(n^*-1)a < t^* < n^*a$ and n^* is an integer. Also recurrence relations between the expectations of $S_n \triangleq S(na)$ and $W_n \triangleq W(na)$, $n = n^*, n^*+1, \dots$ are derived. Because of the special assumptions made in Model B we need a careful look at the transition from phase I to phase II during the interval $[t^*-a, n^*a)$ (see Section 5.2.5).

5.2.1 Assumptions

Unless restated, the assumptions made in Section 5.1.0 also apply to Model B. Here we make further assumptions that are unique to Model B.

1. A wheat grain is subject to attacks by the weevils until a mature weevil emerges from it. If none of the eggs oviposited in a grain develop into adult weevils, then the grain is regarded destroyed at the time when all the

eggs are expected to have developed into adults. A maximum of one adult may emerge from a grain.

2. The eggs laid in the developmental period $[na,(n+1)a)$, $n \geqslant n^*$, and successfully emerge into adults, do so at time $(n+1)a$. This assumption tends to imply that eggs emerge into adults prematurely - instead of emerging continuously in time, the emergence of adults from the eggs is forced to occur at the beginnings of developmental periods. This may not be a bad approximation since, according to an ecological hypothesis, the young weevils are more dispersive than the old ones and therefore most of them would tend to emigrate before they can contribute significantly to the changes to the system. Consequently it does not matter very much at what instant of a developmental period an adult emerges from an egg. An attempt to incorporate the hypothesis that young weevils are more dispersive than the old ones is made through assumption 4 below.

3. If the number of intact grains at time na is s_n, then according to assumption 1, the total number of grains susceptible to attacks at any time $t \in [na,(n+1)a)$ is s_n. So if at time t the number of intact grains is $S(t)$, then the probabilistic rate at which the intact grains are attacked (and therefore damaged), at that time, is proportional to $S(t)/s_n$. We shall take it to be

$$\alpha(t) = (\nu + \lambda)S(t)/s_n = \alpha_n S(t), \text{ say,}$$

where ν and λ are the constant rates of consumption and oviposition, respectively, during phase I, and $\alpha_n = (\nu+\lambda)/s_n$.

In other words, the rates of consumption and oviposition by an individual weevil at time $t \in [na,(n+1)a)$ are $\nu S(t)/s_n$ and $\lambda S(t)/s_n$ respectively.

Let us note that in Mertz and Davies (1968) discussion of the cannibalism of the pupal stage by the adult beetles (*Tribolium Castaneum*), Mertz and Davies make the same assumption on the rate at which the pupae are attacked. That is the probabilistic rate at which the pupal population is attacked by an individual beetle is proportional to the ratio of the live pupae to the total number of pupae at the beginning of a time interval. In our case the pupae would be replaced by the grains and the adult beetles by the weevils. However, in the Mertz and Davies investigation the number of predators (that is the adult beetles; weevils in our case) was taken to be fixed during the entire period in which the pupae are vulnerable to attacks. In our grain-weevil system the predator (weevil) population is a death process over the developmental period.

4. The probability that a weevil leaves the system during a short time interval $(t,t+\delta t)$ increases as the food ratio $S(t)/W(t)$ decreases. As already used in Model A, one of the possible forms for the rate of emigration per weevil is

$$\varepsilon(t) = \varepsilon + b\varepsilon(C - S(t)/W(t)) \qquad (5.2.0)$$

where the constants ε, b and C are the same as in Model A.

According to assumption 2 we would expect a greater number of emigrants per unit time at the beginning of the interval $[na,(n+1)a)$ than at any later instant of the interval. One way of incorporating this hypothesis is to revise the emigration rate (5.2.0) as follows. Given $S(na) = s_n$ and $W(na) = w_n$,

$$\varepsilon(t) = \varepsilon + b\varepsilon(C - s_n/w_n) = \varepsilon_n, \text{ say }, \qquad (5.2.1)$$

for $na \leqslant t < (n+1)a$. That is the emigration rate is constant over $[na,(n+1)a)$. So, since over the interval the weevil population is a death-emigration process, there are more weevils and therefore more emigrants per unit time at the beginning of the interval than at any latter instant. Hence the hypothesis is incorporated.

5.2.2 Joint distribution of weevils and intact grains during a developmental period

According to the assumptions 1 - 4 in Section 5.2.1, given $S(na) = s_n$ and $W(na) = w_n$ the possible transitions for the bivariate process $\{(S(t),W(t)),\ na \leqslant t < (n+1)a\}$ and the corresponding probabilities over the time interval $(t,t+\delta t) \subset [na,(n+1a)$ are:

Transition	Probability
$(S,W) \to (S,W-1)$	$(\mu + \varepsilon_n)W\delta t + 0(\delta t)$
$(S,W) \to (S-1,W)$	$\alpha_n SW\delta t + 0(\delta t)$
$(S,W) \to (S,W)$	$1 - [\alpha_n S + \mu + \varepsilon_n]W\delta t + 0(\delta t)$
Others	$0(\delta t)$

where μ is the mortality rate as used before. Then, for $na \leqslant t < (n+1)a$, the conditional probabilities

$$p_{sw}(t;s_n,w_n) \triangleq P(S(t) = s,\ W(t) = w | S_n = s_n,\ W_n = w_n)$$

satisfy the differential difference equation

$$\frac{d}{dt}(p_{sw}) = -(\kappa_n w + \alpha_n sw)p_{sw} + \alpha_n(s+1)wp_{s+1,w} + \kappa_n(w+1)p_{s,w+1}, \tag{5.2.1}$$

where $\kappa_n = \mu + \varepsilon_n = \mu + \varepsilon(1+bC) - b\varepsilon s_n/w_n$

and $\alpha_n = (\nu + \lambda)/s_n$.

From (5.2.1) we can show that the conditional joint p.g.f. $G_n(t;x,y)$ of $(S(t),W(t))$ given $S_n = s_n$ and $W_n = w_n$ defined by

$$G_n(t,x,y) = \sum_s \sum_w x^s y^w p_{sw}(t;s_n,w_n), \quad |x|,|y| \leqslant 1$$

satisfies the equation

$$\frac{\partial G_n}{\partial t} = -\kappa_n(y-1)\frac{\partial G_n}{\partial y} - \alpha_n y(x-1)\frac{\partial^2 G_n}{\partial x \partial y} \tag{5.2.2}$$

with the initial condition

$$G_n(na,x,y) = x^{s_n} y^{w_n} \quad . \tag{5.2.3}$$

Equation (5.2.2) is similar to some equations for carrier-borne epidemics models (see Bailey, 1975, Chapter 10). Now using Bailey's technique let us look for a solution of (5.2.2) in the form

$$G_n(t,x,y) = \sum_{r=0}^{\infty} (x-1)^r f_{nr}(t,y) \tag{5.2.4}$$

where the functions f_{nr} are differentiable in both t and y , and are such that the series is convergent.

Substituting for G_n defined by (5.2.4) in (5.2.2) and equating the coefficients of $(x-1)^r$ we obtain

$$\frac{\partial f_{nr}}{\partial t} + (\kappa_n(y-1) + r\alpha_n y)\frac{\partial f_{nr}}{\partial y} = 0 \tag{5.2.5}$$

for $r = 0,1,2,\ldots$.

By rewriting the initial condition (5.2.3) as

$$G_n(na,x,y) = [1 + (x-1)]^{s_n} y^{w_n} = \sum_{r=0}^{s_n} \binom{s_n}{r} (x-1)^r y^{w_n}$$

we deduce the initial condition to (5.2.5) to be

$$f_{nr}(na,y) = \binom{s_n}{r} y^{w_n} \tag{5.2.6}$$

where $\binom{s_n}{r}$ takes on the conventional zero value for $r < 0$ or $r > s_n$. Then the solution to (5.2.5) with the initial condition (5.2.6) is

$$f_{nr}(t,y) = \binom{s_n}{r}\left[\frac{(\beta_{nr}y-\kappa_n)e^{-\beta_{nr}(t-na)} + \kappa_n}{\beta_{nr}}\right]^{w_n} \tag{5.2.7}$$

where $\beta_{nr} = \kappa_n + r\alpha_n$.

Definitely $f_{nr}(t,y)$ are differentiable in both t and y and since, $f_{nr}(t,y) \equiv 0$ for $r < 0$ or $r > s_n$, the series in (5.2.4) is convergent. So (5.2.4) reduces to

$$G_n(t,x,y) = \sum_{r=0}^{s_n} (x-1)^r f_{nr}(t,y) . \tag{5.2.8}$$

Distribution of the number of weevils $W(t)$, $na \leq t < (n+1)a$

The conditional p.g.f. of $W(t)$ given $S_n = s_n$ and $W_n = w_n$ is, from (5.2.4),

$$G_n(t,y) = G_n(t,1,y) = f_{n0}(t,y) .$$

Therefore from (5.2.7) we have

$$G_n(t,y) = [1 + (y-1)e^{-\kappa_n(t-na)}]^{w_n} \tag{5.2.9}$$

which is a p.g.f. of the binomial distribution $b(w_n, e^{-\kappa_n(t-na)})$. Hence the conditional mean and variance of $W(t)$ given $S_n = s_n$ and $W_n = w_n$ are

$$E[W(t); s_n, w_n] = w_n e^{-\kappa_n(t-na)} \qquad (5.2.10)$$

and

$$\text{Var}[W(t); s_n, w_n] = w_n e^{-\kappa_n(t-na)}(1 - e^{-\kappa_n(t-na)}). \qquad (5.2.11)$$

Distribution of the number of intact grain $S(t)$, $na \leqslant t < (n+1)a$

The conditional p.g.f. of $S(t)$ given $S_n = s_n$ and $W_n = w_n$ can be obtained by setting $y = 1$ in (5.2.8). However, it suffices to look at the factorial moments $E[S^{(r)}(t); s_n, w_n]$, $r = 0,1,2,\ldots,$ which, from (5.2.8), are given by

$$E[S^{(r)}(t); s_n, w_n] = \frac{\partial^r G_n(t,1,1)}{\partial x^r} = r!\ f_{nr}(t,1)$$

(where by $X^{(r)}$ I mean $X(X-1)\ \ldots\ (X-r+1)$).

In particular the conditional mean and variance of $S(t)$ given $S_n = s_n$ and $W_n = w_n$ are

$$E[S(t); s_n, w_n] = f_{n1}(t,1) \qquad (5.2.12)$$

and

$$\text{Var}[S(t); s_n, w_n] = 2f_{n2}(t,1) + f_{n1}(1 - f_{n1})(t,1) \qquad (5.2.13)$$

where according to (5.2.7)

$$f_{nr}(t,1) = \binom{s_n}{r}\left[\frac{r\alpha_n e^{-\beta_{nr}(t-na)} + \kappa_n}{\beta_{nr}}\right]^{w_n}. \qquad (5.2.14)$$

5.2.3 Distribution of eggs per grain

Let $I(t)$ denote the number of eggs oviposited in a grain over the time interval $[na,t)$ and denote by

$$p_i(t|s_n,W(\cdot)) = P(I(t) = i|S_n = s_n,\{W(\tau),\ na \leqslant \tau < t\}) .$$

Now, according to assumption 3 of Section 5.2.1, eggs are oviposited into a grain by the $W(t)$ weevils in the system at time t at the rate $\tilde{\lambda}(t) = \lambda W(t)/s_n$. So over the developmental period $[na,(n+1)a)$ the probabilities $p_i(t|s_n,W(\cdot))$ satisfy the following differential difference equation

$$\frac{dp_i}{dt} = \frac{\lambda}{s_n} W(t)[p_{i-1} - p_i] \qquad (5.2.15)$$

with $p_i \equiv 0$ for $i < 0$.

According to assumption 2 of Section 5.2.1 we start the developmental period $[na,(n+1)a)$ with none of the grains containing any eggs. Hence the initial condition for (5.2.15) is

$$p_i(na|S_n = s_n,W_n = w_n) = \begin{cases} 1 & \text{for } i = 0 \\ 0 & \text{for } i \neq 0 . \end{cases} \qquad (5.2.16)$$

From (5.2.15) we can show that the conditional p.g.f. of $I(t)$ given $S_n = s_n$ and $\{W(\tau),na \leqslant \tau < t\}$,

$$G(t,v|s_n,W(\cdot)) = \sum_{i=0}^{\infty} v^i p_i(t|s_n,W(\cdot)),$$

satisfies the differential equation

$$\left.\begin{array}{c}\frac{\partial G}{\partial t} = \lambda_n (v-1) W(t) G \\ \text{with the initial condition (according to (5.2.16)} \\ G(na, v; s_n, w_n) = v^0 = 1\end{array}\right\} \quad (5.2.17)$$

where $\lambda_n = \lambda/s_n$.

The solution to (5.2.17) is

$$G(t, v | s_n, W(\cdot)) = \exp[(v-1) A_n(t)] \qquad (5.2.18)$$

where $A_n(t) = \lambda_n \int_{na}^{t} W(\tau) d\tau$.

Now taking the expectation of (5.2.18) with respect to $\{W(\tau), na \leqslant \tau < t\}$ we obtain the p.g.f. of the number of eggs at time t , given $S(na) = s_n$ and $W(na) = w_n$, to be

$$G(t, v; s_n, w_n) = E[\exp\{\lambda_n (v-1) \int_{na}^{t} W(\tau) d\tau\}] .$$

The right-hand side can be easily deduced from the results of Section 4.6 in which we determined an expression for

$$H_1(t, y, z) \triangleq E[y^{W_1(t)} e^{zQ_1(t)}]$$

where $\{W_1(\tau), 0 < \tau < t\}$ is a death-emigration process and $Q_1(t) = \int_0^t W_1(\tau) d\tau$. Thus to obtain the expression for $G(t, v; s_n, w_n)$ we would set $y = 1$ and $z = \lambda_n (v-1)$. Then we get

$$G(t, v; s_n, w_n) = [h(t-na, 1, z)]^{w_n} \qquad (5.2.19)$$

where according to (4.6.8) we have

$$h(t-na,1,z) = \frac{ze^{(z-\kappa_n)(t-na)} - \kappa_n}{z - \kappa_n}$$

$$= \frac{\lambda_n(v-1)e^{[\lambda_n(v-1)-\kappa_n](t-na)} - \kappa_n}{\lambda_n(v-1) - \kappa_n} . \quad (5.2.20)$$

Then the conditional expectation of $I(t)$ given $S_n = s_n$ and $W_n = w_n$ is

$$E[I(t);s_n,w_n] = \left.\frac{\partial G(t,v;s_n,w_n)}{\partial v}\right|_{v=1}$$

$$= \lambda_n w_n \frac{\partial h(t-na,1,0)}{\partial z}$$

$$= \frac{\lambda w_n[1 - e^{-\kappa(t-na)}]}{s_n\kappa_n} , \quad (5.2.21)$$

where, recall, $\kappa_n = \mu + \varepsilon_n = \mu + \varepsilon + b\varepsilon(C - s_n/w_n)$. The conditional variance is

$$\mathrm{Var}[I(t);s_n,w_n] = w_n\left\{\left(\frac{\lambda_n}{\kappa_n}\right)^2 \left[1 - e^{-2\kappa_n(t-na)}\right]\right.$$

$$+ \frac{\lambda}{\kappa_n}\left[1 + (2\lambda_n(t-na)-1)e^{-\kappa_n(t-na)}\right] .$$

(5.2.22)

5.2.4 Recurrence relations for the moments of the weevils and the grains at beginnings of consecutive developmental periods

We should note that though the variable $S(t)$ is continuous at $t = (n+1)a$, the variable $W(t)$, because of assumption 2 of Section 5.2.1, is discontinuous at $t = (n+1)a$. New offsprings emerge at that time. So (5.2.8) and therefore (5.2.10) and (5.2.11) are not valid at $t = (n+1)a$. The random variable W_{n+1} for the number of adult weevils at time $(n+1)a$ is given by

$$W_{n+1} = \lim_{t\uparrow(n+1)a} \{p'(s_n - S(t)) + W(t)\}$$

$$= p'(s_n - S_{n+1}) + \lim_{t\uparrow(n+1)a} W(t) \qquad (5.2.23)$$

where p' is the proportion of the attacked grains from which we expect adults to emerge. If a weevil emerges from each grain in which eggs have been oviposited, then $p' = \lambda/(\nu + \lambda)$ otherwise $p' < \lambda/(\nu + \lambda)$.

From (5.2.23) we obtain the conditional mean and variance of W_{n+1} given $S_n = s_n$ and $W_n = w_n$. Taking the expectation of (5.2.23) and then using (5.2.10) we have

$$E[W_{n+1};s_n,w_n] = w_n e^{-\kappa n a} + p'\{s_n - E[S_{n+1};s_n,w_n]\}. \qquad (5.2.24)$$

From (5.2.23) in conjunction with (5.2.11) we obtain

$$\mathrm{Var}[W_{n+1};s_n,w_n]$$

$$= w_n e^{-\kappa n a}(1 - e^{-\kappa n a}) - \lim_{t\uparrow(n+1)a} 2p'\mathrm{Cov}[S(t),W(t);s_n w_n]$$

$$+ (p')^2\mathrm{Var}[S_{n+1};s_n w_n] \ , \qquad (5.2.25)$$

where, from the joint p.g.f. (5.2.8) of $S(t)$ and $W(t)$

$$\lim_{t\uparrow(n+1)a} \mathrm{Cov}[S(t),W(t);s_n,w_n]$$

$$= \frac{\partial f_{n1}((n+1)a,1)}{\partial y} - w_n f_{n1}((n+1)a,1)e^{-\kappa n a},$$

and $E[S_{n+1};s_n,w_n]$ and $\mathrm{Var}[S_{n+1};s_n,w_n]$ are obtained by setting $t = (n+1)a$ in (5.2.12) and (5.2.13) respectively.

From (5.2.13) and (5.2.25) it is clear that the expressions for the variances of S_{n+1} and W_{n+1} are not easy to handle. We shall, therefore, try to use the means to investigate the states of the system at the beginnings of consecutive developmental periods. First from (5.2.12) let us consider $E(S_{n+1};s_n,w_n) = f_{n1}(n+1)a,1)$. Substituting for f_{n1} from (5.2.7) we get

$$E(S_{n+1}|s_n,w_n) = s_n[d(s_n,w_n)]^{w_n} \qquad (5.2.26)$$

where

$$d(s_n,w_n) = 1 - \frac{\alpha_n(1 - e^{-\beta_{n1}a})}{\beta_{n1}} \quad . \qquad (5.2.27)$$

Let us note that $0 \leqslant d(s_n,w_n) \leqslant 1$ and therefore $\ell_n \triangleq [d(s_n,w_n)]^{w_n}$ is the expected fraction of the intact grains at time na still unattacked at time $(n+1)a$. So let us investigate how large ℓ_n can be and/or how quickly it decreases through the developmental periods.

Proposition 5.1 The *sufficient* condition that ℓ_n is

(i) an increasing function of s_n

and (ii) a decreasing function of w_n

is that

$$s_n/w_n < \beta/(2b\varepsilon) \quad . \qquad (5.2.28)$$

[The proof is given in Appendix 5.1.]

So according to (i), for a given number of weevils, the larger the number of intact grains at the beginning of a developmental period, the greater the number of intact grains remaining in the system at the end of the period. According to (ii) the larger the number of weevils at the beginning of the period the greater the number of grains that are attacked in the period and therefore the less the number of intact grains remaining at the end of the period.

If the value of the constant b (see end of Section 2.2.2) is such that $C < \beta/(2b\varepsilon)$, then (5.2.28) is satisfied even at the time t^* when the critical food ratio is reached for the first time; since $S(t^*)/W(t^*) = C < \beta/(2b\varepsilon)$. But as pointed out in Section 5.1.0 it is highly likely that $S_n/W_n < C$ for all $na > t^*$. So it is very likely that (5.2.28) is satisfied for all developmental periods after t^*. Then from (i) we have

$$\ell_n < \left[d\left(\frac{\beta w_n}{2b\varepsilon}, w_n\right)\right]^{w_n} = g(w_n), \text{ say .}$$

Because of the complexity of the expression for $g(w_n)$ it is not easy to determine its maximum value or to establish a meaningful upper bound for it. However, for a set of possible values of the parameters involved we may be able to demonstrate that $g(w_n)$ is a decreasing function of w_n and it would be possible to calculate maximum values of the fraction ℓ_n for various values of the number of weevils, w_n, at the beginning of the period. In Example 5.1 below in which we demonstrate that $g(w_n)$ is a decreasing function of w_n, we make use of the value of $g(w_n)$ as $w_n \to \infty$. The value is calculated from the limit

$$\lim_{w_n \to \infty} g(w_n) = \exp\left\{-\frac{4(\nu+\lambda)b\varepsilon}{\beta^2}(1 - e^{-\beta a/2})\right\}$$

which is obtained after some tedious and lengthy manipulation.

Example 5.1

With $\nu = 0.021285$, $\lambda = 1.0$, $\varepsilon = 0.006436$, $\mu = 0.008333$, $C = 10.0$, $b = 0.12$ and $a = 50$ we have (5.2.28) satisfied even at the time t^* when the critical food ratio is reached. Using these values we obtain:

Table 5.1

w_n	10	100	500	10^3	2×10^3	5×10^3	10^4	$+\infty$
$g(w_n)$	0.073311	0.068862	0.068493	0.068448	0.068425	0.068412	0.068407	0.068402

Table 5.1 clearly indicates that, for the given values of the parameters, $g(w_n)$ is a decreasing function of w_n. For example, for $w_n \geqslant 100$ we have

$$E[\, S_{n+1}; s_n, w_n] < (0.0689) s_n \,. \tag{5.2.29}$$

Then from (5.2.10) and (5.2.23) we have

$$E[\, W_{n+1}; s_n, w_n] > (0.9311) p' s_n + w_n \, e^{-\kappa_n a} \,.$$

But $w_n \, e^{-\kappa_n a} = w_n \, e^{-\beta a} \, e^{b\varepsilon a s_n / w_n} \geqslant (w_n + b\varepsilon a s_n) e^{-\beta a}$.

Hence for $w_n \geqslant 100$ we have

$$E[\, W_{n+1}; s_n, w_n] > [\,(0.9311) p' + b\varepsilon a e^{-\beta a}]\, s_n + w_n \, e^{-\beta a} \,. \tag{5.2.30}$$

From (5.2.29) and (5.2.30) we can deduce that for $E(W_n) \geqslant 100$,

$$E[S_{n+1}] < (0.0689)E[S_n] \tag{5.2.31}$$

and

$$E[W_{n+1}] > [(0.9311)p + b\varepsilon a\, e^{-\beta a}]E[S_n] + E[W_n]e^{-\beta a}. \tag{5.2.32}$$

It is clear from (5.2.30) or (5.2.32) that the extinction of the population of the weevils (including the eggs) is not possible before intact grains get finished; even if $\lim_{t \uparrow (n+1)a} W(t) = 0$, $E[W_{n+1}; s_n, w_n] > 0$ provided $s_n > 0$.

Let us recall that according to Model A we obtained the mean of the number of intact grains as $E[S(t)] = S^* e^{-\hat{\alpha}(t-t^*)}$ (see equations (5.1.15)). According to this solution the expected number of intact grains at the end of a developmental period would be the fraction $e^{-\hat{\alpha}a}$ of the number at the beginning of the period. Now with $\hat{\alpha} = (\nu+\lambda)/C$ and with ν, λ, a and C taking on the values used in Example 5.1, $e^{-\hat{\alpha}a} = 0.0060577$. Comparing this value with the values of $g(w_n)$ in Table 5.1 we deduce that, according to Model B the number of intact grains remaining after one developmental period (or any interval of time) could be as high as 11 times the number that would be remaining according to Model A; the initial numbers of intact grains at the beginning of the period being the same. This is expected because in Model B even the already attacked grains may be used again by the weevils whereas in Model A once a grain is attacked it is regarded destroyed and it cannot be used again.

5.2.5 The transition from Phase I to Phase II

We should not forget that there is a delay in the emergence of an adult from an egg. So we should look at the interval $[t^*-a, n^*a)$ carefully so that the complete output of phase I can be used as the input to phase II.

We shall assume that over the interval $[t^*, n^*a)$ the wheat grains susceptible to attacks by the weevils are those which are intact at time t^*. Then the derivation of the distribution of the bivariate process $\{(S(t), W(t)), t^* \leq t \leq n^*a\}$ would be the same as in Section 5.2.2. So by replacing na, s_n and w_n by t^*, s^* and w^* respectively and setting $t = n^*a$ in (5.2.12) and (5.2.14) we obtain

$$E[S(n^*a) \mid S(t^*) = s^*, W(t^*) = w^*] = s^* g^*(w^*)$$

where $g^*(w^*)$ (obtained by using $s^* = Cw^*$) works out to

$$g^*(w^*) = \left[1 - \frac{\nu+\lambda}{\nu+\lambda+Cw^*(\mu+\varepsilon)} \exp\left\{-\left(\mu+\varepsilon+\frac{\nu+\lambda}{Cw^*}\right)\left(n^*a - t^*\right)\right\}\right]^{w^*} .$$

It is not clear whether $g^*(w^*)$ is an increasing or a decreasing function of w^*. Intuitively $g^*(w^*)$ should be a decreasing function; for the larger the value of w^* the greater the rate at which the grains will be attacked and therefore the smaller the number of intact grains left in the system at time n^*a. But a demonstration of this intuition, as we did for $g(w_n)$ in Example 5.1, is not possible because t^* is not specified.

Over the interval (t^*, n^*a), $W(t)$ is a binomial random variable with parameters w^* and $\exp[-(\mu+\varepsilon)(t-t^*)]$. We account for all eggs laid in the interval $[t^*-a, n^*a)$ by assuming that they die or emerge into adults at time n^*a. Thus the size of the population of the adult weevils at time n^*a is

$$W(n^*a) = \lim_{t \uparrow n^*a} W(t) + p'(S(t^*-a) - S(n^*a)) .$$

Hence
$$E[W(n^*a)] = E[W^*] \exp\{-(\mu+\varepsilon)(n^*a-t^*)\} + p'(E[S(t^*-a)] - E[S(n^*a)])$$

where, once the value of t^* has been determined or estimated (see Section 4.8), $E[W^*]$ can be evaluated using equation (4.3.11) and a lower bound for $E[S(t^*-a)]$ is evaluated by using (4.7.4) and (4.5.7).

5.2.6 Generalising some of the assumptions

The assumptions in Section 5.2.1 are such that we have been able to derive and solve the equation for the functions $f_{nr}(t,y)$. As it is apparent from the marginal distributions of $S(t)$ and $W(t)$, these functions play a basic role in the essential structure of our problem. However, if we wish to revise or generalise the assumptions we may not be able to derive an equation for $f_{nr}(t,y)$. Even if we are able to derive the equation it may not be possible to solve the equation directly, for example, without taking transforms of it. In this section we shall look at a generalization of some of the assumptions and still be able to determine the functions f_{nr}.

We shall relax assumption 3 of Section 5.2.1 so as to let the rate at which the intact grains are attacked to be a product of $S(t)$ and an arbitrary function of the number of adult weevils $W(t)$. That is, given that $S(na) = s_n$ and $W(na) = w_n$,

(i) $\alpha_n(t) = S(t)\xi(W(t),s_n,w_n)$ for $na \leqslant t < (n+1)a$, where ξ is the arbitrary function. Also we shall let the emigration rate $\varepsilon(t)$ and the death rate μ be functions of $W(t)$ instead of being constants during a developmental period as used in Section 5.2.2. That is the emigration and death rates, for $na \leqslant t < (n+1)a$, are

(ii) $\varepsilon_n(t) = \varepsilon(W(t),s_n,w_n)$ and $\mu_n(t) = \mu(W(t),s_n,w_n)$

respectively.

With the rates (i) and (ii) we can regard our system as a Carrier-borne epidemic in which the grains are the susceptibles and the weevils are the carriers. Then, according to Henderson's (1979) technique we can write the p.g.f. $G_n(t,x,y)$ in the form

$$G_n(t,x,y) = \sum_{s=0}^{s_n} (x-1)^s \binom{s_n}{s} \sum_w y^w q_{sw}(t) \qquad (5.2.33)$$

where

$$q_{sw}(t) = P\left[\begin{array}{l}\text{there are } w \text{ weevils (carriers) at time}\\ t \text{ and a fixed predetermined group of } s\\ \text{grains (susceptibles) is still intact at}\\ \text{time } t\end{array}\right]$$

Using this approach we could also have different groups of weevils. In our case the obvious groups would be those of the eggs, larvae, pupae, pre-emergence adults, mature females and mature males. Then $w(t)$ becomes a vector $\underset{\sim}{w}(t) = (w_1(t),\ldots,w_n(t))$ where $w_i(t)$ is the size of the i-th group at time t. However, for our discussion here we shall consider the case of one group of weevils (the mature adults). The results for more than one group can be obtained using a similar line of argument.

Comparing (5.2.8) and (5.2.33) we deduce that

$$f_{ns}(t,y) = \binom{s_n}{s} \sum_w y^w q_{sw}(t) \quad . \tag{5.2.34}$$

So here f_{ns} has been broken up into the functions $g_{sw}(t)$ of one independent variable t . Note that this is actually what we did in Section 5.2.2 when we broke up $G_n(t,x,y)$ into the functions $f_{nr}(t,y)$. In general it is simpler to solve for functions with fewer arguments. Thus if we can solve for $q_{sw}(t)$ we can obtain an expression for $f_{ns}(t,y)$ using (5.2.34).

According to the formulas (i) and (ii) for the rates $\alpha_n(t)$, $\varepsilon_n(t)$ and $\mu_n(t)$ the probabilities $q_{sw}(t)$ satisfy the equations

$$\left.\begin{aligned} \frac{dq_{sw}}{dt} &= -\gamma_s(w)q_{sw} + \beta(w+1)q_{s,w+1} \\ \text{and} \qquad \frac{dq_{so}}{dt} &= \beta(1)q_1 \end{aligned}\right\} \tag{5.2.35}$$

with $q_{sw}(t) = 0$ for $w < 0$ or $w > w_n$, $na \leqslant t < (n+1)a$ where

$$\gamma_s(w) = s\ \xi(w,s_n,w_n) + (\mu+\varepsilon)(w,s_n,w_n)$$

and $$\beta(w) = (\mu+\varepsilon)(w,s_n,w_n) \quad .$$

The initial condition for (5.2.35) is

$$q_{sw}(na) = \begin{cases} 0 & \text{for} \quad w \neq w_n \\ 1 & \text{for} \quad w = w_n \quad . \end{cases}$$

Note that because the generating function

$$J_s(t,y) \triangleq \sum_w q_{sw}\, y^w = f_{ns}(t,y)\Big/\binom{s_n}{s} \ , \tag{5.2.36}$$

we would not try to use the method of generating function for the q_{sw} to solve the equations (5.2.35); for if we cannot solve the equation for the functions f_{ns} we cannot solve the equation for $J_s(y,t)$. So if we are to solve (5.2.35) the remaining alternative is to solve them recursively in w either directly or by first taking Laplace transforms and then inverting the results.

Now define the transformation functions

$$\hat{Q}_w(z) = \int_{na}^{\infty} q_w(t)\, e^{-zt} dt$$

for $\mathrm{Re}\ z >$ some $R > -\infty$ so that the integral is convergent; where the subscript s has been supressed. Then from (5.2.35) we obtain

$$\left.\begin{aligned} (z+\gamma(w))\hat{Q}_w(z) &= q_w(na^+)e^{-zna} + \beta(w+1)\hat{Q}_{w+1}(t) \\ \text{and}\qquad q_0(t) &= \beta(1)\int_{na}^{t} q_1(\tau)d\tau\,. \end{aligned}\right\} \quad (5.2.37)$$

Now solving (5.2.37) using the initial condition $q_w(na) = \delta_{w,w_n}$ and the boundary condition $q_w(t) = 0$ (and therefore $\hat{Q}_w(z) = 0$) for $w > w_n$, we obtain

$$\hat{Q}_{w_n}(z) = \frac{e^{-zna}}{z+\gamma(w_n)}$$

and

$$\hat{Q}_w(z) = \frac{\beta(w+1)\hat{Q}_{w+1}(z)}{z+\gamma(w)} \quad \text{for} \quad 1 \leqslant w < w_n\,.$$

$$= \left[\prod_{r=w+1}^{w_n-1}\beta(r)\right] e^{-zna}\Big/\prod_{r=w}^{w_n}(z+\gamma(r))$$

$$= \left[\prod_{r=w+1}^{w_n-1}\beta(r)\right] e^{-zna}\sum_{r=w}^{w_n}\frac{C_r}{z+\gamma(r)} \qquad (5.2.38)$$

where $C_r = \prod_{\substack{j=w \\ j\neq r}}^{w_n} (\gamma(j) - \gamma(r))$.

Now noting that

$$\int_{na}^{t} e^{-\gamma(w)(t-na)} e^{-zt} dt = \frac{e^{-zna}}{z+\gamma(w)} ,$$

the inverse of the transform (5.2.38) is

$$\left.\begin{aligned} q_w(t) &= \left[\prod_{r=w+1}^{w_n-1} \beta(r)\right] \sum_{r=w}^{w_n} C_r\, e^{-\gamma(r)(t-na)}, \quad 1 \leqslant w < w_n \\ q_{w_n}(t) &= e^{-\gamma(w_n)(t-na)} \end{aligned}\right\} \qquad (5.2.39)$$

and $q_0(t)$ is evaluated from the second equation of (5.2.37).

So resupplying the subscript s and substituting for $q_{sw}(t)$ in (5.2.34) and (5.2.33) we obtain expressions for $f_{ns}(t,y)$ and $G_n(t,x,y)$ respectively.

Example 5.2

Suppose that, according to assumption 3 of Section 5.2.1, we still have

$$\alpha(t) = (\nu + \lambda)S(t)/s_n = \alpha_n\, S(t)$$

but the emigration rate (5.2.1) is revised to

$$\begin{aligned} \varepsilon(t) &= \varepsilon + b\varepsilon(C - s_n/W(t)) \\ &= \kappa + b\varepsilon s_n/W(t) \end{aligned} \qquad (5.2.40)$$

and the death rate $\mu(t) = \mu$ (a constant).

Then we can show that the generating function

$$J(t,y) \triangleq \sum_{w=0}^{w_n} y^w\, q_w(t)$$

(where the subscript s is suppressed again) satisfies the equation

$$\frac{\partial J}{\partial t} = -\left[\alpha_n s + \kappa(y-1)\right]\frac{\partial J}{\partial y} + b\varepsilon s_n\left(1 - \frac{1}{y}\right)J$$

$$- b\varepsilon s_n\left(1 - \frac{1}{y}\right)q_0(t) \quad . \qquad (5.2.41)$$

According to (5.2.36) $f_n(t,y)$ would satisfy the same equation (5.2.41) except that the last term of the right-hand side of (5.2.41) would be multiplied by $\binom{s_n}{s}$. The unknown term $- b\varepsilon s_n\left(1 - \frac{1}{y}\right)q_0(t)$ in (5.2.41) makes it difficult to solve for $J(t,y)$ directly from the equation. But according to the procedure used to obtain (5.2.39), expressions for the functions $q_w(t)$ (and hence the function $f_n(t,y)$ can be easily obtained. Thus this example illustrates that the equation for the functions $f_n(t,y)$ may not be simple enough to apply straight-forward methods to solve it whereas the equations for $q_w(t)$ can be easily solved.

5.3 DISCUSSION

As already noted in Section 5.1.2, according to Model A , exact equations for the distribution of the weevils could not be obtained. In order to be able to make some inferences about the weevil population I introduced an artificial random variable $\hat{W}(t)$. Model B offers an alternative way by which an introduction of the artificial random variable can be avoided. This is achieved by dividing the time line into developmental periods and assuming that all the eggs laid during a developmental period emerge into adults at the beginning of the next one. At this point let me mention Neyman, Park and Scott (1956) model for a situation similar to the grain-weevil system. In their investigation of cannibalism of eggs by the adult beetle, *Tribolium*, they divided time into successive "seasons" and assumed that the female laid *all* its eggs at the beginning of a season. Then the eggs would be subject to attacks by the adults during part of the season. The survivors become mature adults at the beginning of the next season. However we should note the differences between Neyman *et al* problem and our grain-weevil problem. In their model the beetles eat what they lay (in other words there is an increase in the food supply at the beginning of each season) whereas in our case the food supply is strictly decreasing. Our Model B allows oviposition through the developmental periods whereas in Neyman *et al* model a female beetle lays all its eggs once and for all.

According to Model A the possibility that more than one egg could be oviposited in a grain could not be explicitly considered. But according to Model B a grain (whether already containing eggs or not) is susceptible to attacks by the weevils until the end of a developmental period. Thus according to the Model B formulation the intact grains are used at a slower rate than in Model A and the distribution of the number of eggs oviposited in a single grain during any interval of time (within a developmental period) can be determined. Also a combination of the assumption that young adults emerge at the beginning of a developmental period and the assumption that the emigration rate is constant during the developmental period incorporates the hypothesis that young adults are more dispersive than the old ones (see Section 5.2.1).

Now turning to the solutions let us note that according to Model A $S(t)$ (that is the number of intact grains at time t) is binomially distributed. However, as already mentioned, the exact distribution of $W(t)$ (that is the number of adult weevils at time t) could not be obtained. But the expectation and variance of the artificial variable $\hat{W}(t)$ were shown (under certain assumptions; see Section 5.1.5) to be a lower bound for the expectation and an upper bound for the variance, respectively, of $W(t)$. According to Model B $W(t)$ is binomially distributed during a developmental period but the equations for the distribution of $S(t)$ are more difficult to handle. From the recurrence relations (derived in Section 5.2.4) between the expectations of $S(t)$ and $W(t)$ at the beginnings of two consecutive developmental periods we could determine the maximum fraction of intact grains that are *not* attacked during a developmental period. Comparing the solutions for $S(t)$ by the two models, for a given set of values of the parameters, we could deduce that according to Model B the number of intact grains not attacked during a developmental period could be as high as 11 times the corresponding number in Model A. Also from the recurrence relations we can deduce that the extinction of the weevil population is not possible until all the intact grains have been utilised. But even then the weevil population would not come to an end immediately intact grains are finished. It has been observed (Coombs and Woodroffe, 1973) that when intact grains are finished the weevils feed on frass and the husks of the grains from which young ones have emerged. So I would say that then the weevil population becomes a death-emigration process in which the longevity of an individual is very much reduced. In our two models the reduction in longevity is achieved through the increased rate of emigration when the grains get finished. Some of the weevils that would have died in the system, because of lack of food and ovipositional sites, are free to emigrate. From the grain-weevil system viewpoint emigrants can be regarded dead. Hence those which emigrate have a short life-span as far as the system is concerned.

Finally I would like to note that a revision of the assumptions made in the two models remains open. As shown in Section 5.2.6 there are other ways of formulating our problem and still be able to solve the equations. However, we should have it borne in mind that a drastic revision may not relate to the situation we are considering.

CHAPTER 6

SPATIAL DISTRIBUTION OF INSECTS (WEEVILS) WITHIN STORED GRAIN

6.1 INTRODUCTION

In the previous chapters we have not taken into account the spatial distribution (dispersal) of the weevils within the wheat they are infesting. The spatial distribution influences the activities of the weevils. For example, as pointed out at the end of Section 3.2.8, when the weevils are sparsely distributed within the wheat the oviposition rate may be very low due to lack of copulation. For sure the spatial distribution influences the rate of emigration; for the weevils can only emigrate from the surfaces open to the outside environment. It is also of interest to determine whether there are aggregations of the weevils in some particular sections of the stored wheat.

The model, in this chapter, is concerned with the dispersal of weevils within wheat stored in a container. The container could be small or as big as a silo. Initially we have all the wheat grains intact and the initial distribution of a given number of weevils within the grain is known.

This dispersal problem could be regarded as a diffusion problem with the diffusion coefficients as functions of the local conditions. In the next section I mention models that are related to our problem, but because of the special nature of the grain-weevil system the models cannot fit exactly the assumptions made about the system. I therefore derive and solve dispersal equations from first principles. The basic assumption for the derivation is that the length of time a weevil spends in a section of the wheat depends on the availability of intact grains in the section. A weevil is more likely to stay longer in a section where the food ratio is high than in a section where the food ratio is low.

The equations derived are for the number of weevils and the number of intact grains per unit volume. In order to solve these equations the method of *separation of variables* is applied and then a Laplace transform technique is used to determine the exact solution to a resulting *delay integro-differential equation*. Though this delay equation is of higher difficulty than the delay differential equations of Chapter 2, it is shown that we could still solve it by the rather natural method of steps.

6.2 BASIC ASSUMPTIONS AND RELATED MODELS

We shall assume that the container in which the wheat is stored is cylindrical. However, for the formulation of the problem we shall represent the container by a line segment. Thus a point on the line segment represents a cross-section of the container.

The time a weevil spends in a section of the container is a function of the *food ratio* (that is the average number of intact grains to a weevil) in that section. A weevil is likely to stay longer in a section where the food ratio is high than in a section where the food ratio is low.

Let $s(x,t)$ and $w(x,t)$ be the number of intact grains and the number of weevils, respectively, per unit volume in section x of the container (or at point x when referring to the representative line) at time t. Then we define the food ratio in section x at time t as

$$F(x,t) = s(x,t)/w(x,t) \tag{6.2.1}$$

One of the possible equations that could model the dispersal (distribution) of the weevils within the wheat is the equation for "diffusion under a potential field". That is $w(x,t)$ could satisfy an equation of the form

$$\frac{\partial w}{\partial t} = \tilde{D}\,\frac{\partial^2 w}{\partial x^2} + \tilde{\mu}(x)\,\frac{\partial w}{\partial x}$$

where

$$\tilde{\mu}(x) = (\text{constant}) \times \frac{\partial P}{\partial x}$$

and P is the potential function (Chesson, 1976). In our case P could be a function of the food ratio $F(x,t)$. In particular we could take $P(x,t) = F(x,t)$. However, if we do so, we would be assuming that the weevils would move (drift) in directions of increasing food ratio. I do not think that the weevils can determine the direction of greatest increase from where they are. Instead, I feel, it is the local conditions, such as the local food ratio, that determine whether a weevil is going to move or to stay for a while. Once it has decided to move, its immediate direction of motion is arbitrary. Thus it is not obvious how we can relate the movements of the weevils to the food ratio potential field.

Kiester and Slatkin (1974) derived an equation for the dispersal of lizards in a linear habitat. They based their derivation on the hypothesis that the probability that an individual moves in a given direction $x \to x + \delta x$ in a small interval of time is proportional to the length of the interval and to the directional increase $E(x+\delta x) - E(x)$, where $E(x)$ is the free-time available at position x after an individual has performed the essential activities such as looking for food and eating at x. Kiester *et al* assume that the probability of moving in the direction in which $E(x)$ is decreasing is zero. As I can see their argument would apply to situations in which the habitat is stationary (that is not time-dependent) and the individual animals have already explored the habitat so as to know the favourable places, within the habitat, for different activities! In our case the habitat is not stationary; as the weevils move among the wheat grains they reduce the food availability in the habitat.

For our problem we make the following assumption. "In a small interval of time $(t, t+\delta t)$ a weevil will either leave or stay in the section of the container it is in at time t. If the weevil decides to leave then the probability that it moves up (right of the axis of the container is horizontal) is a half (½). The probability $\beta(x,t)$ that a weevil stays in the section x over the time interval $(t,t+\delta t)$ is proportional to the mean food ratio in the section." That is

$$\beta(x,t) = D\, s(x,t)/w(x,t) \tag{6.2.2}$$

where D is a constant. Skellam (1951) refers to this kind of movement (dispersal) as due to "random blindness" - an individual moves because of cumulative effect of local irregularities but then it "may not discriminate between two parts of a habitat differing considerably in their effect on survival".

Of course the other processes that take place in our system are the emergence of young weevils from the eggs and the dying and emigration of the adults. As in previous chapters (except section 3.2.2) we shall assume it takes a days for an egg to develop into a mature adult. The movements of the adult weevils past a grain in which an egg has been oviposited has no effect on the rate of the development of the egg. A weevil may leave the container only from the top surface of the wheat.

6.3 DERIVATION OF THE EQUATIONS

Let the depth of the wheat in the container be L. For the sake of the derivation of the dispersal equation let us divide the wheat into sections of width h; the middle of the i-th section being $(i-\frac{1}{2})h$ distance units above the bottom of the container. We shall consider movements of a weevil during a short time interval $(t,t+\delta t)$ where h and δt are such that the probability, $\beta(i,t)$, that an individual will not leave section i in the time interval is independent of h and δt. In other words if we make h smaller we also reduce the value of δt in such a way that the probability $\beta(i,t)$ is unchanged. For if we are to reduce h without reducing δt then the region over which a weevil would wander for the same length of time (without leaving the section) will be smaller. This would tend to decrease the probability $\beta(i,t)$. However by reducing δt in an appropriate way we can have $\beta(i,t)$ remaining constant.

Let, according to (6.2.2),

$$\begin{aligned}\beta(i,t) &= \kappa(\nu+\lambda)s(i,t)/w(i,t)\\ &= \kappa\alpha s(i,t)/w(i,t)\end{aligned} \tag{6.3.1}$$

where κ is an arbitrary constant $(D = \kappa\alpha)$, ν is the rate at which the grains are eaten by an individual weevil and λ is the rate of oviposition of eggs per weevil. [For the choice of the values of κ see the paragraph after relation (6.4.20).]

First of all let us derive the equation for the dispersal aspect of our process. The possible transitions (movements) and the corresponding probabilities, in the time interval $(t,t+\delta t)$, by a weevil in section i at time t are:

transition	probability
$i \to i$	$\beta(i,t)$
$i \to i-1$	$\frac{1}{2}[1-\beta(i,t)]$
$i \to i+1$	$\frac{1}{2}[1-\beta(i,t)]$.

Therefore with $w(i,t)$ as the expected number of weevils in section i at time t, the expected number of weevils in the section at time $t+\delta t$ is

$$w(i,t+\delta t) = \beta(i,t)w(i,t) + \frac{1}{2}[1-\beta(i+1,t)]w(i+1,t) + \frac{1}{2}[1-\beta(i-1,t)]w(i-1,t) \qquad (6.3.2)$$

Hoppensteadt [1976, Chapter VIII] uses similar arguments to derive a diffusion approximation to a propagation of a biological activity along a grid of cells. However in his derivation the probability β is constant unlike our $\beta(i,t)$ which depends on the local conditions. Therefore his final result cannot fit our situation.

Let us represent section i by a single variable x. For example x could be the height, $(i-\frac{1}{2})h$, of the middle of section i above the bottom of the container. So substituting for $\beta(i,t)$ from (6.3.1) and then replacing i by x, $i+1$ by $x+h$ and $i-1$ by $x-h$, equation (6.3.2) becomes

$$w(x,t+\delta t) = \kappa\alpha s(x,t) + \frac{1}{2}[w(x+h,t)-\kappa\alpha s(x+h,t)] + \frac{1}{2}[w(x-h,t)-\kappa\alpha s(x-h,t)]. \quad (6.3.3)$$

Now from the Taylor's series expansion of $w(x,t+\delta t)$ about (x,t) with respect to t and the Taylor's series expansion of the right-hand side (RHS) of (6.3.3) about (x,t) with respect to x we obtain

$$\frac{\partial w}{\partial t}\delta t + \frac{1}{2}\frac{\partial^2 w}{\partial t^2}(\delta t)^2 + o[(\delta t)^2] = \frac{1}{2}h^2\frac{\partial^2}{\partial x^2}(w-\kappa\alpha s) + o(h^2) .$$

Dividing this equation by δt and taking limits as $\delta t \to 0$ and $h \to 0$ in such a way that

$$h^2/\delta t \to \sigma^2 \quad \text{(a constant)}$$

and

$$h^r/\delta t \to 0 \quad \text{for} \quad r > 2 ,$$

we obtain

$$\frac{\partial w}{\partial t} = \frac{1}{2}\sigma^2\frac{\partial^2}{\partial x^2}(w-\kappa\alpha s) . \quad (6.3.4)$$

The constant σ^2 is arbitrary. However condition (6.4.20) (in section 6.4.2) indicates how the values of σ^2, in conjunction with the values of κ, may be chosen so as to ensure a solution to our problem.

6.3.1 Deaths, Emergence and Emigration Incorporated

In deriving (6.3.4) we considered only the movement of the weevils. But as they move, they also oviposit eggs and eat up the grain, some die, young ones emerge from eggs laid a days ago and some emigrate from the top surface. If the dispersal of the weevils is not considered the equation for the expected number of weevils per unit volume, $w(x,t)$, would be

$$\frac{\partial w(x,t)}{\partial t} = -\mu w(x,t) + p\lambda w(x,t-a) \qquad (6.3.5)$$

where μ is the mortality rate for an individual weevil, p is the proportion of the eggs that develop into adults, and λ is the oviposition rate as defined before. Note that $\lambda w(x,t-a)$ is the total rate of oviposition of eggs in section x at time $t-a$. The total emergence rate in the section at time t is a proportion of this oviposition rate - hence the second term in the RHS of (6.3.5).

Now combining (6.3.4) and (6.3.5) we get

$$\frac{\partial w(x,t)}{\partial t} = -\mu w(x,t) + p\lambda w(x,t-a) + \frac{1}{2}\sigma^2 \frac{\partial^2}{\partial x^2}(w(x,t)-\kappa\alpha s(x,t)). \qquad (6.3.6)$$

The expected number of intact grains per unit volume, $s(x,t)$, satisfies the equation

$$\frac{\partial s(x,t)}{\partial t} = -\alpha w(x,t) \qquad (6.3.7)$$

where $\alpha w(x,t)$ is the total rate at which the weevils use up the grains in section x at time t.

The *initial conditions* to (6.3.6) and (6.3.7) are

$$w(x,0) = \frac{N_0}{L}\,\phi(x) \qquad (6.3.8)$$

and

$$s(x,0) = \frac{S_0}{L} \qquad (6.3.9)$$

for $0 \leqslant x \leqslant L$ and where $\phi(x)$ is a known function. For example if the weevils are initially released at the top surface we would have $\phi(x) = \delta(x-L)$. S_0 is the initial number of intact grains and N_0 is the number of adult weevils initially introduced into the system.

The weevils leave (emigrate from) the wheat at the rate of ε weevils per unit time per weevil in the top surface. Thus the *boundary conditions* to equation (6.3.6) are

$$\left.\frac{\partial w}{\partial x}\right|_{x=L} = \varepsilon w(L,t) \qquad (6.3.10)$$

and

$$\left.\frac{\partial w}{\partial x}\right|_{x=0} = 0 \qquad (6.3.11)$$

where, of course, equation (6.3.11) implies that the weevils cannot leave the system through the bottom of the container. We should note that though weevils may leave the habitat they cannot come back. In other words there is no immigration into the system.

6.4 SOLUTION OF THE EQUATIONS

6.4.1 Separation of Variables

Integrating (6.3.7) subject to the initial condition (6.3.9) we get

$$s(x,t) = \frac{S_0}{L} - \alpha \int_0^t w(x,\tau)\,d\tau \qquad (6.4.1)$$

Then substituting for $s(x,t)$ in (6.3.6) we have

$$\frac{\partial w(x,t)}{\partial t} = p\lambda w(x,t-a) - \mu w(x,t)$$

$$+ \frac{1}{2}\sigma^2 \frac{\partial^2}{\partial x^2}\left(w(x,t) + \kappa\alpha^2 \int_0^t w(x,\tau)\,d\tau\right). \qquad (6.4.2)$$

Let us look for a solution to equation (6.4.2) of the form

$$w(x,t) = N(x)T(t) .$$

Then from (6.4.2) we obtain

$$\frac{T'(t) + \mu T(t) - p\lambda T(t-a)}{T(t) + \kappa\alpha^2 \int_0^t T(\tau)\,d\tau} = -\frac{c^2}{2} = \frac{\sigma^2}{2}\frac{1}{N}\frac{d^2N}{dx^2}$$

where c is a parameter.

So we have

$$\frac{d^2N}{dx^2} + \gamma^2 N = 0 \qquad (6.4.3)$$

and

$$\frac{dT}{dt} + (\mu + \tfrac{1}{2}\sigma^2\gamma^2)T(t) + \tfrac{1}{2}\kappa\alpha^2\sigma^2\gamma^2 \int_0^t T(\tau)\,d\tau - p\lambda T(t-a) = 0, \qquad (6.4.4)$$

where

$$\gamma^2 = c^2/\sigma^2 .$$

From the boundary conditions (6.3.10) and (6.3.11) we have

$$\left.\frac{dN}{dx}\right|_{x=L} = \varepsilon N(L) \qquad (6.4.5)$$

and

$$\left.\frac{dN}{dx}\right|_{x=0} = 0 \qquad (6.4.6)$$

The general solution to (6.4.3) is

$$N(x) = K_1 \cos \gamma x + K_2 \sin \gamma x$$

where K_1 and K_2 are constants. The boundary condition (6.4.6) implies that $K_2 = 0$.

So

$$N(x) = K_1 \cos \gamma x \, . \qquad (6.4.7)$$

Now applying boundary condition (6.4.5) to the solution (6.4.7) we obtain

$$\tan \gamma L = \varepsilon / \gamma \, . \qquad (6.4.8)$$

So the eigenvalues of the equation (6.4.3) are the roots of (6.4.8). From Figure 6.1 it is clear that the r-th positive eigenvalue is

$$\gamma_r^+ = (r-1)\frac{\pi}{L} + \frac{\theta_r}{L} \quad , \quad r = 1,2,\ldots$$

where $0 < \theta_r < \pi/2$ and $\theta_r \to 0$ as $r \to \infty$.

The r-th negative eigenvalue is

$$\gamma_r^- = -(r-1)\frac{\pi}{L} - \frac{\theta_r}{L} = -\gamma_r^+ \quad , \quad r = 1,2,\ldots$$

Because of the evenness of the solution (6.4.7) and because it is the square of γ that appears in the equation (6.4.4) we shall consider only the positive eigenvalues. Denote the r-th eigenvalue by γ_r. Then

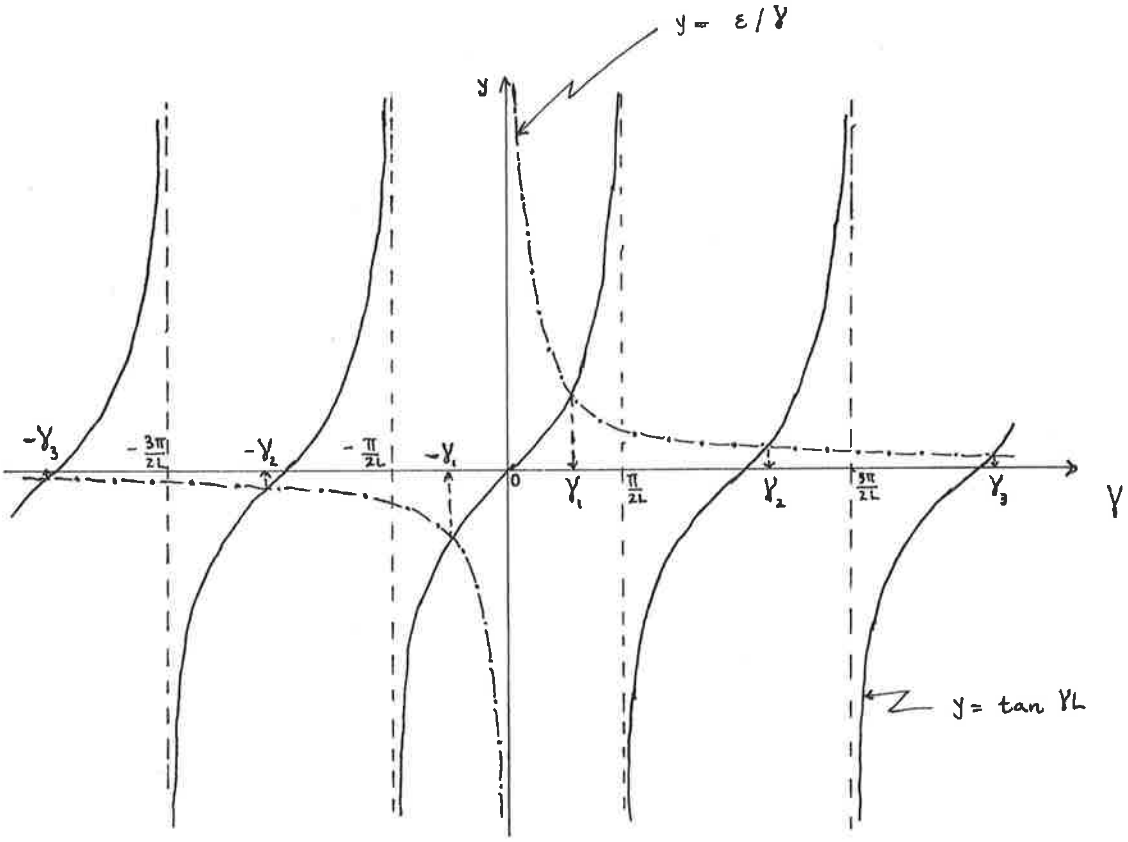


FIGURE 6.1: The locations of the real roots ..., $-\gamma_2$, $-\gamma_1$, γ_1, γ_2, γ_3, ... of the equation $\tan \gamma L = \varepsilon/\gamma$.

the general solution to (6.4.2) is of the form

$$w(x,t) = \sum_{r=1}^{\infty} T_r(t) \cos \gamma_r x \qquad (6.4.9)$$

where $T_r(t)$ is the solution to (6.4.4) corresponding to the eigenvalue γ_r.

6.4.2 Laplace Transform Technique

Let us rewrite equation (6.4.4) as

$$T'(t) + b_1 T(t) + b_2 \int_0^t T(\tau)d\tau - b_3 T(t-a) = 0 \qquad (6.4.10)$$

where $b_1 = \mu + \frac{1}{2}\sigma^2\gamma^2$, $b_2 = \frac{1}{2}\kappa\alpha^2\sigma^2\gamma^2$ and $b_3 = p\lambda$. Note that $b_i > 0$, $i = 1,2,3$.

According to Bellman and Cooke (1963), the Laplace transform of a delay equation such as (6.4.10) can be useful in discussing the asymptotic behaviour of the solution as $t \to \infty$. However for our grain-weevil system we cannot wait that long - all the wheat grains will have been destroyed. The solution for the first few days, weeks or months is more important than the long-run solution. For this reason we shall use the Laplace transform to determine the solution to (6.4.4) (or (6.4.10)) as an explicit function of time t. Then we can easily deduce the solutions over several of the developmental periods, $na \leqslant t < (n+1)a$, $n = 0,1,2,\ldots$, in the earlier part of the storage of the wheat.

Denote the Laplace transform of $T(t)$ by

$$\hat{T}(z) = \mathcal{L}(T(t)) \triangleq \int_0^\infty e^{-zt}T(t)\,dt$$

where the integral is assumed convergent for $\mathrm{Re}Z >$ some $R > -\infty$. Now taking the Laplace transform of (6.4.10) we get

$$(z + b_1 + \frac{b_2}{z} - b_3e^{-az})\hat{T}(z) = T(0^+) .$$

So

$$\hat{T}(z) = \frac{T(0^+)z}{z^2+b_1z+b_2-b_3ze^{-az}}$$

$$= \frac{T(0^+)z}{Q(z)(1-b_3ze^{-az}/Q(z))} \qquad (6.4.11)$$

where

$$Q(z) = z^2+b_1z+b_2 = (z-q_1)(z-q_2), \quad \text{say.}$$

Expanding the RHS of (6.4.11) in powers of $b_3ze^{-az}/Q(z)$, we obtain

$$\hat{T}(z) = T(0^+) \sum_{k=0}^{\infty} b_3{}^k e^{-kaz}[z/Q(z)]^{k+1} . \qquad (6.4.12)$$

Let

$$\hat{\psi}_k(z) = \frac{z^{k+1}}{Q^{k+1}(z)} = \frac{z^{k+1}}{(z-q_1)^{k+1}(z-q_2)^{k+1}} .$$

Now let us note that

$$\mathcal{L}(H(t-b)f(t-b)) = e^{-bz}\hat{F}(z)$$

where $H(t)$ is the Heaviside unit function, that is

$$H(t) = \begin{cases} 0 & \text{for} \quad t < 0 \\ 1 & \text{for} \quad t \geqslant 0 \, , \end{cases}$$

$f(t)$ is an arbitrary function and $\hat{F}(z)$ is the Laplace transform, $\mathcal{L}(f(t))$, of $f(t)$. So the *inverse* Laplace transform of (6.4.12) is

$$T(t) = T(0^+) \sum_{k=0}^{\infty} b_3{}^k H(t-ka)\psi_k(t-ka) \, . \tag{6.4.13}$$

Thus we need to determine $\psi_k(t)$ which is the inverse Laplace transform of $\hat{\psi}_k(z)$.

Note that $\hat{\psi}_k(z)$ is a quotient of two polynomials. The numerator is of degree $(k+1)$ and the denominator is of degree $2(k+1)$ with each of the factors $(z-q_1)$, $(z-q_2)$ repeated $k+1$ times. Therefore we can write $\hat{\psi}_k(z)$ in the partial fractions form:

$$\hat{\psi}_k(z) = \sum_{i=0}^{k} \frac{A_i}{(z-q_1)^{i+1}} + \sum_{i=0}^{k} \frac{B_i}{(z-q_2)^{i+1}} \tag{6.4.14}$$

where the coefficients A_i, B_i, $i = 0,1,\ldots,k$ are obtained from

$$z^{k+1} \equiv (z-q_2)^{k+1} \sum_{i=0}^{k} A_i (z-q_1)^{k-i}$$

$$+ (z-q_1)^{k+1} \sum_{i=0}^{k} B_i (z-q_2)^{k-i} \tag{6.4.15}$$

by, for example, comparing coefficients of the polynomials of the LHS and RHS of (6.4.15). Then the inverse Laplace transform of (6.4.14) gives

$$\psi_k(t) = \sum_{i=0}^{k} A_i \frac{t^i e^{q_1 t}}{i!} + \sum_{i=0}^{k} B_i \frac{t^i e^{q_2 t}}{i!} .$$

Hence from (6.4.13) we have

$$T(t) = T(0^+) \sum_{k=0}^{\infty} b_3{}^k H(t-ka) \sum_{i=0}^{k} \frac{(t-ka)^i}{i!} [A_i e^{q_1(t-ka)} + B_i e^{q_2(t-ka)}] \tag{6.4.16}$$

Solution for $na \leqslant t < (n+1)a$, where integer $n \geqslant 0$.

For $na \leqslant t < (n+1)a$ and $k > n$, we have $t-ka < 0$ and therefore $H(t-ka) \equiv 0$. Then from (6.4.16) we have

$$T(t) = T^{(n)}(t) \triangleq T(0^+) \sum_{k=0}^{n} b_3{}^k \sum_{i=0}^{k} \frac{(t-ka)^i}{i!} \times [A_i^{(n)} e^{q_1(t-ka)} + B_i^{(n)} e^{q_2(t-ka)}] \tag{6.4.17}$$

for $na \leqslant t < (n+1)a$. The constants $A_i^{(n)}$, $B_i^{(n)}$ are the values of A_i, B_i, respectively, when $na \leqslant t < (n+1)a$.

Thus, for example, for $0 \leqslant t < a$, we have $n=0$ and therefore

$$T(t) = T(0^+)(A_o^{(o)} e^{q_1 t} + B_o^{(o)} e^{q_2 t}) . \tag{6.4.18}$$

Now using (6.4.16), and since according to (6.4.17) $k = 0$, we have

$$z = (z-q_2) A_o^{(o)} + (z-q_1) B_o^{(o)}$$

which gives

$$\left.\begin{aligned} A_o^{(o)} &= \frac{q_1}{q_1-q_2}\ , \\ B_o^{(o)} &= \frac{q_2}{q_2-q_1}\ . \end{aligned}\right\} \qquad (6.4.19)$$

On the roots q_1,q_2.

Since we do not expect any periodic or oscillatory behaviour for our system we would require q_1,q_2 to be real. Let us recall that q_1,q_2 are the roots of the equation

$$Q(z) \triangleq z^2 + b_1z + b_2 = 0$$

where $b_1,b_2 > 0$. So q_1,q_2 are real if $b_1^2 - 4b_2 \geqslant 0$, that is, if

$$(\mu+\tfrac{1}{2}\sigma^2\gamma^2)^2 - 2\kappa\alpha^2\sigma^2\gamma^2 \geqslant 0.$$

For positive values of σ,κ and γ this condition reduces to

$$\mu + \tfrac{1}{2}\sigma^2\gamma^2 - \alpha\sigma\gamma\sqrt{2\kappa} \geqslant 0\ . \qquad (6.4.20)$$

Since the LHS of (6.4.20) is quadratic in γ with a minimum value, (6.4.20) is satisfied for all eigenvalues γ_r, $r=1,2,\ldots$ if the values of σ and κ are suitably chosen. Then, because $b_1,b_2 > 0$, we have both $q_1,q_2 < 0$.

So far $T(0^+)$ has remained unspecified. In order to determine $T(0^+)$ we shall use the initial condition (6.3.8). But before we do so let us introduce some notation. Denote the solution to (6.4.4) corresponding to the eigenvalue γ_r of (6.4.3), for $na \leqslant t < (n+1)a$, by $T_r^{(n)}(t)$ and let q_{r1}, q_{r2} be the corresponding zeros of $Q(z)$. That is, from (6.4.17),

$$T_r^{(n)}(t) = T_r(0^+) \sum_{k=0}^{n} b_3{}^k \sum_{i=0}^{k} \frac{(t-ka)^i}{i!} [A_{ri}^{(n)} e^{q_{r1}(t-ka)} + B_{ri}^{(n)} e^{q_{r2}(t-ka)}] \qquad (6.4.21)$$

where $A_{ri}^{(n)}$, $B_{ri}^{(n)}$ are the coefficients corresponding to the eigenvalue γ_r for $na \leqslant t < (n+1)a$.

Thus for $na \leqslant t < (n+1)a$ equation (6.4.9) becomes

$$w(x,t) = \sum_{r=1}^{\infty} T_r^{(n)}(t) \cos \gamma_r x$$

and the number of intact grains per unit volume remaining at time t in section x of the container is given by

$$s(x,t) = \frac{S_0}{L} - \int_0^t \alpha w(x,\tau) d\tau$$

$$= s(x,na) - \sum_{r=1}^{\infty} \int_{na}^{t} \alpha (T_r^{(n)}(\tau) d\tau) \cos \gamma_r x.$$

So

$$w(x,0) = \sum_{r=1}^{\infty} T_r^{(o)}(0) \cos \gamma_r x \quad .$$

Now substituting for $T_r^{(o)}(0)$ from (6.4.18) we have

$$w(x,0) = \sum_{r=0}^{\infty} T_r(0^+)(A_{r0}^{(o)}+B_{r0}^{(o)}) \cos \gamma_r x \, .$$

But according to (6.4.19)

$$A_{r0}^{(o)} + B_{r0}^{(o)} = 1 \, .$$

Hence, using the initial condition (6.3.8), we have

$$\frac{N_0}{L} \phi(x) = \sum_{r=0}^{\infty} T_r(0^+) \cos \gamma_r x \, . \qquad (6.4.22)$$

It can be verified that the eigenfunctions $\cos \gamma_r x$ are orthogonal on the interval $[0,L]$. So multiplying (6.4.22) by $\cos \gamma_r x$ and integrating with respect to x we get

$$\frac{N_0}{L} \int_0^L \phi(x) \cos \gamma_r x \, dx = T_r(0^+) \int_0^L \cos^2 \gamma_r x \, dx$$

Now using equation (6.4.9), that is

$$\tan \gamma_r L = \varepsilon/\gamma_r \, ,$$

we can show that

$$\int_0^L \cos^2 \gamma_r x \, dx = \frac{1}{2} L + \frac{1}{2} \varepsilon/(\gamma_r^2+\varepsilon^2) \, .$$

Hence for the given function $\phi(x)$, $T_r(0^+)$ is given by

$$T_r(0^+) = \frac{2N_0(\gamma_r^2+\varepsilon^2)}{L[\varepsilon+L(\gamma_r^2+\varepsilon^2)]} \int_0^L \phi(x) \cos \gamma_r x \, dx \qquad (6.4.23)$$

Example 6.1

If the weevils are released at the top surface $\phi(x) = \delta(x-L)$.

Then, according to (6.4.23),

$$T_r(0^+) = \frac{2N_0(\gamma_r^2+\varepsilon^2)\cos\gamma_r L}{L[\varepsilon+L(\gamma_r^2+\varepsilon^2)]} \quad . \qquad (6.4.24)$$

Example 6.2

Suppose the weevils cannot emigrate. Then it can be shown that the results for the non-emigration system can be obtained from those for the emigration system by setting the emigration rate ε to zero. Then the eigenvalues γ_r are given by

$$\gamma_r = (r-1)\frac{\pi}{L} \quad , \quad r=1,2,\ldots$$

If in addition the weevils are initially at the bottom of the container, that is $\phi(x) = \delta(x)$, then from (6.4.23) we have

$$T_r(0^+) = \frac{2N_0}{L^2} \quad . \qquad (6.4.25)$$

Then from (6.4.18) and (6.4.19) we can deduce that $T_r(t) > 0$ for $0 \leqslant t < a$. Now, since

$$w(x,t) = \sum_{r=1}^{\infty} T_r(t) \cos\gamma_r x \ ,$$

the positiveness of $T_r(t)$ implies that a maximum density of weevils per unit volume occurs at the bottom of the container at least in the first developmental period $[0,a)$.

6.4.3 The Method of Steps

It is worth noting that the rather natural "method of steps" [El'sgol'ts and Norkin (1973), Driver (1977)] could be used to solve the delay integrodifferential equation (6.4.4). In order to use the method we set $T(t) = 0$ (or a constant) for $-a \leqslant t < a$. Then we solve the equation for $0 \leqslant t < a$ in which case $T(t-a)$ is a known function. Using the solution for $0 \leqslant t < a$ we solve the equation for $a \leqslant t < 2a$. This procedure can be continued to $2a \leqslant t < 3a$ and the following intervals as demonstrated below.

Differentiating (6.4.4) or (6.4.10) we have

$$\frac{d^2T(t)}{dt^2} + b_1 \frac{dT(t)}{dt} + b_2 T(t) - p\lambda \frac{dT(t-a)}{dt} = 0 \ . \qquad (6.4.26)$$

Solution for $0 \leqslant t < a$

With $T(t) = 0$ (or a constant) for $t < 0$ equation (6.4.26) reduces to

$$\frac{d^2T}{dt^2} + b_1 \frac{dT}{dt} + b_1 T = 0 \quad . \qquad (6.4.27)$$

Now if we look for a solution of the form $T(t) = e^{qt}$, the characteristic equation for (6.4.27) is

$$q^2 + b_1 q + b_2 = 0 \ . \qquad (6.4.28)$$

Note that (6.4.28) is the same as the equation

$$Q(z) = z^2 + b_1 z + b_2 = 0$$

in Section 6.4.2. Hence the roots of (6.4.28) are q_1, q_2 as in Section 6.4.2.

As before let q_{r1}, q_{r2} be the characteristic roots corresponding to the eigenvalue γ_r of (6.4.3). Then the solution to (6.4.27) corresponding to γ_r is

$$T_r(t) = C_r\, e^{q_{r1} t} + D_r\, e^{q_{r2} t} \tag{6.4.29}$$

where C_r, D_r are the constants of integration.

At this point let us recall that we obtained (6.4.27) by differentiating (6.4.4). Therefore we must ensure that the solution (6.4.29) satisfies (6.4.4). Substituting $T_r(t)$ in (6.4.4) or (6.4.10) we obtain

$$C_r/q_{r1} + D_r/q_{r2} = 0 \; . \tag{6.4.30}$$

Now the solution to (6.4.2) as given by (6.4.9) is

$$w(x,t) = \sum_{r=1}^{\infty} (C_r e^{q_{r1} t} + D_r e^{q_{r2} t}) \cos \gamma_r x \; . \tag{6.4.31}$$

Then from (6.4.1) and using (6.4.30) we have

$$s(x,t) = \frac{S_0}{L} - \alpha \sum_{r=1}^{\infty} \left(\frac{C_r e^{q_{r1} t}}{q_{r1}} + \frac{D_r e^{q_{r2} t}}{q_{r2}}\right) \cos \gamma_r x \tag{6.4.32}$$

Another equation for C_r and D_r is obtained by applying the initial condition (6.3.8)

$$w(x,0) = \frac{N_0}{L}\,\phi(x)$$

in the same way as in section 6.4.2. Then we obtain

$$C_r+D_r = \frac{2N_0(\gamma_r^2+\varepsilon^2)}{L[\varepsilon+L(\gamma_r^2+\varepsilon^2)]}\int_0^L \phi(x)\,\cos\gamma_r x\,dx\,. \qquad (6.4.33)$$

So C_r and D_r can be determined from (6.4.30) and (6.4.33).

Let us note the relationships between C_r, D_r and $A_r^{(o)}, B_r^{(o)}$ and $T_r(0^+)$. Comparing (6.4.23) and (6.4.33) we notice that

$$C_r + D_r = T_r(0^+) \qquad (6.4.34)$$

Setting $n=0$ in (6.4.21) and comparing the result with (6.4.29) we have

$$\left.\begin{aligned} C_r &= A_{r0}^{(o)}T_r(0^+) \\ D_r &= B_{r0}^{(o)}T_r(0^+) \end{aligned}\right\} \qquad (6.4.35)$$

Note that (6.4.35) satisfies (6.4.34) since according to (6.4.19) $A_{r0}^{(o)} + B_{r0}^{(o)} = 1$.

Solution for $a \leqslant t < 2a$

Let us denote the solution to (6.4.27) corresponding to the eigenvalue γ_r by

$$T_r^{(1)}(t) = C_r^{(1)}e^{q_1 t} + D_r^{(1)}e^{q_2 t}\ ;$$

or if we supress the subscript r we have the solution to

(6.4.26) as

$$T(t) = T^{(1)}(t) = C^{(1)}e^{q_1 t} + D^{(1)}e^{q_2 t} \qquad (6.4.36)$$

for $0 \leqslant t < a$.

Then for $a < t < 2a$ (6.4.26) becomes

$$\frac{d^2T}{dt^2} + b_1\frac{dT}{dt} + b_2T = p\lambda[C^{(1)}q_1e^{q_1(t-a)}+D^{(1)}q_2e^{q_2(t-a)}]. \quad (6.4.37)$$

The general solution to (6.4.37) is

$$T^{(2)}(t) = C^{(2)}e^{q_1(t-a)}+D^{(2)}e^{q_2(t-a)}+k_1(t-a)e^{q_1(t-a)}$$
$$+k_2(t-a)e^{q_2(t-a)} \qquad (6.4.38)$$

where

$$\left.\begin{aligned} k_1 &= -p\lambda C^{(1)}q_1/(q_2-q_1) \\ \text{and} \quad k_2 &= p\lambda D^{(1)}q_2/(q_2-q_1) \end{aligned}\right\} \qquad (6.4.39)$$

Now applying continuity of $T(t)$ at $t=a$, that is $T(a^-) = T(a^+) = T(a)$, (6.4.29) and (6.4.38) give

$$C^{(2)} + D^{(2)} = C^{(1)}\, e^{q_1 a} + D^{(1)}\, e^{q_2 a} . \qquad (6.4.40)$$

Equation (6.4.4), that is

$$\frac{dT}{dt} + b_1T + b_2\int_0^t T(\tau)d\tau = p\lambda T(t-a) ,$$

should still be satisfied for $a \leqslant t < 2a$.

Note that for $a < t < 2a$

$$\int_0^t T(\tau)d\tau = \int_0^a T^{(1)}(\tau)d\tau + \int_a^t T^{(2)}(\tau)d\tau$$

So using the solutions (6.4.36) and (6.4.38) in (6.4.4) we can show that

$$q_2C^{(2)} + q_1D^{(2)} = q_2C^{(1)}e^{q_1a} + q_1D^{(1)}e^{q_2a}$$
$$- p\lambda(q_2C^{(1)}-q_1D^{(1)})/(q_2-q_1) \qquad (6.4.41)$$

Solving for $C^{(2)}$ and $D^{(2)}$ from (6.4.40) and (6.4.41) we get

$$\left.\begin{aligned} & C^{(2)} = C^{(1)}e^{q_1a} - 2p\lambda q_2C^{(1)}/(q_2-q_1)^2 \\ \text{and} \qquad & D^{(2)} = D^{(1)}e^{q_2a} - 2p\lambda q_1D^{(1)}/(q_2-q_1)^2 \end{aligned}\right\} \quad (6.4.42)$$

where we have used

$$q_1D^{(1)} + q_2C^{(1)} = 0 \quad \text{(from (6.4.30))} .$$

Let $T_r^{(2)}(t)$ be the solution to (6.4.37) corresponding to the eigenvalue γ_r. Then substituting for $C^{(2)}, D^{(2)}$, k_1 and k_2 in (6.4.38) we obtain

$$T_r^{(2)}(t) = C_r^{(1)}\left[e^{q_{r1}t} - \frac{2p\lambda q_{r2}e^{q_{r1}(t-a)}}{(q_{r2}-q_{r1})^2} - \frac{p\lambda q_{r1}(t-a)e^{q_{r2}(t-a)}}{q_{r2}-q_{r1}}\right]$$
$$+ D_r^{(1)}\left[e^{q_{r2}t} - \frac{2p\lambda q_{r1}e^{q_{r2}(t-a)}}{(q_{r2}-q_{r1})^2} + \frac{p\lambda q_{r2}(t-a)e^{q_{r2}(t-a)}}{q_{r2}-q_{r1}}\right]$$
$$(6.4.43)$$

where q_{ri} $(i=1,2)$ are the characteristic roots for (6.4.27) corresponding to the eigenvalue γ_r and $C_r^{(1)}$

and $D_r^{(1)}$ are determined from (6.4.30) and (6.4.33).

So the general solution for our system, for $a \leqslant t \leqslant 2a$ is

$$w(x,t) = \sum_{r=1}^{\infty} T_r^{(2)}(t) \cos \gamma_r x$$

and

$$s(x,t) = s(x,a) - \sum_{r=1}^{\infty} \alpha\left(\int_a^t T_r^{(2)}(\tau)d\tau\right) \cos \gamma_r x \, .$$

Solution for $na \leqslant t < (n+1)a$

The procedure used for $0 \leqslant t < a$ and $a \leqslant t < 2a$ can be extended to $2a \leqslant t < 3a$ and the following intervals. Then, recursively, the solution to (6.4.26) for $na \leqslant t < (n+1)a$, $n=0,1,2,\ldots,$ is deduced to be of the form

$$T^{(n)}(t) = \sum_{i=0}^{n} C_i^{(n)}(t-na)^i e^{q_1(t-na)} + \sum_{i=0}^{n} D_i^{(n)}(t-na)^i e^{q_2(t-na)} \tag{6.4.44}$$

where the constants $C_i^{(n)}, D_i^{(n)}$, $i=1,2,\ldots,n$ are related by the difference equations

$$(q_1-q_2)(i+1)C_{i+1}^{(n)} + (i+2)(i+1)C_{i+2}^{(n)} = p\lambda[q_1 C_i^{(n-1)} + (i+1)C_{i+1}^{(n-1)}] \tag{6.4.45}$$

$$(q_2-q_1)(i+1)D_{i+1}^{(n)} + (i+2)(i+1)D_{i+2}^{(n)} = p\lambda[q_2 D_i^{(n-1)} + (i+1)D_{i+1}^{(n-1)}] \tag{6.4.46}$$

$$C_{n+j}^{(n)} \equiv 0 \equiv D_{n+j}^{(n)} \quad \text{for} \quad j \geqslant 1 \, . \tag{6.4.47}$$

So having determined $C_i^{(n-1)}, B_i^{(n-1)}$, $i=0,1,2,\ldots,n-1$, the coefficients $C_i^{(n)}, D_i^{(n)}$, $i=1,2,\ldots,n$ can be obtained recursively from (6.4.45) and (6.4.46).

The constants $C_0^{(n)}$ and $D_0^{(n)}$ cannot be obtained from (6.4.45) and (6.4.46). In order to determine the values for these constants we use

(i) $T^{(n-1)}(na) = T^{(n)}(na)$,

that is $T(t)$ is continuous at $t = na$;

(ii) $T^{(n)}(t)$ must satisfy (6.4.4). That is we have to ensure that the equation

$$\frac{dT}{dt} + b_1 T + b_2 \int_0^t T(\tau)\,d\tau - p\lambda T(t-a) = 0$$

is satisfied by $T^{(n)}(t)$.

Though the solution (6.4.44), by the method of steps, and the solution (6.4.17) may look different it can be shown recursively, with respect to n, that (6.4.44) in conjunction with (6.4.45) and (6.4.46) is the same as (6.4.17).

6.4.4 Remarks on the Two Methods

According to the method of steps the solution for $na \leqslant t < (n+1)a$ depends on the solution for $(n-1)a \leqslant t < na$. For this reason it becomes cumbersome to use for large values of n. However for the first few (two or three) of the developmental periods $[na,(n+1)a)$, $n=0,1,2,\ldots$, the method may be more straight forward than the Laplace transform method in that not much computation is involved; the expressions involved are still simple to handle. The advantage of the Laplace transform method is that the solution for $na \leqslant t < (n+1)a$ can be obtained independently of the solution over the previous intervals except that we use the initial interval $0 \leqslant t < a$ to determine $T_r(0^+)$, $r=1,2,\ldots$.

How far, as regards the intervals $[na,(n+1)a)$, we would try to determine the solution to (6.4.4) would depend on the situation we are considering. For example in laboratory experiments the quantities of wheat used are usually small. In such a situation the dispersal of the weevils within the wheat and the destruction of the wheat might be rapid. Solutions over the first two or three developmental periods would be sufficient to give us a picture of what has gone on in each section of the wheat grain. So in this case the method of steps would be appropriate. For large quantities of wheat stored in big containers such as silos, the initial numbers of weevils are, in most cases, relatively small. Hence the dispersal of the weevils within the grain would be slow. So we would need to determine the solution over relatively many developmental periods before we can establish how far the population of the weevils has spread. However, even with the Laplace transform method, the expressions for the solution to the model become more and more difficult to handle as we move to higher developmental periods.

6.5 DISCUSSION

In formulating the model we assumed that it is only the food ratio that prompts a weevil to move away or to continue staying in a section of the wheat for a while. Other conditions such as temperature and moisture content of the grain are optimal. When a weevil decides to leave a section, its immediate motion is random. Surties' (1963) observations support the random movements at the optimal temperature of 25°C and moisture content of 14% for *Sitophilus granarius*.

Howe (1951) observed that there was a tendancy of the weevils to move down in towers filled with wheat. This would imply that if the weevils are initially released at or near the bottom of the container then the density of weevils per unit volume would continue to be higher in the neighbourhood of the bottom surface. This supports the solution for Example 6.2 in which $w(x,t)$ is maximum at $x=0$ for $0 \leqslant t < a$. Howe's observations were made over short periods (the longest being of 28 days). For *Sitophilus granarius* it takes at least 36 days for an adult to emerge from an egg (see row 1 of Table A.1). Therefore in his experiments no observations were made on the effect of the emergence of young ones on the distribution of the weevils within the wheat. The solution to the model in this chapter enables us to determine the distribution (or at least an approximation to the distribution) at any time t.

Though we have confined our discussion to the wheat-weevil system the model can be applied to similar grain-insect systems. The equations can be modified to include renewability of the food supply, for example by modifying equation (6.3.7). Also the formulation could be extended to non-granular systems. For example we could apply it to a system of insects laying eggs and feeding on the leaves of a tree. In this case, unlike in the grain-weevil system, new leaves come up. So the food resource for the insects is renewable.

I should point out that the model discussed in this chapter is for the purpose of predicting what might happen to a quantity of cereal if it were stored for some length of time and it happened that pests such as insects were initially present. The solution to the model would help in devising control measures and/or formulating control models.

CHAPTER 7

DISCUSSION

7.1 SCOPE AND RESULTS OF THE MODELS

As mentioned in Chapter 1 the models were intended for the study of infestation of stored cereal products by pests such as the grain weevil, *Sitophilus granarius* and the rice weevil, *Sitophilus oryzae*. From the cited literature and the data used in this thesis I would say that the models are more relevant to small quantities of grain, such as those used in laboratory experiments, than to large quantities of grain. However the models have led us to suggest possible ways of tackling situations with large amounts of grain (for example, see end of Chapter 3).

The basic assumption of the models is that the activities of the adult weevils, such as the oviposition of eggs and emigration, are functions of the food ratio (that is the number of intact grains per adult weevil). There is a critical food ratio C above which the available number of intact grains does not influence the activities. Below C the activities become influenced by the availability of the intact grains per weevil. This led to the consideration of a two-phase grain-weevil system; during phase I the food ratio $> C$ and the parameters for the system are constant and during phase II the food ratio $\leqslant C$ and the parameters are functions of the food ratio.

The weevil, *Sitophilus*, used in this study has the special characteristic that all the immature stages of development take place within a grain in which the egg is laid. So it is not essential to consider the stages of the larva, pupa and the pre-emergence adult separately. For this reason the weevil was modelled to go through two stages of development: (i) the immature stage constituted by the egg, larval, pupal and pre-emergence stages and (ii) the mature stage at which the weevil is sexually mature and can emigrate. In short our grain-weevil system is a *two-stage* system going through *two phases*.

In the analytic solutions of the models other environmental conditions such as temperature, relative humidity or moisture content of the grain (other than the food ratio) were taken to be optimal. Some of the expressions for the solutions were not simple enough to indicate the general properties of the solutions. This prompted me to use the computer to obtain graphical form of the solutions for the deterministic models (see Chapter 3). Also with the use of the computer it was possible to incorporate temperature into the equations. We should note that under optimal (or constant) temperature conditions the length of the developmental period (egg to newly emerged adult) was taken to be constant. This is because all the immature stages of development take place within a grain and as a result the density of adult weevils per intact grain does not affect the rate of development of the egg. But when temperature was incorporated the computer output showed that the developmental period could be as long as 220 days for the eggs which develop through the months of Autumn, Winter and Spring and as short as 31 days for the eggs that develop through Summer. These computed lengths of the developmental period were in good agreement with those which have been observed in laboratory experiments (see Section 3.2.8).

According to the solutions to the deterministic models the size of the population of the adult weevils decreases over the first developmental period (since there are no new young ones coming up in this period). As the young ones emerge, in the second developmental period, the population size increase rapidly well beyond the end of phase I. According to the computer output the population size increases for over another developmental period (about 60 days when the developmental period was taken as 50 days) from the time the critical food ratio is reached. Then it decreases monotomically. The number of intact grains are finished long before the weevil population becomes extinct. The incorporation of temperature has the significant effect of slow growth of the weevil population (and therefore a slower rate of depletion of the intact grains; see Tables 3.1 and 3.2).

The food ratio increases over the first developmental period. As the young ones start emerging the ratio decreases and continues to do so until it is zero (that is when intact grains get finished).

In Section 2.1.3 the relations that the initial food ratio has to satisfy so as the critical food ratio is reached in the first developmental period, in or after the second developmental period were derived. According to these relations it can be deduced that, for such initial food ratios as those used in laboratory experiments, it is likely that the critical food ratio is reached in the second developmental period. The computer output for the initial numbers of 240, 120, 60 and 30 weevils to 20,000 wheat grains confirmed this (see Table 3.1). For this reason, in the phase I models, I concentrated on determining solutions for the first two developmental periods. However where possible, I have indicated how we can obtain the solutions for the third and higher developmental periods if required.

The stochastic models in Chapter 4 and Section 5.1 were intended for checking the deterministic solutions of the models in Chapter 2 and for the derivation of expressions for the variances of the variables involved. For phase I it worked out that the stochastic mean and the deterministic value of the number of adult weevils are the same but the deterministic value for the number of intact grains is a lower bound for the stochastic mean. For phase II the reverse happens: the stochastic mean and the deterministic value of the number of intact grains are the same, but, under certain assumptions (see Section 5.1.5), the deterministic value of the number of weevils is a lower bound for the stochastic mean.

The stochastic Model B for phase II incorporates explicitly the possibility that more than one egg may be oviposited in a grain. This was achieved by dividing time into developmental periods. During a developmental period a grain (whether already containing eggs or not) is continuously susceptible to attacks by the weevils. Those grains that are attacked are regarded useless at the end of the period. The distribution of the number of eggs oviposited in a single grain was derived. The eggs that are laid into grains already containing eggs were regarded lost since a maximum of one adult may emerge from a grain. Thus, according to Model B, the fraction of the number of eggs that are expected to develop into mature adults is less than that according to Model A.

Also by defining the emigration rate as a step function with respect to the developmental periods the total number of emigrants per unit time would be higher at the beginning of a developmental period than at any later instant of the period. Since according to Model B the young weevils emerge at the beginning of the period and since age was considered not important,this tends to incorporate the ecological hypothesis that young weevils are more dispersive than the old ones.

The number of grains that escape the attacks by the weevils during a developmental period (or any interval of time within the period) in Model B could be as high as 11 times the number in Model A.

Also according to Model B it was shown that the extinction of the weevil population is not possible until the intact grains are finished. Then the population becomes a death-emigration process.

7.2 MATHEMATICAL METHODS USED

Due to the delay of emergence of adults from the eggs, some of the equations for our grain-weevil system are delay differential equations (Chapter 2) or delay integro-differential equations (Chapter 6). Since we are concerned with the damage done to the wheat by the weevils, long run (or asymptotic) solutions are not of interest to us. It is more important predicting the destruction that is likely to occur in the early stages of storage than, for example, knowing what happens when the grains are finished. For this reason the *method of steps* (see Sections 2.1.2 and 6.4.3) was appropriate to use in solving the equations. However if the method is to be used for several developmental periods the computations may become cumbersome to handle. In such a case solving the equations by the use of Laplace transforms (see Sections 2.1.2 and 6.4.2) may prove to be less involving.

In the stochastic model for phase I an artificial variable was introduced to represent the number of intact grains. This was done for the purpose of simplifying the computation. It was, however, a rewarding exercise in that we could prove that the expectation of this artificial random variable was the same as the value of the number of intact grains obtained by the deterministic model. Also the expectation was used to show, as already mentioned, that the deterministic value of the number of intact grains is a lower bound for (that is it underestimates) the expected number of intact grains in the system.

By treating the emergence process of the young weevils from the eggs as an immigration process into, but independent of, the adult weevil population two methods were used to derive an approximate expression for the joint p.g.f. of the artificial variable and the number of weevils. The first method gives insights into the techniques that are used to derive the Puri's (1975, Eqn. 14) result. The second method (that is the method of "marks and catastrophe", Section 4.6.2) has notable techniques that can be applied to a wide range of problems.

In the stochastic version of the phase II determinsitic model an artificial random variable was introduced to represent the number of weevils. Again, in this case, the expectation of this artificial r.v. worked out to be the same as the deterministic value - implying that the actual stochastic mean of the number of weevils is not the same as the deterministic value.

We should note that the technique used in solving for the p.g.f. $G_n(t,x,y)$ of the number of intact grains and the weevils by writing it in the series form

$$G_n(t,x,y) = \sum_s (x-1)^s f_{ns}(t,y)$$

and then solving for the functions $f_{ns}(t,y)$, could be tried on partial differential equations of the form (5.2.2) not necessarily arising from probabilistic applications. In section 5.2.6 it was shown that for more generalised assumptions than those considered in Model B the functions f_{ns}, too, could be broken down into functions which would prove simpler to derive.

In Chapter 6 the method of separation of variables was used in determining the spatial distribution of the weevils in a container storing wheat. The equation for the time factor obtained after separating the spatial and the time factors was a delay integro-differential equation. A Laplace transform technique was used to solve the equation. Also it was shown that even for this hard delay equation the method of steps could be used to solve it.

7.3 APPLICATION AND FUTURE DEVELOPMENT

With the parameters taking on appropriate values the solutions to the models could be used to predict what would happen when small quantities of stored grain get infested with pests such as the weevils. The solutions may not apply very well to large quantities of grain. As indicated at the end of Chapter 3 it may be necessary to consider the grain-weevil system to go through three phases: one for low density of weevils per intact grain, the optimal density phase which would correspond to the phase I in this thesis and the high density phase (corresponding to our phase II). According to MacLagan (1932) this high density phase could still be divided into two subphases. One of the subphases would correspond to the density of more than 4 females per intact grain at which oviposition stops completely. Thus a consideration of multiphase system (with more than 2 phases) is relevant to our problem.

Also, as pointed out at the end of Chapter 3, at very low density the weevil population may not survive for a long time unless the weevils congregate to create some sort of partnership environment. So in a low density situation the consideration of the patchness of the distribution of the weevils within the system may be relevant.

It was hoped that the age of a weevil did not have much influence on its activities. This was because, for small quantities of grain, by the time age starts having a significant influence on an individual's activities most of the grains would have been destroyed. However for large quantities of grain several generations of the weevil population are possible before a substantial damage is done. In this case it would be essential to consider the influence of age by, for example, making the oviposition and emigration rates functions of the age.

As far as emigration is concerned we did not worry what happens to the emigrants. In the laboratory experiments they die. However if the wheat is stored in several units between which the movement of the weevils is possible then the consideration of where a weevil goes after leaving a unit is essential - for the infestation is likely to spread over all the units. This would give rise to a dispersal problem which is worth studying.

As indicated in Section 5.2.6 it is possible to reformulate the rate of emigration and the rate at which the intact grains are attacked, and still be able to solve the equations involved. However whatever reformulation we may do it should not be abstract; it should relate to the real situation under study.

APPENDICES

APPENDIX 1.1

TABLE A.1: Values of parameters as cited or estimated from existing literature

Key to Table:
R.H. = relative humidity
m.c. = (grain) moisture content
S.O. = *Sitophilus oryzae*
S.G. = *Sitophilus granarius*
/w = per weevil
/d = per day

Note: 1. The oviposition rates given in the Table are for female weevil. If we assume that the sex ratio is 1:1 then the oviposition rates for an individual weevil (female or male) is taken to be a half those given in the Table.

2. In the calculation of the emigration rate (see row 9 of the Table) the second and third fortnights were used because it was hoped that by then the weevils would have settled down in their new habitat and no young adults would have emerged to increase interaction between the weevils.

Parameter	Species	Researcher or Reference	Determined or Estimated Value(s)	Environmental Conditions	Comment
1. Length of the developmental period, a (days)	S.O.	Birch (1953)	4.0 weeks = 28 days	29.1°C, 14% m.c.	
		"	4.9 weeks = 34.3 days	25.5°C, 14% m.c.	
		"	32.9 weeks = 230.3 days	15.2°C, 14% m.c.	
		Golebiowska (1969)	30-46 days (mean = 31.4 days)	28°C, 70% R.H.	
		Hardman (1977)	436 day-degrees (D$^{\circ}$) (≡ 49 days, 53 days)	(at mean temperatures 22.7°C, 23.18°C)	Note that Hardman (1978) estimated it to be 422.7D$^{\circ}$.
		MacLagan & Dunn (1935)	24-28 days	25°C, 90% R.H.	Rather short compared with other estimates.
	S.G.	Coombs & Woodroffe (1973)	60 days	20°C, 60% R.H.	
		"	160 days	15°C, 60% R.H.	
		Golebiowska (1969)	58-64 days	28°C, 70% R.H.	
		"	(40 + 8) days	24°C, ?	40 days to develop into adult, 8 days for adult to mature.
		Howe (1966) Howe & Hole (1967)	36-64 days	25°C, 70% R.H.	Howe (1966) noted that < 1% of developmental periods exceeded 48 days.
2. Proportion of Survival of immature stages, p	S.O.	Birch (1953)	0.0	13.0°C, 14% m.c.	He has more values of p at several other temperatures.
		"	0.25	15.2°C, "	
		"	0.93	25.5°C, "	
		"	0.25	33.5°C, "	
	S.G.	Coombs & Woodroffe (1973)	0.75	?	
		Richards (1947)	(0.75 - 8.0)*	25°C, 70% R.H.	* is the proportion of eggs which hatch. So proportion of eggs that fully develop into adults is less than .75, especially at low temperatures.

TABLE A.1 (Continued)

Parameter	Species	Researcher or Reference	Determined or Estimated Value(s)	Environmental Conditions	Comment
3. Longevity (for adult weevil)	S.O.	Birch (1953)	On average 16.58 weeks = 116.06 days	29.1°C, 70% R.H.	For small strain of S.O. infecting wheat.
		"	10.78 weeks = 75.46 days	32.3°C, 70% R.H.	
		MacLagan & Dunn (1935)	About 4 months ≃120 days	25°C, 90% R.H.	
	S.G.	Coombs & Woodroffe (1973)	250 days	20°C, 60% R?H?	
		Golebiowska (1969)	On average 150 days	?	
		Richards (1947)	174.5 days	25°C, 70% R.H.	For an isolated adult female. The longevity is less in mass cultures.
4. Mortality rate μ w/d/w	S.O.	Golebiowska (1969)	$\frac{0.08}{30} = 0.002667$ w/d/w	28°C, 70% R.H.	Deduced from "on average 92% beetles were alive at the end of 30 days".
		If we use "Longevity $= \frac{1}{\mu}$"	$\mu = \frac{1}{\text{Longevity}} \simeq \frac{1}{120}$ $\simeq 0.008333$ w/d/w	$\left\{\begin{array}{l}25^{\circ}\text{C, 90\% R.H.}\\ \text{or } 29.1^{\circ}\text{C, 70\% R.H.}\end{array}\right\}$	Using Longevity of 120 days according tp MacLagan & Dunn and Birch respectively.
	S.G.	If we use Longevity $= \frac{1}{\mu}$	$\frac{1}{250} < \mu < \frac{1}{150}$ w/d/w i.e. $0.00400 < \mu < 0.006667$ w/d/w		Maximum value obtained from Golebiowska's Longevity. Minimum value obtained from Coombs & Woodroffe Longevity.
5. (Rate of) Consumption (ν grains/w/d)	S.O.	Golebiowska (1969) (quoted Hurlock, 1965)	(a) Immature Stages: 30 mg/larva ≅0.8571 of a grain of Olympic wheat	-	1 grain of Olympic wheat weighs 35 mg on average (see Hardman, 1977).
		Golebiowska (1969)	(b) Adults: 0.490 mg/w/d ≅0.0140 grains/w/d	28°C, 75% R.H.	So $0.01400 \leq \nu \leq 0.02857$
		Golebiowska (1969) (quotes Steffan, 1963)	1 mg/w/d ≅0.02857 grains/w/d	28°C, 70% R?H?	

TABLE A.1 (Continued)

Parameter	Species	Researcher or Reference	Determined or Estimated Value(s)	Environmental Conditions	Comment
5. (Continued) (Rate of) Consumption (ν grains/w/d)	S.G.	Coombs & Woodroffe (1964)	(a) Immature Stages: 2/3 of a grain per larva	-	The fraction is > 2/3 if more than one egg is oviposited in the grain.
		Golebiowska (1969) (quotes Hurlock, 1965)	30 mg/larva $\cong$ 0.8571 grains/larva		
		Golebiowska (1969) (He quotes Steffan 1963)	(b) Adults: 0.5188 mg/w/d $\cong$ 0.01482 grains/w/d	24°C	We therefore have $0.01482 \leq \nu \leq 0.02857$
			1 mg/w/d $\cong$ 0.02857 grains/w/d		
6(a). Progeny (Total number of eggs laid by a female)	S.O.	Birch (1953)	0 eggs/female	13°C, 14 m.c.	
		"	266 "	23°C, 14 m.c.	
		"	344 "	25.5°C, 14 m.c.	
		"	384 "	29.1°C, 14 m.c.	
		"	197 "	32.3°C, 14 m.c.	
		"	0 "	35°C, 14 m.c.	
		MacLagan & Dunn (1935)	380 eggs/female	"favourable" environment	
	S.G.	Coombs & Woodroffe (1973)	125 eggs/female in 250 days	20°C, 60% R.H.	This gives oviposition rate λ = 125/250 = 0.5
		Richards (1947)	89-362 eggs/female (191.5 eggs/female on average)		

TABLE A.1 (Continued)

Parameter	Species	Researcher or Reference	Determined or Estimated Value(s)	Environmental Conditions	Comment
6(b) Oviposition rate λ eggs/female/day	*S.O.*	Birch (1953)	$\frac{266}{120} < \lambda < \frac{384}{120}$ i.e. $2.2167 < \lambda < 3.2000$	23.0°C – 29.1°C, 70% R.H.	λ is calculated using his longevity and progeny data at 23°C and 29.1°C.
		Golebiowska (1969)	$2.00 < \lambda < 6.00$	28°C, 70% R.H.	Deduced from "progeny per 100 weevils per day over a period of 30 days.
		Hardman (1977)	$\lambda = \frac{3980}{46 \times 50} = 1.7304$	23°C, 14% m.c.	3980 eggs were laid by 46 females, on average, in 50 days.
	S.G.	Evans (1977)	$0.01429 \leq \lambda \leq 1.6743$ (average value $= 0.8500$)	15°C	Calculated from number of eggs per female per fortnight over a period of 20 weeks.
		Richards (1947)	$1.49 \leq \lambda \leq 3.33$	25°C, 70% R.H.	For weevils ranging from 16 days to 106 days old.
7. Critical food ratio C grains/weevil	*S.O.* and *S.G.*	Coombs & Woodroffe (1973)	10 grains/female	-	
		Hardman (1977) MacLagan & Dunn (1935)	12.5 grains/weevil		
		Richards (1947)	10 grains/female		C could lie in [10, 20].

TABLE A.1 (Continued)

Parameter	Species	Researcher or Reference	Determined or Estimated Value(s)	Environmental Conditions	Comment
8. Temperature thresholds and optimal temperatures	*S.O.*	Hardman (1977) - uses Birch's (1945) data	Lower threshold for development $= 13.7^\circ C$	–	N.B. Lower temperature thresholds for development are not necessarily the same as those for oviposition.
		Howe(1965)	Lower threshold for population increase $= 17^\circ C$. Opt.range: $27-31^\circ C$		
		Richards (1947)	Oviposition ceases at and below $9.5^\circ C$		
	S.G.	Evans (1977)	Lower threshold for development is $15^\circ C$		
		"	Optimal temperature $= 26^\circ C$		
		Howe (1965)	Lower threshold for population increase $= 15^\circ C$		
		"	Optimal range $26-30^\circ C$		
9. Emigration rate. ε, w/d/w	At the Waite Agricultural Research Institute, University of Adelaide, Mr Mlambo conducted experiments to study the emigration process of weevils from wheat stored in containers. From his average numbers of emigrants during the 2nd and 3rd fortnights, from containers initially holding 600 g ($\cong$ 20,000 intact grains) of Olympic wheat (Variety 8156) and 240, 120, 60, 30 weevils, I calculated the mean emigration rates. These worked out to be 0.006436 w/d/w for *S.O.* and 0.0005478 w/d/w for *S.G.*.				

APPENDIX 3.1

COMPUTER PROGRAMME I

This programme is for solving equations (3.1.1) under *optimal* temperature conditions.

```
      PROGRAM OPTCOND(OUTPUT)
      DIMENSION  WO(4)   ,EG(458),U(458),W(458),S(458),FDR(458),R(458),
     +EMGT(458),IDAY(458)  ,DAY(466),Y(1382),ZA(924)
      EQUIVALENCE (S(1),Y(1)),(W(1),Y(459)),(FDR(1),Y(917)          ,ZA(1
     +)),(EMGT(1),ZA(459))
C
C    PARAMETERS $ THEIR VALUES
C      OVIPOSITION RATE  V=1.0 EGGS/DAY/WEEVIL
C      MORTALITY RATE D=0.00833 WEEVILS/DAY/WEEVIL
C      CONSUMPTION RATE C=0.02128 GRAINS/DAY/WEEVIL
C      EMEGRATION TATE E=.006436 WEEVILS/DAY/WEEVIL
C      PROPORTION OF SURVIVORSHIP OF EGGS IS P
C      CRITICAL FOOD RATIO CFDR=10. GRAINS/WEEVIL
C      DEVELOPMENTAL PERIOD A IS 49-53 DAYS FOR S.O., 45-60 DAYS FOR S.G.
C
C    VALUES OF PARAMETERS AT OPTIMAL TEMPARATURE
       C=0.021285
       V=1.0
       E=0.006436
       D=0.008333
       P=.7
       CFDR=10.
       B=0.12
       A=50. $ IA=A
C
C    NAMES USED IN THE PROGRAM
C      EG=NO. OF EGGS LAID THE PREVIOUS DAY
C      U=EGGS+LARVAE+PUPAE+UNEMERGED ADULTS
C      W=NO. OF ADULT WEEVILS
C      S=NO. OF UNUSED GRAINS OF WHEAT
C      FDR=S/W=FOOD RATIO(DENSITY)
C      R=TOTAL NO. OF EMEGRANTS UP TO DATE
C      EMGT=EMEGRANTS DURING THE PREVIOUS DAY
C    INITIAL NO. OF WHEAT GRAINS
         SO=20000.
C    INITIAL NO. OF ADULT WEEVILS
       WO(1)=240. $ WO(2)=120. $ WO(3)= 60. $ WO(4)=30.
C
       DO 1001 M=1,4

       S(1)=SO
       W(1)=WO(M)
       EG(1)=0.
       EMGT(1)=0. $R(1)=0.
       U(1)=0.
       FDR(1)=S(1)/W(1)
       IDAY(1)=0
       DAY(1)=0.
       PRINT 41,WO(M)
       PRINT 40
       LINES=8
    41 FORMAT(1H1,*  INITIAL NO OF GRAINS =20000.*/*              NO OF WEEVI
     +LS = *,F4.0//)
    40 FORMAT( 1X,*  DAY    NO OF  ADULT  EGGS LAID TOTAL NO EMIGRTS  TOT
     +AL NO    FOOD*,/*           GRAINS  WEEVILS  THAT DAY OF EGGS  THAT D
     +AY OF EMIGRTS  RATIO*,//)
       PRINT 22, IDAY(1),            S(1),W(1),EG(1),U(1),EMGT(1),R(1),FDR(
     +1)
       LINES=LINES+1
       DO 777 K=2,458
       L=K-1
       IDAY(K)=L
       IF(L.LE.420) DAY(K)=L
       IF (FDR(L).LE.CFDR) GO TO 17
       EG(K)=V*W(L)
       EMGT(K)=E*W(L)
       COSMD=C*W(L)
    15 R(K)=R(L)+EMGT(K)
       S(K)=S(L)-COSMD -EG(K)
       IF(L.LE.IA) GO TO 83
       Z=EG(L-IA)
       GO TO 85
    83 Z=0.
    85 W(K)=(1.-D)*W(L) -EMGT(K)+P*Z
       U(K)=U(L)+EG(K)-Z
       FDR(K)=S(K)/W(K)
```

```
      GO TO 18
   17 LL=L-1
      IF (FDR(LL).LE.CFDR) GO TO 45
      PRINT 14,IDAY(L)
      LINES=LINES+4
      IF(LINES.LT.57) GO TO 45
      PRINT 41,WO(M)
      PRINT 40
      LINES=8
   14 FORMAT(//,*      CRITICAL FOOD RATIO REACHED DURING THE *,I3,*-TH D
     +AY *,//)
   45 EG(K)=V*S(L)/CFDR
      EMGT(K)=E*(1.+B*CFDR)*W(L)-E*B*S(L)
      COSMD=C*S(L)/CFDR
      GO TO 15
   18 IF (S(K).GT.0.) GO TO 19
      S(K)=0.
      FDR(K)=0.
      IF (S(L).EQ.0.) GO TO 19
      PRINT 16,IDAY(L)
      LINES=LINES+4
      IF(LINES.LT.57) GO TO 19
      PRINT 41,WO(M)
      PRINT 40
      LINES=8
   16 FORMAT (//,*      WHEAT GRAINS WERE FINISHED DURING THE *,I3,*-TH D
     +AY *,//)
C
   19 IF (W(K).GT.0.) GO TO 77
      W(K)=0.
      PRINT 20, IDAY(K)
      LINES=LINES+4
      IF(LINES.LT.57) GO TO 77
      PRINT 41,WO(M)
      PRINT 40
      LINES=8
   20 FORMAT (//,*      AN EXTINCTION OF ADULT WEEVIL POPULATION OCCURS D
     +URING THE *,I3,*-TH DAY *,//)
   77 PRINT 22,IDAY(K),              S(K),W(K),EG(K),U(K),EMGT(K),R(K),FDR(K
     +)
      LINES=LINES+1
      IF(LINES.LT.57) GO TO 777
      PRINT 41,WO(M)
      PRINT 40
      LINES=8
   22 FORMAT (3X,I3,            6F9.2,F10.4)
  777 CONTINUE
      CALL SCALE(DAY,35.,60,7)
      CALL SCALE(S,15.,60,7)
      CALL SCALE(W,15.,60,7)
      CALL SCALE(FDR, 9.,60,7)
      CALL SCALE(U,15.,60,7)
      CALL SCALE(R,15.,60,7)
      PRINT 23,FDR(421),FDR(428),S(421),S(428),U(421),U(428),W(421),W(42
     +8),R(421),R(428)
   23 FORMAT(/////,1X,*     VARIABLE      ORIGIN VALUE      SCALE FACTOR*/
     +*          FDR      *,2(5X,E11.3)/*            S       *,2(5X,E11.3)/*
     +  U      *,2(5X,E11.3)/*             W       *,2(5X,E11.3)/*           R      *
     +,2(5X,E11.3))
      CALL PAUPLOT(22HUSE BLANK PAPER PLEASE,22)
      CALL PAUPLOT(21HUSE DARKER INK PLEASE,21)
      CALL PLOT25
      CALL AXIS(0.,0.,41HGRAINS(ADULT WEEVILS MULTIPLIED BY 3.3..),41,15
     +.0,90.,S(421),S(428),-1)
      CALL AXIS(0.,0.,12HTIME IN DAYS,-12,24.0,0.,DAY(421),DAY(428),0)
      CALL AXIS(21.,0.,10HFOOD RATIO,-10,15.0,90.,FDR(421),FDR(428),-1)
      CALL LINE(DAY(1),S(1),60,7,1,1)
      CALL LINE(DAY(1),W(1)    ,60,7,1,0)
      CALL LINE(DAY(1),FDR(1),60,7,1,4)
      CALL SYMBOL(8.,14.8,0.2, 14H     FOOD RATIO,0.,14)
      CALL SYMBOL(8.,14.4,0.2,27H     NUMBER OF INTACT GRAINS, 0.,27)
      CALL SYMBOL(8.,14.0,0.2,27H     NUMBER OF ADULT WEEVILS, 0.,27)
      CALL PLOT(30.,0.,-3)
      CALL AXIS (0.,0.,30HADULT WEEVILS (TOTAL EMIGRANT),30, 15.0,90.,W(
     +421),W(428),-1)
      CALL AXIS(0.,0.,12HTIME IN DAYS,-12,24.0,0.,DAY(421),DAY(428),0)
```

```
      CALL AXIS(21.,0.,22HSIZE OF IMMATURE GROUP,-22,15.0,90.,U(421),U(4
     +28),-1)
      CALL LINE(DAY(1),W(1)   ,60,7,1,0)
      CALL LINE(DAY(1),R(1)   ,60,7,1,2)
      CALL LINE(DAY(1),U(1)   ,60,7,1,11)
      CALL SYMBOL(12., 9.8,0.2,18H    NUMBER OF EGGS,0.,18)
      CALL SYMBOL(12.,9.4,0.2,27H    NUMBER OF ADULT WEEVILS, 0.,27)
      CALL SYMBOL(12.,9.0,0.2,29H    TOTAL NUMBER OF EMIGRANTS, 0.,29)
      CALL PLOT(30.,0.,-3)
 1001 CONTINUE
  514 STOP
      END
```

APPENDIX 3.2

COMPUTER PROGRAMME II

This programme is for

(a) Computing heating day-degrees

(b) Solving the equations (3.1.1) under variable temperature

The solution of (3.1.1) is based on the linear interpolation (3.2.5) and the formulae (3.2.1), (3.2.2), (3.2.3) and (3.2.4).

```
      PROGRAM TEMPTUR (INPUT,OUTPUT)
      DIMENSION  WO(4)   ,EG(428),U(428),W(428),S(428),FDR(428),AHDD(428)
     +,JTCAP(428),R(428),EMGT(428),IDAY(428),TEMP(429,2),AVTEMP(428),DP(
     +428),HDD(2),CDD(2),ACDD(428),DAY(428)
      COMMON TEMPL,TEMPT,TEMPU
C
C   PARAMETERS $ THEIR VALUES
C      OVIPOSITION RATE    IS V EGGS/DAY/WEEVIL
C      MORTALITY RATE  IS D      WEEVILS/DAY/WEEVIL
C      EMEGRATION TATE     IS E     WEEVILS/DAY/WEEVIL
C      PROPORTION OF SURVIVORSHIP OF EGGS IS P
C      CONSUMPTION RATE C=0.02128 GRAINS/DAY/WEEVIL
C      CRITICAL FOOD RATIO CFDR=10. GRAINS/WEEVIL
C      DEVELOPMENTAL PERIOD A=422.7 DAY-DEGREES
C   VALUES OF PARAMETERS AT OPTIMAL TEMPARATURE
C
      C=0.021285
      DT=0.0083333
      E0=0.008436
      V0=1.0
      P=.7
      CFDR=10.
      A=422.7
      B=0.12
C
C   OPTIMAL
      TEMPT=22.
C   LOWER THRESHOLD
      TEMPL=12.
C   UPPER THRESHOLD
      TEMPU=26.
C   VALUES AT LOWER TEMP THRESHOLD
      VL=0.
      DL=    DT
      EL=0.10*E0
C   PARAMETER VALUES AT UPPER TEMP THRESHOLD
      VU=0.
      DU =2.*DT
      EU=2.*E0
C   NAMES USED IN THE PROGRAM
C     TEMP=TEMPARATURE
C     EG=NO. OF EGGS LAID THE PREVIOUS DAY
C     U=EGGS+LARVAE+PUPAE+UNEMERGED ADULTS
C     W=NO. OF ADULT WEEVILS
C     S=NO. OF UNUSED GRAINS OF WHEAT
C     FDR=S/W=FOOD RATIO(DENSITY)
C     AHDD,ACCUMULATED HEATING DAY-DEGREES
C     JTCAP=TIME AT WHICH AN EMERGING ADULT WAS LAID
C     R=TOTAL NO. OF EMEGRANTS UP TO DATE
C     EMGT=EMEGRANTS DURING THE PREVIOUS DAY
C   SUBPROGRAM TO COMPUTE HEATING DAY-DEGREES
C   SCAL =A RADIAN TO DAYS CONVERSION:1/(2*PI)
C   TIME BETWEEN MAX AND MIN TEMPARATURES IS 12 HOURS
      DATA PIBY2/1.570796328/
C
      DO 1 L=1,43
      N=10*(L-1)+1
      KK=N+9
    1 READ 5,((TEMP(I,J),J=1,2),I=N,KK)
    5 FORMAT(20F4.1)
C
      TUP=1000.
      TLO=13.
C
      TDIF=TUP-TLO
      AVTEMP(1)=0.
      AHDD(1)=0.
      ACDD(1)=0.
      AVTEMP(1)=0.
      IDAY(1)=0
      DAY(1)=0
      DO 116 L=2,428
      KL=0
      K=KL+1
      IDAY(L)=L-1
      DAY(L)=IDAY(L)
```

```
      AVTEMP(L)=(TEMP(L,1)+TEMP(L,2))/2.
C
      TMIN=TEMP(L,1)
      TMAX=TEMP(L,2)
C
  100 AMPL=(TMAX-TMIN)/2.
      TBAR=(TMAX+TMIN)/2.
      IF(TMIN.LT.TLO) GO TO 4
      THETA1=-PIBY2
      COS1=0.
      GO TO 101
    4 IF(TMAX.GT.TLO) GO TO 102
      THETA1=PIBY2
      COS1=0.
      GO TO 101
  102 THETA1=ASIN((TLO-TBAR)/AMPL )
      COS1=COS(THETA1)
  101 IF(TMAX.GT.TUP)  GO TO 203
      THETA2=PIBY2
      COS2=0.
      GO TO 104
  203 THETA2=ASIN((TUP-TBAR)/AMPL)
      COS2=COS(THETA2)
  104 SCAL       =1./(4.*PIBY2)
      HDD(K)=SCAL       *((TBAR-TLO)*(THETA2-THETA1)+AMPL*(COS1-COS2)+TDIF
     +*(PIBY2-THETA2))
      CDD(K)=SCAL       *((TLO-TBAR)*(THETA1+PIBY2)+AMPL*COS1)
      KL=KL+1
      IF(KL.LT.2) GO TO 105
      AHDD(L)=AHDD(L)+HDD(K)
      ACDD(L)=ACDD(L)+CDD(K)
      GO TO 116
  105 AHDD(L)=AHDD(L-1)+HDD(K)
      ACDD(L)=ACDD(L-1)+CDD(K)
      TMIN=TEMP(L+1,1)
      K=K+1
      GO TO 100
  116 CONTINUE
C  ********  SUBPROGRAM ENDS HERE  *********
      PRINT 8
      LINES=5
    8 FORMAT (1H1,*    THE EXPERIMENT STARTED ON DECEMBER 1, 1977 *)
      PRINT 9
      LINES=2
      DO 6 L=1,428
      AVTEMP(L)=(TEMP(L,1)+TEMP(L,2) +TEMP(L+1,1))/3.
      IDAY(L)=L-1
      DAY(L)=IDAY(L)
C  JTCAP CALCULATED
      X=AHDD(L)-A
      IF (X.LE.0.) GO TO 7
      DO 11 K=1,428
      IF (AHDD(K).LE.X) GO TO 11
      JTCAP(L)=IDAY(K)
      DP(L)=IDAY(L)-IDAY(K)
      PRINT 12, IDAY(L),TEMP(L,1),TEMP(L,2),AVTEMP(L),AHDD(L),JTCAP(L),
     +DP(L)
      LINES=LINES+1
      IF(LINES.NE.60) GO TO 6
      PRINT 9
      LINES=2
      GO TO 6
   11 CONTINUE
    7 PRINT 10, IDAY(L),TEMP(L,1),TEMP(L,2),AVTEMP(L),AHDD(L)
      LINES=LINES+1
      IF(LINES.NE.80) GO TO 6
      PRINT 9
      LINES=2
    9 FORMAT(1H1,* DAY  MIN   MAX  MEAN  ACCUMULATED  HATCHING   DEVELOP
     +*,/*         TEMP  TEMP TEMP      HDD      EGG LAID ON  PERIOD*)
   12 FORMAT (2X,I3,3( 2X,F4.1),2X,E10.4,4X,I3,6X,F5.1)
   10 FORMAT (2X,I3,3( 2X,F4.1),2X,E10.4)
    6 CONTINUE
          S0=20000.
      W0(1)=240. $ W0(2)=120. $ W0(3)= 60. $ W0(4)=30.
      DO 1001 M=1,4
```

```
C   INITIAL VALUES DATA
      S(1)=S0
      W(1)=W0(M)
      EG(1)=0.
      EMGT(1)=0. SR(1)=0.
      U(1)=0.
      FDR(1)=S(1)/W(1)
      PRINT 41,W0(M),V0,DT,E0,P,TEMPL,TEMPT,TEMPU
      PRINT 40
      LINES=10
   41 FORMAT(1H1,*  INTIAL NO OF GRAINS = 20000      INITIAL NO OF ADULT
     +WEEVILS =*,F4.0/,* OPTIMAL RATES OF (1) OVIPOSITION =*,F4.2,*   (2)
     + MORTALITY =*,F8.6,*   (3)  EMIGRATION =*,F8.6/,* PROPORTION OF EGG
     +S THAT SURVIVE =*,F4.2/,* LOWER THRESHOLD TEMP. =*,F4.1,*      OPTI
     +MAL TEMP. =*,F4.1,*      UPPER THRESHOLD TEMP. =*,F4.1,//)
   40 FORMAT( 1X,*  DAY    MEAN     NO OF   ADULT  EGGS LAID TOTAL NO EMIGR
     +TS  TOTAL NO     FOOD*,/*              TEMP  GRAINS  WEEVILS  THAT DAY O
     +F EGGS  THAT DAY OF EMIGRTS  RATIO*,//)
      PRINT 22, IDAY(1),AVTEMP(1),S(1),W(1),EG(1),U(1),EMGT(1),R(1),FDR(
     +1)
      LINES=LINES+1
      TEMP(429,1)=18.0
      DO 777 K=2,428
      L=K-1
C   CALCULATION OF PARAMETER VALUES
      V=PAR(AVTEMP(L),VL,V0,VU)
      D=PAR(AVTEMP(L),DL,DT,DU)
      E=PAR(AVTEMP(L),EL,E0,EU)
C
      IF (FDR(L).LE.CFDR) GO TO 17
      EG(K)=V*W(L)
      EMGT(K)=E*W(L)
      COSMD=C*W(L)
   15 R(K)=R(L)+EMGT(K)
      S(K)=S(L)-COSMD -EG(K)
      IF(AHDD(L).LE.A)  GO TO 83
      JC=JTCAP(L)
      IF (AHDD(L-1).LT.A) GO TO 31
      JTL=JTCAP(L-1)
      GO TO 32
   31 JTL=0
   32 IF (JC.EQ.JTL) GO TO 83
      NON=JTL+1
      IF (JC.GT.NON) GO TO 103
      Z=EG(JC)
      GO TO 85
  103 LSUM=JC-JTL
      Z=0.
      DO 67 I=1,LSUM
      JT=JTL+I
   67 Z=Z+EG(JT)
      GO TO 85
   83 Z=0.
   85 W(K)=(1.-D)*W(L) -EMGT(K)+P*Z
      U(K)=U(L)+EG(K)-Z
      FDR(K)=S(K)/W(K)
      GO TO 18
   17 LL=L-1
      IF (FDR(LL).LE.CFDR) GO TO 45
      PRINT 14,IDAY(L)
      LINES=LINES+4
      IF(LINES.LT.80) GO TO 45
      PRINT 41,W0(M),V0,DT,E0,P,TEMPL,TEMPT,TEMPU
      PRINT 40
      LINES=10
   14 FORMAT(//,*     CRITICAL FOOD RATIO REACHED DURING THE *,I3,*-TH D
     +AY *,//)
   45 EG(K)=V*S(L)/CFDR
      EMGT(K)=E*(1.+B*CFDR)*W(L)-E*B*S(L)
      COSMD=C*S(L)/CFDR
      GO TO 15
   18 IF (S(K).GT.0.) GO TO 19
      S(K)=0.
      FDR(K)=0.
      IF (S(L).EQ.0.) GO TO 19
```

```
      PRINT 16,IDAY(L)
      LINES=LINES+4
      IF(LINES.LT.60) GO TO 19
      PRINT 41,WO(M),VO,DT,EO,P,TEMPL,TEMPT,TEMPU
      PRINT 40
      LINES=10
   16 FORMAT (//,*      WHEAT GRAINS WERE FINISHED DURING THE *,I3,*-TH D
     +AY *,//)
C
   19 IF (W(K).GT.0.) GO TO 77
      W(K)=0.
      PRINT 20, IDAY(K)
      LINES=LINES+4
      IF(LINES.LT.60) GO TO 77
      PRINT 41,WO(M),VO,DT,EO,P,TEMPL,TEMPT,TEMPU
      PRINT 40
      LINES=10
   20 FORMAT (//,*      AN EXTINCTION OF ADULT WEEVIL POPULATION OCCURS D
     +URING THE *,I3,*-TH DAY *,//)
   77 PRINT 22,IDAY(K),AVTEMP(K),S(K),W(K),EG(K),U(K),EMGT(K),R(K),FDR(K
     +)
      LINES=LINES+1
      IF(LINES.LT.60) GO TO 777
      PRINT 41,WO(M),VO,DT,EO,P,TEMPL,TEMPT,TEMPU
      PRINT 40
      LINES=10
   22 FORMAT (3X,I3,2X,F5.1,6F9.2,F10.4)
  777 CONTINUE
      CALL SCALE(DAY,35.,60,7)
      CALL SCALE(S,15.,60,7)
      CALL SCALE(W,15.,60,7)
      CALL SCALE(FDR, 9.,60,7)
      CALL SCALE(U,15.,60,7)
      CALL SCALE(R,15.,60,7)
      CALL SCALE(AVTEMP,15.,60,7)
      PRINT 23,FDR(421),FDR(428),S(421),S(428),U(421),U(428),W(421),W(42
     +8),R(421),R(428),AVTEMP(421),AVTEMP(428)
   23 FORMAT(/////,1X,*      VARIABLE       ORIGIN VALUE       SCALE FACTOR*/
     +*         FDR       *,2(5X,E11.3)/*                    S        *,2(5X,E11.3)/*
     +  U       *,2(5X,E11.3)/*                  W        *,2(5X,E11.3)/*            R      *
     +,2(5X,E11.3)/*   AVTEMP      *,2(5X,E11.3))
      CALL PAUPLOT(21HUSE DARKER INK PLEASE,21)
      CALL PAUPLOT(22HUSE BLANK PAPER PLEASE,22)
      CALL PLOT25
      CALL AXIS (0.,0.,14H   GRAINS      ,                   14,15.0,90., S(421)
     +,S(428),-1)
      CALL AXIS(0.,0.,12HTIME IN DAYS,-12,24.0,0.,DAY(421),DAY(428),0)
      CALL AXIS(21.,0.,10HFOOD RATIO,-10,15.0,90.,FDR(421),FDR(428),-1)
      CALL LINE(DAY(1),S(1),60,7,1,1)
      CALL LINE(DAY(1),W(1)   ,60,7,1,0)
      CALL LINE(DAY(1),FDR(1),60,7,1,4)
      CALL LINE(DAY(1),AVTEMP(1),60,7,1,3)
      CALL SYMBOL(8.,14.8,0.2, 14H    FOOD RATIO,0.,14)
      CALL SYMBOL(8.,14.4,0.2,27H    NUMBER OF INTACT GRAINS, 0.,27)
      CALL SYMBOL(8.,14.0,0.2,27H    NUMBER OF ADULT WEEVILS, 0.,27)
      CALL SYMBOL(8.,13.6,0.2,23H    AVERAGE TEMPERATURE, 0.,23)
      CALL PLOT(30.,0.,-3)
      CALL AXIS (0.,0.,30HADULT WEEVILS (TOTAL EMIGRANT),30, 15.0,90.,W(
     +421),W(428),-1)
      CALL AXIS(0.,0.,12HTIME IN DAYS,-12,24.0,0.,DAY(421),DAY(428),0)
      CALL AXIS(21.,0.,19HAVERAGE TEMPERATURE,-19,15.0,90.,AVTEMP(421),
     +AVTEMP(428),-1)
      CALL LINE(DAY(1),W(1)   ,60,7,1,0)
      CALL LINE(DAY(1),R(1)   ,60,7,1,2)
      CALL LINE(DAY(1),U(1)   ,60,7,1,11)
      CALL LINE(DAY(1),AVTEMP(1)   ,60,7,1,3)
      CALL SYMBOL(8.0,14.8,0.2,19HAVERAGE TEMPERATURE,0.,19)
      CALL SYMBOL(8.0,14.4,0.2,36H0.44..THE SIZE OF THE IMMATURE GROUP,
     +0.,36)
      CALL SYMBOL(8.0,14.,0.2,27H    NUMBER OF ADULT WEEVILS, 0.,27)
      CALL SYMBOL(8.,13.6,0.2,29H    TOTAL NUMBER OF EMIGRANTS, 0.,29)
      CALL PLOT(30.,0.,-3)
 1001 CONTINUE
  225 STOP
      END
```

```
C   SUBPROGRAM FOR EVALUATING PARAMETER  VALUES
       FUNCTION PAR(T,VHL,VHO,VHU)
       COMMON  TEMPL,TEMPT,TEMPU
       IF (T.LE.TEMPT) GO TO 52
       X=VHO+(VHU-VHO)*(T-TEMPT)/(TEMPU-TEMPT)
    51 IF(X.LT.0.) GO TO 54
       PAR=X
       GO TO 53
    52 X=VHL+(VHO-VHL)*(T-TEMPL)/(TEMPT-TEMPL)
       GO TO 51
    54 PAR=0.
    53 RETURN
       END
```

APPENDIX 5.1

Proof of Proposition 5.1 (of Section 5.2.4)

(i) For a given w_n we have to prove that $d(s_n,w_n)$ is an increasing function of s_n. Now with

$$\beta_{n1} = \kappa_n + \alpha_n = \beta - b\varepsilon\, s_n/w_n + (\nu + \lambda)/s_n$$

where

$$\beta = \mu + \varepsilon(1 + bC),$$

$$\alpha_n/\beta_{n1} = (\lambda + \nu)/\{(\lambda + \nu)\beta\, s_n - b\varepsilon s_n^2/w_n\} .$$

Then

$$\frac{\partial d(s_n,w_n)}{\partial s_n} = \frac{\alpha_n}{\beta_{n1}}[b\varepsilon/w_n + (\lambda + \nu)/s_n]e^{-\beta_{n1}a}$$

$$+ (\lambda + \nu)(\beta - 2b\varepsilon s_n/w_n)(1 - e^{-\beta_{n1}a})/$$

$$[\lambda + \nu + \beta s_n - b\varepsilon s_n^2/w_n]^2 .$$

The first term of the RHS > 0. It is only the second term that could be negative. So $\beta - 2b\varepsilon s_n/w_n > 0$, that is $s_n/w_n < \beta/(2b\varepsilon)$, is a sufficient condition for $\frac{\partial d(s_n,w_n)}{\partial s_n} > 0$ and therefore for $d(s_n,w_n)$ to be an increasing function of s_n.

(ii)
$$\ell_n = [d(s_n,w_n)]^{w_n}$$

$$= [1 - X(s_n,w_n)]^{w_n}$$

where

$$X = \frac{\alpha_n}{\beta_{n1}}(1 - e^{-\beta_{n1}a}) < 1 .$$

Now taking the logarithm of ℓ_n and differentiating with respect to w_n we have

$$\frac{1}{\ell_n}\frac{\partial \ell_n}{\partial w_n} = \frac{1}{1-X}\left\{(1-X)\ln(1-X) + w_n\frac{\partial d(s_n,w_n)}{\partial w_n}\right\} \qquad (5.A.1)$$

where

$$w_n\frac{\partial d}{\partial w_n} = \frac{\alpha_n b\varepsilon s_n}{w_n\beta_{n1}^2}[1-(1+\beta_{n1}a)e^{-\beta_{n1}a}]$$

$$< \frac{\alpha_n b\varepsilon s_n}{w_n\beta_{n1}^2}[1-e^{-\beta_{n1}a}] \quad .$$

So if $s_n/w_n < \beta/(2b\varepsilon)$

$$w_n\frac{\partial d}{\partial w_n} < \frac{\alpha_n\beta}{2\beta_{n1}^2}(1-e^{-\beta_{n1}a}) \quad . \qquad (5.A.2)$$

Since $0 < X < 1$

$$\ln(1-X) = -X - \frac{X^2}{2} - \frac{X^3}{3} - \ldots \quad .$$

Hence $(1-X)\ln(1-X) < -X(1-X)$

$$= -\frac{\alpha_n}{\beta_{n1}}(1-e^{-\beta_{n1}a})\left[1-\frac{\alpha_n}{\beta_{n1}}(1-e^{-\beta_{n1}a})\right]$$

$$< -\frac{\alpha_n}{\beta_{n1}}(1-e^{-\beta_{n1}a})(1-\alpha_n/\beta_{n1}) \quad . \qquad (5.A.3)$$

So using (5.A.2) and (5.A.3) we have the contents of { } in (5.A.1)

$$< \frac{\alpha_n}{\beta_{n1}}(1-e^{-\beta_{n1}a})\left(\frac{\beta-2(\beta_{n1}-\alpha_n)}{2\beta_{n1}}\right) . \qquad (5.A.4)$$

But $\beta_{n1} - \alpha_n = \beta - b\varepsilon s_n/w_n > \beta - \beta/2 = \beta/2$

when $s_n/w_n < \beta/(2b\varepsilon)$.

Hence RHS of (5.A.4) < 0 .

Therefore from (5.A.1) $\frac{\partial \ell_n}{\partial w_n} < 0$. Hence ℓ_n is a decreasing function of w_n.

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