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A POPULATION OF INSECTS INFESTING A STORED QUANTITY OF WHEAT[1]

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Abstract. This paper presents a mathematical model to determine the development of a population of weevils in stored wheat and the damage the weevils do to the wheat. The system is considered to go through two phases: in the first phase the number of wheat grains available per weevil is still sufficiently large, and in the second phase this number is below the critical food ratio C. Because of the time it takes the egg to develop into a mature weevil, the equations of the model are delay differential equations. Analytical solutions and/or bounds on the solutions can be obtained.

Introduction

I shall be concerned with a determistic model for the study of a population of weevils (*Sitophilus granarius* or *Sitophilus oryzae*) and the destruction they do to stored wheat.

The weevils destroy the wheat grains in two ways: (1) by ovipositing eggs into the grains and (2) by eating the grains. The egg develops through all the immature stages of larva, pupa and pre-emergence adult within the grain in which it is oviposited (Richards, 1947). Almost the whole grain is used up for the complete development of the egg. If more than one egg is oviposited in a grain, usually at most one adult emerges from the grain. This is because of competition that develops between the larvae within the grain. On average an egg takes 50 days to develop into a mature adult.

We shall consider a two-phase system in which *Phase I* corresponds to the situation where the ratio of the number of intact (unused) grains to the total number of adult weevils (referred to as the *food ratio*) is greater than a specified value C. *Phase II* is when the ratio is below C. The ratio C is to be referred to as the *critical food ratio*.

The existence of such critical food ratio in a real ecological system has been described by 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 (1975) gave the critical food ratio as 10 grains per female.

For the Phase I situation we set up delay differential equations for the number of weevils W(t) and the number of intact wheat grains S(t) at time t. From the solution for Phase I we determine the time T* at which the "critical food ratio" C is reached for the first time.

For the Phase II model parameters such as the oviposition rate and the emigration rate depend on the food radio $F(t)=S(t)/W(t)$.

The dependence of these parameters on F(t) was deduced from existing literature and collected data (MacLagan, 1932; Arditi *et al.* 1978).

Notation and assumptions

For Phase I the food ratio (*i.e.*, number of intact grains to a weevil) $F(t)=S(t)/W(t)$ is $>C$ and for Phase II $F(t) \leq C$.

In Phase I a female tries to avoid ovipositing eggs into grains already containing large larvae (Richards 1947). We therefore assume that a grain will contain at most one immature weevil. However, for Phase II more than one egg may be oviposited in a single grain (MacLagan and Dunn 1935) but a maximum of one adult may emerge from such a grain.

We assume that the wheat is stored under optimal environmental conditions as regards temperature, relative humidity and the moisture content of the grain.

The age of an adult weevil is assumed to have a negligible effect on its activities in the first few developmental periods for which we shall be solving our equations. However, we shall be concerned with two age-groups: (i) the immature age-group consisting of eggs, larvae, pupae and the pre-emergence adults and (ii) the mature adult age-group.

Let $\lambda(t)$, $\nu(t)$, $\epsilon(t)$ and $\mu(t)$ be the rates of oviposition, consumption, emigration and mortality respectively, at time t. It will be assumed that the expected length of the developmental period (*i.e.*, from egg to mature adult) is *a* days (assumed to be constant).

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The proportion of eggs expected to survive the developmental stages is p.

For Phase II both the oviposition rate $\lambda(t)$ and the consumption rate $\nu(t)$ are proportional to the food ratio (MacLagan 1932). The emigration rate is linear in F(t) but increases as the food ratio decreases.

According to the assumptions made above we shall take:

$$\lambda(t) = \begin{cases} \lambda & \text{(a constant) for Phase I} \\ \dfrac{\lambda}{C}\,\dfrac{S(t)}{W(t)} & \text{for Phase II} \end{cases}$$

$$\nu(t) = \begin{cases} \nu & \text{(a constant) for Phase I} \\ \dfrac{\nu}{C}\,\dfrac{S(t)}{W(t)} & \text{for Phase II} \end{cases} \qquad (2.1)$$

$$\mu(t) = \mu \qquad \text{(a constant) for both Phases}$$

$$\epsilon(t) = \begin{cases} \epsilon & \text{(a constant) for Phase I} \\ \epsilon + b\epsilon\,(C - S(t)/W(t)) & \text{for Phase II} \end{cases}$$

where the emigration rate is very small compared with the oviposition rate (*i.e.* $\nu \ll \lambda$), b is a constant, and C is the critical food ratio.

The phase I model

According to the assumptions made above the variables S(t) and W(t) satisfy the equations

$$\frac{dS}{dt} = -(\lambda+\nu)\,W(t) \qquad (3.1)$$

$$\frac{dW}{dt} = p\lambda W(t-a) - (\mu+\epsilon)\,W(t) \qquad (3.2)$$

These equations are subject to the initial conditions

$$S(0) = S_o,\ W(0) = W_o$$

and

$$W(t) \equiv 0 \text{ for } t<0.$$

To solve (3.2) we use the method of steps or Laplace transform technique.

Either way we get

$$W(t) = \sum_{r=0}^{n} \frac{(\lambda\, p)^r}{r!}\, e^{-k(t-ra)} \times (t-ra)^r \qquad (3.3)$$

over the n-th developmental period

$na \le t < (n+1)\,a$, $n = 0, 1, 2, \ldots$ (where $k = \mu+\epsilon$).

Then

$$S(t) = S_o - (\lambda+\nu) \int_o^t W(\gamma)\, d\gamma$$

or

$$S(t) = S\,(na) - (\lambda+\nu) \int_{na}^t W(\gamma)\, d\gamma. \qquad (3.4)$$

For example:

for $0 \le t < a$

$$W(t) = W_o\, e^{-kt}$$

$$S(t) = S_o - \left(\frac{\lambda+\nu}{k}\right) W_o\,(1-e^{-kt})$$

For $a \le t < 2a$

$$W(t) = W_o\,\{e^{-kt} + p\lambda\,(t-a)\, e^{-k(t-a)}\}$$

$$S(t) = S_o - \frac{(\lambda+\nu)}{k}\, W_o\, \{(1-e^{-kt}) - p\lambda\,(t-a)\, e^{-k(t-a)} + \frac{p\lambda}{k}\,(1-e^{-k(t-a)})\}.$$

We can continue to higher developmental periods and be able to sketch the graphs for S(t) and W(t). The shapes of the graphs will depend on the values of the parameters λ, μ, ϵ, p and ν and the initial numbers of the wheat grains and mature weevils (Fig. 1).

There is one very important quantity to determine using the solutions of Phase I. This is the time T^* at which the critical food ratio C is reached (for the first time). By numerical evaluation of (3.3) and solution of (3.4) T^* can be found.

Example 1: For $a = 50$ days, $\lambda = 0.5$, $\nu = 0.01863$, $\mu = 0.0267$, $\epsilon = 0.00278$, $p = 0.8$ and $C = 10$ (grains to a weevil); and for the initial number of wheat grains $S_o = 19{,}900$ ($\simeq 600$ gm in weight). Table 1 gives the values of T^* for the initial numbers of 240, 120, 60 and 30 weevils.

Table 1: The times T^* at which the critical food ratio C ($= 10$ grains per weevil) is first reached.

Initial No. of weevils W_o in 19900 grains	240	120	60	30
Day T^* at which the critical food ratio C is reached	63	75	96	114

The value $T^* = 75$ days for $W_o = 120$ weevils is close to that of 84 days given by Hardman's (1977) experiment in which he had 100 adult weevils to 19900 grains at the beginning of the experiment. It is worth noting

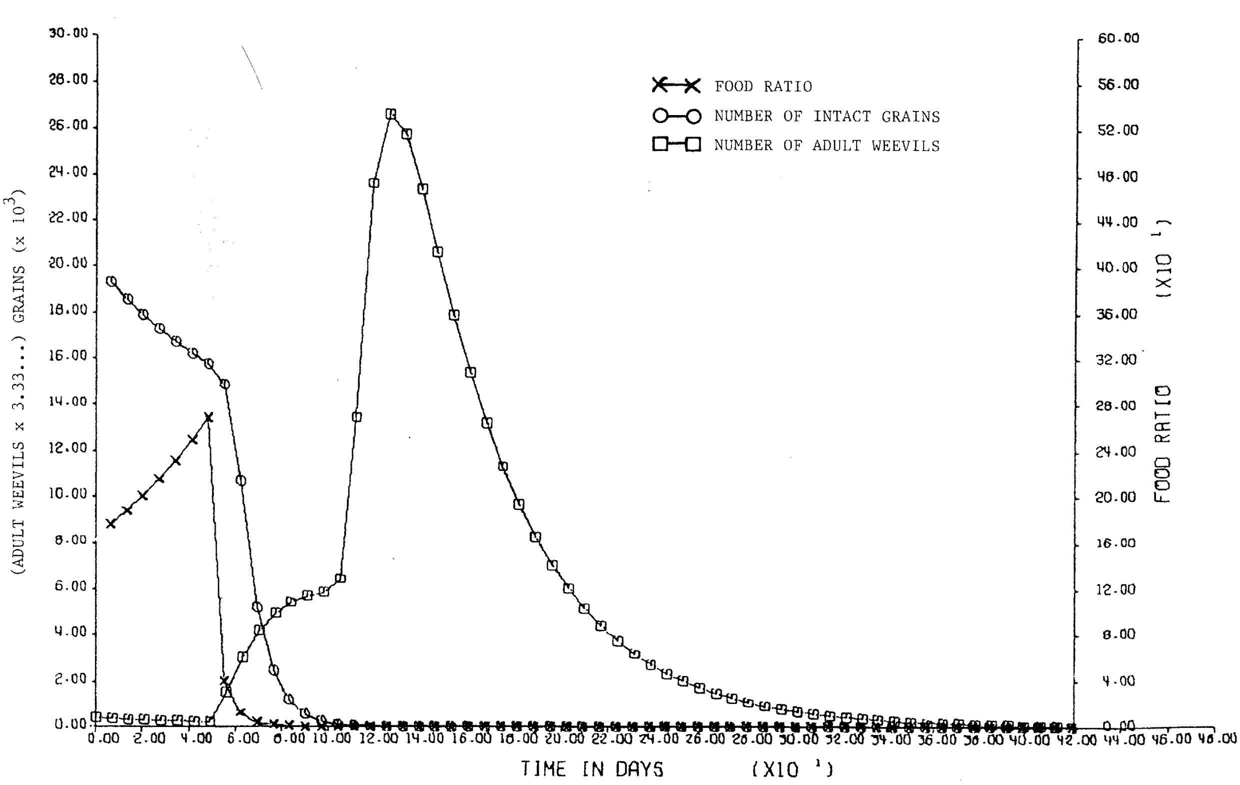

Fig. 1. The curves for (1) the food ratio F(t), (2) number of intact grains S(t) and (3) number of adult weevils for 120 weevils initially in 19,900 grains for the values of parameters as in Example 1 in Section 3.

that in both cases the critical food ratio is reached during the second developmental period.

Phase II model

According to (2.1), for Phase II we have

$$(\lambda, \nu)(t) = \left(\frac{\lambda}{C}, \frac{\nu}{C}\right) S(t)/W(t) \qquad (4.1)$$

$$\mu(t) = \text{constant}$$

and

$$\epsilon(t) = \epsilon + b\epsilon\,(C - S(t)/W(t)) \qquad (4.2)$$

It is important that the food ratio never rises again above the value C. If this happens then (4.1) and (4.2) would no longer apply.

Thus it is important that once F(t) drops below C it cannot rise again above C. A conditional relation connecting the parameters can be derived to ensure this. For example for $(\nu+\lambda)/C > \mu + \epsilon\,(1+bC)$ is a *sufficient condition* that the food ratio F(t) is a decreasing function for $t > T^*$ (Luboobi, 1980 Section 2.2.2).

Thus for the values of the parameters in the example at the end of Section 3 it has been demonstrated numerically that $F(t) < C$ for all $t > T^*$ (refer to Figure 1).

The Equations for Phase II

With the revision of the parameters as per (4.1) and (4.2) the equations (3.1) and (3.2) become

$$\frac{dS}{dt} = -\frac{(\lambda+\nu)}{C} S(t) \qquad (\text{for } t \geq T^*) \qquad (4.3)$$

$$\frac{dW}{dt} = p\lambda\, W(t-a) - (\mu+\epsilon+b\,\epsilon\, C)\, W(t) + b\,\epsilon\, S(t)$$

$$(\text{for } T^* \leq t < T^* + a) \qquad (4.4)$$

$$\frac{dW}{dt} = \frac{p\lambda}{C} S(t-a) - (\mu+\epsilon+b\epsilon\, C)\, W(t) + b\,\epsilon\, S(t)$$

$$\text{for } t > T^* + a \qquad (4.5)$$

These equations (i.e. (4.3), (4.4), and (4.5) turn out to be easier to solve than those of Phase I.

For example

$$S(t) = S(T^*)\, e^{-(\lambda+\nu)(t-T^*)/C} \qquad (4.6)$$

Then equation (4.5) becomes an ordinary differential equation; no delays are involved. From the expressions for W(t) obtained by solving (4.5) we can establish bounds on W(t).

For example if $\lambda + \nu < CB$ then

$$W(t) < Q^* e^{-Bt} \qquad \text{for } t > T^* + a$$

where $B = \mu + \epsilon\,(1 + b)$

$$\text{and } Q^* = W(T^* + a) + \left(\frac{k}{C} - B\right) S(T^*) \left\{\frac{\lambda\, p_e{-ka/C}}{C} + b\epsilon\right\}$$

Discussion

In Section 3 and 4 I demonstrated that the critical food ratio is reached during the second developmental period for an initial food ratio less than 663 grains per weevil. However, even for the initial food ratio greater than 663 grains per weevil (for example for 30 weevils initially in 19,900 grains), the critical food ratio is reached soon after the beginning of the third developmental period. Hence our solutions in Section 3 and 4 remain tractable; we need not seek solutions for many developmental periods. Moreover, after the critical food ratio is reached the equations become even simpler to solve.

We should note that when the food ratio falls below the critical value C it never rises above that level again, but continues to decrease monotonically to zero.

It should also be noted that even after the critical food ratio is reached the number of weevils continues to increase for some time before it decreases exponentially (Figure 1). This continued growth of the weevil population is due to the emergence of young from the eggs laid before time T^*, when the critical food ratio is reached.

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