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# Modeling dynamical temperature influence on tick *Ixodes scapularis* population

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**Abstract:** Lyme disease has been recognised as one of the emerging vector borne diseases in Canada. Ticks, *Ixodes scapularis* SAY, play a major role as vectors of Lyme disease causative agent *Borrelia burgdorferi*. Ticks become infected with *Borrelia* while feeding on the primary hosts (mice, squirrels, shrews, and other small vertebrates). Deers are primary source of nourishment for each gravid female *I. scapularis* and are fundamental to the tick establishment without infection. The life cycle of tick, *I. scapularis*, is very complex and takes nearly two years to reach adult stage from egg. Studies have shown that tick life cycle is heavily influenced by changes in the climate. In particular, increasing temperature was shown to facilitate the rapid geographical expansion of vector *I. scapularis* and such an expansion might establish the disease in non-endemic areas of Canada. Hence, we tried to predict the temperature impact on the complex tick population life cycle as well as on their establishment conditions in the presence of primary and secondary hosts. This tick population model was based on the Ogden's process-based system, which comprises 12 mutually exclusive tick stages. Tick developmental rates were modelled as temperature dependent based on the earlier studies. We found the threshold condition, in terms of the basic reproduction number ( $R_0$ ), for tick persistence and showed the existence, uniqueness and stability of an endemic equilibrium. We also conducted some numerical simulations to illustrate the analytical results. These simulation results seem to be in good agreement with the previous studies on Lyme disease ecology, and our analysis indicates that temperature can be used as determining parameter to predict the distribution, establishment of tick populations and Lyme disease in the new regions.

**Keywords:** *Ixodes scapularis*, Mathematical Model, Temperature, Lyme Disease, Dynamics

## 1 INTRODUCTION

Lyme disease was first time described in 1977 following the investigation of a cluster of arthritis cases among children living near Lyme, Connecticut (Steere et al, 1977). Lyme disease is the most common tick borne disease in United States (Daniels et al, 1995), where approximately 20,000 cases reported annually (Bacon et al, 2008). Lyme disease has been recognised as an emerging disease in Canada, hence placed in the priority list of National Notifiable Diseases (Doherty, 2006). Distribution of Lyme disease in Canada is currently limited to parts of southern Ontario, southern Quebec, southeastern Manitoba, Nova Scotia, New Brunswick (Ogden et al, 2005; Ogden et al, 2008) and in British Columbia (Lane et al, 2001; Holden et al, 2006; Ogden et al, 2008). Increasing temperature with climatic changes encourage the rapid geographical expansion of vector *I. scapularis* that could establish the disease in non-endemic areas of Canada (Brownstein et al, 2005; Ogden et al, 2006).

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Causative agent of Lyme disease is a spirochete bacterium *Borrelia burgdorferi* transmitted by the principal vector of black-legged tick species, *Ixodes scapularis* SAY, in north-eastern regions of North America (Dolan et al, 2004, Kurtenbach et al, 2006). Natural reservoirs of *B.burgdorferi* include mice, squirrels and shrews, and other small vertebrates (Dennis and Piesman, 2005; Slowik and Lane, 2009) act as primary hosts. While feeding on these reservoirs ticks, *I.scapularis* become infected with *B.burgdorferi* and can transmit infection during the subsequent blood meals among hosts or to incidental hosts, including humans. White-tailed deer (*Odocoileus virginianus* Zimmerman) are not infected with *B.burgdorferi* (Telford et al, 1988), but they play a role in transporting ticks and maintaining tick population as primary source of nourishment for gravid females (Rand et al, 2003; Rand et al, 2004). The life cycle of tick, *I.scapularis*, is very complex and takes place nearly two years to reach adult stage from egg. After hatching from eggs, they pass through three developmental stages: larva, nymph, adult. Each of the three immature stages exhibits their activity in different seasons. Eggs are laid by an adult female tick in the spring and larvae hatch during the late summer. In all three stages, larvae, nymph and adult ticks, seek to attach a host to draw a blood meal, and then drop off to digest the meal. The fed larvae in the spring or summer moult and over winter as nymphs; the very few larvae fed after September over winter as engorged larvae and ready to moult in the next spring. Unfed larvae survive less than one year hence no overlap can be seen with the successive cohorts. Most nymphs fed in spring or early summer will moult to adult ticks. Unfed nymphs able to survive throughout the spring or summer to the next year overlap with new generation of nymph cohorts. Adult ticks feed during fall and spring. The gravid females lay their eggs in early spring and die shortly. Unfed adults of fall over winter and resume host-seeking in the spring and die, unless they feed during their first season, of questing (Daniels et al 1989; Yuval and Spielman, 1990; Lord, 1993; Porco, 1999; Ogden et al, 2004). Many researchers stated that interstadial developmental rates of ixodes ticks are determined in part by temperature and this phenomenon is usually nonlinear (Chilton and Bull, 1994; Peavey and Lane, 1996; Randolph, 1997; Randolph et al, 2002; and Ogden et al, 2004)

Over the years, several mathematical and system-based computational models have been developed for specific questions to understand the interwoven relationships of the climate and tick and host population dynamics (Gardiner, W.P., Gettinby, 1983; King et al, 1988; Sandberg et al, 1992; Kitron and Mannelli, 1994; Randolph and Rogers, 1997; Porco, 1999; Mwambi et al, 2000; Ghosh and Pugliese, 2004; Awerbuch-Friedlander et al, 2005; Brownstein et al, 2005; Ogden et al, 2005; Rosa and Pugliese, 2007). We developed here an ordinary differential equation model based on the process-based dynamic population model (Ogden et al, 2005), which comprises of 12 mutually exclusive states (Figure 1) and investigate the influence of temperature on the density of tick population. Tick developmental rates were modeled as temperature dependent based on the earlier studies (Chilton and Bull, 1994; Peavey and Lane, 1996; Randolph, 1997; Randolph et al, 2002; and Ogden et al, 2004). For the model, we find a threshold condition for tick persistence, and show the existence, uniqueness and stability of the endemic equilibrium. We also give some numerical simulations to illustrate the theoretical results.

## 2 MODEL FORMATION

The life cycle of ticks have three developmental stages: larva, nymph and adult. Each stage subdivides in turn according to the phase of activity: ‘questing’, in which the unfed tick seeks a host; ‘feeding’, in which the attached tick feeds; and ‘engorged’ after feeding and then drop off their hosts. In the model, ticks are classified 12 different states: eggs ( $x_2$ ), hardening larvae ( $x_3$ ), questing larvae ( $x_4$ ), nymphs ( $x_7$ ) and adults ( $x_{10}$ ), feeding larvae ( $x_5$ ), nymphs ( $x_8$ ) and adults females ( $x_{11}$ ), engorged larvae ( $x_6$ ), nymphs ( $x_9$ ) and adults females ( $x_{12}$ ) and egg-laying adults females ( $x_1$ ). Each state represents a specific point in the life of the ticks. Differently from other models for tick population, here we follow (Ogden et al, 2005) and consider an additional state hardening larvae, because hatched larvae undergo a 21 days ‘hardening’ prior to becoming questing larvae (Dennis et al, 1996).

Tick’s development is highly constrained by many factors including biotic (host kind, host densities and habitat) and abiotic such as climate. In particular, the abiotic environment plays a vital

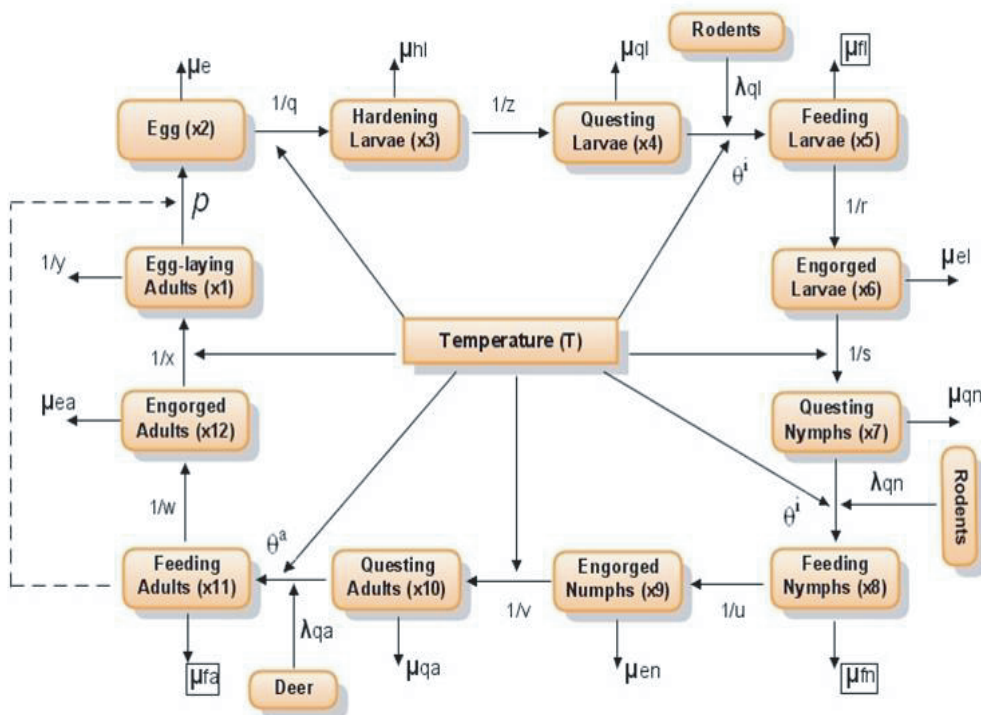


Figure 1: Tick population model flowdiagram, using Gliffy online diagram software

role in the development of *I. scapularis*. Because 98% of the 2-year life cycle occurs on the host, climate should act as an essential determinant of distribution of tick population. Therefore, we assume the tick's development periods  $q$  (pre-eclosion period, the period between commencement of egg-laying and larval hatching),  $s$  (period engorged larvae develop into questing nymphs),  $v$  (period engorged nymphs develop into questing adults) and  $x$  (pre-oviposition period, the period between adult female engorgement and egg laying) as functions of a variable temperature, see Table 1 in detail. Assume the number of eggs produced by each engorged adult female was set to  $p$  (3000) (Mount et al, 1997), and total number of eggs is reduced by a density-dependent factor  $f(x_{11})$ , and they are all dead after 1 day.

Let

- $x_1$  = Number of egg-laying adult females;
- $x_2$  = Number of eggs;
- $x_3$  = Number of hardening larvae;
- $x_4$  = Number of questing larvae;
- $x_5$  = Number of feeding larvae;
- $x_6$  = Number of engorged larvae;
- $x_7$  = Number of questing nymphs;
- $x_8$  = Number of feeding nymphs;
- $x_9$  = Number of engorged nymphs;
- $x_{10}$  = Number of questing adults;
- $x_{11}$  = Number of feeding adult females;
- $x_{12}$  = Number of engorged adult females.

The model equations that describe tick population dynamics are as follows:

$$\frac{dx_1}{dt} = \frac{1}{x}x_{12} - \frac{1}{y}x_1; \quad (1)$$

$$\frac{dx_2}{dt} = x_1 \times f(x_{11}) \times p - \left(\frac{1}{q} + \mu_e\right)x_2; \quad (2)$$

$$\frac{dx_3}{dt} = \frac{1}{q}x_2 - \left(\frac{1}{z} + \mu_{hl}\right)x_3; \quad (3)$$

$$\frac{dx_4}{dt} = \frac{1}{z}x_3 - (\lambda_{ql} \times \theta^i + \mu_{ql})x_4; \quad (4)$$

$$\frac{dx_5}{dt} = \lambda_{ql} \times \theta^i x_4 - \left(\frac{1}{r} + \mu_{fl}(x_5)\right)x_5; \quad (5)$$

$$\frac{dx_6}{dt} = \frac{1}{r}x_5 - \left(\frac{1}{s} + \mu_{el}\right)x_6; \quad (6)$$

$$\frac{dx_7}{dt} = \frac{1}{s}x_6 - (\lambda_{qn} \times \theta^i + \mu_{qn})x_7; \quad (7)$$

$$\frac{dx_8}{dt} = \lambda_{qn} \times \theta^i x_7 - \left(\frac{1}{u} + \mu_{fn}(x_8)\right)x_8; \quad (8)$$

$$\frac{dx_9}{dt} = \frac{1}{u}x_8 - \left(\frac{1}{v} + \mu_{en}\right)x_9; \quad (9)$$

$$\frac{dx_{10}}{dt} = \frac{1}{v}x_9 - (\lambda_{qa} \times \theta^a + \mu_{qa})x_{10}; \quad (10)$$

$$\frac{dx_{11}}{dt} = \frac{1}{2}\lambda_{qa} \times \theta^a x_{10} - \left(\frac{1}{w} + \mu_{fa}(x_{11})\right)x_{11}; \quad (11)$$

$$\frac{dx_{12}}{dt} = \frac{1}{w}x_{11} - \left(\frac{1}{x} + \mu_{ea}\right)x_{12}, \quad (12)$$

where the biological meaning and numerical values of parameters are given in **Table 1** with relevant references. Most parameter values of the parameters are from (Ogden et al, 2005). All parameters of the model are assumed to be non-negative, with all the death rates and development rates positive.

Note that  $f(x_{11}) = A_1 - A_2 \ln(A_3 + x_{11}R^{-1})$ , where  $A_1, A_2, A_3, R$  are positive constants. To obtain the nonnegativity of  $f(x_{11})$ , we note that  $x_{11} \leq \bar{x}_{11} = R(e^{A_1/A_2} - A_3)$ . Substituting  $\bar{x}_{11}$  into equation (11), we obtain  $x_{10} \leq \bar{x}_{10} = 2\left(\frac{1}{w} + \mu_{fa}(\bar{x}_{11})\right)\bar{x}_{11}(\lambda_{qa} \times \theta^a)^{-1}$ . Continuing the same process, we get  $x_i \leq \bar{x}_i, i = 1, \dots, 12$ , for constants  $\bar{x}_i$  that can be explicitly given. It is therefore natural to consider the region  $\Omega = \prod_{i=1}^{12}[0, \bar{x}_i]$ . It can be shown that all solutions of the model system starting in  $\Omega$  remain in  $\Omega$  for all  $t \geq 0$ . Thus,  $\Omega$  is positively invariant and we will restrict our attention to solutions in  $\Omega$ .

### 3 EQUILIBRIA AND BASIC REPRODUCTION NUMBER

System (1)-(12) has a tick-free equilibrium denoted by  $E_0 := (x_1, x_2, \dots, x_{12}) = (0, 0, \dots, 0)$ . The following analysis of the local stability of  $E_0$  yields a threshold condition, under which the number of ticks in all different stages will increase or decrease exponentially. This threshold condition is characterized by the so-called basic reproductive number, denoted by  $R_0$  (Diekman and Heesterbeek, 2000).

The Jacobian matrix of (1)-(12) at  $E_0$  has the form  $J_1 = T - D$ , where  $T$  and  $D$  are give

Table 1: Parameter definitions and numerical values

y	Average period for 'oviposition' (1 day)
q	Average period for the pre-eclosion period of eggs ( $34, 234 \times T^{-2.27}$ )
z	Average period for hardening of larvae (21 days)
r	Average feeding period of larvae (3 days)
s	Average period for engorged larva to nymph development ( $101, 181 \times T^{-2.55}$ )
u	Average feeding period of nymphs (5 days)
v	Average period for engorged nymph to adult females ( $1596 \times T^{-1.21}$ )
w	Average feeding period of adult females (10 days)
x	Average period for the pre-oviposition period ( $1300 \times T^{-1.42}$ )
$\mu_e$	Daily, per capita mortality rate of eggs (0.002)
$\mu_{hl}$	Daily, per capita mortality rate of hardening larvae (0.006)
$\mu_{ql}$	Daily, per capita mortality rate of questing larvae (0.006)
$\mu_{qn}$	Daily, per capita mortality rate of questing nymphs (0.006)
$\mu_{qa}$	Daily, per capita mortality rate of questing adults (0.006)
$\mu_{el}$	Daily, per capita mortality rate of engorged larvae (0.003)
$\mu_{en}$	Daily, per capita mortality rate of engorged nymphs (0.002)
$\mu_{ea}$	Daily, per capita mortality rate of engorged adults (0.0001)
$\mu_{fl}(x_5)$	Density-dependent, per capita mortality of feeding larvae on rodents ( $0.65 + [0.049Ln(\{1.01 + x_5\}/R)]$ )
$\mu_{fn}(x_8)$	Density-dependent, per capita mortality of feeding nymphs on rodents ( $0.55 + [0.049Ln(\{1.01 + x_8\}/R)]$ )
$\mu_{fa}(x_{11})$	Density-dependent, per capita mortality of feeding adults on deer ( $0.5 + [0.049Ln(\{1.01 + x_{11}\}/D)]$ )
R	Number of rodents
D	Number of deers
p	Per capita egg production by egg-laying females (3000)
$f(x_{11})$	Density-dependent reduction in fecundity of egg-laying females ( $1 - [0.01 + (0.04 \times Ln\{1.01 + x_{11}/D\})]$ )
$\theta^i$	Temperature-variable factor for questing activity of immature ticks (see Ogden et al. 2005)
$\theta^a$	Temperature-variable factor for questing activity of adult ticks (see Ogden et al. 2005)
$\lambda_{ql}$	Daily host-finding probability for questing larvae ( $0.0013R^{0.515}$ )
$\lambda_{qn}$	Daily host-finding probability for questing nymphs ( $0.0013R^{0.515}$ )
$\lambda_{qa}$	Daily host-finding probability for questing adults ( $0.0086D^{0.515}$ )

respectively by

$$T = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{x} \\ f(0) \times p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{q} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{z} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \lambda_{ql} \times \theta^i & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{r} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{s} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \lambda_{qn} \times \theta^i & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{u} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{v} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2} \lambda_{qa} \times \theta^a & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{w} & 0 \end{pmatrix}$$

and

$$D = diag \left( \frac{1}{y}; \frac{1}{q} + \mu_e; \frac{1}{z} + \mu_{hl}; \lambda_{ql} \times \theta^i + \mu_{ql}; \frac{1}{r} + \mu_{fl}(0); \frac{1}{s} + \mu_{el}; \lambda_{qn} \times \theta^i + \mu_{qn}; \frac{1}{u} + \mu_{fn}(0); \frac{1}{v} + \mu_{en}; \lambda_{qa} \times \theta^a + \mu_{qa}; \frac{1}{w} + \mu_{fa}(0); \frac{1}{x} + \mu_{ea} \right)$$

The characteristic equation of matrix  $TD^{-1}$  is  $\lambda^{12} - R_0 = 0$ , where

$$R_0 = \frac{\frac{1}{q}}{\frac{1}{q} + \mu_e} \frac{\frac{1}{z}}{\frac{1}{z} + \mu_{hl}} \frac{\lambda_{ql} \times \theta^i}{\lambda_{ql} \times \theta^i + \mu_{ql}} \frac{\frac{1}{r}}{\frac{1}{r} + \mu_{fl}(0)} \frac{\frac{1}{s}}{\frac{1}{s} + \mu_{el}} \frac{\lambda_{qn} \times \theta^i}{\lambda_{qn} \times \theta^i + \mu_{qn}} \frac{\frac{1}{u}}{\frac{1}{u} + \mu_{fn}(0)} \frac{\frac{1}{v}}{\frac{1}{v} + \mu_{en}} \frac{\frac{1}{2} \lambda_{qa} \times \theta^a}{\lambda_{qa} \times \theta^a + \mu_{qa}} \frac{\frac{1}{w}}{\frac{1}{w} + \mu_{fa}(0)} \frac{\frac{1}{x}}{\frac{1}{x} + \mu_{ea}} \frac{f(0) \times p}{\frac{1}{y}}. \quad (13)$$

This eigenvalue is, in module, smaller than one if and only if  $R_0 < 1$ . The definition, given in Diekmann and Heesterbeek(2000), yields the reproductive number of such a system (though not really an epidemic model) as  $\sqrt[12]{R_0}$ . Regardless, we conclude that  $E_0$  is asymptotically stable if and only if  $R_0 < 1$ .

$R_0$  as a threshold can be better illustrated when we consider the existence and stability of an endemic equilibrium. We assume in the remaining part of this section that  $R_0 > 1$ .

Setting the right-hand sides of (1)-(12) to zeros, we obtain the following equation:

$$f(x_{11}) \times k_1 - \left(\frac{1}{r} + \mu_{fl}(x_5)\right) \left(\frac{1}{u} + \mu_{fn}(x_8)\right) \left(\frac{1}{w} + \mu_{fa}(x_{11})\right) = 0, \quad (14)$$

where

$$k_1 = \frac{\frac{1}{q}}{\frac{1}{q} + \mu_e} \frac{\frac{1}{z}}{\frac{1}{z} + \mu_{hl}} \frac{\lambda_{ql} \times \theta^i}{\lambda_{ql} \times \theta^i + \mu_{ql}} \frac{\frac{1}{s}}{\frac{1}{s} + \mu_{el}} \frac{\lambda_{qn} \times \theta^i}{\lambda_{qn} \times \theta^i + \mu_{qn}} \frac{\frac{1}{v}}{\frac{1}{v} + \mu_{en}} \frac{\frac{1}{2} \lambda_{qa} \times \theta^a}{\lambda_{qa} \times \theta^a + \mu_{qa}} \frac{\frac{1}{x}}{\frac{1}{x} + \mu_{ea}} \frac{1}{w} \times \frac{p}{y} \times \frac{1}{r} \times \frac{1}{u} > 0.$$

In order to find positive solutions of , we need to know the relationships between  $x_5$  or  $x_8$  and  $x_{11}$ . Setting the right-hand sides of (6)-(11) to zeros again, we obtain

$$x_8 = k_2 \left(\frac{1}{w} + \mu_{fa}(x_{11})\right) x_{11}, x_5 = k_3 \left(\frac{1}{u} + \mu_{fn}(x_8)\right) x_8,$$

where

$$k_2 = \frac{\frac{1}{v} + \mu_{en}}{\frac{1}{u}} \times \frac{\lambda_{qa} \times \theta^a + \mu_{qa}}{\frac{1}{v}} \cdot \frac{1}{\frac{1}{2}\lambda_{qa} \times \theta^a} > 0$$

and

$$k_3 = \frac{\frac{1}{s} + \mu_{el}}{\frac{1}{r}} \times \frac{\lambda_{qn} \times \theta^i + \mu_{qn}}{\frac{1}{s}} \cdot \frac{1}{\lambda_{qn} \times \theta^i} > 0.$$

From the formula  $\mu_{fl}(x_5)$ ,  $\mu_{fn}(x_8)$  and  $\mu_{fa}(x_{11})$ , it is easy to check that all of the terms  $x_5$ ,  $x_8$ ,  $\mu_{fl}(x_5)$ ,  $\mu_{fn}(x_8)$  and  $\mu_{fa}(x_{11})$ , which are functions of  $x_{11}$ , are strictly increasing functions of  $x_{11}$ . Moreover,  $f(x_{11})$  is a strictly decreasing function of  $x_{11}$ . Hence, there exists an endemic equilibrium if and only if there exists a positive solution  $x_{11}$  to (14).

Define

$$F(x_{11}) = \left(\frac{1}{r} + \mu_{fl}(x_5)\right)\left(\frac{1}{u} + \mu_{fn}(x_8)\right)\left(\frac{1}{w} + \mu_{fa}(x_{11}) - f(x_{11})\right) \times k_1. \quad (15)$$

Hence,  $F(x_{11})$  is a strictly increasing function with respect to  $x_{11}$ . Note that  $\lim_{x_{11} \rightarrow \bar{x}_{11}} F(x_{11}) > 0$ . Then there exists a unique endemic solution of  $F(x_{11}) = 0$  if and only if  $F(0) < 0$ .

On the other hand,

$$\begin{aligned} F(0) &= \left(\frac{1}{r} + \mu_{fl}(0)\right)\left(\frac{1}{u} + \mu_{fn}(0)\right)\left(\frac{1}{w} + \mu_{fa}(0) - f(0)\right) \times k_1 \\ &= \left(\frac{1}{r} + \mu_{fl}(0)\right)\left(\frac{1}{u} + \mu_{fn}(0)\right)\left(\frac{1}{w} + \mu_{fa}(0)(1 - R_0)\right). \end{aligned}$$

Therefore, we conclude that there exists a unique endemic equilibrium if and only if  $R_0 > 1$ .

To address the stability of this unique endemic equilibrium, denoted by  $X^* := (x_1^*, x_2^*, \dots, x_{12}^*) \in \Omega$ . We note that the Jacobian matrix  $J_2$  at the endemic equilibrium can be expressed as  $J_2 := A - B$ , where  $A$  and  $B$  are given respectively by

$$A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{x} \\ f(x_{11}^*)p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -(-x_1^* p f'(x_{11}^*)) & 0 & 0 \\ 0 & \frac{1}{q} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{z} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \lambda_{ql} \cdot \theta^i & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{r} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{s} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \lambda_{qn} \cdot \theta^i & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{u} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{v} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2}\lambda_{qa} \cdot \theta^a & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{w} & 0 & 0 \end{pmatrix}$$

and

$$B = \text{diag} \left( \frac{1}{y}; \frac{1}{q} + \mu_e; \frac{1}{z} + \mu_{hl}; \lambda_{ql} \times \theta^i + \mu_{ql}; \frac{1}{r} + \mu_{fl}(x_5^*) + \mu'_{fl}(x_5^*)x_5^*; \frac{1}{s} + \mu_{el}; \lambda_{qn} \times \theta^i + \mu_{qn}; \frac{1}{u} + \mu_{fn}(x_8^*) + \mu'_{fn}(x_8^*)x_8^*; \frac{1}{v} + \mu_{en}; \lambda_{qa} \times \theta^a + \mu_{qa}; \frac{1}{w} + \mu_{fa}(x_{11}^*) + \mu'_{fa}(x_{11}^*)x_{11}^*; \frac{1}{x} + \mu_{ea} \right).$$



Therefore,  $J_2$  can be written as

$$J_2 := \begin{pmatrix} -a_{1,1} & & & & & & & & & & & a_{1,12} \\ a_{2,1} & -a_{2,2} & & & & & -a_{2,11} & & & & & \\ & a_{3,2} & -a_{3,3} & & & & & & & & & \\ & & \ddots & \ddots & & & & & & & & \\ & & & a_{11,10} & -a_{11,11} & & & & & & & \\ & & & & a_{12,11} & -a_{12,12} & & & & & & \end{pmatrix},$$

where  $a_{i,j} > 0$ . Hence, the endemic equilibrium is locally asymptotically stable if all eigenvalues of  $J_2$  have negative real parts.

Let  $\lambda$  be an eigenvalue of  $J_2$  and a corresponding eigenvector be  $X := (x_1, x_2, \dots, x_{12})^T$ . Then we have

$$(\lambda + a_{1,1})x_1 = a_{1,12}x_{12}, \tag{16}$$

$$(\lambda + a_{2,2})x_2 = a_{2,1}x_1 - a_{2,11}x_{11}, \tag{17}$$

$$(\lambda + a_{i,i})x_i = a_{i,i-1}x_{i-1} \quad i = 3, \dots, 12. \tag{18}$$

It follows from (18) that

$$x_i = \frac{a_{i,i-1}}{\lambda + a_{i,i}}x_{i-1}, \quad i = 3, \dots, 12. \tag{19}$$

Therefore, we have

$$x_{12} = \prod_{i=3}^{12} \frac{a_{i,i-1}}{\lambda + a_{i,i}}x_2, \tag{20}$$

$$x_{11} = \prod_{i=3}^{11} \frac{a_{i,i-1}}{\lambda + a_{i,i}}x_2. \tag{21}$$

Substituting (20) and (21) into (16) and (17) yields

$$\begin{cases} (\lambda + a_{1,1})x_1 - a_{1,12} \prod_{i=3}^{12} \frac{a_{i,i-1}}{\lambda + a_{i,i}}x_2 = 0, \\ -a_{2,1}x_1 + [(\lambda + a_{2,2}) + a_{2,11} \prod_{i=3}^{11} \frac{a_{i,i-1}}{\lambda + a_{i,i}}]x_2 = 0. \end{cases} \tag{22}$$

Then, we arrive at a simplified characteristic equation

$$f(\lambda) = \prod_{i=1}^{12} (\lambda + a_{i,i}) + (\lambda + a_{1,1})(\lambda + a_{12,12})a_{2,11} \prod_{i=3}^{11} a_{i,i-1} - a_{1,12} \prod_{i=2}^{12} a_{i,i-1} = 0. \tag{23}$$

It is tedious but straightforward to verify that

$$\prod_{i=1}^{12} a_{i,i} > a_{1,12} \prod_{i=2}^{12} a_{i,i-1}. \tag{24}$$

Substituting  $\lambda = 0$  into (23) gives  $f(0) > 0$ . Moreover, if  $\lambda > 0$ , then

$$f'(\lambda) = \sum_{j=1}^{12} \prod_{i=1, i \neq j}^{12} (\lambda + a_{i,i}) + (2\lambda + a_{1,1} + a_{12,12})a_{2,11} \prod_{i=2}^{12} a_{i,i-1} > 0. \quad (25)$$

This implies that the characteristic equation (23) has no real positive or zero roots.

Now, assume  $\lambda = \alpha + j\beta$  with  $\alpha \geq 0$  and  $\beta > 0$  is an eigenvalue of (23). Substituting this into (23) and taking module, we get

$$\left| \prod_{i=1}^{12} (\alpha + j\beta + a_{i,i}) + (\alpha + j\beta + a_{1,1})(\alpha + j\beta + a_{12,12})a_{2,11} \prod_{i=3}^{11} a_{i,i-1} \right| = a_{1,12} \prod_{i=2}^{12} a_{i,i-1}. \quad (26)$$

But, using the nonnegativity of  $\alpha, \beta$  and  $a_{i,j}$ , we obtain

$$\begin{aligned} & \left| \prod_{k=1}^{12} (\alpha + j\beta + a_{i,i}) + (\alpha + j\beta + a_{1,1})(\alpha + j\beta + a_{12,12})a_{2,11} \prod_{i=2}^{10} a_{i+1,i} \right| \\ > & \left| \prod_{i=1}^{12} (\alpha + a_{i,i} + j\beta) \right| > \left| \prod_{i=1}^{12} (\alpha + a_{i,i}) \right| \geq \left| \prod_{i=1}^{12} a_{i,i} \right| > a_{1,12} \prod_{i=2}^{12} a_{i,i-1}, \end{aligned}$$

a contradiction.

Therefore, the matrix  $J_2$  has only eigenvalues with negative real part, which implies that the endemic equilibrium is locally asymptotically stable. In summary, we have

**Theorem 3.1.** *Suppose  $R_0 > 1$ . Then an endemic equilibrium exists, is unique and locally asymptotically stable.*

Whether this equilibrium is globally asymptotically stable remains to be an open problem. Here we address a relatively simpler issue, namely we investigate the persistence of the disease.

Recall that  $f(x_{11}) = A_1 - A_2 \ln(A_3 + x_{11}R^{-1})$  with  $A_1, A_2$  and  $A_3$  being positive constants. Then  $0 < f(x_{11}) \leq A_1$ . Replacing  $f(x_{11})$  by  $A_1$  in the system (1)-(12), we get another ordinary differential equations system

$$\dot{\tilde{x}}_i(t) = \tilde{f}_i(\tilde{x}_i, \tilde{x}_{i-1}), \quad i = 1, 2, \dots, 12. \quad (27)$$

Denote by  $\tilde{x}_0 = \tilde{x}_{12}$ . We have the following

**Theorem 3.2.** *For system (27), there exists an unique endemic equilibrium which is globally asymptotically stable, when  $R_0 > 1$ .*

The proof of the existence of the endemic equilibrium is similar to the proof of the similar conclusion for equations (1)-(12), by considering the function

$$G(\tilde{x}_{11}) = \left(\frac{1}{r} + \mu_{fl}(\tilde{x}_5)\right)\left(\frac{1}{u} + \mu_{fn}(\tilde{x}_8)\right)\left(\frac{1}{w} + \mu_{fa}(\tilde{x}_{11})\right) - A_1 k_1. \quad (28)$$

Since system (27) is a positive feedback cycle system, and when  $R_0 > 1$  the system has a unique positive equilibrium in the positively invariant set  $R_+^{12}$ , the forward trajectory of every initial point of  $R_+^{12}$  approaches the equilibrium  $\tilde{X}^*$ .

Now, let  $X(t, X_0)$  be a solution of system (1)-(12) starting at the initial point  $X_0 \in \Omega$ , let  $\tilde{X}(t, X_0)$  be the solution of system (27) with the same initial data. By a standard comparison argument, we get  $X(t, X_0) \leq \tilde{X}(t, X_0), \forall t \geq 0$ . Taking limit on both sides gives  $\lim_{t \rightarrow \infty} X(t, X_0) \leq \lim_{t \rightarrow \infty} \tilde{X}(t, X_0) = \tilde{X}^*$ . Choosing the initial value  $X_0 = X^* \in \Omega \subset R_+^{12}$  in the above inequality gives  $X^* = \lim_{t \rightarrow \infty} X(t, X^*) \leq \lim_{t \rightarrow \infty} \tilde{X}(t, X^*) \leq \tilde{X}^*$ . Moreover,  $\lim_{t \rightarrow \infty} \sup X(t, X_0) \leq \tilde{X}^*$ . This implies, when  $t$  is enough large, that  $0 < X(t, X_0) \leq \tilde{X}^*$ . In particular, for every  $\varepsilon \geq 0$  there exists  $T > 0$  so that for  $t \geq T$  we have  $x_{11}(t, X_0) \leq \tilde{x}_{11}^* + \varepsilon$ . Thus,  $f(x_{11}(t, X_0)) \geq f(\tilde{x}_{11}^*)$  when  $t$  enough large. Now, replacing  $f(x_{11})$  by  $f(\tilde{x}_{11}^*)$  at (2), this arrives at the third system

$$\dot{\hat{x}}_i = \hat{f}_i(\hat{x}_{i-1}, \hat{x}_i), \quad i = 1, \dots, 12 \quad (29)$$

**Theorem 3.3.** *When  $R_0 > 1$ , if  $\frac{f(0)}{R_0} < f(\tilde{x}_{11}^*) < 1$ , then system (29) exists an unique endemic equilibrium  $\hat{X}^* > 0$ . Moreover,*

$$\hat{X}^* \leq X^* \leq \tilde{X}^*, \text{ and } \hat{X}^* \leq X(t, X_0) \leq \tilde{X}^* \text{ when } t \text{ enough large.} \quad (30)$$

**Proof:** Using same arguments as above, we arrive at the following equation

$$H(\hat{x}_{11}) = \left(\frac{1}{r} + \mu_{fl}(\hat{x}_5)\right)\left(\frac{1}{u} + \mu_{fn}(\hat{x}_8)\right)\left(\frac{1}{w} + \mu_{fa}(\hat{x}_{11})\right) - f(\tilde{x}_{11}^*)k_1 = 0. \quad (31)$$

Similarly, the function  $H(\hat{x}_{11})$  is a strictly increasing function of  $\hat{x}_{11}$ . So, equation (31) has an unique positive solution  $\hat{X}^*$  if and only if  $H(0) < 0$ , which is equivalent to  $f(\tilde{x}_{11}^*) > f(0)R_0^{-1}$ .

A standard comparison argument gives

$$\hat{X}(t, X_0) \leq X(t, X_0), \text{ for any given initial value } X_0, \text{ provided } t \text{ enough large.} \quad (32)$$

Choose  $X_0 = X^*$ . Then

$$\hat{X}(t, X^*) \leq X(t, X^*) \quad (33)$$

Since system (29) is also a positive feedback cyclic system, the forward trajectory of every initial point approaches the equilibrium  $\hat{X}^*$ . Taking limit for (33), we obtain

$$\hat{X}^* = \lim_{t \rightarrow \infty} \hat{X}(t, X^*) \leq \lim_{t \rightarrow \infty} X(t, X^*) = X^*. \quad (34)$$

From (33) it follows that

$$\hat{X}^* = \lim_{t \rightarrow \infty} \hat{X}(t, X_0) \leq \lim_{t \rightarrow \infty} \inf X(t, X_0). \quad (35)$$

This implies

$$\hat{X}^* \leq X(t, X_0) \text{ when } t \text{ enough large.} \quad (36)$$

Therefore,  $\hat{X}^* \leq X(t, X_0) \leq \tilde{X}^*$  when  $t$  is enough large and  $\hat{X}^* \leq X^* \leq \tilde{X}^*$ , completing the proof.

#### 4 NUMERICAL ANALYSIS

To illustrate these theoretical results, we performed numerical simulations using MATLAB R2009a version for both case  $R_0 < 1$  and  $R_0 > 1$  using the list of all parameters presented in Table 1. Time is measured in days and vector and host densities are in per hectare.

Figure 2 explains how the basic reproduction number is influenced by the temperature at fixed parameters, with rodents density = 250 and deer density = 30. If  $R_0 < 1$ , temperatures at 14.5 degree celsius would provide favorable environment for the development of vectors and hosts as well as spread of pathogen. Where as  $R_0 > 1$ , temperature equals or above 15.4 degree celsius would not be favorable for the survival of vector and host.

Figures 3a and 3b show the developmental trends of feeding larvae; feeding nymphs and feeding adults over time period based on  $R_0$  value. When,  $R_0 < 1$ , ticks will die out under the certain range of temperature (Figure 3a). This result shows that the tick-free equilibrium is globally asymptotically stable. Tick existence, uniqueness, and local stability of the endemic positive equilibrium are proved when  $R_0 > 1$  (Figure 3b). This result confirms the persistent development of tick population at certain temperature conditions.

In Figure 3a, we also show the dynamics behaviors of the upper value  $\hat{x}^*$  and lower value  $\hat{x}^*$ , they are also globally asymptotically stable from the numerical simulation viewpoint. From Figure 3b, the value  $\hat{x}^*$  and the value  $\hat{x}^*$  are very close to the endemic equilibrium  $x^*$ . ( $\hat{x}_{11}^* = 2.8213$ ,  $x_{11}^* = 2.7701$ ,  $\hat{x}_{11}^* = 2.7693$ ).

Figure 4 shows the effect of hosts density (deer, rodent) on the basic reproduction number  $R_0$  when temperature fluctuates. The surface represents the value of  $R_0 = 1$ , inside the surface the value of  $R_0$  is greater than 1, and outside the surface the value of the  $R_0$  is less than 1. Figure 5 depicts how host abundances will be influenced by temperature and these trends would again show an impact on the tick developmental stages and/or Lyme disease spread if hosts are infected with *Borrelia burgdorferi*.

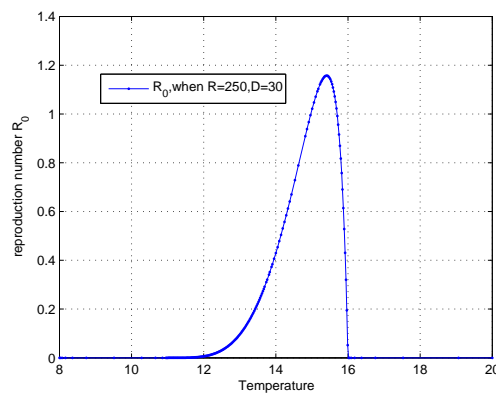


Figure 2: Effects of Temperature on the  $R_0$  condition with a fixed parameters, density of Rodents = 250 and Deer density = 30.

#### 5 SUMMARY AND CONCLUSIONS

We formulated and presented a mathematical model based on the life history of the tick, to analyse the effects of temperature on the tick developmental stages, hosts (rodents and deer) densities and their establishment. Further, this model helps to reveal the role of primary and secondary host activity for *I.scapularis* population sustenance.

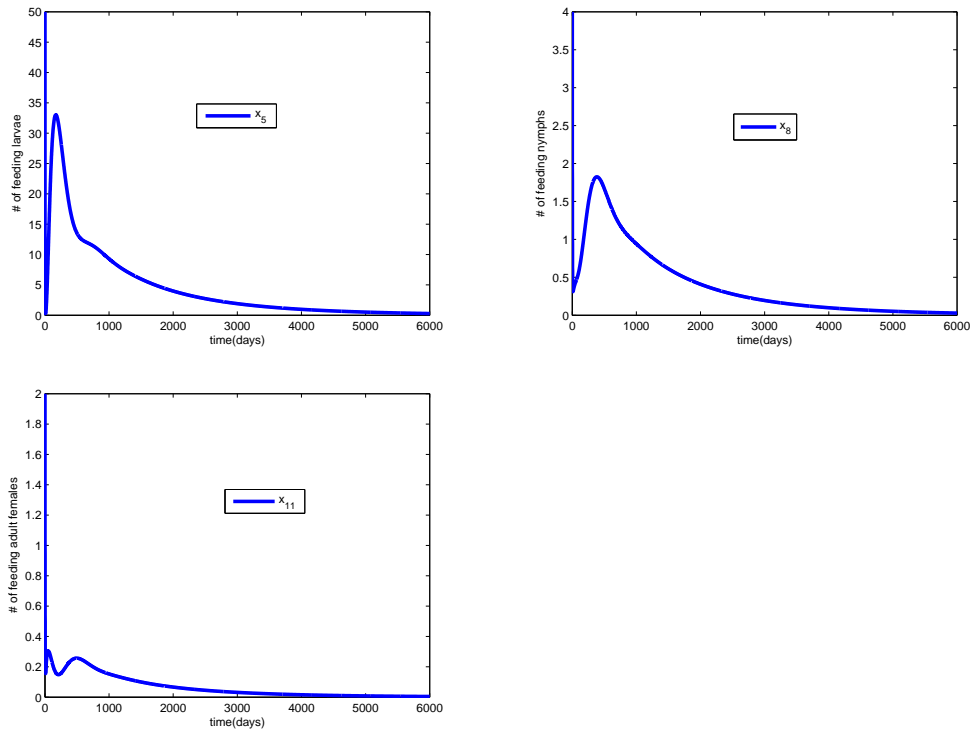


Figure 3a: Temperature influence on the different stages of Tick life cycle when  $R_0 = 0.7115 < 1$ , i. feeding larvae; ii. feeding nymphs and iii. feeding Adults The initial value as  $[0, 20, 30, 75, 50, 350, 100, 4, 50, 2, 2, 20]$  and set temperature as 14.5, Rodents =250 and Deer = 30.

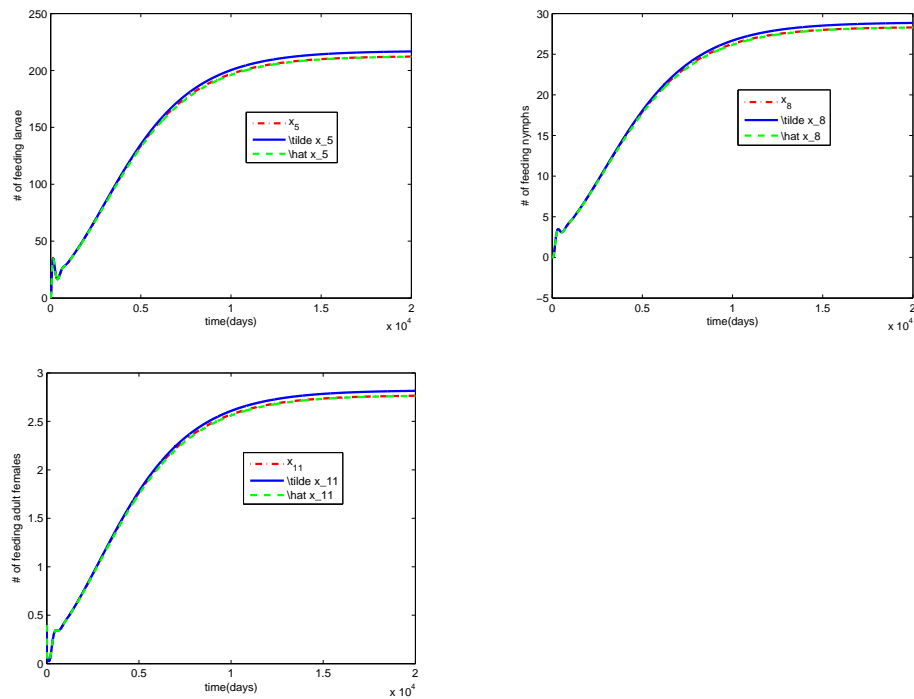


Figure 3b: Temperature influence on the different stages of Tick life cycle when  $R_0 = 2.1904 > 1$ , i. feeding larvae; ii. feeding nymphs and iii. feeding Adults The initial value as  $[0, 0, 0, 0, 0, 0, 0, 0, 0, 10, 0.4, 10]$  and set temperature as 15.4, Rodents =250 and Deer = 30.

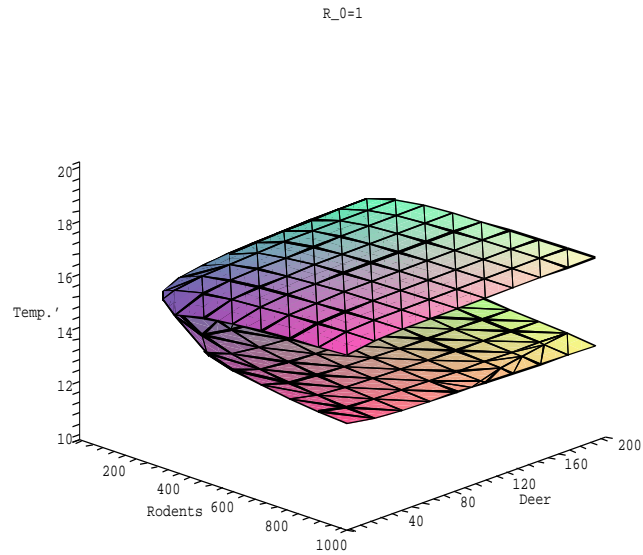


Figure 4: Temperature influence on the host densities according to the  $R_0$  condition.

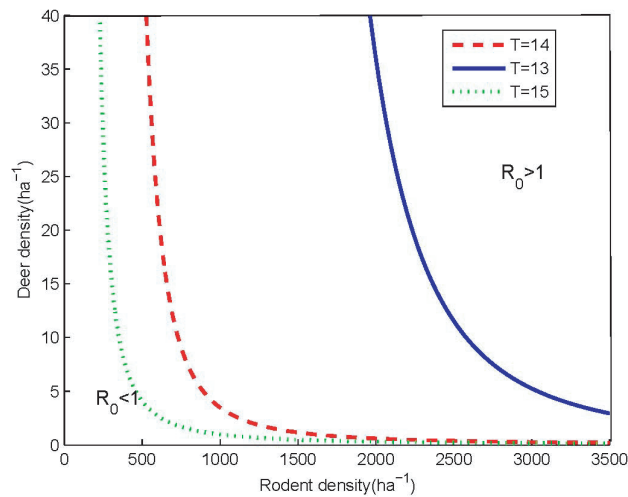


Figure 5: Effects of host densities on the tick life cycle with respect to the temperature.

As observed in the Figure 5, low abundances of hosts due to increase in temperature, could impede the growth of tick developmental stages and Lyme disease propagation due to scarcity of blood meal, infection maintenance and spread (Figure 5). Our findings are in agreement with the earlier research on the Lyme disease ecology and with the earlier tick population and Lyme disease models (Porco, 1990; Buskirk and Ostfeld, 1995; Awerbuch-Friedlander et al, 2005). The interactions of *I. scapularis* and primary hosts (small mammals) would help in tick survival, development and spread of *B.burgdorferi* infection. Where as deers, as secondary hosts, provide nourishment for each gravid female of *I. scapularis* and help in tick establishment and local spread. Significant decline in the sub-adults/adult ticks were found when host densities are extremely low (Wilson et al. 1988; Deblinger et al. 1993; Jones and Kitron, 2000; Telford 2002). In general, our model indicates that temperature can be used as determining parameter to predict the distribution, establishment of tick populations and Lyme disease in the new regions.

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## REFERENCES

- Steere AC, Malawista SE, Snyderman DR, et al Lyme arthritis: an epidemic of oligoarticular arthritis in children and adults in three Connecticut communities. *Arthritis Rheum*, 20:7-17, 1977.
- Daniels, T. J., D. Fish, and R. C. Falco. Evaluation of host-targeted acaricide for reducing risk of Lyme disease in SouthernNewYork State. *J. Med. Entomol*, 28:537-543, 1991.
- Bacon R.M, Kugeler K.J and P.S. Mead. Surveillance for Lyme Disease United States, 1992-2006. *Morbidity and Mortality Weekly Report (MMWR)*, October 3, 2008, 57(SS10):1-9, 2008.
- Doherty JA. Final report and recommendations from the National Notifiable Diseases Working Group. *Can Commun Dis Rep.*, 1 (32):211-25, 2006.
- Ogden NH, Bigras-Poulin M, OCallaghan CJ, et al. A dynamic population model to investigate effects of climate on geographic range and seasonality of the tick *Ixodes scapularis*. *Int J Parasitol.*, 35:375-89, 2005.
- Ogden NH, St-Onge L, Barker IK, et al. Risk maps for range expansion of the Lyme disease vector, *Ixodes scapularis*, in Canada now and with climate change. *Int J Health Geogr.*, 7:24, 2008.
- Lane RS, Foley JE, Eisen L, et al. Acarologic risk of exposure to emerging tick-borne bacterial pathogens in a semirural community in northern California. *Vector Borne Zoonotic Dis.*, 1: 197-210, 2001.
- Holden K, Boothby JT, Kasten RW, et al. Co-detection of *Bartonella henselae*, *Borrelia burgdorferi*, and *Anaplasma phagocytophilum* in *Ixodes pacificus* ticks from California, USA. *Vector Borne Zoonotic Dis.*, 6:99-102, 2006.
- Ogden NH, Lindsay LR, Morshed M, Sockett PN, Artsob H. The rising challenge of Lyme borreliosis in Canada. *Can Commun Dis Rep.*, 34 (1):1-19, 2008.
- Brownstein J.S., Theodore R.Holford and Durland Fish. Effect of climate change on lyme disease risk in North America. *EcoHealth*, 2:38-46, 2005.
- Ogden NH, Maarouf A, Barker IK, et al. Climate change and the potential for range expansion of the Lyme disease vector *Ixodes scapularis* in Canada. *Int J Parasitol.*, 36:63-70, 2006.
- Dolan MC, Maupin GO, Schneider BS, Denatale C, Hamon N, Cole C, Zeidner NS, Stafford KC 3rd. Control of immature *Ixodes scapularis* (Acari: Ixodidae) on rodent reservoirs of *Borrelia burgdorferi* in a residential community of southeastern Connecticut. *J Med Entomol.*, 41 (6): 1043-1054, 2004.
- Kurtenbach K, Hanincova K, Tsao J, Gabriele M, Durland F and Nicholas H. O. Fundamental processes in the evolutionary ecology of Lyme borreliosis. *Nat Rev Microbiol .*, 4:660-669, 2006.
- Dennis DT, and Piesman, JF. Overview of tick-borne infections in humans. *Washington, DC: ASM Press*, :, 2005.
- Slowik TJ, Lane RS. Feeding preferences of the immature stages of three western north American ixodid ticks (Acari) for avian, reptilian, or rodent hosts. *J Med Entomol.* , 46 (1):115-22, 2009.

- Telford, S. R., III, T. N. Mather, S. I. Moore, M. L. Wilson, and A. Spielman. Incompetence of deer as a reservoir of the Lyme disease spirochete. *Am. J. Trop. Med. Hyg.*, 39:105-109, 1988.
- Rand PW, Lubelczyk C, Lavigne GR, Elias S, Holman MS, Lacombe EH, Smith RP Jr. Deer density and the abundance of *Ixodes scapularis* (Acari: Ixodidae). *J Med Entomol.*, 40 (2): 179-84, 2003.
- Rand PW, Lubelczyk C, Holman MS, Lacombe EH, Smith RP Jr. Abundance of *Ixodes scapularis* (Acari: Ixodidae) after the complete removal of deer from an isolated offshore island, endemic for Lyme Disease. *J Med Entomol.*, 41 (4):779-84, 2004.
- Daniels TJ, Fish D, Falco RC. Seasonal activity and survival of adult *Ixodes dammini* (Acari: Ixodidae) in southern New York State. *J Med Entomol.*, 26 (6):610-4, 1989.
- Yuval B, Spielman A. Duration and regulation of the developmental cycle of *Ixodes dammini* (Acari: Ixodidae). *J Med Entomol.*, 27 (2):196-201, 1996.
- Lord C.C. Mortality of unfed nymphal *Ixodes dammini* (Acari:Ixodidae) in field enclosures. *Envir.Ent.*, 22:82-87, 1993.
- Porco TC. A mathematical model of the ecology of Lyme disease. *IMA J Math Appl Med Biol.*, 16 (3):261-96, 1999.
- Ogden NH, Lindsay LR, Beauchamp G, Charron D, Maarouf A, O'Callaghan CJ, Waltner-Toews D, Barker IK. Investigation of relationships between temperature and developmental rates of tick *Ixodes scapularis* (Acari: Ixodidae) in the laboratory and field. *J Med Entomol.*, 41 (4): 622-33, 2004.
- Chilton NB, Bull CM. Influence of environmental factors on oviposition and egg development in *Amblyomma limbatum* and *Aponomma hydrosauri* (Acari: Ixodidae). *Int J Parasitol.*, 24 (1): 83-90, 1994.
- Peavey CA, Lane RS. Field and laboratory studies on the timing of oviposition and hatching of the western black-legged tick, *Ixodes pacificus* (Acari: Ixodidae). *Exp Appl Acarol.*, 20 (12): 695-711, 1996.
- Randolph S.E. and Rogers D.J A generic population model for the African tick *Rhipicephalus appendiculatus*. *Parasitology.*, 115:265, 1997.
- Randolph SE, Green RM, Hoodless AN, Peacey MF. An empirical quantitative framework for the seasonal population dynamics of the tick *Ixodes ricinus*. *Int J Parasitol.*, 32(8):979-89, 2002.
- Gardiner, W.P., Gettinby, G. A weather-based prediction model for the life-cycle of the sheep tick, *Ixodes ricinus* L. *Veterinary Parasitology*, 13(1):77-84, 1983.
- King D, Gettinby G, Newson RM. A weather-based prediction model for the life-cycle of the sheep tick, *Ixodes ricinus* L. *Veterinary Parasitology*, 29(1):41-51, 1998.
- Sandberg, S., Awerbuch, T.E., Spielman, A. A comprehensive multiple matrix model representing the life cycle of the tick that transmits the agent of Lyme disease. *Journal of Theoretical Biology*, 157(2):203-220, 1992.
- Kitron U. and Mannelli A. Modeling the ecological dynamics of tick-borne zoonoses. In: T.N. Mather and D.E. Sonenshine, Editors, *Ecological Dynamics of Tick-borne Zoonoses Oxford University Press, Oxford*, 157(2):198, 1994.
- Randolph S.E. and Rogers D.J. A generic population model for the African tick *Rhipicephalus appendiculatus*. *Parasitology*, 115:265, 1997.
- Mwambi H.G., Baumgartner J. and K.P. Hadel. Ticks and tickborne diseases: a vector-host interaction model for the brown ear tick. *Stat.Methods Med. Res.*, 9:279, 2000.



- Ghosh Mini and Andrea Pugliese. Seasonal population dynamics of ticks, and its influence on infection transmission: a semi-discrete approach. *Bulletin of Mathematical Biology*, 66:1659-1684, 2004.
- Awerbuch-Friedlander T., Levins R. and Predescu M. The role of seasonality in the dynamics of deer tick populations. *Bulletin of Mathematical Biology*, 67:467, 2005.
- Rosa R and Andrea Pugliese. Effects of tick population dynamics and host densities on the persistence of tick-borne infections. *Mathematical Biosciences*, 208:216-240, 2007.
- Daniels T.J., Falco R.C, Curran K.L., Fish D. Timing of *Ixodes scapularis* (Acari:Ixodidae) oviposition and larval activity in southern New York. *J. Med.Entomol.*, 33:140-147, 1996.
- Mount G.A, D.G., Haile, E., Daniels. Simulation of blacklegged tick (Acari:Ixodidae) population dynamics and transmission of *Borrelia burgdorferi*. *J. Med.Entomol.*, 34:461-484, 1997.
- Diekmann O, Heesterbeek J.A.P. Mathematical epidemiology of infectious disease: Model building, analysis and interpretation. *Wiley, New York*, :2000.
- Jones, C.J., Kitron, U.D. Populations of *Ixodes scapularis* (Acari: Ixodidae) are modulated by drought at a Lyme disease focus in Illinois. *J. Med.Entomol.*, 37 (3):408-415, 1997.
- Wilson, M. L., S. R. Telford, III, J. Piesman, and A. Spielman. Reduced abundance of immature *Ixodes dammini* (Acari: Ixodidae) following elimination of deer. *J. Med.Entomol.*, 25:224-228, 1988b.
- Deblinger, R. D., M. L. Wilson, D. W. Rimmer, and A. Spielman. Reduced abundance of immature deer ticks (Acari: Ixodidae) following incremental removal of deer. *J. Med.Entomol.*, 30:144-150, 1993.
- Telford, S. R., III. Deer tick-transmitted zoonoses in the eastern United States, In A. Aguirre, R. S. Ostfeld, G. M. Tabor, C. House, and M. C. Pearl [eds.], *Conservation medicine: ecological health in practice. Oxford University Press, New York.*, :310-324, 2002.
- Van Buskirk J and Ostfeld R.S. Controlling Lyme disease by modifying the density and species composition of tick hosts. *Ecological Applications*, 5 (4):1133-1140, 1995.