A simple parasite model with complicated dynamics

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Abstract. During their first year of life sheep acquire parasites through grazing, and simultaneously build up an immunity to infection. At the beginning of each year non-immune lambs are introduced onto contaminated pasture. We represent this process by differential equations describing the within-year dynamics, and defining a difference equation that describes the between-year dynamics. An example with two system parameters is analysed in detail. It is shown that regions exist in parameter space where periodic (between-year) or aperiodic solutions occur. Parasite control schemes could change the system dynamics from a stable equilibrium to complicated long-term fluctuations.

1 Introduction

A variety of differential equation models has been used to explore the dynamics of nematode parasites (roundworms) of farmed animals (for a review see Smith and Grenfell, 1994). The adult stages of these parasites live in the gastrointestinal tract of the host. The females lay eggs that pass with the host's faeces onto pasture, where they develop into infective larvae. These larvae may be ingested by a host animal during grazing, and subsequently develop into adult parasites. The model proposed by Roberts and Grenfell (1991) consisted of just three equations, and was shown to exhibit within-year and between-year behaviour that qualitatively agreed with available data. Consider the scenario where lambs at weaning are introduced onto pasture that has been previously contaminated with parasites. As the lambs graze they acquire parasites, and an immunity to subsequent infection that is induced by parasite challenge (see also Woolhouse, 1992). Characteristic within-year dynamics are a rapid acquisition of parasites, followed by an exponential decay in parasite

numbers (Vlassoff, 1973). The between-year dynamics are determined by the discrete map between the levels of pasture parasite contamination in consecutive years. This model was extended by Roberts and Heesterbeek (1995) to include heterogeneities in host and parasite, and the development of parasite strains resistant to chemotherapy.

The equations used by Roberts and Grenfell (1991) and Roberts and Heesterbeek (1995) to model the dynamics of nematode populations in farmed ruminants were

$$\frac{dL}{dt} = -(\rho + \beta H)L + q\lambda(r)HA$$

$$\frac{dA}{dt} = \beta p(r)L - \mu(r)A \tag{1}$$

$$\frac{dr}{dt} = \beta L - \sigma r$$

The state variables L, A, and r represent the density of larvae on the pasture, the mean number of adult parasites per host and the mean level of acquired immunity respectively. H is the population density of host animals, assumed to be constant. The parameters q, β and ρ are the probability that a parasite egg develops into an infective larva, the rate at which host animals eat larvae, and the rate at which larvae are lost from the pasture by other means respectively. Acquired immunity is represented as the cumulative larval challenge, discounted at rate σ. The functions $\lambda(r)$, $p(r)$, and $\mu(r)$ are the rate at which individual adult parasites produce eggs, the probability that an ingested larva develops into an adult parasite and the mortality rate of adult parasites respectively. The parasite population is regulated by acquired immunity through one or more of these functions, hence $\lambda'(r) \leqq 0$, $p'(r) \leqq 0$, and $\mu'(r) \geqq 0$.

Define

$$Q(r) = \frac{q\lambda(r)\beta p(r)}{\mu(r)(\rho + \beta H)} H$$

If

$$Q_0 = Q(0) = \frac{q\lambda(0)\beta p(0)}{\mu(0)(\rho + \beta H)} H > 1$$

and $\lim_{r \to \infty} Q(r) < 1$, then equations (1) have a non-zero endemic steady state

$$(L^*, A^*, r^*) = \left(\frac{\sigma}{\beta} r^*, \frac{\sigma p(r^*)}{\mu(r^*)} r^*, r^*\right)$$

where $Q(r^*) = 1$. For r^* to be uniquely defined it is sufficient that $Q'(r^*) \neq 0$.

The state variables in equations (1) are non-dimensionalised by the transformation $(L, A, r) = (L^*x, A^*y, r^*z)$ to obtain the equations

$$\frac{dx}{dt} = -\kappa(x - f(z)y)$$

$$\frac{dy}{dt} = v(g(z)x - h(z)y) \tag{2}$$

$$\frac{dz}{dt} = \sigma(x - z)$$

where $\kappa = \rho + \beta H$, $v = \mu(r^*)$ and

$$(f(z), g(z), h(z)) = \left(\frac{\lambda(r)}{\lambda(r^*)}, \frac{p(r)}{p(r^*)}, \frac{\mu(r)}{\mu(r^*)}\right)$$

We now have $Q_0 = f(0)g(0)/h(0)$, $f'(z), g'(z) \leqq 0$, $h'(z) \geqq 0$, $f(1) = g(1) = h(1) = 1$, and the steady state solution is $x^* = y^* = z^* = 1$.

Typically σ is small, but as $\sigma \to 0$ z becomes constant, and equations (2) become linear. With the rescaling $\tilde{x} = \sigma x$, $\tilde{y} = \sigma y$, then dropping the tilde and letting $\sigma \to 0$ we obtain

$$\frac{dx}{dt} = -\kappa(x - f(z)y)$$

$$\frac{dy}{dt} = v(g(z)x - h(z)y) \tag{3}$$

$$\frac{dz}{dt} = x$$

The only non-trivial steady state solution of equations (3) is $x = y = 0$, $z = z^*$, for any $z^* \geqq 0$. However, we are interested in the situation where periodic perturbations occur; that is whenever t is an integer we reset y and z to zero, but x is continuous. This procedure is used to represent the introduction of new immunologically naive animals onto contaminated pasture at the beginning of each grazing season, replacing the existing animals that had acquired immunity (see Heesterbeek and Roberts, 1995; Roberts, 1995; Roberts and Heesterbeek, 1995). Instead of determining the existence and stability of steady states we are now interested in the existence and stability of dynamic equilibria. This is equivalent to determining the properties of a mapping $\phi: x(0) \to x(1)$. In the next section we consider a two-dimensional model for this problem that retains its essential features, and show that even this simple model can exhibit complicated dynamics. This analysis is relevant for the dynamics of all parasite populations that have an environmental stage and discrete host populations.

2 The two-dimensional model problem

2.1 Introduction

In this and subsequent sections we discuss a system that is simplified by the biological assumption that the free-living larval stages on the pasture have

a much longer life-span than the adult parasites within the host. The corresponding mathematical assumption is that v is much greater than κ. Assuming $v \gg \kappa$ in equation (3) we let $1/v \to 0$ to obtain the two-dimensional model problem

$$\frac{dx}{dt} = \kappa x (Q(z) - 1)$$

$$\frac{dz}{dt} = x$$

(4)

where $Q(z) = f(z)g(z)/h(z)$, hence $Q'(z) \leqq 0$ and $Q(1) = 1$, and we assume that $Q(0) = Q_0 > 1$ and $\lim_{z \to \infty} Q(z) < 1$. Note that formally, and in the spirit of the non-dimensionalisation described in the previous section, we have set $\tilde{Q}(z) = Q(r^*z)$ and then dropped the tilde. The resetting condition is now that z becomes zero whenever t takes an integer value.

To determine the within-year behaviour of the system we solve equations (4) on $(0, 1)$ with $x(0) = X$, $z(0) = 0$. Taking the quotient of equations (4) we obtain

$$x(t) = X + \kappa \int_0^{z(t)} (Q(s) - 1)ds$$

Starting at the point $(x, z) = (X, 0)$ trajectories increase in x until $z = 1$, whereupon they decrease in x. Trajectories always increase in z, and tend to the z axis ($x = 0$) as $t \to \infty$. If two trajectories begin at the initial conditions $(x(0), z(0)) = (X, 0)$ and $(x(0), z(0)) = (\tilde{X}, 0)$, then the distance between them in the x direction is always $|X - \tilde{X}|$. The maximum value of x occurs when $z = 1$ and is given by

$$x_{\text{MAX}} = X + \kappa \int_0^1 (Q(s) - 1)\, ds$$

We are interested in the problem with resetting, i.e. solve the differential equations for $t \in (0, 1)$ then reset z to zero and repeat. Define the map $\phi(X) = x(1)$. The map has the following properties.

Lemma 1. *The map ϕ has a unique fixed point $X^* = \phi(X^*)$.*

Lemma 2. *If $0 < X < X^*$ then $\phi(X) > X$, and if $X > X^*$ then $\phi(X) < X$.*

Lemma 3. *There exists a unique $X^{\#} < X^*$ such that when $X = X^{\#}$, $z(1) = 1$.*

2.2 Proof of lemmas

If $x(1) = X$ then $z(1) = z_1$, which is uniquely determined, independent of X, by

$$\int_0^{z_1} (Q(s) - 1)\, ds = 0$$

To establish the existence of a fixed point for ϕ, we only have to show that for at least one value of X, $z(1) = z_1$. But

$$z(t) = \int_0^t x(\tau)\, d\tau$$

so choose X so that

$$\int_0^1 x(\tau)\, d\tau = z_1 \tag{5}$$

This is possible because, from equation (4)

$$X e^{-\kappa t} \leqq x(t) \leqq X e^{\kappa(Q_0 - 1)t}$$

and therefore

$$\frac{X}{\kappa}(1 - e^{-\kappa}) \leqq \int_0^1 x(\tau)\, d\tau \leqq \frac{X}{\kappa(Q_0 - 1)}(e^{\kappa(Q_0 - 1)} - 1)$$

Choosing

$$X < \frac{\kappa(Q_0 - 1)z_1}{e^{\kappa(Q_0 - 1)} - 1} \Rightarrow \int_0^1 x(\tau)\, d\tau < z_1$$

and choosing

$$X > \frac{\kappa z_1}{1 - e^{-\kappa}} \Rightarrow \int_0^1 x(\tau)\, d\tau > z_1$$

Hence, for some intermediate value, $x(1) = X$, and we have established the existence of a fixed point, $X^* = \phi(X^*)$. To establish uniqueness, suppose there were two values of X that satisfied equation (5). Trajectories do not cross in the (x, z) plane, and using obvious notation $X > \tilde{X} \Rightarrow x(z) > \tilde{x}(z)\ \forall z$. But z_1 is independent of X, and for a fixed point we require

$$\int_0^{z_1} \frac{dz}{x} = \int_0^{z_1} \frac{dz}{\tilde{x}} = 1$$

which is clearly not possible. Hence we have established uniqueness of the fixed point, $X^* = \phi(X^*)$, and completed the proof of Lemma 1.

To prove Lemma 2 we note from the above that there exists an $X < X^*$ such that $\phi(X) > X$, and there exists an $X > X^*$ such that $\phi(X) < X$. The result follows from continuity and the uniqueness of the fixed point $X^* = \phi(X^*)$. Lemma 3 is established by setting $z_1 = 1$ in equation (5) and then repeating the argument that led to the existence and uniqueness of X^*.

In the next section we make a choice for the function $Q(z)$, and use these lemmas to investigate the dynamics of the map ϕ for all parameters $\kappa > 0$ and $Q_0 > 1$.

3 A simple model with complicated dynamics

3.1 Introduction

Now suppose that each host animal can either be *susceptible* or *immune*, the rate of mortality of parasites in both classes of host is the same ($=\kappa$), but

parasites are completely prevented from establishing in immune animals. Hence, we use a step function for $Q(z)$:

$$Q(z) = \begin{cases} Q_0 & \text{for } z < 1 \\ 1 & \text{for } z = 1 \\ 0 & \text{for } z > 1 \end{cases}$$

The solution of equation (4) is then

$$x(t) = \begin{cases} Xe^{\kappa(Q_0-1)t} & \text{for } t \leqq t_1 \\ Xe^{-\kappa t}\left(1 + \dfrac{\kappa(Q_0-1)}{X}\right)^{Q_0/(Q_0-1)} & \text{for } t > t_1 \end{cases}$$

$$z(t) = \begin{cases} \dfrac{X}{\kappa(Q_0-1)}\,(e^{\kappa(Q_0-1)t}-1) & \text{for } t \leqq t_1 \\ Q_0 + \dfrac{X}{\kappa} - e^{-\kappa t}\left(\dfrac{X}{\kappa}+Q_0-1\right)\left(\dfrac{X+\kappa(Q_0-1)}{X}\right)^{1/(Q_0-1)} & \text{for } t > t_1 \end{cases}$$

where t_1 is that value of t for which $z = 1$, i.e. the time at which the host becomes immune,

$$t_1 = \frac{1}{\kappa(Q_0-1)}\log\left(1 + \frac{\kappa(Q_0-1)}{X}\right)$$

The map $\phi(X)$ that expresses the between-year dynamics is

$$\phi(X) = \begin{cases} Xe^{\kappa(Q_0-1)} & \text{for } X \leqq X^{\#} \\ Xe^{-\kappa}\left(1 + \dfrac{\kappa(Q_0-1)}{X}\right)^{Q_0/(Q_0-1)} & \text{for } X > X^{\#} \end{cases}$$

where $X^{\#}$ is that initial value of x for which the parasite population reaches its peak exactly at the end of the year (at $t = 1$),

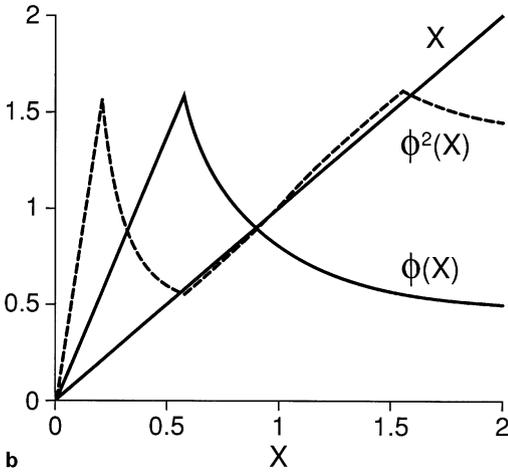$$X^{\#} = \frac{\kappa(Q_0-1)}{e^{\kappa(Q_0-1)}-1}$$

Figures 1a–c show examples of the map $\phi(X)$ for $Q_0 = 1.35$ and $\kappa = 2.2, 3$ and 5. The map $\phi^2(X)$ is also shown.
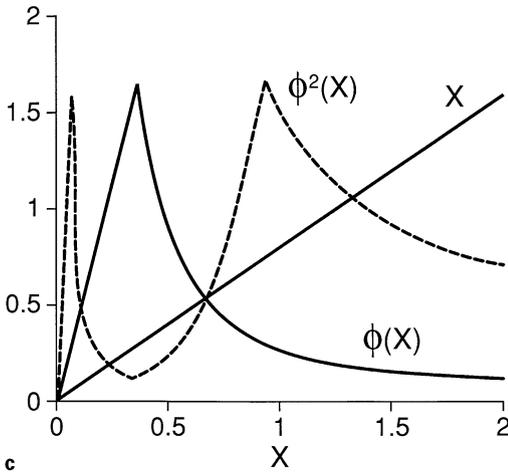
3.2 The period-1 solution

By Lemma 1, the map ϕ has a unique fixed point, and hence equations (4) together with the resetting condition on z have a unique period-1 solution, for all $Q_0 > 1$. We now demonstrate the more surprising result that this becomes unstable when κ exceeds a threshold only if $Q_0 < 2$.
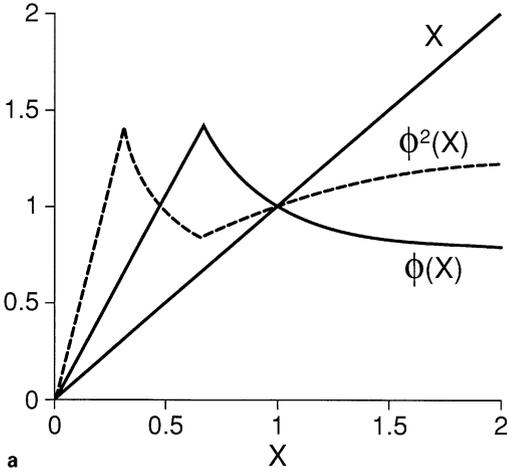
Fig. 1a–c. The functions $\phi(X)$ and $\phi^2(X)$ for **a** $\kappa = 2.2$, **b** $\kappa = 3$, and **c** $\kappa = 5$

Theorem 4. *The map ϕ has a unique fixed point $X^* = \phi(X^*)$ with $X^* > X^\#$. The fixed point is unstable if $1 < Q_0 < 2$ and*

$$\kappa > \kappa_1 = \frac{Q_0}{Q_0 - 1} \log \frac{Q_0}{2 - Q_0} \tag{6}$$

and stable if $Q_0 > 2$, or if $1 < Q_0 < 2$ and $\kappa < \kappa_1$.

Proof. The fixed point is defined by

$$X^* = \frac{\kappa(Q_0 - 1)}{e^{\kappa(Q_0 - 1)/Q_0} - 1}$$

Clearly $X^* > X^\#$. For all $X > X^\#$

$$\phi'(X) = \frac{\phi(X)}{X} \frac{X - \kappa}{X + \kappa(Q_0 - 1)} \tag{7}$$

Hence

$$\phi'(X^*) = \frac{Q_0 e^{-\kappa(Q_0 - 1)/Q_0} - 1}{Q_0 - 1}$$

which is a decreasing function of κ; $\lim_{\kappa \to 0} \phi'(X^*) = 1$ and $\lim_{\kappa \to \infty} \phi'(X^*) = -1/(Q_0 - 1)$. Hence if $1 < Q_0 < 2$ and $\kappa > \kappa_1$ then $\phi'(X^*) < -1$, and the fixed point $X = X^*$ is unstable. If $Q_0 \geqq 2$ or $0 < \kappa < \kappa_1$ then $|\phi'(X^*)| < 1$, and the fixed point is stable. $\square$

Remark 5. If $X = X^*$ then $t_1 = 1/Q_0$, $x(t_1) = \kappa(Q_0 - 1)/(1 - e^{-\kappa(Q_0 - 1)/Q_0})$ and $z(1) = Q_0$. In biological terms, t_1 is the time at which the parasite population attains its peak, $x(t_1)$ is the maximum parasite load, and $z(1)$ is the mean parasite load.

3.3 The period-2 solution

We now explore the dynamics of the system when the fixed point of ϕ is unstable. In particular we investigate conditions for the existence and stability of period-n solutions of equations (4) together with the resetting condition. A period-n solution is one for which $(x(t + n), z(t + n)) = (x(t), z(t))$ for all non-integer t. The function (x, z) corresponding to the initial condition $(x(0), z(0)) = (X, 0)$ is a period-n solution if $X = \phi^n(X)$, that is, if X is a period-n point of the map ϕ. Conditions for the existence and stability of period-2 solutions are established by two theorems:

Theorem 6. *When $1 < Q_0 < 2$ and $\kappa > \kappa_1$ the map $\phi(X)$ has a unique period-2 point defined by $X^{2*} = \phi^2(X^{2*})$, $\phi(X^{2*}) > X^{2*}$.*

Note that the fixed point, $X^* = \phi(X^*)$, is (trivially) a periodic point, and if X^{2*} is a periodic point then so is $\phi(X^{2*})$ (see Fig. 1). As a consequence of Lemma 2, whenever X^{2*} exists then $X^{2*} < X^* < \phi(X^{2*})$.

Theorem 7. *The orbit of the period-2 point defined by Theorem 6 is stable if $\kappa \in (\kappa_1, \kappa_2)$, and unstable if $\kappa > \kappa_2$, where*

$$\kappa_2 = \frac{Q_0}{(Q_0 - 1)(2 - Q_0)} \log\left(\frac{Q_0}{2 - Q_0}\right) \tag{8}$$

The proofs of these theorems are presented in the appendix. First we define a value $\kappa^\#$ such that $\kappa = \kappa^\# \Rightarrow \phi^2(X^\#) = X^\#$, and show that $\kappa^\# \in (\kappa_1, \kappa_2)$. For $\kappa \in (\kappa^\#, \kappa_2)$ we have

$$\phi^2(X) = X e^{\kappa(Q_0 - 2)} \left(1 + \frac{\kappa(Q_0 - 1)}{X e^{\kappa(Q_0 - 1)}}\right)^{Q_0/(Q_0 - 1)}$$

and the period-2 point may be found explicitly:

$$X^{2*} = \frac{\kappa(Q_0 - 1) e^{-\kappa(Q_0 - 1)}}{e^{\kappa(Q_0 - 1)(2 - Q_0)/Q_0} - 1} < X^\# < X^* \tag{9}$$

with

$$\phi(X^{2*}) = \frac{\kappa(Q_0 - 1)}{e^{\kappa(Q_0 - 1)(2 - Q_0)/Q_0} - 1} > X^* > X^\#$$

For $\kappa \in (\kappa_1, \kappa^\#)$, which is the sub-interval adjacent to the bifurcation point with the fixed point, the existence of a period-2 point must be established indirectly. Full details are given in the appendix, together with a proof that the orbit of the period-2 point is stable when $\kappa < \kappa_2$, and unstable when $\kappa > \kappa_2$.

3.4 Period-n solutions

The algebra involved in establishing the existence of periodic points of ϕ with period greater than two, and stability of their orbits, is lengthy. We confine ourselves here to presenting criteria that are sufficient for the existence of a period-n point, $X^{n*} = \phi^n(X^{n*})$, where n is any integer greater than one and $n - 1$ of the points of the orbit have values less than $X^\#$, and for the stability of its orbit. This is the an extension of the "easy" part of the calculation for the period-2 point presented above.

Theorem 8. *If $1 < Q_0 < n/(n - 1)$ and $\kappa > \kappa^b$ where $e^{\kappa^b(Q_0 - 1)}$ solves*

$$e^{\kappa(Q_0 - 1)(n - (n - 2)Q_0)/Q_0} = 2e^{\kappa(Q_0 - 1)} - 1$$

there exists a period-n point, $X^{n*} = \phi^n(X^{n*})$, with $X^{n*} < \phi(X^{n*}) < \ldots < \phi^{n-1}(X^{n*})$ and $\phi^{n-2}(X^{n*}) < X^\# < \phi^{n-1}(X^{n*})$. The orbit of the periodic point is stable when

$$\kappa < \kappa_n = \frac{Q_0}{(Q_0 - 1)(n - (n - 1)Q_0)} \log \frac{Q_0}{2 - Q_0}$$

and unstable when $\kappa > \kappa_n$.

Proof. The periodic point is found to be

$$X^{n*} = \frac{\kappa(Q_0 - 1)}{e^{\kappa n(Q_0 - 1)/Q_0} - e^{\kappa(n-1)(Q_0 - 1)}}$$

which satisfies the specified bounds for the specified ranges of parameters. Now suppose that $X < \phi(X) < \phi^2(X) < \ldots < \phi^{n-1}(X)$ and $\phi^{n-2}(X) < X^{\#} < \phi^{n-1}(X)$. For values of X satisfying these constraints

$$\phi^n(X) = X e^{\kappa(n-1)(Q_0 - 1) - \kappa} \left(1 + \frac{\kappa(Q_0 - 1)}{X e^{\kappa(n-1)(Q_0 - 1)}} \right)^{Q_0/(Q_0 - 1)}$$

and

$$(\phi^n)'(X) = \left(\frac{X e^{\kappa(n-1)(Q_0 - 1)} - \kappa}{X e^{\kappa(n-1)(Q_0 - 1)} + \kappa(Q_0 - 1)} \right) \frac{\phi^n(X)}{X}$$

By direct substitution

$$(\phi^n)'(X^{n*}) = \frac{Q_0 e^{\kappa(Q_0 - 1)/((n-1)Q_0 - n)Q_0} - 1}{Q_0 - 1}$$

The function $(\phi^n)'(X^{n*})$ is analytic and strictly decreasing in κ for $Q_0 < n/(n - 1)$. When $\kappa = 0$, $(\phi^n)'(X^{n*}) = 1$, and when $\kappa = \kappa_n$, $(\phi^n)'(X^{n*}) = -1$. Hence the orbit of the period-n point $X = X^{n*}$ is stable when $\kappa < \kappa_n$ and unstable when $\kappa > \kappa_n$. $\qquad\square$

In particular, we have

Remark 9. A period-3 point is

$$X^{3*} = \frac{\kappa(Q_0 - 1) e^{-2\kappa(Q_0 - 1)}}{e^{\kappa(Q_0 - 1)(3 - 2Q_0)/Q_0} - 1}$$

which exists for $1 < Q_0 < \frac{3}{2}$ and $\kappa > \kappa^{b}$ where $e^{\kappa^{b}(Q_0 - 1)}$ solves

$$e^{\kappa(Q_0 - 1)(3 - Q_0)/Q_0} = 2e^{\kappa(Q_0 - 1)} - 1 \ .$$

Its orbit is stable for

$$\kappa < \kappa_3 = \frac{Q_0}{(Q_0 - 1)(3 - 2Q_0)} \log \frac{Q_0}{2 - Q_0}$$

4 Dynamics and control

The results obtained in the previous section are summarised in Fig. 2. It should be emphasised that we have only established sufficient conditions for solutions with period greater than two, and the system dynamics for parameter combinations outside the labelled regions in Fig. 2 have not been determined analytically. The parameter space has been explored numerically, for example:
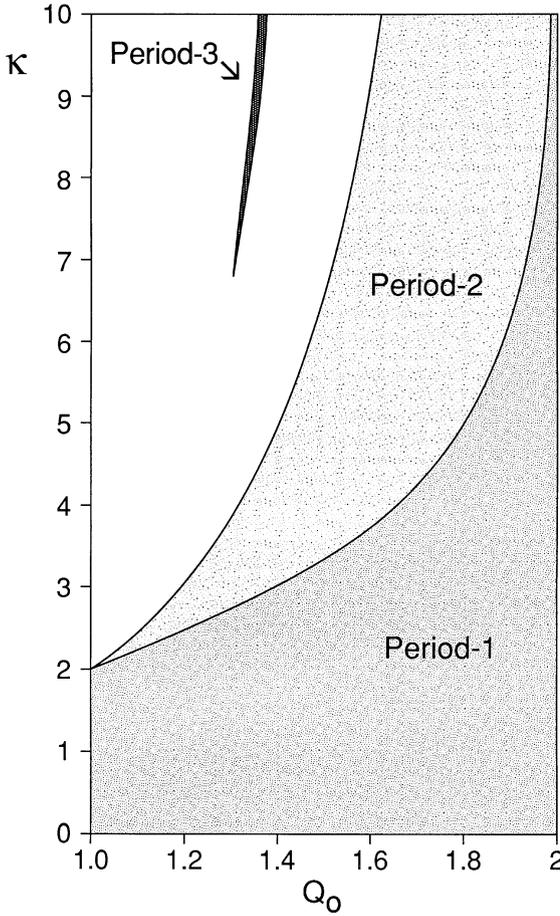
Fig. 2. Regions in the (Q_0, κ) plane for which stable fixed points, period-2 points and period-3 points of ϕ with stable orbits, and hence stable period-1, period-2 and period-3 solutions of the dynamical system with resetting, have been shown to exist

Remark 10. Numerical results (not shown) confirm that for $Q_0 = 1.35$ we have the following: when $\kappa = 1$, repeated iterations of $\phi(X)$ tend to $X^* = 1.183$; $\kappa_1 = 2.819$; $\kappa^{\#} = 2.949$; when $\kappa = 3$, iterations tend to the orbit $X^{2*} = 0.558$, $\phi(X^{2*}) = 1.596$; $\kappa_2 = 4.337$; when $\kappa = 5$, iterations tend to an irregular pattern; $\kappa^{b} = 8.590$ (when $n = 3$); when $\kappa = 9$, iterations tend to the orbit $X^{3*} = 0.006$, $\phi(X^{3*}) = 0.133$, $\phi^2(X^{3*}) = 3.108$; $\kappa_3 = 9.397$; and when $\kappa = 12$, iterations tend to an irregular pattern.

In Fig. 3 a "bifurcation diagram" is presented with $Q_0 = 1.35$ and distinguished parameter κ. Figure 3 was constructed by taking as an initial condition $X = 1.1X^*$, to avoid the fixed point, then iterating the map $\phi(X)$ 960
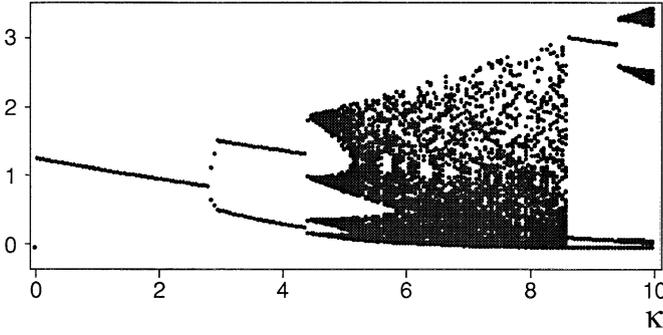
Fig. 3. Bifurcation diagram against κ for $Q_0 = 1.35$

times. Results of the last 80 iterations are plotted for values of κ from 0 to 10, in increments of 0.05.

The objective of an eradication strategy is to reduce Q_0 below one, but control strategies may combine reduction of Q_0 with an increase in κ. As the
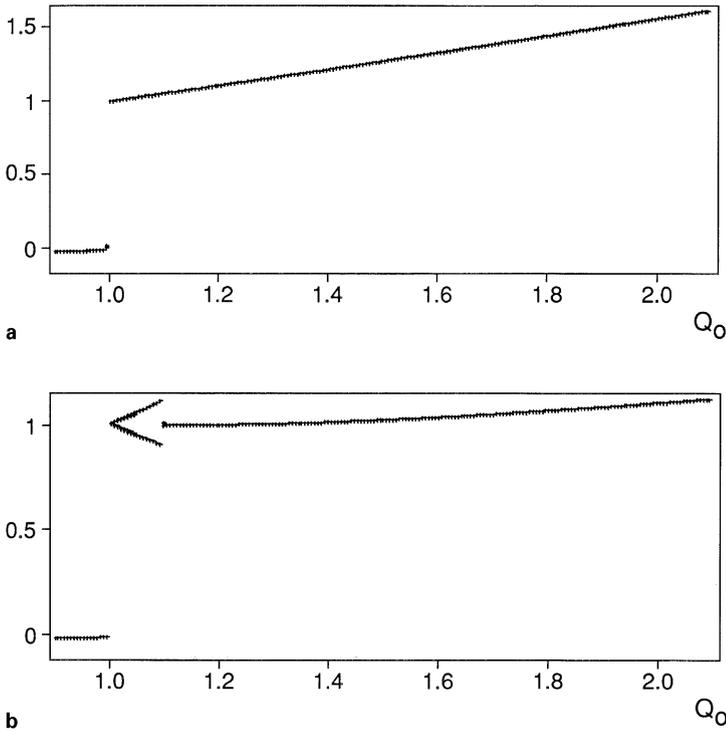

a

b

Fig. 4a–e. Bifurcation diagram against Q_0 for **a** $\kappa = 1$, **b** $\kappa = 2.2$, **c** $\kappa = 3$, **d** $\kappa = 5$ and **e** $\kappa = 9$
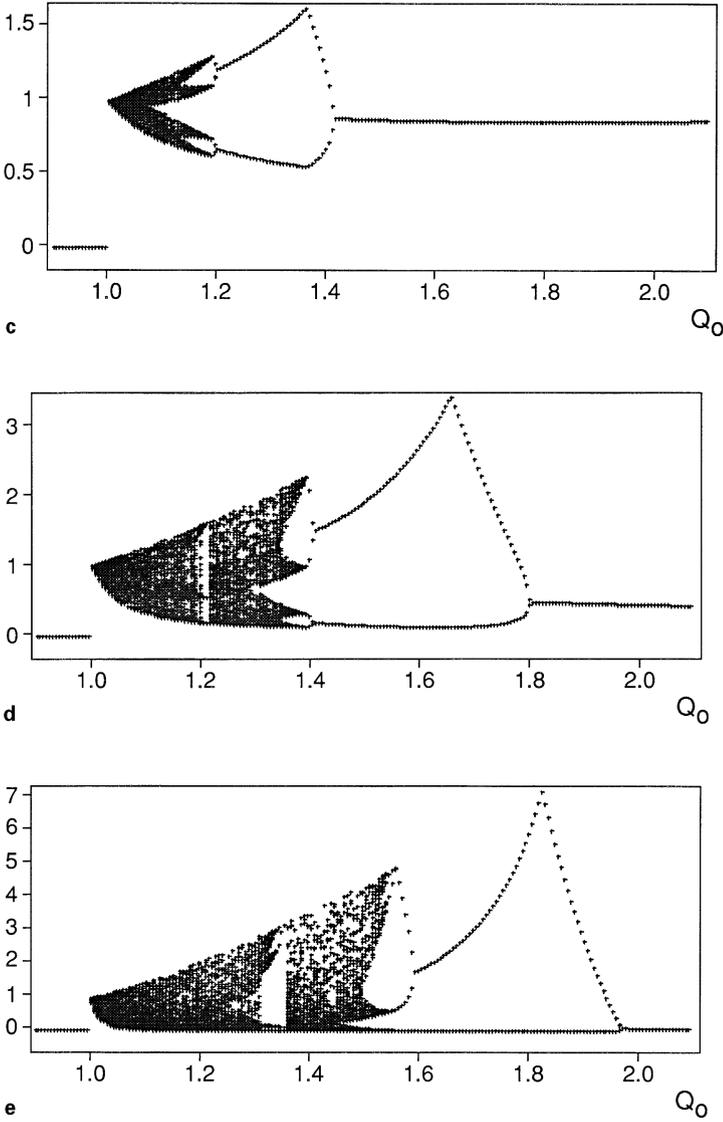
c

d

e

Fig. 4. Continued

fixed point of ϕ is globally stable for $Q_0 > 2$, one effect of a control strategy could be to change the dynamics of the discrete system to a periodic or aperiodic orbit. This is illustrated by the series of bifurcation diagrams presented in Fig. 4, that show how the long-term dynamics respond to changes in Q_0 for fixed values of κ. Figures 4 were constructed using the same method as Fig. 3, except that values of Q_0 were taken from 0.9 to 2.1, in increments of 0.006. In Fig. 4a some spurious points are visible near $Q_0 = 1$,

demonstrating that the iteration was slow to converge for a limited range of parameter values.

5 Discussion

We have shown that a simple prototype model for the dynamics of parasites of farmed animals can exhibit complicated dynamics, and that control interventions could change the qualitative nature of the dynamics, for example by destabilising a between-year equilibrium to induce periodic or aperiodic long-term behaviour. The practical implications of our work are immediate. If the population dynamics of parasites have remained constant on a year to year basis, and then control measures are introduced, the observation that parasite abundance decreases in the following year is not sufficient to conclude that it will continue to decrease. Figure 2 shows that for the majority of that region of parameter space for which $\kappa > 2$ and $1 < Q_0 < 2$ the fixed point of ϕ, and hence the period-1 solution of the dynamical system with resetting, is unstable, and in the long term the solution would tend to a more complicated attractor. On the farm this could translate to an apparently random sequence of observed annual parasite levels. If these are always less than those in pre-control years then the control programme could be regarded as successful, but the complicated nature of the orbits does not guarantee this.

The model that we have discussed is the limit of many other models for nematode parasites of ruminants, being the limit as selected parameters tend to zero or infinity. Hence our results should also hold for these models, although the complicated behaviour could occur at biologically unrealistic parameter values. The approximation $\sigma \to 0$ may be justified when the rate at which acquired immunity is lost is small in comparison to typical rates of parasite dynamics (see Roberts and Grenfell, 1991; Roberts and Heesterbeek, 1995, where $\sigma = 0.01$ was assumed). Typically the immunity of animals tends to increase with their age, and animals that are constantly exposed to parasites will retain their immunity. An experiment to measure σ would have to be conducted in parasite-free conditions. Similarly, it would be difficult to measure the precise form of the function $Q(z)$; a step function is the simplest assumption and one that makes the equations tractable.

The assumption $v \gg \kappa$ introduced in Sect. 2, and used to simplify the model to a two-dimensional problem, is less general. This implies that the life-span of parasites within the host is short in comparison with that of the free-living stages on the pasture. This will be true in temperate climates, but less applicable in hot and dry climates, and will vary between epidemic situations (Smith and Grenfell, 1994). In making this approximation, we constrain the within-host parasite population to "track" the parasites on the pasture. Hence, the statement in Remark 1 that t_1 is the time at which the parasite population reaches its peak is true for both the parasite population on the pasture, and the adult population within the host. Similarly, $x(t_1)$ and $z(1)$ represent the maximum and mean (over year) population density of either

larvae or adult parasites to within a multiplicative constant. The constant ratio between the sizes of the two parasite sub-populations cannot apply over all t, as we require $x(0) > 0$ but $y(0) = 0$. Hence, the two-dimensional model is nevertheless an approximation, and the original three-dimensional model must be analysed to confirm that its qualitative dynamics are similar to those presented in this paper.

It can be seen in Fig. 1 that the shape of the map $\phi(X)$, a linear increase to a cusp, followed by a decreasing curve is characteristic of many maps known to exhibit chaotic dynamics, for example the tent map (see Devaney, 1989). The existence of a region in parameter space where an orbit of period-3 exists is further confirmation of this. The bifurcation diagram (Fig. 3) may be regarded as a plot of iterates of ϕ taken up a vertical transect of the parameter space shown in Fig. 2, at $Q_0 = 1.35$. The period doubling route to chaos is clearly shown, with an interval around $\kappa = 9$ where the period-3 orbit is stable. The series of bifurcation diagrams against Q_0 shown in Fig. 4 may be regarded as plots of iterates of ϕ taken across a horizontal transect of Fig. 3. For $\kappa = 1$ the fixed point is stable for all $Q_0 > 1$. For increasing values of κ we then see an increasing region of instability from $Q_0 = 1$, followed by a stable orbit of period-2, then finally a stable fixed point for some $Q_0 < 2$.

The complicated dynamics generated by our simple model demonstrates the need for a more detailed model of parasite dynamics, and in particular for better mathematical descriptions of the immune response to parasites. However, the results from our model show that short-term field observations may not necessarily translate to correct long-term descriptions of parasite epidemiology. In the future, improved models of host-parasite interactions will lead to better descriptions of the epidemiology and control of parasites of farmed animals.

6 Appendix

In this appendix we prove the existence of a period-2 point of the map $\phi(X)$ when $\kappa > \kappa_1$ (see Theorem 6), the stability of its orbit when $\kappa \in (\kappa_1, \kappa_2)$, and its instability when $\kappa > \kappa_2$ (see Theorem 7).

A period-2 solution of equation (4), with $Q(z)$ defined by a step function and the re-setting condition on z, exists if and only if the mapping $\phi^2(X)$ has a strictly positive fixed point. The expression for $\phi^2(X)$ takes one of three explicit forms, depending on which sub-interval of $(0, \infty)$ contains X.

First, if $0 < X < X^{\#}e^{-\kappa(Q_0 - 1)}$ then both $X < X^{\#}$ and $\phi(X) < X^{\#}$, and we have

$$\phi^2(X) = Xe^{2\kappa(Q_0 - 1)}$$

For X in this interval, $\phi^2(X) > X$, hence no fixed point of $\phi^2(X)$ can exist.

If $X^{\#}\mathrm{e}^{-\kappa(Q_0-1)} < X < X^{\#}$ then $X < X^{\#} < \phi(X)$,

$$\phi^2(X) = X\mathrm{e}^{\kappa(Q_0-2)}\left(1 + \frac{\kappa(Q_0-1)}{X\mathrm{e}^{\kappa(Q_0-1)}}\right)^{Q_0/(Q_0-1)}$$

and we have already demonstrated that a fixed point exits when $\kappa \in (\kappa^{\#}, \kappa_2)$ (see equation (9)). The value $\kappa = \kappa^{\#}$ is obtained by solving the equation $\phi^2(X^{\#}) = X^{\#}$, and in Lemma 11 below we show that $\kappa^{\#} \in (\kappa_1, \kappa_2)$.

If $X > X^{\#}$ then

$$\phi^2(X) = X\mathrm{e}^{-2\kappa}\left(1 + \frac{\kappa(Q_0-1)}{X}\left(1 + \mathrm{e}^\kappa\left(1 + \frac{\kappa(Q_0-1)}{X}\right)^{-1/(Q_0-1)}\right)\right)^{Q_0/(Q_0-1)}$$

(10)

To complete the proof of Theorem 6 we need to demonstrate that ϕ^2 as defined by equation (10) has a unique fixed point $X^{2*} \in (X^{\#}, X^*)$ when $\kappa \in (\kappa_1, \kappa^{\#})$. But first we need to prove:

Lemma 11. *If $1 < Q_0 < 2$ then there exists a unique strictly positive value, $\kappa = \kappa^{\#}$ that solves*

$$\mathrm{e}^{2\kappa(Q_0-1)/Q_0} = 2\mathrm{e}^{\kappa(Q_0-1)} - 1 \tag{11}$$

and $\kappa_1 < \kappa^{\#} < \kappa_2$.

Proof. Define the function $\psi(\xi) = \xi^{2/Q_0} - 2\xi + 1$. This has two roots, $\xi = 1$ and $\xi = \xi^{\#} > 1$. If $\xi \in (1, \xi^{\#})$ then $\xi^{2/Q_0} < 2\xi - 1$, and if $\xi > \xi^{\#}$ then $\xi^{2/Q_0} > 2\xi - 1$. Equation (11) has the solution $\kappa^{\#} = \log \xi^{\#}/(Q_0 - 1)$. Let $\eta = Q_0/(2 - Q_0)$, hence $Q_0 \in (1, 2) \Rightarrow \eta \in (1, \infty)$. Now $\mathrm{e}^{\kappa_1(Q_0-1)} = \eta^{Q_0}$ and $\kappa_1 < \kappa^{\#}$ if and only if

$$\eta^2 < 2\eta^{2\eta/(1+\eta)} - 1 \tag{12}$$

for all $\eta > 1$. Note that we would have equality in (12) for $\eta = 1$. Differentiating the right hand side of (12) with respect to η, then dividing by 2η (the derivative of the left hand side), we see that (12) is true if

$$\theta(\eta) = \frac{2}{1+\eta}\eta^{(\eta-1)/(\eta+1)}\left(1 + \frac{\log \eta}{1+\eta}\right) > 1$$

for all $\eta > 1$. But $\theta(1) = 1$ and

$$\frac{d\theta}{d\eta} = 2\eta^{-2/(1+\eta)}\frac{2\eta \log \eta + \eta^2 - 1}{(1+\eta)^4}\log \eta > 0$$

hence $\kappa_1 < \kappa^{\#}$. To prove that $\kappa^{\#} < \kappa_2$ note that $\mathrm{e}^{\kappa_2(Q_0-1)} = \eta^\eta$, and we need to prove that $\eta^{1+\eta} - 2\eta^\eta + 1 > 0$ for $\eta > 1$. We would have equality for $\eta = 1$. Differentiating the left hand side of the inequality with respect to η we obtain $\eta^\eta(\eta \log \eta + \eta - 2\log \eta - 1)$. The expression in parentheses equals zero when $\eta = 1$, and has derivative $\log \eta + 2 - \frac{2}{\eta}$ which is positive for $\eta > 1$. Hence $\kappa^{\#} < \kappa_2$, and the proof of the lemma is complete. $\square$

6.1 Proof of Theorem 6

We proceed by showing that for $\kappa_1 < \kappa < \kappa^\#$ a period-2 pointof ϕ, $X = X^{2*}$, exists, with $X^\# < X^{2*} < X^*$, and then refer to equation (9) for the existence of a period-2 point with $X^{2*} < X^\#$ when $\kappa > \kappa^\#$.

Now assume $X^\# < X < X^*$. If $\phi^2(X) = X$ then $F(X) = 0$, where

$$F(X) = 1 + e^\kappa \left(1 + \frac{\kappa(Q_0 - 1)}{X} \right)^{-1/(Q_0 - 1)} - \frac{e^{2\kappa(Q_0 - 1)/Q_0} - 1}{\kappa(Q_0 - 1)} X \qquad (13)$$

Note that $F(X^*) = 0$. Differentiating equation (13) with respect to X we obtain

$$\frac{dF}{dX} = \frac{\kappa e^\kappa}{X^2} \left(1 + \frac{\kappa(Q_0 - 1)}{X} \right)^{-Q_0/(Q_0 - 1)} - \frac{e^{2\kappa(Q_0 - 1)/Q_0} - 1}{\kappa(Q_0 - 1)}$$

and substituting $X = X^*$

$$\left. \frac{dF}{dX} \right|_{X = X*} = \frac{2 - Q_0}{\kappa(Q_0 - 1)} \left(e^{\kappa(Q_0 - 1)/Q_0} - \frac{Q_0}{2 - Q_0} \right)$$

which is positive if $\kappa > \kappa_1$. The second derivative of equation (13) is

$$\frac{d^2 F}{dX^2} = \frac{\kappa e^\kappa (\kappa(2 - Q_0) - 2X)}{X^4} \left(1 + \frac{\kappa(Q_0 - 1)}{X} \right)^{-(2Q_0 - 1)/(Q_0 - 1)}$$

which has only one zero for X strictly positive. Hence $F(X)$ can have at most three positive roots. As $F(X)$ is increasing when $X = X^*$, there exists a root in the interval $(X^\#, X^*)$ if $F(X^\#) > 0$. This is established by substituting $X = X^\#$ directly into (13) to obtain

$$F(X^\#) = - \frac{e^{2\kappa(Q_0 - 1)/Q_0} - 2e^{\kappa(Q_0 - 1)} + 1}{e^{\kappa(Q_0 - 1)} - 1}$$

which is positive for $\kappa < \kappa^\#$ (see the proof of Lemma 11). As $\lim_{X \to \infty} F(X) = -\infty$, a third root of $F(X)$ is contained in the region (X^*, ∞). Hence, the condition $\kappa_1 < \kappa < \kappa^\#$ is sufficient for the existence of a unique period-2 point, $X^{2*} = \phi^2(X^{2*}) \in (X^\#, X^*)$ with $\phi(X^{2*}) > X^*$. Combining this result with that presented in equation (9), and the observation that $\phi^2(X^\#) = X^\#$ when $\kappa = \kappa^\#$, the existence of a unique period-2 point whenever $\kappa > \kappa_1$ is established. $\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\square$

6.2 Proof of Theorem 7

In order to establish the stability of the orbit of the period-2 point for $\kappa \in (\kappa_1, \kappa_2)$, we need to show that $|(\phi^2)'(X^{2*})| < 1$. In proving Theorem 6 we showed that the period-2 point $X = X^{2*}$ exists for $\kappa > \kappa_1$, and that the explicit formula for $\phi^2(X)$ is different on the intervals $\kappa \in (\kappa_1, \kappa^\#)$ and $\kappa > \kappa^\#$.

Consider first the period-2 point when $\kappa_1 < \kappa < \kappa^{\#}$, for which $X^{\#} < X^{2*} < X^*$. Using equation (7) we have

$$(\phi^2)'(X) = \frac{\phi^2(X)}{X} \frac{\phi(X) - \kappa}{\phi(X) + \kappa(Q_0 - 1)} \cdot \frac{X - \kappa}{X + \kappa(Q_0 - 1)} \tag{14}$$

and

$$\phi'(X^*) = \frac{X^* - \kappa}{X^* + \kappa(Q_0 - 1)}$$

For $\kappa > \kappa_1$, $\phi'(X^*) < -1$, (see the proof of Theorem 4), hence $(\phi^2)'(X^*) = (\phi'(X^*))^2 > 1$. From the proof of Theorem 6, the function $\phi^2(X) - X$ has three roots, $X^{2*} < X^* < \phi(X^{2*})$, hence we must have $(\phi^2)'(X^{2*}) < 1$ (see Fig. 1). As $\phi'(X^*)$ is negative, $X^* < \kappa$, and hence $\phi'(X) < 0$ for $X \in (X^{\#}, X^*)$. It then follows that $\phi(X) < \phi(X^{\#})$ for $X \in (X^{\#}, X^*)$, but

$$\phi(X^{\#}) = \frac{\kappa(Q_0 - 1)\,e^{\kappa(Q_0 - 1)}}{e^{\kappa(Q_0 - 1)} - 1} < \kappa$$

which immediately gives us $X^{2*} < \phi(X^{2*}) < \kappa$ and $(\phi^2)'(X^{2*}) > 0$ by equation (14). Hence we have established that when $\kappa_1 < \kappa < \kappa^{\#}$, $0 < (\phi^2)'(X^{2*}) < 1$.

Now assume that $\kappa > \kappa^{\#}$, hence $X^{2*} < X^{\#}$ (see equation (9)). For $X < X^{\#}$,

$$\phi^2(X) = X e^{\kappa(Q_0 - 2)} \left(1 + \frac{\kappa(Q_0 - 1)}{X e^{\kappa(Q_0 - 1)}} \right)^{Q_0/(Q_0 - 1)}$$

Differentiating with respect to X, and then substituting $X = X^{2*}$ from equation (9)

$$(\phi^2)'(X^{2*}) = \frac{Q_0 e^{\kappa(Q_0 - 1)(Q_0 - 2)/Q_0} - 1}{Q_0 - 1}$$

The function $(\phi^2)'(X^{2*})$ is analytic and strictly decreasing in κ. When $\kappa = 0$, $(\phi^2)'(X^{2*}) = 1$, and when $\kappa = \kappa_2$, $(\phi^2)'(X^{2*}) = -1$. Hence the orbit of the period-2 point is stable when $\kappa < \kappa_2$, and unstable when $\kappa > \kappa_2$. $\qquad \square$

References

1. Devaney, R. L. (1989) An introduction to chaotic dynamical systems. 2nd ed. Reading Massachusetts: Addison-Wesley
2. Heesterbeek, J. A. P. and Roberts, M. G. (1995) Threshold quantities for helminth infections. Journal of Mathematical Biology 33: 415–434

3. Roberts, M. G. and Grenfell, B. T. (1991) The population dynamics of nematode infections of ruminants: Periodic perturbations as a model for management. IMA Journal of Mathematics Applied in Medicine and Biology 8: 83–93
4. Roberts, M. G. and Heesterbeek, J. A. P. (1995) The dynamics of nematode infections of farmed ruminants. Parasitology 110: 493–502
5. Roberts, M. G. (1995) A pocket guide to host-parasite models. Parasitology Today 11: 172–177
6. Smith, G. and Grenfell, B. T. (1994) Modelling of parasite populations: gastrointestinal nematode models. Veterinary Parasitology 54: 127–143
7. Vlassoff, A. (1973) The seasonal incidence of infective trichostrongyle larvae on pasture grazed by lambs. New Zealand Journal of Experimental Agriculture 1: 293–301
8. Woolhouse, M. E. J. (1992) A theoretical framework for the immunoepidemiology of helminth infection. Parasite Immunology 14: 563–578