A MODEL FOR THE POPULATION DYNAMICS OF INTERNAL PARASITES

BU-176-M Keewhan Choi May, 1965

ABSTRACT

We are interested in the loss of red cells in a parasitized sheep in relation to the contamination of posture by worm eggs and parasites (pupae and adult worms) in a sheep (or any other organism). Discussed in this paper is a simple model for the temporal distributions of eggs in the pasture, red cells in a sheep, and pupae and/or adult worms in a sheep. For a stochastic model difference-differential equations which must be satisfied by the probability distributions of the quantities of interest are obtained easily. However, the resulting equation is not tractable. As for a deterministic model, the solution (an infinite series) is obtained. Since the solution is of no practical use, a recursive scheme of evaluating the solution is given.

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We are interested in the loss of red cells in a parasitized sheep in relation to the contamination of posture by worm eggs and parasites (pupae and adult worms) in a sheep, (or any other organism). Discussed in this paper is a simple model for the temporal distributions of eggs in the pasture, red cells in a sheep, and pupae and/or adult worms in a sheep. For a stochastic model difference-differential equations which must be satisfied by the probability distributions of the quantities of interest are obtained easily. However, the resulting equation is not tractable. As for a deterministic model, the solution (an infinite series) is obtained. Since the solution is of no practical use, a recursive scheme of evaluating the solution is given.

1. Notation and a stochastic model

Let $X(t)$ be the number of eggs in the pasture at time t,
$Y(t)$ " " " " red cells in a sheep at time t,
$Z(t)$ " " " " pupae and adults (worms) in a sheep at time t.

Given at time t, $X(t) = x$, $Y(t) = y$, $Z(t) = z$, we assume that

the probability of $x \to x + 1$ in $(t, t + \Delta t) = \lambda_2 z\Delta t + o(\Delta t)$
" " " $x \to x - 1$ " " $= \mu_2 x\Delta t + o(\Delta t)$
" " " $y \to y + 1$ " " $= \lambda_1 y\Delta t + o(\Delta t)$
" " " $y \to y - 1$ " " $= (\mu_1 y + \mu_2 z)\Delta t + o(\Delta t)$

the probability of x or y changing more than 1 in $(t, t + \Delta t) = o(\Delta t)$. We also assume that

$$Z(t) = \theta X(t - \tau)$$

where $\tau > 0$ is the known maturation period of eggs and $0 < \theta < 1$ is the known proportion of eggs surviving to maturity.

Let $P_x(t)$ denote the probability that $X(t) = x$ and $P_y(t)$ is defined in the same way.

Then it is obvious from the above assumptions that

$$P_x(t + \Delta t) = P_x(t)\,[1 - (\lambda_3 z + \mu_3 x)\Delta t] + P_{x-1}(t)\mu_3 z\Delta t$$
$$+ P_{x+1}(t)\mu_3(x + 1)\Delta t + o(\Delta t) .$$

Hence

$$(\mathrm{I})\quad \begin{cases} \dfrac{dP_x(t)}{dt} = P_{x-1}(t)\mu_3 z - (\lambda_3 z + \mu_3 x)P_x(t) + \mu_3(x + 1)P_{x+1}(t) & x = 1,2,3,\ldots \\ \dfrac{dP_0(t)}{dt} = \mu_3 P_1(t) \end{cases}$$

Similarly, we obtain

$$(\mathrm{II})\quad \begin{cases} \dfrac{dP_y(t)}{dt} = P_{y-1}(t)(\mu_1(y - 1) + \mu_2 z) - [(\lambda_1 + \mu_1)y + (\lambda_2 + \mu_2)z]P_y(t) \\ \qquad\qquad + P_{y+1}(t)[\mu_1(y + 1) + \mu_2 z] & x \geq 1 \\ \dfrac{dP_0(t)}{dt} = P_1(t)[\mu_1 + \mu_2 z] \end{cases}$$

$Z(t)$ is obtained from the assumption

$$Z(t) = \theta X(t - \tau) .$$

Let $P(s, t)$ and $Q(s, t)$ be the probability generating functions of $P_x(t)$ and $P_y(t)$, respectively.

(e.g. $P(s, t) = \sum_{x=0}^{\infty} P_x(t)s^x$)

Then (I) and (II) give us

$$\frac{\partial P(s, t)}{\partial t} = (s - 1)\lambda_3 zP(s, t) + (s^{-1} - 1)\, s\, \frac{\partial P(s, t)}{\partial t}$$
$$= (s - 1)\lambda_3 zP(s, t) + (1 - s)\, \frac{\partial P(s, t)}{\partial t}$$

or

$$(\mathrm{I}') \quad s\,\frac{\partial P(s,\, t)}{\partial t} = (s - 1)\lambda_3 z P(s,\, t)$$

and

$$(\mathrm{II}') \quad \frac{\partial Q(s,\, t)}{\partial t} = (s - 1)[\lambda_1 s\,\frac{\partial Q(s,\, t)}{\partial t} + \lambda_2 z Q(s,\, t)]$$

$$+ (s^{-1} - 1)[s\,\frac{\partial Q(s,\, t)}{\partial t} + \mu_2 z Q(s,\, t)]\ .$$

Neither the solutions of (I) and (II) nor the solutions of (I') and (II') are known.

2. Deterministic model

Using the notation in Section 1 and the corresponding deterministic assumptions, the following set of differential equations can be written immediately.

$$(1) \quad \frac{dX(T)}{d(T)} = \lambda_3 \theta X(T - \tau) - \mu_3 X(T)$$

$$(2) \quad \frac{dY(T)}{d(T)} = (\lambda_1 - \mu_1)Y(T) - \mu_2 \theta X(T - \tau)$$

$$X(T) = X_0 \quad \text{for} \quad T \le 0\ .$$

The equation (1) must be solved first and the solution has to be substituted in the equation (2) before the equation (2) can be solved. In the remainder of the paper only the solution of (1) will be given.

Using the notation $I = \mu_3$, $R = -\lambda_3\theta$ (1) becomes

$$X'(T) + IX(T) + RX(T - \tau) = 0$$

changing the time scale by

$$t = \tau T$$

$$x(t) = e^{IT} X(T)$$

Then $$x'(t) = \tau e^{I\tau t} X'(T) + I\tau e^{I\tau t} X(T)$$

$$x(t - 1) = I^{I\tau(t-1)} X(T - \tau)$$

where $$x' = \frac{dx}{dt}, \quad X' = \frac{dX}{dT}.$$

Then (1) can be written as

$$\frac{1}{\tau} x'(t) + Re^{I\tau} x(t-1) = 0$$

or

$$(1') \qquad \begin{cases} x'(t) + R\tau e^{I\tau} x(t-1) = 0 \\ x(t) = X_0 e^{I\tau t} \text{ for } t \le 0 \end{cases}$$

Denoting $R\tau e^{I\tau} = -\lambda_3 \theta\tau e^{\mu_3 \tau}$ by b, we notice the characteristic equation of (1') is

$$D(Z) \equiv Z + be^{-Z} = 0 .$$

Since $b < 0$, D(Z) has no real roots, but has infinitely many pairs of conjugate complex roots. Let $r_{\pm p}(b)$ denote the conjugate complex roots with positive and negative immaginary roots and larger p refers to the root of the greater magnitude. The Asymptotic expression for $r_{\pm p}(b)$ is given by Pinney (see ordinary difference-differential equations by Pinney, University of California Press, 1958, page 122).

$$r_{\pm p}(b) - \ln(-2p\pi/_b) \pm (2p - \tfrac{1}{2})\pi i + 0\left(\frac{\ln p}{p}\right)$$

Then

$$x(t) = \sum_{j=-\infty}^{\infty}{}' \frac{1}{1 + r_j(b)} e^{r_j(b)t} \left[\frac{I\tau X_0}{I\tau - r_j(b)} \left(1 - e^{r_j(b) - I\tau}\right) - br_j^{-1}(b)X_0\right]$$

$$= X_0 \tau \sum_{j=-\infty}^{\infty}{}' \frac{e^{r_j(b)t}}{1 + r_j(b)} \left[\frac{I - Ie^{r_j(b)-I\tau}}{I\tau - r_j(b)} - \frac{Re^{I\tau}}{r_j(b)}\right]$$

where $\sum'$ denotes that $j = 0$ time is omitted.

In terms of the original time scale T,

$$X(t) = X_0 \tau \sum_{j=\infty}^{\infty}{}' \frac{e^{r_j(b)T/\tau - IT}}{1 + r_j(b)} \left[\frac{I - Ie^{r_j(b)-I\tau}}{I\tau - r_j(b)} - \frac{Re^{I\tau}}{r_j(b)}\right]$$

The explicit solution of X(T) is not much of any practical use because of its form. The following discretization of the equation (1') is more amenable to numerical solution.

Discretize (1') as follows:

$$(1') \qquad \begin{aligned} x'(t) &= -\mu_3 x(t) + \lambda_3 \theta x(t-1) & t \geq 0 \\ x(t) &= x_0(t) \equiv x_0 & 0 \leq t \leq 1 \end{aligned}$$

Define $x_n(t) = x(t+n)$, $\quad 0 \leq t \leq 1$

then (1') is equivalent to

$$b \qquad \begin{cases} x_n'(t) = -\mu_3 x_n(t) + \lambda_3 \theta x_{n-1}(t) \qquad 0 \leq t \leq 1 \\ \quad n = 1,2,\ldots, \quad x_0 \text{ as above.} \\ \text{with the initial condition} \\ x_n(0) = x_{n-1}(1) \end{cases}$$

Let us now solve the above set of difference-differential equations.

$$x_1'(t) = -\mu_3 x_1(t) + \lambda_3 \theta x_0(t)$$

$$x_1'(t) + \mu_3 x_1(t) = \lambda_3 \theta x_0 \qquad \qquad (\text{for } x_1(\theta) \equiv x_0)$$

$$x_1(t) = e^{-\mu_3 t} \lambda_3 \theta x_0 \int_0^t e^{\mu_3 t} dt + c e^{-\mu_3 t}$$

$$= \frac{\lambda_3 \theta x_0}{\mu_3} \left[1 - e^{-\mu_3 t}\right] + c e^{-\mu_3 t}$$

$$c = x_0$$

Hence

$$x_1(t) = \frac{\lambda_3 \theta x_0}{\mu_3} \left[1 - e^{-\mu_3 t}\right] + x_0 e^{-\mu_3 t}$$

Now let us find $x_2(t)$.

$$x_2'(t) = -\mu_3 x_2(t) + \lambda_3 \theta x_1(t)$$

$$x_2(0) = x_1(1) .$$

Hence $$x_2(t) = e^{-\mu_3 t} \lambda_3 \theta \int_0^t x_1(t) e^{\mu_3 t} dt + x_1(1) e^{-\mu_3 t}$$

For general n, we have

$$x_n'(t) = -\mu_3 x_n(t) + \lambda_3 \theta x_{n-1}(t)$$

with $$x_n(0) = x_{n-1}(1)$$

hence $$x_n(t) = e^{-\mu_3 t} \lambda_3 \theta \int_0^t x_{n-1}(t) e^{\mu_3 t} dt + x_{n-1}(1) e^{-\mu_3 t}$$

$$n = 1,2,3,\ldots.$$

Inspection of the solutions $x_1(t)$, $x_2(t)$ convinces us $x_n(t)$ can be evaluated for any integer n in a closed form involving exponential functions.