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**Development of a stage-structured analytical population model
for strategic decision making:
the case of ticks and tick-borne diseases (**)**

dedicated to the memory of Giulio Di Cola

1 - Introduction

In integrated pest control, mathematical models are often used for tactical decision making, for example, whether to apply a pest control method on a population defined in time and space. A second class of models are those developed for strategic decision making such as the evaluation of control strategies or planning and priority setting in research programmes. These models make predictions in an analytical and qualitative way. There are infact two secondary branches emerging from the analytical limb of the modelling tree (Getz and Gutierrez 1982). The first of these branches contains those models designed to explore various population processes such as density-dependent interactions in prey-predator and host-

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parasite systems (Beddington *et al.* 1975, May 1973), the interaction of competing species and the many questions in epidemiology (Anderson and May 1991). The second of these branches contains those models designed to directly address management type questions such as optimal pesticide application schedules (Regev *et al.* 1983), optimal harvesting strategies (Regev and Rieder 1989, Regev *et al.* 1998). In our work we address both issues in relation to the management of vector-borne disease. The purpose of this paper is to develop an analytical model for strategic decision making and to show possible areas of application. We rely on a case study of a three-host tick (e.g. *Rhipicephalus appendiculatus* and *Amblyomma variegatum*) and the interactions with its hosts. It is a three-host tick because it attaches onto a host three times in its lifetime. First as a larva, then as a nymph and finally as an adult (Kettle 1990). The majority of hard ticks (Ixodidae) have this life cycle and are referred to as three-host ticks. The model is developed for this group first, because it can easily be adjusted for one- or two-host ticks and secondly, because these are the most abundant and widely distributed and economically important species of cattle disease vectors throughout east, central and southern Africa (Mukhebi and Perry, 1995). Biological details including the ecology and life cycle of the tick and applications of the model are discussed in detail in Mwambi *et al.* (2000). In sect. 2 the model is derived as a continuous time compartmental model. In sect. 3 a compact form of the characteristic polynomial of the system is obtained. In sect. 4 the interaction between wild hosts, cattle and the tick vector is introduced. Conditions on persistence and existence of the vector and its hosts are derived and analysed. Finally in sect. 5 we give concluding remarks where we discuss the implication of the model to a real field situation and to management strategies.

2 - The compartmental model

The population is structured according to n successive stages. Let the variable x_1, \dots, x_n denote the number of individuals in stages 1 to n . Let $p_i, i = 1, \dots, n-1$, be the rate of transition from stage i to stage $i+1$. Let f_n be the fecundity rate of the adult female stage. In each stage there is a net mortality rate $\mu_i, i = 1, \dots, n$. This includes losses due to natural mortality and losses due to transport by hosts into and out of the area of study. We first assume that the p_i are constant, later we let these quantities depend on host abundance and availability. The model is a cyclic chain model of n linear differential equations with constant

coefficients such that,

$$\begin{aligned}
 \dot{x}_1 &= f_n x_n - p_1 x_1 - \mu_1 x_1 \\
 \dot{x}_2 &= p_1 x_1 - p_2 x_2 - \mu_2 x_2 \\
 &\dots \\
 \dot{x}_i &= p_{i-1} x_{i-1} - p_i x_i - \mu_i x_i \\
 &\dots \\
 \dot{x}_{n-1} &= p_{n-2} x_{n-2} - p_{n-1} x_{n-1} - \mu_{n-1} x_{n-1} \\
 \dot{x}_n &= p_{n-1} x_{n-1} - \mu_n x_n
 \end{aligned}
 \tag{2.1}$$

where $\dot{x}_i = \partial x_i / \partial t$, $i = 1, \dots, n$. For a given system n will be known and the parameters in Eq. (2.1) given precise meaning.

In general system (2.1) can be written in matrix notation as

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \vdots \\ \dot{x}_{n-1} \\ \dot{x}_n \end{pmatrix} = \begin{pmatrix} -a_1 & 0 & 0 & \dots & 0 & f_n \\ p_1 & -a_2 & 0 & \dots & 0 & 0 \\ 0 & p_2 & -a_3 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & p_{n-1} & -p_n \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_{n-1} \\ x_n \end{pmatrix}
 \tag{2.2}$$

where $a_i = p_i + \mu_i$, $i = 1, 2, \dots, n - 1$. More compactly system (2.2) can be written as

$$\dot{\mathbf{x}} = A\mathbf{x}
 \tag{2.3}$$

where A is the $n \times n$ matrix in Eq. (2.2) and $\mathbf{x} = (x_1, \dots, x_n)^T$. For a small interval of time δ a discretized version of Eq. (2.3) is given by

$$\mathbf{x}_{t+1} = (I + \delta A) \mathbf{x}_t = L\mathbf{x}_t
 \tag{2.4}$$

where $L = I + \delta A$ is a discrete type Leslie matrix recently reviewed by Di Cola *et al.* (1998, 1999). The relationship between equations (2.3) and (2.4) has been discussed in detail in Mwambi (1997) in the context of the current study.

The matrix $A = (a_{ij})$ is of a type called essentially nonnegative and irreducible. Thus to this matrix the Perron-Frobenius theorem can be applied. The spectral bound of the matrix is a simple real root of its characteristic polynomial and all other eigenvalues have strictly smaller real parts. Corresponding to the spectral bound there is a positive eigenvector. There are no positive eigenvectors to any other eigenvalues. The spectral bound governs the stability of the zero solution of the differential equation. If the spectral bound is positive, the population will grow exponentially, and if it is negative it will decay.

3 - The characteristic polynomial

In general the characteristic polynomial can be obtained by expanding the determinant $|A - \lambda I|$. In the case of the matrix A in Eq. (2.3) the characteristic polynomial is best obtained from the corresponding linear system rather than by expanding determinants. Thus to obtain the polynomial from $A\mathbf{x} = \lambda\mathbf{x}$, we have to eliminate the x_i 's from the system of equations given below

$$\begin{aligned}
 \lambda x_1 &= f_n x_n - p_1 x_1 - \mu_1 x_1 \\
 \lambda x_2 &= p_1 x_1 - p_2 x_2 - \mu_2 x_2 \\
 &\dots\dots\dots \\
 \lambda x_i &= p_{i-1} x_{i-1} - p_i x_i - \mu_i x_i \\
 &\dots\dots\dots \\
 \lambda x_{n-1} &= p_{n-2} x_{n-2} - p_{n-1} x_{n-1} - \mu_{n-1} x_{n-1} \\
 \lambda x_n &= p_{n-1} x_{n-1} - \mu_n x_n.
 \end{aligned}
 \tag{3.1}$$

Starting from the last equation of system (3.1) and recursively eliminating the x_i 's from the system we finally get a compact form of the characteristic polynomial as

$$P(\lambda) = \prod_{i=1}^n (p_i + \mu_i + \lambda) - f_n \prod_{i=1}^{n-1} p_i
 \tag{3.2}$$

with $p_n = 0$ because n is the last stage in the life cycle.

Now consider any nonnegative matrix (a_{ij}) . Then the Perron Frobenius theorem (classical version) applies. In particular one can look at matrices of the Leslie type. Also one can consider the class of stochastic matrices and the class of stochastic companion matrices. These type of matrices have a characteristic poly-

mial of the type similar to a Cauchy polynomial. The eigenvalues lie in the disc $\{\lambda : |\lambda| \leq s_0\}$ and $\lambda = s_0$ is an eigenvalue. For a Cauchy polynomial $s_0 = 1$ and except 1, no positive number can be a root of the polynomial.

In the present case of matrices related to the continuous time evolution we have quite similar properties that have to be discussed. Two results about the system are stated without proof. The proofs are presented elsewhere in the appendix of Mwambi *et al.* (2000).

The first result states that the tick population will grow with exponent s_0 , which is the spectral bound of matrix A , if

$$(3.3) \quad f_n > \mu_n \prod_{i=1}^{n-1} \left(1 + \frac{\mu_i}{p_i} \right)$$

and s_0 is the unique zero of the characteristic polynomial in the interval $(-m, \infty)$ where m is a positive real number.

In biological terms inequality (3.3) says that the tick population persists if the fecundity rate exceeds the product on the right hand side. This product measures the mortalities against the average sojourn times in the corresponding compartments. The second result states that the spectral bound s_0 is a decreasing function of the mortalities; $\mu_i, i = 1, \dots, n$ and it is an increasing function of the transition rates p_i if $s_0 > -\mu_i$ for all i .

Thus, for an increasing tick population, increasing any p_i leads to an increase of s_0 . In biological terms, accelerating the development process increases the rate of exponential growth. The eigenvector of the matrix A corresponding to the eigenvalue s_0 describes the ‘persistent’ stage distribution at exponential growth (or decay). From Eq. (3.1) we find, by normalizing the adults to $x_n = 1$,

$$(3.4) \quad x_i = \prod_{j=i+1}^n (p_j + \mu_j + s_0) \left/ \prod_{j=i}^{n-1} p_j \right.$$

The persistent stage distribution is the stage distribution attained when the system reaches stability. Its distribution determines the future population structure and its growth rate is governed by the spectral bound s_0 of the matrix A in Eq. (2.2).

4 - Vector-host interaction model

Model (2.1) does not incorporate any factors that would limit population growth, in particular host abundance and availability. We introduce a variable y to describe the number of available natural animals and a quantity z that counts the

domestic animals (mainly cattle) serving as hosts for the ticks. We assume the quantity z is not a dynamic variable but a parameter, for the simple reason that cattle density will be controlled by actions not within the framework of the model. Hence $h = y + z$ is the total of available hosts. In our model the effect of reduced host densities implies a reduction of the transition rates. In other words there is a critical host density below which the vector population goes to extinction.

One could imagine that hosts avoid heavily tick infested areas. This would mean that if tick abundance goes up then host density goes down, in specific grazing areas. Thus we get a situation similar to a predator prey model. The host equation is therefore given by

$$(4.1) \quad \dot{y} = r - dy - \mathbf{c}^T \mathbf{x}y$$

where r is the inflow of the hosts into a given grazing area. The parameter d is the host mortality which is assumed to be constant and it does not depend on tick density and disease prevalence. The constant (row) vector $\mathbf{c}^T = (c_1, \dots, c_n)$ measures the effect on the host population by the different stages of the vector population present in the area. We assume $c_i \geq 0$ with $c_i > 0$ if i is a questing stage. The vector \mathbf{x} has the same meaning as before.

To develop a theoretical basis for the instantaneous host searching model we follow Gutierrez (1996). Let the variables X_i and h_a respectively denote the initial number of questing ticks in stage i and the number of hosts attacked during an infinitesimally small period of time dt . The parameter b denotes the physiological demand rate for hosts per tick during the small time period dt and the variable h the number of hosts. The variable A denotes a typical grazing area or in other words a possible search area for ticks. We assume the functional response model

$$(4.2) \quad \frac{\partial h_a}{\partial h} = f(X_i, h_a) = X_i A (X_i b - h_a).$$

The model indicates that $\partial h_a / \partial h$ declines as h_a approaches $X_i b$ (the tick vector is satiated). The area of search A , however should decrease as $X_i \rightarrow \infty$ because of increased competition for hosts. Thus

$$\frac{dA}{dX_i} = -\beta \frac{A}{X_i}$$

where β is the coefficient of competition. Integrating the above equation yields

$$(4.3) \quad A = sX_i^{-\beta}$$

with search coefficient s , which means that as $X_i \rightarrow \infty$ then $A \rightarrow 0$. Substituting (4.3) into (4.2) we get

$$\frac{\partial h_a}{\partial h} = sX_i^{1-\beta}(X_i b - h_a).$$

Then by separation of variables we solve for the proportion $q_i(h) = h_a/(X_i b)$ which gives the proportion of attaching ticks as

$$0 \leq q_i(h) = (1 - e^{-\left(\frac{a}{b}\right)X_i^{1-\beta}h}) \leq 1$$

where $s = a/b$. The case of $\beta = 2$ gives the case of intraspecific competition for hosts by questing ticks therefore

$$q_i(h) = (1 - e^{-\left(\frac{a}{b}\right)\frac{h}{X_i}}) = (1 - e^{-q_i h})$$

where $q_i = a/(bX_i)$. By expanding $e^{-q_i h}$ and assuming that X_i is large, we get $q_i(h) = q_i h$. A similar model has been used by Di Cola and collaborators (Buffoni *et al.*, 1995, 1997).

Host preference by ticks is not modelled at this stage. We denote the transition rates for the different stages in a unified form as $p_i + q_i h$. The new system of differential equations is now given by

$$\begin{aligned}
 \dot{x}_1 &= f_n x_n - (p_1 + hq_1) x_1 - \mu x_1 \\
 \dot{x}_2 &= (p_1 + hq_1) x_1 - (p_2 + hq_2) x_2 - \mu_2 x_2 \\
 &\dots\dots\dots \\
 \dot{x}_j &= (p_{j-1} + hq_{j-1}) x_{j-1} - (p_j + hq_j) x_j - \mu_j x_j \\
 &\dots\dots\dots \\
 \dot{x}_{n-1} &= (p_{n-2} + hq_{n-2}) x_{n-2} - (p_{n-1} + hq_{n-1}) x_{n-1} - \mu_{n-1} x_{n-1} \\
 \dot{x}_n &= (p_{n-1} + hq_{n-1}) x_{n-1} - \mu_n x_n \\
 \dot{y} &= r - dy - \mathbf{c}^T \mathbf{x}y .
 \end{aligned}
 \tag{4.5}$$

The system of equations (4.5) can be expressed in matrix notation as follows. First define the matrices

$$(4.6) \quad D = \begin{pmatrix} -1 & 0 & 0 & \cdots & 0 & 0 \\ 1 & -1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & 0 \end{pmatrix},$$

$$(4.7) \quad F = \begin{pmatrix} 0 & 0 & 0 & \cdots & f_n \\ 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 \end{pmatrix}.$$

We further define three diagonal matrices P , Q , and M given by

$$(4.8) \quad P = (p_i \delta_{ij}), \quad Q = (q_i \delta_{ij}), \quad M = (\mu_i \delta_{ij}).$$

Thus in matrix notation the system of equations (4.5) may be written as

$$(4.9) \quad \begin{aligned} \dot{\mathbf{x}} &= F\mathbf{x} + D(P + (y + z) Q)\mathbf{x} - M\mathbf{x} \\ \dot{y} &= r - dy - \mathbf{c}^T \mathbf{x} y. \end{aligned}$$

Putting

$$(4.10) \quad A = F + DP - M, \quad B = DQ,$$

this system assumes the form

$$(4.11) \quad \begin{aligned} \dot{\mathbf{x}} &= (A + (y + z) B) \mathbf{x} \\ \dot{y} &= r - dy - \mathbf{c}^T \mathbf{x} y. \end{aligned}$$

A two dimensional caricature when x is just one compartment and consequently A , B , C are constants is discussed in Mwambi *et al.* (2000). We go straight to the analysis of system (4.11) or the full model. Here one finds similar phenomena as in the caricature but in addition we are able to find expressions for the stage distribution of ticks as a function of the host density h .

Theorem 4.1. *There exists a threshold host density h_0 such that the tick population can persist on host population $h > h_0$ and cannot persist on host population of density $h < h_0$.*

Proof. At a stationary state (\bar{x}, \bar{y}) the following two equations must hold

$$(4.19) \quad \begin{aligned} \mathbf{0} &= (A + (y + z) B) \bar{\mathbf{x}} \\ 0 &= r - d\bar{y} - \bar{\mathbf{c}}^T \bar{\mathbf{x}} \bar{y}. \end{aligned}$$

For fixed $y + z$, the first equation is a homogeneous linear system for the vector \mathbf{x} . Thus a necessary condition for the existence of nonzero \mathbf{x} is that the determinant of the matrix $A + (y + z)B$ must vanish, that is

$$(4.20) \quad \det(A + (y + z) B) = 0$$

which can be expanded to give the linear system

$$(4.21) \quad \begin{aligned} 0 &= f_n x_n - (p_1 + hq_1) x_1 - \mu_1 x_1 \\ 0 &= (p_1 + hq_1) x_1 - (p_2 + hq_2) x_2 - \mu_2 x_2 \\ &\dots\dots\dots \\ 0 &= (p_{j-1} + hq_{j-1}) x_{j-1} - (p_j + hq_j) x_j - \mu_j x_j \\ &\dots\dots\dots \\ 0 &= (p_{n-2} + hq_{n-2}) x_{n-2} - (p_{n-1} + hq_{n-1}) x_{n-1} - \mu_{n-1} x_{n-1} \\ 0 &= (p_{n-1} + hq_{n-1}) x_{n-1} - \mu_n x_n. \end{aligned}$$

This system compares with system (3.1) with $\lambda = 0$ and p_i replaced by $p_i + hq_i$. Then from Eq. (3.2) one sees that the quantity h must be a zero of the polynomial

$$(4.22) \quad \tilde{P}(h) = \prod_{i=1}^n (p_i + hq_i + \mu_i) - f_n \prod_{i=1}^{n-1} (p_i + hq_i).$$

This polynomial can also be written in the form

$$(4.23) \quad \tilde{P}(h) = \mu_n \prod_{i \notin E} (p_i + \mu_i) \prod_{i \in E} (hq_i + \mu_i) - h^m f_n \prod_{i \notin E} p_i \prod_{i \in E} q_i$$

where $E \subset \{1, 2, \dots, n\}$ is the set of questing states and m the number of these

states. Now we define the quantity

$$(4.24) \quad R_0(h) = \frac{f_n}{\mu_n} \prod_{i \notin E} \frac{p_i}{p_i + \mu_i} \prod_{i \in E} \frac{hq_i}{hq_i + \mu_i},$$

which is the average number of ticks produced by one adult female tick in its life time. This number $R_0(h)$ is the basic reproduction number of the tick population on a host population of density h . We see that

$$(4.25) \quad R_0(\infty) = \frac{f_n}{\mu_n} \prod_{i \notin E} \frac{p_i}{p_i + \mu_i}.$$

If $R_0(\infty) > 1$ then the tick population can persist on sufficiently dense host populations. The critical host density is h_0 , where h_0 is the unique positive root of the equation $R_0(h) = 1$. Thus the tick population can persist on host populations with density $h > h_0$ and cannot persist on host populations with $h < h_0$ which completes the proof. Now at any nontrivial equilibrium we would have $R(h) = 1$, thus $h = h_0$. Then solving system (4.21) recursively for x_i gives the non-normalized tick distribution according to stage as

$$(4.26) \quad \bar{x}_i = x_n \prod_{j=i+1}^n (p_j + h_0 q_j + \mu_j) \left| \prod_{j=i}^{n-1} (p_j + h_0 q_j) \right|, \quad i = 1, \dots, n-1.$$

Furthermore the three populations of wildlife, cattle and ticks must satisfy

$$(4.27) \quad r - dy - \mathbf{c}^T \mathbf{x} y = 0 \quad \text{and} \quad y + z = h_0.$$

Case I: When $z > h_0$ then the equation $y + z = h_0$ cannot be satisfied with $y > 0$. In this case we have $R_0(z) > 1$. Thus, at the given level of domestic animals, the tick population can survive on cattle alone, the tick population grows exponentially, and the wild animals disappear. Factually, cattle breeding at this density (with the given transition rates) is impossible.

Case II: When $z < h_0$ then at equilibrium $y = \bar{y}$, where

$$\bar{y} = h_0 - z.$$

The tick population $\tilde{\mathbf{x}}$, at equilibrium is the solution to the equation

$$r - d\bar{y} = \mathbf{c}^T \tilde{\mathbf{x}}.$$

Hence there are again two cases.

Case IIa): $\bar{y} > r/d$ or $r < d\bar{y}$.

In this case

$$\bar{y} = h_0 - z > r/d .$$

Then $(z + r/d) < h_0$ and the tick population cannot survive on the joint wild and domestic animals.

Case IIb): $\bar{y} < r/d$ or $r > d\bar{y}$.

In this case

$$\bar{y} = h_0 - z < r/d .$$

Then $z + r/d > h_0$. Thus, due to the assumed possibility that wild animals avoid heavily tick infested areas, an equilibrium density of wild animals \bar{y} establishes itself. The cattle density is z , the density of wildlife animals is $\bar{y} = h_0 - z$ and the total population size of ticks is determined from

$$(4.28) \quad \mathbf{c}^T \mathbf{x} = \frac{r - d\bar{y}}{\bar{y}} .$$

The right hand side of Eq. (4.28) is positive, since $r/d > h_0 - z = \bar{y}$. A parameter plane for the full model is obtained by partitioning the (z, r) plane into three regions according to the three cases *I, IIa* and *IIb*.

5 - Concluding remarks

The analysis of the model shows that for the tick population to thrive, host abundance and distribution is crucial. The analysis shows that at low cattle density the threshold levels of wildlife becomes important for the tick population to be maintained while at high cattle densities this contribution is insignificant. The models developed thus far can be used to evaluate control measures acting on fecundity, mortality and developmental times. Moreover it has helped us to identify future research direction such as modelling host mortality and disease dynamics including spatial variation in the risk of infection (O'Callaghan *et al.* 1999). The paper demonstrates the capacity of an analytical model for guiding research activities including the evaluation of control options. Further, analytical models are an efficient tool to synthesize existing information and a basis for the development of models with wider areas of applications.

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- [13] DEVELOPMENT OF A STAGE-STRUCTURED ANALYTICAL POPULATION MODEL... 169
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Abstract

*Mathematical models are an important tool for understanding disease systems in general and as aids for designing control and management strategies both for vectors and vector-borne diseases. In this paper a model is derived for the interaction of the brown ear tick (*Rhipicephalus appendiculatus*) with its hosts. First a general model consisting of a system of differential equations with constant coefficients on a stage structured tick population with unlimited host density is presented. The model is then improved by incorporating host abundance and availability by means of a demand-driven, ratio-dependent functional response model. The improved model adequately represents the dynamics of a stage structured vector population under conditions of varying host density. The model efficiently synthesizes existing information allowing for a qualitative evaluation of several management strategies and the identification of gaps in the actual understanding of the system. The model is expected to guide future research work in the area.*
