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The Contribution of Wildlife Hosts to the Rise of Ticks and Tick-Borne Diseases in North America

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Abstract

Wildlife vertebrate hosts are integral to enzootic cycles of tick-borne pathogens, and in some cases have played key roles in the recent rise of ticks and tick-borne diseases in North America. In this forum article, we highlight roles that wildlife hosts play in the maintenance and transmission of zoonotic, companion animal, livestock, and wildlife tick-borne pathogens. We begin by illustrating how wildlife contribute directly and indirectly to the increase and geographic expansion of ticks and their associated pathogens. Wildlife provide blood meals for tick growth and reproduction; serve as pathogen reservoirs; and can disperse ticks and pathogens—either through natural movement (e.g., avian migration) or through human-facilitated movement (e.g., wildlife translocations and trade). We then discuss opportunities to manage tick-borne disease through actions directed at wildlife hosts. To conclude, we highlight key gaps in our understanding of the ecology of tick–host interactions, emphasizing that wildlife host communities are themselves a very dynamic component of tick–pathogen–host systems and therefore complicate management of tick-borne diseases, and should be taken into account when considering host-targeted approaches. Effective management of wildlife to reduce tick-borne disease risk further requires consideration of the 'human dimensions' of wildlife management. This includes understanding the public's diverse views and values about wildlife and wildlife impacts—including the perceived role of wildlife in fostering tick-borne diseases. Public health agencies should capitalize on the expertise of wildlife agencies when developing strategies to reduce tick-borne disease risks.

Key words: Ixodidae, ticks, tick-borne disease, emergence, wildlife

In recent decades, rising incidence and expanding geographic distribution of zoonotic and veterinary tick-borne diseases have been of increasing concern in North America (Eisen et al. 2017, Little et al. 2021). Examples of rising tick-borne zoonoses include Lyme disease (borreliosis), human anaplasmosis, babesiosis, human monocytic ehrlichiosis, spotted fever group rickettsioses, and Powassan virus (POWV) encephalitis (Rosenberg et al. 2018). Examples of rising veterinary diseases of companion animals include canine anaplasmosis and feline cytauxzoonosis. Recent increases in tick-borne diseases of livestock are less common, in part, due to the use of antiparasitic treatments and other prophylactic measures. Livestock nevertheless

remain at risk from ticks, as evidenced by the substantial resources invested in the Cattle Fever Tick Eradication Program over many decades (Pegram et al. 2000) and the recent invasion of the Asian longhorned tick *Haemaphysalis longicornis* Neumann) (Acari: Ixodidae) with consequent cases of theileriosis in cattle (Oakes et al. 2019). Finally, some wild species can themselves be adversely affected by ticks, as illustrated by mortality of moose heavily infested with winter ticks (Jones et al. 2019).

Many factors have contributed to the recent and ongoing rise of ticks and tick-borne diseases (TTBDs), including changes in habitat, land use, and landscape (Diuk-Wasser et al. 2020 (this issue))
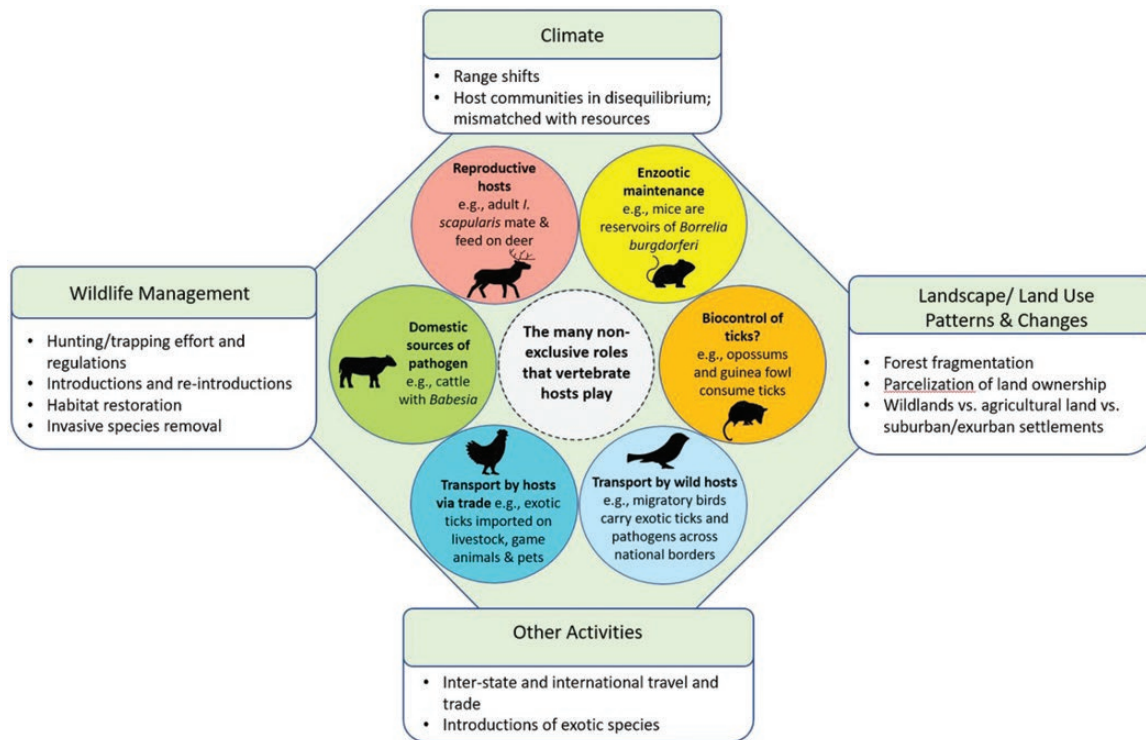
Fig. 1. Wildlife hosts contribute to the rise of TTBD in several nonexclusive roles. Many factors influence the distribution and abundance of these wildlife species, including wildlife management practices, climate, landscape, and land use; these factors often act synergistically.

and climate (Sonenshine 2018, Ogden et al. 2020 (this issue)). Nevertheless, because ticks are obligate parasites, interactions with their hosts are central to tick and tick-borne pathogen dynamics. Wildlife play diverse roles in the maintenance and spread of zoonotic, companion animal, livestock, and wildlife pathogens (Fig. 1; for a more quantitative understanding, see also Randolph 1998, 2004; Ogden et al. 2005, 2007; Hartemink et al. 2008; Ogden and Tsao 2009; Gaff et al. 2020).

Here we highlight some key roles that wildlife hosts have played in the spread and/or maintenance of selected TTBDs. We first focus on their contributions in introducing, sustaining, and dispersing ticks and pathogens. We then review how wildlife may affect the local dynamics of enzootic cycles. Given the importance of wildlife hosts for maintaining enzootic cycles (and challenges with other currently available prevention measures), we discuss opportunities for managing tick-borne disease through host-targeted methods. We then highlight key gaps in our understanding of the basic ecology of tick–host interactions, emphasizing that wildlife host communities are themselves a very dynamic component of tick–pathogen–host systems. We conclude by discussing proactive approaches to best manage wildlife to reduce TTBDs, including taking into account 'human dimensions' of wildlife and working with wildlife agencies.

Contribution of Wildlife to the Increase and Spread of Ticks

TTBDs rise when changes in ecological factors favor the persistence and growth of tick populations (Wu et al. 2013) and/or the persistence and growth of pathogens carried by ticks (Hartemink et al. 2008). All else equal, increased abundance of hosts will increase

ticks' host finding and feeding success, thereby increasing the probabilities of pathogen transmission and persistence as well as the number of offspring in the next tick generation (Randolph 2004, Ogden et al. 2007, Ogden and Tsao 2009).

Rising TTBDs Due to Increased Abundance and Range Expansion of Key Hosts for Adult Ticks

Tick abundance is linked to the abundance of their vertebrate hosts, which in turn depends on climate, habitat, resource levels, and myriad intra- and interspecific interactions, including with predators, competitors, pathogens, and parasites. In North America this linkage is illustrated by the response of tick populations to historical changes in the abundance and distribution of the white-tailed deer (*Odocoileus virginianus*, deer), which is a key host for the adult stage of two tick species that significantly impact humans, companion animals, domestic animals, and wildlife. Increases in the abundance and distribution of deer have strongly affected the emergence and spread of blacklegged ticks (*Ixodes scapularis* Say = deer ticks) (Acari: Ixodidae) and lone star ticks (*Amblyomma americanum* (Linneaus)) (Acari: Ixodidae) (Barbour and Fish 1993, Spielman 1994, Paddock and Yabsley 2007). Both tick species are three-host ixodids that feed on a broad range of host species as juveniles, which has contributed to their broad geographic ranges. The link between the abundance of deer and that of ticks has been demonstrated empirically for blacklegged ticks by a variety of exclusion and removal studies (e.g., Daniels et al. 1993, Rand et al. 2004, Kilpatrick et al. 2014). This relationship between the abundance of the two species, however, is nonlinear: i.e., above a threshold level, additional increases in deer density do not appreciably increase blacklegged tick abundance, including the abundance of infected nymphs (the epidemiologically important metric for estimating the environmental risk for Lyme disease; see Elias et al. 2020 for a recent review).

Recovery of deer populations across North America during the 20th century, following previous near-extirpation by European settlers, has provided an opportunity for tick populations 1) to increase in abundance locally, and 2) to expand geographically into areas where conditions for off-host survival have been suitable. Deer populations on their own, however, cannot support enzootic cycles for many of the pathogens transmitted by these ticks; for example, deer are not competent for the Lyme disease pathogen that is transmitted by the blacklegged tick in the eastern United States (Telford et al. 1988). Nevertheless, the successional habitats that favor deer also support wildlife species that feed juvenile ticks and are reservoirs for many pathogens, including the agent of Lyme disease.

The magnitude of historical changes in deer abundance in North America is illustrated in Fig. 2. Native Americans significantly impacted wildlife diversity, distribution, and abundance prior to the arrival of Europeans in North America in the late 1400s (McCabe and McCabe 1984). The introduction of firearms, coupled with high European demand for deer products, greatly increased harvest rates and caused deer abundance to decline. The forest and wildlife resources of eastern North America in the early 1600s, however, still were perceived by the arriving European settlers as near-limitless and were exploited as such. Unregulated market hunting of deer, now primarily by European settlers, combined with extensive habitat loss due to the needs of the expanding settler population, greatly accelerated the decline of the national deer population during the 1800s—to the point where deer were locally extirpated from many areas. In response, an increasing number of state and federal regulations were introduced to curb overhunting of deer (e.g., the Lacey Act of 1900, which banned interstate sales of wildlife). Other management efforts included hunting restrictions, habitat restoration, translocation and reintroduction of deer from remaining populations, and predator suppression programs.

The recovery of deer populations in the 20th century was facilitated greatly by changes in the landscape that promoted early successional habitats that augmented wildlife conservation efforts. Early forestry practices such as clear-cut logging created secondary successional habitat that provided more abundant and nutritious forage than did mature forests. Similarly, in the latter half of the 20th century, intentional management of timber harvesting to create gaps in forests continued to favor populations of deer and other successional wildlife species such as wild turkey (*Meleagris gallopavo*). The

creation of fragmented agroforested landscapes—consisting of forest remnants that provided shelter and ecotonal successional forage, intermixed with crops and pastures that provided additional nutritional resources—produced highly productive landscapes for deer, as did replacement of forests and agricultural lands with semiforested suburban and 'exurban' landscapes. These land use and landscape changes, beginning in the last century and continuing to the present day, have promoted high deer populations in areas where people reside and recreate. From a low of around 350,000 deer in 1900, the deer population rebounded to between 24 and 34 million nationwide by the end of the 20th century (McCabe and McCabe 1984, VerCauteren et al. 2018).

Deer are the preferred host for adult *I. scapularis* and *A. americanum*, but these adults (and other life stages) can also feed on other medium and large mammals. Childs and Paddock (2003) suggest that coyotes (*Canis latrans*) and raccoons (*Procyon lotor*) have contributed to the expanding geographic distribution of *A. americanum*, and these host species are also important for sustaining another common human-biting species, the American dog tick (*Dermacentor variabilis* Say) (Acari: Ixodidae) (Sonenshine and Stout 1971). Population sizes and ranges of coyotes, raccoons, and red fox (*Vulpes vulpes*) have expanded in recent decades, due, in part, to declines in the apex predators—grizzly bear (*Ursus arctos*) and gray wolf (*Canis lupus*)—in landscapes with high human influence (Laliberte and Ripple 2004). Raccoons thrive in suburban and urban landscapes, where their densities are often greater than in rural areas (Prange et al. 2003).

As habitat generalists, in addition to influencing forest-associated ticks, deer also have facilitated the spread and establishment of several tick species primarily associated with unforested habitats and livestock, such as cattle fever ticks ((*Rhipicephalus* (*Boophilus*) *annulatus* Say) (Acari: Ixodidae) and *R.* (*B.*) *microplus* (Canestrini) (Acari: Ixodidae)); the Gulf Coast tick (*A. maculatum* Koch) (Acari: Ixodidae); and the recently introduced H. longicornis. *Rhipicephalus* (*B.*) *microplus* infestations of cattle recently have spread to counties in Texas that lie beyond the fever tick quarantine zone; spillover of these ticks to wildlife species including deer (see below) is facilitating spread and impeding control of these outbreaks (Miller et al. 2013, Wang et al. 2016). *Amblyomma maculatum* probably was introduced to the central United States via transport of infested cattle moved
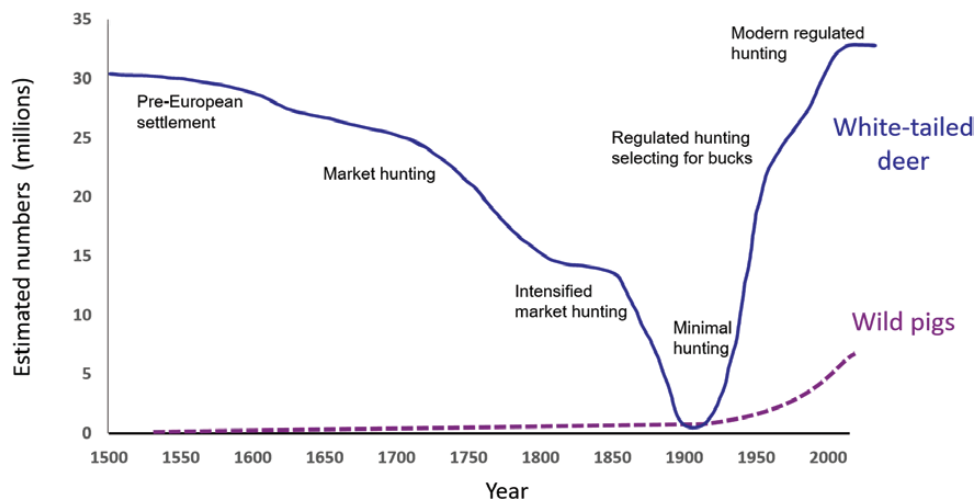

Fig. 2. Decline and recovery of native white-tailed deer (*Odocoileus virginianus,* solid line) populations and history of invasive pig (*Sus scrofa,* dashed line) populations in the United States (adapted from VerCauteren et al. 2018).

from the Gulf Coast region (Semtner and Hair 1973); Paddock and Goddard (2015) suggest that the restoration of deer and the invasion of feral swine (*Sus scrofa*) facilitated subsequent geographic spread of these ticks. Furthermore, deer and other medium-sized mammals serve as primary hosts for adult *A. maculatum* in southeastern Virginia, where *A. maculatum* is emerging and where livestock densities are low (Paddock and Goddard 2015, Nadolny and Gaff 2018). *Haemaphysalis longicornis* similarly has become abundant in several areas where livestock densities are low (e.g., southern New York and northeastern New Jersey; Tufts et al. 2019, Piedmonte et al. 2021, White et al. 2020). A wide range of wildlife species, including deer and medium-sized mammals in multiple eastern states (Beard et al. 2018, Tufts et al. 2021, White et al. 2020), have been found to be infested with *H. longicornis*, and consequently, eradication of this recently introduced tick is likely infeasible (Haddow 2019).

Geographic Expansion of North American Tick Populations Due to Movement of Infested Hosts

When hosts disperse ticks and their associated pathogens into new and suitable environments, a rise in TTBDs may follow. The hurdles common to many species invasions (Lodge et al. 2006), however, mean that only a small proportion of invading ticks that are transported to a new site survive, establish a population, spread, and then go on to cause ecological, human health, or economic impacts. In this section we provide examples of wildlife host movement pathways - both natural and anthropogenic - that have enabled ticks and pathogens to surmount some or all of these invasion hurdles.

Migration of infested hosts.
Migratory species can spread infectious pathogens over long distances over relatively short periods of time (e.g., Altizer et al. 2011), and such periods of host movement provide dispersal opportunities for ticks and their associated pathogens. Migration often comprises large groups of animals moving together, which aggregates ticks and hosts, some of whom will be infected, in both time and space, thereby further increasing the potential for pathogen transmission and spread. Additionally, if detachment of ticks is concentrated along a migratory path, there may be increased likelihood that surviving ticks will find mates.

Wild passerines and several western ungulate species are important tick hosts that undergo seasonal migration (Kauffman et al. 2020). Little is known, however, about the role of ungulate migration in the spread of TTBDs (Mysterud et al. 2016), which remains an underexplored topic given that ungulates serve as the definitive host for several important tick species, and therefore may be key to seeding some new populations.

In North America, wild passerines increasingly are recognized as sculpting patterns of TTBDs across the landscape (Hasle 2013, Loss et al. 2016). For example, inspection of tens of thousands of northward-migrating birds arriving at banding stations in eastern Canada has revealed an overall low tick infestation prevalence (0.4–2.2%) and an overall low burden of ticks on infested birds (mean of 1.66 ticks per bird). Nevertheless, the vast number of seasonal migrants into the region means that millions of *I. scapularis* ticks likely are dispersed into Canada each spring (Ogden et al. 2008). Past climate was unsuitable for successful invasion by these bird-imported 'adventitious' ticks, but recent climate warming has supported the northward range expansion of *I. scapularis* populations into southeastern Canada, with a subsequent dramatic increase in the incidence of human Lyme disease in the region (Bouchard et al. 2015).

Two islands off the coast of Maine further illustrate the role birds can play in introducing ticks to new areas. *Ixodes scapularis* is not established on either island due to a lack of hosts for the adult stage (Smith et al. 1996, Rand et al. 2004). Yet both spring migrant birds infested with immature *I. scapularis* and host-seeking adult ticks are frequently collected on these islands. Thus, it seems likely that a population of bird-introduced ticks could become self-sustaining on these islands if an adequate density of hosts for the adult ticks were present (Elias et al. 2011).

Similarly, *A. americanum* has been detected parasitizing birds far north of established populations of this tick (e.g., Scott et al. 2001, 2010; Ogden et al. 2008; Elias et al. 2011; Loss et al. 2016; and see Stafford et al. 2018 for a review). Although these ticks may survive one molt, it seems they usually are unable to reproduce and/or become established. For example, Walker et al. (1998) reported submissions by citizens of 111 *A. americanum* over a 12-yr period (1985–1996), yet during that period no evidence could be found of established populations in Michigan. In recent years, *A. americanum* has become more frequently detected in Wisconsin (Christenson et al. 2017) and Ontario (Nelder et al. 2019), and can now be considered 'established' by CDC criteria (Springer et al. 2014) in Connecticut (Stafford et al. 2018). Based on geography and proximity to established populations, dispersal by migrating passerines seems a highly likely origin of these new populations.

Amblyomma maculatum has been detected on migrating birds in several studies (Ogden et al. 2008, Scott et al. 2010, Elias et al. 2011, Loss et al. 2016), and birds likely are playing a role in the dispersal and establishment of this tick in the central United States and mid-Atlantic states (Keirans and Durden 1998, Rainwater et al. 2007, Florin et al. 2014). Paddock and Goddard (2015) suggest that recent restoration of prairie habitat in the central United States has increased grassland bird populations that are frequently parasitized by *A. maculatum* immatures, such as eastern and western meadowlarks (*Sturnella neglecta* and *S. magna*), which are migratory species, as well as bobwhite quail (*Colinus virginianus*), which do not migrate (Teel et al. 1998).

Finally, turning to the southern border of North America, two studies observing Neotropical migrant birds when they first make landfall on the Gulf Coast have documented the importation of Neotropical ticks (Mukherjee et al. 2014, Cohen et al. 2015). Several of the attached ticks have been species that can be infected with spotted fever group *Rickettsia* species of human and animal health concern (Mukherjee et al. 2014, Cohen et al. 2015). Neotropical ticks also have been detected on spring migrant birds captured further inland north of the Gulf Coast (see references in Cohen et al. 2015). Two of the attached tick species—*Haemaphysalis leporispalustris* (Packard) (Acari: Ixodidae) and *A. maculatum*—are native to both hemispheres, but of the six and eight species detected in Mukherjee et al. (2014) and Cohen et al. (2015), respectively, four and seven are not known to be established in North America.

Cohen et al. (2015) estimate that more than 19 million Neotropical ticks are imported annually during birds' spring migration, but despite the likelihood of high annual propagule introduction pressure, it seems that biotic and/or abiotic barriers currently prevent these exotic ticks and disease agents from establishing in the North America. There are sporadic reports of Neotropical tick species collected from vegetation or from nonmigratory native fauna in the United States. For example, a questing adult *Amblyomma longirostre* (Koch) (Acari: Ixodidae) was collected in Oklahoma (Noden et al. 2015), and an adult *Haemaphysalis juxtokochi* Cooley (Acari: Ixodidae) was found attached to a deer in Ohio (Keirans and Restifo 1993). Detection of these adult ticks indicates partial

progress along the invasion 'pathway', because these ticks most likely were transported as immatures and then survived at last one molt locally. Climate warming might facilitate establishment of these species in North America in coming decades.

Dispersal of the tropical bont tick *Amblyomma variegatum* (Fabricius) (Acari: Ixodidae) has been linked to migratory movements of the cattle egret (*Bubulcus ibis*). Although *A. variegatum* has yet to be detected from vegetation or wildlife in the continental United States, its emergence in the Caribbean Islands has raised concern about the high potential for future invasion into the southeastern United States (Corn et al. 1993), as it is the vector of several pathogens of concern to the livestock industry, most notably *Ehrlichia ruminantium* (the agent of heartwater disease).

Nonmigratory range expansions of hosts

Naturally dispersing hosts can carry ticks; therefore, the dispersal range of these hosts determines the distance and habitat types where ticks may be dropped off. Long distances may be traveled during certain periods in an individual's life, such as when juveniles disperse from their natal range, or for male ungulates during the rut. Landscape features affect dispersal movements; for example, many birds and mammals follow riverine corridors, and this behavior in deer is believed to have contributed to the observed spatiotemporal pattern of establishment of *I. scapularis* in Illinois and, perhaps more broadly, in the Midwest (Cortinas et al. 2002).

Climate and landscapes are dynamic in ways that have flow-on effects on hosts' geographic ranges and thus patterns of TTBDs. For example, the white-footed mouse (*Peromyscus leucopus noveboracensis*) has been expanding northwards during the last four decades in both the northern Great Lakes region (Myers et al. 2009) and southern Quebec, Canada (Roy-Dufresne et al. 2013). Myers et al. (2009) hypothesized that a warming climate during this period, which resulted in shorter winters and an earlier onset of spring weather, increased the reproductive capacity of *P. leucopus* more than that of the woodland deer mouse (*P. maniculatus gracilis*), which formerly dominated these northern forests. Researchers further hypothesize that the northward expansion of this key rodent reservoir of the Lyme disease agent has hastened the northward spread of Lyme disease. Roy-Dufresne et al. (2013) found a positive association of the agent of Lyme disease with the presence of *P. leucopus* in southern Quebec. Whether the enhanced rate of invasion of *B. burgdorferi* at these sites with *P. leucopus* is due to host differences in reservoir competence, parasitism rates, and/or other processes requires further study.

Anthropogenic movement of wildlife: managed and invasive species

Given sufficient data we can predict how a tick may naturally diffuse across a landscape bounded by suitable habitat and climate for the tick and its hosts. Superimposed on these natural movements, however, can be abrupt and unpredictable movements of ticks caused by anthropogenic events. White-tailed deer, wild turkey, and many other game species were driven to near-extirpation by the early 1900s, as discussed previously. To help restore these populations, deer, elk (*Cervus canadensis*), turkey, and other species were frequently translocated between states (Kallman 1987), thereby increasing the availability of hosts and potential geographic range of ticks and tick-borne pathogens that parasitize them. Additionally, attached ticks inadvertently could have been introduced with translocated hosts. For example, a northern U.S. clade of *Dermacentor albipictus* (Packard) (winter ticks) (Acari: Ixodidae) can now be found on elk translocated to Tennessee's Smoky Mountains (G. J. Hickling, unpublished data).

The wild turkey is an important host for immature *A. americanum* (Kollars et al. 2000). Wild turkey populations have followed a trajectory of decline and recovery similar to that of deer: loss of woodland habitat and unrestricted hunting extirpated wild turkeys from most of their ancestral range by the mid-1800s, with 1930–1940 representing a population low point of around 200,000 birds (Kennamer et al. 1992). Restoration efforts then intensified, including stocking of suitable habitats in many states with translocated birds. By the 1970s, wild turkey populations had recovered to harvestable levels in 39 states, 16 of which were outside the wild turkey's historical range (Mosby 1975). By 2004 the national population had reached 6.6–6.9 million birds (Tapley et al. 2005). Some investigators (e.g., Mock et al. 2001) have suggested that this recovery of wild turkey populations helped drive the numerical and geographic expansion of *A. americanum*. Because the rebound of turkey populations broadly coincided with the expansion of deer, however, the relative contributions of these two hosts to the rise of *A. americanum* remain uncertain.

In recent decades, captive game ranching of native and exotic ungulates has increased in many states (Miller and Miller 2016). Proximity of these 'farmed wildlife' to livestock has created opportunities for the sharing and spread of ticks and tick-borne pathogens. This scenario, for example, has become an impediment to the eradication of cattle fever ticks in southern Texas (Lohmeyer et al. 2018). Cattle fever ticks (*R. (B.) annulatus* and *R. (B.) microplus*) are one-host ticks, so removal of all cattle from pasture for a suitable interval historically has been an effective method of cattle fever tick control. The effectiveness of this approach is declining, however, with control failures attributed to the presence of wild white-tailed deer and nilgai (*Boselaphus tragocamelus*) on the vacated pastures, where they provide an alternative source of blood meals for the ticks when cattle are removed (Olafson et al. 2018).

Nilgai were introduced from India to a ranch in southern Texas in the 1920s later escaped and became established in multiple southern Texas counties and adjacent Mexican provinces. Both nilgai and white-tailed deer have been implicated in the movement of cattle fever ticks northwards beyond current cattle fever quarantine areas (Foley et al. 2017 and references therein). Nilgai are of particular concern to disease managers, because they have larger home ranges and can disperse further than white-tailed deer. There are several additional species of exotic ungulates free-ranging in southern Texas, and their potential contributions to maintaining and spreading ticks and tick-borne pathogens are also of concern (Lohmeyer et al. 2018).

First introduced into southeastern North America by Spanish explorers in the 16th century, European swine now number more than 6 million and are found in at least 38 U.S. states (Bevins et al. 2014, VerCauteren et al. 2018). Based on current trends, wild pig populations are predicted to more than triple in population size and continue to expand in distribution (Fig. 2; Snow et al. 2017, Vercauteren et al. 2018). Feral swine can host many tick species (Sanders et al. 2013), but have not as yet been implicated as having any major role spreading TTBDs in North America, although Paddock and Goddard (2015) speculate that feral swine have contributed to the northward spread of *A. maculatum*. High survival rates, high reproductive rates, and rapid spread of feral swine mean their importance as tick hosts may be increasing. Indeed, Florida researchers recently have proposed their use as sentinel species for the detection of newly invasive ticks (Merrill et al. 2018).

Anthropogenic movement of tick-infested animals and products through wildlife trade, baggage, and cargo

Inadvertent importation of ticks is an ongoing biosecurity risk at U.S. borders. Exotic ticks and pathogens can enter the United States on wild animals, or wildlife-related products, that cross the border

as baggage or cargo (see Keirans and Durden 2001 for a review of all imported ticks submitted to the U.S. National Tick Collection). For example, non-native ticks have been found on numerous species of imported reptiles (Burridge et al. 2006), with several of the detected species being known vectors of livestock and veterinary pathogens. Several of these non-native ticks will feed on multiple wild lizard, mammal, and bird species (Burridge 2001), which increases their potential for local establishment if they were to be escape into the wild. *Amblyomma marmoreum* Koch (Acari: Ixodidae)—a tortoise tick that is a competent vector of the agent of heartwater—has been detected on imported tortoises, local dogs, and vegetation at a reptile-breeding facility in Florida (Allan et al. 1998). Exotic reptile ticks also have been collected from free-ranging exotic and native reptiles in Florida (Corn et al. 2011 and references therein). Given the growing demand for exotic reptile pets (Roth and Merz 1997), legal and illegal importations of reptiles have been increasing (Hoover 1999), increasing the risk of introduction of non-native ticks.

Non-native ticks also enter the United States associated with vertebrate host material such as wildlife trophies and skins (Becklund 1968). To explore the range of propagule ticks imported to the United States through airports, maritime ports, and land borders, we recently requested and analyzed relevant USDA data via a Freedom of Information Act request. The records we obtained listed all ticks intercepted from cargo and baggage arriving to the United States from selected regions of Latin America and Africa between 2012 and 2016 (these regions of origin represent areas of endemicity for the heartwater tick and cattle fever tick, among others). Of 264 Ixodid ticks detected, the most abundant genus was *Dermacentor* (179 individuals, 67.8% of the total), followed by *Rhipicephalus* (8.3%), *Amblyomma* (7.6%), *Boophilus* (8.7%), *Ixodes* (1.1%), and *Haemaphysalis* (0.4%) (Table 1). Overall, 72.3% of the intercepted ticks from baggage/cargo were found on vertebrate host materials, such as skins of *Odocoileus* spp. and other undisclosed species. Many were detected in privately owned vehicles at border crossings between Mexico and either Texas or Arizona. Whether ticks found attached to wildlife hides were dead or alive was not recorded, but if some were alive, this entry pathway could circumvent current fever tick surveillance efforts that focus on inspection of live cattle and live wildlife in the quarantine zone. These USDA data can be viewed as the 'tip of the iceberg', since not all imported ticks will have been intercepted. Thus, cross-border transport of animal skins and trophies—and also the pet trade (Molaei et al. 2019)—should be addressed in future efforts to reduce non-native tick incursions.

Contribution of Wildlife to the Rising Prevalence of Tick-Borne Disease Agents in North America

In this section we illustrate ways in which wildlife hosts can affect the prevalence and/or abundance of infected ticks. Our objective is not to provide a comprehensive survey of diseases, but rather to illustrate how wildlife hosts are important determinants of disease risk to humans, companion animals, livestock, and (occasionally) the wildlife themselves. Before we describe specific enzootic cycles, we first consider how pathogen transmission routes fundamentally affect the roles that wildlife can play.

The qualitative and quantitative importance of hosts for pathogen persistence and spread will vary depending on the route(s) of transmission used by the pathogen, which can be vertical (i.e., transovarial) or horizontal (Randolph et al. 1996, Hartemink et al. 2008). Horizontal transmission of disease agents from infected ticks to uninfected ticks can occur via a host that is systemically infected

(i.e., a 'competent' or 'reservoir' host). Alternatively, horizontal transmission can occur from infected to uninfected ticks that are cofeeding in close proximity in space and time on a host that is not systemically infected (Labuda et al. 1993a, Gern and Rais 1996) or has acquired immunity from a prior infection (Labuda et al. 1997). Thus, the role of wildlife in maintaining a tick-borne pathogen (beyond serving as a blood meal source) can be direct (as a reservoir), indirect (as a 'bridge' in cofeeding transmission), or inconsequential (in the case of vertical transmission).

Broadly speaking, for cofeeding transmission in the absence of vertical transmission, the quantitative importance of a host species will depend on the proportion of bloodmeals provided by that host and degree of aggregation of multiple life stages feeding at the same time on the same individual host (i.e., the degree to which questing phenologies of the ticks' life stages are synchronous) (Randolph et al. 2000). If vertical transmission occurs, then aggregation of ticks within a life stage may also contribute to the pathogen's reproductive number, which will increase the importance of hosts that tend to feed just one life stage (and may relax the constraint of synchronous phenologies).

For systemic transmission in the absence of vertical transmission, as with cofeeding transmission in the absence of vertical transmission, the quantitative importance of a host species depends on the proportion of bloodmeals provided by that host for multiple life stages. Additionally, the host's mortality rate and the duration of infectivity are important (Ogden et al. 2007), especially if the questing phenologies of the different life stages involved with maintaining the pathogen are highly asynchronous, or are broadly synchronous over an extended period. For vertically transmitted pathogens, if the transmission efficiency is less than 100%, the pathogen will eventually die out unless some form of horizontal transmission also occurs to help amplify the pathogen (Fine 1975). Therefore, even for pathogens that rely primarily on vertical transmission for persistence, there may be certain hosts that are nevertheless critical for maintaining the pathogen cycle by cofeeding or systemic transmission (even if that route is relatively inefficient).

Contribution of Wildlife Hosts to Rising Tick-Borne Disease Risk to Humans

We focus this section on the role of wildlife on *I. scapularis*-associated pathogen dynamics, because *I. scapularis* is the most significant North American vector of human disease. For a review of the enzootic cycles of other TTBDs in North America, including host relationships, see Eisen et al. (2017) and references therein.

Currently, *I. scapularis* is known to transmit seven zoonotic pathogens (*A. phagocytophilum*, *Babesia microti*, *B. burgdorferi* sensu stricto, *B. mayonii*, *B. miyamotoi*, *Ehrlichia muris euclairensis*, and POWV). Our level of understanding varies regarding how each of these pathogens is maintained in nature, but we do know that they rely on the different routes of transmission (described previously) to differing degrees. Consequently, the importance of wildlife hosts for the enzootic maintenance of these pathogens also varies (Table 2) (Davis and Bent 2011, States et al. 2017). For example, vertical transmission occurs in both *B. miyamotoi* and POWV, but not for the other pathogens. Horizontal transmission via a reservoir appears to occur for all of the pathogens, but the duration of host infectivity varies and may even be fleeting, and the contribution of systemic transmission for some of the pathogens may be small. Cofeeding transmission has been established empirically in the laboratory for *A. phagocytophilum*, *B. burgdorferi* sensu stricto, and *E. muris euclairensis* (see below and references in Davis and Bent 2011) and

Table 1. Interceptions of Ixodid ticks at U.S. land borders, maritime ports, and airports in baggage and cargo arriving from selected regions in Latin America and Africa, 2012–2016

Genus	Species	Origin of the intercepted baggage/cargo/shipment									
		Costa Rica	Ecuador	El Salvador	Ghana	Guatemala	Honduras	Mexico	Peru	Unknown	All
Amblyomma	*americanum*							1			1
	cajennense		2					6			8
	dissimile		1								1
	maculatum							1			1
	mixtum		1								1
	undetermined							8			8
Boophilus	*annulatus*							2			2
	microplus							6			6
	undetermined							15			15
Dermacentor	*albipictus*							104			104
	hunteri							2			2
	variabilis		1					59			60
	undetermined							13			13
Haemaphysalis	undetermined							1			1
Ixodes	undetermined							3			3
Rhipicephalus	*sanguineus*		4	1		1		2	1		9
	undetermined		2	1	1	1	2	6			13
Undetermined	undetermined	1	2				2	10		1	16
All		1	13	2	1	2	4	239	1	1	264

Table 2. Examples of host-targeted methods for reducing acarological risk. Not all these examples presently are likely to be economically feasible to use over large areas, and some methods do not yet exist.

Primary life stage fed by targeted wildlife host	Adult (hosts may or may not be reservoirs)			Juvenile (hosts are reservoirs)		
Intervention	Remove host	Treat host		Remove host	Treat host	
		acaricide	anti-pathogen		acaricide	anti-pathogen
Mechanism for reducing the abundance of infected vectors	• Tick control (most directly by reducing the next generation of larvae) and • Reducing pathogen transmission if vertical transmission occurs		• Reducing pathogen transmission by reducing the number of infected vectors	• Tick control (most directly by reducing the subsequent numbers of infected nymphs; can reduce the number of adults but may be a minor effect overall on the tick population) • Reducing pathogen transmission in the enzootic cycle by reducing the number of infected nymphs		• Reducing pathogen transmission by reducing the number of infected nymphs
Ecological questions	• What proportion of bloodmeals does the targeted species provide? • How likely will ticks use alternative hosts?	• Not applicable	• Not applicable	• What proportion of bloodmeals does the targeted species provide? • How likely will ticks use alternative hosts?	• Not applicable	• Not applicable
Examples	• Lethal • Fencing	• Acaricide ('4-poster') • Anti-tick vaccine	• None known at this time	• Lethal	• Bait tubes • Bait boxes • Anti-tick vaccine	• Anti-pathogen vaccine • Antibiotic
Selected comments and concerns	• Lethal: social acceptance • Fencing: if small mammals and birds are not excluded by fencing, infected vectors may be imported into the fenced area	• Anti-tick/acaricide treatments will have a negative effect on the enzootic cycles for all pathogens vectored by the tick • Withdrawal period of acaricide must be considered for game species • Vaccines or therapeutics must be considered safe for human consumption if the host is a game species • Concern for secondary poisoning of predators/scavengers		• Lethal: social acceptance	• Anti-tick/acaricide treatments will have a negative effect on the enzootic cycles for all pathogens vectored by the tick • Withdrawal period of acaricide must be considered for game species • Vaccines or therapeutics must be considered safe for human consumption if the host is a game species • Concern for secondary poisoning of predators/scavengers	

likely also occurs for POWV (Ebel 2010). Below we discuss these seven pathogens in greater detail.

Lyme disease is the most commonly reported tick-borne disease in North America (Rosenberg et al. 2018), with more than 90% of reported cases transmitted by *I. scapularis* (Schwartz et al. 2017). The etiologic agents of Lyme disease on this continent are *Borrelia burgdorferi* sensu stricto and the recently discovered *B. mayonii* (Pritt et al. 2016), which presently appears to be limited to the north central United States (Lehane et al. 2020). Vertical transmission has not been demonstrated for either pathogen (Rollend et al. 2013, Breuner et al. 2018). Horizontal transmission between systemically infected reservoir hosts (e.g., white-footed mouse, *Peromyscus leucopus*) and immature *I. scapularis* is highly efficient for both *B. burgdorferi* ss (e.g., Donahue et al. 1987) and *B. mayonii* (Parise et al. 2020). Cofeeding transmission has been reported as being inefficient for *B. burgdorferi* ss (Piesman and Happ 2001), but further research is warranted given recent reports of cofeeding transmission of *B. mayonii* (Breuner et al. 2018) and of European Lyme spirochetes (Voordouw 2015). In the following, we focus on *B. burgdorferi* ss, as more studies are needed to unravel the host ecology of *B. mayonii*.

Immature *I. scapularis* feed on a broad range of mammals, birds, and lizards (Barbour and Fish 1993, Keirans et al. 1996, Piesman and Gern 2004). These species vary in their competence for *B. burgdorferi* ss, which is broadly determined by the alternative pathway of the host complement system (Kurtenbach et al. 2002). Several small mammals and passerines are highly competent, while

several other hosts, including reptiles and medium and large mammals, are either weakly competent or incompetent (Keirans et al. 1996). Hosts also vary in their quality for ticks, as evident from host-dependent variation in the proportion of ticks that successfully attach, feed, and successfully molt to the next stage (Keesing et al. 2009). Immature *I. scapularis* reliably feed successfully on small mammals, and in particular, white-footed mice, which are highly abundant in the habitats that also favor *I. scapularis* and deer (Levine et al. 1985, Ostfeld et al. 2006). Consequently, much research has investigated how biotic and abiotic factors might affect the abundance of mice (e.g., Levi et al. 2012) and the spatial and temporal dynamics in Lyme disease risk, as measured by the density of infected *I. scapularis* nymphs (the life stage most responsible for transmission of infection to humans). Additional reservoirs that are important hosts of immature *I. scapularis* include eastern chipmunks (Tamias striatus) and shrews (Blarina brevicauda and Sorex cinereus) (Slajchert et al. 1997, Brisson et al. 2008).

Depending on geographic location and year, rodent population numbers in temperate forests can be regulated by either bottom-up or top-down processes (Ostfeld et al. 2018). For example, positive correlations between increased food supply, increased rodent density, and lagged increase in the density of infected *I. scapularis* nymphs have been reported (Ostfeld et al. 2001). In other studies, infection prevalence of *I. scapularis* nymphs decreased with increased predation of small rodents (Ostfeld et al. 2018). Levi et al. (2012) suggested that displacement of foxes (*V. vulpes*) by coyotes in the eastern

United States in recent decades reduced the top-down pressure of fox predation on mice and thereby contributed to rising Lyme disease risk. This argument has been challenged by Way and White (2013), in part, because Levi et al. (2012) provided no evidence of a rodent population response of the type posited. Rather than a numerical effect on rodent populations, Hofmeester et al. (2017) have proposed that predators can affect tick-borne disease dynamics by modifying prey behavior; i.e., the 'ecology of fear': if rodents limit their movements in the presence of predators, they may contact fewer ticks and pathogens (Moll et al. 2020).

Considering the entire host community more broadly, Ostfeld and Keesing (2000) proposed that host biodiversity is an important driver of the Lyme disease system in the eastern United States (LoGiudice et al. 2003). They suggested that disturbed, fragmented ecosystems typically have low host diversity and are dominated by generalist wildlife species such as deer and mice that support robust cycles of *B. burgdorferi*. In contrast, landscapes with large intact forests typically support a higher diversity of less competent hosts and proportionately fewer mice on which immature ticks can feed, thereby suppressing *B. burgdorferi* transmission (Ostfeld and Keesing 2000, Allan et al. 2003). This 'dilution hypothesis' (Schmidt and Ostfeld 2001, Keesing et al. 2006), when applied universally to Lyme disease systems, remains controversial (Randolph and Dobson 2012, Wood and Lafferty 2013), in part, because increasing species richness of the host community can have either amplifying or diluting effects on pathogen transmission, depending on the numerical response of ticks to varying abundance of the various host species (Ogden and Tsao 2009). A key question, with regard to feeding immature ticks, is whether additional host species act compensatorily or additively? The infection prevalence will decrease in both cases, but the density of infected nymphs, and therefore disease risk, can stay the same or increase in the latter case. Diuk-Wasser et al. (2020) (this issue) provides a more extensive discussion on this topic.

Scaling up to the continental level, one striking epidemiological pattern is the very strong latitudinal gradient in Lyme disease incidence in the eastern United States: states in the northeastern and north central typically report Lyme disease annual incidences at least two orders of magnitude higher than in the Southeast (Schwartz et al. 2017). Covarying with this gradient are several factors that may reduce disease risk in the southern United States, including concomitant changes in the host community and host-use by juvenile *I. scapularis* (Keirans et al. 1996). In northern states, *B. burgdorferi* is maintained by high-efficiency horizontal transmission among juvenile *I. scapularis*, reservoir-competent white-footed mice, several other small mammal species, and a few bird species (Mather et al. 1989, LoGiudice et al. 2003, Brinkerhoff et al. 2011). In contrast, throughout the southeastern and south central United States, juvenile ticks feed primarily on skinks that are abundant but have low reservoir competence for *B. burgdorferi* (Apperson et al. 1993, Levin et al. 1996, Ginsberg et al. 2021). Ostfeld and Keesing (2000) hypothesized that the gradient in disease incidence may be driven by increased host biodiversity in the South, but Ginsberg et al. (2021) suggest it is the use of poorly competent skinks, rather than biodiversity per se, that is one of several key factors. Other factors include the latitudinal change in host-seeking behavior of *I. scapularis* immatures (Diuk-Wasser et al. 2010, Arsnoe et al. 2019) and overall lower *I. scapularis* population densities in the Southeast (Ginsberg et al. 2021).

In the western United States, where *I. pacificus Cooley & Kohls (Acari: Ixodidae)* is the primary vector of *B. burgdorferi*, there are many ecological parallels to the eastern United States 'Lyme system', including a latitudinal gradient in acarologic risk and Lyme disease incidence (Eisen et al. 2006). Several rodent species have been implicated as amplifying or reservoir hosts of the spirochetes,

including the dusky-footed wood rat (*Neotoma fuscipes*), deer mouse (*P. maniculatus*), and western gray squirrel (*Sciurus griseus*) (Eisen et al. 2003, Lane et al. 2005). Juvenile *I. pacificus*, however, frequently feed on the western fence lizard (*Sceloporus occidentalis*), which is an incompetent host of *B. burgdorferi* due to complement-mediated killing through the alternative pathway (Lane and Loye 1989, Kuo et al. 2000). As in the eastern United States, it has been hypothesized that these lizards divert vector ticks from feeding on reservoir-competent hosts, thereby reducing the *B. burgdorferi* prevalence in vector ticks, as well as human Lyme disease risk (but see Salkeld and Lane 2010). Experimental removal of western fence lizards from a California field site resulted, however, in a decrease, rather than increase, in Lyme disease risk (Swei et al. 2011), illustrating our less-than-complete understanding of the complex relationship between host diversity and Lyme disease risk.

Just as host dynamics and dispersal can affect tick spread, they can affect pathogen spread as well, and so birds are considered to have the greatest effect on long-distance dispersal of Lyme spirochetes to previously uninfected areas. A recent study (Walter et al. 2017) reconstructed the evolutionary history of *B. burgdorferi* ss through sequencing of genomes from across the North American continent. High levels of gene flow, and evidence of long-distance migration events between the three geographic regions sampled (north central, northeastern, and southeastern United States), were attributed to long-distance, bird-mediated dispersal. Thus, although small mammals are believed to be the most important reservoirs for maintaining enzootic cycles of *B. burgdorferi*, population genomics data support the hypothesis that birds disperse *B. burgdorferi* over long distances and have a homogenizing role on *B. burgdorferi* genetics. This can be most clearly seen in European studies, where there is strong host association of several *B. burgdorferi* sensu lato species (Kurtenbach et al. 2006). Owing to high rates of migration and mixing facilitated by avian hosts (Vollmer et al. 2011, Norte et al. 2020), the bird-associated species (*B. garinii* and *B. valaisiana*) show low geographic genetic structuring throughout Europe, when compared to the small mammal-associated species (*B. afzelii*). Underscoring the vagile nature of bird-associated Lyme borrelia, *B. garinii* and *B. bavariensis* (Asian lineage) have been detected in sea bird ticks *Ixodes uriae* White (Acari: Ixodidae) collected from islands off the coast of North America (Smith et al. 2006; Munro et al. 2017, 2019). It is possible that *B. garinii* or *B. bavariensis* from these island disease systems eventually will reach mainland North America.

Finally, the maintenance and dispersal of different Lyme borrelia spirochetes by different wildlife hosts could potentially have epidemiological consequences beyond simple increase in risk, because in North America there appears to be strain-associated *B. burgdorferi* ss clinical manifestations (Wormser et al. 1999, 2008; Dykhuizen et al. 2008). At this time, however, evidence for host association of North American strains remains tenuous (Hanincová et al. 2006, Brisson et al. 2008, Brinkerhoff et al. 2010, Mechai et al. 2016).

The importance of reservoir host ecology for tick-borne pathogen dynamics is nicely illustrated by contrasting *B. burgdorferi* ss with *Ba. microti*, the etiologic agent of human babesiosis (Vannier et al. 2015). Reservoir hosts for *Ba. microti* are limited to small mammals, predominantly *P. leucopus* (Spielman et al. 1981). Being constrained to reservoirs with small home ranges and short dispersal distances appears to have contributed to more limited, slower expansion and greater genetic structure of *Ba. microti*, when compared with *B. burgdorferi* (Lemieux et al. 2016, Goethert et al. 2018). Furthermore, *Ba. microti* is not transmitted as efficiently as *B. burgdorferi* ss (Dunn et al. 2014), and model analysis has estimated its reproductive number (R_0) to be <1, implying it should not persist in nature (Davis and Bent 2011). Laboratory

experiments have demonstrated, however, that mice coinfected with *B. burgdorferi* show increased transmission efficiency of *Ba. microti* to *I. scapularis* (Dunn et al. 2014). In other words, the competence of mice for *Ba. microti* is increased by coinfection with *B. burgdorferi* (Dunn et al. 2014), and so areas with established enzootic cycles of *B. burgdorferi* may be more permissive for invasion, establishment, and maintenance of *Ba. microti* (Diuk-Wasser et al. 2016). This may explain the wide range of nymphal infection prevalences reported for *Ba. microti* (0–20%) (Diuk-Wasser et al. 2014). Unlike all other *I. scapularis*-borne pathogens, *Ba. microti* can be transmitted transplacentally (i.e., vertically) from the infected female *P. leucopus* and *Microtus pennsylvanicus* (meadow vole) to offspring (Tufts and Diuk-Wasser 2018). Thus, transplacental transmission, which was not considered in Davis and Bent (2011), may be contributing to the persistence of *Ba. microti* in nature.

Human granulocytic anaplasmosis (HGA)—caused by infection with *Anaplasma phagocytophilum*—is the second most reported TBD in the United States (Rosenberg et al. 2018). Its emerging geographic distribution is similar to that of Lyme disease. Although the enzootic cycle maintaining *A. phagocytophilum* comprises several of the same reservoir hosts (including small mammals and birds) as that for *B. burgdorferi* ss, the duration of peak infectivity is shorter (Levin and Ross 2004), and immunity gained from a prior infection with *A. phagocytophilum* will reduce the transmission efficiency of subsequent infections. Cofeeding transmission is possible (Levin and Fish 2000a) and may contribute to enzootic maintenance especially in the north central United States, where host-seeking phenologies of nymphal and larval *I. scapularis* are more synchronous compared with the northeastern United States (Ogden et al. 2007).

Anaplasma phagocytophilum exhibits complex enzootic cycles involving multiple strains associated with multiple species of wildlife hosts and tick vectors (Stuen et al. 2013). Based on a fragment of the *16s RNA* gene, there are two important variants of *A. phagocytophilum* broadly distributed in North America: *A. phagocytophilum* human-active (Ap-ha), which is known to be pathogenic to humans, and *A. phagocytophilum* variant-1 (Ap-v1), which is not pathogenic (Massung et al. 2003). In the eastern United States, white-footed mice are considered the most competent reservoir hosts for the human pathogenic strain (Massung et al. 2003), whereas deer are considered the main reservoir host for the nonpathogenic variant (Massung et al. 2005). Eastern chipmunks and shrews are also considered potentially important reservoir hosts for the Ap-ha variant (Keesing et al. 2012). It is possible, therefore, that the composition of the wildlife community will help determine the relative infection prevalence of *A. phagocytophilum*-ha and *A. phagocytophilum*-v1 in the tick population in a given area, with implications for human disease risk.

Ehrlichia muris eauclairensis is an example of an emerging *I. scapularis*-borne pathogen whose enzootic maintenance remains poorly understood. The pathogen was first detected in symptomatic patients in Wisconsin and Minnesota in 2009 (Pritt et al. 2011) and subsequently in *I. scapularis* and *P. leucopus* in the Upper Midwest, but not yet in the Northeast (Stromdahl et al. 2014, Castillo et al. 2015, Johnson et al. 2015, Xu et al. 2018). Reservoir competence of *P. leucopus* has been demonstrated in the laboratory (Lynn et al. 2017), but the infectious period is short (less than 4 wk), host mortality is high, and survivors clear their infection. Cofeeding transmission can occur and may be an important additional (or main) mechanism for *E. muris eauclairensis* maintenance (Karpathy et al. 2016, Lynn et al. 2017). Alternatively, it is possible that an unidentified host other than *P. leucopus* may be the key reservoir (Lynn et al. 2017).

POWV, which can cause a rare, fatal neuroinvasive disease in humans, is the only member of the tick-borne encephalitis (TBE) serogroup recognized in North America (Ebel 2010). The role of wildlife reservoirs for its enzootic maintenance is unclear, and perhaps negligible (Ebel 2010, Mlera and Bloom 2018). In Europe, it has been argued that TBEV is maintained mainly by vertical and cofeeding transmission among ticks, as systemic infection of hosts is short-lived (Labuda et al. 1993b, Randolph et al. 1996, Michelitsch et al. 2019), and this may be true for POWV as well (Ebel 2010, Davis and Bent 2011, Mlera and Bloom 2018).

Molecular phylogenetics indicate that POWV consists of two genotypes that are maintained in two different enzootic cycles: POWV prototype lineage (Lineage I), and deer tick virus (DTV) lineage (Lineage II) (Beasley et al. 2001, Ebel et al. 2001, Kuno et al. 2001). POWV cycles between *I. cookei (Acari: Ixodidae)*, groundhogs (*Marmota monax*) (McLean et al. 1964), and striped skunks (*Mephitis mephitis*) (Main et al. 1979), and between *I. marxi* Banks (Acari: Ixodidae) and red squirrels (*Tamiasciurus hudsonicus*) (McLean and Larke 1963). Although no virus has been detected, serological evidence suggests that DTV is maintained in a cycle between *I. scapularis* and white-footed mice (Telford et al. 1997, Ebel et al. 2000).

POWV encephalitis has been emerging over the last two decades (Campbell and Krause 2020 and references therein, Eisen et al. 2017). Most human cases occur in the Northeast and Upper Midwest. Given that *I. cookei* infrequently bites humans (but see Smith et al. 1992, Rand et al. 2007), the increase in incidence has been attributed to a rise in *I. scapularis* bite rates (Campbell and Krause 2020), which implies that factors promoting the increase and spread of *I. scapularis* also may be driving the increase in POWV. Supporting this hypothesis is the significant increase in prevalence of POWV antibodies in deer observed in Connecticut from 1979 to 2009 (Nofchissey et al. 2013), most likely reflecting the emergence of new *I. scapularis* populations in this area. Aggregation of adult female *I. scapularis* on deer may be an opportunity for cofeeding transmission, thereby increasing the prevalence of infection in adult females and the probability of transovarial transmission (Mlera and Bloom 2018). Other host species that could be investigated as a potential reservoir for POWV are voles (*Myodes* spp.) based on 1) the detection of POWV antibodies in northern (*Myodes rutilis*) and southern (*Myodes gapperi*) red-backed voles in Alaska (Ebel et al. 2000, Deardorff et al. 2013); and 2) *I. scapularis* parasitizes *M. gapperi* in the north central United States (Russart et al. 2014, Ginsberg et al. 2021).

Borrelia miyamotoi, a relapsing fever group *Borrelia* spirochete, is transmitted by *I. ricinus* complex ticks (Scoles et al. 2001, Fraenkel et al. 2002, Fomenko et al. 2010). We highlight it here as an example of a vertically transmitted pathogen for which the role of wildlife in the maintenance and transmission is not well-defined. *Borrelia miyamotoi* has been detected in a number of wildlife hosts in North America in both *I. scapularis*- and *I. pacificus*-driven cycles. Since *B. miyamotoi* circulates in areas where white-footed mice are key reservoir hosts for *B. burgdorferi*, these mice also have an important role in *B. miyamotoi* maintenance and transmission. However, brief infectivity and low transmission efficiency of white-footed mice for *B. miyamotoi* suggest that mice are not highly competent reservoirs for the spirochete (Scoles et al. 2001). Vertical transmission, however, is probably insufficient to fully support *B. miyamotoi* maintenance in tick populations (Han et al. 2019), such that occasional horizontal transmission involving wildlife reservoirs or cofeeding transmission is required for persistence of *B. miyamotoi* (Han et al. 2016, Sambado et al. 2020).

Thus, further research is needed to clarify the importance of wildlife hosts for *B. miyamotoi* maintenance.

This section has focused on *I. scapularis*-borne zoonotic pathogens. It should be appreciated that certain aspects of the biology of *B. burgdorferi*—such as the wide host range and long period of infectivity of reservoir hosts to ticks—are very different from other pathogens transmitted by *I. scapularis*, which vary in host range, duration of infectivity, and for which the role of wildlife for pathogen persistence may be more limited. Similarly, for several rickettsial agents transmitted by other vectors (e.g., *D. variabilis*, *A. americanum*, *A. maculatum*), hosts may be infectious for such short periods that cofeeding transmission (and/or vertical transmission if it occurs), rather than systemic transmission, may be required for their maintenance in nature (e.g., Zemtsova et al. 2010, Moraru et al. 2013, Levin et al. 2017). For such pathogens, there may be no significant vertebrate reservoir in the transmission system (Tomassone et al. 2018); rather, the key host species simply will be those whose blood meals help to support large tick populations.

Contribution of Wildlife Hosts to Rising Tick-Borne Disease in Companion Animals

The rise of some TTBDs threatens the health of companion animals such as dogs and cats (Little et al. 2010, Nicholson et al. 2010, Herrmann et al. 2014). Companion animals that spend time outdoors are typically at greater risk of exposure to ticks and tick-borne pathogens than are humans (Eng et al. 1988), because they spend more time in the environment and have behaviors that may increase their chances of encountering ticks (e.g., rooting in the leaf litter, stalking prey in the leaf litter, and investigating holes in which wild animals live). Given their greater risk and close association with their human companions, dogs often have been used as sentinels for emerging TTBDs (Eng et al. 1988, Johnson et al. 2004, Mead et al. 2011, Self et al. 2019, Little et al. 2021).

In North America, humans are most commonly bitten by a few hard tick species: *A. americanum*, *D. variabilis*, *I. scapularis*, and *I. pacificus* (Nieto et al. 2018). In contrast, recent national surveys of companion animals brought to veterinary clinics reveal that dogs (Saleh et al. 2019) and cats (Little et al. 2018, Saleh et al. 2019) are bitten by at least 14 and 12 species of ticks, respectively, although the most commonly reported are similar to that biting humans. For dogs, *R. sanguineus* (sensu lato) (Acari: Ixodidae), *A. americanum*, *D. variabilis*, and *I. scapularis* were the most frequently submitted (Saleh et al. 2019). For cats, *A. americanum*, *D. variabilis*, and *I. scapularis* were the most frequently submitted (Little et al. 2018, Saleh et al. 2019). The ecology of these four tick species are relatively well-studied, whereas much less is known about how wildlife affect the population dynamics of the other tick species and enzootic cycles for associated pathogens. As the discussion in the previous section about the role of wildlife in the rise of *I. scapularis*-borne zoonotic pathogens applies to companion animals, below we briefly discuss two examples that are of greater concern for companion animals.

Rhipicephalus sangineus Latreille (Acari: Ixodidae), the brown dog tick, has a global distribution and can be a major pest and disease vector for companion dogs. *Rhipicephalus sanguineas* is a vector of *Ehrlichia canis*, several babesia species, and *Rickettsia rickettsii*, the agent of Rocky Mountain Spotted Fever (RMSF). Because all three life stages highly prefer dogs, and because it is a nidicolous tick, humans are rarely bitten. Some circumstances, however, can result in "spillover" bites and pathogen transmission to humans, as recently occurred on American Indian reservations in southwestern United States (Demma et al. 2006). Large numbers of dogs, many

free-roaming, resulted in heavy infestations of *R. sanguineas* on dogs as well as in the environment in domestic and peridomestic settings, leading to outbreaks of RMSF among people (Demma et al. 2006, Nicholson et al. 2006, Drexler et al. 2014). Wildlife do not appear to be important for the maintenance of *R. sanguineus* nor the pathogens it transmits, so although *R. sanguineus* is expected to respond to warming climate, changes in abundance and distribution are unlikely to be driven by wildlife.

Cytauxzoonosis is a tick-borne protozoal disease impacting cats; the causative agent is *Cytauxzoon felis* (Wagner 1976). Cytauxzoonosis has been reported in south central, southeastern, and mid-Atlantic regions of the United States (Birkenheuer et al. 2006). The primary reservoir hosts are bobcats (*Lynx rufus*), with *C. felis* transmitted from bobcats to domestic cats by *D. variabilis* ticks (Blouin et al. 1984). Bobcat densities decline with urbanization (including exurban, low-density development), but if wildland habitats (or suitably large green spaces) are maintained adjacent to development, bobcats populations can persist and will use these exurban/suburban landscapes (Tigas et al. 2002, Lewis et al. 2015). Thus, in areas with appropriate habitat for *D. variabilis*, overlap in space use by bobcats, feral cats, and domestic cats may increase, leading to greater exposure risk to *C. felis*.

Contribution of Wildlife Hosts to Rising Tick-Borne Disease in Livestock

Ticks can have significant economic impacts on the livestock industry by reducing weight gain, increasing feed per pound of gain, decreasing milk production and hide value, and increasing livestock mortality (Eskezia and Desta 2016). Tick management in the livestock industry is beyond the scope of this article, but we emphasize that movement of ticks and tick-borne pathogens between free-ranging and captive species is a 'two-way street' whenever these species overlap or have fence-line contact. For example, *H. longicornis*, which is native to East Asia, has long been considered a significant threat to the cattle industry in New Zealand, parts of Australia, and the Pacific Islands (Heath 2016), because it is the primary vector for the hemoparasite *Theileria orientalis*. In 2017, the first known *H. longicornis* infestation in North America was discovered on a domestic sheep from New Jersey (Rainey et al. 2018). Subsequent surveys revealed that *H. longicornis* was also infesting wildlife near where the sheep had grazed, and subsequent efforts to eradicate the wildlife infestation have been unsuccessful. The tick has since spread rapidly across the eastern United States (Beard et al. 2018), with natural movement of infested wildlife and transportation of infested livestock both contributing to that spread. Recently, *H. longicornis* has been implicated in cattle infection with *T. orientalis* in Virginia (Oakes et al. 2019).

As mentioned previously, feral swine are an example of a free-ranging species that hosts multiple tick species and is reservoir-competent for several tick-borne pathogens of livestock concern (Bevins et al. 2014). For example, African Swine Fever (ASF) is a foreign animal disease that can be spread directly or through the bite of infected soft ticks in the genus *Ornithodoros (Acari: Argasidae)*. In recent years, ASF has emerged or reemerged in Europe, Asia, and Central and South America (Brown and Bevins 2018). There is considerable concern that if ASF reached North America, it could become enzootic among native ticks of feral swine or peccaries (Golnar et al. 2019).

In western North America, wild ungulates such as bighorn sheep (*Ovis canadensis*), elk (*Cervus elaphus*), and mule deer (*Odocoileus*

hemionus) overlap in habitat use with domestic sheep (*O. aries*), cattle (*Bos taurus*), and other livestock, thereby sharing ticks and pathogens. Examples of shared ticks include *D. occidentalis Marx (Acari: Ixodidae)*, *D. andersoni Stiles (Acari: Ixodidae)*, and *D. albipictus*, all of which are competent vectors of *A. marginale* and *A. ovis* (Stiller et al. 1999). *Dermacentor hunter* Bishopp (Acari: Ixodidae), which feeds primarily on bighorn sheep, is another competent vector of both *Anaplasma* species (Crosbie et al. 1997). Infection with *A. ovis* usually causes mild disease in domestic sheep (Splitter and Anthony 1956) but severe disease in bighorn sheep (Tibbitts et al. 1992).

In recent decades, numerous state legislatures have allowed various ungulate species to be managed as 'livestock' within captive cervid facilities that are regulated by state agriculture and/or state wildlife agencies. New TTBD challenges have arisen within these captive cervid facilities. For example, *Babesia odocoilei* transmitted by *I. scapularis* ticks is historically associated with white-tailed deer, which show few if any signs of disease. Clinical babesiosis, however, has now been seen in captive elk, reindeer, and caribou (Holman et al. 1994, Bartlett et al. 2009). As *I. scapularis* emerges in new areas, babesiosis may become an increasing threat to captive and perhaps wild cervids. In parts of Canada where *I. scapularis* has been presumed to be absent, *Ba. odocoilei* and babesiosis have been detected among captive cervid herds (Mathieu et al. 2018)—these captive cervids inadvertently may have played a role as sentinels for *I. scapularis* and therefore wildlife and human health.

Contribution of Wildlife Hosts to Rising Tick-Borne Disease in Wildlife

Reports of clinical manifestations of tick-borne disease in wild animals are not common, but this does not necessarily imply nonpathogenicity of these pathogens to wildlife species because diseases, and even substantial die-offs, in wildlife populations often go unnoticed and are rarely quantified. Nevertheless, it is to be expected that natural, long-term interactions among wildlife hosts, vectors, parasites, and their environment will often produce persistent enzootic cycles of disease agents with little measurable effect on overall wildlife population health and abundance.

Anthropogenic influences such as habitat degradation or climate change may disrupt these cycles, leading to epizootic outbreaks of tick-borne disease in wildlife populations (Höfle et al. 2004, Nijhof et al. 2005). For example, epizootics of *D. albipictus* triggered by climate change are a suspected cause of high mortality of moose (*Alces alces*) calves and reduced reproductivity of yearling and adult moose in the northeastern United States (Jones et al. 2019). Moose with severe tick infestations may be fed on by tens of thousands of winter ticks resulting emaciation, severe metabolic imbalance, and hair loss, which in combination can be a primary cause of mortality (Jones et al. 2019). A spring 2002 epizootic of winter ticks in New Hampshire that caused over 50% mortality of moose calves was associated with a mild preceding winter that increased tick loads on moose (Musante et al. 2010). Three successive years (2014–2016) of winter tick epizootics in the Northeast caused high (88%) mortality of moose calves that contributed to declines in regional moose populations (Jones et al. 2017, 2019). Tick-borne pathogens have not as yet been implicated in directly contributing to moose morbidity or mortality.

As mentioned previously, *Ba. odocoilei* has been reported as causing severe or fatal babesiosis in elk (*Cervus elaphus canadensis*) (Gallatin et al. 2003), reindeer (*Rangifer tarandus tarandus*) (Langton et al. 2003), caribou (*R. tarandus caribou*) (Petrini et al. 1995), and a

captive juvenile African wild dog (*Lycaon pictus*) (Colly and Nesbit 1992). These clinical observations were from individual animals or captive herds; population-level impacts of babesiosis on free-ranging herds of these species remain uncertain. Benign *Ba. odocoilei* infections have been observed among experimentally inoculated white-tailed deer, which is suggestive of a stable enzootic cycle for this host species, although Emerson and Wright (1968) and Holman et al. (2000) have reported decreased body condition among infected free-ranging deer.

Wildlife Host-Targeted Approaches to Combat the Rise of TTBD

Since wildlife play a critical role in the maintenance of TTBDs, host-targeted control measures are—at least in principle—a promising route toward managing TTBD risks. Host-targeted measures, for example, provide an opportunity to avoid the nontarget impacts and public concerns associated with broad-scale applications of chemical acaracides. Host-targeted strategies also may have value when used in conjunction with other tick control approaches, as part of an integrated tick management (ITM) program.

Broadly speaking, host-targeted approaches involve either: 1) reducing the availability of hosts (e.g., by hunting or exclusion fencing) or 2) using the host to deliver a product (e.g., an acaracide or a vaccine) to the tick (Table 3). When targeting the hosts of adult ticks, the focus is on breaking or weakening the enzootic cycle indirectly by reducing overall tick density, because each adult female that feeds successfully will produce thousands of larvae. If the pathogen of concern can be vertically transmitted, targeting the host of the adult stage will also weaken that route of transmission. In contrast, when targeting the reservoir hosts of the larval and nymphal stages, the desired impacts are to reduce the numbers of infected nymphs and to directly break the enzootic cycle.

One significant difficulty with a host-targeted approach is that the tick species that are most problematic for humans and companion animals tend to be host-generalists. Since control measures typically target the most important reproductive or reservoir host, the efficacy of that measure will greatly depend on the extent to which some ticks already are feeding on other host species in the community (Tsao et al. 2004), and therefore how readily ticks can 'switch' to alternative hosts in response to control measures. Having said that, methods targeting deer can have added value because the adults of multiple tick species that feed on deer (e.g., blacklegged tick, lone star tick, Gulf Coast tick, and Asian long-horned tick) can be targeted simultaneously.

When developing host-targeted control plans the detailed ecology of each tick–pathogen cycle needs to be considered—along with the ecological and social context in which researchers, public health, and communities wish to explore a particular control approach. Below we provide selected examples of host-targeted approaches; for in-depth reviews of the research into these methods, see Eisen and Dolan (2016) and White and Gaff (2018). Most of these strategies aim to reduce the risk for Lyme disease, but many of the lessons learned and knowledge gaps identified are applicable to other emerging TTBDs.

Targeting Wildlife Hosts of Adult Ticks

As with the management of other wildlife diseases, reducing the population density of key hosts is a logical approach. Efforts to rid a landscape of a wildlife host are usually impractical, but in

Table 3. Summary of knowledge of modes of transmission of seven pathogens transmitted by *Ixodes scapularis*.

Pathogen	Vertical transmission	Horizontal transmission via		Reservoir hosts	Estimated duration of infectivity of reservoir host post-exposure
		Co-feeding or non-systemic transmission	Systemic transmission		
Anaplasma phagocytophilum	No evidence[1]	Yes[2]	Yes[3]	*Peromyscus leucopus,* but also other species[4]	~ 2 mos, but peaks ~1–3 wks post-exposure[5]
Babesia microti	No evidence in the tick[6], but can occur in the vertebrate host[7]	Unknown	Yes[8]	*P. leucopus,* but also other species[9]	At least 7 wks - 4 mos, peaks ~ 2 wks post-exposure[10]; transmission efficiency may be boosted if host is also infected with *B. burgdorferi*[11]
Borrelia burgdorferi sensu stricto	No evidence in North America[12]	Yes[13]	Yes[14]	*P. leucopus,* but also other species[1]	At least 6 mos, peaks ~ 2–3 wks post-exposure, but strain-dependent, but strain-dependent[16]
Borrelia mayonii	No evidence[17]	Unknown (but probable)[18]	Yes[19]	Perhaps: *P. leucopus* and *Tamiasciurus hudsonicus*[20]	May be lifelong[21] but declines from 4 to 12 wks post-exposure[22]
Borrelia miyamotoi	High, but < 100%[23]	Yes[24]	Yes[25]	*P. leucopus*[26]	Brief (< 3 wks)[27]
Ehrlichia muris euclairensis	Unknown but unlikely based on phylogeny[28] and lack of evidence in ovarian tissue[29]	Yes[30]	Yes[3]	*P. leucopus* possibly[32]	Mainly 1–2 wks, limited in part due to a high mortality rate of infected hosts (in the lab)[33]
Powassan encephalitis virus/Deer tick virus	Yes[34]	Very probable[35]	Yes[36]	POWV[37]: *Marmota monax, Mephitis mephitis, Tamiasciurus hudsonicus* (maintained by other *Ixodes* spp.) DTV[38]: *P. leucopus*	Probably brief (< 8–11 d) based on few studies, but infection experiments conducted by tick-bite are needed to mimic natural exposure[39]

Much of the presented evidence is inferred from studies conducted with laboratory animal species.

[1]Dunning Hotopp et al. 2006, Rikihisa 2011, Stuen et al. 2013; [2]Levin and Fish 2000a; [3]Telford et al. 1996, Des Vignes and Fish 1997; [4]Levin and Fish 2000b, Keesing et al. 2012; [5]Levin and Ross 2004; [6]Oliveira and Kreier 1979; [7]Friedhoff 1988, Tufts and Diuk-Wasser 2018; [8]Spielman et al. 1981, Mather et al. 1990; [9]Spielman et al. 1981, Telford and Spielman 1993, Hersh et al. 2012; [10]Spielman et al. 1981, Dunn et al. 2014; [11]Dunn et al. 2014; [12]Rollend et al. 2013; [13]Patrican 1997, Piesman and Happ 2001,Voordouw 2015, States et al. 2017; [14]Donahue et al. 1987; [15]Levine et al. 1985, Donahue et al. 1987, LoGiudice et al. 2003, Hanincová et al. 2006; [16]Donahue et al. 1987, Hanincová et al. 2008; [17]Breuner et al. 2018; [18]Breuner et al. 2018; [19]Parise et al. 2020; [20]Johnson et al. 2017; [21]Dolan et al. 2017; [22]Parise et al. 2020; [23]Scoles et al. 2001, Han et al. 2019; [24]Scoles et al. 2001, van Duijvendijk et al. 2016; [25]Scoles et al. 2001; [26]Scoles et al. 2001; [27]Scoles et al. 2001; [28]Dunning Hotopp et al. 2006; [29]Lynn et al. 2015; [30]Karpathy et al. 2016, Lynn et al. 2017; [31]Saito and Walker 2015, Karpathy et al. 2016, Lynn et al. 2017; [32]Castillo et al. 2015; [33]Lynn et al. 2017; [34]Costero and Grayson 1996; [35]Ebel 2010, Hermance and Thangamani 2018; [36]Costero and Grayson 1996, Telford III et al. 1997, Ebel and Kramer 2004; [37]McLean and Larke 1963, McLean et al. 1964, Main et al. 1979; [38]Telford III et al. 1997, Ebel et al. 2000; [39]Ebel 2010, Hermance and Thangamani 2018, Mlera and Bloom 2018.

the rare cases when it has been achieved, it can be successful. For example, after all the deer were removed from an island off the coast of Maine (Rand et al. 2004), the blacklegged tick population collapsed. Removing deer on the mainland, however, is far more challenging. Although intensive deer removal operations on the mainland have in some cases successfully reduced tick abundance and TBD incidence (Kilpatrick et al. 2014), these benefits are only seen when populations are reduced to very low levels due to the nonlinear relationship between deer density and tick abundance discussed previously. Near-elimination of a valued species like deer is socially and politically infeasible in most cases, so intensive deer removal as a control method is not a realistic option for most communities (Kugeler et al. 2016). Deer exclusion by fencing has been suggested as a method to create areas of low risk, but smaller animals that can cross the fences may still import infected ticks into the fenced area.

A method shown to be effective at reducing the abundance of blacklegged and lone star tick populations is the '4-poster' device (Pound et al. 2000b), whereby deer are attracted to a bait station that will apply a topical acaricide when deer reach down through impregnated rollers to eat corn (Pound et al. 2000a, Brei et al. 2009). Four-posters are expensive to maintain, however, and their effect is relatively localized, making them impractical for tick control over large areas (Harmon et al. 2011). Furthermore, baiting deer is controversial and frequently banned in areas where bovine tuberculosis and chronic wasting disease have infected the free-ranging deer population.

Immunization with an anti-tick vaccine has been used in the control of cattle fever ticks on cattle (de la Fuente et al. 1999) and an initial field trial of a deer-targeted anti-tick vaccine has been conducted in Spain (Contreras et al. 2020). These vaccines reduce the ability of ticks to feed to repletion and thereby reduce their reproductive

capacity. Given the evidence from other deer-targeted approaches, broad vaccine coverage of the deer population is necessary for an epidemiologically meaningful reduction of disease risk.

As mentioned above, a key concern with targeting deer for tick control is the degree to which alternative hosts contribute to feeding adult ticks. Alternative hosts can maintain a tick population in the absence of deer (Sidge 2016), although the resulting size of the population and disease risk likely depends on several factors including the species composition and abundance of the alternative hosts. Thus, control measures like an anti-tick vaccine that kills ticks or otherwise reduces the fecundity of deer-fed ticks after they have been successfully recruited from the environment to a deer may be more effective than deer removal, because such measures do not result in ticks using alternative hosts.

Targeting Wildlife Hosts of Juvenile Ticks

An alternative approach to reducing disease risk is to target hosts important for feeding and infecting juvenile ticks (i.e., reservoir hosts). For example, mice and chipmunks can be treated with synthetic acaricides using bait tubes or bait boxes (e.g., Mather et al. 1987, Dolan et al. 2004, Schulze et al. 2017) or with entomopathogenic fungi (Hornbostel et al. 2005, Williams et al. 2018). Effects on tick loads and disease risk have been promising (Schulze et al. 2017, Williams et al. 2018, Little et al. 2020), but variability across studies (as reviewed in Eisen and Dolan 2016) requires further research to better understand factors affecting success and the possibility of scaling up to large areas (Williams et al. 2018, Jordan and Schulze 2019, Machtinger and Li 2019). Similar to reducing the feeding success of the adult life stage by vaccinating hosts against ticks, hosts of juvenile ticks also can be targeted. Alternatively, one could develop a vaccine to block acquisition or transmission of a tick-borne pathogen (i.e., reservoir-targeted vaccines) (Tsao et al. 2004, Richer et al. 2014, Stafford et al. 2020) or make hosts refractory to infestation and/ or infection by ticks using gene editing tools (Buchthal et al. 2019). A further approach is to treat hosts with an antibiotic that clears infection in the host and thereby reduces transmission to feeding larvae (Dolan et al. 2017). Small mammal populations can respond quickly to food supplementation, so care needs to be taken to ensure that their populations will not increase as a result of bait consumption during these kinds of management efforts (White and Gaff 2018, Stafford et al. 2020). Furthermore, strategies need to factor in the contributions of alternative hosts for feeding and infecting immatures (Tsao et al. 2004), and whether contributions are compensatory or additive, particularly if population dynamics of the targeted host species are volatile. For example, bloodmeal analysis of questing nymphs (i.e., indicating the source of the larval blood meal) collected over 2 yr from two mainland and two island sites in New England, suggested that although *B. burgdorferi-* and *Ba. microti*-infected nymphs overall were more likely to have fed on mice compared with deer, in four of the eight site-year samples, <20% of nymphs had fed on mice (Goethert et al. 2021). Thus, an understanding of how climate, geography, food resources, and predators interact to predict the stability of small mammal communities is critical to the success of reservoir-targeted strategies (Ostfeld et al. 2018).

Wildlife as Potential Predator Control for Ticks

Chickens and other domestic and wild fowl consume arthropods and are frequently proposed as potential biological control agents for ticks (e.g., Duffy et al. 1992, Hassan et al. 1992). Aside from questionable efficacy, managers contemplating introducing fowl for tick control must also consider the potential for unintended consequences. For example, to control *Hyalomma* spp. ticks—which

vector Crimean–Congo hemorrhagic fever (CCHF) virus—the Turkish government introduced thousands of exotic helmeted guinea fowl (*Numida meleagris*). The outcome, however, was that the birds consumed few ticks, but served as bloodmeal hosts to immature *Hyalomma marginatum* Koch (Acari: Ixodidae); tick population suppression was not achieved (Şekercioğlu 2013). In South Africa, stomach content analysis indicated that <1% of guineafowl stomachs examined contained ticks (Petney and Kok 1993) and some birds were found to be host for hundreds of *Hyalomma* ticks (Van Niekerk et al. 2006). In New York State, Duffy et al. (1992) compared the abundance of questing *I. scapularis* ticks at properties with and without free-ranging guineafowl. Although the density of questing adults was lower at properties where guineafowl occurred, there was no statistical difference in the density of nymphal ticks, which pose the greatest risk for transmission of the Lyme disease spirochete to humans. There was also concern that the feed left uneaten by the guinea fowl would attract rodents and other wildlife hosts for the ticks.

Based on laboratory observations of field-captured opossums, Keesing et al. (2009) inferred that opossums are highly efficient groomers of larval blacklegged ticks and thereby help to reduce the abundance of *B. burgdorferi*-infected nymphal blacklegged ticks in nature. Using calculations based on opossum population densities reported from the literature and mean larval loads from their own data, their model predicted that the presence of opossums in the host community has a negative effect on the density of infected nymphs assuming that opossums divert larvae away from reservoirs like mice and chipmunks and kill them. Nevertheless, many areas in eastern North America that are considered high risk for Lyme disease also support substantial opossum populations (as evidenced, in part, by their status as a game species with no bag limits). Thus, even if opossums may act as 'ecological traps' for ticks, evidence supporting their efficacy for effectively reducing Lyme disease risk broadly is lacking and thus remains an open question.

Conclusions

Ecological knowledge gaps

Tick-borne disease systems are complex, often involving many wildlife host species; this complexity inherently poses challenges for control of TTBDs. Despite decades of research and many research studies, our understanding of the role hosts play in TTBD dynamics remains incomplete. Kilpatrick et al. (2017) listed uncertainties and research needs associated with Lyme disease ecology, several of which pertain to hosts: 1) the relationship between deer abundance and the abundance of larval *I. scapularis* in the presence of alternative large mammal hosts; 2) the factors determining the abundance of important hosts for larval ticks across time and space, including along gradients of land cover/land use; 3) the factors influencing tick burdens on different species, across a range of host communities and host abundances; and 4) the degree to which the restoration of predator communities of the key hosts—ungulates, rodents, and shrews—would reduce tick abundance or infection prevalence. To this list we add: 5) the interplay of abiotic and biotic factors that limit and/or regulate tick populations.

Given the extremely high potential fecundity of ticks, but relatively modest volatility in adult tick abundance from year to year under most North American conditions, there clearly are strong limitations to unchecked tick population growth. Two lines of evidence suggest that larval *I. scapularis* feeding success is often host-limited: firstly, the nonlinear relationship between deer and blacklegged nymph abundance discussed previously, and secondly, the often

positive relationship between rodent numbers in one year and nymphal density in the next year (Ostfeld et al. 2018, Ginsberg et al. 2020). Although these observations relate to the ecology of Lyme disease, the general conclusions may also apply to other TTBDs in North America. Future efforts to better understand the relationships between host abundance and tick abundance would provide a stronger foundation for development of host-targeted control measures for ticks and TBDs.

The rise of TTBDs in a changing environment

As researchers work to unravel the complexities of tick enzootic cycles, the system is changing around them. Wildlife host communities are dynamic, with perhaps unanticipated consequences for TTBDs. For example, three wildlife species that feed several tick species—coyotes, American black bears (*Ursus americanus*), and feral swine—are currently undergoing significant range expansions. All three species are highly adaptable, can disperse long distances, and can be found in agricultural and/or suburban habitats where they could directly affect human TTBD risk. Levi et al. (2012) hypothesized that the establishment of coyote populations can increase Lyme disease risk through their trophic interactions with other tick hosts. Coyotes themselves, however, can serve as hosts for blacklegged, lone star, American dog, Asian long-horned, and Gulf Coast ticks, so predicting the consequences of coyote range expansion for TTBDs is not straightforward (Way and White 2013). Black bears host human-biting tick species including the American dog, blacklegged, lone star tick, and Gulf Coast tick (Yabsley et al. 2009, Al-Warid et al. 2017), while also harboring several *I. scapularis*-borne pathogens (Zolnik et al. 2015, Chern et al. 2016). No significant effects by invasive feral swine on the spread of ticks or pathogens are yet apparent, but surveillance efforts of swine should continue given their ecology and high reproductive capacity. As mentioned previously, there is concern that *A. variegatum* could be carried from the Caribbean Islands to the continental United States by cattle egrets. This concern is reasonable, given that in a parallel situation in the Mediterranean, cattle egrets are speculated to have imported a juvenile *A. variegatum* to the island of Corsica from sub-Saharan Africa (Cicculli et al. 2019).

Host population changes driven by changes in land use and landscape can be expected to alter geographic patterns of disease risk. Conversion of natural and agricultural land into suburban housing divisions will continue to create habitat conducive for TTBDs. Trends toward cultivating more natural landscapes that attract wildlife (e.g., through planting native pollinator gardens or encouraging wildland vegetation between golf course fairways) may further increase peridomestic and recreational TTBD risk. Socioeconomic changes in rural areas also may affect TTBDs in unintended ways. For example, Campa et al. (2011) describe a national trend toward land 'parcelization' for low-density rural housing, whereby large tracts of land with single ownership are subdivided into multiple parcels of land with multiple owners. Parcelization tends to increase the edge habitats preferred by deer and other early successional wildlife species important to several TTBDs. Furthermore, parcelization poses challenges for effective deer management, as the original rural owners are replaced by owners from suburban or urban areas who typically have less enthusiasm for management of deer by harvesting. Parcelization thus tends to draw more humans into areas of improved habitat for more lightly hunted deer populations, with foreseeable consequences for rising TTBD risk.

Wildlife as a management lever for TTBDs

There is growing recognition that ITM approaches are needed to address the problem of rising TTBDs. Given the central role of wildlife in the maintenance and dispersal of ticks and tick-borne pathogens, management of wildlife needs to be recognized as one of the key management tools for future ITM. Eisen (2020) proposes that the responsibility for reducing environmental risk of TTBDs should be shared between the public and professionally staffed tick management programs, similar to the programs that exist for mitigating risk from mosquito-borne diseases. Eisen and Stafford (2020) discuss barriers to implementing ITM and further recommend that the responsibility for such programs be broadened to include: 1) the public (both at the individual and community levels); 2) public health agencies and researchers; and 3) industry/commercial partners. To facilitate informed decisions about managing wildlife to reduce TTBD risk, all three groups need to explicitly take into account the biological, environmental, and human dimensions of wildlife management. Thus, as an addition to Eisen and Stafford's (2020) (this issue) 'tick management triad' framework, we emphasize the importance of partnerships with the stakeholders who exert influence on the distribution and abundance of wildlife hosts.

Most obviously, we advocate communications with state and federal natural resource agencies, and within them, the wildlife agencies, as these entities are entrusted to manage wildlife for the current and future benefit of the public. These agencies are charged with the responsibility to develop and implement management plans for many game species, including deer, wild turkey, furbearers (e.g., raccoons, opossums, fox, coyotes, bear), and invasive species such as feral swine. They track trends in population abundance and spatial distribution of these species, which is key information needed to anticipate future trends in TTBDs. State wildlife agencies have staff who are determining what actions can be taken to mitigate climate change effects on wildlife diversity, abundance, and health. These agencies should be encouraged to collaborate with their public health counterparts to assess jointly the implications of predicted changes in wildlife and their habitat for future TTBD risk.

Managing wildlife often translates into managing their habitat, so in addition to collaboration with wildlife agencies, ITM teams need to communicate with forestry agencies and other nongovernmental entities whose mission is to acquire and manage land to conserve or increase biodiversity (e.g., The Nature Conservancy). Similarly, there needs to be proactive communication with municipal planners as they make decisions regarding land development as well as designing green spaces and recreational areas that are likely to attract wildlife. Models predicting future wildlife communities and landscapes based on future climate and socioeconomic scenarios may aid further planning (e.g., Pearman-Gillman et al. 2020).

Finally, effective wildlife management requires understanding the public's diverse views and values about wildlife and wildlife impacts—including the perceived role of wildlife in fostering TTBDs—and thereafter incorporating those views into the agencies' objectives for management. Wildlife agencies already have experience incorporating human dimensions into the management of wildlife diseases such as bovine tuberculosis and chronic wasting disease. Public health agencies should capitalize on that expertise, especially when considering management of deer (McShea 2012). To borrow from the field of wildlife disease management, "a wildlife disease management model includes risk perception, impact tolerance, and social acceptability of management actions that contribute to perceived impacts of wildlife disease and management responses" (Decker et al. 2006). For example, when developing an ITM program to reduce the risk of TTBDs, the public needs to recognize that planting native shrubs and plants in backyards can attract wildlife hosts of ticks as can preservation or restoration of natural wildlife habitat around recreation areas. Similarly, when we pay farmers to set aside land to maintain wildlife habitat,

or when we conduct controlled burns to maintain early successional habitats, we are valuing wildlife, but we also need to recognize the potential negative impact of increased risk of TTBDs. Communities need to decide what level of TTBD risk is tolerable and to determine what kinds of wildlife management actions to reduce disease risk would be effective, affordable, and socially acceptable. Stakeholder engagement is critical for successful wildlife host management and is well aligned with the tick management triad Eisen and Stafford (2020), whereby the public is a key part of the solution for combating the rise of TTBDs.

Acknowledgments

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