# A stage structured stochastic epidemic model for tick borne diseases

ANNE WANGOMBE *†

School of Mathematics, University of Nairobi,P.O Box 30197 00100, Nairobi

MIKAEL ANDERSSON ‡and 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.

*Corresponding author. Tel +254722370875. E-mail: wachiraanne@hotmail.com

†author did this study partially in Department of Mathematics, Stockholm University.

‡E-mail: mikaela@math.su.se

§E-mail: tomb@math.su.se

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# 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 ([1]). High costs associated with the control of ticks and treatment of the diseases further contributes to the poverty of cattle owners and there is therefore a continuous effort to manage these diseases ([1]; 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: [2]-[8]. Several authors have also developed mathematical models for tick borne diseases affecting humans,([9]-[11]) 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

([1]). 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 ([12]). 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.*[8] 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 of [8] 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 [8]. 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 "homogeneous 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 model in [8]. 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 $K_A$, $K_A = L_A + N_A + A_A$.

## 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 $\mu M$ constant and each host have a death rate $\mu$, 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 $\rho$ 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 $K_A(t)$, 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 $\alpha_L$, $\alpha_N$ or $\alpha_A$. The functions chosen for the attachment rates of larvae, nymph and adult stages are $\frac{\alpha_L H(t)}{1+K_A(t)}$, $\frac{\alpha_N H(t)}{1+K_A(t)}$ and $\frac{\alpha_A H(t)}{1+K_A(t)}$ 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 $\delta_L$, $\delta_N$ and $\delta_A$.

### 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 $\lambda_N$, 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 $\lambda_A$ 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 $\beta_L$, 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 $\beta_N$, 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 $\mu$ or recovers at the rate $\gamma$, 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:

$$(L_{DS}, L_{AS}, L_{AI}, N_{DS}, N_{AS}, N_{DI}, N_{AI}, A_{DS}, A_{AS}, A_{DI}, A_{AI}, H_S, H_I, H_R) =$$

$$\{L_{DS}(t), L_{AS}(t), L_{AI}(t), N_{DS}(t), N_{AS}(t), N_{DI}(t), N_{AI}(t), A_{DS}(t), A_{AS}(t),$$

$$A_{DI}(t), A_{AI}(t), H_S(t), H_I(t), H_R(t); t > 0\}$$

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 $\rho A_A$ and $\mu M$.

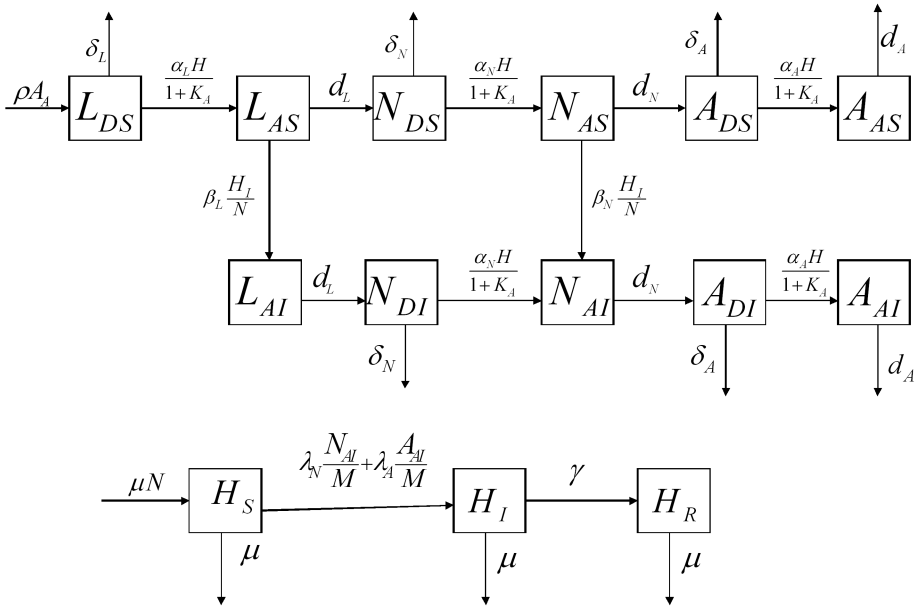


Figure 1: Schematic representation of the model

*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.

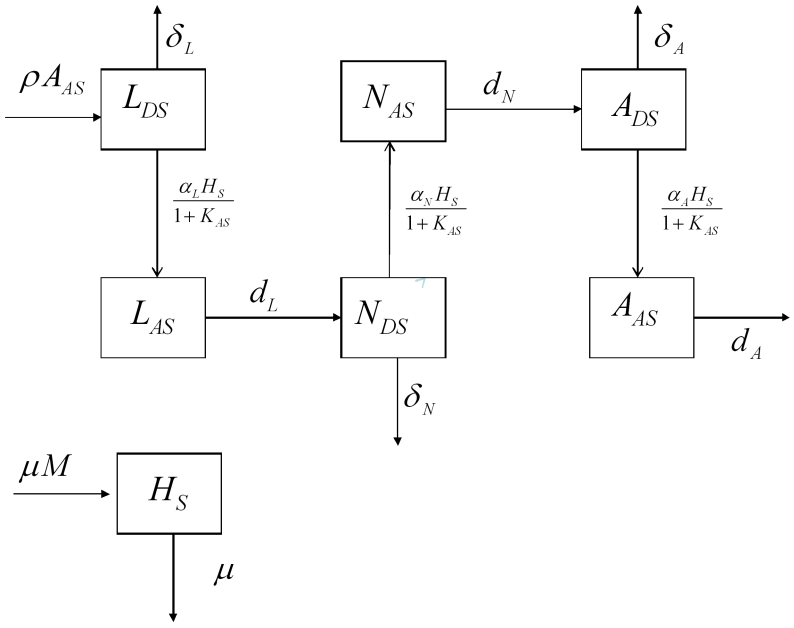


Figure 2: Schematic representation of the stages of the disease-free tick-host interaction system

## 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

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

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;

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

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

$$\begin{aligned}
\hat{L}_{DS} &= \frac{\rho\alpha_A M}{d_A(\delta_L \hat{K}_{AS} + \alpha_L M)} \hat{A}_{DS} \\
\hat{L}_{AS} &= \frac{\rho\alpha_L M}{d_L(\delta_L \hat{K}_{AS} + \alpha_L M)} \hat{A}_{AS} \\
\hat{N}_{DS} &= \frac{\alpha_L M}{\delta_N \hat{K}_{AS} + \alpha_N M} \hat{L}_{DS} \\
\hat{N}_{AS} &= \frac{d_L\alpha_N M}{d_N(\delta_N \hat{K}_{AS} + \alpha_N M)} \hat{L}_{AS} \\
\hat{A}_{DS} &= \frac{\alpha_N M}{\delta_A \hat{K}_{AS} + \alpha_A M} \hat{N}_{DS} \\
\hat{A}_{AS} &= \frac{d_N\alpha_A M}{d_A(\delta_A \hat{K}_{AS} + \alpha_A M)} \hat{N}_{AS}
\end{aligned} \tag{1}$$

where $\hat{K}_{AS} = \hat{L}_{AS} + \hat{N}_{AS} + \hat{A}_{AS}$. There is no explicit solution for (1). However from the equations the average number of attached ticks per host $\frac{\hat{K}_{AS}}{M}$ at equilibrium satistifies the condition

$$\left(\delta_L \frac{\hat{K}_{AS}}{M} + \alpha_L\right)\left(\delta_N \frac{\hat{K}_{AS}}{M} + \alpha_N\right)\left(\delta_A \frac{\hat{K}_{AS}}{M} + \alpha_A\right) = \alpha_L\alpha_N\alpha_A \frac{\rho}{d_A}. \tag{2}$$

For Equation (2) to have a positive solution for $\frac{\hat{K}_{AS}}{M}$, it is necessary that $\rho > d_A$. Since only attached adult ticks give birth to new ticks, the tick birth rate $\rho$ has to be greater than the detachment rate $d_A$ for the tick population to be able to survive. 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 ([13], [14]). 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 ([15],Ch 11; [16], Ch 4)

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

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

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

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 $\beta_L \frac{\alpha_N M}{\delta_N \hat{K}_A + \alpha_N M} I \frac{\hat{L}_{AS}}{M}$ . Thus the number of infective attached nymphs, $X_{01}$, produced is mixed Poisson distributed

and the expected number is;

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

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 $\frac{\alpha_A M}{\delta_A \hat{K}_A + \alpha_A M}$; $X_{02}$ 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

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

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 $\lambda_N$ 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

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

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

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

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 $\lambda_A$ 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;

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

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

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

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

$$\begin{aligned} T_* &= \frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{K}_A + \alpha_N M)(\mu+\gamma)} \frac{\lambda_N}{d_N+\lambda_N} + \frac{\alpha_A \beta_N \hat{N}_A}{(\delta_A \hat{K}_A + \alpha_A M)(\mu+\gamma)} \frac{\lambda_A}{d_A+\lambda_A} \\ &\quad + \frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{K}_A + \alpha_N M)(\mu+\gamma)} \frac{\alpha_A M}{\delta_A \hat{K}_A + \alpha_A M} \frac{\lambda_A}{d_A+\lambda_A} > 1. \end{aligned} \tag{3}$$

$T_*$ 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. $T_*$ 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), we observe that $T_*$ also increases in the tick birth rate. The expression $T_*$ 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 $\frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{K}_A + \alpha_N M)(\mu+\gamma)}$ 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 $\frac{\alpha_A \beta_N \hat{N}_A}{(\delta_A \hat{K}_A + \alpha_A M)(\mu+\gamma)}$ infected adult ticks and each adult infects a susceptible host with probability $\frac{\lambda_A}{d_A+\lambda_A}$; and finally, each of the $\frac{\alpha_N \beta_L \hat{L}_A}{(\delta_N \hat{K}_A + \alpha_N M)(\mu+\gamma)}$ infected nymphs produced by an infectious host will produce an infected adult with probability $\frac{\alpha_A M}{\delta_A \hat{K}_A + \alpha_A M}$ and the infected adult will then infect a susceptible host with probability $\frac{\lambda_A}{d_A+\lambda_A}$. Therefore $T_*$ 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 $T_*$ is a threshold quantity obtained by Rosà *et al.*[11] for a deterministic model for tick borne diseases transmitted by three-host ticks. The main difference is that in [11], the infection transmission is defined in terms of 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 $b_1 = \frac{\alpha_N \beta_L \hat{L}_{AS}}{\delta_N \hat{K}_A + \alpha_N M}$, $b_2 = \frac{\alpha_A \beta_N \hat{N}_{AS}}{\delta_A \hat{K}_A + \alpha_A M}$

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

$$G_0(\mathbf{s}) = \frac{(\mu+\gamma)}{(\mu+\gamma)+\frac{\alpha_N\beta_L\hat{L}_A(1-s_1)}{(\delta_N\hat{K}_A+\alpha_N M)}+\frac{\alpha_A\beta_N\hat{N}_A(1-s_2)}{(\delta_A\hat{K}_A+\alpha_A M)}} \tag{4}$$

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

$$\begin{aligned} G_1(\mathbf{s}) &= E\left[s_0^{X_{10}} s_1^{X_{11}} s_2^{X_{12}}\right] = E[s_0^{X_{10}}]E[s_2^{X_{12}}] \\ &= \left(P(X_{10}=0)s_0^0 + P(X_{10}=1)s_0^1\right)\left(P(X_{12}=0)s_2^0 + P(X_{12}=1)s_2^1\right) \\ &= \left[\frac{d_N+\lambda_N s_0}{d_N+\lambda_N}\right]\left[\frac{\delta_N\hat{K}_A+\alpha_N M s_2}{\delta_N\hat{K}_A+\alpha_N M}\right] \end{aligned} \tag{5}$$

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

$$\begin{aligned} G_2(\mathbf{s}) &= E\left[s_0^{X_{20}} s_1^{X_{21}} s_2^{X_{22}}\right] \\ &= E[s_0^{X_{20}}] = \left(P(X_{20}=0)s_0^0 + P(X_{20}=1)s_0^1\right) \\ &= \frac{d_A+\lambda_A s_0}{d_A+\lambda_A} \end{aligned} \tag{6}$$

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 $T_* \leq 1$ and $q_0 < 1$,$q_1 < 1$, $q_2 < 1$ when $T_* > 1$.

(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, $T_*$ is used to assess this equilibrium. If the disease is present initially in the tick-host system, then when $T_* \leq 1$ very few infections occur and the epidemic fades out quickly. On the other hand when $T_* > 1$ 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 [18] and [19], 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

$$\begin{aligned}
l'_{DS}(t) &= \rho a_A(t) - \delta_L l_{DS}(t) - \frac{\alpha_L h(t) l_{DS}(t)}{K_A(t)} \\
l'_{AS}(t) &= \frac{\alpha_L h(t) l_{DS}(t)}{K_A(t)} - d_L l_{AS}(t) - \beta_L h_I(t) l_{AS}(t) \\
l'_{AI}(t) &= \beta_L h_I(t) l_{AS}(t) - d_L l_{AI}(t) \\
n'_{DS}(t) &= d_L l_{AS}(t) - \delta_N n_{DS}(t) - \frac{\alpha_N h(t) n_{DS}(t)}{K_A(t)} \\
n'_{AS}(t) &= \frac{\alpha_N h(t) n_{DS}(t)}{K_A(t)} - d_N n_{AS}(t) - \beta_N h_I(t) n_{AS}(t) \\
n'_{DI}(t) &= d_L l_{AI}(t) - \delta_N n_{DI}(t) - \frac{\alpha_N h(t) n_{DI}(t)}{K_A(t)} \\
n'_{AI}(t) &= \frac{\alpha_N h(t) n_{DI}(t)}{K_A(t)} + \beta_N h_I(t) n_{AS}(t) - d_N n_{AI}(t) \\
a'_{DS}(t) &= d_N n_{AS}(t) - \delta_A a_{DS}(t) - \frac{\alpha_A h(t) a_{DS}(t)}{K_A(t)} \\
a'_{AS}(t) &= \frac{\alpha_A h(t) a_{DS}(t)}{K_A(t)} - d_A a_{AS}(t) \\
a'_{DI}(t) &= d_N n_{AI}(t) - \delta_A a_{DI}(t) - \frac{\alpha_A h(t) a_{DI}(t)}{K_A(t)} \\
a'_{AI}(t) &= \frac{\alpha_A h(t) a_{DI}(t)}{K_A(t)} - d_A a_{AI}(t) \\
h'_S(t) &= \mu - \mu h_S(t) - (\lambda_N n_{AI}(t) + \lambda_A a_{AI}(t)) h_S(t) \\
h'_I(t) &= (\lambda_N n_{AI}(t) + \lambda_A a_{AI}(t)) h_S(t) - \mu h_I(t) - \gamma h_I(t) \\
h'_R(t) &= \gamma h_I(t) - \mu h_R(t)
\end{aligned} \tag{7}$$

For the model of Equation (7),

(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 $T_* \leq 1$, 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 $T_* > 1$, 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:

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

Equating this system of equations to zero;

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

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 $T_* \leq 1$, 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 $T_* > 1$, then the epidemic may attain an endemic equilibrium state. This state is the solution of the system of equations in (7) with all derivatives equated to zero.

Using $h(t) = 1$ and $\hat{k}_A = \frac{\hat{K}_A}{M}$, the solution can be shown to satisfy

$$\begin{aligned}
\hat{l}_{DS} &= \frac{\rho \hat{a}_A \hat{k}_A}{\alpha_L + \delta_L \hat{k}_A} \\
\hat{l}_{AS} &= \frac{\alpha_L \hat{l}_{DS}}{\hat{k}_A(d_L + \beta_L \hat{h}_I)} \\
\hat{l}_{AI} &= \frac{\beta_L \hat{h}_I \hat{l}_{AS}}{d_L} \\
\hat{n}_{DS} &= \frac{d_L \hat{k}_A \hat{l}_{AS}}{\alpha_N + \delta_N \hat{k}_A} \\
\hat{n}_{AS} &= \frac{\alpha_N \hat{n}_{DS}}{\hat{k}_A(d_N + \beta_N \hat{h}_I)} \\
\hat{n}_{DI} &= \frac{d_L \hat{k}_A \hat{l}_{AI}}{\alpha_N + \delta_N \hat{k}_A} \\
\hat{n}_{AI} &= \frac{\alpha_N \hat{n}_{DI} + \beta_N \hat{h}_I \hat{n}_{AS} \hat{k}_A}{\hat{k}_A d_N} \\
\hat{a}_{DS} &= \frac{d_N \hat{k}_A \hat{n}_{AS}}{\alpha_A + \delta_A \hat{k}_A} \\
\hat{a}_{AS} &= \frac{\alpha_A \hat{a}_{DS}}{d_A \hat{k}_A} \\
\hat{a}_{DI} &= \frac{d_N \hat{k}_A \hat{n}_{AI}}{\alpha_A + \delta_A \hat{k}_A} \\
\hat{a}_{AI} &= \frac{\alpha_A \hat{a}_{DI}}{d_A \hat{k}_A} \\
\hat{h}_S &= \frac{\mu}{\mu + \lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI}} \\
\hat{h}_I &= \frac{\mu(\lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI})}{(\mu + \gamma)(\mu + \lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI})} \\
\hat{h}_R &= \frac{\gamma(\lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI})}{(\mu + \gamma)(\mu + \lambda_N \hat{n}_{AI} + \lambda_A \hat{a}_{AI})}
\end{aligned} \tag{8}$$

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.*[8] 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 of [8] 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).

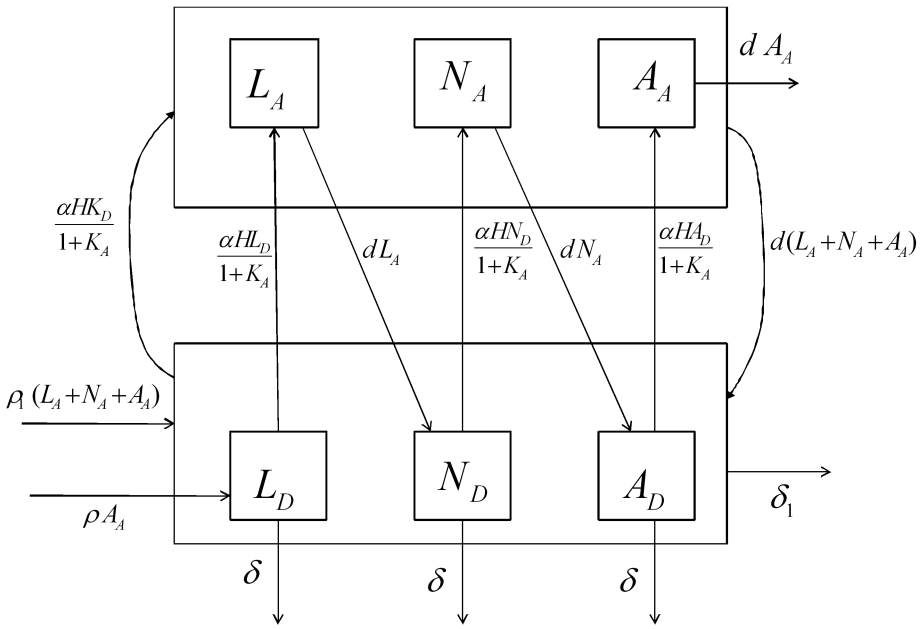


Figure 3: An illustration of the difference between the homogeneous and one-state model, the big boxes and arrows to and from them represent the one-state model while the smaller boxes with arrows to and from them represent the homogeneous model.

Let $\rho_1$ and $\delta_1$ 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 $\rho_1$ and $\delta_1$ we use Equations (1) and (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),

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

Using the result for $\frac{\hat{K}_A}{M}$ in Equation (1),

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

Thus

$$\begin{aligned}\rho_1 &= \frac{\rho\hat{A}_A}{\hat{L}_A+\hat{N}_A+\hat{A}_A} \\ &= \frac{\rho}{\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}}+\left(\frac{\rho}{d}\right)^{\frac{1}{3}}+1\right)}, \end{aligned} \tag{9}$$

and

$$\begin{aligned}\delta_1 &= \delta+\frac{\hat{A}_A}{\hat{L}_D+\hat{N}_D+\hat{A}_D} \\ &= \left(\frac{\rho}{\rho-d}\right)\delta. \end{aligned} \tag{10}$$

For the one-state model, the average number of attached ticks per host is

$$\frac{\alpha\rho_1}{\delta_1 d},$$

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

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

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

For the one-state model, the average number of detached ticks per host is

$$\frac{\alpha\rho_1^2}{d\delta^2},$$

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

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 $T_*^{(1)}$ and for the homogeneous model be $T_*^{(2)}$. The threshold quantity for the one-state model ( reffered to as $T$ in [8]) is

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

Using Equations (9) and (10)

$$T_*^{(1)} = \frac{\beta\alpha\lambda\left(\left(\frac{\rho}{d}\right)^{\frac{1}{3}} - \frac{d}{\rho}\right)}{\delta(\mu+\gamma)(\lambda+d)}. \tag{11}$$

Using Equation (3), the threshold quantity for the homogeneous model is

$$T_*^{(2)} = \frac{\beta\lambda\alpha\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}} + \left(\frac{\rho}{d}\right)^{\frac{1}{3}} - 2\right)}{\delta(\lambda+d)(\mu+\gamma)\left(\left(\frac{\rho}{d}\right)^{\frac{2}{3}} + \left(\frac{\rho}{d}\right)^{\frac{1}{3}} + 1\right)}. \tag{12}$$

This implies that

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

From this we conclude that $T_*^{(2)} < T_*^{(1)}$. The new model hence always has a smaller threshold $T_*$. 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 $T_*^{(1)}$ and $T_*^{(2)}$ 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 $\beta_1$ and $\lambda_1$ 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 $\beta$ and $\lambda$ 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 [20], [21], [4] and [7]. 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 [8], 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 (1), (2) and (3); we compute the threshold quantity for the sixteen cases. The results are summarised in Table 1. From the results we observe that $T_*$ has the largest value when the tick attachment rates and the infection transmission rates are high and tick detachment rates are low. Also $T_*$ 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 $\beta_L$, $\beta_N$, $\lambda_N$, $\lambda_A$ $\alpha_L$ , $\alpha_N$, $\alpha_A$,$d_L$ $da_N$, $d_A$; and the corresponding threshold parameter $T_*$ with fixed values $\delta_L$=0.02, $\delta_N$=0.015, $\delta_A$ =0.005, $\rho$=0.75, $\mu$=0.0006 and $\gamma$=0.05.

| Case | $\beta_L$ | $\beta_N$ | $\lambda_N$ | $\lambda_A$ | $\alpha_L$ | $\alpha_N$ | $\alpha_A$ | $d_L$ | $d_N$ | $d_A$ | $T_*$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 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 (4)-(6) 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 $T_* > 1$ 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 $T_*$ 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 $T_*$ increases. We ran 1000 simulations for the epidemic process for each of the five cases where $T_* > 1$ 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 $T_* > 1$.

| Case | $T_*$ | $q_1$ | $q_2$ | $q_3$ | $(1-\pi)$ | $(1-\tilde{\pi})$ |
|---|---|---|---|---|---|---|
| 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 (8) to obtain the endemic level for the cases where $T_*$ 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). 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 $T_* > 1$.

| 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 $T_* > 1$.

| 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 |

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

| 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 |

To illustrate the full distribution of the simulated endemic levels of the susceptible and infected hosts, attached nymphs and attached adult ticks for case 11, we have plotted histograms in Figures 4-6.

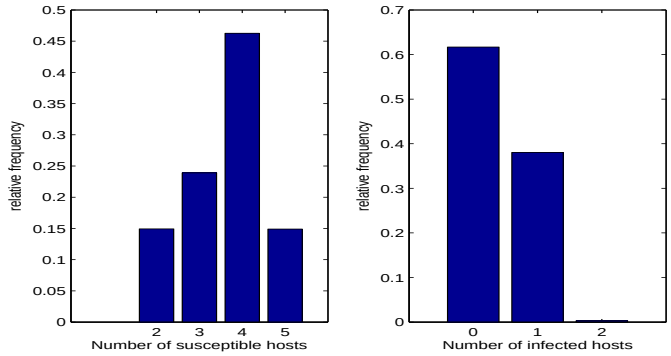


Figure 4: Distribution (over time in the simulation) of susceptible and infective hosts at the endemic level for parameters chosen for case 11.

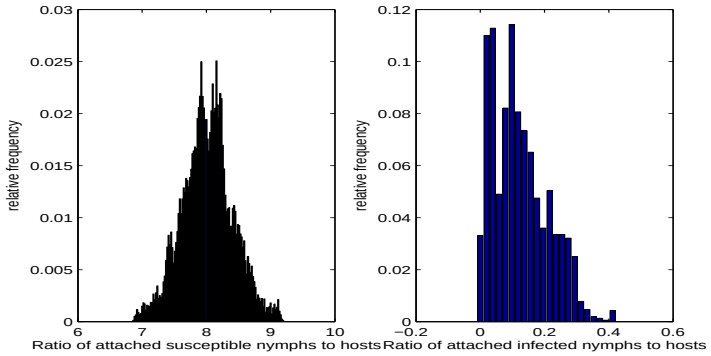


Figure 5: Distribution (over time in the simulation) of the number of attached susceptible and infective nymphs per host at the endemic level for parameters chosen for case 11.

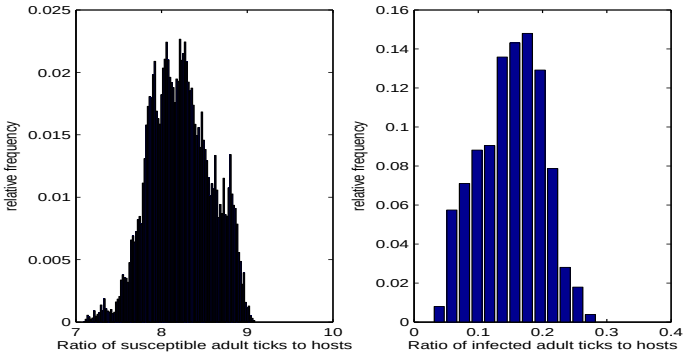


Figure 6: Distribution (over time in the simulation) of the number of attached susceptible and infective adult ticks per host at the endemic level for parameters chosen for case 11.

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 (9) and (10), we obtain values for $\rho$ 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 $T_*^{(1)}$ and $T_*^{(2)}$ are summarised in Table 6 (where $T_*^{(1)}$ refers to the one-state model and $T_*^{(2)}$ to the homogeneous model) .

Table 6: Different parameter values for $\beta$, $\lambda$, $\alpha$ 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.

| $\beta$ | $\lambda$ | $\alpha$ | $T_*^1$ | $T_*^2$ |
|---|---|---|---|---|
| 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 |

Using Equations (4)-(6), 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.

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

| $T_*^1$ | $T_*^2$ | $(1-\pi^{(1)})$ | $(1-\pi^{(2)})$ | $(1-\tilde{\pi}^{(1)})$ | $(1-\tilde{\pi}^{(2)})$ |
|---|---|---|---|---|---|
| 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 |

Both theoretical probabilities are presented in Table 7 as $(1-\pi^{(1)})$ for the one-state model and $(1-\pi^{(2)})$ for the homogeneous model. The 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 (8) 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.

| $\hat{K}_{AS}^{(1)}$ | $\hat{K}_{AS}^{(2)}$ | $\hat{K}_{AI}^{(1)}$ | $\hat{K}_{AI}^{(2)}$ | $\hat{K}_{DS}^{(1)}$ | $\hat{K}_{DS}^{(2)}$ | $\hat{K}_{DI}^{(1)}$ | $\hat{K}_{DI}^{(2)}$ |
|---|---|---|---|---|---|---|---|
| 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 $\beta_1$, the infection transmission rate from host to tick and $\lambda_1$, the infection transmission rate from tick to host for the one-state model and then choose

values for $\beta$ and $\lambda$ 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.

| $\beta_1$ | $\beta$ | $\lambda_1$ | $\lambda$ | $T_*^{(1)}$ | $T_*^{(2)}$ | $(1-\pi^{(1)})$ | $(1-\pi^{(2)})$ | $(1-\tilde{\pi}^{(1)})$ | $(1-\tilde{\pi}^{(2)})$ |
|---|---|---|---|---|---|---|---|---|---|
| 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 $\beta$ and $\lambda$ 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 $T_*^{(2)} < 1$, 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.*[8]. 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). 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 in [11]. 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 [8]. 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 [8]. 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. Though our main focus was on the effects of the three stages of a tick vector on the disease dynamics, we expect that the two-host ticks have less impact as an infected tick of this species can only infect at most one host during its life cycle.

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 [4]. 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 ([4]). 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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