Stockholm University

Stochastic epidemic models for tick-borne diseases

Anne Wangombe

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Anne Wangombe *†

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Abstract

This thesis consists of two papers

1. Wangombe A., Andersson M., Britton T. (2009): A stochastic epidemic model for tick borne diseases: initial stages of an outbreak and endemic levels, (submitted).
2. Wangombe A., Andersson M., Britton T. (2009): A stage-structured stochastic epidemic model for tick borne diseases, (Manuscript).

Both papers deal with the formulation of stochastic models for the spread of tick-borne diseases amongst cattle. Multi-type branching process approximation of the early stages of the epidemic process is used to derive a threshold quantity which determines whether an epidemic may take off in the tick-host system as well as outbreak probabilities when above threshold. Expressions of the endemic level in case of a major outbreak are also derived. A "homogeneous version" of the stage-structured model is defined and compared with the one-stage model. It is shown that the two models are different.

Keywords: endemic equilibrium; epidemic model; multi-type branching process; threshold quantity; tick-borne diseases

*Present address: Mathematical Statistics, Stockholm University, SE-10691, Sweden

†Permanent address: School of Mathematics, University of Nairobi, P.O Box 30197-00100, Nairobi. E-mail: wachiraanne@hotmail.com

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1 Introduction

Mathematical models have become important tools in analysing the spread and control of infectious diseases. The models are either deterministic or stochastic in nature. When dealing with large population sizes, deterministic models are often appropriate as they model the average large scale behaviour of the random phenomenon of the epidemic process. Stochastic models on the other hand capture the random variations of the epidemic process and are therefore better suited for describing the epidemic, especially for small populations, where these variations cannot be neglected. Stochastic models have the advantage that outbreak probabilities, final size distribution and expected duration of an epidemic can be derived. They 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, even though they are less tractable and more complex to analyse than deterministic models, they are more ideal if one can construct a manageable and tractable model.

One question where stochastic models are important is the conditions under which an epidemic may take off infecting a large community fraction (possibly leading to an endemic situation). This is achieved through *coupling* the epidemic process with a branching process (see Ball, 1983; Ball & Donnelly, 1995). These conditions which give the threshold of the disease are defined in terms of a threshold parameter commonly referred to as the basic reproduction number R_0 for simple models and for more complex models, threshold quantities with similar properties to those of R_0. If $R_0 \leq 1$, the epidemic cannot take off in the population , whereas if $R_0 > 1$, there is a positive probability that there is a major outbreak. The threshold quantities as well as R_0 are defined in terms of the spectral radius of the next-generation matrix, which gives the expected number of infections given the distribution of infectious individuals in the present generation. Outbreak probabilities are also derived using the same branching process approximation.

Tick-borne diseases like other vector-borne diseases can be modelled using S-I-R compartmental models for the hosts ans S-I models for the vector. However ticks have unique life histories that create epidemics that differ from other vector-borne diseases, they need to attach to one or more hosts during their developmental stages. A tick has four developmental stages: egg, larvae, nymph and adult, and it requires to attach to a host for a blood meal at least once at the stages of larvae, nymph and/or adult stage. Our focus is on the ticks that attach at the three stages and are hence referred to as three-host ticks (see Figure 1).

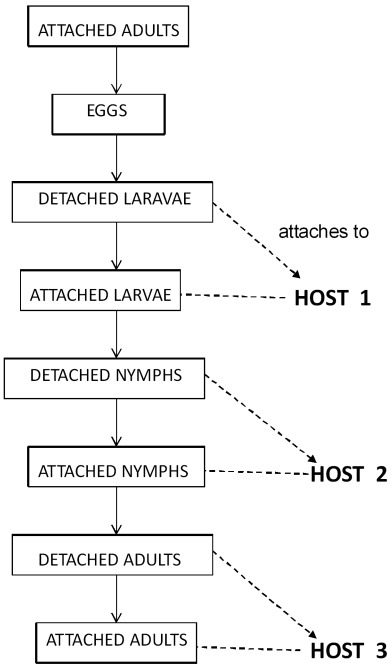

Figure 1: The developmental stages in the life cycle of a three-host tick.

It is during the attachment that a tick may transmit the disease if infected and is attached to a susceptible host, or it can get infected if susceptible and attached to an infectious host. A simple way of describing the transmission dynamics would be to disregard the stage structure of the tick as is done in Paper 1. On the other hand it is of interest to find out if anything is gained by including the stage structure of the tick as is done in Paper 2. A brief summary of both papers is now given below.

In the first paper, we define a stochastic model motivated by the deterministic model developed by Mwambi (2002). We combine all the stages of the tick into one compartment and only classify a tick according to its infectious state and whether or not it is attached to a host, and the host population is categorised as susceptible, infected or recovered. The model developed is a seven dimensional Markov process. For this model, a tick may attach and detach several times before dying, and this will have an impact on the transmission dynamics of the disease. Using a three-type branching process approximation, a threshold parameter, which determines whether the epidemic may take off in the tick-cattle system, is derived. The threshold parameter is shown to increase in the infection transmission rate from host to tick, the transmission rate from tick to host, 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. The threshold parameter derived is reasonably similar to the one obtained for the related deterministic model developed by Mwambi(2002) with minor differences as a result of definition of some of the parameters. Outbreak probabilities are computed using the branching process approximation and expressions for endemic level

in case of a major outbreak are derived. All results obtained are illustrated using numerical examples and simulations. The outbreak probabilities as well as the infectious proportions of the hosts and ticks at the endemic level increase as the threshold parameter increases.

In the second paper, a stochastic model that incorporates the stage structure of the tick is formulated with an aim of developing a more realistic model than the one developed in the first paper. The model is therefore an extension of the model developed in Paper 1 and is a fourteen dimensional Markov process. With the incorporation of the stage structure, a tick can only attach three times and of this, it can get infected only at the larvae and nymph stages and may infect a susceptible host only at the nymph and adult stages. The transmission dynamics will therefore differ with those of the simpler model in Paper 1. The threshold condition for the persistence of the disease, the probability of a major outbreak and endemic level of the disease are derived. The threshold condition is defined in terms of a threshold quantity which depends on the population dynamics parameters of the tick-host system as well as the transmission parameters. It is shown that the number of infectives in the tick-host system increase when the tick attachment rates of the different stages of the tick, the transmission rates from host to larvae (nymph) and the transmission rate from nymph (adult) to host increase; and decrease when the tick detachment rates for the different stages of the tick increase. A threshold quantity similar to the one derived in this paper is obtained using a deterministic model by Rosà *et al.* (2007). A comparison of a "homogeneous version" of the more complicated model and the one stage model is done. The two models (one stage and homogeneous version) are made as similar as possible through calibration of their model parameters. It is shown that the two models are genuinely different with the homogenous version having smaller threshold quantity and lower outbreak probabilities. The reason for this is that an infected tick in the stage structured model infects fewer susceptible hosts (at most two) than in the one stage model. These results are illustrated using numerical examples and simulations.

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

ANNE WANGOMBE*†, MIKAEL ANDERSSON‡, TOM BRITTON§
Department of Mathematics, Stockholm University, SE-10691 Stockholm, Sweden

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

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 *babesia bigemina* and spread by the tick vector *Boophilus microplus* and East Coast Fever caused by *Theileria parva* and spread by the tick vector *Rhicephalus appendiculatus*, also

*E-mail: wachiraanne@hotmail.com
†Permanent adress: School of Mathematics, University of Nairobi, P.O Box 30197-00100, Nairobi.
‡E-mail: mikaela@math.su.se
§E-mail: tomb@math.su.se

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

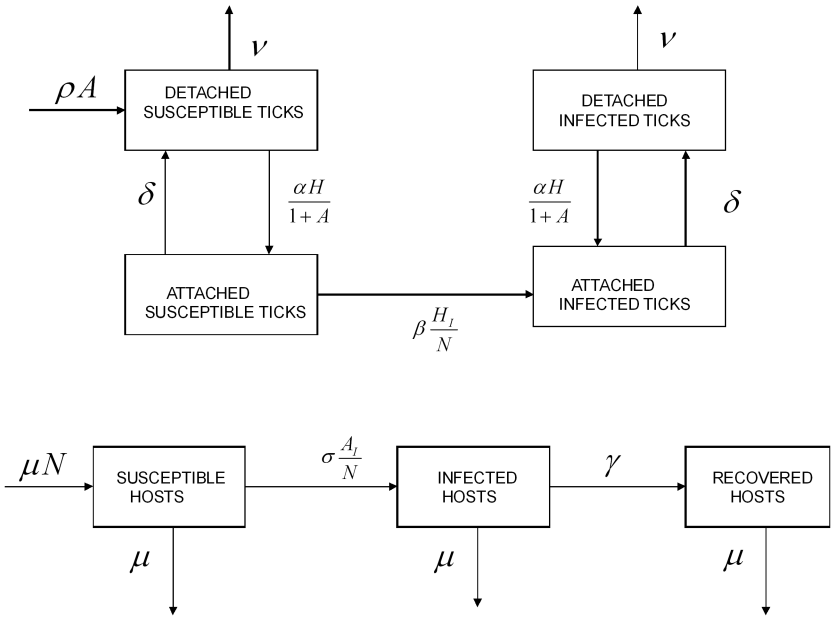

Figure 1: Schematic representation of the model.

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

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

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

$\hat{H}_S$, $\hat{A}_S$ 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 equlibrium 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 $\left(\frac{H_S(t)}{N} \simeq 1\right)$. 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

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

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

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

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

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

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

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

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

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

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

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

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

$$
\begin{aligned}
G_3(\mathbf{s}) &= E\left[s_1^{X_{21}} s_2^{X_{22}} s_3^{X_{23}}\right] = \sum_x s_2^x P(X_{32}=x) \\
&= \sum_x s_2^x \int_0^\infty (\mu+\gamma) e^{-(\mu+\gamma)t} \frac{e^{\left(\beta\frac{\hat{A}}{N}t\right)}\left(\beta\frac{\hat{A}}{N}t\right)^x}{x!} dt \\
&= \int_0^\infty (\mu+\gamma) e^{-(\mu+\gamma+\beta\frac{\hat{A}}{N})t} \left\{\sum_{x=0}^\infty s_2^x \frac{\left(\beta\frac{\hat{A}}{N}t\right)^x}{x!}\right\} dt \\
&= \int_0^\infty (\mu+\gamma) e^{-(\mu+\gamma+\beta\frac{\hat{A}}{N})t} e^{\beta\frac{\hat{A}}{N}ts_2} dt \\
&= (\mu+\gamma)\int_0^\infty e^{-(\mu+\gamma+\beta\frac{\hat{A}}{N}-\beta\frac{\hat{A}}{N}s_2)t} dt \\
&= \frac{N(\mu+\gamma)}{N(\mu+\gamma)+\beta\hat{A}-\beta\hat{A}s_2}.
\end{aligned}
$$

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

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

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

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

and extinction probabilities are given by π_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 $t = 0$,

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

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

then

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

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

as $N \to \infty$ 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

$$\begin{aligned}
d'_S(t) &= \rho a(t) + \delta a_S(t) - \nu d_S(t) - \frac{\alpha h(t) d_S(t)}{a(t)} && (10)\\
d'_I(t) &= \delta a_I(t) - \nu d_I(t) - \frac{\alpha h(t) d_I(t)}{a(t)} && (11)\\
a_S^{\prime(t)} &= \frac{\alpha h(t) d_S(t)}{a(t)} - \delta a_S(t) - \beta h_I(t) a_S(t) && (12)\\
a'_I(t) &= \frac{\alpha h(t) d_I(t)}{a(t)} + \beta h_I(t) a_S(t) - \delta a_I(t) && (13)\\
h'_S(t) &= \mu - \mu h_S(t) - \sigma a_I(t) h_S(t) && (14)\\
h'_I(t) &= \sigma a_I(t) h_S(t) - \mu h_I(t) - \gamma h_I(t) && (15)\\
h'_R(t) &= \gamma h_I(t) - \mu h_R(t) && (16)
\end{aligned}$$

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 $t \to \infty$, 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

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

and

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

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:

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

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

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

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

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

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

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

$\left(\hat{d}_S, \hat{d}_I, \hat{a}_S, \hat{a}_I, \hat{h}_S, \hat{h}_I, \hat{h}_R\right)$ is unique and is the endemic equilibrium state. It only exists if $T > 1$. The state $\left(N\hat{d}_S, N\hat{d}_I, N\hat{a}_S, N\hat{a}_I, N\hat{h}_S, N\hat{h}_I, N\hat{h}_R\right)$ 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 ν=0.01, ρ=0.05, μ=0.0006 and γ=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 probabilty 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.

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

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 posssibility 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 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%

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

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.

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

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 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 illstrate 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

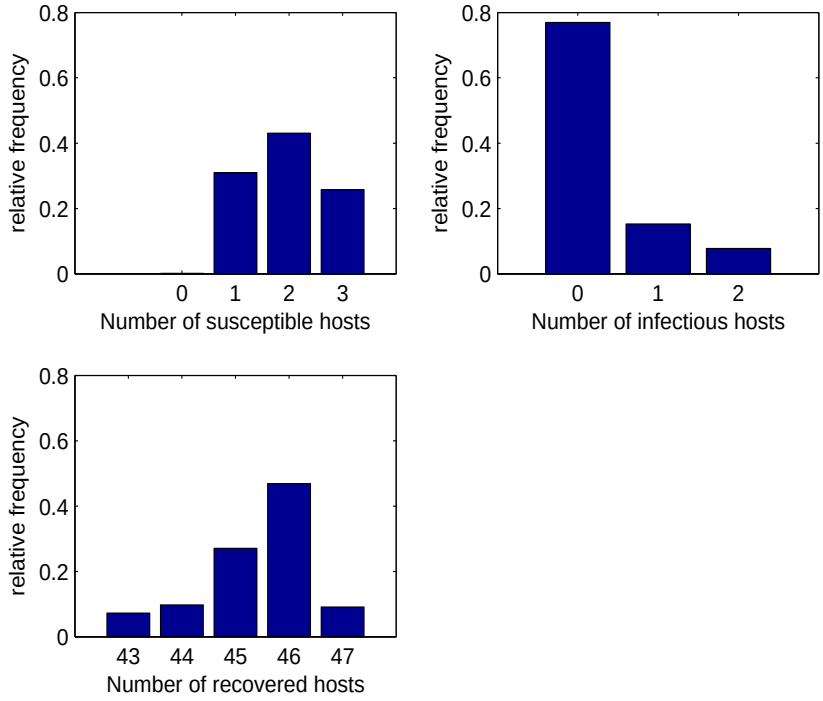

Figure 2: Distribution (over time in the simulation) of susceptible, infective and recovered hosts at endemic level for parameters chosen for case 15.

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

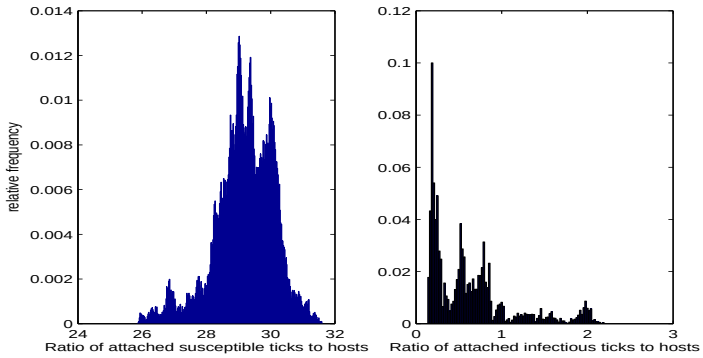

Figure 3: Distribution (over time in the simulation) of the number of attached susceptible and infective ticks per host at endemic level for parameters chosen for case 15.

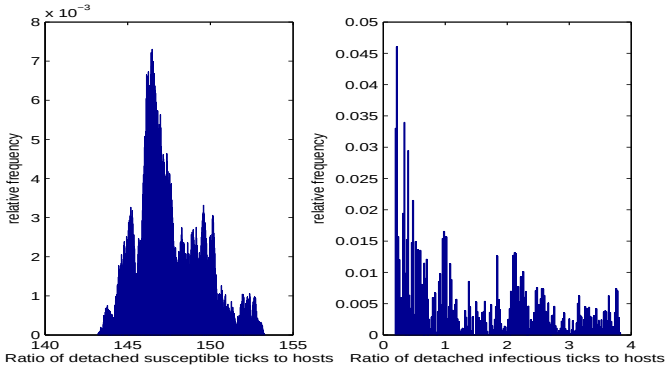

Figure 4: Distribution (over time in the simulation) of the number of attached susceptible and infective ticks per host at endemic level for parameters chosen for case 15.

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.

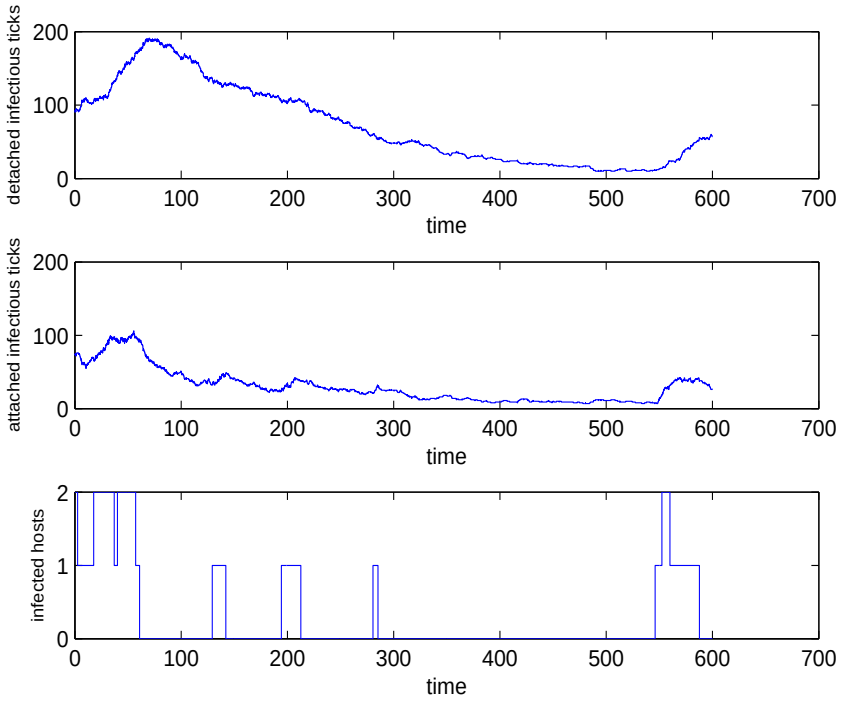

Figure 5: Plot of the distribution of infectious ticks (detached and attached) and infected hosts over time starting at the endemic level for case 15.

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 detachement 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 determinstic models which simply state with certainity 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 not withstanding, we believe our results are a first step towards more realistic stochastic modelling of tick borne diseases.

Acknowledgement

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A stage-structured stochastic epidemic model for tick-borne diseases

ANNE WANGOMBE*†, MIKAEL ANDERSSON‡, TOM BRITTON§
Department of Mathematics, Stockholm University, SE-10691 Stockholm, Sweden

Abstract

In this paper a stochastic model for the spread of tick-borne diseases amongst cattle, that incorporates the stage structure of the tick vector, is formulated. Using a three-type branching process approximation, a threshold quantity, determining if a major outbreak is possible, is derived as well as outbreak probabilities when above threshold. The approximation is based on the assumption that, at the initial stages of the epidemic, the sub-populations of susceptible larvae, nymphs and adult ticks as well as cattle are sufficiently large, while those of the infectives are small. Expressions for the endemic levels in case of a major outbreak are also derived.
The results are compared with those of a one stage model. It is shown that the two models are distinctively different, with the "homogeneous version" of the present model having a smaller threshold quantity, smaller outbreak probability and lower endemic levels of infectives.

Keywords: endemic equilibrium; multi-type branching process; parameters calibration; threshold quantity; tick-borne diseases

1 Introduction

In sub-Saharan Africa, ticks and tick-borne diseases are a major economic constraint to livestock production. The tick-borne diseases that pose a threat to livestock in this region include East Coast Fever transmitted by the parasite *Theileria parva* and spread by the tick vector *Rhicephalus appendiculatus*, heartwater caused by *Cowdria ruminatium* and spread by the tick vector *Amblyomma hebraeum* and babesiosis caused by *Babesia bigemina* and spread by the tick vector *Boophilus microplus*. These diseases have a massive impact through loss of animals and reduction of their productivity when they recover (Minijauw & Mc Leod, 2003). High costs associated with the control of ticks and treatment of the diseases

*E-mail: wachiraanne@hotmail.com
†Permanent adress: School of Mathematics, University of Nairobi, P.O Box 30197-00100, Nairobi.
‡E-mail: mikaela@math.su.se
§E-mail: tomb@math.su.se

further contributes to the poverty of cattle owners and there is therefore a continuous effort to manage these diseases (Minijauw & Mc Leod, (2003); International Livestock Research Institute website,`www.ilri.org`). Concern over these diseases has led to the development of mathematical models either describing the tick population and/or the disease transmission dynamics by several authors: Perry *et al.* (1993); Medley (1994); O'Callaghan *et al.* (1998); Mwambi *et al.* (2000); Mwambi (2002); Gilioli *et al.* (2009) and Wangombe *et al.* (2009). Several authors have also developed mathematical models for tick borne diseases affecting humans, Gilbert *et al.* (2001); Norman *et al.* (2003) and Rosa *et al.* (2007) among others.

The life cycle of a tick consists of four developmental stages namely egg, larvae, nymph and adult. Ticks are generally categorised according to the number of stages of the tick that require to attach on to a host for a blood meal. There are one-host ticks that attach only once at the larvae stage, there are two-host ticks that attach at the larvae and adult stages and finally the three-host ticks that attach at the larvae, nymph and adult stages (Minijauw & Mc Leod, 2003). The disease transmission dynamics therefore vary as the parasites which cause the diseases are transmitted by both the tick and host through feeding on the host. The model to be developed in the present paper considers a three-host tick as they are more abundant in Sub-Saharan Africa. Moreover the tick vectors *Cowdria ruminatium* and *Rhicephalus appendiculatus*, which transmit heartwater and East Coast Fever diseases that have the largest impact on the community, are three-host ticks (Torr *et al.*, 2002). For the three-host ticks, larvae and nymphs develop to nymphs and adults respectively after a complete blood meal and detachment from a host. For an adult tick, after detaching from a host it either dies or lays eggs if it is a female and then dies. For a tick to get infected and become infectious, it must feed on an infectious host, detach and develop to the next stage. Therefore only the larvae and nymphs can get infected and only the nymphs and adults can infect susceptible hosts. Once a tick is infectious it remains so throughout its remaing life cycle, thus a larvae that gets infected can infect at most two hosts at its nymph and adult stages.

Wangombe *et al.* (2009) developed a stochastic model describing the disease dynamics for a tick borne disease amongst cattle. The model defined is a seven dimensional Markov process. In the model, the three stages of the tick vector were combined into one compartment and the tick was only classified according to its infection status and whether or not it is attached to a host. For the host population it was categorised as susceptible, infected or recovered. Using a branching process approximation, a threshold condition which determines whether the epidemic may take off in the tick-cattle system was derived. Also the probabilty that an epidemic takes off is derived as well as expressions for the endemic level.

In the present paper we build on the model developed by Wangombe *et al.* (2009) by dividing the ticks into the three developmental stages of larvae, nymph and adult.

A threshold quantity which is a function of the population dynamics and transmission parameters and the probability of a major outbreak occurring are derived using branching process approximation. In case of a major outbreak, expressions for endemic level are also derived. Model parameters of a "homogeneous version" of the present model are compared with the one stage model of Wangombe *et al.*(2009). One comparison involves calibrating the population dynamics of the tick-host system while the other comparison involves calibrating the endemic levels of the attached ticks and hosts for both models. For both comparisons, we compare the thresholds and probability of an outbreak and it is shown that the "homogenous version" of the present model has a smaller threshold quantity and lower probability of a major outbreak occurring for both comparisons.
The rest of the paper is organized as follows: In Section 2 we describe the model. In Section 3 we derive the threshold conditions for the persistence of the disease as well as the probability of a major outbreak occurring using branching process approximations. The endemic levels are also derived for the case of being above threshold. In Section 4 we calibrate the model parameters and compare the present model with the one developed by Wangombe *et al.* (2009). In Section 5 we assess the results of Sections 3 and 4 using numerical examples and simulations. Finally in Section 6 we have a discussion and summary of results obtained.

2 A stochastic epidemic model

A stochastic epidemic model incorporating the different stages a tick vector undergoes in its life cycle is defined. The host population is classified as susceptible (H_S), infected (H_I) and recovered (H_R). The tick population is classified according to the three developmental stages as larvae (L), nymphs (N) and adults (A). The egg stage is not incorporated into the model as it is not directly related to the disease transmission dynamics. Each tick stage is further classified according to whether it is attached to a host or detached as well as its infection status (susceptible or infected). This classification of the ticks leads to categories such as L_{DS}, the number of detached susceptible larvae; L_{AI}, the number of attached infected larvae and so on. For each stage the first index denotes detachment/attachment and the second index denotes the infection status. The categories are eleven in total. Eggs laid by female adult ticks that hatch to become detached larvae are susceptible and hence there are no detached infected larvae (L_{DI}). Let the total number of attached larvae, nymphs and adults be denoted by L_A, N_A and A_A; i.e $L_A = L_{AS} + L_{AI}$, $N_A = N_{AS} + N_{AI}$ and $A_A = A_{AS} + A_{AI}$. Similarly let $L_D = L_{DS}$, $N_D = N_{DS} + N_{DI}$ and $A_D = A_{DS} + A_{DI}$ be the total number of detached larvae, nymphs and adult ticks. Finally let the total number of attached ticks be T_A, $T_A = L_A + N_A + A_A$.

2.1 Model definition

2.1.1 Host population dynamics without ticks and disease

We want a model such that the host population (per unit area) fluctuates around a constant value M, i.e $H(t) \simeq M$. The simple way to achieve this is to have the host birth rate μM constant and each host have a death rate μ, implying that the overall death rate is $\mu H(t)$.

2.1.2 Vector-host interaction system without the disease

The tick population is assumed to have no impact on the births and deaths in the host population so the host dynamics remain as described above.
The production rate of eggs is assumed to be proportional to the total number of attached adult ticks, $A_A(t)$. The eggs produced then hatch to become larvae and therefore we can let the rate at which larvae are produced be proportional to the attached adult ticks. Let ρ be the rate at which larvae are produced per attached adult tick, then the rate at which detached larvae are produced is $\rho A_A(t)$.
At each stage of larvae, nymph and adult; a tick attaches to a host. The attachment rate of each stage is treated as a decreasing function of the total number of attached ticks $T_A(t)$, and an increasing function of the host population $H(t)$. A tick at the larvae, nymph or adult stage encounters a host at the rates α_L, α_N or α_A. The functions chosen for the attachment rates of larvae, nymph and adult stages are $\frac{\alpha_L H(t)}{1+T_A(t)}$, $\frac{\alpha_N H(t)}{1+T_A(t)}$ and $\frac{\alpha_A H(t)}{1+T_A(t)}$ respectively. These functions are one of the many possible choices of the attachment rates that can be used.
Attached ticks at the larvae, nymph and adult stages detach at the respective rates d_L, d_N and d_A. Mortality of attached ticks is neglected. Detached ticks at larvae, nymph and adult stages die at respective rates δ_L, δ_N and δ_A.

2.1.3 Vector-Host-Disease interaction system

The nymph and adult ticks as well as the hosts may transmit the parasite that causes the disease. An infective nymph, while attached to a susceptible host infects the host at the rate λ_N, and the probability that the nymph is attached to a susceptible host is $\frac{H_S}{M}$, hence the overall infection transmission rate from nymph to host is $\lambda_N N_{AI}(t)\frac{H_S(t)}{M}$. Similarly, an infected adult tick may infect a susceptible host it is attached to at the rate λ_A and hence the overall infection transmission rate from an adult tick to a host is $\lambda_A A_{AI}(t)\frac{H_S(t)}{M}$.
While infectious, a host may infect a susceptible larvae attached to it at the rate β_L, and since the average number of susceptible attached larvae per host is $\frac{L_{AS}}{M}$, the overall transmission rate from host to larvae is $\beta_L H_I(t)\frac{L_{AS}(t)}{M}$. Similarly, an infective host may infect a susceptible nymph attached to it at the rate β_N, hence the overall transmission rate from host to nymph is $\beta_N H_I(t)\frac{N_{AS}(t)}{M}$. A susceptible adult tick that gets infected plays

no role in the epidemic process as it dies after detaching from the host it was attached to or if it is a female it lays uninfected eggs and dies.
An infected host dies at the rate μ or recovers at the rate γ, hence the overall death and recovery rates are $\mu H_I(t)$ and $\gamma H_I(t)$ respectively. Recovered hosts die at the rate $\mu H_R(t)$ The model is denoted by:

$$\begin{aligned}(L_{DS}, L_{AS}, L_{AI}, N_{DS}, N_{AS}, N_{DI}, N_{AI}, A_{DS}, A_{AS}, A_{DI}, A_{AI}, H_S, H_I, H_R) = \\ \{L_{DS}(t), L_{AS}(t), L_{AI}(t), N_{DS}(t), N_{AS}(t), N_{DI}(t), N_{AI}(t), A_{DS}(t), A_{AS}(t), \\ A_{DI}(t), A_{AI}(t), H_S(t), H_I(t), H_R(t); t > 0\}\end{aligned}$$

It is a fourteen dimensional Markov process with respective jump intensities as illustrated in Figure 1. The jump intensities are rates per individual host or tick except for ρA_A and μM.
Assumptions of the model:
We have made the following assumptions;

(i) There is uniform mixing of the hosts and ticks. This implies that any larvae has an equal chance of attaching to a host and similarly for the nymph and adult tick.

(ii) The environmental conditions are constant and ticks are constantly developing into various stages.

(iii) Susceptible attached larvae and nymphs get infected at a rate proportional to the total number of infectious hosts and thus the infection status of the actual host the larvae (nymph) is attached to is not relevant.

(iv) The attachment rate of each stage of the tick is proportional to the total number of ticks attached in the system and not the number attached to a particular host.

(v) All hosts have the same susceptibility and that there is no increased death rate of infectious hosts due to the disease.

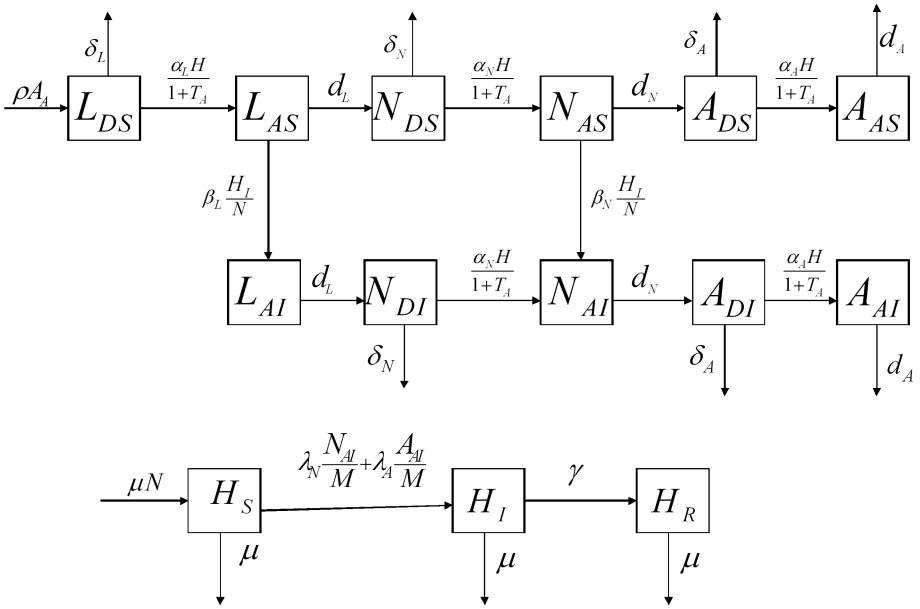

Figure 1: Schematic representation of the model

2.2 Disease free equilibrium state

Let us first consider the tick-host system before any disease is introduced.The uninfected tick-host interaction system is a Markov process with jump rates as illustrated in Figure 2. This sub-system is in equilibrium when the rates at which the individuals of the various subpopulations enter the subsystem are equal to the rates at which they leave the subsystem. Beginning with the host population,

$$\mu M = \mu H_S(t),$$

thus giving

$$\hat{H}_S = M.$$

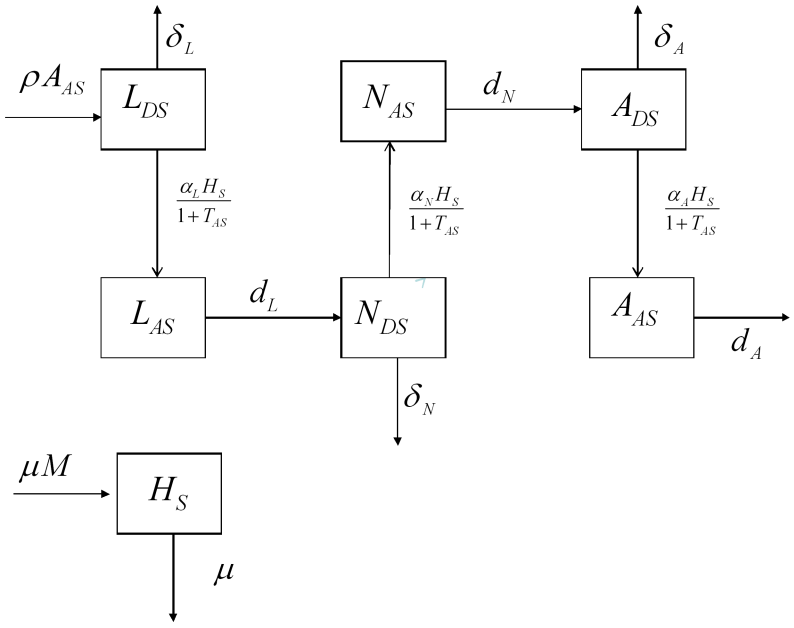

Figure 2: Schematic representation of the stages of the disease-free tick-host interaction system

For the tick population, it is at equilibrium when the incoming rates are equal to the outgoing rates for each tick stage, (see Figure 2). Thus;

$$\begin{aligned}
\rho A_{AS}(t) &= \left(\delta_L + \frac{\alpha_L H_S(t)}{1+T_{AS}(t)}\right) L_{DS}(t) \\
\frac{\alpha_L H_S(t)}{1+T_{AS}(t)} L_{DS}(t) &= d_L L_{AS}(t) \\
d_L L_{AS}(t) &= \left(\delta_N + \frac{\alpha_N H_S(t)}{1+T_{AS}(t)}\right) N_{DS}(t) \\
\frac{\alpha_N H_S(t)}{1+T_{AS}(t)} N_{DS}(t) &= d_N N_{AS}(t) \\
d_N N_{AS}(t) &= \left(\delta_A + \frac{\alpha_A H_S(t)}{1+T_{AS}(t)}\right) A_{DS}(t) \\
\frac{\alpha_A H_S(t)}{1+T_{AS}(t)} A_{DS}(t) &= d_A A_{AS}(t).
\end{aligned}$$

Using $1 + T_{AS} \simeq T_{AS}$, we obtain;

$$\begin{aligned}
\hat{L}_{DS} &= \frac{\rho\alpha_A M}{d_A(\delta_L \hat{T}_{AS} + \alpha_L M)}\hat{A}_{DS} \\
\hat{L}_{AS} &= \frac{\rho\alpha_L M}{d_L(\delta_L \hat{T}_{AS} + \alpha_L M)}\hat{A}_{AS} \\
\hat{N}_{DS} &= \frac{\alpha_L M}{\delta_N \hat{T}_{AS} + \alpha_N M}\hat{L}_{DS} \\
\hat{N}_{AS} &= \frac{d_L\alpha_N M}{d_N(\delta_N \hat{T}_{AS} + \alpha_N M)}\hat{L}_{AS} \\
\hat{A}_{DS} &= \frac{\alpha_N M}{\delta_A \hat{T}_{AS} + \alpha_A M}\hat{N}_{DS} \\
\hat{A}_{AS} &= \frac{d_N\alpha_A M}{d_A(\delta_A \hat{T}_{AS} + \alpha_A M)}\hat{N}_{AS}
\end{aligned} \tag{2.1}$$

where $\hat{T}_{AS} = \hat{L}_{AS} + \hat{N}_{AS} + \hat{A}_{AS}$. There is no explicit solution for (2.1). However from the equations the average number of attached ticks per host $\frac{\hat{T}_{AS}}{M}$ at equilibrium satistifies the condition

$$\left(\delta_L \frac{\hat{T}_{AS}}{M} + \alpha_L\right)\left(\delta_N \frac{\hat{T}_{AS}}{M} + \alpha_N\right)\left(\delta_A \frac{\hat{T}_{AS}}{M} + \alpha_A\right) = \alpha_L\alpha_N\alpha_A\frac{\rho}{d_A}. \tag{2.2}$$

For Equation (2.2) to have a positive solution for $\frac{\hat{T}_{AS}}{M}$, it is necessary that $\rho > d_A$, and from now on we assume that $\rho > d_A$.

3 Branching process

At the early stages of an epidemic in a population which is divided into several categories of distinguishable individuals, each having a large number of susceptible individuals and few infected 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 offsprings of possibly all types and individuals of the same type have the same offspring distribution of all type of individuals (Ch 11, Karlin & Taylor, 1975; Ch 4, Jagers, 1975)

In the present model, the disease is spread by individuals of three types: infective attached nymphs, infective attached adult ticks and infective hosts. An infective attached nymph produces one infective attached adult tick when it detaches from a host, develops to become an infected detached adult and then attaches to a host. It may also produce one infective host if attached to a susceptible host. An infective attached adult tick produces

one infective host if it infects the susceptible host it is attached to. Finally, an infective host may infect susceptible larvae and nymphs attached to it, which in turn detach, moult and may attach to other hosts becoming attached infected nymphs and attached infected adults respectively. Assuming the uninfected tick-host interaction system is in equilibrium at the time when the disease is introduced in the system with a few infectives of the three types then at the early stages the number of infectives in the population can be approximated by a three type branching process.

3.1 Threshold condition for persistence of disease

Let the infected host be of type 0, infected attached nymphs be of type 1 and infected attached adults be of type 2. Further let $\{X_{ij}; i, j = 0, 1, 2\}$ be the number of infectives of type j produced by an infective of type i and let $c_{ij} = E[X_{ij}]$. We derive the offspring distribution and its mean matrix.

An infected host infects larvae according to a Poisson process with rate $\beta_L \frac{\hat{L}_{AS}}{N}$ during its infectious period which is exponentially distributed with intensity $(\mu + \gamma)$. The Poisson distribution is an approximation since assume that the average number of susceptible larvae per host is large and constant over the infectious period so that the binomial distribution can be approximated using Poisson. An infected larvae then becomes an infected attached nymph with probability $\frac{\alpha_N M}{\delta_N \hat{T}_{AS} + \alpha_N M}$ as a detached infected nymph either attaches at the rate

$$\frac{\alpha_N H(t)}{1 + T_A(t)} \simeq \frac{\alpha_N \hat{H}_S}{\hat{T}_A} \simeq \frac{\alpha_N M}{\hat{T}_A}$$

since we assume large populations for the susceptible ticks and hosts, or it dies at the rate δ_N.

Conditioning on the length I of the infectious period, the number of infective nymphs produced by one infective host,X_{01}, is Poisson distributed with rate $\beta_L \frac{\alpha_N M}{\delta_N \hat{T}_A + \alpha_N M} I \frac{\hat{L}_{AS}}{M}$. Thus the number of infective attached nymphs, X_{01}, produced is mixed Poisson distributed and the expected number is;

$$\begin{aligned} E[X_{01}] &= E(E[X_{01}|I]) \\ &= E\left[\beta_L \frac{\hat{L}_A}{M} \frac{\alpha_N M}{\delta_N \hat{T}_A + \alpha_N M} I\right] \\ &= \left[\frac{\alpha_N \beta_L \hat{L}_A}{\delta_N \hat{T}_A + \alpha_N M}\right] E[I] \\ &= \frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu + \gamma)} \end{aligned}$$

as $\hat{L}_{AS} = \hat{L}_A$ at the initial stages of the epidemic.

In a similar manner, an infectious host produces infective attached adult ticks when it infects

susceptible nymphs attached to it which then become infected attached adults. Given that the infected host infects the nymphs according to a Poisson process with rate $\beta_N \frac{\hat{N}_A}{M}$, ($\hat{N}_{AS} = \hat{N}_A$) and the infected nymphs become attached infected adults with probability $\frac{\alpha_A M}{\delta_A \hat{T}_A + \alpha_A M}$; X_{02} too is mixed Poisson distributed (the mean of the distribution is given below).

An infectious host can not directly infect another host thus $X_{00} \equiv 0$.

The expected number of infective hosts, infective attached nymphs and infective attached adults produced by one infective host are hence

$$\begin{aligned} c_{00} &= E[X_{00}] = 0, \\ c_{01} &= E[X_{01}] = \frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu + \gamma)}, \\ c_{02} &= E[X_{02}] = \frac{\alpha_A \beta_N \hat{N}_A}{(\delta_A \hat{T}_A + \alpha_A M)(\mu + \gamma)}. \end{aligned}$$

An infected attached nymph produces one infective host if it attaches onto a susceptible host and infects it before detaching. While attached to the host for a period that is exponentially distributed with intensity d_N, it infects it at the rate λ_N since the probability of attaching to a susceptible host at the initial stages is one ($\frac{H_S}{M} \simeq 1$). Thus

$$\begin{aligned} P(X_{10} = 0) &= \frac{d_N}{d_N + \lambda_N}, \\ P(X_{10} = 1) &= \frac{\lambda_N}{d_N + \lambda_N}. \end{aligned}$$

An infected attached nymph can not directly infect an attached nymph hence $X_{11} \equiv 0$.

An infected attached nymph becomes an infected attached adult if it detaches, successfully develops to become an infected detached adult which then attaches onto a host before dying. Thus

$$\begin{aligned} P(X_{12} = 0) &= \frac{\delta_A \hat{T}_A}{\delta_A \hat{T}_A + \alpha_A M}, \\ P(X_{12} = 1) &= \frac{\alpha_A M}{\delta_A \hat{T}_A + \alpha_A M}. \end{aligned}$$

The expected number of infective hosts, infective attached nymphs and infective attached adults produced by one infective attached nymph are hence

$$\begin{aligned} c_{10} &= E[X_{10}] = \frac{\lambda_N}{d_N + \lambda_N}, \\ c_{11} &= E[X_{11}] = 0, \\ c_{12} &= E[X_{12}] = \frac{\alpha_A M}{\delta_A \hat{T}_A + \alpha_A M}. \end{aligned}$$

An infected attached adult tick can only produce an infected host hence $X_{21} \equiv X_{22} \equiv 0$. While an infected adult is attached to a susceptible host for a time period which is exponentially distributed with intensity d_A, it infects the host at the rate λ_A before detaching. Thus

$$\begin{aligned} P(X_{20}=0) &= \frac{d_A}{d_A+\lambda_A}, \\ P(X_{20}=1) &= \frac{\lambda_A}{d_A+\lambda_A}. \end{aligned}$$

The expected number of infective hosts, infective attached nymphs and infective attached adults produced by one infective attached adult are hence

$$\begin{aligned} c_{20} &= E[X_{20}] = \frac{\lambda_A}{d_A+\lambda_A}, \\ c_{21} &= E[X_{21}] = 0, \\ c_{22} &= E[X_{22}] = 0. \end{aligned}$$

Let $C = \{c_{ij}\}_{i,j=0}^{2}$ be the expectation matrix;

$$C = \begin{pmatrix} 0 & \frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu+\gamma)} & \frac{\alpha_A \beta_N \hat{N}_A}{(\delta_A \hat{T}_A + \alpha_A M)(\mu+\gamma)} \\ \frac{\lambda_N}{d_N+\lambda_N} & 0 & \frac{\alpha_A M}{\delta_A \hat{T}_A + \alpha_A M} \\ \frac{\lambda_A}{d_A+\lambda_A} & 0 & 0 \end{pmatrix}.$$

Let the characteristic polynomial of C be $f(\lambda)$;

$$\begin{aligned} f(\lambda) &= \lambda^3 - \lambda \left(\frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu+\gamma)} \frac{\lambda_N}{d_N+\lambda_N} + \frac{\alpha_A \beta_N \hat{N}_A}{(\delta_A \hat{T}_A + \alpha_A M)(\mu+\gamma)} \frac{\lambda_A}{d_A+\lambda_A} \right) \\ &\quad - \frac{\lambda_A}{d_A+\lambda_A} \frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu+\gamma)} \frac{\alpha_A M}{\delta_A \hat{T}_A + \alpha_A M}. \end{aligned}$$

The eigen-values of C are the roots of the equation,

$$f(\lambda) = 0.$$

From the signs of the coefficients of $f(\lambda)$, we can conclude that $f(\lambda)$ has an unique positive root and since C is a non-negative matrix, the largest positive root is greater than one if and only if $f(1) < 0$, that is if

$$\begin{aligned} R_* &= \frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu+\gamma)} \frac{\lambda_N}{d_N+\lambda_N} + \frac{\alpha_A \beta_N \hat{N}_A}{(\delta_A \hat{T}_A + \alpha_A M)(\mu+\gamma)} \frac{\lambda_A}{d_A+\lambda_A} \\ &\quad + \frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu+\gamma)} \frac{\alpha_A M}{\delta_A \hat{T}_A + \alpha_A M} \frac{\lambda_A}{d_A+\lambda_A} > 1. \end{aligned} \tag{3.1}$$

R_* is the threshold quantity for the tick-host system when the disease is introduced at equlibrium. It increases in the attachment rates for nymphs and adults; infection rates from nymphs and adults to hosts respectively as well as the infection rates from hosts to nymphs and adults respectively. It decreases in the detachment rates for nymphs and adults; the mortality rates of the nymphs and adults; the death and recovery rate of the hosts. R_* also depends on the average number of attached susceptible ticks per host in the system. If we express the number of attached susceptible ticks in terms of the average number attached per host as in Equation (2.2), we observe that R_* also increases in the tick birth rate. The expression R_* can be interpreted as the average number of infectious hosts produced indirectly by one primary infectious host: for the first term of the sum, an infectious host produces on average $\frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu+\gamma)}$ infected nymphs and each nymph will infect a susceptible host with probability $\frac{\lambda_N}{d_N+\lambda_N}$; for the second term, an infectious host produces on average $\frac{\alpha_A \beta_N \hat{N}_A}{(\delta_A \hat{T}_A + \alpha_A M)(\mu+\gamma)}$ infected adult ticks and each adult infects a susceptible host with probability $\frac{\lambda_A}{d_A+\lambda_A}$; and finally, each of the $\frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{T}_A + \alpha_N M)(\mu+\gamma)}$ infected nymphs produced by an infectious host will produce an infected adult with probability $\frac{\alpha_A M}{\delta_A \hat{T}_A + \alpha_A M}$ and the infected adult will then infect a susceptible host with probability $\frac{\lambda_A}{d_A+\lambda_A}$. Therefore R_* is the mean of a single type branching process approximation for the hosts. This approximation is otherwise rather complicated to calculate as the probability distribution of the offspring distribution is not easily attainable. A result that is almost similar to R_* is a threshold quantity obtained by Rosà *et al.* (2007) for a deterministic model for tick borne diseases transmitted by three-host ticks. The main difference is that Rosa *et al.* (2007) considered the infection transmission as related to detached (questing) ticks while in this paper we define the infection transmission in terms of attached ticks.

3.2 Probability of a major outbreak occurring

Let the probability generating function of the offspring distribution of infectives produced by an infective of type i $(i = 0, 1, 2)$, be $G_i(\mathbf{s}) = E\left[\prod_{j=0}^{2} s_j^{X_{ij}}\right]$, where X_{ij} is as defined in the previous section and $\mathbf{s} = (s_0, s_1, s_2)$. The probability that a minor outbreak of the disease occurs given that there are k_i infectives initially of each of the three types is $\pi = q_0^{k_0} q_1^{k_1} q_2^{k_2}$, where $\mathbf{q}$ is the solution of $\mathbf{s} = G(\mathbf{s})$ that is closest to the origin in the unit cube $[0, 1]^3$.

Since X_{01} and X_{02} are Poisson distributed conditioned on the infectious period I of the host, and $X_{00} \equiv 0$; the probability generating function of the number of infected hosts,

infected attached nymphs and infected attached adults produced by one infected host is;

$$\begin{aligned} G_0(\mathbf{s}) &= E\left[s_0^{X_{00}} s_1^{X_{01}} s_2^{X_{02}}\right] = E\left[E[s_1^{X_{01}} s_2^{X_{02}}|I]\right] \\ &= E\left(E\left[s_1^{X_{01}}|I\right] E\left[s_2^{X_{02}}|I\right]\right) \end{aligned}$$

Let $b_1 = \frac{\alpha_N \beta_L \hat{L}_{AS}}{\delta_N \hat{T}_A + \alpha_N M}$, $b_2 = \frac{\alpha_A \beta_N \hat{N}_{AS}}{\delta_A \hat{T}_A + \alpha_A M}$
Now,

$$\begin{aligned} E\left[s_1^{X_{01}}|I = t\right] &= \sum_{x=0}^{\infty} s_1^x \frac{(b_1 t)^x \, e^{-b_1 t}}{x!} \\ &= e^{-(b_1 t)(1-s_1)} \end{aligned}$$

Similarly,

$$E\left[s_2^{X_{02}}|I = t\right] = e^{-(b_2 t)(1-s_2)}$$

Thus

$$\begin{aligned} E\left[E\left(s_1^{X_{01}}|I\right)\left(s_2^{X_{02}}|I\right)\right] &= E[e^{-(b_1(1-s_1)+b_2(1-s_2))I}] \\ &= \int_0^{\infty} (\mu+\gamma) \quad e^{-(\mu+\gamma)t} e^{-(b_1(1-s_1)+b_2(1-s_2))I} dI \\ &= \frac{\mu+\gamma}{\mu+\gamma+b_1(1-s_1)+b_2(1-s_2)}. \end{aligned}$$

Substituting b_1 and b_2, the probability generating function is

$$G_0(\mathbf{s}) = \frac{(\mu+\gamma)}{(\mu+\gamma) + \frac{\alpha_N \beta_L \hat{L}_A (1-s_1)}{(\delta_N \hat{T}_A + \alpha_N M)} + \frac{\alpha_A \beta_N \hat{N}_A (1-s_2)}{(\delta_A \hat{T}_A + \alpha_A M)}} \tag{3.2}$$

Since $X_{11} \equiv 0$, X_{10} and X_{12} are either equal to 0 or 1, the probability generating function of the number of infected hosts, infected attached nymphs and infected attached adults produced by one infected attached nymph is

$$\begin{aligned} G_1(\mathbf{s}) &= E\left[s_0^{X_{10}} s_1^{X_{11}} s_2^{X_{12}}\right] \\ &= E[s_0^{X_{10}}] E[s_2^{X_{12}}] \\ &= \left(P(X_{10}=0)s_0^0 + P(X_{10}=1)s_0^1\right)\left(P(X_{12}=0)s_2^0 + P(X_{12}=1)s_2^1\right) \\ &= \left[\frac{d_N + \lambda_N s_0}{d_N + \lambda_N}\right]\left[\frac{\delta_N \hat{T}_A + \alpha_N M s_2}{\delta_N \hat{T}_A + \alpha_N M}\right] \end{aligned} \tag{3.3}$$

Finally, $X_{21} \equiv X_{22} \equiv 0$ and X_{20} is either equal to zero or one, therefore the probability generating function of the number of infected hosts, infected attached nymphs and infected attached adults produced by one infected attached adult is

$$\begin{aligned} G_2(\mathbf{s}) &= E\left[s_0^{X_{20}} s_1^{X_{21}} s_2^{X_{22}}\right] \\ &= E[s_0^{X_{20}}] = \left(P(X_{20}=0)s_0^0 + P(X_{20}=1)s_0^1\right) \\ &= \frac{d_A + \lambda_A s_0}{d_A + \lambda_A} \end{aligned} \tag{3.4}$$

The analytic solution for $\mathbf{s} = G(\mathbf{s})$ is quite complex to derive but let $\hat{s}_0$, $\hat{s}_1$ and $\hat{s}_2$ denote the solutions. Further let q_i=min(1,$\hat{s}_i$), $i = 0, 1, 2$,and k_0, k_1, k_2 be the initial number of infective hosts, attached infective nymphs and attached infective adults; then it follows from branching process theory (Ch II, Harris, 1989) that

(i) $q_0 = q_1 = q_2 = 1$ when $R_* \leq 1$ and $q_0 < 1$,$q_1 < 1$, $q_2 < 1$ when $R_* > 1$.

(ii) the probability of a minor outbreak occuring is $\pi = q_0^{k_0} q_1^{k_1} q_2^{k_2}$

(iii) the probabilty of a major outbreak is $1 - \pi$.

3.3 Endemic level

We now consider states where the system may be in equilibrium, the disease free equilibrium was already derived in Section 2.2. For the model defined, R_* is used to assess this equilibrium. If the disease is present initially in the tick-host system, then when $R_* \leq 1$ very few infections occur and the epidemic fades out quickly. On the other hand when $R_* > 1$ the epidemic may take off in the system and become endemic, taking the tick and host populations to an infection level known as the endemic level. At this level, the tick-host system is said to be in an endemic equilibrium state. This state is actually not a true equilibrium when considering a finite population; eventually the disease will die out. Prior to this the endemic equilibrium is a so called quasi-stationary distribution.

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 fourteen dimensional stochastic process converges to the trajectories of a fourteen dimensional deterministic dynamical system.
As $M \to \infty$, then suppose at $t = 0$,

$$\begin{aligned}
\left(\frac{L_{DS}(0)}{M}, \frac{L_{AS}(0)}{M}, \frac{L_{AI}(0)}{M}\right) &\xrightarrow{p} (l_{DS}(0), l_{AS}(0), l_{AI}(0)) \\
\left(\frac{N_{DS}(0)}{M}, \frac{N_{AS}(0)}{M}, \frac{N_{DI}(0)}{M}, \frac{N_{AI}(0)}{M}\right) &\xrightarrow{p} (n_{DS}(0), n_{AS}(0), n_{DI}(0), n_{AI}(0)) \\
\left(\frac{A_{DS}(0)}{M}, \frac{A_{AS}(0)}{M}, \frac{A_{DI}(0)}{M}, \frac{A_{AI}(0)}{M}\right) &\xrightarrow{p} (a_{DS}(0), a_{AS}(0), a_{DI}(0), a_{AI}(0))) \\
\left(\frac{H_S(0)}{M}, \frac{H_I(0)}{M}, \frac{H_R(0)}{M}\right) &\xrightarrow{p} (h_S(0), h_I(0), h_R(0))
\end{aligned}$$

then at time t, $0 < t \leq u$,(u is any finite time),

$$\begin{aligned}
\left(\frac{L_{DS}(t)}{M}, \frac{L_{AS}(t)}{M}, \frac{L_{AI}(t)}{M}\right) &\xrightarrow{p} (l_{DS}(t), l_{AS}(t), l_{AI}(t)) \\
\left(\frac{N_{DS}(t)}{M}, \frac{N_{AS}(t)}{M}, \frac{N_{DI}(t)}{M}, \frac{N_{AI}(t)}{M}\right) &\xrightarrow{p} (n_{DS}(t), n_{AS}(t), n_{DI}(t), n_{AI}(t)) \\
\left(\frac{A_{DS}(t)}{M}, \frac{A_{AS}(t)}{M}, \frac{A_{DI}(t)}{M}, \frac{A_{AI}(t)}{M}\right) &\xrightarrow{p} (a_{DS}(t), a_{AS}(t), a_{DI}(t), a_{AI}(t)) \\
\left(\frac{H_S(t)}{M}, \frac{H_I(t)}{M}, \frac{H_R(t)}{M}\right) &\xrightarrow{p} (h_S(t), h_I(t), h_R(t)).
\end{aligned}$$

The vector

$$(l_{DS}(t), l_{AS}(t), l_{AI}(t), n_{DS}(t), n_{AS}(t), n_{DI}(t), n_{AS}(t), a_{DS}(t), a_{AS}(t), a_{DI}(t), a_{AI}(t), h_S(t), h_I(t), h_R(t))$$

is deterministic and is the solution of

$$\begin{aligned}
l'_{DS}(t) &= \rho a_A(t) - \delta_L l_{DS}(t) - \frac{\alpha_L h(t) l_{DS}(t)}{t_A(t)} \\
l'_{AS}(t) &= \frac{\alpha_L h(t) l_{DS}(t)}{t_A(t)} - d_L l_{AS}(t) - \beta_L h_I(t) l_{AS}(t) \\
l'_{AI}(t) &= \beta_L h_I(t) l_{AS}(t) - d_L l_{AI}(t) \\
n'_{DS}(t) &= d_L l_{AS}(t) - \delta_N n_{DS}(t) - \frac{\alpha_N h(t) n_{DS}(t)}{t_A(t)} \\
n'_{AS}(t) &= \frac{\alpha_N h(t) n_{DS}(t)}{t_A(t)} - d_N n_{AS}(t) - \beta_N h_I(t) n_{AS}(t) \\
n'_{DI}(t) &= d_L l_{AI}(t) - \delta_N n_{DI}(t) - \frac{\alpha_N h(t) n_{DI}(t)}{t_A(t)} \\
n'_{AI}(t) &= \frac{\alpha_N h(t) n_{DI}(t)}{t_A(t)} + \beta_{HN} h_I(t) n_{AS}(t) - d_N n_{AI}(t) \qquad (3.5) \\
a'_{DS}(t) &= d_N n_{AS}(t) - \delta_A a_{DS}(t) - \frac{\alpha_A h(t) a_{DS}(t)}{t_A(t)} \\
a'_{AS}(t) &= \frac{\alpha_A h(t) a_{DS}(t)}{t_A(t)} - d_A a_{AS}(t) \\
a'_{DI}(t) &= d_N n_{AI}(t) - \delta_A a_{DI}(t) - \frac{\alpha_A h(t) a_{DI}(t)}{t_A(t)} \\
a'_{AI}(t) &= \frac{\alpha_A h(t) a_{DI}(t)}{t_A(t)} - d_A a_{AI}(t) \\
h'_S(t) &= \mu - \mu h_S(t) - (\lambda_N n_{AI}(t) + \lambda_A a_{AI}(t)) h_S(t) \\
h'_I(t) &= (\lambda_N n_{AI}(t) + \lambda_A a_{AI}(t)) h_S(t) - \mu h_I(t) - \gamma h_I(t) \\
h'_R(t) &= \gamma h_I(t) - \mu h_R(t)
\end{aligned}$$

For the model of Equation (3.5),

(i) If $l_{AI}(0) = n_{DI}(0) = n_{AI}(0) = a_{DI}(0) = a_{AI}(0) = h_I(0) = 0$, then the tick-host system starts in disease free equilibrium and it remains in that state.

(ii) If $l_{AI}(0) + n_{DI}(0) + n_{AI}(0) + a_{DI}(0) + a_{AI}(0) + h_I(0) > 0$ and $R_* \leq 1$, then the tick-host system converges to the disease free equilibrium as $t \to \infty$.

(iii) If $l_{AI}(0) + n_{DI}(0) + n_{AI}(0) + a_{DI}(0) + a_{AI}(0) + h_I(0) > 0$ and $R_* > 1$, a unique endemic equilibrium for the tick-host system exists.

Disease free equilibrium:
If $l_{AI}(0) = n_{DI}(0) = n_{AI}(0) = a_{DI}(0) = a_{AI}(0) = h_I(0) = 0$ the deterministic system is:

$$\begin{aligned}
l'_{DS}(t) &= \rho a_A(t) - \delta_L l_{DS}(t) - \frac{\alpha_L h(t) l_{DS}(t)}{t_A(t)} \\
l'_{AS}(t) &= \frac{\alpha_L h(t) l_{DS}(t)}{t_A(t)} - d_L l_{AS}(t) \\
n'_{DS}(t) &= d_L l_{AS}(t) - \delta_N n_{DS}(t) - \frac{\alpha_N h(t) n_{DS}(t)}{t_A(t)} \\
n'_{AS}(t) &= \frac{\alpha_N h(t) n_{DS}(t)}{t_A(t)} - d_N n_{AS}(t) \\
a'_{DS}(t) &= d_N n_{AS}(t) - \delta_A a_{DS}(t) - \frac{\alpha_A h(t) a_{DS}(t)}{t_A(t)} \\
a'_{AS}(t) &= \frac{\alpha_A h(t) a_{DS}(t)}{t_A(t)} - d_A a_{AS}(t) \\
h'_S(t) &= \mu - \mu h_S(t)
\end{aligned}$$

Equating this system of equations to zero;

$$\begin{aligned}
\hat{l}_{DS} &= \frac{\rho \hat{a}_A \hat{t}_A}{\alpha_L + \delta_L \hat{t}_A} \\
\hat{l}_{AS} &= \frac{\alpha_L \hat{l}_{DS}}{\hat{t}_A d_L} \\
\hat{n}_{DS} &= \frac{d_L \hat{t}_A \hat{l}_{AS}}{\alpha_N + \delta_N \hat{t}_A} \\
\hat{n}_{AS} &= \frac{\alpha_N \hat{n}_{DS}}{\hat{t}_A d_N} \\
\hat{a}_{DS} &= \frac{d_N \hat{t}_A \hat{n}_{AS}}{\alpha_A + \delta_A \hat{t}_A} \\
\hat{a}_{AS} &= \frac{\alpha_A \hat{a}_{DS}}{d_A \hat{t}_A} \\
\hat{h}_S &= 1
\end{aligned}$$

Further $\hat{l}_{DS} = \hat{l}_D$, $\hat{l}_{AS} = \hat{l}_A$, $\hat{n}_{DS} = \hat{n}_D$, $\hat{n}_{AS} = \hat{n}_A$, $\hat{a}_{DS} = \hat{a}_D$, $\hat{a}_{AS} = \hat{a}_A$ and $\hat{h}_S = \hat{h}$.

Alternatively, if $l_{AI}(0) + n_{DI}(0) + n_{AI}(0) + a_{DI}(0) + a_{AI}(0) + h_I(0) > 0$ and $R_* \leq 1$, then

$$[l_{AI}(t), n_{DI}(t), n_{AI}(t), a_{DI}(t), a_{AI}(t), h_I(t), h_R(t)] \to [0, 0, 0, 0, 0, 0, 0] \quad \text{as} \quad t \to \infty$$

and

$$[l_{DS}(t), l_{AS}(t), n_{DS}(t), n_{AS}(t), a_{DS}(t), a_{AS}(t), h_S(t)] \to [\hat{l}_D, \hat{l}_A, \hat{n}_D, \hat{n}_A, \hat{a}_D, \hat{a}_A, \hat{h}] \quad \text{as} \quad t \to \infty$$

Endemic equilibrium state:
When $R_* > 1$, then the epidemic may attain an endemic equilibrium state. This state is the solution of the system of equations in (3.5) with all derivatives equated to zero. Using $h(t) = 1$ and $\hat{t}_A = \frac{\hat{T}_A}{M}$, the solution can be shown to satisfy

$$\begin{aligned}
\hat{l}_{DS} &= \frac{\rho \hat{a}_A \hat{t}_A}{\alpha_L + \delta_L \hat{t}_A} \\
\hat{l}_{AS} &= \frac{\alpha_L \hat{l}_{DS}}{\hat{t}_A (d_L + \beta_L \hat{h}_I)} \\
\hat{l}_{AI} &= \frac{\beta_L \hat{h}_I \hat{l}_{AS}}{d_L} \\
\hat{n}_{DS} &= \frac{d_L \hat{t}_A \hat{l}_{AS}}{\alpha_N + \delta_N \hat{t}_A} \\
\hat{n}_{AS} &= \frac{\alpha_N \hat{n}_{DS}}{\hat{t}_A (d_N + \beta_N \hat{h}_I)} \\
\hat{n}_{DI} &= \frac{d_L \hat{t}_A \hat{l}_{AI}}{\alpha_N + \delta_N \hat{t}_A} \\
\hat{n}_{AI} &= \frac{\alpha_N \hat{n}_{DI} + \beta_N \hat{h}_I \hat{n}_{AS} \hat{t}_A}{\hat{t}_A d_N} \\
\hat{a}_{DS} &= \frac{d_N \hat{t}_A \hat{n}_{AS}}{\alpha_A + \delta_A \hat{t}_A} \\
\hat{a}_{AS} &= \frac{\alpha_A \hat{a}_{DS}}{d_A \hat{t}_A} \\
\hat{a}_{DI} &= \frac{d_N \hat{t}_A \hat{n}_{AI}}{\alpha_A + \delta_A \hat{t}_A} \\
\hat{a}_{AI} &= \frac{\alpha_A \hat{a}_{DI}}{d_A \hat{t}_A} \\
\hat{h}_S &= \frac{\mu}{\mu + \lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI}} \\
\hat{h}_I &= \frac{\mu(\lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI})}{(\mu + \gamma)(\mu + \lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI})} \\
\hat{h}_R &= \frac{\gamma(\lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI})}{(\mu + \gamma)(\mu + \lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI})}
\end{aligned} \tag{3.6}$$

In the stochastic model $(M\hat{l}_{DS}, M\hat{n}_{DS}, M\hat{n}_{DI}, M\hat{a}_{DS}, M\hat{a}_{DI},)$ is the endemic level for the detached ticks; $(M\hat{l}_{AS}, M\hat{l}_{AI}, M\hat{n}_{AS}, M\hat{n}_{AS}, M\hat{a}_{AS}M\hat{a}_{AI})$ for the attached ticks and $(M\hat{h}_S, M\hat{h}_I, M\hat{h}_R)$ for the host population. The tick-host system will fluctuate around this level for a long period of time for large M before going into extinction.

4 Calibration of the models

We now compare the threshold quantity, the probability of a major outbreak occurring and the endemic level of the present model and the one developed by Wangombe *et al.* (2009) where all stages of a tick are combined in one compartment. The purpose of the comparison is to find out if the more detailed model for the tick life cycle significantly changes the behaviour of the model after we make the two models as similar as possible through calibrating their model parameters.

To begin with, we define what we call the homogeneous version of the present model. For the homogeneous setting, we let $\alpha_L = \alpha_N = \alpha_A =: \alpha$, $d_L = d_N = d_A =: d$, $\delta_L = \delta_N = \delta_A =: \delta$, $\beta_L = \beta_N =: \beta$ and $\lambda_N = \lambda_A =: \lambda$. The homogeneous version of the present model and the model developed by Wangombe *et al.*(2009) will henceforth be referred to as the homogeneous model and one-state model respectively.

4.1 Equating the population dynamics and transmission parameters

To equate the population dynamics and infection transmission parameters; let the tick attachment rate, tick detachment rate, host birth (death) rate, host recovery rate, transmission rate from host to tick and transmission rate from tick to host have the same notation for both models.

Two parameters will differ for the two models, the tick birth rate and tick death rate. With regard to the tick birth rates, for the one-state model, the birth rate of the ticks is proportional to the total number of attached ticks whereas in the homogeneous model the tick birth rate is proportional to the total number of adult attached ticks. Also with regard to the tick death rates, for the one-state model ticks leave the system through death of detached ticks and in the present model, the ticks leave the system through death of detached larvae, detached nymphs, detached adults (before attaching) and attached adults who detach and die. Thus to make the population dynamics of the tick-host system equal in the two models we adjust the birth and death rates of the homogeneous model (see Fig.3).

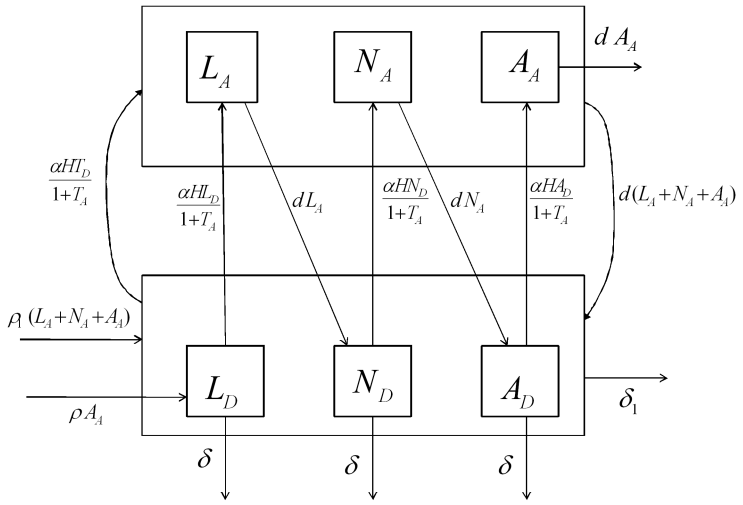

Figure 3: An illustration of the difference between the homogeneous and one-state model, the big boxes and arrows to and from them represent the one-state model while the smaller boxes with arrows to and from them represent the homogeneous model.

Let ρ_1 and δ_1 be the tick birth and death rates for the one-state model. Then we want

$$\begin{aligned} \rho_1(L_A(t) + N_A(t) + A_A(t)) &= \rho A_A(t), \\ \delta_1(L_D(t) + N_D(t) + A_D(t)) &= \delta(L_D(t) + N_D(t) + A_D(t)) + dA_A(t). \end{aligned}$$

To solve for ρ_1 and δ_1 we use Equations (2.1) and (2.2) so as to obtain the total number of attached (detached) larvae, nymphs and adult ticks. Substituting the parameters of the homogeneous model in Equation (2.1),

$$\begin{aligned} \left(\delta\frac{\hat{T}_A}{M} + \alpha\right)^3 &= \alpha^3\frac{\rho}{d} \\ \hat{T}_A &= \frac{\alpha M}{\delta}\left(\left(\frac{\rho}{d}\right)^{\frac{1}{3}} - 1\right). \end{aligned}$$

Using the result for $\hat{T}_A$ in Equation (2.1),

$$\begin{aligned}
\hat{L}_A &= \frac{\alpha\left(\frac{\rho}{d}-\left(\frac{\rho}{d}\right)^{\frac{2}{3}}\right)M}{\delta\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}+\left(\frac{\rho}{d}\right)^{\frac{1}{3}}+1\right)},\\
\hat{N}_A &= \frac{\alpha\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}-\left(\frac{\rho}{d}\right)^{\frac{1}{3}}\right)M}{\delta\left(\left(\frac{\rho}{\delta}\right)^{\frac{2}{3}}+\left(\frac{\rho}{\delta}\right)^{\frac{1}{3}}+1\right)},\\
\hat{A}_A &= \frac{\alpha\left(\left(\frac{\rho}{d}\right)^{\frac{1}{3}}-1\right)M}{\delta\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}+\left(\frac{\rho}{d}\right)^{\frac{1}{3}}+1\right)},\\
\hat{L}_D &= \frac{\rho\alpha}{\delta^2}\frac{\left(\left(\frac{\rho}{d}\right)^{\frac{1}{3}}-1\right)^2 M}{\left(\frac{\rho}{d}\right)^{\frac{1}{3}}\left(\frac{\rho}{d}\right)^{\frac{1}{3}}\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}+\left(\frac{\rho}{d}\right)^{\frac{1}{3}}+1\right)},\\
\hat{N}_D &= \frac{\rho\alpha}{\delta^2}\frac{\left(\left(\frac{\rho}{d}\right)^{\frac{1}{3}}-1\right)^2 M}{\left(\frac{\rho}{d}\right)^{\frac{2}{3}}\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}+\left(\frac{\rho}{d}\right)^{\frac{1}{3}}+1\right)},\\
\hat{A}_D &= \frac{\rho\alpha}{\delta^2}\frac{\left(\left(\frac{\rho}{d}\right)^{\frac{1}{3}}-1\right)^2 M}{\frac{\rho}{d}\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}+\left(\frac{\rho}{d}\right)^{\frac{1}{3}}+1\right)}.
\end{aligned}$$

Thus

$$\begin{aligned}
\rho_1 &= \frac{\rho\hat{A}_A}{\hat{L}_A+\hat{N}_A+\hat{A}_A}\\
&= \frac{\rho}{\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}+\left(\frac{\rho}{d}\right)^{\frac{1}{3}}+1\right)}, \qquad (4.1)
\end{aligned}$$

and

$$\begin{aligned}
\delta_1 &= \delta+\frac{\hat{A}_A}{\hat{L}_D+\hat{N}_D+\hat{A}_D}\\
&= \left(\frac{\rho}{\rho-d}\right)\delta. \qquad (4.2)
\end{aligned}$$

For the one-state model, we have $\hat{T}_A=\frac{\alpha\rho_1}{\delta_1 d}M$,

$$\begin{aligned}
\frac{\alpha\rho_1}{\delta_1 d}M &= \frac{\alpha M}{d}\frac{\rho}{\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}+\left(\frac{\rho}{d}\right)^{\frac{1}{3}}+1\right)}\frac{\rho-d}{\rho\delta}\\
&= \frac{\alpha M}{\delta}\left(\left(\frac{\rho}{d}\right)^{\frac{1}{3}}-1\right).
\end{aligned}$$

Let the total number of detached larvae, nymphs and adults be T_D, then $\hat{T}_D = \hat{L}_D + \hat{N}_D + \hat{A}_D$,

$$\hat{T}_D = \frac{\alpha M}{\delta^2} d \left(\left(\frac{\rho}{d} \right)^{\frac{1}{3}} - 1 \right)^2.$$

Similarly for the one-state model, we have

$$\begin{aligned} \hat{T}_D &= \frac{\alpha \rho_1^2 M}{d\delta^2} = T_A \frac{\rho_1}{\delta_1} \\ &= \frac{\alpha M}{\delta} \left(\left(\frac{\rho}{d} \right)^{\frac{1}{3}} - 1 \right) \frac{\rho}{\left(\left(\frac{\rho}{d} \right)^{\frac{2}{3}} + \left(\frac{\rho}{d} \right)^{\frac{1}{3}} + 1 \right)} \frac{\rho - d}{\rho \delta} \\ &= \frac{\alpha M}{\delta^2} d \left(\left(\frac{\rho}{d} \right)^{\frac{1}{3}} - 1 \right)^2, \end{aligned}$$

where the last equality follows from simple algebra. The tick-host system is in the same equilibrium state for the two models.

Comparison of threshold quantity

Let the threshold quantity for the one-state model be $R_*^{(1)}$ and for the homogeneous model be $R_*^{(2)}$. From Wangombe *et al.* (2009), the threshold quantity for the one-state model is

$$\frac{\beta \lambda \alpha \left(1 + \frac{\rho_1}{d} \right)}{\delta_1 (\lambda + d)(\mu + \gamma)}.$$

Using Equations (4.1) and (4.2)

$$R_*^{(1)} = \frac{\beta \alpha \lambda \left(\left(\frac{\rho}{d} \right)^{\frac{1}{3}} - \frac{d}{\rho} \right)}{\delta (\mu + \gamma)(\lambda + d)}. \tag{4.3}$$

Using Equation (3.1), the threshold quantity for the homogeneous model is

$$R_*^{(2)} = \frac{\beta \lambda \alpha \left(\left(\frac{\rho}{d} \right)^{\frac{2}{3}} + \left(\frac{\rho}{d} \right)^{\frac{1}{3}} - 2 \right)}{\delta (\lambda + d)(\mu + \gamma) \left(\left(\frac{\rho}{d} \right)^{\frac{2}{3}} + \left(\frac{\rho}{d} \right)^{\frac{1}{3}} + 1 \right)}. \tag{4.4}$$

This implies that

$$\frac{R_*^{(1)}}{R_*^{(2)}} = \frac{\left(\left(\frac{\rho}{d} \right)^{\frac{1}{3}} - \frac{d}{\rho} \right) \left(\left(\frac{\rho}{d} \right)^{\frac{2}{3}} + \left(\frac{\rho}{d} \right)^{\frac{1}{3}} + 1 \right)}{\left(\left(\frac{\rho}{d} \right)^{\frac{2}{3}} + \left(\frac{\rho}{d} \right)^{\frac{1}{3}} - 2 \right)} > 1, \quad \text{since} \quad \rho > d.$$

From this we conclude that $R_*^{(2)} < R_*^{(1)}$. The new model hence always has a smaller threshold R_*. The reason for this is that a tick can only infect at most two hosts in the new model whereas it may infect more in the one-state model. Analysis of this result is explored using numerical examples in Section 5. For cases where both $R_*^{(1)}$ and $R_*^{(2)}$ are larger than one, we compare the probability of major outbreak and endemic level.

4.2 Equating the endemic levels of attached ticks and hosts

In the previous subsection, we saw that the threshold quantity of the homogeneous model is lower than that of the one-state model and consequently we expect the probability of a major outbreak occurring and endemic levels of the homogeneous model to be lower. We now adjust the calibration by making the endemic levels of the attached ticks and hosts identical in the two models. It is not possible to have all the three endemic levels of detached ticks, attached ticks and hosts identical so we exclude the detached ticks as they do not directly lead to infection of either ticks or hosts.
Let β_1 and λ_1 be the infection transmission rate from host to tick and tick to host respectively for the one-state model. We fix these values for the one-state model and then find values for β and λ for the homogeneous model that give the same endemic levels. Using numerical examples we will compare the probability of a major outbreak occurring and the threshold quantity for the two models using this calibration.

5 Numerical examples

In this section we give examples to illustrate the results obtained in Sections 3 and 4.

5.1 The stage-structured stochastic epidemic model

The parameter values of the tick and host population dynamics as well as the infection transmission are based on the work of Branagan (1973), Randolph *et al.* (2004), O'Callaghan *et al.* (1998) and Gilioli *et al.* (2009). The tick attachment rates, tick detachment rates, tick mortality rates, host birth rate, host recovery rate are reciprocal of mean time (in days) to the event. The tick birth rate is the number of eggs laid per adult attached tick per day while the infection transmission rates have been estimated using the same idea as Wangombe *et al.* (2009), i.e for the transmission rate from nymph (adult) to host, it is a product of the rate at which the nymph (adult) feeds on the host and the probability that an infectious nymph (adult) transmits the infection. Similarly, the transmission rate from host to larvae (nymph) is a product of the feeding rate and the probability that an infectious host transmits the infection.We vary the tick attachment, tick detachment and the infection transmission rates simultaneously for the different stages of larvae, nymph and adult while keeping the rest of the parameters fixed. The resulting cases are sixteen and are given in Table 1.

5.1.1 Threshold quantity

Using Equations (2.1), (2.2) and (3.1); we compute the threshold quantity for the sixteen cases. The results are summarised in Table 1. From the results we observe that R_* has the largest value when the tick attachment rates and the infection transmission rates are high and tick detachment rates are low. Also R_* increases when the tick attachment rates and infection rates are increased individually while holding all other parameters constant. The results concur with the dependencies observed earlier in Section 3.

Table 1: Different parameter values for β_L, β_N, λ_N, λ_A α_L , α_N, α_A,d_L da_N, d_A; and the corresponding threshold parameter R_* with fixed values δ_L=0.02, δ_N=0.015, δ_A =0.005, ρ=0.75, μ=0.0006 and γ=0.05.

Case	β_L	β_N	λ_N	λ_A	α_L	α_N	α_A	d_L	d_N	d_A	R_*
1	0.01	0.016	0.005	0.008	0.05	0.1	0.15	0.5	0.2	0.125	0.03
2	0.05	0.08	0.005	0.008	0.05	0.1	0.15	0.5	0.2	0.125	0.15
3	0.05	0.08	0.020	0.032	0.05	0.1	0.15	0.5	0.2	0.125	0.50
4	0.01	0.016	0.020	0.008	0.05	0.1	0.15	0.5	0.2	0.125	0.10
5	0.01	0.016	0.005	0.008	0.05	0.1	0.15	0.1	0.07	0.05	0.19
6	0.05	0.08	0.005	0.008	0.05	0.1	0.15	0.1	0.07	0.05	0.97
7	0.05	0.08	0.02	0.032	0.05	0.1	0.15	0.1	0.07	0.05	2.06
8	0.01	0.016	0.02	0.032	0.05	0.1	0.15	0.1	0.07	0.05	0.41
9	0.01	0.016	0.005	0.008	0.2	0.3	0.5	0.1	0.07	0.05	0.73
10	0.05	0.08	0.005	0.008	0.2	0.3	0.5	0.1	0.07	0.05	2.37
11	0.05	0.08	0.02	0.032	0.2	0.3	0.5	0.1	0.07	0.05	6.91
12	0.01	0.016	0.02	0.032	0.2	0.3	0.5	0.1	0.07	0.05	1.38
13	0.01	0.016	0.005	0.008	0.2	0.3	0.5	0.5	0.2	0.125	0.12
14	0.05	0.08	0.005	0.008	0.2	0.3	0.5	0.5	0.2	0.125	0.62
15	0.05	0.08	0.02	0.032	0.2	0.3	0.5	0.5	0.2	0.125	2.10
16	0.01	0.016	0.02	0.032	0.2	0.3	0.5	0.5	0.2	0.125	0.42

5.1.2 Probability of a major outbreak

We have solved Equations (3.2)-(3.4) to obtain the probability of a major outbreak occurring when one infectious host, one infectious attached nymph and one infectious attached adult are introduced into a susceptible tick-host system. For cases where $R_* > 1$ out of the 16 cases above, the theoretical probabilities are summarised in Table 2. For all the other cases where the threshold quantity is below one, the probability of a major outbreak is

zero. We observe that the probability of a major outbreak $(1-\pi)$ does not increase as R_* increases. The trend ususally is that the probability of an outbreak increases as the threshold increases for simple epidemic models but there are exceptions for more complex models. However for cases 10, 11 and 12 where the population dynamics parameters are the same and only the infection transmission parameters vary, the outbreak probability increases as R_* increases. We ran 1000 simulations for the epidemic process for each of the five cases where $R_* > 1$ to obtain the fraction of major outbreaks occurring $(1-\tilde{\pi})$ and compared the results with the corrresponding theoretical probability $(1-\pi)$. For cases 10, 11 and 12, the tick population (before disease introduction) was in equilibrium with 12893 susceptible detached larvae, 781 suceptible attached larvae, 3243 susceptible detached nymphs, 421 susceptible attached nymphs, 1463 susceptible detached adult ticks and 448 susceptible attached adult ticks. Case 15 was in equilibrium with 8700 susceptible detached larvae, 205 suceptible attached larvae, 3135 susceptible detached nymphs, 277 susceptible attached nymphs, 1607 susceptible detached adult ticks and 378 susceptible attached adult ticks. Finally Case 7 was in equilibrium with 3646 susceptible detached larvae, 202 suceptible attached larvae, 775 susceptible detached nymphs, 123 susceptible attached nymphs, 397 susceptible detached adult ticks and 132 susceptible attached adult ticks. The susceptible host population (before disease introduction) was 50. The disease was introduced in the system by one infective attached nymph, one infective attached adult tick and one infective host. Each simulation was run until either there were no infectives in the system or there were 20 infectives in the system. It is assumed that if the number of infectives reaches 20 the epidemic will not go extinct thus leading to a major outbreak. The probability of a major outbreak is approximated by the fraction of simulations that reaches 20 infectives. The results are presented in Table 2 and they are overestimates of the theoretical probabilities though the values do not differ very much.

Table 2: Values of the theoretical probability of a major outbreak for all cases where $R_* > 1$.

Case	R_*	q_1	q_2	q_3	$(1-\pi)$	$(1-\tilde{\pi})$
12	1.38	0.835	0.938	0.933	0.274	0.287
7	2.06	0.555	0.834	0.826	0.617	0.648
15	2.10	0.512	0.904	0.900	0.583	0.595
10	2.37	0.485	0.940	0.928	0.577	0.599
11	6.91	0.169	0.716	0.676	0.918	0.946

5.1.3 Endemic level

We have solved the system of equations (3.6) to obtain the endemic level for the cases where R_* is larger than one. The results are summarised in Tables 3-5 for the host population, the attached ticks and detached ticks respectively. The endemic level for the infected hosts remains fairly constant for all cases while that of the susceptible hosts varies from 7% to 34%. For the ticks, we observe that the endemic levels vary and this is because the tick population sizes are different depending on the population parameters as is seen in Equation (2.2). For cases 10, 11 and 12 which have the same tick population size, the infectious proportions increase as the threshold quantity and probability of a major outbreak increases.
One simulation was carried out for case 11 for a duration of two years, beginning the process at the endemic level and the time averages during this period were used to obtain the endemic proportion of the host population and the average number of attached (detached) larvae, nymphs and adult ticks per host at the endemic level. The simulated values obtained are $\tilde{h}_S = 0.075$, $\tilde{h}_I = 0.008$, $\tilde{h}_R = 0.917$, $\tilde{l}_{AS} = 15.417$, $\tilde{l}_{AI} = 0.06$, $\tilde{n}_{AS} = 8.465$, $\tilde{n}_{AI} = 0.129$, $\tilde{a}_{AS} = 8.681$, $\tilde{a}_{AI} = 0.158$, $\tilde{l}_{DS} = 255.56$, $\tilde{n}_{DS} = 64.11$, $\tilde{n}_{DI} = 0.3$, $\tilde{a}_{DS} = 28.68$ and $\tilde{a}_{DI} = 0.47$. The results are very close to the numerical solutions for case 11 given in Tables 3-5.

Table 3: Endemic proportion for host population where $R_* > 1$.

Case	$\hat{h}_S$	$\hat{h}_I$	$\hat{h}_R$
12	0.340	0.008	0.652
7	0.231	0.009	0.760
15	0.282	0.008	0.71
10	0.275	0.009	0.716
11	0.069	0.011	0.920

Table 4: Endemic proportion for attached ticks per host where $R_* > 1$.

Case	$\hat{l}_{AS}$	$\hat{l}_{AI}$	$\hat{n}_{AS}$	$\hat{n}_{AI}$	$\hat{a}_{AS}$	$\hat{a}_{AI}$
12	15.620	0.012	8.400	0.020	8.850	0.020
7	4.040	0.018	2.430	0.030	2.620	0.030
15	4.090	0.003	5.510	0.024	7.530	0.033
10	15.560	0.061	8.310	0.120	8.740	0.120
11	15.540	0.090	8.270	0.150	8.710	0.160

To illustrate the full distribution of the simulated endemic levels of the susceptible

Table 5: Endemic proportion for detached ticks per host where $R_* > 1$.

Case	$\hat{l}_{DS}$	$\hat{n}_{DS}$	$\hat{n}_{DI}$	$\hat{a}_{DS}$	$\hat{a}_{DI}$
12	257.86	64.82	0.05	29.190	0.08
7	72.930	15.45	0.06	7.85	0.08
15	174.01	62.65	0.05	32.02	0.14
10	257.86	64.59	0.28	28.86	0.41
11	257.86	64.51	0.35	28.74	0.52

and infected hosts, attached nymphs and attached adult ticks for case 11, we have plotted histograms in Figures 4-6.

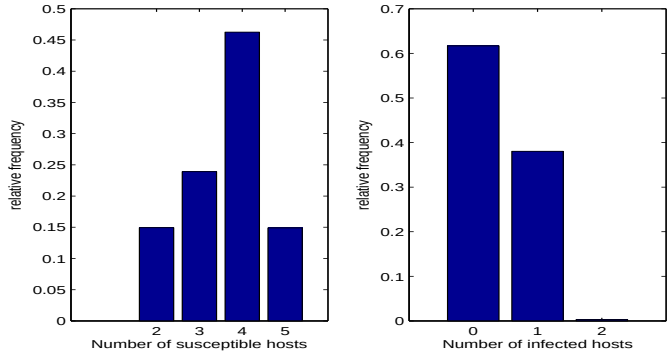

Figure 4: Distribution (over time in the simulation) of susceptible and infective hosts at the endemic level for parameters chosen for case 11.

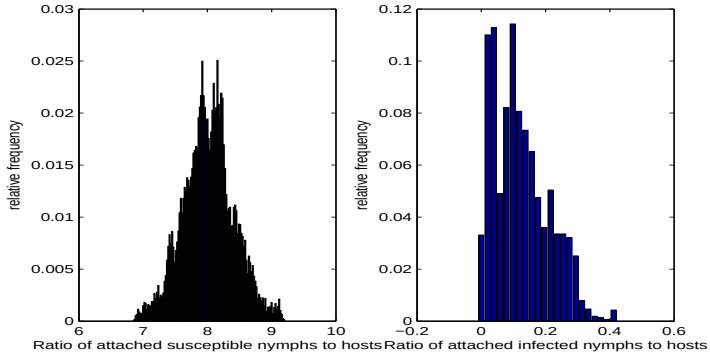

Figure 5: Distribution (over time in the simulation) of the number of attached susceptible and infective nymphs per host at the endemic level for parameters chosen for case 11.

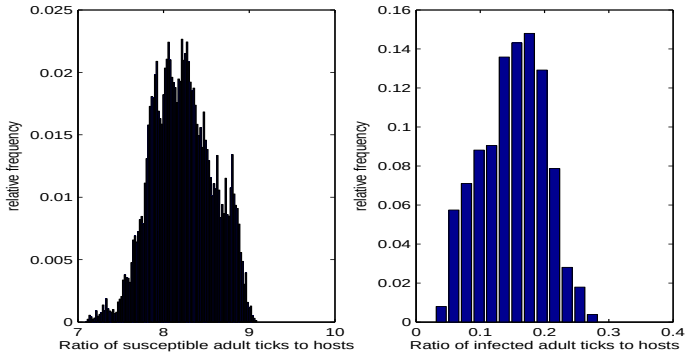

Figure 6: Distribution (over time in the simulation) of the number of attached susceptible and infective adult ticks per host at the endemic level for parameters chosen for case 11.

From Figure 4, we observe that the endemic proportion of the suceptible hosts ranges from 0.04 to 0.1 while that of the infected hosts ranges from 0 to 0.04. From Figure 5 we observe that the average number of attached susceptible nymphs per host varies between 6.84 and 9.2 and that of the infected attached nymphs varies between 0 and 0.35. Finally the average number of attached susceptible adult ticks varies between 7.1 and 9.1 while that of the attached infected adult ticks varies between 0.04 and 0.27 (Figure 6). In total there are two infectious ticks per host at the endemic level including the average number of attached infected larvae, detached infected nymphs and detached infected adult ticks.

5.2 Comparison of the two calibrated models

5.2.1 Equal population dynamics and transmission parameters

As mentioned earlier, we fix the population dynamics and transmission parameters for the one-state model and then obtain values for the tick birth and death parameters for the homogeneous model so that the population dynamics are equal for both models. All other parameters of the homogeneous model take on the same values as the one-state model. Using Equations (4.1) and (4.2), we obtain values for ρ and d from parameter values used in the one-state model. The threshold quantity, probability of a major outbreak occurring and endemic levels (where applicable) are computed for five sets of parameter values. The values are chosen so that we have a situation where both threshold quantities are larger than 1 and also where one quantity is below 1 and the other above 1. The results for $R_*^{(1)}$ and $R_*^{(2)}$ are summarised in Table 6 (where $R_*^{(1)}$ refers to the one-state model and $R_*^{(2)}$ to the homogeneous model) . Using Equations (3.2)-(3.4), we compute the probability of a major outbreak occurring for the cases presented in Table 6 and compare the results with those obtained for the one-state model. Both theoretical probabilities are presented in Ta-

Table 6: Different parameter values for β, λ, α and their corresponding threshold quantity values with $d = 0.05$, $\mu = 0.0006$, $\gamma = 0.05$, $\rho_1 = 0.05$, $\delta_1 = 0.01$, $\rho \approx 0.311$ and $\delta \approx 0.0084$ for the one-state and homogeneous model.

β	λ	α	R_*^1	R_*^2
0.01	0.005	0.3	1.08	0.33
0.05	0.02	0.03	1.69	0.52
0.01	0.02	0.3	3.39	1.05
0.05	0.005	0.3	5.39	1.66
0.05	0.02	0.3	16.94	5.22

ble 7 as $(1 - \pi^{(1)})$ for the one-state model and $(1 - \pi^{(2)})$ for the homogeneous model. The

Table 7: Values of the theoretical and simulated probabilities of a major outbreak for one-state and homogeneous model.

R_*^1	R_*^2	$(1 - \pi^{(1)})$	$(1 - \pi^{(2)})$	$(1 - \tilde{\pi}^{(1)})$	$(1 - \tilde{\pi}^{(2)})$
1.08	0.33	0.084	0.000	0.122	0.005
1.69	0.52	0.517	0.000	0.494	0.005
3.39	1.05	0.797	0.069	0.735	0.110
5.39	1.66	0.840	0.446	0.806	0.467
16.94	5.22	0.965	0.894	0.959	0.907

probabilites for the homogeneous model are lower than those of the one-state model. We ran 1000 simulations for the epidemic process of both models for the five cases in Table 7. Both of the tick-host systems were in equilibrium with 7500 susceptible detached ticks, 1500 susceptible attached ticks and 50 susceptible hosts. The procedure of estimating the probability of a major outbreak is as described in the earlier section. The results are presented in Table 7 as $(1 - \tilde{\pi}^{(1)})$ for the one-state model and $(1 - \tilde{\pi}^{(2)})$ for the homogeneous model. For both models the simulated values are relatively close to the theoretical probabilities.
The system of equations (3.6) is solved for the endemic level of the homogeneous model and compared with results obtained for the one-state model and the results are presented in Tables 8 and 9 for the host and tick populations respectively (the superscript 1 represents the one-state model and 2, the homogeneous model). As a consequence of the probability of a major outbreak being lower for the homogeneous model, the endemic levels for the susceptible sub-populations are higher.

Table 8: Theoretical endemic proportion for host population for one-state and homogeneous model where both the threshold quantities are larger than one.

$\hat{h}_S^{(1)}$	$\hat{h}_S^{(2)}$	$\hat{h}_I^{(1)}$	$\hat{h}_I^{(2)}$	$\hat{h}_R^{(1)}$	$\hat{h}_R^{(2)}$
0.211	0.463	0.009	0.006	0.780	0.531
0.172	0.374	0.010	0.007	0.818	0.619
0.043	0.094	0.011	0.011	0.946	0.895

Table 9: Theoretical values of the average number of attached ticks and detached ticks per host for one-state and homogeneous model where both threshold quantities are larger than one.

$\hat{t}_{AS}^{(1)}$	$\hat{t}_{AS}^{(2)}$	$\hat{t}_{AI}^{(1)}$	$\hat{t}_{AI}^{(2)}$	$\hat{t}_{DS}^{(1)}$	$\hat{t}_{DS}^{(2)}$	$\hat{t}_{DI}^{(1)}$	$\hat{t}_{DI}^{(2)}$
29.89	29.94	0.11	0.06	149.72	149.88	0.28	0.12
29.42	29.68	0.58	0.32	148.60	149.5	1.40	0.5
29.33	29.54	0.67	0.46	148.30	149.27	1.70	0.73

5.2.2 Equal endemic levels for attached ticks and hosts

We now calibrate the two models by instead equating the endemic levels as described in Section 4.2. We fix values for β_1, the infection transmission rate from host to tick and λ_1, the infection transmission rate from tick to host for the one-state model and then choose values for β and λ for the homogeneous model so that the endemic levels coincide. Using the results obtained and the values of the other parameters as given in the earlier example, we compute the probability of a major outbreak occurring and the threshold quantity. The results are summarised in Table 10.

Table 10: Infection parameters, threshold quantity, theoretical and simulated probability of a major outbreak for one-state and homogeneous models with equal endemic levels for attached ticks and hosts.

β_1	β	λ_1	λ	$R_*^{(1)}$	$R_*^{(2)}$	$(1-\pi^{(1)})$	$(1-\pi^{(2)})$	$(1-\tilde{\pi}^{(1)})$	$(1-\tilde{\pi}^{(2)})$
0.01	0.014	0.005	0.008	1.08	0.69	0.084	0.000	0.122	0.01
0.05	0.069	0.02	0.032	1.69	0.99	0.517	0.000	0.494	0.008
0.01	0.014	0.02	0.032	3.39	2.00	0.797	0.676	0.735	0.696
0.05	0.069	0.005	0.008	5.39	3.48	0.840	0.771	0.806	0.780
0.05	0.069	0.02	0.032	16.94	9.85	0.965	0.961	0.959	0.964

The threshold quantity is still considerably lower for the homogenous model. As for the probability of a major outbreak occurring, we observe that the values are relatively close

for the last case in Table 10 but differ considerably for the other two cases. We conclude that even though we increase the disease transmission rates, the threshold quantity and probability of a major outbreak are still lower for the homogeneous model. As in the previous subsection, we ran 1000 simulations using the same procedure for the homogeneous model with the new parameters for β and λ and the results of the proportions that do not go extinct are presented in Table 10 as $(1 - \tilde{\pi}^{(2)})$. Again the proportions are close to the theoretical probabilities. For the first two cases in Table 10 where $R_*^{(2)} < 1$, the endemic levels are very low and not sustainable for practical purposes. We expect that the endemic state is unstable and hence the disease free state is stable.

6 Discussion

In the present paper we have formulated a stochastic model for the spread of tick-borne diseases which incorporates the life stage structure of the ticks. The aim of this was to develop a more realistic model than the one developed earlier by Wangombe *et al.* (2009). The threshold condition for the persistence of the disease, the probability of a major outbreak and endemic level of the disease are derived. The threshold condition is defined in terms of a threshold quantity which depends on the population dynamics parameters of the tick-host system as well as the transmission parameters, Equation (3.1). In Sections 3.1 and 5.1.1, it was shown that the number of infectives in the tick-host system increase when the tick attachment rates of the different stages of the tick, the transmission rates from host to larvae (nymph) and the transmission rate from nymph (adult) to host increase; and decrease when the tick detachment rates for the different stages of the tick increase. Thus these parameters play a key role in the transmission dynamics of the disease when the tick-host system is in equilibrium. Any control strategy for the disease should therefore aim for a reduction in the parameters that enhance the disease and/or an increase in those that lead to a reduced spread. Similar results for the threshold quantity can be obtained using deterministic models as shown by Rosà *et al.* (2007). However the stochastic version has the advantage that we can calculate the probability of a major outbreak occurring, something which is not possible for a deterministic model.

We also compared the present three stage model with the one stage model in Wangombe *et al.* (2009). This is done to determine if anything is gained by making the model more complicated. To make meaningful comparisons, we defined a homogeneous version of the present model, and then calibrated the parameters of the homogeneous version and the one stage model of Wangombe *et al.* (2009). From the results in Sections 4 and 5.2, we see that the homogeneous version has smaller threshold and lower probability of a major outbreak despite the calibrations made of the two models. We therefore conclude that the two models

are genuinely different and that the present model gives a more realistic representation of the transmission dynamics of the disease. The main reason for better realism, as mentioned earlier, is that a tick in the present model infects fewer hosts (at most two in its life cycle) than in the previous model. By neglecting that a tick goes through several stages, the one stage model can be above threshold whereas in fact it is below when admitting the tick life stages. From a prevention perspective this is infact good news: The necessary amount of change in various parameters so as to come below threshold is *smaller* if admitting the tick life stages.

The present model has some limitations that could be incorporated to make the model more realistic. For example we assume that there is no increased mortality of infectious hosts due to the disease and yet as mentioned in the Introduction, the tick-borne diseases do lead to death of cattle. One possible extension of the present model is hence to consider increased mortality due to the disease as done in O'Callaghan *et al.* (1998). The role of wildlife that share open fields with the cattle is not considered and their presence could influence the population dynamics of the ticks and therefore lead to a dilution or enhancement of the disease. The role of carrier cattle may also be considered as they may lead to an enhancement of the disease even though their ability to transmit the infection is greatly reduced (O'Callaghan *et al.* (1998)). Lastly, assumptions like exponential life length for hosts and that attachment rates depend on the total number of attached ticks (rather than the number of attached ticks on the specific host in question) can be relaxed to make the model more realistic.

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Department of Mathematics
Stockholm University
SE-106 91 Stockholm

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