

A Stochastic epidemic model for tick borne diseases: Initial stages of an outbreak and endemic levels

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A stochastic model describing the disease dynamics for a tick borne disease amongst cattle is developed. The spread of the disease at its initial stages is approximated by a three-type branching process assuming that the initial sub-populations of susceptible ticks (attached and detached) and cattle are large; while those of the infected ticks and cattle are small. Using this approximation, a threshold condition which determines whether the epidemic may take off in the tick-cattle system is derived. This condition expressed as a threshold parameter, is shown to increase in the infection transmission rates, the tick attachment rate and the tick birth rate. It decreases in the tick detachment rate, the tick mortality rate as well as in the host mortality and recovery rates. Outbreak probabilities and endemic levels in case of a major outbreak are also calculated.

Keywords: tick-borne diseases; multi-type branching process; threshold parameter; disease persistence; deterministic system; endemic level

1 Introduction

Tick borne diseases affecting cattle pose major health and management problems in Sub Saharan Africa (Norval *et al.*, 1992; Latif, 1993). The prevalence of these diseases have therefore been given considerable attention in an attempt to find ways of managing and controlling them (International Livestock Research Institute website, www.ilri.org). The tick borne diseases affecting cattle in this region include heartwater caused by *Cowdria ruminantium* and spread by the tick vector *Amblyomma hebraeum*, babesiosis caused by

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babesia bigemina and spread by the tick vector *Boophilus microplus* and East Coast Fever caused by *Theileria parva* and spread by the tick vector *Rhipicephalus appendiculatus*, also known as the brown ear tick. Of these diseases, heartwater and East Coast Fever lead to huge economic losses through appreciable mortality and morbidity, and also through reduction in growth rates and productivity of recovered cattle (Young *et al.*, 1988; ICIPE, 2005). The biology and epidemiology of *Theileria parva* and *Cowdria ruminantium* have been reviewed by several authors, Norval *et al.* (1992); Medley (1994); O'Callaghan *et al.* (1998); Mc Dermott *et al.* (2000) and Makala *et al.* (2003) among others. The problem of transmission dynamics of these parasites in endemically stable environments have been studied mathematically by Medley *et al.* (1993); Norval *et al.* (1992) and Mwambi (2002). Most models developed for tick borne diseases are deterministic. Although these models have contributed much to the understanding of the biological processes which underlie the spread of disease, the importance of random effects in determining population dynamic patterns of disease incidence and persistence is not reflected. One question where stochastic models are important is the conditions under which the epidemic process may become endemic depending on its spread at the early stages. Another problem is the probability of a major outbreak occurring, i.e that an epidemic takes off in a population. Stochastic models are also appropriate in describing an epidemic process that moves from an endemic state to the disease extinction state (Andersson & Britton, 2000, ch 8). Therefore they are more ideal if one can construct a manageable and tractable model.

Mwambi (2002) developed a deterministic transmission model for tick borne disease for cattle. The model is a seven dimensional system of ordinary differential equations in which he combined the larvae, nymph and adult stages of the tick into one compartment and assumed a constant host density per unit area. He investigated conditions for the persistence of a steady tick population. He also derived a threshold quantity for the disease which is dependent on the host density, the parameters of the tick-cattle interaction system and the two disease transmission rates from tick vector to cattle host and vice versa.

In the present paper we define a stochastic model related to the deterministic model developed by Mwambi and derive properties of it. However, in the model developed in this paper, functions of some parameters differ in definition from those in the deterministic model. These differences are mentioned in the discussion when we make comparisons of the threshold quantities derived in both models.

One of the main results of the study is the derivation of the necessary condition for the possibility of a major outbreak in the tick-cattle system when randomness is taken into account, given that the disease is introduced when the susceptible tick and cattle populations are in equilibrium. This condition is formulated in terms of a threshold parameter

which depends on the parameters governing the tick-cattle system as well as the infection transmission rates of both the ticks and the cattle. A consequence of this result is the possibility of attaining an endemic equilibrium state in the system when the threshold parameter is larger than one. Another main result is the derivation of the probability of an outbreak occurring (leading to endemicity) under the same conditions. This is achieved by a branching process approximation.

The paper is structured as follows: In Section 2, the stochastic model for the tick and cattle populations and epidemic is described in detail. In Section 3, a three-type branching process is used to approximate the initial stages of the epidemic process. This approximation is used to derive threshold conditions for the possibility of the disease becoming endemic. In Section 4, expressions for the probability of a major outbreak under different circumstances are derived. In Section 5, we derive an endemic equilibrium using the embedded deterministic system of the stochastic model defined in Section 2. In Section 6, the main results are examined using numerical examples and simulations. Finally in Section 7, we give a brief discussion on the study, its limitations as well as suggestions for possible further work.

2 A stochastic model for tick borne disease

Motivated by the deterministic model developed by Mwambi (2002), we now define a model which is a stochastic version of the deterministic model. In the model, the individuals in the host (cattle) population are categorised as Susceptible (H_S), Infectious (H_I) and Recovered (H_R). The individuals in the tick population are categorised as: detached and infectious (D_I); detached and susceptible (D_S); attached and infectious (A_I) and attached and susceptible (A_S). These categories of the tick vector depend on a tick's infection status as well as whether it is attached to a host or not. Once a tick get infected it remains infectious until it dies.

2.1 Model definition

2.1.1 Host population dynamics without ticks and disease

For the model, we want the size of the host population $H(t)$ (per unit area) to fluctuate around a constant value, N ; i.e $H(t) = H_S(t) + H_I(t) + H_R(t) \approx N$ at any time t . This is obtained by having a constant birth rate μN , and each host having an exponential life-length with death rate μ .

2.1.2 Tick-host interaction system without the disease

The host population is not affected by susceptible ticks and therefore its dynamics remain as mentioned in the previous section.

For the tick population, ticks require a blood meal from a host in order to develop fully and for females to reproduce. Since, in nature, adult female ticks lay eggs after detaching, we could let the number of newborn ticks depend on the number of newly detached ticks. However, since it is not easy to keep track of the number of newly detached ticks (and this also ruins the Markovian property of the model), the birth rate of ticks is defined to be proportional to the total number of attached ticks $A(t)$; ($A(t) = A_S(t) + A_I(t)$); as it is roughly proportional to the number of newly detached ticks. An individual tick gives birth at the rate ρ , hence new ticks are born at the rate $\rho A(t)$.

The attachment rate of a tick is treated as a decreasing function of the total number of attached ticks $A(t)$ in the system and an increasing function of the host population $H(t)$. We have chosen the functional relationship, $\frac{\alpha H(t)}{1+A(t)}$, as the attachment rate of a detached tick. The constant 1 is added to $A(t)$ in the denominator so that if the number of attached ticks is zero then the overall attachment rate of a tick will be $\alpha H(t)$ rather than infinity. For large populations (which we assume in the study) the effect of the constant is negligible, i.e. $\frac{\alpha H(t)}{1+A(t)} \simeq \alpha \frac{H(t)}{A(t)}$. The overall attachment rate is $\frac{\alpha H(t)}{1+A(t)} D(t)$, where $D(t) = D_S(t) + D_I(t)$. An attached tick detaches at the rate δ , hence the overall detachment rate is $\delta A(t)$.

Tick mortality is considered only for detached ticks which die at rate ν independent of everything else. The mortality rate of ticks is hence $\nu D(t)$.

2.1.3 Host-tick-disease interaction system

Both ticks and hosts transmit the parasite that causes the disease. While infectious, a host infects each susceptible tick attached to it at rate β , so the overall infection transmission rate from hosts to ticks is $\beta H_I(t) \frac{A_S(t)}{N}$. The infectious hosts may either recover from the disease at the rate γ , hence $\gamma H_I(t)$ is the overall recovery rate; or die at the rate μ , hence $\mu H_I(t)$ is the death rate. Recovered hosts are considered immune to the disease but ticks may still attach to them. A recovered host dies at the rate μ , hence the overall death rate is $\mu H_R(t)$.

While attached to susceptible hosts, infectious attached ticks may infect their host at the rate σ , so the overall infection transmission rate from ticks to hosts is $\sigma A_I(t) \frac{H_S(t)}{N}$.

The stochastic model for the process

$(D_S(t), D_I(t), A_S(t), A_I(t), H_S(t), H_I(t), H_R(t), t > 0)$ is summarised in Table 1, (having initial values $(D_S(0), D_I(0), A_S(0), A_I(0), H_S(0), H_I(0), H_R(0))$). It is a seven dimensional,

integer-valued Markov process with respective jump intensities as illustrated in Fig. 1. In the model defined we have made the simplification that susceptible attached ticks get infected at a rate proportional to the total number of infectious hosts. This means that the infection status of the actual host the tick is attached to is irrelevant. Another simplification is that the attachment rate is proportional to the total number of attached ticks in the system and not the number of attached ticks on a particular host that a tick wants to attach to. We have also assumed that the host and tick populations mix uniformly implying that any tick has an equal chance of attaching to any host in the system. Further, we have assumed no increased death rate of host or tick population due to the disease. Finally we have assumed that there are no seasonal effects in the system.

Table 1: Stochastic model for tick-host-disease system starting from $(D_S, D_I, A_S, A_I, H_S, H_I, H_R)$.

| to | transition rate | event |
|---|----------------------------|---|
| $\rightarrow (D_S + 1, D_I, A_S, A_I, H_S, H_I, H_R)$ | ρA | birth of a susceptible tick |
| $\rightarrow (D_S - 1, D_I, A_S + 1, A_I, H_S, H_I, H_R)$ | $\frac{\alpha H}{1+A} D_S$ | attachment of a susceptible detached tick |
| $\rightarrow (D_S + 1, D_I, A_S - 1, A_I, H_S, H_I, H_R)$ | δA_S | detachment of a susceptible attached tick |
| $\rightarrow (D_S - 1, D_I, A_S, A_I, H_S, H_I, H_R)$ | νD_S | death of a susceptible detached tick |
| $\rightarrow (D_S, D_I - 1, A_S, A_I + 1, H_S, H_I, H_R)$ | $\frac{\alpha H}{1+A} D_I$ | attachment of an infectious detached tick |
| $\rightarrow (D_S, D_I + 1, A_S, A_I - 1, H_S, H_I, H_R)$ | δA_I | detachment of an infectious attached tick |
| $\rightarrow (D_S, D_I - 1, A_S, A_I, H_S, H_I, H_R)$ | νD_I | death of an infectious detached tick |
| $\rightarrow (D_S, D_I, A_S - 1, A_I + 1, H_S, H_I, H_R)$ | $\beta H_I \frac{A_S}{N}$ | infection of a susceptible attached tick |
| $\rightarrow (D_S, D_I, A_S, A_I, H_S - 1, H_I + 1, H_R)$ | $\sigma A_I \frac{H_S}{N}$ | infection of a susceptible host |
| $\rightarrow (D_S, D_I, A_S, A_I, H_S + 1, H_I, H_R)$ | μN | birth of a susceptible host |
| $\rightarrow (D_S, D_I, A_S, A_I, H_S - 1, H_I, H_R)$ | μH_S | death of a susceptible host |
| $\rightarrow (D_S, D_I, A_S, A_I, H_S, H_I - 1, H_R)$ | μH_I | death of an infectious host |
| $\rightarrow (D_S, D_I, A_S, A_I, H_S, H_I - 1, H_R + 1)$ | γH_I | recovery of an infectious host |
| $\rightarrow (D_S, D_I, A_S, A_I, H_S, H_I, H_R - 1)$ | μH_R | death of a recovered host |

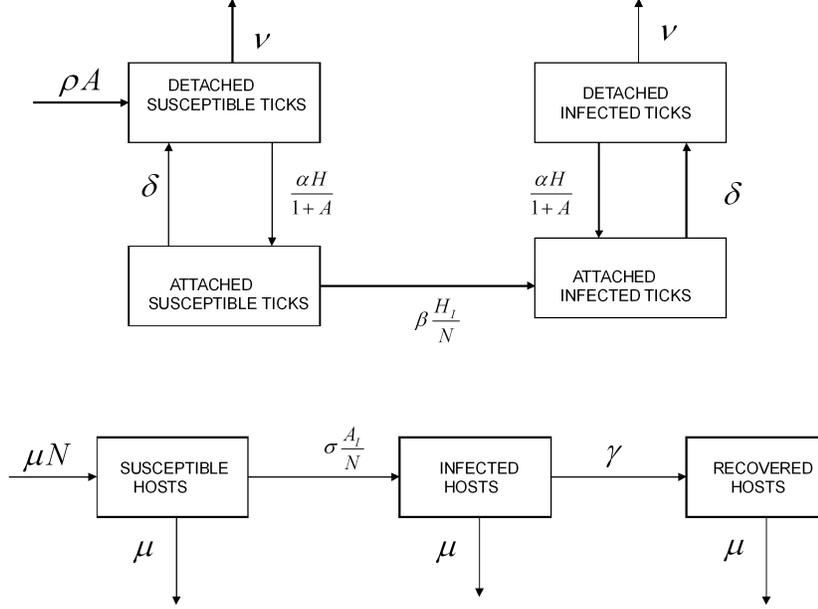


Figure 1: Schematic representation of the model.

2.2 Disease free tick-host subsystem

One of the sub-systems that is of interest is that of a disease-free population, where all individuals are susceptible. This sub-system is a Markov process with jump intensities as defined in Table 2. We now derive the disease free tick-host system $(\hat{H}_S, \hat{A}_S, \hat{D}_S)$, where all states have equal rates of entering and leaving the state. Given that the host population is

Table 2: Stochastic model for uninfected subsystem.

| to | transition rate | Event |
|---|--------------------------------|--------------------|
| $(D_S, A_S, H_S) \rightarrow (D_S + 1, A_S - 1, H_S)$ | δA_S | detachment of tick |
| $(D_S, A_S, H_S) \rightarrow (D_S - 1, A_S + 1, H_S)$ | $\frac{\alpha H_S}{1+A_S} D_S$ | attachment of tick |
| $(D_S, A_S, H_S) \rightarrow (D_S + 1, A_S, H_S)$ | ρA_S | birth of tick |
| $(D_S, A_S, H_S) \rightarrow (D_S - 1, A_S, H_S)$ | νD_S | death of tick |
| $(D_S, A_S, H_S) \rightarrow (D_S, A_S, H_S + 1)$ | μN | birth of host |
| $(D_S, A_S, H_S) \rightarrow (D_S, A_S, H_S - 1)$ | μH_S | death of host |

in equilibrium;

$$\mu N = \mu H_S(t)$$

and hence

$$\hat{H}_S = N, \tag{1}$$

then for the subsystem to attain a steady state the tick vector population should be in equilibrium. At equilibrium, the birth and death rates of ticks are equal as well as the detachment and attachment rates. Thus,

$$\begin{aligned}\rho A_S(t) &= \nu D_S(t) \\ \frac{\alpha H_S(t)}{1 + A_S(t)} D_S(t) &= \delta A_S(t).\end{aligned}$$

By solving the two equations we obtain,

$$\hat{A}_S = \frac{\alpha \rho \hat{H}_S}{\delta \nu} - 1 = \frac{\alpha \rho N}{\delta \nu} - 1 \approx \frac{\alpha \rho N}{\delta \nu} \quad (2)$$

$$\hat{D}_S = \frac{\rho \hat{A}_S}{\nu} = \frac{\alpha \rho^2 N}{\delta \nu^2} - \frac{\rho}{\nu} \approx \frac{\alpha \rho^2 N}{\delta \nu^2} = \frac{\rho}{\nu} \hat{A}_S \quad (3)$$

\hat{H}_S , \hat{A}_S and \hat{D}_S are the population sizes of susceptible hosts, susceptible attached ticks and susceptible detached ticks in the disease free equilibrium.

3 Initial stages of the epidemic process

3.1 Branching process approximation

During the early stages of an epidemic in a large population which is distinctively divided into various sub-populations of distinguishable individuals, each having a very large number of susceptible individuals and few infectious individuals; the number of infectives can often be approximated by a multi-type branching process (Ball, 1983; Ball & Donnelly, 1995). In multi-type branching processes, individuals in the population are categorised into a finite number of types and each individual behaves independently. An individual of a given type can produce offspring of possibly all types and individuals of the same type have the same offspring distribution (Ch 11, Karlin & Taylor, 1975; Ch 4, Jagers, 1975)

In the present model, the disease is spread by individuals of three types: infectious detached ticks, infectious attached ticks and infectious hosts. Infectious detached ticks produce (or rather become) infectious attached ticks when they attach to a host. Infectious attached ticks produce (i.e. become) infectious detached ticks when they detach from a host. While attached to susceptible hosts, infectious ticks may infect the host they are attached to. Finally, infectious hosts may infect susceptible ticks attached to them thus producing infectious attached ticks. Therefore the number of infectives in the tick-host system during the early stages of the epidemic process can be approximated by a three type branching process. This can be proved using similar arguments as in Ball & Donnelly(1995).

3.2 Threshold condition for disease outbreak

Let N , the average population size of hosts, be sufficiently large and assume that the tick and host populations are in equilibrium before the disease is introduced in the system. During the early stages of the epidemic the population sizes of the susceptible ticks and hosts are very large compared to the population sizes of the infectious ticks and hosts. As a consequence the attachment rate of a tick is approximately,

$$\frac{\alpha H(t)}{1 + A(t)} \simeq \frac{\alpha N}{\hat{A}} = \frac{\delta \nu}{\rho}$$

where $H(t)$ and $A(t)$ are the total host population and the number of attached ticks at time t ; and \hat{A} ($\hat{A} = \hat{A}_S$) is the total number of attached ticks in equilibrium state (given in Equation 2).

Suppose the disease is introduced by a few infectious hosts and/or infectious ticks, then the infectious detached ticks, infectious attached ticks and infectious hosts will spread the disease. Let the infectious detached ticks be of type 1, infectious attached ticks be of type 2 and infectious hosts be of type 3. Further let $\{X_{ij}; i, j = 1, 2, 3\}$ be the number of infectives of type j produced by an infective of type i and $m_{ij} = E[X_{ij}]$. We now derive the offspring distributions and its expected values for the approximating branching process.

Beginning with the infectious detached ticks; an infectious detached tick produces at most one single infectious attached tick but no other offspring, hence $X_{11} \equiv X_{13} \equiv 0$.

While on the ground, an infectious detached tick either dies at rate ν or it attaches to a host at rate $\frac{\alpha N}{\hat{A}}$ and becomes an infectious attached tick; so

$$\begin{aligned} P(X_{12} = 0) &= \frac{\nu}{\nu + \frac{\alpha N}{\hat{A}}} = \frac{\nu \hat{A}}{\nu \hat{A} + \alpha N}, \\ P(X_{12} = 1) &= \frac{\alpha N}{\nu \hat{A} + \alpha N}. \end{aligned}$$

The expected numbers of infectious detached ticks, infectious attached ticks and infectious hosts produced by one infectious detached tick are hence

$$\begin{aligned} m_{11} &= E[X_{11}] = 0, \\ m_{12} &= E[X_{12}] = \frac{\alpha N}{\nu \hat{A} + \alpha N}, \\ m_{13} &= E[X_{13}] = 0. \end{aligned}$$

Next, an infectious attached tick detaches producing a detached infectious tick with certainty, so $X_{21} \equiv 1$. An infectious attached tick does not produce another infectious attached tick, hence $X_{22} = 0$. Finally an infectious attached tick (one that is attached to a susceptible host) produces at most one infectious host. Since nearly all hosts are susceptible in

the early stages of the epidemic process, the probability that an infectious tick is attached to a susceptible host during this period is approximately one ($\frac{H_S(t)}{N} \simeq 1$). An infectious tick is attached to a susceptible host for a time duration which is exponentially distributed with intensity δ (δ is the detachment rate), and it infects the susceptible host at the rate σ before detaching. Thus

$$\begin{aligned} P(X_{23} = 0) &= \frac{\delta}{\delta + \sigma}, \\ P(X_{23} = 1) &= \frac{\sigma}{\delta + \sigma}. \end{aligned}$$

The expected numbers of infectious detached ticks, infectious attached ticks and infectious hosts produced by one infectious attached tick are hence

$$\begin{aligned} m_{21} &= E[X_{21}] = 1, \\ m_{22} &= E[X_{22}] = 0, \\ m_{23} &= E[X_{23}] = \frac{\sigma}{\delta + \sigma}. \end{aligned}$$

Finally, for the infectious hosts; an infectious host can only produce infectious attached ticks, hence $X_{31} \equiv X_{33} \equiv 0$. A host is infectious for a time period that is exponentially distributed with intensity $\mu + \gamma$ (it either dies at the rate μ or it recovers at the rate γ). During this period it infects susceptible ticks attached to it according to a Poisson process with intensity $\beta \frac{\hat{A}}{N}$; since $\frac{A_S}{N} = \frac{\hat{A}}{N}$ at the initial stages of the epidemic process. Here we make the simplifying assumption that the number of susceptible attached ticks remains fairly constant throughout the infectious period.

Conditioning on I , the length of the infectious period, the expected number of susceptible ticks that get infected before this period ends is

$$\begin{aligned} E[X_{32}] &= E(E[X_{32}|I]) = E\left(\beta \frac{\hat{A}}{N} I\right) \\ &= \beta \frac{\hat{A}}{N} E[I] = \frac{\beta \hat{A}}{N(\mu + \gamma)} \\ &= \frac{\beta \hat{A}}{N(\mu + \gamma)}. \end{aligned}$$

The expected numbers of infectious detached ticks, infectious attached ticks and infectious hosts produced by one infectious host are hence

$$\begin{aligned} m_{31} &= E[X_{31}] = 0, \\ m_{32} &= E[X_{32}] = \frac{\beta \hat{A}}{N(\mu + \gamma)}, \\ m_{33} &= E[X_{33}] = 0. \end{aligned}$$

Let $M = \{m_{ij}\}_{i,j=1}^3$ be the expectation matrix of the form

$$M = \begin{pmatrix} 0 & \frac{\alpha N}{\alpha N + \nu \hat{A}} & 0 \\ 1 & 0 & \frac{\sigma}{\sigma + \delta} \\ 0 & \frac{\beta \hat{A}}{N(\mu + \gamma)} & 0 \end{pmatrix}.$$

If the largest real-valued eigenvalue of M is less than or equal to one, the epidemic dies out fairly quickly. On the other hand, if the largest real-valued eigenvalue of M is greater than one, then there is a positive probability that the epidemic takes off (Karlin & Taylor, 1975, p. 412).

The eigenvalues of M are the roots of the characteristic equation

$$\lambda^3 - \lambda \left(\frac{\beta \hat{A}}{N(\mu + \gamma)} \frac{\sigma}{\sigma + \delta} + \frac{\alpha N}{\alpha N + \nu \hat{A}} \right) = 0. \quad (4)$$

From Equation(4), the largest eigenvalue is the positive root of the expression

$$\lambda^2 = \frac{\beta \sigma \hat{A}(\alpha N + \nu \hat{A}) + \alpha N^2(\mu + \gamma)(\sigma + \delta)}{N(\alpha N + \nu \hat{A})(\mu + \gamma)(\sigma + \delta)}.$$

Since we are interested in the case where the largest eigenvalue is greater than one, then $\lambda > 1$ implies that $\lambda^2 > 1$.

Thus for λ to be greater than 1, then we must have that

$$\beta \sigma \hat{A}(\alpha N + \nu \hat{A}) + \alpha N^2(\mu + \gamma)(\sigma + \delta) > N(\alpha N + \nu \hat{A})(\mu + \gamma)(\sigma + \delta),$$

This expression reduces to

$$\frac{\beta \sigma(\alpha N + \nu \hat{A})}{N \nu(\sigma + \delta)(\mu + \gamma)} > 1. \quad (5)$$

Using Equation(2), the value of \hat{A} will be

$$\hat{A} = \hat{A}_S \simeq \frac{N \alpha \rho}{\delta \nu}$$

since we assume that all susceptible sub-populations are sufficiently large.

Substituting for \hat{A} in Equation(5), we obtain

$$T = \frac{\beta \sigma \alpha (1 + \frac{\rho}{\delta})}{\nu(\sigma + \delta)(\mu + \gamma)}. \quad (6)$$

T is the threshold quantity when the tick-host system is in equilibrium at the time of disease introduction. From Equation(6) we see that T has a monotonic dependence on all the eight model parameters. It decreases in the tick detachment rate δ , host birth and mortality rate

μ , tick mortality rate ν and host recovery rate γ . It increases in the tick-host encounter rate α , the infection transmission rate from tick to host σ , the infection transmission rate from host to tick β as well as the tick birth rate ρ . When $T \leq 1$, the epidemic dies out fairly quickly and when $T > 1$, the epidemic may take off in the system and has a chance of becoming endemic.

4 The probability of a major outbreak

Let the probability generating function of the offspring distribution of infectives produced by an infective of type i ($i = 1, 2, 3$), be $G_i(\mathbf{s}) = E \left[\prod_{j=1}^3 s_j^{X_{ij}} \right]$, where X_{ij} is as defined in the previous section and $\mathbf{s} = (s_1, s_2, s_3)$. The probability that a minor outbreak of the disease occurs given that there are a_i infectives initially of each of the three types is $\pi = \pi_1^{a_1} \pi_2^{a_2} \pi_3^{a_3}$. Since M is irreducible, we know that $\pi_1 = \pi_2 = \pi_3 = 1$ if $T \leq 1$ or that $\phi = (\pi_1, \pi_2, \pi_3)$ is the unique root of $\mathbf{s} = \mathbf{G}(\mathbf{s})$ that satisfies $\pi_1 < 1$, $\pi_2 < 1$ and $\pi_3 < 1$ if $T > 1$.

Since $X_{11} \equiv X_{13} \equiv 0$ and X_{12} equals zero or one, the probability generating function of offspring produced by one infectious detached tick is

$$\begin{aligned} G_1(\mathbf{s}) &= E \left[s_1^{X_{11}} s_2^{X_{12}} s_3^{X_{13}} \right] = P(X_{12} = 0) s_2^0 + P(X_{12} = 1) s_2^1 \\ &= \frac{\nu \hat{A}}{\alpha N + \nu \hat{A}} + \frac{\alpha N}{\alpha N + \nu \hat{A}} s_2. \end{aligned}$$

Since $X_{21} \equiv 1$, $X_{22} \equiv 0$ and X_{23} equals zero or one, the probability generating function of offspring produced by one infectious attached tick is

$$\begin{aligned} G_2(\mathbf{s}) &= E \left[s_1^{X_{21}} s_2^{X_{22}} s_3^{X_{23}} \right] = s_1^1 \left[P(X_{23} = 0) s_3^0 + P(X_{23} = 1) s_3^1 \right] \\ &= \left(\frac{\delta}{\sigma + \delta} + \frac{\sigma}{\sigma + \delta} s_3 \right) s_1. \end{aligned}$$

Since $X_{31} \equiv X_{33} \equiv 0$ and X_{32} is Poisson distributed conditioned on that the infectious period $I = t$ (as explained in the previous section), the probability generating function of offspring produced by one infectious host is

$$\begin{aligned} G_3(\mathbf{s}) &= E \left[s_1^{X_{31}} s_2^{X_{32}} s_3^{X_{33}} \right] = \sum_x s_2^x P(X_{32} = x) \\ &= \sum_x s_2^x \int_0^\infty (\mu + \gamma) e^{-(\mu + \gamma)t} \frac{e^{\left(\beta \frac{\hat{A}}{N} t\right)} \left(\beta \frac{\hat{A}}{N} t\right)^x}{x!} dt \end{aligned}$$

$$\begin{aligned}
&= \int_0^\infty (\mu + \gamma) e^{-(\mu + \gamma + \beta \frac{\hat{A}}{N})t} \left\{ \sum_{x=0}^\infty s_2^x \frac{\left(\beta \frac{\hat{A}}{N} t\right)^x}{x!} \right\} dt \\
&= \int_0^\infty (\mu + \gamma) e^{-(\mu + \gamma + \beta \frac{\hat{A}}{N})t} e^{\beta \frac{\hat{A}}{N} t s_2} dt \\
&= (\mu + \gamma) \int_0^\infty e^{-(\mu + \gamma + \beta \frac{\hat{A}}{N} - \beta \frac{\hat{A}}{N} s_2)t} dt \\
&= \frac{N(\mu + \gamma)}{N(\mu + \gamma) + \beta \hat{A} - \beta \hat{A} s_2}.
\end{aligned}$$

Substituting $\hat{A} = \frac{N\rho\alpha}{\delta\nu}$; the non-trivial solutions \hat{s}_1 , \hat{s}_2 and \hat{s}_3 for the equations $s_i = G_i(\mathbf{s})$, $i = 1, 2, 3$ can be shown to satisfy

$$\hat{s}_1 = \frac{(\sigma + \delta)[\beta\alpha\rho(\delta + \rho) + \delta^2\nu(\mu + \gamma)]}{\beta\alpha(\rho + \delta)[\sigma(\rho + \delta) + \rho\delta]} \quad (7)$$

$$\hat{s}_2 = \frac{\delta[\nu(\mu + \gamma)(\delta + \sigma) + \beta\alpha\rho]}{\beta\alpha[\rho\delta + \sigma(\delta + \rho)]} \quad (8)$$

$$\hat{s}_3 = \frac{(\mu + \gamma)\delta\nu[\sigma(\delta + \rho) + \rho\delta]}{\sigma[\beta\alpha\rho(\delta + \rho) + \delta^2\nu(\mu + \gamma)]} \quad (9)$$

and extinction probabilities are given by $\pi_i = \min(1, \hat{s}_i)$. The analytical solution in this case can be derived which is not common for multi-type branching processes.

In Section 6, π_1, π_2, π_3 and $(1 - \pi)$ are computed numerically for some examples.

5 Endemic level of the epidemic process

Assume that the tick-host system is in equilibrium before the disease is introduced. The threshold value T defined in (6) is useful in determining the possibility of the epidemic taking off in the system. If $T \leq 1$ then the epidemic will die out fairly quickly and the tick-host system will attain a disease-free equilibrium state. On the other hand if $T > 1$, then either a minor outbreak occurs where only few ticks and hosts get infected before the infection disappears from the population; or else a major outbreak occurs and the disease may become endemic (taking the host and tick populations to a substantial infection level known as the endemic level). At this level, the tick-host system is said to be in an endemic equilibrium state.

Using similar arguments as in Ethier & Kurtz (1986) and Andersson & Britton (2000), as the tick vector and host populations increase then, by the law of large numbers, the seven dimensional stochastic process (developed in Section 2) converges to the trajectories of a

seven dimensional deterministic dynamical system.

Suppose at $t = 0$,

$$\left(\frac{D_S(0)}{N}, \frac{D_I(0)}{N}, \frac{A_S(0)}{N}, \frac{A_I(0)}{N}, \frac{H_S(0)}{N}, \frac{H_I(0)}{N}, \frac{H_R(0)}{N} \right) \xrightarrow{p}$$

$$(d_S(0), d_I(0), a_S(0), a_I(0), h_S(0), h_I(0), h_R(0))$$

then

$$\left(\frac{D_S(t)}{N}, \frac{D_I(t)}{N}, \frac{A_S(t)}{N}, \frac{A_I(t)}{N}, \frac{H_S(t)}{N}, \frac{H_I(t)}{N}, \frac{H_R(t)}{N} \right) \xrightarrow{p}$$

$$(d_S(t), d_I(t), a_S(t), a_I(t), h_S(t), h_I(t), h_R(t))$$

as $N \rightarrow \infty$ on $[0, t_0]$ (t_0 is any finite value).

The vector $(d_S(t), d_I(t), a_S(t), a_I(t), h_S(t), h_I(t), h_R(t))$ is deterministic and is the solution of

$$d'_S(t) = \rho a(t) + \delta a_S(t) - \nu d_S(t) - \frac{\alpha h(t) d_S(t)}{a(t)} \quad (10)$$

$$d'_I(t) = \delta a_I(t) - \nu d_I(t) - \frac{\alpha h(t) d_I(t)}{a(t)} \quad (11)$$

$$a'_S(t) = \frac{\alpha h(t) d_S(t)}{a(t)} - \delta a_S(t) - \beta h_I(t) a_S(t) \quad (12)$$

$$a'_I(t) = \frac{\alpha h(t) d_I(t)}{a(t)} + \beta h_I(t) a_S(t) - \delta a_I(t) \quad (13)$$

$$h'_S(t) = \mu - \mu h_S(t) - \sigma a_I(t) h_S(t) \quad (14)$$

$$h'_I(t) = \sigma a_I(t) h_S(t) - \mu h_I(t) - \gamma h_I(t) \quad (15)$$

$$h'_R(t) = \gamma h_I(t) - \mu h_R(t) \quad (16)$$

where $h(t) = h_S(t) + h_I(t) + h_R(t) \equiv 1$ and $a(t) = a_S(t) + a_I(t) = \hat{a}$; the ratio $\frac{\hat{A}}{N} = \hat{a} = \frac{\alpha \rho}{\delta \nu}$ is the same at all time points t since the system is in equilibrium. These equations are derived from the transition events with respect to each sub-population in the system as illustrated in Figure 1.

As $t \rightarrow \infty$, the deterministic system converges to one of the two equilibrium states;

- (i) The disease free equilibrium state if $d_I(0) = a_I(0) = h_I(0) = 0$ or if $d_I(0) + a_I(0) + h_I(0) > 0$ and $T \leq 1$
- (ii) The endemic equilibrium state if $d_I(0) + a_I(0) + h_I(0) > 0$ and $T > 1$.

Disease free equilibrium state:

This state can be attained in two ways:

- (i) If the disease is not present in the system initially, i.e. $d_I(0) = a_I(0) = h_I(0) = 0$, then for $d_S(t)$, $a_S(t)$ and $h_S(t)$, the deterministic system is:

$$\begin{aligned} d'_S(t) &= (\rho + \delta)a_S(t) - \frac{\alpha h_S(t)d_S(t)}{a_S(t)} - \nu d_S(t) \\ a'_S(t) &= \frac{\alpha h_S(t)d_S(t)}{a_S(t)} - \delta a_S(t) \\ h'_S(t) &= \mu(1 - h_S(t)) \end{aligned}$$

The solution of this system of equations all equated to zero gives us;

$$\hat{d}_S = \frac{\rho^2 \alpha}{\delta \nu^2}, \quad \hat{a}_S = \frac{\rho \alpha}{\delta \nu}, \quad \hat{h}_S = 1$$

corresponding to Equations (1-3).

- (ii) If the disease is present initially in the system, i.e $d_I(0) + a_I(0) + h_I(0) > 0$ and $T \leq 1$, then

$$[d_I(t), a_I(t), h_I(t), h_R(t)] \rightarrow [0, 0, 0, 0]$$

and

$$d_S(t) \rightarrow \hat{d}_S = \frac{\rho^2 \alpha}{\delta \nu^2}, \quad a_S(t) \rightarrow \hat{a}_S = \frac{\rho \alpha}{\delta \nu}, \quad h_S(t) \rightarrow \hat{h}_S = 1.$$

Therefore the disease free equilibrium state will have $d_I(t) = a_I(t) = h_I(t) = h_R(t) = 0$ and the proportions $d_S(t)$, $a_S(t)$ and $h_S(t)$ will converge to the values $(\hat{d}_S, \hat{a}_S, \hat{h}_S)$.

Endemic equilibrium state:

When $T > 1$, then the tick-host system can converge to an endemic equilibrium state. If this state is attained then it is the positive solution of the system of Equations (10-16) having derivatives all equal to zero.

Using the values $\hat{h} = 1$, $\hat{a} = \frac{\alpha \rho}{\delta \nu}$ and $\hat{d} = \frac{\rho^2 \alpha}{\delta \nu^2}$ obtained for the disease free state, the solution can be shown to satisfy:

$$\hat{d}_S = \frac{\rho^2 [\sigma \alpha \rho (\delta (\rho + \delta) (\mu + \gamma) + \beta \mu (\rho + \delta)) + \delta^3 \nu \mu (\mu + \gamma)]}{\sigma \delta \nu^2 (\rho + \delta) [\rho \delta (\mu + \gamma) + \beta \mu (\rho + \delta)]} \quad (17)$$

$$\hat{d}_I = \frac{\rho^2 \mu [\alpha \beta \sigma (\rho + \delta) - \delta^2 \nu (\mu + \gamma)]}{\sigma \nu^2 (\rho + \delta) [\rho \delta (\mu + \gamma) + \beta \mu (\rho + \delta)]} \quad (18)$$

$$\hat{a}_S = \frac{\rho (\mu + \gamma) [\alpha \rho \sigma + \delta \nu \mu]}{\sigma \nu [\rho \delta (\mu + \gamma) + \beta \mu (\rho + \delta)]} \quad (19)$$

$$\hat{a}_I = \frac{\rho \mu [\alpha \beta \sigma (\rho + \delta) - \delta^2 \nu (\mu + \gamma)]}{\sigma \delta \nu [\rho \delta (\mu + \gamma) + \beta \mu (\rho + \delta)]} \quad (20)$$

$$\hat{h}_S = \frac{\delta\nu[\rho\delta(\mu + \gamma) + \beta\mu(\rho + \delta)]}{(\rho + \delta)\beta[\delta\nu\mu + \sigma\alpha\rho]} \quad (21)$$

$$\hat{h}_I = \frac{\rho\mu[\alpha\beta\sigma(\rho + \delta) - \delta^2\nu(\mu + \gamma)]}{(\mu + \gamma)(\rho + \delta)\beta[\delta\nu\mu + \sigma\alpha\rho]} \quad (22)$$

$$\hat{h}_R = \frac{\rho\gamma[\alpha\beta\sigma(\rho + \delta) - \delta^2\nu(\mu + \gamma)]}{(\mu + \gamma)(\rho + \delta)\beta[\delta\nu\mu + \sigma\alpha\rho]} \quad (23)$$

$(\hat{d}_S, \hat{d}_I, \hat{a}_S, \hat{a}_I, \hat{h}_S, \hat{h}_I, \hat{h}_R)$ is unique and is the endemic equilibrium state. It only exists if $T > 1$. The state $(N\hat{d}_S, N\hat{d}_I, N\hat{a}_S, N\hat{a}_I, N\hat{h}_S, N\hat{h}_I, N\hat{h}_R)$ is known as the endemic level of the stochastic epidemic process. The epidemic eventually dies out but when $T > 1$ this will take very long in a large population, and prior to extinction it will fluctuate around the endemic level.

6 Numerical examples

We illustrate the results of the study using sixteen numerical examples (varying four parameters at two different levels). In each case, we have computed the threshold parameter T , the probability of a major outbreak $(1 - \pi)$ occurring and the endemic proportion for the host population as well as the ratio of attached and detached ticks to the host population at the endemic level. The choice of parameters values is based on values reported by O'Callaghan *et al.* (1998), Medley (1994) and Mwambi (2002). Each parameter value is expressed per individual host or tick per day.

The parameter values for the host birth and mortality rate μ , the host recovery rate γ , the tick mortality rate ν , the tick-host encounter rate α and the tick detachment rate δ are the reciprocals of the expected durations of time it takes before the respective events occur. Thus, for example if a tick on average stays attached to a host for 4 days before detaching, the detachment rate is 0.25. For the infection transmission rate σ from tick to host, it is the product of the rate at which ticks feed on host and the probability that an infectious tick infects a susceptible host (Medley, 1994; O'Callaghan *et al.*, 1998). We use similar arguments to estimate the infection transmission rate β from host to tick as the product of the rate at which ticks feed on host and the probability that an infectious host infects a susceptible attached tick. Finally, the tick birth rate ρ is the average number of ticks produced per tick per day.

For α , β , δ and σ ; we choose two values for each parameter; one high and one low value; and combine these values to obtain sixteen possible cases. These parameters are considered to be most influential in determining the infection dynamics in the tick-host-disease system when both the host and tick populations are sufficiently large (Mwambi, 2002; O'Callaghan

et al., 1998). The other parameters are set to be fixed.

6.1 Threshold parameter T

The parameter values chosen are summarised in Table 3 as well as the threshold parameter T obtained from Equation(6). From the values of T obtained for the sixteen cases considered, we observe that increasing the value of δ , while holding all other parameters constant, decreases T . On the other hand, increasing the value of each of the parameters α , β or σ individually, while holding all other parameters constant, increases T . This result is consistent with the monotonic dependencies observed earlier in Section 3. We also observe that for most cases where T is larger than one (Cases 3,7,11,15); the parameter α has a high value while δ has a low value. For cases where both the parameters β and σ have high values, the disease has a possibility of spreading when the parameter α has a low value (Case 13).

Table 3: Different parameter values for β , σ , α , δ ; and the corresponding threshold parameter T with fixed values $\nu=0.01$, $\rho=0.05$, $\mu=0.0006$ and $\gamma=0.05$.

| Case | β | σ | α | δ | T |
|------|---------|----------|----------|----------|-------|
| 1 | 0.01 | 0.005 | 0.03 | 0.05 | 0.11 |
| 2 | 0.01 | 0.005 | 0.03 | 0.5 | 0.006 |
| 3 | 0.01 | 0.005 | 0.3 | 0.05 | 1.08 |
| 4 | 0.01 | 0.005 | 0.3 | 0.5 | 0.06 |
| 5 | 0.01 | 0.02 | 0.03 | 0.05 | 0.39 |
| 6 | 0.01 | 0.02 | 0.03 | 0.5 | 0.03 |
| 7 | 0.01 | 0.02 | 0.3 | 0.05 | 3.39 |
| 8 | 0.01 | 0.02 | 0.3 | 0.5 | 0.25 |
| 9 | 0.05 | 0.005 | 0.03 | 0.05 | 0.54 |
| 10 | 0.05 | 0.005 | 0.03 | 0.5 | 0.03 |
| 11 | 0.05 | 0.005 | 0.3 | 0.05 | 5.39 |
| 12 | 0.05 | 0.005 | 0.3 | 0.5 | 0.32 |
| 13 | 0.05 | 0.02 | 0.03 | 0.05 | 1.69 |
| 14 | 0.05 | 0.02 | 0.03 | 0.5 | 0.13 |
| 15 | 0.05 | 0.02 | 0.3 | 0.05 | 16.94 |
| 16 | 0.05 | 0.02 | 0.3 | 0.5 | 1.25 |

6.2 Probability of a major outbreak

Using Equations (7-9) and the properties presented in Section 4, we calculate the theoretical probability $(1 - \pi)$ of a major outbreak occurring starting with only one infectious detached tick, one infectious attached tick and one infectious host initially in the epidemic process. Though it is not realistic for an epidemic to be introduced by only one infective for each sub-population, similar results for the probability of a major outbreak occurring can be obtained using a few infectives for each sub-population. For all cases in Table 3 where $T < 1$, the probability of a major outbreak is zero. For the rest of the cases where the threshold parameter T is larger than one, the results are presented in Table 4, (the cases are ordered according to their threshold value T). The results show that this probability increases as the threshold parameter T increases and that an outbreak is almost certain for parameter values chosen for Case 15. We ran 1000 simulations for the epidemic process for cases 7, 11 and 15 in Table 4 to obtain the fraction of major outbreaks occurring $(1 - \tilde{\pi})$ and compared the result with the theoretical probability $(1 - \pi)$ obtained for these cases; the other cases 3, 13 and 16 were omitted since larger populations than those chosen for the simulations are needed to avoid extinction of the disease in the near future event though the branching process initially may increase. The infection-free tick-host system was in equilibrium with 50 susceptible hosts, 1500 susceptible attached ticks and 7500 susceptible detached ticks, and the disease was introduced in the system by one infective member for each of the three subpopulations. Each simulation was run until either there were no infectives in the system (extinction) or there were 20 infectives in the system. The choice of 20 is arbitrary but it is assumed that if the number of infectives reaches 20 the epidemic will not go extinct. The probability of a major outbreak is estimated by the proportion of the simulations that do not go extinct before reaching 20 infectives. The results are presented in Table 4. The proportions obtained are in good agreement with those of the theoretical probabilities.

6.3 Endemic level

Equations (16-21) are used for calculations of the endemic proportions for the host population and the average number of ticks (attached and detached) per host at endemic level. For cases in Table 3 where $T < 1$, there is no possibility of a major outbreak occurring hence no endemic proportions for the host population or average number of ticks per host at endemic level can be obtained. For cases where $T > 1$, the results are summarised in Tables 5 as $\hat{h}_S, \hat{h}_I, \hat{h}_R$, and in Table 6 as $\hat{a}_S, \hat{a}_I, \hat{d}_S, \hat{d}_I$.

From Table 5, we observe that the proportion of infectious hosts increases as the

Table 4: Values of the theoretical probability of a major outbreak and the probability of major outbreak for simulated values of cases 7,11 and 15.

| Case | T | π_1 | π_2 | π_3 | $(1 - \pi)$ | $(1 - \tilde{\pi})$ |
|------|-------|---------|---------|---------|-------------|---------------------|
| 3 | 1.08 | 0.994 | 0.988 | 0.933 | 0.084 | |
| 16 | 1.25 | 0.944 | 0.938 | 0.845 | 0.252 | |
| 13 | 1.69 | 0.909 | 0.818 | 0.649 | 0.517 | |
| 7 | 3.39 | 0.843 | 0.687 | 0.350 | 0.797 | 0.754 |
| 11 | 5.39 | 0.932 | 0.864 | 0.199 | 0.840 | 0.810 |
| 15 | 16.94 | 0.791 | 0.582 | 0.075 | 0.965 | 0.954 |

Table 5: Theoretical and simulated values of the endemic proportion for host population where the threshold parameter is above one.

| Case | T | \hat{h}_S | \tilde{h}_S | \hat{h}_I | \tilde{h}_I | \hat{h}_R | \tilde{h}_R |
|------|-------|-------------|---------------|-------------|---------------|-------------|---------------|
| 3 | 1.08 | 0.844 | | 0.002 | | 0.154 | |
| 16 | 1.25 | 0.769 | | 0.003 | | 0.228 | |
| 13 | 1.69 | 0.427 | | 0.007 | | 0.566 | |
| 7 | 3.39 | 0.211 | 0.223 | 0.009 | 0.002 | 0.780 | 0.775 |
| 11 | 5.39 | 0.172 | 0.176 | 0.010 | 0.004 | 0.818 | 0.820 |
| 15 | 16.94 | 0.043 | 0.041 | 0.011 | 0.007 | 0.946 | 0.952 |

threshold parameter T increases though the percentage is fairly constant ranging between 0.2% and 1.1% of the host population. The percentage of susceptible hosts on the other hand seems to decrease rapidly from 84.4% to 4.3% as T increases. For Case 15 where a major outbreak leading to endemicity is almost certain to occur, approximately 4% and 1% of the hosts are susceptible and infective respectively, and the remaining 95% are immune at the endemic level. This result is close to the one obtained by Medley(1994) where he considered the endemic stability of the East Coast Fever disease in Eastern Africa.

From Table 6, we observe that the average number of infectious ticks (attached and detached) per host increases as the threshold parameter T increases. For the attached ticks, the average number increases more than thirty fold from 0.02 to 0.67 and that of the detached ticks increases with an almost thirty fold from 0.06 to 1.7. The average number of susceptible attached and detached ticks per host remain fairly constant.

No simulations were carried out for cases 3, 13 and 16 where T is slightly above one as the endemic levels are too close to disease extinction because the population sizes chosen are

Table 6: Theoretical and simulated values of the average number of attached ticks and detached ticks per host for cases where the threshold parameter is above one.

| Case | T | \hat{a}_S | \tilde{a}_S | \hat{a}_I | \tilde{a}_I | \hat{d}_S | \tilde{d}_S | \hat{d}_I | \tilde{d}_I |
|------|-------|-------------|---------------|-------------|---------------|-------------|---------------|-------------|---------------|
| 3 | 1.08 | 29.98 | | 0.02 | | 149.94 | | 0.06 | |
| 16 | 1.25 | 2.99 | | 0.01 | | 14.96 | | 0.04 | |
| 13 | 1.69 | 2.96 | | 0.04 | | 14.90 | | 0.10 | |
| 7 | 3.39 | 29.89 | 29.96 | 0.11 | 0.05 | 149.72 | 149.82 | 0.28 | 0.21 |
| 11 | 5.39 | 29.42 | 29.43 | 0.58 | 0.57 | 148.60 | 148.75 | 1.40 | 1.27 |
| 15 | 16.94 | 29.33 | 29.38 | 0.67 | 0.63 | 148.30 | 148.52 | 1.70 | 1.50 |

small. For cases 7, 11 and 15, one simulation for each case was carried out for a duration of three years, beginning the process at the endemic level and the results were compared with the numerical solutions obtained. For each simulation, the first year was disregarded and the time averages of the remaining duration were used to obtain the endemic proportion of the host population and the average number of ticks (attached and detached) per host at the endemic level. The results are presented in Tables 5 and 6. The simulated values are all relatively close to those of the numerical solutions for each of the subpopulations of the susceptible and the infective hosts and ticks.

To illustrate the full distribution of the different states, we have plotted histograms of case 15 in Figs 2-4.

The results show that the endemic level of the susceptible hosts varies between 0 and 3 while that of the infectious hosts varies between 0 and 2. These numbers give endemic proportions ranging from 0 to 0.06 for susceptible hosts and 0 to 0.04 for the infective hosts (Fig. 2). Even though the numbers of the susceptible and infective host are small, endemicity is still attainable because there are many infectious ticks in the system. From Fig. 3, we observe that the ratio of attached susceptible ticks to host population varies between 25.8 and 31.6 and the ratio of attached infectious ticks varies between 0.15 and 2.2. Finally the ratio of susceptible detached ticks varies between 143.2 and 153.3 and the ratio of detached infectious ticks varies between 0.2 and 3.9 (Fig. 4). In total, there are in the range one to six infectious ticks per host at the endemic level. The distributions of the number of infected ticks (attached and detached) per host appear to be multi-modal. The reason for this multi-modal distribution is a consequence of the importance of the present number of infectious hosts. In Fig. 5 this is seen: when there are no infectious hosts, the number of infectious ticks decreases whereas they increase when there are infectious hosts, in particular if there are two of them.

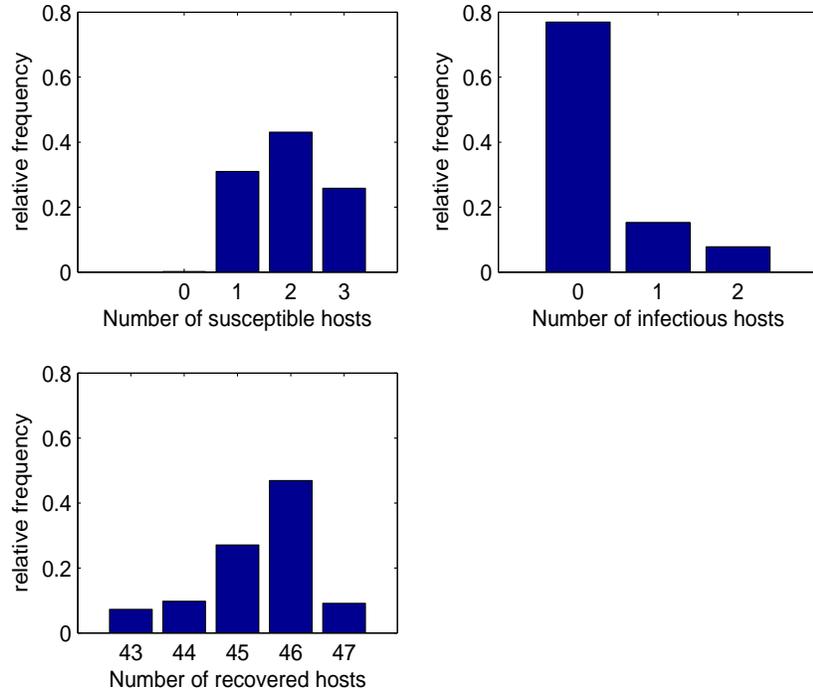


Figure 2: Distribution (over time in the simulation) of susceptible, infective and recovered hosts at endemic level for parameters chosen for case 15.

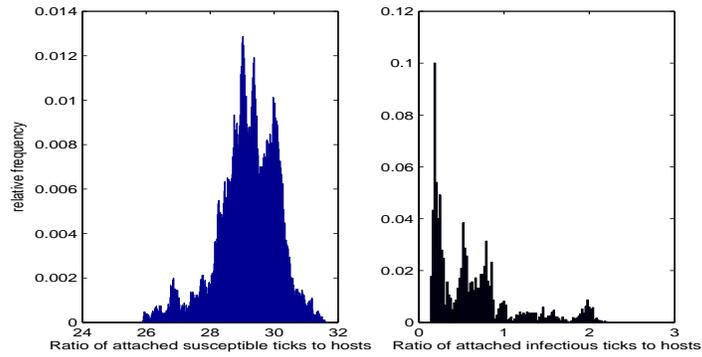


Figure 3: Distribution (over time in the simulation) of the number of attached susceptible and infective ticks per host at endemic level for parameters chosen for case 15.

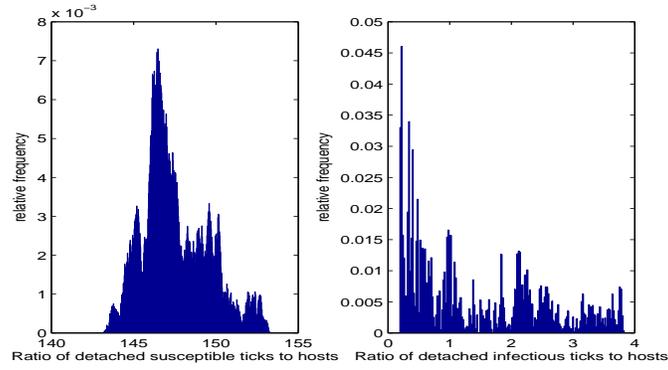


Figure 4: Distribution (over time in the simulation) of the number of attached susceptible and infective ticks per host at endemic level for parameters chosen for case 15.

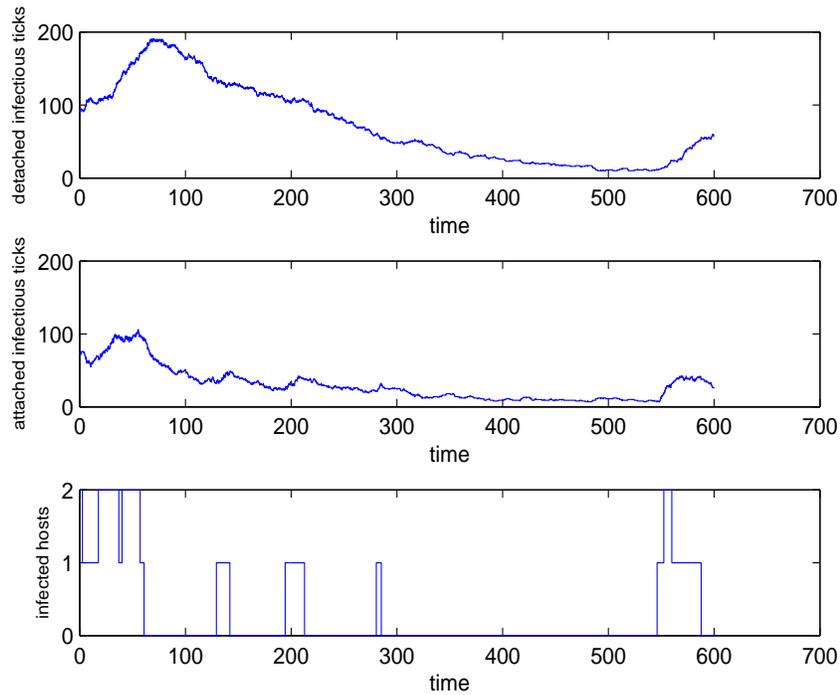


Figure 5: Plot of the distribution of infectious ticks (detached and attached) and infected hosts over time starting at the endemic level for case 15.

7 Discussion

In this paper, we have developed a stochastic epidemic model for tick-borne diseases and considered the threshold properties for the persistence of the disease, the probability of an epidemic occurring and the endemic levels of the disease.

We observed that the necessary condition for the persistence of the disease, if it is introduced when the tick-host interaction system is in equilibrium, depends on the parameters governing the population dynamics of the system as well as the infection transmission between ticks and hosts, Equation(6). The effect of these parameters on the persistence of the disease can therefore be determined. From numerical examples in Section 6, we observe how the parameters that are considered most influential in determining the disease transmission dynamics affect the tick-host-disease system. An increase in the values of the two infection transmission rates and/or the tick-host encounter rate (and consequently the tick attachment rate) lead to an increase in the number of infectives while an increase of the value of the tick detachment rate leads to a decrease in the number of infectives at the endemic level. With reliable data for various parameter values in the model, Equation(6) can be a useful tool in application to disease control strategies with efforts focused on reducing parameters that enhance the spread of the epidemic and simultaneously increasing parameters that reduce the spread. One way of achieving this is by making hosts resistant to tick infestation (Mwambi, 2002) as well as vaccination (O’Callaghan *et al.*,1999).

The threshold parameter derived is reasonably similar to the one obtained for the related deterministic model developed by Mwambi(2002). Both thresholds are increasing in the attachment rate, tick birth rate, and the infection transmission rates. They both decrease in tick mortality rate for detached ticks, host recovery rate, host mortality rate and tick detachment rate. One difference in the two quantities is that the threshold quantity obtained by Mwambi depends on parameters governing the tick-host-disease system as well as the host density whereas the one we obtain depends only on the parameters governing the tick-host-disease system. The reason that the threshold obtained in this study does not depend on host density is that we define the tick-host ratio in terms of the parameters governing the disease free tick-host interaction system (Section 2.2). The other difference is in the choice of functions of the tick detachment rate and tick mortality rate for attached ticks. Mwambi (2002) considers the tick detachment rate as an increasing function of the host population whereas in our model it is independent of the host population. The detachment of an attached tick occurs when it has had a complete blood meal or when it falls off the host due to reasons (like the host shaking it off) not dependent on whether there are other

hosts to attach onto, hence we consider detachment to be independent of host population. The tick mortality rate for attached ticks is incorporated in the deterministic model defined by Mwambi but in our model we disregard it. Most literature on epidemic modelling for tick borne diseases (O’Callaghan *et al.* (1998), Gilbert *et al.*, (2001) and Rosa *et al.*, (2007) among others) do not cite mortality of ticks while attached to hosts, therefore we did not include it in our model.

One advantage of stochastic models is that the probability that an epidemic (major outbreak) occurs can be derived. In our model we have shown that this probability can be obtained from the parameters governing the tick-host-disease system. From Section 6, we see that reducing T also reduces the probability of a major outbreak, hence any measures taken to reduce T simultaneously reduces $(1 - \pi)$. This result can not be obtained from deterministic models which simply state with certainty that either an epidemic occurs or it does not.

The model developed here has some limitations which should be addressed in order to for it to be more accurate in modelling the tick-host system as well as making it more useful in its application to control and intervention strategies. One limitation is the simplification of the stage structure of the tick vector. In reality, the tick vector goes through four different stages in its life cycle which in our model we have grouped into one compartment. However as noted in Perry *et al.* (1993) and O’Callaghan *et al.* (1998), each developmental stage has different effects on the tick-host interaction system as well as the disease transmission dynamics. Another limitation is in the role of recovered hosts. We have assumed that recovered cattle become immune and play no further role in the spread of the disease. In reality, most of these animals may get infected again (secondary infection) and become carriers of the disease. Susceptible ticks attaching to them may get infected and since they remain infectious for long periods of time, the disease may persist for a long time leading to an endemic state (Medley, 1994). Another limitation is that the infectious periods and life durations are assumed to be exponentially distributed. Lastly, we model the attachment rate as a decreasing function of the overall number of attached ticks rather than the actual number on the host in question.

The limitations notwithstanding, we believe our results are a first step towards more realistic stochastic modelling of tick borne diseases.

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