

Annotated List of the Hard Ticks (Acari: Ixodida: Ixodidae) of New Jersey

James L. Occi,^{1,4} Andrea M. Egizi,^{1,2} Richard G. Robbins,³ and Dina M. Fonseca¹

¹Center for Vector Biology, Department of Entomology, Rutgers University, 180 Jones Ave, New Brunswick, NJ 08901-8536, ²Tick-borne Diseases Laboratory, Monmouth County Mosquito Control Division, 1901 Wayside Road, Tinton Falls, NJ 07724, ³Walter Reed Biosystematics Unit, Department of Entomology, Smithsonian Institution, MSC, MRC 534, 4210 Silver Hill Road, Suitland, MD 20746-2863 and ⁴Corresponding author, e-mail: james.occi@rutgers.edu

Subject Editor: Rebecca Eisen

Received 1 November 2018; Editorial decision 8 January 2019

Abstract

Standardized tick surveillance requires an understanding of which species may be present. After a thorough review of the scientific literature, as well as government documents, and careful evaluation of existing accessioned tick collections (vouchers) in museums and other repositories, we have determined that the verifiable hard tick fauna of New Jersey (NJ) currently comprises 11 species. Nine are indigenous to North America and two are invasive, including the recently identified Asian longhorned tick, *Haemaphysalis longicornis* (Neumann, 1901). For each of the 11 species, we summarize NJ collection details and review their known public health and veterinary importance and available information on seasonality. Separately considered are seven additional species that may be present in the state or become established in the future but whose presence is not currently confirmed with NJ vouchers. We compare our list of hard ticks in NJ with those from neighboring states (Connecticut, New York, Pennsylvania, Delaware, and Maryland), discuss the importance of vouchers in tick research and surveillance, and examine the likelihood and public health consequences of additional hard tick species becoming established in NJ.

Key words: surveillance, vouchers, accession, invasive, health

The State of New Jersey (NJ) is located on the northeastern coast of the United States and is characterized by a convergence of features that may favor tick abundance and diversity as well as human exposure to tick-borne pathogens: 1) although NJ is one of the smallest U.S. states, due to its physiography and elongate outline with an approximately north-south axis, it has five distinct climatic zones that range from temperate to humid subtropical (Collins and Anderson 1994); 2) NJ is on the Atlantic flyway for migratory birds, which often transport ticks, especially from southern localities (Ogden et al. 2008) and references therein); and 3) NJ is the most densely populated U.S. state (U.S. Census Bureau, <https://factfinder.census.gov/>; last accessed 29 January 2019), where former farmland has now largely been replaced by suburban developments (Olson and Lyson 1999) situated near or within patches of second-growth forest that provide habitat for wild vertebrates, which may host a variety of tick species (Paddock and Yabsley 2007, Falco et al. 2008) and serve as reservoirs of tick-borne pathogens (Wood and Lafferty 2013).

To thoroughly understand the risks of tick-borne diseases to humans, domestic animals, and wildlife, it is important to know which tick species occur in a given area. Best practices for surveying ticks depend on the life history and ecology of particular species. For example, species that spend most of their lives in the nests and burrows of their hosts (i.e., nidicolous ticks) are unlikely to be collected from the environment by dragging, which is currently the most commonly used method to sample so-called hard ticks (family Ixodidae) (Gray et al. 2012) and favors collection of species that host-seek by clinging to vegetation (i.e., openly questing ticks). Surveying for nidicolous ticks often requires trapping hosts (Obsomer et al. 2013), which can be cumbersome and even dangerous (Animal Care and Use Committee 1998), and partly explains why they are often poorly studied.

While several hard tick species are recognized as occurring in NJ, a formal tally has previously not been available and is the objective of this review. Species often encountered by NJ residents, such as the American dog tick, *Dermacentor variabilis* Say, the lone star tick,

Amblyomma americanum Linnaeus, and the blacklegged tick, *Ixodes scapularis* Say (Acar: Ixodidae) (previously known as the ‘deer tick’), are obviously present (Smart and Caccamise 1988, Schulze et al. 2006, Egizi et al. 2017). However, as this review demonstrates, information on the occurrence of other hard tick species in the state is limited. Less commonly encountered species of hard ticks, or species unlikely to bite humans, may still play a pivotal role in the local transmission of pathogens, thereby driving epizootics that can spill over to humans (Foley et al. 2011, Randolph 2011).

Here we present an annotated list of hard ticks that have been documented from NJ and discuss some other species that may already be present, but undocumented, or that may become established in the future. Our hope is that this work will aid in the development of standardized hard tick surveillance across NJ, thus facilitating more accurate assessments of tick-borne disease risk as well as the development of strategies to minimize such risk statewide.

Materials and Methods

We conducted computerized bibliographic searches using internet databases, such as PubMed and Google Scholar, to identify all studies of ixodid ticks in NJ that have been published in peer-reviewed journals. Search terms used were: ‘ticks, New Jersey’; ‘ixodid, New Jersey’; and iterations thereof, substituting individual tick genera or species. The United States National Tick Collection (USNTC), housed at Georgia Southern University (<http://cosm.georgiasouthern.edu/usntc/>; last accessed 29 January 2019), provided lists of accessioned NJ tick collections (accession numbers beginning with RML). Voucher specimens reported for the first time in this manuscript were deposited in the permanent research collections of the USNTC and are summarized in [Supp Table 1 \[online only\]](#). We also queried institutions in Connecticut (University of Connecticut), Delaware (University of Delaware, Wesley University), Maryland (University of Maryland), New York (State University of New York College of Environmental Science and Forestry at Syracuse, New York State Museum), and Pennsylvania (Academy of Natural Sciences of Drexel University) to obtain any formal or informal tick lists for their respective states.

For each species, we provide a brief review of its known importance as a vector of pathogens to humans, companion animals, livestock, and wildlife and summarize its known or likely seasonal

activity and, for questing tick species, their known (or predicted) habitat associations in NJ. Note that ‘activity’ for questing ticks is determined by flagging, while ‘activity’ for midicolous ticks is based on trapping or animal surveys, which may depend on the seasonal activity of the hosts.

Results

Ixodid Ticks Demonstrably Present in New Jersey

Our analyses yielded records for 11 ixodid tick species that occur or have occurred in NJ ([Table 1](#)) since vouchers have been identified. We present collection records for these species, arranged alphabetically, together with data for the earliest known museum voucher specimens of each species. Where applicable, common names accepted by the Entomological Society of America (<https://www.entsoc.org/common-names>; last accessed 29 January 2019) are provided alongside each tick species’ Latin name.

Amblyomma americanum (Linnaeus, 1758), the lone star tick

Kalm (1754) was the first to report the lone star tick, described as ‘*Acarus ovalis planus ruber, macula dorsali alba*’ (roughly translated as ‘an oval shaped, flat, red (mite or tick) with a white dorsal spot’) from the forests of Pennsylvania and New Jersey, but no vouchers are known. Leidy (1890) recorded what were most likely lone star ticks collected from his dog in Beach Haven Township, Ocean County, in June 1890, although he did not preserve specimens. The first voucherized specimen of *A. americanum* from NJ with full collection data was a single nymph collected by N. Adams, C. Flint, and O. Flint from Pakim Pond, Burlington County, on 7 June 1991 ([Table 1](#)).

This species is of significant public health and veterinary importance because it readily feeds on humans and pets as well as wildlife, such as white-tailed deer (*Odocoileus virginianus*), which routinely host all stages of this tick and often suffer heavy infestations (Bloemer et al. 1988). In Monmouth County, NJ, *A. americanum* is the tick species most often submitted by residents to the Mosquito Control Division’s Tick Identification Program (Egizi et al. 2017).

Amblyomma americanum transmits the agents of human ehrlichiosis, *Ehrlichia chaffeensis* and *E. ewingii* (Goddard and Varela-Stokes 2009). Ehrlichiosis is also a veterinary problem in NJ, where 5,383 canine cases were reported in 2017 by the Companion

Table 1. Annotated list of ixodid ticks of New Jersey, with first known vouchered collection and accompanying data, if available

Species	Accession #	Date collected	Location (county)	Sex/stage	Source ^a
<i>Amblyomma americanum</i>	RML120584	7 June 1991	Pakim Pond (Burlington)	1 nymph	Environment
<i>Dermacentor albipictus</i>	RML119098	19 Dec. 1987	Fort Monmouth (Monmouth)	1 nymph	Environment
<i>Dermacentor variabilis</i>	RML18497	5 July 1909	Lakehurst (Ocean)	1 adult,	NA
	RML59481	8 May 1915	Pemberton (Burlington)	1 female	NA
<i>Haemaphysalis leporispalustris</i>	RML128851	11 June 2018	Teterboro Airport(Bergen)	2 male, 2 female	<i>Sylvilagus floridanus</i>
<i>Haemaphysalis longicornis</i>	RML128847	23 Apr. 2018	Watchung Reservation (Union)	5 larvae	Environment
	RML128848	26 June 2018	Watchung Reservation (Union)	6 nymphs, 1 female	Environment
<i>Ixodes brunneus</i>	RML115824	23 Mar. 1943	Shiloh (Cumberland)	1 female	<i>Troglodytes hiemalis</i>
<i>Ixodes cookei</i>	RML64968	Prior to 1966	NA	6 nymphs, 1 larva	Environment
<i>Ixodes dentatus</i>	RML122095	May 1995	Cranford (Union)	2 nymphs	Environment
<i>Ixodes scapularis</i>	RML18554	1 Dec. 1933	Princeton (Mercer)	1 nymph	<i>Sylvilagus floridanus</i>
<i>Ixodes texanus</i>	RML122620	Feb. 1998	Cranford (Union)	3 females	<i>Procyon lotor</i>
<i>Rhipicephalus sanguineus</i>	RML60065	6 June 1936	Atlantic City (Atlantic)	32 females	Environment

RML, Rocky Mountain Laboratories accession number; collection currently at Georgia Southern University, Statesboro, GA.

^aEnvironment = collected from vegetation, except in the case of *R. sanguineus*, where Environment = collected by flagging indoors or removal from bedding; NA = source of collection (host or environment) unknown.

Animal Parasite Council (<https://www.capcvet.org/>; last accessed 29 January 2019). Additionally, *A. americanum* transmits the agent of 'bobcat fever,' *Cytauxzoon felis*, to wild and domestic cats (Birkenheuer et al. 2006). Bobcats (*Lynx rufus*) are the primary reservoir for this protozoan (Shock et al. 2011), and though their populations in NJ are small, they are reportedly increasing (<https://www.nj.gov/dep/fgw/ensp/pdf/end-thrtened/bobcat.pdf>). Additionally, this species has been associated with human alpha gal 'red meat' allergy (Commins and Platts-Mills 2013).

In NJ, *A. americanum* adults and nymphs become active in April and will continue to seek hosts until early August, although most activity occurs in June and July (Schulze et al. 1986). Larvae emerge in late April and early May with a second period of activity beginning in August, peaking in September and disappearing by the end of October. Larvae are more abundant during the second peak compared with the first (Schulze et al. 1986) possibly indicating overwintering mortality. According to Childs and Paddock (2003), *A. americanum* overwinters as replete larvae, unfed or replete nymphs, or unfed adults but only cite studies from Oklahoma (Hair and Howell 1970). In Oklahoma, unfed larvae are unlikely to survive the winter (Hair and Howell 1970), and the appearance of larvae in NJ only after adults have become active in the Spring may indicate the same is true there.

In NJ, the lone star tick is established in the southern counties although there are indications it is spreading north (Springer et al. 2015). In much of this portion of the state the lone star tick can be found in forests, woodlands, fields, and ecotones (Schulze et al. 2011).

Dermacentor albipictus (Packard, 1869), the winter tick

A single nymph of *D. albipictus*, collected at Fort Monmouth, Monmouth County, on 19 December 1987 by J. Hornberger, constitutes the first voucherized specimen of this species from NJ (Table 1).

Schulze et al. (1984) have shown that in northern NJ the winter tick feeds primarily on white-tailed deer, while in the north-central United States and Canada this tick can develop large infestations on moose (*Alces alces*), to the extent that these animals become seriously weakened or die of exsanguination (Samuels 2004). *D. albipictus* does not appear to target livestock and is not considered an important vector of human pathogens. Although Magnarelli et al. (1986) claimed to have detected *Borrelia burgdorferi* in *D. albipictus* collected from white-tailed deer in Connecticut, the polyclonal sera used has been shown to cross react with *B. miyamotoi* (Scoles et al. 2001). Since deer are incompetent for *B. burgdorferi* (Telford et al. 1988), *D. albipictus* may in fact not be able to acquire *B. burgdorferi*.

In Alberta, western Canada, *D. albipictus* larvae emerge in September and feed until November. *Dermacentor albipictus* is a one-host tick, so larvae molt on the host and when nymphs emerge, between October and March, they too feed and molt on the host (Samuels 2004). Adults emerge from February to May, feed, mate, and the replete females drop off in late spring. Based on these observations, a limiting factor on *D. albipictus* populations appears to be the ability of larvae (the only host-seeking stage) to find a host before the winter sets in (Holmes et al. 2018).

Dermacentor variabilis (Say, 1821), the American dog tick

Although Banks (1908) mentioned that this species is widespread in North America, he did not list specific states. The first NJ specimen of *D. variabilis* accessioned into the USNTC was an adult from Lakehurst, Ocean County, dated 5 July 1909. The collector is unknown. The first accessioned specimen with full collection

data was a female collected on 28 May 1915 by H. K. Plank in Pemberton, Burlington County (Table 1).

Immature stages of *D. variabilis* occur often on small rodents, especially meadow voles (*Microtus pennsylvanicus*) (Smart and Caccamise 1988), while adult ticks are more abundant on medium-sized mammals (Burgdorfer 1969). During 2013–2015, J. L. Occi collected adult *D. variabilis* from coyotes (*Canis latrans*), black bears (*Ursus americanus*), raccoons (*Procyon lotor*) and woodchucks, also known as groundhogs (*Marmota monax*); representative specimens from each host were deposited in the USNTC (Supp Table 1 [online only]).

Dermacentor variabilis is considered an important vector of *Rickettsia rickettsii*, the agent of Rocky Mountain spotted fever, and *Francisella tularensis*, the tularemia bacterium (Bishopp and Trembley 1945). However, recent studies have failed to identify a high prevalence of *R. rickettsii* in *D. variabilis* from across the United States (Stromdahl et al. 2011). Female *D. variabilis* can cause tick paralysis in humans and dogs (Hicks and Elston 2018).

In a Massachusetts-based study, larval and nymphal activity began in early spring, but nymphal and adult activity extended into the summer (Smith et al. 1946). Likewise, in NJ, Smart and Caccamise (1988) reported bimodal activity for larvae and nymphs, peaking on hosts in mid spring and again in late summer. Adult activity started in mid-March and ceased each year after the third week in August.

D. variabilis is desiccation-tolerant in the adult stage and will quest on exposed vegetation in ecotones, roadsides, utility rights-of-way, and even beach grass (Trout Fryxell et al. 2015). Underscoring this habitat association, in NJ juvenile *D. variabilis* are more often found on meadow voles that are common in meadows and fields, than on white-footed mice (*Peromyscus leucopus*), more common in woods and forests (Smart and Caccamise 1988). Juvenile *D. variabilis* are rarely flagged and are thought to be nidicolous since trapping small mammal hosts is the most reliable way of sampling them (Wilson 1994).

Haemaphysalis leporispalustris (Packard, 1869), the rabbit tick

Clifford et al. (1961) reported the rabbit tick from every state in the eastern United States except Vermont, while Bequaert (1945) reported collections from NJ, but neither collection data nor voucher specimens were mentioned in these accounts. According to Lindquist et al. (2016), *H. leporispalustris* is widespread in Canada, the United States and parts of Mexico, but there are no NJ voucher specimens in the USNTC. Two male and two female *H. leporispalustris* obtained by J. L. Occi from T. Riotto (USDA) and collected on 11 June 2018 from eastern cottontail rabbits (*Sylvilagus floridanus*) at the Teterborough Airport, Bergen County, were submitted to the USNTC in October 2018 (Table 1). A female collected by J. L. Occi in 2001, again from an eastern cottontail rabbit captured in Cranford Township, Union County, was submitted as an additional voucher (Supp Table 1 [online only]).

Adult *H. leporispalustris* are thought to feed almost exclusively on lagomorphs, but immatures may feed on birds and other small mammals (Hooker et al. 1912) and this species is likely involved in the enzootic maintenance of tularemia and possibly *Rickettsia* spp. (Eremeeva et al. 2018).

Haemaphysalis leporispalustris is a nidicolous tick and all three life-stages have been taken from rabbits throughout the year, although larvae and nymphs are more numerous in late summer and fall (Bequaert 1945). Males, females, and larvae have been removed from eastern cottontail rabbits in January on Martha's Vineyard, MA (Bishopp and Trembley 1945).

Haemaphysalis longicornis (Neumann, 1901), the Asian longhorned tick

This species, new to the North American tick fauna, was intercepted in 1969 on a horse during a U.S. Department of Agriculture (USDA) quarantine inspection in NJ (Burridge 2011) but was not detected outside of quarantine until 2017. Rainey et al. (2018) were the first to report multiple life stages of *H. longicornis* in NJ, from an Icelandic sheep (*Ovis aries*) and its paddock in Hunterdon County in August 2017. Since this initial discovery, *H. longicornis* has been found in Bergen, Mercer, Middlesex, Monmouth, Somerset, and Union Counties, NJ (Beard et al. 2018). Specimens collected in Union County in 2018 by J. L. Occi have been submitted to the USNTC (Table 1).

In NJ, *H. longicornis* has been found feeding on white-tailed deer, raccoon, Virginia opossum (*Didelphis virginiana*), sheep, and goat (*Capra aegagrus hircus*) (Beard et al. 2018). This tick is native to parts of eastern Russia, China, Korea, and Japan (Chen et al. 2012). In different parts of its native range, it has been shown to transmit severe fever with thrombocytopenia syndrome virus (SFTSV) and has been implicated in the transmission of *Rickettsia japonica*, the agent of Japanese spotted fever (Tabara et al. 2011). Additionally, it has been found infected with a variety of other pathogens, but it is unknown whether it can transmit them (Kang et al. 2016). *Haemaphysalis longicornis* is also invasive in parts of Australia and New Zealand, where it is a significant problem for the livestock industry (Heath 2016). Some populations of *H. longicornis* are parthenogenetic, resulting in the development of large infestations on domestic animals and wildlife in a relatively short period of time (Heath 2016). The current U.S. introduction appears to be parthenogenetic (Rainey et al. 2018).

The phenology of *H. longicornis* in NJ is still under investigation. During our own preliminary surveys, we found overlapping life stages throughout spring and summer, although the relative abundance of each stage varied, with nymphs appearing to peak in the spring to early summer, adults in midsummer, and larvae in late summer to early fall. This pattern of activity was similar to that found in central Japan (Tsunoda 2007), northern China, (Zheng et al. 2012) and south Korea (Chong et al. 2013), where *H. longicornis* is indigenous. In contrast, in New Zealand, where *H. longicornis* was introduced in the early 1900s, there appears to be more extensive temporal overlap in activity of all stages (Hearth 2016), possibly a result of the milder climate.

Studies in South Korea (e.g., Chong et al. 2013) and New Zealand (Heath 2016) indicate that *H. longicornis* thrive in tall grasses (meadows, paddocks) in areas where average precipitation is higher than 50 mm/month. However, studies in China found an association with shrub and forest areas (Zheng et al. 2012, Liu et al. 2014), although high humidity still seems to be critical. Of note, in eastern Asia (China, Korea, Japan), *H. longicornis* occurs as both bisexual and parthenogenetic populations while in Australia and New Zealand only the parthenogenetic form has been found. The preferred habitat of *H. longicornis* in NJ is still under investigation.

Ixodes brunneus (Koch, 1844)

Bequaert (1945) published the first record of *I. brunneus* in NJ but provided neither collection data nor voucher specimens. In a subsequent review of the larval ixodid ticks of the eastern United States, Clifford et al. (1961) described and illustrated the larva of *I. brunneus*, again citing its occurrence in NJ, but without further information. Keirans and Clifford (1978) presented scanning electron photomicrographs of the adults of all *Ixodes* species then

known from the United States and listed *I. brunneus* as having been found in NJ, but on the authority of Bequaert (1945). The first USNTC specimen of *I. brunneus* from NJ was a female removed from a winter wren (*Troglodytes hiemalis*) on 23 March 1943 by F. Beaudette in Shiloh Township, Cumberland County (Table 1).

Because all three stages of this species feed primarily on birds (Banks 1908), *I. brunneus* is considered of minor economic importance, although infestations can cause tick paralysis in wild birds (Luttrell et al. 1996). Sonenshine and Stout (1970) reported that all stages of *I. brunneus* were found on small passerine birds between November and April in the piedmont sections of Virginia and North Carolina.

Ixodes cookei (Packard, 1869)

Although Banks (1908) reported *I. cookei* from NJ, no collection data or information concerning voucher specimens was provided. The earliest extant collection record of *I. cookei* in NJ was submitted by F. C. Bishop, whose six nymphs and one larva were retained by the USNTC (Table 1). While there is no collection date for these specimens, the entirety of Bishop's tick collection was accessioned by the Smithsonian in 1966, so it must have occurred prior to that year (Smith et al. 1971). One larva was reported flagged in Bergen County in 1993 (Risley and Hahn 1994), but the specimen was not vouchered. One male, five nymphs, and one larva of *I. cookei* collected from a mink (*Neovison vison*) by J. L. Occi and M. J. Scaloni at Fort Dix, Burlington County, in December 1999 were submitted to the USNTC (Supp Table 1 [online only]).

This species commonly feeds on woodchucks but will also feed on other small and medium-sized mammals (Ko 1972). *Ixodes cookei* can harbor Powassan virus (POWV), which is maintained in an enzootic cycle in woodchucks (Main et al. 1979). This tick is considered an infrequent parasite of humans (Smith et al. 1992).

Fish and Dowler (1989) found that in southern New York all stages of *I. cookei* were active throughout the year, but larvae were most abundant in May, nymphs were most abundant in November, and adult activity peaked in May.

Ixodes dentatus (Marx, 1899)

The first report of *I. dentatus* in NJ was from Island Beach State Park in Ocean County, where this species was found on migrating birds by Snetsinger et al. (1970), although voucher specimens were not retained. Later, *I. dentatus* was flagged in Bergen County (39 larvae and three nymphs) and in Passaic County (26 larvae) by Risley and Hahn (1994), but again, no vouchers were designated. During May 1995, Occi (1996) flagged two nymphal *I. dentatus* in Cranford, Union County, which were deposited in the USNTC (Table 1). Additionally, 2 female and 2 male *I. dentatus* recovered from an eastern cottontail rabbit in May of 2001, also in Cranford by J. L. Occi, were submitted to the USNTC (Supp Table 1 [online only]).

Ixodes dentatus commonly feeds on small mammals and birds and is often found on the eastern cottontail rabbit. Although this tick rarely bites humans, it may be involved in the enzootic transmission of *B. burgdorferi* (Telford and Spielman 1989, Hamer et al. 2011).

Kollars and Oliver (2003) report that in southern Missouri, all stages of *I. dentatus* were collected on eastern cottontail rabbits throughout the year, although larval activity was bimodal, with peaks in May and later in September. Nymphal activity was erratic but peaked in the fall and winter months. Adult peak activity occurred in May. Further north, in Michigan, nymphal *I. dentatus* were often found on birds from May through July and larvae from September through November (Hamer et al. 2012).

Ixodes scapularis (Say, 1821), the blacklegged tick

Say collected this tick species in Maryland and states to the south, but apparently not farther north (Say 1821). A single nymphal *I. scapularis* removed from an eastern cottontail rabbit in Princeton Township, Mercer County, on 1 December 1933 (collector not recorded) was the first NJ specimen of this tick submitted to the USNTC (Table 1). Later, blacklegged ticks were reported during a survey for '*I. dammini*,' a junior synonym of *I. scapularis* (Schulze et al. 1984), in the central and southern parts of the state but were used for pathogen analysis and none were submitted as vouchers. Sometime during the 1980s, *I. scapularis* expanded into the northern third of the state (Schulze et al. 1984) and is currently established in all 21 counties (Eisen et al. 2016). The first complete voucher specimens of *I. scapularis* from NJ are two males and two females collected by flagging in 2017 by J. L. Occi in Barnegate Light Township, Ocean Co., deposited in the USNTC (Supp Table 1 [online only]).

The economic and human health importance of *I. scapularis* cannot be overstated. In NJ, this species transmits several human pathogens, including *Borrelia burgdorferi* (Lyme disease), *B. miyamotoi*, *Anaplasma phagocytophilum*, and *Babesia microti* (Eisen and Eisen 2018) and has been found infected with 'deer tick virus' (DTV), which is closely related to Powassan virus (Dupuis et al. 2013). Lyme disease is by far the most common tick-borne disease in the United States, and the nationwide total of approximately 30,000 confirmed cases per year results in an annual expenditure of over 1 billion dollars for diagnosis and treatment (Adrion et al. 2015). Immature stages of *I. scapularis* commonly feed on the white-footed mouse, which is an important reservoir of *B. burgdorferi*, *Babesia microti*, and *Anaplasma phagocytophilum* (Eisen and Eisen 2018). Adult *I. scapularis* feed on white-tailed deer, which are routinely encountered in suburban settings (Levi et al. 2012). However, *I. scapularis* is an indiscriminate feeder that will attack almost any host, including birds and small, medium-sized, and large mammals (Zolnik et al. 2015). While *I. scapularis* will also feed on reptiles, in NJ eastern fence lizards are rare and, therefore, have a minimal role in *B. burgdorferi* transmission (Rulison et al. 2014). Locally abundant tick, mouse, and deer populations, combined with a dense human population, make *I. scapularis*-borne pathogens a common cause of morbidity in NJ.

In NJ, *I. scapularis* larvae hatch in August and September. The following year, beginning in April, they emerge as nymphs and remain active until July. Adults emerge in the fall with peak activity in November, but remain active all winter, questing for large vertebrate hosts, such as deer, during times of moderate temperatures. This same cohort of adults becomes active in April and May of the following year (Schulze et al. 1986).

Ixodes scapularis is very sensitive to desiccation and is usually found in moist microhabitats such as leaf litter and underbrush in shady, wooded areas (Sonenshine 2018).

Ixodes texanus (Banks, 1909)

We found only one prior report of this species from NJ, a single female specimen that was removed from a raccoon trapped in a training area at Fort Dix, Burlington County, in 1974 (Harlan and Kramer 1979). The specimen had been identified by a local medical entomologist but the identification was never confirmed by a professional taxonomist. Regrettably, that specimen was later lost (H. Harlan, personal communication). The first voucher specimens of *I. texanus* from NJ are three females removed from a raccoon in February 1998 by J. L. Occi in Cranford, Union County, that were deposited in the USNTC (Table 1).

The preferred host of *I. texanus* is the raccoon, but this tick has been found on many different medium-sized mammals (Bishopp and Trembley 1945). Thus far, no tick-borne disease outbreaks have been associated with *I. texanus*, but in one North Carolina study, 2 (0.54%) out of 368 *I. texanus* were positive for *B. burgdorferi* (Ouellette et al. 1997). *Ixodes texanus* removed from raccoons in Connecticut have been found infected with *Babesia lotori*, but the pathogenicity of this protozoan in vertebrates has not been studied thoroughly (Anderson et al. 1981).

Fish and Dowler (1989) reported that this species is active throughout the year in southern New York State, with peak activity in February. All three active stages overlap and can be taken from the same individual host. This species is also cold-tolerant and is often taken from hosts in the winter (Darsie and Anastos 1957).

Rhipicephalus sanguineus (Latreille, 1806), the brown dog tick

In NJ, the brown dog tick was first reported from Atlantic City, Atlantic County, in 1936 when 32 females were collected by C. Gilpin (Table 1). *Rhipicephalus sanguineus* is an invasive species, which likely arrived with immigrants or cargo from northern Africa or the Mediterranean region, but until recently its taxonomic status had been uncertain because the type was lost and North American populations are likely a complex of closely related, cryptic species (Dantas-Torres 2010). This situation has now been somewhat clarified with the designation of a neotype from France, the original type locality (Nava et al. 2018). The brown dog tick has been reported in every U.S. state (Clifford et al. 1961).

Although *R. sanguineus sensu lato* is tropical (Dantas-Torres 2008), it is unique among ixodid ticks in its ability to complete its life cycle indoors. It is important to note that this endophilic life cycle can make eradication difficult because *R. sanguineus* spends most of its time off-host. Thus, in kennels and other areas with brown dog tick infestations and large dog populations, ticks will hide in floorboards and under the bedding of their hosts (Dantas-Torres 2010).

As its common name attests, dogs are the primary host of this tick, although it may also feed on other animals and humans. In the United States, the brown dog tick can transmit a number of pathogens, such as *E. canis* and *R. rickettsii*, but its economic importance chiefly lies in its ubiquity as an indoor pest whose populations can quickly and dramatically increase (Gray et al. 2013). Worldwide, members of the *R. sanguineus* complex are potentially able to transmit many additional pathogens, such as *Anaplasma* spp., *Babesia* spp., *Coxiella burnetti*, *Hepatazoon canis*, and *Theileria equi* (Dantas-Torres 2008). Pesticide resistance has been widely reported in this tick (Eiden et al. 2016). All stages of this species can be present throughout the year indoors (Dantas-Torres 2010).

Ixodid Ticks Known From Neighboring States That may Occur in New Jersey

Here we consider five tick species that have either been reported in NJ but are not represented by voucher specimens or that occur in states within a 300 km radius of NJ (Table 2).

Haemaphysalis chordeilis (Packard, 1869), the bird tick

According to Weiss (1915), this species 'undoubtedly occurs in New Jersey' but no specimens have ever been reported. This is not entirely unusual since, as its name implies, the bird tick is most often found on birds, making collections sporadic. *Haemaphysalis chordeilis* has been reported in New York, Pennsylvania (Clifford et al. 1969), Connecticut (Clifford et al. 1961), and Maryland (Keirans and Clifford 1978) (Table 2). The public health and veterinary importance of this tick species is unclear.

***Ixodes angustus* (Neumann 1899)**

This species has been reported in New York and Pennsylvania (Jammback 1969, Keirans and Clifford 1978, Robbins and Keirans 1992, Table 2) and is widespread in northern North America as well as northeastern Asia (Robbins and Keirans 1992), but it has never been reported from NJ. *Ixodes angustus* commonly feeds on rodents and other small mammals. The human health and veterinary importance of this tick are still unclear. In the Pacific Northwest, *I. angustus* has been associated with a syndrome resembling Lyme disease (Damrow et al. 1989); more recently, it has been associated with enzootic cycles of *B. burgdorferi* (Peavey et al. 2000).

***Ixodes banksi* (Bishopp 1911)**

This species has been reported in Connecticut (Anderson and Magnarelli 1980), New York (Durden and Keirans 1996), and Pennsylvania (Serfass et al. 1992) (Table 2). *Ixodes banksi* is commonly found on beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*) and attaches deep within the ear canals. The public health and veterinary importance of this species is unknown, but in 1956 *I. banksi* was implicated in a large beaver die-off in Michigan (Lawrence et al. 1956).

***Ixodes marxi* (Banks 1908)**

In 1920, Cooley and Kohls (1945) stated that they removed a *I. marxi* from an American red squirrel (*Tamiasciurus hudsonicus*) in Riverton, Burlington County, NJ. However, there is no indication that the specimen was vouchered, and the USNTC has no record of *I. marxi* specimens from NJ. This tick has also been reported in Delaware, Maryland, New York, and Pennsylvania (Keirans and Clifford 1978), and in Connecticut by the Connecticut Agricultural Experiment Station. (<https://www.ct.gov/caes/cwp/view>).

asp?a=2815&q=385290; last accessed 29 January 2019). *Ixodes marxi* has been found infected with POWV in Ontario, California (McLean and Larke 1963).

***Ixodes muris* (Bishopp and Smith 1937)**

This species has been reported in Connecticut (Carey et al. 1980), New York, Pennsylvania (Keirans and Clifford 1978), and Maryland (Scharf 2004) (Table 2). *Ixodes muris* feeds on small rodents and birds (Anastos 1947), and Dolan et al. (2000) have shown that *I. muris* is a competent laboratory vector of *B. burgdorferi*. This tick was thought to be the vector of *Babesia microti* on Nantucket Island, MA, during the 1930s (Spielman et al. 1984). These authors theorized that *I. scapularis* has replaced *I. muris* in much of the Northeast. In Maine, the bite of *I. muris* has been shown to cause severe swelling at the site of attachment in dogs and cats (Lacombe et al. 1999).

Ixodid Ticks Undergoing a Northern Expansion That may Become Established in NJ in the Near Future

Many factors, such as larger host populations (Falco et al. 2008), favorable climatic conditions (Sonenshine 2018), or subtle changes in plant communities (Williams and Ward 2010) can cause tick populations to expand and establish themselves in new areas. While migrating birds often transport ticks (Hasle 2013), anthropogenic activity can also facilitate tick movement and population growth (Lastavica et al. 1989, Paddock and Yabsley 2007). Indeed, humans and their companion animals often introduce ticks to new areas; *H. longicornis* and *R. sanguineus* probably entered NJ in this way. While it is difficult to predict the introduction and establishment of exotics, the two species listed below are currently undergoing a northern range expansion within the United States and may be detected in NJ in the future.

Table 2. Ixodid species reported in the literature from states within a 300 km radius of New Jersey

Species	Connecticut	New York	New Jersey	Pennsylvania	Delaware	Maryland
<i>Amblyomma americanum</i>	X	X	X	X	X	X
<i>A. maculatum</i>					X	X
<i>Dermacentor albipictus</i>	X	X	X ^c	X		X
<i>D. variabilis</i>	X	X	X	X	X	X
<i>Haemaphysalis chordeilis</i>		X ^b		X		
<i>H. leporispalustris</i>	X	X	X ^c	X	X	X ^e
<i>H. longicornis</i>		X	X	X		X
<i>Ixodes angustus</i>		X		X		
<i>I. banksi</i>	X ^a	X		X ^d		
<i>I. brunneus</i>	X	X ^b	X	X		X ^e
<i>I. cookei</i>	X	X ^b	X	X ^d	X	X
<i>I. dentatus</i>	X	X ^b	X	X	X	X ^e
<i>I. kingi</i>						X
<i>I. marxi</i>	X	X ^b		X	X	X
<i>I. muris</i>	X	X ^b		X		X ^e
<i>I. texanus</i>	X ^a	X	X		X	X
<i>I. scapularis</i>	X	X	X	X	X	X
<i>Rhipicephalus sanguineus</i>	X	X	X	X	X	X
Total per state	13	16	11	15	10	15

'X' means the species is listed in the literature for that state but, except for New Jersey, voucher specimens were not confirmed. A blank space means the species has not been listed for that state.

State specific references: ^aAnderson et al. 1981, Anderson and Magnarelli 1980; ^bGood 1972, Jammback 1969, Robbins and Keirans 1992, Anastos 1947; ^cKalm 1754, Risley and Hahn 1994, Schulze et al. 2011, Snetsinger 1970, Harlan and Kramer 1979; ^dRobbins and Keirans 1992, Serfass et al. 1992; ^eScharf 2004, Clifford et al. 1969. General regional references: Bequaert 1945, Banks 1908, Bishopp and Trembley 1945, Clifford et al. 1961, Cooley and Kohls 1945, Durden and Keirans 1996, Keirans and Clifford 1978, Lindquist et al. 2016.

***Amblyomma maculatum* (Koch, 1844), the Gulf Coast tick**

This species has recently been reported as far north as Delaware's Bombay Hook National Wildlife Refuge (Florin et al. 2013), less than 20 km across the Delaware Bay from NJ. Historically, however, the distribution of *A. maculatum* extended no farther up the Atlantic coast than North Carolina (Paddock and Goddard 2015). The Gulf Coast tick is primarily associated with open grassy areas and low-lying vegetation (Nadolny and Gaff 2018). While often found on deer, *A. maculatum* is an aggressive biter of humans and companion animals and can transmit *R. parkeri*, the agent of *Rickettsia parkeri* rickettsiosis, also known as Tidewater spotted fever, to humans (Paddock and Goddard 2015). Fortunately, infection with *R. parkeri* is relatively mild when compared with *R. rickettsii*, but any infection requires antibiotic treatment and may leave sequelae (Paddock et al. 2004). *Amblyomma maculatum* can also transmit *Hepatazoon americanum*, the causative agent of canine hepatozoonosis (Nadolny and Gaff 2018).

***Ixodes affinis* (Neumann, 1899)**

This species is also currently expanding its range northward. Originally known only from the southeasternmost United States (Florida, Georgia, South Carolina), *I. affinis* is now found as far north as Virginia (Heller et al. 2016). *Ixodes affinis* immatures commonly feed on birds, but adults share hosts with *I. scapularis*, a species with which *I. affinis* is often confused. Importantly, *I. affinis* is a competent enzootic vector of *B. burgdorferi* (Oliver et al. 2003).

Discussion

We have identified 11 (nine native and two exotic) ixodid tick species in NJ whose presence is supported by vouchers in U.S. collections. These species have widely variable behaviors, feeding preferences, and ecological niches and include both species rarely collected, such as *I. texanus* and *H. leporispalustris*, and those commonly encountered by NJ residents, such as *A. americanum*, *D. variabilis*, and *I. scapularis* (Egizi and Jordan 2019). These differences in human–tick encounter frequency may derive from real differences in tick population density or host seeking behavior, or from differences in degree of overlap with humans. For example, ticks that quest for hosts by climbing on vegetation and waiting for a host to approach often attach to and feed on humans, companion animals, or livestock. In contrast, most of the rarely encountered species are nidicolous and are unlikely to leave the nests and burrows of their hosts unless they are already feeding (i.e., attached) on a host. As a result, we know comparatively little about their biology, ecology, and involvement in enzootic pathogen transmission.

We chose not to include *I. marxi* in our list of ticks present in NJ because, while it is known from neighboring states and has been reported in NJ, no voucher specimens exist in collections, public, or private. Although we expect *I. marxi* to be present in NJ, by not including this species in the 'official' list we wish to highlight the need for vouchers to facilitate species confirmation and encourage further studies, especially as taxonomic methodologies such as molecular genetic testing allow examination of changes over time (Suarez and Tsutsui 2004). Other seemingly uncommon species, such as *I. banksi*, are known from nearby states and may eventually be found in NJ. Their occurrence, as well as that of tick species currently moving northward along the Atlantic coast, such as *A. maculatum*, should be considered when developing standardized tick surveillance programs, especially when tick-borne disease risk analyses are undertaken. While some of the more reclusive, nidicolous species are unlikely to bite or

transmit pathogens to humans directly, their role in enzootic pathogen transmission cycles has the potential to 'spill over' to humans or domestic animals and should not be ignored.

It is clear that elucidation of the NJ tick fauna is still a work in progress. Further research on tick diversity, host relationships, and population dynamics is needed throughout the many natural and human-altered habitats that extend from NJ's northwestern highlands to the Atlantic coastal plain. A carefully tailored statewide tick surveillance program could provide basic but necessary information on which tick species are present, their principal hosts, and any pathogens that they may carry and transmit. With this information in hand, public health professionals and physicians would be better able to inform and protect the public from tick-borne diseases.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

Acknowledgments

Colleen R. Evans, College of Science and Mathematics, Georgia Southern University, generously provided all New Jersey tick records in the U.S. National Tick Collection. Harold J. Harlan, U.S. Army (retired), graciously shared his *Ixodes texanus* collection data with us. Martin 'Joe' Scanlon (deceased) of the New Jersey Trappers Association and Terri Riotti of the USDA helpfully offered numerous legally trapped New Jersey animals as sources of ticks. We thank Dr. Richard C. Falco (Fordham University) and Dr. Cesar Rodriguez-Saona (Rutgers University) for their critical reviews of earlier versions of the manuscript. This research was partly supported by Multistate NE-1043 Biology, Ecology & Management of Emerging Disease Vectors to DMF.

References Cited

Adrion, E. R., J. Aucott, K. W. Lemke, and J. P. Weiner. (2015). Health care costs, utilization and patterns of care following Lyme disease. *PLoS One*. 10(2): e0116767. doi:10.1371/journal.pone.0116767.

Anastos, G. 1947. Hosts of certain New York ticks. *Psyche*. 54: 178–180.

Anderson, J. F., and L. A. Magnarelli. 1980. Vertebrate host relationships and distribution of ixodid ticks (Acar: Ixodidae) in Connecticut, USA. *J. Med. Entomol.* 17: 314–323.

Anderson, J. F., L. A. Magnarelli, and A. J. Sulzer. 1981. Raccoon babesiosis in Connecticut, USA: *Babesia lotori* sp. n. *J. Parasitol.* 67: 417–425.

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *J. Mammal.* 79: 1416–1431.

Banks, N. 1908. Revision of the Ixodidae, or ticks of the United States, Bureau of Entomology Tech. Ser. U.S. Department of Agriculture, Washington, DC.

Beard, C. B., J. Occi, D. L. Bonilla, A. M. Egizi, D. M. Fonseca, J. W. Mertins, B. P. Backenson, W. I. Bajwa, A. M. Barbarin, M. A. Bertone, et al. 2018. Multistate infestation with the exotic disease-vector tick *Haemaphysalis longicornis*—United States, August 2017–September 2018. *MMWR. Morb. Mortal. Wkly. Rep.* 67: 1310–1313.

Bequaert, J. 1945. The ticks or Ixodidae of the northeastern United States and eastern Canada. *Entomol. Amer.* 25: 181–232.

Birkenheuer, A. J., J. A. Le, A. M. Valenzisi, M. D. Tucker, M. G. Levy, and E. B. Breitschwerdt. 2006. *Cytauxzoon felis* infection in cats in the mid-Atlantic states: 34 cases (1998–2004). *J. Am. Vet. Med. Assoc.* 228: 568–571.

Bishopp, F. C., and H. L. Trembley. 1945. Distribution and hosts of certain North American ticks. *J. Parasitol.* 31: 1–41.

Bloemer, S. R., R. H. Zimmerman, and K. Fairbanks. 1988. Abundance, attachment sites, and density estimators of lone star ticks (Acar: Ixodidae) infesting white-tailed deer. *J. Med. Entomol.* 25: 295–300.

Burgdorfer, W. 1969. Ecology of tick vectors of American spotted fever. Bull. World Health Organ. 40: 375–381.

Burridge, M. J. 2011. Non-native and invasive ticks. Threats to human and animal health in the United States. University of Florida Press, Gainesville, FL.

Carey, A. B., W. L. Krinsky, and A. J. Main. 1980. *Ixodes dammini* (Acar: Ixodidae) and associated ixodid ticks in South-central Connecticut, USA. J. Med. Entomol. 17: 89–99.

Chen, Z., X. Yang, F. Bu, X. Yang, and J. Liu. 2012. Morphological, biological and molecular characteristics of bisexual and parthenogenetic *Haemaphysalis longicornis*. Vet. Parasitol. 189: 344–352.

Childs, J. E., and C. D. Paddock. 2003. The ascendancy of *Amblyomma americanum* as a vector of pathogens affecting humans in the United States. Annu. Rev. Entomol. 48: 307–337.

Chong, S. T., H. C. Kim, I. Y. Lee, T. M. Kollars, Jr, A. R. Sancho, W. J. Sames, and T. A. Klein. 2013. Comparison of dragging and sweeping methods for collecting ticks and determining their seasonal distributions for various habitats, Gyeonggi Province, Republic of Korea. J. Med. Entomol. 50: 611–618.

Clifford, C. M., G. Anastos, and A. Elbl. 1961. The larval ixodid ticks of the eastern United States (Acarina-Ixodidae), pp. 213–237. Misc. Publ. Entomol. Soc. Am., Lanham, MD.

Clifford, C. M., D. E. Sonenshine, E. L. Atwood, C. S. Robbins, and L. E. Hughes. 1969. Tests on ticks from wild birds collected in the eastern United States for rickettsiae and viruses. Am. J. Trop. Med. Hyg. 18: 1057–1061.

Collins, B. R., and K. Anderson. 1994. Plant communities of New Jersey: a study of landscape diversity. Rutgers University Press, New Brunswick, NJ.

Commins, S. P., and T. A. Platts-Mills. 2013. Tick bites and red meat allergy. Curr. Opin. Allergy Clin. Immunol. 13: 354–359.

Cooley, R. A., and G. M. Kohls. 1945. The genus *Ixodes* in North America, pp. 246. In U. S. G. P. Office (ed.). National Institutes of Health Bulletin No. 184, Washington, DC.

Damrow, T., H. Freedman, R. S. Lane, and K. L. Preston. 1989. Is *Ixodes (Ixodiopsis) angustus* a vector of Lyme disease in Washington State? West. J. Med. 150: 580–582.

Dantas-Torres, F. 2008. The brown dog tick, *Rhipicephalus sanguineus* (Latreille, 1806) (Acar: Ixodidae): from taxonomy to control. Vet. Parasitol. 152: 173–185.

Dantas-Torres, F. 2010. Biology and ecology of the brown dog tick, *Rhipicephalus sanguineus*. Parasit. Vectors. 3: 26.

Darsie, R., and G. Anastos. 1957. Geographical distribution and hosts of *Ixodes texanus* Banks (Acar: Ixodidae). Ann. Entomol. Soc. Am. 50: 295–301.

Dolan, M. C., E. H. Lacombe, and J. Piesman. 2000. Vector competence of *Ixodes muris* (Acar: Ixodidae) for *Borrelia burgdorferi*. J. Med. Entomol. 37: 766–768.

Dupuis, A. P., II, R. J. Peters, M. A. Prusinski, R. C. Falco, R. S. Ostfeld, and L. D. Kramer. 2013. Isolation of deer tick virus (Powassan virus, lineage II) from *Ixodes scapularis* and detection of antibody in vertebrate hosts sampled in the Hudson Valley, New York State. Parasit. Vectors. 6: 185.

Durden, L. A., and J. E. Keirans. 1996. Nymphs of the genus *Ixodes* (Acar: Ixodidae) of the United States: taxonomy, identification key, distribution, hosts, and medical/veterinary importance, pp. 95. Entomological Society of America, Lanham, MD.

Egizi, A., and R. A. Jordan. 2019. The growing importance of lone star ticks in a Lyme disease endemic county: passive tick surveillance in Monmouth County, NJ, 2006–2016. PLoS One. In press.

Egizi, A., N. H. Fefferman, and R. A. Jordan. 2017. Relative risk for Ehrlichiosis and Lyme disease in an area where vectors for both are sympatric, New Jersey, USA. Emerg. Infect. Dis. 23: 939–945.

Eiden, A. L., P. E. Kaufman, S. A. Allan, and F. Oi. 2016. Establishing the discriminating concentration for permethrin and fipronil resistance in *Rhipicephalus sanguineus* (Latreille) (Acar: Ixodidae), the brown dog tick. Pest Manag. Sci. 72: 1390–1395.

Eisen, R. J., and L. Eisen. 2018. The Blacklegged Tick, *Ixodes scapularis*: an increasing public health concern. Trends Parasitol. 34: 295–309.

Eisen, R. J., L. Eisen, and C. B. Beard. 2016. County-scale distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acar: Ixodidae) in the Continental United States. J. Med. Entomol. 53: 349–386.

Eremeeva, M. E., L. M. Weiner, M. L. Zambrano, G. A. Dasch, R. Hu, I. Vilcins, M. B. Castro, D. L. Bonilla, and K. A. Padgett. 2018. Detection and characterization of a novel spotted fever group *Rickettsia* genotype in *Haemaphysalis leporispalustris* from California, USA. Ticks Tick. Borne. Dis. 9: 814–818.

Falco, R. C., G. P. Wormser, and T. J. Daniels. 2008. Suburbanization in developed nations, pp. 138–170. In K. Mayer and H. Pizer (eds.), The social ecology of infectious disease. Elsevier, New York.

Fish, D., and R. C. Dowler. 1989. Host associations of ticks (Acar: Ixodidae) parasitizing medium-sized mammals in a Lyme disease endemic area of southern New York. J. Med. Entomol. 26: 200–209.

Florin, D. A., J. Jiang, R. G. Robbins, and A. L. Richards. 2013. Infection of the Gulf Coast tick, *Amblyomma maculatum* (Acar: Ixodidae), with *Rickettsia parkeri*: first report from the State of Delaware. Syst. Appl. Acarol. 18: 27–30.

Foley, J., D. Rejmanek, K. Fleer, and N. Nieto. 2011. Nidicolous ticks of small mammals in *Anaplasma phagocytophylum*-enzootic sites in northern California. Ticks Tick. Borne. Dis. 2: 75–80.

Goddard, J., and A. S. Varela-Stokes. 2009. Role of the lone star tick, *Amblyomma americanum* (L.), in human and animal diseases. Vet. Parasitol. 160: 1–12.

Gray, J. S., A. Estrada-Peña, and L. Vial. 2012. Ecology of nidicolous ticks, pp. 39–60. In D. E. Sonenshine and R. M. Roe (eds.), Biology of Ticks Vol. II. Oxford University Press, New York, NY.

Gray, J., F. Dantas-Torres, A. Estrada-Peña, and M. Levin. 2013. Systematics and ecology of the brown dog tick, *Rhipicephalus sanguineus*. Ticks Tick. Borne. Dis. 4: 171–180.

Hair, J. A., and D. E. Howell. 1970. Lone star ticks: their biology and control in Ozark recreation areas. Okla. State Univ. Agric. Exp. Stat. Bull. B-679: 1–47.

Hamer, S. A., G. J. Hickling, J. L. Sidge, M. E. Rosen, E. D. Walker, and J. I. Tsao. 2011. Diverse *Borrelia burgdorferi* strains in a bird-tick cryptic cycle. Appl. Environ. Microbiol. 77: 1999–2007.

Hamer, S. A., G. J. Hickling, R. Keith, J. L. Sidge, E. D. Walker, and J. I. Tsao. 2012. Associations of passerine birds, rabbits, and ticks with *Borrelia miyamotoi* and *Borrelia andersonii* in Michigan, U.S.A. Parasit. Vectors. 5: 231.

Harlan, H. J., and R. D. Kramer. 1979. Ectoparasites of mammals and birds from Fort Dix, New Jersey. Entomol. News. 90: 79–87.

Hasle, G. 2013. Transport of ixodid ticks and tick-borne pathogens by migratory birds. Front. Cell. Infect. Microbiol. 3: 48.

Heath, A. 2016. Biology, ecology and distribution of the tick, *Haemaphysalis longicornis* Neumann (Acar: Ixodidae) in New Zealand. N.Z. Vet. J. 64: 10–20.

Heller, E. L., C. L. Wright, R. M. Nadolny, W. L. Hynes, H. D. Gaff, and E. L. Walters. 2016. New records of *Ixodes affinis* (Acar: Ixodidae) parasitizing avian hosts in southeastern Virginia. J. Med. Entomol. 53: 441–445.

Hicks, A. B., and D. M. Elston. 2018. What's eating you? Clinical manifestations of Dermacentor tick bites. Cutis. 101: 19;20;36.

Holmes, C. J., C. J. Dobrotka, D. W. Farrow, A. J. Rosendale, J. B. Benoit, P. J. Pekins, and J. A. Yoder. 2018. Low and high thermal tolerance characteristics for unfed larvae of the winter tick *Dermacentor albipictus* (Acar: Ixodidae) with special reference to moose. Ticks Tick. Borne. Dis. 9: 25–30.

Hooker, W. A., F. C. Bishopp, and H. P. Wood. 1912. The life history and bionomics of some North American ticks. U.S. Department of Agriculture, Washington, DC.

Jamnback, H. 1969. Bloodsucking flies and other outdoor nuisance arthropods of New York State, Volumes 19–20. pp. 36–41, vols. 19–20. New York State Science Museum, Science Series.

Kalm, P. 1754. Berättelse om et slags yrfä i Norra America (translated by Larsen, EL. 1955. Pehr Kalm's description of a type of creature in North America called the wood tick. Ann. Entomol. Soc. Am. 48:178–180).

Skogs-Löss kalladt. Kongl. Svenska Vetenskaps Academiens Handlingar. 15: 19–31.

Kang, J. G., S. Ko, W. B. Smith, H. C. Kim, I. Y. Lee, and J. S. Chae. 2016. Prevalence of *Anaplasma*, *Bartonella* and *Borrelia* Species in *Haemaphysalis longicornis* collected from goats in North Korea. *J. Vet. Sci.* 17: 207–216.

Keirans, J. E., and C. M. Clifford. 1978. The genus *Ixodes* in the United States: a scanning electron microscope study and key to the adults. *J. Med. Entomol. Suppl.* 2: 1–149.

Ko, R. C. 1972. Biology of *Ixodes cookei* Packard (Ixodidae) of groundhogs (*Marmota monax* Erxleben). *Can. J. Zool.* 50: 433–436.

Kollars, T. M., Jr, and J. H. Oliver, Jr. 2003. Host associations and seasonal occurrence of *Haemaphysalis leporispalustris*, *Ixodes brunneus*, *I. cookei*, *I. dentatus*, and *I. texanus* (Acar: Ixodidae) in Southeastern Missouri. *J. Med. Entomol.* 40: 103–107.

Lacombe, E. H., P. W. Rand, and R. P. Smith, Jr. 1999. Severe reaction in domestic animals following the bite of *Ixodes muris* (Acar: Ixodidae). *J. Med. Entomol.* 36: 227–232.

Lastavica, C. C., M. L. Wilson, V. P. Berardi, A. Spielman, and R. D. Deblinger. 1989. Rapid emergence of a focal epidemic of Lyme disease in coastal Massachusetts. *N. Engl. J. Med.* 320: 133–137.

Lawrence, W. H., L. D. Fay, and S. A. Graham. 1956. A report on the beaver die-off in Michigan. *J. Wildl. Manag.* 20: 184–187.

Leidy, J. 1890. Remarks on ticks. *Proc. Phila. Acad. Nat. Sci.* 42: 278–281.

Levi, T., A. M. Kilpatrick, M. Mangel, and C. C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. *Proc. Natl Acad. Sci. USA.* 109: 10942–10947.

Lindquist, E. E., T. D. Galloway, H. Artsob, L. R. Lindsay, M. Drebot, H. Wood, and R. G. Robbins. 2016. A Handbook to the Ticks of Canada (Ixodida: Ixodidae, Argasidae). Biological Survey of Canada Monograph Series No. 7.

Liu, K., N. Cui, L. Q. Fang, B. J. Wang, Q. B. Lu, W. Peng, H. Li, L. Y. Wang, S. Liang, H. Y. Wang, et al. 2014. Epidemiologic features and environmental risk factors of severe fever with thrombocytopenia syndrome, Xinyang, China. *Plos Negl. Trop. Dis.* 8: e2820.

Luttrell, M. P., L. H. Creekmore, and J. W. Mertins. 1996. Avian tick paralysis caused by *Ixodes brunneus* in the southeastern United States. *J. Wildl. Dis.* 32: 133–136.

Magnarelli, L. A., J. F. Anderson, C. S. Apperson, D. Fish, R. C. Johnson, and W. A. Chappell. 1986. Spirochetes in ticks and antibodies to *Borrelia burgdorferi* in white-tailed deer from Connecticut, New York State, and North Carolina. *J. Wildl. Dis.* 22: 178–188.

Main, A. J., A. B. Carey, and W. G. Downs. 1979. Powassan virus in *Ixodes cookei* and Mustelidae in New England. *J. Wildl. Dis.* 15: 585–591.

McLean, D. M., and R. P. Larke. 1963. Powassan and Silverwater viruses: ecology of two Ontario arboviruses. *Can. Med. Assoc. J.* 88: 182–185.

Nadolny, R. M., and H. D. Gaff. 2018. Natural history of *Amblyomma maculatum* in Virginia. *Ticks Tick. Borne. Dis.* 9: 188–195.

Nava, S., L. Beati, J. M. Venzel, M. B. Labruna, M. P. J. Szabó, T. Petney, M. N. Saracho-Bottero, E. L. Tarragona, F. Dantas-Torres, M. M. S. Silva, et al. 2018. *Rhipicephalus sanguineus* (Latreille, 1806): neotype designation, morphological re-description of all parasitic stages and molecular characterization. *Ticks Tick. Borne. Dis.* 9: 1573–1585.

Obsomer, V., M. Wirtgen, A. Linden, E. Claerebout, P. Heyman, D. Heylen, M. Madder, J. Maris, M. Lebrun, W. Tack, et al. 2013. Spatial disaggregation of tick occurrence and ecology at a local scale as a preliminary step for spatial surveillance of tick-borne diseases: general framework and health implications in Belgium. *Parasit. Vectors.* 6: 190.

Occi, J. L. 1996. Detection of the Lyme disease spirochete, *Borrelia burgdorferi*, in *Ixodes* ticks. M.S. thesis, Seton Hall University, South Orange, NJ.

Ogden, N. H., L. R. Lindsay, K. Hanincová, I. K. Barker, M. Bigras-Poulin, D. F. Charron, A. Heagy, C. M. Francis, C. J. O'Callaghan, I. Schwartz, et al. 2008. Role of migratory birds in introduction and range expansion of *Ixodes scapularis* ticks and of *Borrelia burgdorferi* and *Anaplasma phagocytophilum* in Canada. *Appl. Environ. Microbiol.* 74: 1780–1790.

Oliver, J. H., Jr, T. Lin, L. Gao, K. L. Clark, C. W. Banks, L. A. Durden, A. M. James, and F. W. Chandler, Jr. 2003. An enzootic transmission cycle of Lyme borreliosis spirochetes in the southeastern United States. *Proc. Natl Acad. Sci. USA.* 100: 11642–11645.

Olson, R. K., and T. A. Lyson. 1999. Under the blade: the conversion of agricultural landscapes. Westview Press, Taylor and Francis, New York, NY.

Ouellette, J., C. S. Apperson, P. Howard, T. L. Evans, and J. F. Levine. 1997. Tick-raccoon associations and the potential for Lyme disease spirochete transmission in the coastal plain of North Carolina. *J. Wildl. Dis.* 33: 28–39.

Paddock, C. D., and J. Goddard. 2015. The evolving medical and veterinary importance of the Gulf Coast tick (Acar: Ixodidae). *J. Med. Entomol.* 52: 230–252.

Paddock, C. D., and M. J. Yabsley. 2007. Ecological havoc, the rise of white-tailed deer, and the emergence of *Amblyomma americanum*-associated zoonoses in the United States. *Curr. Top. Microbiol. Immunol.* 315: 289–324.

Paddock, C. D., J. W. Sumner, J. A. Comer, S. R. Zaki, C. S. Goldsmith, J. Goddard, S. L. McLellan, C. L. Tamminga, and C. A. Ohl. 2004. *Rickettsia parkeri*: a newly recognized cause of spotted fever rickettsiosis in the United States. *Clin. Infect. Dis.* 38: 805–811.

Peavey, C. A., R. S. Lane, and T. Damrow. 2000. Vector competence of *Ixodes angustus* (Acar: Ixodidae) for *Borrelia burgdorferi* sensu stricto. *Exp. Appl. Acarol.* 24: 77–84.

Rainey, T., J. L. Occi, R. G. Robbins, and A. Egizi. 2018. Discovery of *Haemaphysalis longicornis* (Ixodida: Ixodidae) parasitizing a sheep in New Jersey, United States. *J. Med. Entomol.* 55: 757–759.

Randolph, S. E. 2011. Transmission of tick-borne pathogens between co-feeding ticks: Milan Labuda's enduring paradigm. *Ticks Tick. Borne. Dis.* 2: 179–182.

Risley, L. S., and S. Hahn. 1994. Lyme disease in northern New Jersey: distribution of blacklegged ticks (*Ixodes scapularis*) and prevalence of the spirochete *Borrelia burgdorferi*. *Bull. N.J. Acad. Sci.* 39: 17–21.

Robbins, R. G., and J. E. Keirans. 1992. Systematics and ecology of the subgenus *Ixodiopsis* (Acar: Ixodidae: *Ixodes*), pp. 159. Entomological Society of America, Lanham, MD.

Rulison, E. L., K. T. Kerr, M. C. Dyer, S. Han, R. L. Burke, J. I. Tsao, and H. S. Ginsberg. 2014. Minimal role of eastern fence lizards in *Borrelia burgdorferi* transmission in central New Jersey oak/pine woodlands. *J. Parasitol.* 100: 578–582.

Samuels, B. 2004. White as a ghost: winter ticks and moose. Federation of Alberta Naturalists Publishing, Alberta, Canada.

Say, T. 1821. An account of the Arachnides of the United States. *J. Acad. Nat. Sci. Phila.* 2: 59–83.

Scharf, W. C. 2004. Immature ticks on birds: temporal abundance and reinestation. *Northeast. Nat.* 11: 143–150.

Schulze, T. L., M. F. Lakat, G. S. Bowen, W. E. Parkin, and J. K. Shisler. 1984. *Ixodes dammini* (Acar: Ixodidae) and other ixodid ticks collected from white-tailed deer in New Jersey, USA. I. Geographical distribution and its relation to selected environmental and physical factors. *J. Med. Entomol.* 21: 741–749.

Schulze, T. L., G. S. Bowen, M. F. Lakat, W. E. Parkin, and J. K. Shisler. 1986. Seasonal abundance and hosts of *Ixodes dammini* (Acar: Ixodidae) and other ixodid ticks from an endemic Lyme disease focus in New Jersey, USA. *J. Med. Entomol.* 23: 105–109.

Schulze, T. L., R. A. Jordan, S. P. Healy, V. E. Roegner, M. Meddis, M. B. Jahn, and D. L. Guthrie, Sr. 2006. Relative abundance and prevalence of selected *Borrelia* infections in *Ixodes scapularis* and *Amblyomma americanum* (Acar: Ixodidae) from publicly owned lands in Monmouth County, New Jersey. *J. Med. Entomol.* 43: 1269–1275.

Schulze, T. L., R. A. Jordan, J. C. White, V. E. Roegner, and S. P. Healy. 2011. Geographical distribution and prevalence of selected *Borrelia*, *Ehrlichia*, and *Rickettsia* infections in *Amblyomma americanum* (Acar: Ixodidae) in New Jersey. *J. Am. Mosq. Control Assoc.* 27: 236–244.

Scoles, G. A., M. Papero, L. Beati, and D. Fish. 2001. A relapsing fever group spirochete transmitted by *Ixodes scapularis* ticks. *Vector Borne Zoo. Dis.* 1: 21–34.

Serfass, T. L., L. M. Rymon, and R. P. Brooks. 1992. Ectoparasites from river otters in Pennsylvania. *J. Wildl. Dis.* 28: 138–140.

Shock, B. C., S. M. Murphy, L. L. Patton, P. M. Shock, C. Olfenbuttel, J. Beringer, S. Prange, D. M. Grove, M. Peek, J. W. Butfiloski, et al. 2011. Distribution and prevalence of *Cytauxzoon felis* in bobcats (*Lynx rufus*),

the natural reservoir, and other wild felids in thirteen states. *Vet. Parasitol.* 175: 325–330.

Smart, D. L., and D. F. Caccamise. 1988. Population dynamics of the American dog tick (Acari: Ixodidae) in relation to small mammal hosts. *J. Med. Entomol.* 25: 515–522.

Smith, C., M. Cole, and H. Gouck. 1946. Biology and control of the American dog tick, pp. 1–74, U.S. Department of Agriculture. Technical Bulletin No. 905

Smith, C. N., A. W. Lindquist, and J. A. Fluno. 1971. Fred Corry Bishop 1884–1970. *J. Econ. Entomol.* 64: 1341–1342.

Smith, R. P., Jr, E. H. Lacombe, P. W. Rand, and R. Dearborn. 1992. Diversity of tick species biting humans in an emerging area for Lyme disease. *Am. J. Pub. Health.* 82: 66–69.

Snetsinger, R., D. Bordner, and J. Luke. 1970. Ixodid tick populations on fall migrating birds at Island Beach State Park, New Jersey. *Melsheimer Entomol. Ser.* 6: 1–4.

Sonenshine, D. E. 2018. Range expansion of tick disease vectors in North America: implications for spread of tick-borne disease. *Int. J. Environ. Res. Pub. Health.* 15 (3). doi:10.3390/ijerph15030478.

Sonenshine, D. E., and I. J. Stout. 1970. A contribution to the ecology of ticks infesting wild birds and rabbits in the Virginia-North Carolina Piedmont (Acarina: Ixodidae). *J. Med. Entomol.* 7: 645–654.

Spielman, A., J. F. Levine, and M. L. Wilson. 1984. Vectorial capacity of North American Ixodes ticks. *Yale J. Biol. Med.* 57: 507–513.

Springer, Y. P., C. S. Jarnevich, D. T. Barnett, A. J. Monaghan, and R. J. Eisen. 2015. Modeling the present and future geographic distribution of the lone star tick, *Amblyomma americanum* (Ixodida: Ixodidae), in the continental United States. *Am. J. Trop. Med. Hyg.* 93: 875–890.

Stromdahl, E. Y., J. Jiang, M. Vince, and A. L. Richards. 2011. Infrequency of *Rickettsia rickettsii* in *Dermacentor variabilis* removed from humans, with comments on the role of other human-biting ticks associated with spotted fever group Rickettsiae in the United States. *Vector Borne Zoo. Dis.* 11: 969–977.

Suarez, A. A., and N. D. Tsutsui. 2004. The value of museum collections for research and society. *BioScience.* 54: 66–74.

Tabara, K., H. Kawabata, S. Arai, A. Itagaki, T. Yamauchi, T. Katayama, H. Fujita, and N. Takada. 2011. High incidence of rickettsiosis correlated to prevalence of *Rickettsia japonica* among *Haemaphysalis longicornis* tick. *J. Vet. Med. Sci.* 73: 507–510.

Telford, S. R., III, and A. Spielman. 1989. Enzootic transmission of the agent of Lyme disease in rabbits. *Am. J. Trop. Med. Hyg.* 41: 482–490.

Telford, S. R., III, T. N. Mather, S. I. Moore, M. L. Wilson, and A. Spielman. 1988. Incompetence of deer as reservoirs of the Lyme disease spirochete. *Am. J. Trop. Med. Hyg.* 39: 105–109.

Trout Fryxell, R. T., J. E. Moore, M. D. Collins, Y. Kwon, S. R. Jean-Philippe, S. M. Schaeffer, A. Odoi, M. Kennedy, and A. E. Houston. 2015. Habitat and vegetation variables are not enough when predicting tick populations in the southeastern United States. *PLoS One.* 10: e0144092.

Tsunoda, T. 2007. Seasonal change in habitat use by *Haemaphysalis longicornis* (Acari: Ixodidae): plant, litter, and soil. *J. Med. Entomol.* 44: 575–579.

Weiss, H. B. 1915. Preliminary list of New Jersey Acarina. *Ent. News.* 26: 149–152.

Williams, S. C., and J. S. Ward. 2010. Effects of Japanese barberry (Ranunculales: Berberidaceae) removal and resulting microclimatic changes on *Ixodes scapularis* (Acari: Ixodidae) abundances in Connecticut, USA. *Environ. Entomol.* 39: 1911–1921.

Wilson, M. L. 1994. Population ecology of tick vectors: interaction, measurement and analysis, pp. 20–44. In D. E. Sonenshine and T. N. Mather (eds.), chap. 2, *Ecological dynamics of tick-borne zoonoses*. Oxford University Press, New York, NY.

Wood, C. L., and K. D. Lafferty. 2013. Biodiversity and disease: a synthesis of ecological perspectives on Lyme disease transmission. *Trends Ecol. Evol.* 28: 239–247.

Zheng, H., Z. Yu, L. Zhou, X. Yang, and J. Liu. 2012. Seasonal abundance and activity of the hard tick *Haemaphysalis longicornis* (Acari: Ixodidae) in North China. *Exp. Appl. Acarol.* 56: 133–141.

Zolnik, C. P., A. M. Makkay, R. C. Falco, and T. J. Daniels. 2015. American black bears as hosts of blacklegged ticks (Acari: Ixodidae) in the Northeastern United States. *J. Med. Entomol.* 52: 1103–1110.