Models for regional heartwater epidemiology in a variable environment

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ABSTRACT

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A model of the epidemic dynamics of heartwater within a cattle production unit was presented by Yonow *et al.* (1998). Here, the model is expanded to a region consisting of several farms to study the effect of environmental variability on control strategies. We have shown that:

- In a region, where the environment of each farm is modelled with constant epidemiologic parameter values, while the between-farm parameter values differ, regional variation in the removal rate of infected cattle increases the average fraction of infected cattle across the region, while regional variation in the transmission rate of infection from ticks to cattle decreases the average fraction of infected cattle, thereby requiring control measures that keep the removal rate uniform and the transmission rate variable.
- In a region, where in addition to regional variation between farms, the epidemiologic parameters of each farm are time-variant, then temporal variation in both the transmission rate and removal rate increases the average fraction of infected cattle across the region, thereby requiring control measures that keep both parameters uniform.

Keywords: Concave, convex, heartwater, time averaging, time-variant, variable environment

INTRODUCTION

Yonow, Brewster, Allen & Meltzer (1998) presented a model for the determination of the epidemiology of heartwater within a cattle production unit and found the equilibrium values for the fraction of cattle infected and fraction of infected ticks. However, when the scope of the study is expanded from an individual farm to a region consisting of several farms, a range of conditions on the parameters has to be included. It will be shown that parameter variation affects the epidemiology, the estimates of transmission and acquisition rates, as well as the strategy for control.

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The model used by Yonow *et al.* (1998) is a non-linear system of two ordinary differential equations, describing the dynamic interaction between the cattle and ticks in a farm. The system is adapted from the original equations developed by Ross (1911) and Macdonald (1957) to study the epidemiology of malaria.

$$\frac{dx}{dt} = Cy(1-x) - rx \qquad (1)$$

$$\frac{dy}{dt} = Ax(1-y) - \mu y \qquad (2)$$

where x is the fraction of cattle infected;
y is the fraction of ticks infected;
C is the transmission rate from ticks to cattle;
A is the acquisition rate by ticks from cattle;
r is the rate of removal of infected cattle by death or culling; and
μ is the death rate of ticks.

It is further assumed that all the system parameters are constant. At the steady state, when $\frac{dx}{dt} = \frac{dy}{dt} = 0,$ we can solve for the equilibrium values of x and y to get:

$$x^* = \frac{AC - \mu r}{A(C + r)} \quad (3)$$

$$y^* = \frac{AC - \mu r}{C(A + \mu)} \quad (4)$$

Here x^* and y^* represent the equilibrium values of x and y, respectively. However, when one moves from an individual farm to a region consisting of different farms, then under this "spatial" variability, although the parameter values may be constant in each separate farm, in principle they vary from farm to farm. This inherent variability can be further complicated by making the system parameters time-dependent in each farm so that the environment of a farm is no longer driven by constant parameter values. Therefore under spatial variability of a region, in section 2, we consider the situation when parameters are constant in each farm but vary across the farms in a region; then in section 3, we remove the constancy assumption and instead assume that some or all of the system parameters are time-variant in each farm so that a farm is now taken to be a variable environment. Furthermore, in each section we make diagnostic use of the results and interpret them as effective control strategies.

SPATIAL VARIATION

Suppose that the system of equations 1–2 holds for each separate farm, but the parameter values vary from farm to farm. Then the regional value of each parameter is obtained by averaging across a sample of farms. However, if a variable is a *non-linear* function of some parameter, then the average of the function is not the same as the function evaluated at the average value of the parameter. This crucial observation is the key to making inferences about devising effective control strategies.

Consider x^* as a function of the removal rate r. Clearly x^* is a non-linear, concave, function of r, as can be detected from Fig. 1 and equation 3. Therefore, if r varies around some average value $\bar{r}$, then x^* increases faster for $r < \bar{r}$ than when it decreases for $r > \bar{r}$ (cf. Fig. 1). Hence on average x^* increases in the region if r varies from farm to farm; the concavity of the curve results in the average fraction of infected cattle being greater than the fraction infected at the average value $\bar{r}$. Therefore, when r varies, for a given level of tick infection, we observe more cattle being infected than would be expected. But if the average regional fraction of infected cattle is falsely assumed to be the fraction of infected cattle at the

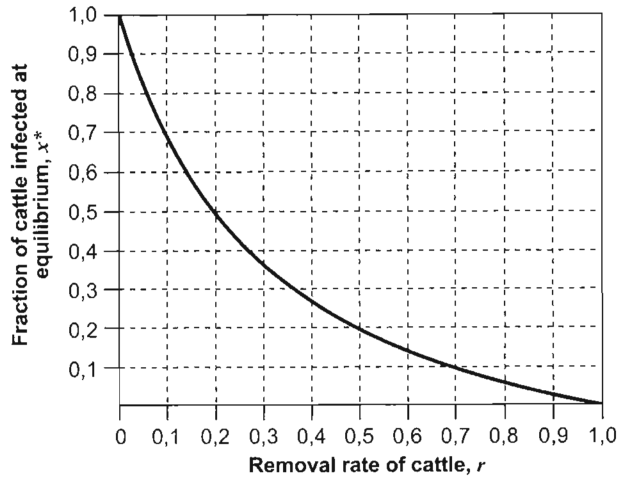

FIG. 1 Fraction of cattle infected at equilibrium x^*, as a function of the removal rate of infected cattle r, where $0 \leq r \leq 1$. The concavity of the curve results in the average fraction of infected cattle being greater than the fraction infected at average value $\bar{r}$. The constants of the system are: A = 0,25; C = 0,32; and μ = 0,08

average value $\bar{r}$, then observing a greater fraction of infected cattle may result in overestimating the transmission rate of the disease. On the other hand, y^* is a linear function of r (cf. equation 4), and its average value over the region is not affected by variation in r.

This implies that an effective control strategy should aim at increasing the average value r in the region, but at the same time reducing the variance of r from farm to farm. In other words, a program should begin with increasing r in the farms with the lowest r-values. Hence, improvement begins with the worst off.

Similarly, since x^* is a linear function of the death rate of ticks μ, if there is variation in μ from farm to farm, this will not affect the average level of infected cattle. However, since y^* is a non-linear, concave, function of μ (cf. equation 4), variation in μ will increase the regional average fraction of infected ticks. But if the average regional fraction of infected ticks is falsely assumed to be the fraction of infected ticks at the average value μ, then this would result in underestimating the ticks' vectorial capacity.

Suppose now that the contagion rate C varies across a region. Since y is the fraction of the tick population infected, C depends on the absolute number of ticks so that Cy measures the vulnerability of cattle to infection. C may vary if the absolute size of the tick population varies or if the rate of successful transmission per tick bite varies. Now x^* is a convex function of $\bar{C}$, as can be detected from Fig. 2 and equation 3. Therefore, if C varies around some average value $\bar{C}$, then x^* decreases faster for $C < \bar{C}$ than when it increases for $C > \bar{C}$ (cf. Fig. 2). Thus the variation in C is beneficial: it reduces the average fraction of cattle infected and therefore leads to underestimates

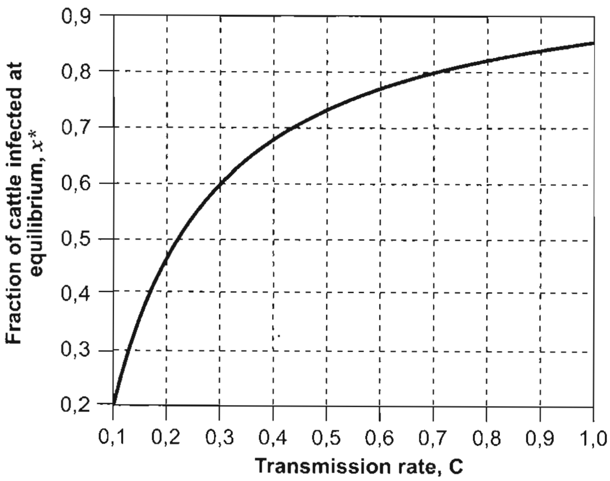

FIG. 2 Fraction of cattle infected at equilibrium x^*, as a function of the transmission rate C, where $0{,}1 \leq C \leq 0{,}86$. The convexity of the curve results in the average fraction of infected cattle being smaller than the fraction infected at average value $\bar{C}$. Here C depends both on the absolute population size of ticks and the probability of successful transmission per tick bite. Any resistance among the cattle will reduce C. The constants of the system are: $A = 0{,}2$; $r = 0{,}1$; and $\mu = 0{,}12$

of vectorial capacity. The convexity of the curve results in the average fraction of infected cattle being smaller than the fraction infected at the average value $\bar{C}$. Therefore in order to reduce the regional average fraction of cattle infected, a reduction in the tick population is desired, but beginning with those farms in which the tick populations are already low. In other words, this strategy starts improvement with the best off.

Finally, since C depends on the tick population it will vary with the rate of fecundity as well as that of mortality of ticks. Let f denote the rate of fecundity of ticks. Suppose further that C is a decreasing function of mortality, e.g. $C = \frac{f}{\mu}$. Then x^* will be a nonlinear, concave, function of tick mortality μ, and therefore the greatest improvement will come about by increasing the tick mortality where it is the lowest, i.e. improvement from below.

SPATIAL AND TEMPORAL VARIATION

Suppose now that some or all of the system parameters are time-variant for each farm. In a varying environment the derivatives of x and y average to zero in the long run. This property is used in the method of "time averaging", developed by Puccia & Levins (1985), to derive explicit solutions for the average values of the variables under study in order to learn about the existing correlations between different variables and the time varying parameters. Divide equation 2 by 1 to get:

$$\frac{dy}{dt(1-y)} = Ax - \frac{\mu y}{1-y} \quad (5)$$

The left hand side of equation 5 is the derivative of $-\log(1-y)$, and therefore has an average value of zero (see Puccia & Levins 1985). Take expected value from both sides of equation 5 to get:

$$\mathrm{E}\{x\} = \frac{\mu}{A}\mathrm{E}\frac{y}{\{1-y\}} \quad (6)$$

where E stands for expected or average value. Clearly, $\mathrm{E}\{x\}$ is a concave function of y. Therefore, $\mathrm{E}\{x\}$ is increased by any environmental variation that causes y to vary. Suppose now that A and μ are constant but there is temporal variation in r or C. Then, in order to reduce $\mathrm{E}\{x\}$, we need to make r or C more uniform. C depends on the total tick population and will vary seasonally; therefore control measures should be focused on the season of greatest population. The removal rate r is more accessible: the screening for sick or infected animals should be done uniformly throughout the year.

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