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A MATHEMATICAL MODEL FOR *TRIBOLIUM CONFUSUM* POPULATIONS

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Abstract. A deterministic mathematical model is constructed to describe the population growth in colonies of the grain beetle, *Tribolium confusum,* under laboratory conditions. It is shown how (1) changes in the egg laying rate and adult mortality, (2) the destruction of some eggs by larvae as well as by adults, and (3) the destruction of some small larvae by larvae and adults, lead to a theoretical population growth which agrees closely with the laboratory experiments.

INTRODUCTION

A previous mathematical model describing the behavior of laboratory populations of the grain beetle, *Tribolium confusum,* has shown how the main features of the population growth can be explained by the tendency of adults to destroy eggs (Taylor 1965). Although there were some errors, as indicated below, in the numerical values used in that model, the general conclusions remain unaltered.

In the present paper an alternative description of the model is given in a form more suitable for mechanical computation. The program is devised so that the computer itself mimics the population. Hence, corresponding to a given instant, it reproduces simultaneously the numbers present in each of the various forms, adults, eggs, larvae, and pupae. In a model of this type, improvements and extensions can be incorporated easily, and it is shown how some of these allow it to describe features of the population history more closely than the previous model.

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THE FUNDAMENTAL EQUATIONS

Let the subscripts 0, 1, 2, 3, and 4 refer respectively to the adults, eggs, small larvae, large larvae, and pupae. Then

$N_j(t)$ = number in jth stage at time t,
$\Delta N_j(\tau, t)$ = number in jth stage aged between $\tau - \Delta t$ and τ at time t,
a_j = age span in jth stage,
b = egg laying rate per adult,
c = mortality rate of adults per adult,
$\alpha_j(\tau)$ = probability of survival of jth stage from age τ to $\tau + \Delta t$.

The method consists in finding the populations at time $t + \Delta t$ in terms of the populations at time t.

For the adults, the number at time $t + \Delta t$ is equal to the number at time t, less those dying in time Δt, plus those hatching from pupae which reach the full age span a_4 in this time. Hence

$$(1)\ N_0(t + \Delta t) = N_0(t) - c\, N_0(t)\, \Delta t + \Delta N_4(a_4, t).$$

For the eggs, the number at time $t + \Delta t$ in the youngest age range of Δt will be the number laid in time Δt, reduced by a factor between 1 and $\alpha_1(0)$ due to losses in this time. If Δt is small, then, approximately,

$$(2)\ \Delta N_1(\Delta t, t + \Delta t) = b\, N_0(t)\, \Delta t \times \alpha_1(0).$$

Also, the number of eggs at time $t + \Delta t$ in each subsequent age range of Δt is the number in the corresponding previous age range at time t, reduced by the survival factor. Hence,

$$(3)\ \Delta N_1(\tau + \Delta t, t + \Delta t) = \Delta N_1(\tau, t) \times \alpha_1(\tau)$$

for $\tau = \Delta t$ to $a_1 - \Delta t$. So, from (2) and (3), the total number of eggs at time $t + \Delta t$ is

$$(4)\ N_1(t + \Delta t) = b\, N_0(t)\, \Delta t \times \alpha_1(0) + \sum_{\tau = \Delta t}^{a_1 - \Delta t} \Delta N_1(\tau, t) \times \alpha_1(\tau).$$

For the small larvae, similarly,

$$(5)\ \Delta N_2(\Delta t, t + \Delta t) = \Delta N_1(a_1, t) \times \alpha_2(0)$$

and

$$(6)\ \Delta N_2(\tau + \Delta t, t + \Delta t) = \Delta N_2(\tau, t) \times \alpha_2(\tau)$$

for $\tau = \Delta t$ to $a_2 - \Delta t$. So

$$(7)\ N_2(t + \Delta t) = \Delta N_1(a_1, t) \times \alpha_2(0) + \sum_{\tau = \Delta t}^{a_2 - \Delta t} \Delta N_2(\tau, t) \times \alpha_2(\tau).$$

For the large larvae,

$$(8)\ \Delta N_3(\Delta t, t + \Delta t) = \Delta N_2(a_2, t) \times \alpha_3(0)$$

and

$$(9)\ \Delta N_3(\tau + \Delta t, t + \Delta t) = \Delta N_3(\tau, t) \times \alpha_3(\tau)$$

for $\tau = \Delta t$ to $a_3 - \Delta t$. So

$$(10)\ N_3\,(t + \Delta t) = \Delta N_2\,(a_2, t) \times \alpha_3\,(0) + \sum_{\tau=\Delta t}^{a_3-\Delta t} \Delta N_3\,(\tau, t) \times \alpha_3\,(\tau).$$

For the pupae,

$$(11)\ \Delta N_4\,(\Delta t, t + \Delta t) = \Delta N_3\,(a_3, t) \times \alpha_4\,(0)$$

and

$$(12)\ \Delta N_4\,(\tau + \Delta t, t + \Delta t) = \Delta N_4\,(\tau, t) \times \alpha_4\,(\tau)$$

for $\tau = \Delta t$ to $a_4 - \Delta t$. So

$$(13)\ N_4\,(t + \Delta t) = \Delta N_3\,(a_3, t) \times \alpha_4\,(0) + \sum_{\tau=\Delta t}^{a_4-\Delta\tau} \Delta N_4\,(\tau, t) \times \alpha_4\,(\tau).$$

If Δt is not very small, some refinements must be included in these formulae. For example, the summations must be adjusted to give more accurate expressions for approximate integration. One way of doing this is shown in the next section It is a simple matter to include these adjustments in the program, and to include also possible dependence of b and c on the numbers present in the population and the time.

Some assumptions must now be made concerning the α_j.

To determine the α_1, it will be assumed that the main factor affecting the mortality of eggs is the cannibalism by adults and large larvae.

Let

k_0 = proportion of eggs destroyed by an adult in unit time,

k_3 = proportion of eggs destroyed by a large larva in unit time.

In general, these quantities will be functions of the population numbers. The subscript denotes the stage which does the killing.

In the time Δt previous to t, let v be the fraction of the medium explored by the cannibals, and hence the fraction of the eggs destroyed. Let dv be the additional fraction lost in the further infinitesimal time dt. This will be a fraction $(k_0 N_0(t) + k_3 N_3(t))dt$ of the number of eggs remaining. So

$$dv = (1 - v)\,(k_0\,N_0 + k_3\,N_3)\,dt.$$

Hence

$$1 - v = \exp\left\{-\int_{t-\Delta t}^{t} (k_0\,N_0 + k_3\,N_3)\,dt\right\}.$$

This is the fraction of eggs surviving through the time Δt. If Δt is small, then

$$(14)\ \alpha_1\,(\tau) = \exp\left\{-[k_0\,N_0\,(t) + k_3\,N_3\,(t)]\,\Delta t\right\}.$$

Thus $\alpha_1(\tau)$ is a function of t. Adjustments can be made to give a more accurate formula. Usually, the term $(k_0N_0 + k_3N_3)$ will be fairly large (of the order of unity), and so variations of N_0 and N_3 during the time Δt should be taken into account.

To determine α_2, it will be assumed that destruction by adults and large larvae is also the main cause of mortality of the small larvae.

Let

l_0 = proportion of small larvae destroyed by an adult in unit time,

l_3 = proportion of small larvae destroyed by a large larva in unit time.

Then, as before,

$$(15)\ \alpha_2\,(\tau) = \exp\left\{-(l_0\,N_0\,(t) + l_3\,N_3\,(t)\,)\,\Delta t\right\}.$$

It will be assumed that the deaths of large larvae and pupae are accidental, and so the probability of survival remains the same throughout the respective lifetimes. The probability of survival of these forms is usually so much greater than that of the eggs and small larvae that comparatively little error is introduced by this assumption.

Let

p_3 = probability of survival of a large larva,

p_4 = probability of survival of a pupa.

Then

$$(16)\ \alpha_j\,(\tau) = (p_j)^{\Delta t/a_j} \quad \text{for } j = 3, 4.$$

The equations (14), (15), and (16) take into account the main factors affecting the populations of the immature forms. Substituting from these into the equations (1) to (13), the properties of the population at time $t + \Delta t$ can be determined from the properties at time t, and so the history of the population can be traced.

With the present assumptions, each $\alpha_j(\tau)$ is independent of the age τ, and so could be written simply as α_j.

The additional complications introduced here make mathematical expressions for the steady state populations more difficult to obtain than in the previous model. However, the actual values can be found easily by allowing the program to run for a sufficient time on the computer.

ADJUSTMENTS TO THE FORMULAE

To accomplish the calculation reasonably quickly so that computer time is not wasted, the interval Δt must not be too small. It is then necessary to replace the summations in the formulae (4), (7), (10), and (13) by more accurate expressions for numerical integration. The trapezoidal rule, although less accurate than most of the usual devices, requires only a small alteration to the equations. The additional terms

$$\tfrac{1}{2}\, b\, N_0\,(t)\,\Delta t - \tfrac{1}{2}\,\Delta N_1\,(a - \Delta t, t) \times \alpha_1\,(a_1 - \Delta t)$$

must be included on the right hand side of (4), and the equations (7), (10), and (13) treated similarly. When the egg number becomes large, there will be a strong, approximately exponential decrease in number with age, due to the relatively small probability of survival of eggs. The trapezoidal rule will then leave noticeable errors, particularly in the initial stages of the egg population, and so a further adjustment must be made. A similar correction might be necessary also in the case of small larvae. Amended formulae replacing (4), (7), (10), and (13) are, for the case where the α_j are independent of age,

$$\begin{aligned} N_1\,(t + \Delta t) &= b\, N_0\,(t)\,\Delta t\,\alpha_1 + \sum_{\tau=\Delta t}^{a_1-\Delta t} \Delta N_1\,(\tau, t)\,\alpha_1 \\ &\quad + \tfrac{1}{2}\left\{1 - \tfrac{1}{6}\,(1 - \alpha_1)\right\} \\ &\quad \times \left\{b\, N_0\,(t)\,\Delta t - \alpha_1\,\Delta N_1\,(a_1 - \Delta t, t)\right\}. \end{aligned} \tag{17}$$

$$\begin{aligned} N_2\,(t + \Delta t) &= \Delta N_1\,(a_1, t)\,\alpha_2 + \sum_{\tau=\Delta t}^{a_2-\Delta t} \Delta N_2\,(\tau, t)\,\delta\,\alpha_2 \\ &\quad + \tfrac{1}{2}\left\{1 - \tfrac{1}{6}\,(1 - \alpha_2)\right\} \\ &\quad \times \left\{\Delta N_1\,(a_1, t) - \alpha_2\,\Delta N_2\,(a_2 - \Delta t, t)\right\}, \end{aligned} \tag{18}$$

$$\begin{aligned} N_3\,(t + \Delta t) &= \Delta N_2\,(a_2, t)\,\alpha_3 + \sum_{\tau=\Delta t}^{a_3-\Delta t} \Delta N_3\,(\tau, t)\,\alpha_3 \\ &\quad + \tfrac{1}{2}\left\{\Delta N_2\,(a_2, t) - \alpha_3\,\Delta N_3\,(a_3 - \Delta t, t)\right\}, \end{aligned} \tag{19}$$

$$\begin{aligned} N_4\,(t + \Delta t) &= \Delta N_3\,(a_3, t)\,\alpha_4 + \sum_{\tau=\Delta t}^{a_4-\Delta t} \Delta N_4\,(\tau, t)\,\alpha_4 \\ &\quad + \tfrac{1}{2}\left\{\Delta N_3\,(a_3, t) - \alpha_4\,\Delta N_4\,(a_4 - \Delta t, t)\right\}. \end{aligned} \tag{20}$$

The total number of larvae is given by adding the results of (18) and (19).

COMPARISON WITH EXPERIMENT

The experimental population consisted of replicates in 40 g of medium at 29°C and 70% relative humidity (Brereton 1962). An example of a theoretical population and its comparison with this experimental one has been given in a previous paper (Taylor 1965). Unfortunately, there were errors in some of the numerical values used there. The average mortality rate of adults was taken to be 0.02 per adult per day instead of 0.002. Also, the resultant probability of survival of larvae was taken to be 0.62, the value given by Brereton for survival from the small larval stage only. The losses in the small larval stage, which lasts only for about 3 days of a total 16, were incorrectly assumed to be negligible. These errors do not affect the conclusion reached in that paper, that the destruction of eggs by adults causes the population to tend to a steady state after an initial overshooting. However, there are some features not explained by the simple theoretical investigation.

The theoretical approach of the present paper, besides being suitable for electronic computation, readily allows the simple model to be extended. The inclusion in the program of cannibalism of eggs and small larvae by large larvae and of small larvae by adults are examples of this. Dependence of the egg laying rate on adult numbers and of the mortality rate on time also can be incorporated. In Figure 1, the numerical values used differing from those in the previous paper were determined by the following considerations.

(1) Reference to the previous results shows that the initial growth of the experimental egg population is about three times as fast as that given by the theoretical curve. In the present case it was assumed that the egg laying rate started at 3.0 per adult per day when the number of adults was 18, and decreased with increase in population to 1.1 when the number reached 30. Table VII of Brereton's paper (1962) also gives some indication of a decrease in egg laying rate with increase in adult numbers. The final value of 1.1 agrees more closely with the results shown in that table than the 1.0 previously taken. Park, Mertz, and Petrusewicz (1961) describe variations in fecundity with age. They also note differences in longevity of male and female adults which will alter the sex-ratio, and hence the average egg laying rate. Since the cannibalism of males differs from that of females, it will also affect the egg eating rate. These effects have been ignored in the present calculations. The cannibalism rate has been taken as constant at 0.0011 of the total eggs per adult per day, in agreement with Brereton's Table VII.

(2) If the destruction of eggs by adults is the only type of cannibalism taken into account, the initial overshooting in the adult and larval populations is too great. Preliminary trials on the new model showed that a smoothing effect of the

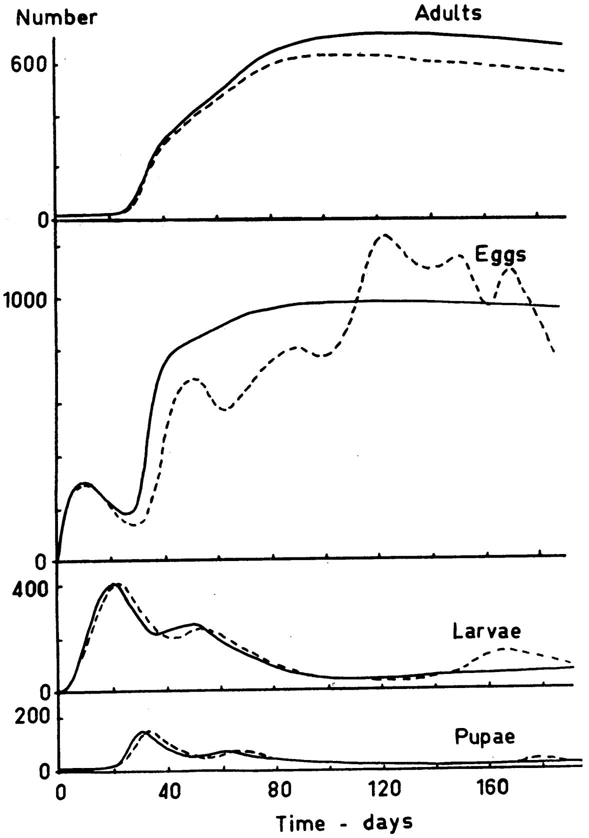

FIG. 1. Comparison of the theoretical and experimental population growths. The solid lines show the theoretical and the dotted lines the experimental growths.

required order could be obtained by assuming a small amount of destruction of eggs by larvae. It is known in fact that all moving forms attack all inert forms. For the curves shown in Figure 1, each large larva was assumed to destroy 0.0003 of the eggs per day. There is no direct experimental evidence for this value. It was chosen because it produces the desired effect in the growth curves.

(3) The mortality of small larvae could be due to eating or some other interference by large larvae and adults. It is known that large larvae do attack small larvae. However, the experimental growth curve for the larvae could not be explained by this effect alone. The theoretical curve contained a distortion which was removed by assuming that adults also attack small larvae. The value chosen for the rate of destruction of small larvae by large larvae and by adults was taken to be 0.0003 in each case. Again, there is no direct evidence for this figure except for the effect it produces on the curves.

Experiments by Park, Mertz, Grodzinski, and Prus (1965) indicate that the destruction of small larvae by large larvae is rather less than this, but that there is some loss due to accident. Taking this into account in the calculations, there is little alteration in the theoretical curves, since accidental loss has an effect very similar to destruction by large larvae, provided the losses are not excessive. Accidental losses can be included in the calculations if the right hand side of the equation (15) is multiplied by an expression like that in (16).

(4) Since the natural life span of an adult is about 200 days, it is expected that the mortality rate will approach 0.005 per adult per day after a sufficient time has elapsed. Hence, the mortality rate of adults was taken to be 0.002 for the first 100 days, increasing to 0.005 at about 200 days after the commencement. The experimental figures show a high mortality rate in the very early stages, but this was neglected since the total number of adults then is small. A drop in mortality below the figure of 0.002 for a considerable period also was ignored.

From the above observations, the present model uses the following values: $a_1 = 6$ days; $a_2 = 3$ days; $a_3 = 13$ days; $a_4 = 6$ days; $b = 3.0$ eggs per adult per day when $N_0 = 18$, decreasing to 1.1 when $N_0 \geqq 30$; $c = 0.002$ of the adults per day, increasing to 0.005 during the period 100-200 days; $k_0 = 0.0011$ of the total eggs per adult per day; $k_3 = 0.0003$ of the total eggs per large larva per day; $l_0 = 0.0003$ of the small larvae per adult per day; $l_3 = 0.0003$ of the small larvae per large larva per day; $p_3 = 0.62$; $p_4 = 0.89$.

The initial populations chosen were those of the experiments, $N_0(0) = 18$, $N_1(0) = 23$, $N_2(0) = 0$, $N_3(0) = 9$, $N_4(0) = 1$.

From the similarity between the theoretical and experimental curves, it appears that the destruction of eggs by larvae and the destruction of small larvae by large larvae and by adults are significant factors in determining the history of the populations.

The number of eggs in the model varies much more smoothly than in the experimental population, but follows roughly the mean growth. In trying out various numerical values, it was found that fluctuations could be induced easily by small increases in the egg cannibalism of larvae, and so differences in the theoretical and experimental egg populations are probably not significant. These fluctuations did not cause much effect on the adult population growth in the model. In fact, it is shown in the next section that the other populations are relatively stable even for the complete removal of eggs at a given instant.

Discrepancies so far not resolved in the theoretical curves are the noticeably high adult numbers, and the small decrease in the time scale,

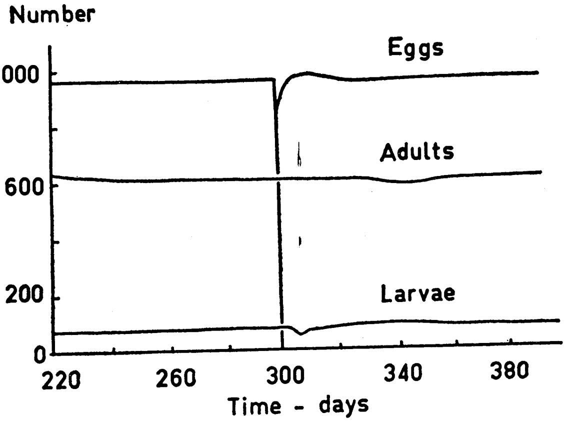

FIG. 2. The effect of the removal of eggs. All eggs were removed at the time 300 days.

particularly in the egg population in the region where the major growth occurs.

REMOVAL OF EGGS

An example is given here of the way in which the model can be extended without difficulty to deal with certain special cases.

In one of Brereton's experiments, all the eggs were removed from some of the replicates on one occasion. Details are not given in his paper (1962), but an examination of the original figures shows that this had little effect on the population history. Figure 2 demonstrates the effect in the theoretical model of putting all the ΔN_1 equal to zero at the instant $t = 300$ days. The populations of the various components soon return to their steady states, in agreement with Brereton's observations.

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EFFECT OF POPULATION DENSITY ON THE VIABILITY AND FECUNDITY IN *NASONIA VITRIPENNIS* WALKER (HYMENOPTERA, PTEROMALIDAE)[1]

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Abstract. Viability and oviposition of the parasitic wasp *Nasonia vitripennis* on its host *Phaenicia sericata* at various parasite-host densities were analyzed. As the parasite density becomes excessive, an increasing portion of the progeny is reduced. These density-dependent reduction mechanisms are: retention of eggs if a sufficient number of hosts is not available; death and decomposition of superparasitized host pupae resulting in death of the parasite larvae; food shortage within the host leading to parasite mortality shortly before and during metamorphosis; reduced longevity and fecundity of viable female offspring from superparasitized hosts and a decreasing portion of female progeny as the parasite number on a given host supply increases. This change in sex ratio is relatively independent of the number of eggs laid per parasite female or per host pupa. It is mainly determined by the number of simultaneously ovipositing females: the more dense the ovipositing females, the less fertilized eggs they produce.

Two categories of density-dependent regulation mechanisms are distinguished: behavioural and pathological mechanisms. The significance of the two categories for the existence of a theoretical population equilibrium on the one hand and for a real equilibrium on the other hand is discussed.

INTRODUCTION

In order to reach an understanding of the density fluctuations in a host-parasite population the density-dependent biological interactions between the two organisms have to be known. Density-dependent fecundity and viability factors may be—according to the definition of Nicholson (1933)—mechanisms of population regulation sensu stricto.

According to the mathematical population model of Pimentel (1961) the genetic nature of the interacting organisms would be continuously altered by a "feed back" mechanism, which would ultimately lead to an equilibrium between host and parasite

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