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Review article

The role of *Ixodes scapularis*, *Borrelia burgdorferi* and wildlife hosts in Lyme disease prevalence: A quantitative review

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ABSTRACT

Due to the ongoing expansion of *Ixodes scapularis* (blacklegged tick) throughout the northeastern and mid-western United States, there is need to identify the role wildlife hosts play in the establishment and maintenance of tick populations. To quantify and synthesize the patterns of *I. scapularis* and *Borrelia burgdorferi* sensu stricto and sensu lato prevalence relative to wildlife hosts, we reviewed the findings of independent studies conducted throughout the United States. We performed a comprehensive literature search from 1970 to 2017 using the ISS Web of Science Core Collection and the keywords “*Ixodes scapularis*,” “*Ixodes dammini*” and “*Borrelia burgdorferi*.” We identified 116 studies for inclusion in our meta-analysis, with 187,414 individual wildlife hosts captured and examined for *I. scapularis* and either the host or ticks collected subsequently tested for *B. burgdorferi*. We found that only 13% of the wildlife mammals sampled comprised species other than *Odocoileus virginianus* (white-tailed deer) and *Peromyscus leucopus* (white-footed mouse). To examine whether there were regional differences between the Northeast, Midwest and the Southeast U.S. in *I. scapularis* infestation rates on wildlife hosts, we used general linear models (glm), with post hoc pairwise comparisons. In most cases, detection of *I. scapularis* and *B. burgdorferi* was significantly higher in the Northeast than the Midwest. Using data on host-specific *I. scapularis* infestation prevalence, *B. burgdorferi* prevalence in feeding larvae, and host permissiveness, we developed an epizootiological model to determine the relative contributions of individual hosts to *B. burgdorferi*-infected nymphs. Our model provides additional evidence that wildlife hosts other than *P. leucopus* may contribute more to Lyme disease risk than commonly thought. To aid in understanding the ecology of Lyme disease, we propose that additional studies sample non-*Peromyscus* spp. hosts to obtain more detailed tick and pathogen infestation and infection estimates, respectively, for these less frequently sampled wildlife hosts.

1. Introduction

The discovery that *Ixodes scapularis* (blacklegged tick) is responsible for the transmission of *Borrelia burgdorferi*, the causative agent of Lyme disease, spurred research to quantify the distribution and abundance of this tick species (Steere and Malawista, 1979; Steere et al., 1978). Among the earliest findings was that the geographic distribution of *I. scapularis* was expanding from two focal populations in the Northeast and upper Midwest regions of the United States (Anderson et al., 1987), resulting in urgent efforts to identify and prevent the establishment of new tick populations over the past four decades (Dennis et al., 1998; Eisen et al., 2016). Despite extensive data collection, our knowledge of *I. scapularis* population ecology remains limited to a few wildlife host species (Hamer et al., 2010; Ostfeld, 2011). Most studies on *I. scapularis* emphasize two host species as important to establishing and

maintaining *I. scapularis* populations: *Odocoileus virginianus* (white-tailed deer) and *Peromyscus leucopus* (white-footed mouse) (Fish and Dowler, 1989; Madhav et al., 2004). However, *I. scapularis* is a host generalist that has been detected on over 125 wildlife species (Keirans et al., 1996). Understanding tick population biology will thus require researchers to consider a broader suite of potential wildlife host species (Krasnov et al., 1997).

A disproportionate focus on examining conspicuous wildlife hosts can lead to a dismissal of the influence that other wildlife hosts play in the dynamics of *I. scapularis* populations. The presence of different wildlife host species can affect tick population sizes by providing additional blood meals or serving as ecological traps by killing the ticks that attempt to feed on them (Keesing et al., 2006). This variation in host suitability is referred to as ‘host permissiveness’ and frequently is measured by the proportion of ticks attempting to obtain a blood meal

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from a host that successfully feed and survive host grooming (Keesing et al., 2009). In addition, wildlife hosts vary in reservoir competency for *B. burgdorferi* which may influence the maintenance of the pathogen within the community (LoGiudice et al., 2003; Piesman and Sinsky, 1988). Although only *B. burgdorferi sensu stricto* contributes to Lyme disease, older methods were limited to detecting the *Borrelia* complex are collectively called *B. burgdorferi sensu lato* (Baranton et al., 1992). Regionally, reservoir potential of hosts (i.e., estimated relative contribution to infection of larval ticks) for *B. burgdorferi* may differ as well (Mather et al., 1989; Piesman and Happ, 2001).

The goal of our review is to identify and synthesize the patterns of *I. scapularis* and *B. burgdorferi* prevalence relative to wildlife hosts. To our knowledge, there has not been a systematic investigation of *I. scapularis* infestation rates and *B. burgdorferi* infection prevalence among wildlife hosts in North America. Therefore, we examined studies that reported the presence or prevalence of the tick or pathogen and corresponding wildlife hosts to calculate the prevalence of infestation (i.e. the proportion of hosts infested), intensity of infestation (i.e. the average number of ticks per host) and *B. burgdorferi sensu stricto* and *sensu lato* infection prevalence (i.e., either the proportion of ticks removed from hosts that tested positive or the proportion of wildlife hosts which tested positive) for each host species. We specifically sought to determine whether there are regional differences in prevalence and intensity of *I. scapularis* as well as *B. burgdorferi* prevalence between the Northeast, Midwest, and Southeast U.S. (Schwartz et al., 2017; United States Census Bureau, 2010). We then used data on the prevalence of *I. scapularis* larvae feeding on wildlife hosts, the prevalence of *B. burgdorferi*-infected larvae feeding on wildlife hosts, and host permissiveness, to develop a regional scale epizootiological model for eight wildlife host species. Our model calculates the relative host-specific contributions to feeding and infecting larval *I. scapularis* with *B. burgdorferi*, as these individuals become infected nymphs, the life-stage that poses the greatest risk to humans for exposure to Lyme disease (Mather et al., 1996). The results of this quantitative review will contribute to our understanding of the ecology of Lyme disease by helping to identify mechanistically the relative contributions of different wildlife hosts to disease risk as well as providing direction for future research in determining the interactions between *I. scapularis*, *B. burgdorferi* and wildlife hosts, which ultimately determine human risk of exposure to Lyme disease.

2. Methods

2.1. Literature search and study selection

We identified relevant peer-reviewed articles published through October 2017 by searching the ISI Web of Science Core Collection database using the following terms: *Ixodes scapularis*, *Ixodes dammini*, and *Borrelia burgdorferi*. Prior to 1996, *I. scapularis* and *I. dammini* were considered two distinct species, but now *I. dammini* is considered a junior synonym and has been replaced by *I. scapularis* (Keirans et al., 1996). We also examined the citations within relevant papers to identify additional studies. Inclusion criteria for this meta-analysis required that studies were conducted in the United States or Canada and involved the capture of potential wildlife hosts and subsequent examination for *I. scapularis* or *B. burgdorferi*. Studies must also have provided information for the calculation of at least one of the following: the wildlife species-specific prevalence of *I. scapularis* (i.e., proportion of hosts parasitized), the intensity of *I. scapularis* infestation (i.e., numbers of parasites per host), prevalence of *B. burgdorferi*-infected feeding *I. scapularis* (i.e., proportion of ticks which tested positive) and the sero-prevalence of *B. burgdorferi* infection (i.e., proportion of wildlife hosts which tested positive). We excluded data derived from passive surveillance (i.e., data from tick mail-ins) and experimental manipulation of habitat to reduce *I. scapularis* abundance (e.g., prescribed burning, deer removal, pesticides). However, data from control sites in experimental studies were used in this meta-analysis.

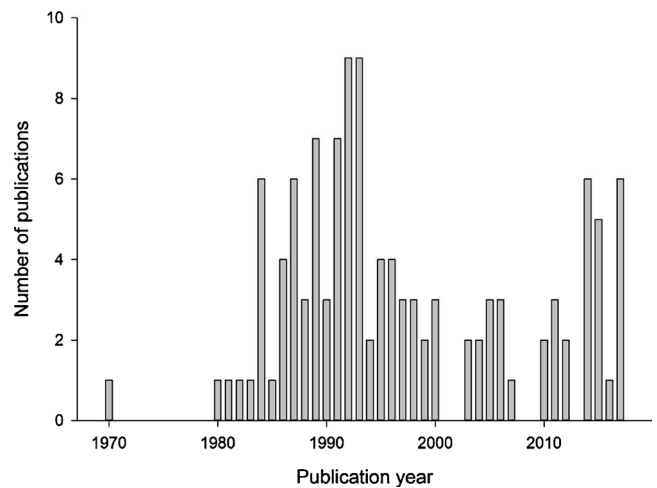


Fig. 1. Number of studies published by year in which (1) animal captures took place in the United States, (2) animals were examined for *I. scapularis*, or (3) either the host or ticks collected were subsequently tested for *B. burgdorferi*.

2.2. Data extraction and preparation

Data collected from all articles included citation, study site name, county, state, data collection year, and data collection month. For each wildlife species examined, we recorded the scientific name, number of individual hosts captured, number of individuals examined for ticks, number of individual hosts tested for *B. burgdorferi*, number of individual hosts testing positive for *B. burgdorferi*, method of *B. burgdorferi* detection, number of individual hosts infested with *I. scapularis* (larvae, nymphs, adults), total number of ticks collected (larvae, nymphs, adults), number of feeding *I. scapularis* (larvae, nymphs, or adults) tested for *B. burgdorferi*, as well as the number of feeding *I. scapularis* that tested positive for *B. burgdorferi*. We divided our analysis into three regions (Midwest, Northeast and Southeast) using a combination of US census designation as well as phylogenetic studies and host-seeking behavior of *I. scapularis* (Schwartz et al., 2017; United States Census Bureau, 2010; Fig. 1). We grouped each wildlife host into categories of projected host permissiveness (high, medium and low) based on similarities in body mass and species classification (i.e. class and order) to the six hosts examined by Keesing and colleagues (2009; Table S1). Low permissive hosts tend to have few ticks surviving host grooming (i.e. 3.5%), whereas tick feeding success on medium permissive hosts ranges from 17 to 26% and on a highly permissive host (i.e., *P. leucopus*) ticks have an approximately 49% feeding success rate. Due to no similar examination of host permissiveness for deer (i.e., white-tailed and sika), the American black bear and reptiles, we were not able to categorize these hosts. For those studies from which we could not directly extract the data due to either summarization of data or inclusion of data in figures instead of tables or text, we requested data via email from the corresponding author. When we were unable to contact the author, we used Plot Digitizer v.2.6.6 to extract the relevant data from figures (Huwaldt and Steinhorst, 2014).

2.3. Statistical analysis

We developed generalized linear models, incorporating the year in which the data were collected as a covariate to control for differing levels of surveillance effort over time, to test for differences between the three focal regions (Midwest, Northeast, and Southeast) in the prevalence of infestation of *I. scapularis* for all wildlife host species, and intensity of infestation of *I. scapularis* for *O. virginianus* and *P. leucopus*. For intensity of infestation, we analyzed only *O. virginianus* and *P. leucopus* because for those species there were sufficient data throughout all three regions and through time. We examined all models for an

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