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Tick-borne infectious agents in nature: Simulated effects of changes in host density on spatial-temporal prevalence of infected ticks

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ABSTRACT

Ticks (Ixodidae) are important vectors of infectious agents that affect human and animal health, and the spatial-temporal dynamics of tick-host-pathogen-landscape interactions are difficult to understand based on empirical observations alone. We used a spatially explicit simulation model to examine the effects of changes in host density on the prevalence of a hypothetical transstadially transmitted infectious agent in a population of a prototypical three-host tick under ecological conditions representative of the predominantly forested areas of the south-central United States. The model was parameterized such that baseline conditions yielded a landscape-level nymphal infection prevalence (NIP) fluctuating seasonally around a threshold of 0.1 (indicative of pathogen endemicity in some disease systems) roughly paralleling seasonal fluctuations in wildlife host densities, with seasonal highs in late summer and early fall and seasonal lows in winter and spring. In simulated scenarios of both small-sized and medium-sized host reduction, the densities of both uninfected and infected off-host nymphs decreased markedly from year-to-year. The number of habitat patches in which NIP > 0.1, however, increased when small-sized hosts were removed, yet decreased when medium-sized hosts were removed. Simulation of the reduction in density of large-sized hosts resulted in trends similar to those produced by reducing density of small-sized hosts, but trends were less pronounced. Under the conditions simulated, both NIP and off-host nymph densities (DON) were particularly sensitive to changes in the proportion of larvae obtaining their blood meal from medium-sized hosts. Variation in simulated NIP values can be explained by the fact that larval, nymphal, and adult tick loads were distributed differently among the different-sized hosts, each with their distinct range of movement and degree of variation in population size. Simulation results of this hypothetical case study offer insight into the complex landscape-level interactions of a prototypical 3-host tick and suggest that medium-sized hosts could play a key role in sustaining and dispersing a tick-borne infectious agent in nature.

1. Introduction

Emerging zoonoses from wildlife represent a significant and increasing threat to global public and animal health with economic and poverty impacts (Daszak et al., 2000; Jones et al., 2008; Rich and Perry, 2011). Yet, significant gaps exist in understanding complex factors driving zoonotic systems and disease emergence (Plowright et al., 2008; Lloyd-Smith et al., 2009). The emergence of infectious diseases is driven by biological and environmental factors that alter the spatial distribution and intensity of transmission of zoonotic infectious agents, as well as by demographic and sociological changes that influence the likelihood of human exposure to sources of infection (Vanwambeke et al., 2010). Zoonotic infectious diseases are linked inextricably to the natural system of which the infectious agent is a part. For example, a study by Schauber et al. (2005) found that predictors of Lyme disease risk based upon acorn production, mouse densities, and weather were variable depending on spatial scale, leading to the conclusion that additional predictors or combinations of predictors were necessary to capture the complexity of the system. Infectious agents often seemingly appear and disappear quickly in nature, making the apparent prevalence of infection both spatially and temporally discontinuous and rendering the occurrence of human or animal disease or seroconversion as insensitive indicators of the dynamics of infectious agent transmission (Childs and Paddock, 2003). For vector-borne infectious agents, local differences in host species diversity and sporadic fluctuations in host population density can promote or hinder the persistence, prevalence and rate of spread of infection (Tabor et al.,

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2001). Detection and effective control of human diseases caused by these infectious agents frequently depends on targeting local vector or reservoir populations (Childs and Paddock, 2003). Although general distribution and density of hosts and vectors is determined by environmental conditions (Pavlovsky, 1966; Kitron, 1998), and macro-scale correlative models are useful in delineating areas of potential disease risk and targeting general surveillance measures (Guerra et al., 2002; Brownstein et al., 2003), such models do not identify conditions fostering disease emergence and hence do not provide information needed to design preemptive management schemes (Kiel et al., 2009).

Ticks (*Ixodidae*) are important vectors of infectious agents that can cause morbidity and mortality in human and animal populations and often cause substantial economic losses. Numerous simulation models of tick population dynamics have been developed over the past two decades. Some have emphasized the effect of environmental factors on off-host tick survival (Mount and Haile, 1989; Mount et al., 1991, 1993, 1997), including predictions of tick populations as a result of projected scenarios of climate change (Ogden et al., 2005, 2008, 2014; Dobson and Randolph, 2011; Wu et al., 2013). Others have focused on the role of hosts in affecting local distributions of ticks (Teel et al., 1996, 1998, 2003; Corson et al., 2001, 2003, 2004; Hoch et al., 2010), while still others have emphasized the role of fluctuations in host population sizes (Gaff and Gross, 2007; Dobson and Randolph, 2011). Simulation models of tick-borne diseases have explored the role of host community composition, including the timing of seasonal fluctuations of hosts relative to that of the various tick life stages, on disease ecology (Schmidt and Ostfeld, 2001; Schauber and Ostfeld, 2002), as well as the timing of pathogen invasion relative to tick invasion (Ogden et al., 2013), and the basic reproduction number for a pathogen in a multi-host disease system (Dunn et al., 2013). Most models have been spatially implicit or have represented small landscapes composed of a dozen or fewer habitat cells, however, Madhav et al. (2004) describe a spatially explicit, cellular automata model representing tick range expansion over a large, simplified landscape. Recently, however, Wang et al. (2012) developed a model capable of simulating the spatial-temporal dynamics of ticks within a heterogeneous landscape resulting from seasonal and year-to-year fluctuations in host densities.

In the present paper, we modified the model of Wang et al. (2012) to examine the effects of changes in host density on the spatial-temporal prevalence of infected ticks within the landscape. We were particularly interested in the effects of altering the relative density of small-, medium-, and large-sized mammalian hosts. Our focus was not on differences among host ability to transmit pathogens *per se*, but rather on differences in tick-host-landscape interactions that sustain and disperse ticks with a hypothetical horizontally transmitted pathogen. Small-sized rodents, medium-sized carnivores/omnivores, and large-sized ungulates differ with regard to the numbers of larval, nymphal, and adult ticks they can carry, and with regard to the sizes of their activity ranges. As a hypothetical case study, we simulated the spatial-temporal dynamics of a three-host tick within a community of mammalian hosts in a forested area under climatic conditions representative of the south-central United States. We monitored the resulting spatial-temporal patterns in the nymphal infection prevalence (NIP) under several scenarios representing changes to the densities of various-sized hosts, and examined the processes generating these patterns.

2. Methods

We modified the model developed by Wang et al. (2012), which simulates the spatial-temporal dynamics of a common three-host tick and their mammalian hosts under climatic conditions and landscapes representative of the predominantly forested regions of the south-central U.S., to include the transmission of bacterial infectious agents among the different tick life stages and the different types of hosts (Fig. 1). A detailed model description following the protocol suggested by Grimm et al. (2006) is available in Wang et al. (2012). Briefly, the model is a spatially structured, individual-based, stochastic model consisting of a square lattice of 400 cells, each representing a 30 m by 30 m (0.09 ha) habitat patch within a (≈40 ha) simulated landscape. Within each habitat cell, the numbers of ticks in each life stage (eggs, larvae, nymphs, and adults) change from week to week in response to variations in climatic conditions (temperature, relative humidity, and day length) and availability of hosts (small-, medium-, and large-sized mammals), whose numbers also change weekly in response to seasonal climatic variations. Individual hosts collect ticks from habitat cells within their activity range depending on the relative density of actively host-seeking life stages and the proportion of time spent in each cell, and deposit engorged (blood-fed) ticks into habitat cells depending on the proportion of time spent in each cell. The model determines the number of ticks in each life stage collected from each habitat cell each time step by first calculating, separately for each life stage, the total number of host-seeking ticks within the activity range of the host, then setting the number of ticks the host would collect (N) equal to this total number of host-seeking ticks, or equal to the maximum number of ticks the host can carry, whichever was less. Small-, medium-, and large-sized hosts differ with regard to the numbers of larval, nymphal, and adult ticks they can carry, and with regard to the sizes of their activity ranges. Finally, the model calculates the proportion of N collected from each habitat cell as:

$$D_i = \frac{HP_i \cdot N_i}{\sum_i (HP_i \cdot N_i)}$$

where D_i is the proportion of the total number of ticks in a given life stage (calculated separately for larvae, nymphs, and adults) collected by an individual host that were collected from habitat cell i, N_i is the number of host-seeking ticks in that life stage in habitat cell i, and HP_i is the relative preference of the host for the habitat type in cell i ($0 \leq HP_i \leq 1$).

To include the transmission of bacterial infectious agents, we added to the model a hypothetical horizontally transmitted agent capable of infecting tick hosts of all size categories. Each uninfected host is examined each week to see if it has collected infected ticks. If infected ticks have been collected, tick-to-host transmission occurs probabilistically. Uninfected on-host ticks are also examined each week to see if they have been feeding upon an infected host. If feeding upon an infected host has occurred, host-to-tick transmission occurs probabilistically. To represent the agent-vector-host transmission process, we made a series of simplifying assumptions based on transmission dynamics that have been well-described for various tick-borne disease systems, which we feel represent a plausible transmission environment for our hypothetical pathogen transmitted by a prototypical three-host tick. We assumed: (1) all hosts and all post-embryonic tick life stages can become infected (Stromdahl et al., 2000; Yabsley, 2010), (2) transstadial transmission in ticks occurs (Dennis and Piesman, 2005), (3) no transovarial transmission in ticks occurs (Groves et al., 1975; Long et al., 2003); (4) lifelong infection of hosts (Monack et al., 2004), and (5) no transplacental transmission by hosts (Mather et al., 1991). To help isolate the effects of changes in host density on the prevalence of infected ticks, we also assumed that tick-to-host and host-to-tick transmission probabilities were the same. That is, we used a single parameter (α_{ij}) to represent both the capability of the donor organism (i) to transmit the infectious agent and the susceptibility of the recipient organism (j) to infection. We calibrated α ($\alpha = 0.19$) such that NIP values simulated under baseline conditions (see next