# Persistence and transmission dynamics of emerging tick-borne pathogens:

## Extending a 2-pathogen, 1-host, 1-vector SIR metapopulation model


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## ABSTRACT

Novel extensions to a published SIR compartment model describing the dynamics of vector-borne disease in a 2-pathogen/1-vector/1-host system are proposed. The goals of these model extensions are to analyze the resulting changes to the transmission dynamics of two established pathogens induced by the introduction of novel diversity in the form of either a newly emerged (i.e., competing) pathogen or the expansion of the pathogens' ecological niche to new vectors and new hosts. While our proposed model extensions are theoretical by design, we aim to derive plausible initial values gleaned from real-world case studies of applicable vector-borne model systems to demonstrate realistic parameter ranges that may underly similar biological systems as they occur in nature. Extended epidemic models such as those included in this proposal have potential to become valuable tools in the public health science toolbox by helping scientists and decision-makers evaluate threats posed by -for example- the emergence of new vector-borne pathogens or by the expansion of the host or geographic range of established pathogens due to climate change.



## KEYWORDS

SIR models, transmission dynamics, vector-borne diseases, metapopulation models

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## Introduction

The diversity and zoonotic potential of tickborne diseases has been reported with increasing frequency over the past decade, increasing the threat to human and veterinary health (Rondino et al. 2020). Ticks belong to the arachnid order and are classified into two broad types: hard-bodied ticks (family Ixodidae) and soft-bodied ticks (family Argasidae) (Durden and Beati 2013). The ixodid ticks are the most common ectoparasites of humans and mammals in the United States with an average of approximately 50,000 cases of tickborne diseases reported each year, estimated to be 77-95% of the reported cases of vector-borne disease (Rondino et al. 2020; cdc.gov/ticks/data-summary, accessed 2022-10-04). The tick life cycle includes three obligate parasitic stages: larva, nymph, and adult. Each stage is characterized by the need for a blood meal from a suitable host, during which the feeding tick attaches to the host, consumes a meal, and then detaches to molt to the next stage (Figure 1, below).

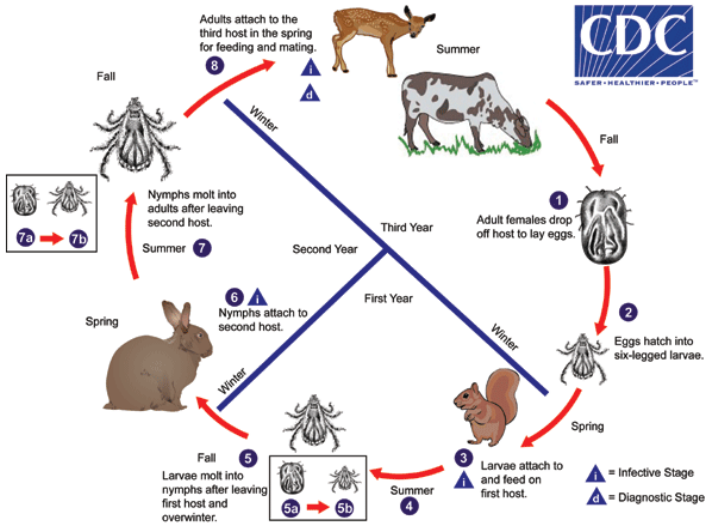


**Figure 1:** Typical life cycle of tick vectors. Reproduced from URL: https://www.cdc.gov/ticks/tickbornediseases/

During this feeding process, some infectious agents, such as *Rickettsia spp.* (spotted fevers), *Borrelia burgdorferi* (Lyme disease), and *Ehrlichia chaffeensis* (heartwater), which are occasionally present in the host, can be transmitted to the feeding tick via the consumed blood meal (Madison-Antenucci et al. 2020). Following host-to-tick transmission, the newly-acquired pathogen(s) colonize the mid- or hindgut of the tick and can be further transmitted by the tick vector to new hosts on which the infected tick feeds (cdc.gov/ticks/life_cycle_and_hosts, accessed 2022-10-04). Once colonized (="infected"), molting larvae

or nymphal ticks retain the commensal pathogen as they advance to their next life stage (known as trans-stadial transmission). Similarly, adult female ticks can vertically transmit infection to her offspring when eggs are laid (called trans-ovarial transmission), thus the newly hatched larvae are infectious prior to consuming any blood meal and capable of tick-to-host transmission when they attach to their first host (Rondino et al. 2020).

Modelling vector-borne disease with compartment models such as SIR represents a powerful way to examine population dynamics of tick vectors and the zoonotic pathogens they transmit. The standard SIR model can be extended to capture unique dynamics of vector-borne pathogen transmission, including published models which reflect the multiple modes of transmission and additional states/compartments required to accurately describe a biological system that includes the vector(s), host(s), and the infectious agent(s) at play (White et al. 2019). Further extensions to these existing compartment models can better portray the populations dynamics and expected pathogen persistence, defined as the pathogen's ability to survive environmental disturbances, as they occur in nature by attempting to capture additional parameters of natural systems and using fewer simplifying assumptions. In this proposal, we will analyze a published 2-pathogen/1-vector/1-host compartment model (hereafter referred to as the "2-1-1" model) which models the dynamics of two species of rickettsial pathogen, the ixodid tick vector *Amblyomma*, and a white-tailed deer host population. We aim to extend the deterministic differential equations (ODEs) underlying this model to include additional pathogens, vectors, and hosts with an eye towards better understanding the epidemic potential, transmission dynamics, and persistence of the competing pathogen species as additional diversity is introduced into the model. While theoretical, our proposed extensions to the 2-1-1 model may be useful to examine potential scenarios of public health concern such as emerging zoonoses as "old" pathogens expand their ecological niche by gaining new vectors or host species, or in which they may be outcompeted by the introduction of new pathogens.

## Goals and Hypothesis

Our overall aims are to study the effects on transmission dynamics between competing *Rickettsia* pathogens by extending the 2-1-1 SIR compartment model outlined in White et al. (2019). Briefly, this metapopulation model describes a model system in which two pathogen species, both belonging to the genus *Rickettsia,* are transmitted by infected tick vectors to susceptible hosts. Our model extensions will focus on modelling theoretical population dynamics between pathogen/vector/host in three areas: (i) in the presence of three pathogen species (i.e. a 3-1-1 model), (ii) with two co-occurring vectors (a 2-2-1 model), and (iii) with two susceptible hosts (a 2-1-2 model). Our specific aims are outlined below.

**Aim 1.** Extend the 2-1-1 SIR compartment model equations to include the additional metapopulation conditions described above.

**Aim 2**. Calculate the basic reproductive numbers $R_1$, $R_2$ for each pathogen species under each of the three extended model conditions (including $R_3$ for the 3-1-1 extension).

- ***Hypothesis 1****:* Basic reproductive numbers of Pathogen 1 and Pathogen 2 will decrease compared to the published 2-1-1 model upon the introduction of Pathogen 3 in an extended 3-1-1 model.
- ***Hypothesis 2****:* Basic reproductive numbers for all modelled pathogens will increase from the 2-1-1 model baseline as the ecological niche is expanded in a 2-vector and 2-host extended model (2-2-1 and 2-1-2 models).

**Aim 3**. Calculate the invasion reproductive numbers $\tilde{R}_1$, $\tilde{R}_2$ ($\tilde{R}_3$) as a measure of the expected ability of each pathogen to persist under each of the extended model conditions.

- ***Hypothesis 3:*** Invasive reproductive numbers will be greater than 1.0 for all pathogens under all three model extensions, demonstrating sustainable persistence over time due to stable equilibria points. Invasive reproductive numbers >= 1.0 can be

understood to be evidence of long-term persistence.

## Preliminary Data

**State Descriptions and Initial Values.**

Initial values for the base 2-1-1 model are given in Table 1 of White et al. (2019). These initial conditions have been derived from previously published models and real-world data including field sampling of ticks (Gaff and Gross 2007). We have reproduced and extended Table 1 to include additional state variables applicable to the planned model extensions (below). Descriptions of initial SIR parameter values, such as transmission and recovery rates, are given in Supplemental Tables 1-3 at the end of this document for brevity. For the third pathogen in the 3-1-1 model, initial values were adapted from published prevalence and virulence data of *Rickettsia rickettsii,* the causative agent of Rocky Mountain Spotted Fever (Infante 2017). All other initial values are defined following original values given in White et al. 2019 and subject to refinement pending additional literature search.

| State Variable | Description | Initial Value | Model Extension |
|---|---|---|---|
| $N$ | Total Number of Hosts | 20 | |
| $N_1$ | Number of Host Species 1 | 10 | 2-1-2 |
| $N_2$ | Number of Host Species 2 | 10 | 2-1-2 |
| $V$ | Total Number of Ticks | 4000 | |
| $V_1$ | Number of Vector Species 1 | 3000 | 2-2-1 |
| $V_2$ | Number of Vector Species 2 | 1000 | 2-2-1 |
| $Y_1$ | Number of Hosts Infected with Pathogen 1 | 1 | |
| $X_1$ | Number of Ticks Infected with Pathogen 1 | 200 | |
| $Y_2$ | Number of Hosts Infected with Pathogen 2 | 0 | |
| $X_2$ | Number of Ticks Infected with Pathogen 2 | 150 | |
| $Y_3$ | Number of Hosts Infected with Pathogen 3 | 0 | 3-1-1 |
| $X_3$ | Number of Ticks Infected with Pathogen 3 | 175 | 3-1-1 |
| $Y_{12}$ | Number of Coinfected Hosts with Pathogens 1,2 | 0 | |
| $X_{12}$ | Number of Coinfected Ticks with Pathogens 1,2 | 10 | |
| $Y_{13}$ | Number of Coinfected Hosts with Pathogens 1,3 | 0 | 3-1-1 |
| $X_{13}$ | Number of Coinfected Ticks with Pathogens 1,3 | 10 | 3-1-1 |
| $Y_{23}$ | Number of Coinfected Hosts with Pathogens 2,3 | 0 | 3-1-1 |
| $X_{23}$ | Number of Coinfected Ticks with Pathogens 2,3 | 5 | 3-1-1 |
| $Y^*$ | Number of Coinfected Hosts with Pathogens 1,2,3 | 0 | 3-1-1 |
| $X^*$ | Number of Coinfected Ticks with Pathogens 1,2,3 | 1 | 3-1-1 |

**Table 1:** Description of state variables according to proposed model extensions (partially reproduced from White et al. 2019). Rows using gray highlighting indicate new state variables unique to this study. Text is additionally colored to visually separate states unique to specific model extensions.

**Model Assumptions.**

In this proposed study design, we have made the simplifying assumption that all ticks have an equal ability to acquire and/or transmit infection regardless of life stage. We have made the additional assumption that infection with any pathogen is not fatal to the acquiring host and that birth/death rates among tick vectors and hosts are independent of one another (Table 2).

## Proposed Analysis Plan

We will implement and test our model in two stages. Stage 1 will implement the proposed extended ODEs and solve a deterministic model following the underlying assumptions of homogenous population mixing, and (ii) by implementing the 3-1-1 model as a stochastic agent-based simulation using the NetLogo platform (Tisue and Wilensky 2004). The use of NetLogo allows for the inclusion of (2-D) space as an additional parameter of the population dynamics under investigation. We will compare the expected (theoretical) SIR curves and associated basic and invasion reproductive numbers against the resulting curves from the NetLogo model. Our proposed project timeline is described in Figure 2 (below). All development, documentation, and results will be versioned using Git and hosted on Github as an open-source public repository.

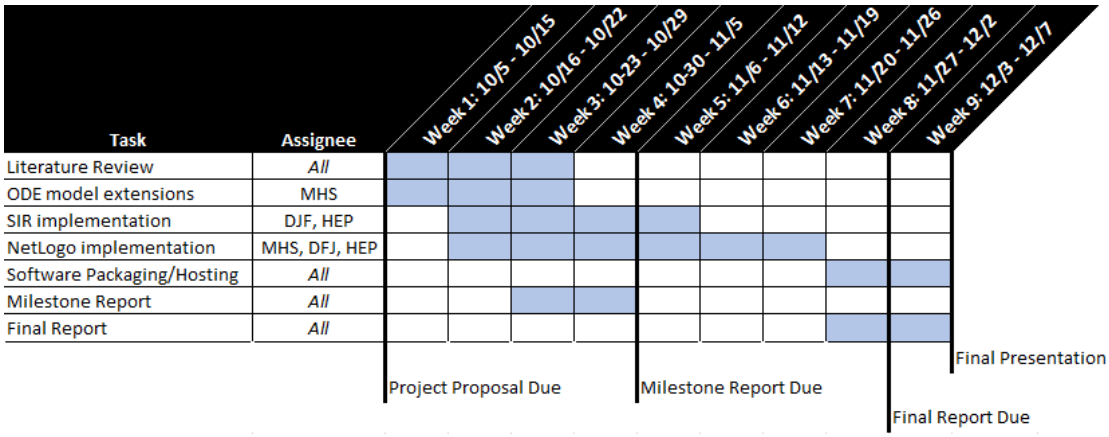


**Figure 2:** Gantt chart describing proposed project timeline, touchstone deliverables, and tentative assignment of tasks to specific team members.

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## SUPPLEMENTAL MATERIALS

| Parameter | Description | Initial Value | Model Extension |
|---|---|---|---|
| Â1 | Host-to-Tick Pathogen 1 Transmission Rate | 0.07 | |
| Â2 | Host-to-Tick Pathogen 2 Transmission Rate | 0.07 | |
| Â3 | Host-to-Tick Pathogen 3 Transmission Rate | 0.07 | 3-1-1 |
| Â12 | Host-to-Tick Coinfection Transmission Rate Pathogens 1,2 | 0.035 | |
| Â13 | Host-to-Tick Coinfection Transmission Rate Pathogens 1,3 | 0.035 | 3-1-1 |
| Â23 | Host-to-Tick Coinfection Transmission Rate Pathogens 2,3 | 0.035 | 3-1-1 |
| A1 | Tick-to-Host Pathogen 1 Transmission Rate | 0.02 | |
| A2 | Tick-to-Host Pathogen 2 Transmission Rate | 0.02 | |
| A3 | Tick-to-Host Pathogen 3 Transmission Rate | 0.02 | 3-1-1 |
| A12 | Tick-to-Host Coinfection Transmission Rate Pathogens 1,2 | 0.01 | |
| A13 | Tick-to-Host Coinfection Transmission Rate Pathogens 1,3 | 0.01 | 3-1-1 |
| A23 | Tick-to-Host Coinfection Transmission Rate Pathogens 2,3 | 0.01 | 3-1-1 |
| γ1 | Tick Transovarial and Transstadial Transmission of Pathogen 1 | 0.4 | |
| γ2 | Tick Transovarial and Transstadial Transmission of Pathogen 2 | 0.4 | |
| γ3 | Tick Transovarial and Transstadial Transmission of Pathogen 3 | 0.4 | 3-1-1 |
| γ12 | Coinfected Tick Transovarial and Transstadial Transmission (1,2)→1 | 0.2 | |
| γ21 | Coinfected Tick Transovarial and Transstadial Transmission (1,2)→2 | 0.2 | 3-1-1 |
| γ13 | Coinfected Tick Transovarial and Transstadial Transmission (1,3)→1 | 0.2 | 3-1-1 |
| γ31 | Coinfected Tick Transovarial and Transstadial Transmission (1,3)→3 | 0.2 | 3-1-1 |
| γ23 | Coinfected Tick Transovarial and Transstadial Transmission (2,3)→2 | 0.2 | 3-1-1 |
| γ32 | Coinfected Tick Transovarial and Transstadial Transmission (2,3)→3 | 0.2 | 3-1-1 |
| μ1 | Tick Cofeeding Transmission Rate of Pathogen 1 | 0.01 | |
| μ2 | Tick Cofeeding Transmission Rate of Pathogen 2 | 0.01 | |
| μ2 | Tick Cofeeding Transmission Rate of Pathogen 3 | 0.01 | 3-1-1 |
| μ12 | Tick Cofeeding Coinfection Transmission Rate Pathogens 1,2 | 0.005 | |
| μ13 | Tick Cofeeding Coinfection Transmission Rate Pathogens 1,3 | 0.005 | 3-1-1 |
| μ23 | Tick Cofeeding Coinfection Transmission Rate Pathogens 2,3 | 0.005 | 3-1-1 |
| ν1 | Host Recovery Rate for Pathogen 1 | 0.166 | |
| ν2 | Host Recovery Rate for Pathogen 2 | 0.166 | |
| ν3 | Host Recovery Rate for Pathogen 3 | 0.166 | 3-1-1 |
| ν12 | Host Recovery Rate of Coinfection Pathogens (1,2)→1 | 0.166 | |
| ν21 | Host Recovery Rate of Coinfection Pathogens (1,2)→2 | 0.166 | |
| ν23 | Host Recovery Rate of Coinfection Pathogens (2,3)→2 | 0.166 | 3-1-1 |
| ν32 | Host Recovery Rate of Coinfection Pathogens (2,3)→3 | 0.166 | 3-1-1 |
| ν13 | Host Recovery Rate of Coinfection Pathogens (1,3)→1 | 0.166 | 3-1-1 |
| ν31 | Host Recovery Rate of Coinfection Pathogens (1,3)→3 | 0.166 | 3-1-1 |
| K | Host Carrying Capacity | 20 | |
| β | Tick Population Growth Rate | | |
| b | Host Background Density-Independent Mortality Rate | | |
| b̂ | Tick Background Density-Independent Mortality Rate | | |

**Supplemental Table 1:** SIR model parameters and initial values for the base 2-1-1 and extended 3-1-1 model (partially reproduced from White et al. 2019). Rows using gray highlighting indicate new state variables unique to this study. Wherever possible, variable symbols follow White et al. (2019).

**Supplemental Table 2:** SIR model parameters and initial values for the base 2-1-1 and extended 2-1-2 (2 [illegible] gray [illegible] to this study. Wherever possible, variable symbols follow White et al. (2019).

| Parameter | Description | Initial Value | Model Extension |
|---|---|---|---|
| Â11 | Host1-to-Tick Pathogen 1 Transmission Rate | 0.07 | |
| Â21 | Host2-to-Tick Pathogen 1 Transmission Rate | 0.07 | 2-1-2 |
| Â12 | Host1-to-Tick Pathogen 2 Transmission Rate | 0.07 | |
| Â22 | Host2-to-Tick Pathogen 2 Transmission Rate | 0.07 | 2-1-2 |
| Â*1 | Host1-to-Tick Coinfection Transmission Rate Pathogens 1,2 | 0.035 | |
| Â*2 | Host2-to-Tick Coinfection Transmission Rate Pathogens 1,2 | 0.035 | 2-1-2 |
| A11 | Tick-to-Host1 Pathogen 1 Transmission Rate | 0.02 | |
| A21 | Tick-to-Host2 Pathogen 1 Transmission Rate | 0.02 | 2-1-2 |
| A12 | Tick-to-Host1 Pathogen 2 Transmission Rate | 0.02 | |
| A22 | Tick-to-Host2 Pathogen 2 Transmission Rate | 0.02 | 2-1-2 |
| A*1 | Tick-to-Host1 Coinfection Transmission Rate Pathogens 1,2 | 0.01 | |
| A*2 | Tick-to-Host2 Coinfection Transmission Rate Pathogens 1,2 | 0.01 | 2-1-2 |
| $\gamma 1$ | Tick Transovarial and Transstadial Transmission of Pathogen 1 | 0.4 | |
| $\gamma 2$ | Tick Transovarial and Transstadial Transmission of Pathogen 2 | 0.4 | |
| $\gamma 12$ | Coinfected Tick Transovarial and Transstadial Transmission (1,2)→1 | 0.2 | |
| $\mu 1$ | Tick Cofeeding Transmission Rate of Pathogen 1 | 0.01 | |
| $\mu 2$ | Tick Cofeeding Transmission Rate of Pathogen 2 | 0.01 | |
| $\mu 12$ | Tick Cofeeding Coinfection Transmission Rate Pathogens 1,2 | 0.005 | |
| $\nu 11$ | Host1 Recovery Rate for Pathogen 1 | 0.166 | |
| $\nu 12$ | Host1 Recovery Rate for Pathogen 2 | 0.166 | 2-1-2 |
| $\nu 21$ | Host2 Recovery Rate for Pathogen 2 | 0.166 | |
| $\nu 22$ | Host2 Recovery Rate for Pathogen 2 | 0.166 | 2-1-2 |
| $\nu 11$ | Host1 Recovery Rate of Coinfection Pathogens (1,2)→1 | 0.166 | |
| $\nu 12$ | Host1 Recovery Rate of Coinfection Pathogens (1,2)→2 | 0.166 | |
| $\nu 21$ | Host2 Recovery Rate of Coinfection Pathogens (1,2)→1 | 0.166 | 2-1-2 |
| $\nu 22$ | Host2 Recovery Rate of Coinfection Pathogens (1,2)→2 | 0.166 | 2-1-2 |
| K1 | Host1 Carrying Capacity | 20 | |
| K2 | Host2 Carrying Capacity | 20 | 2-1-2 |
| M | Maximum Ticks per Host | 200 | |
| $\beta 1$ | Host1 Population Growth Rate | 0.2 | |
| $\beta 2$ | Host1 Population Growth Rate | 0.2 | 2-1-2 |
| $\beta$ | Tick Population Growth Rate | 0.75 | |
| b1 | Host1 Background Density-Independent Mortality Rate | 0.01 | |
| b2 | Host2 Background Density-Independent Mortality Rate | 0.01 | 2-1-2 |
| $\hat{b}$ | Tick Background Density-Independent Mortality Rate | 0.001 | |

| | |
|---|---|
| $\hat{b}1$ | Tick1 Background Density-Independent Mortality Rat |
| $\hat{b}2$ | Tick2 Background Density-Independent Mortality Rat |

vector) model, partially reproduced from White et al. 2019. Rows using gray highlighting indicate new state variables unique to this study. Wherever possible, variable symbols follow White et al (2019).

| Parameter | Description | Initial Value | Model Extension |
|---|---|---|---|
| $\hat{A}11$ | Host-to-Tick1 Pathogen 1 Transmission Rate | 0.07 | |
| $\hat{A}12$ | Host-to-Tick1 Pathogen 2 Transmission Rate | 0.07 | |
| $\hat{A}21$ | Host-to-Tick2 Pathogen 1 Transmission Rate | 0.07 | 2-2-1 |
| $\hat{A}22$ | Host-to-Tick2 Pathogen 2 Transmission Rate | 0.07 | 2-2-1 |
| $\hat{A}*1$ | Host-to-Tick1 Coinfection Transmission Rate Pathogens 1,2 | 0.035 | |
| $\hat{A}*2$ | Host-to-Tick2 Coinfection Transmission Rate Pathogens 1,2 | 0.035 | 2-2-1 |
| A11 | Tick1-to-Host Pathogen 1 Transmission Rate | 0.02 | |
| A12 | Tick1-to-Host Pathogen 2 Transmission Rate | 0.02 | |
| A21 | Tick2-to-Host Pathogen 1 Transmission Rate | 0.02 | 2-2-1 |
| A22 | Tick2-to-Host Pathogen 2 Transmission Rate | 0.02 | 2-2-1 |
| A*1 | Tick1-to-Host Coinfection Transmission Rate Pathogens 1,2 | 0.01 | |
| A*2 | Tick2-to-Host Coinfection Transmission Rate Pathogens 1,2 | 0.01 | 2-2-1 |
| $\gamma 11$ | Tick1 Transovarial and Transstadial Transmission of Pathogen 1 | 0.4 | |
| $\gamma 12$ | Tick1 Transovarial and Transstadial Transmission of Pathogen 2 | 0.4 | |
| $\gamma*1$ | Coinfected Tick1 Transovarial and Transstadial Transmission (1,2)→1 | 0.2 | |
| $\gamma 21$ | Tick2 Transovarial and Transstadial Transmission of Pathogen 1 | 0.6 | 2-2-1 |
| $\gamma 22$ | Tick2 Transovarial and Transstadial Transmission of Pathogen 2 | 0.6 | 2-2-1 |
| $\gamma*2$ | Coinfected Tick2 Transovarial and Transstadial Transmission (1,2)→1 | 0.3 | 2-2-1 |
| $\mu 11$ | Tick1 Cofeeding Transmission Rate of Pathogen 1 | 0.01 | |
| $\mu 12$ | Tick1 Cofeeding Transmission Rate of Pathogen 2 | 0.01 | |
| $\mu*1$ | Tick1 Cofeeding Coinfection Transmission Rate Pathogens 1,2 | 0.005 | |
| $\mu 21$ | Tick2 Cofeeding Transmission Rate of Pathogen 1 | 0.02 | 2-2-1 |
| $\mu 22$ | Tick2 Cofeeding Transmission Rate of Pathogen 2 | 0.02 | 2-2-1 |
| $\mu*2$ | Tick2 Cofeeding Coinfection Transmission Rate Pathogens 1,2 | 0.1 | 2-2-1 |
| $\nu 1$ | Host Recovery Rate for Pathogen 1 | 0.166 | |
| $\nu 2$ | Host Recovery Rate for Pathogen 2 | 0.166 | |
| $\nu 12$ | Host Recovery Rate of Coinfection Pathogens (1,2)→1 | 0.166 | |
| $\nu 21$ | Host Recovery Rate of Coinfection Pathogens (1,2)→2 | 0.166 | |
| K | Host Carrying Capacity | 20 | |
| M1 | Maximum Ticks1 per Host | 150 | |
| M2 | Maximum Ticks2 per Host | 50 | 2-2-1 |
| $\beta$ | Host Population Growth Rate | 0.2 | |
| $\beta 1$ | Tick1 Population Growth Rate | 0.75 | |
| $\beta 2$ | Tick2 Population Growth Rate | 0.75 | 2-2-1 |
| b | Host Background Density-Independent Mortality Rate | 0 | |