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Ticks Tick Borne Dis. Author manuscript; available in PMC 2026 April 01.

Published in final edited form as:

Ticks Tick Borne Dis. 2026 May ; 17(3): 102622. doi:10.1016/j.ttbdis.2026.102622.

Why are the ticks winning, and what can we do about it?

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Abstract

Human illness associated with tick bites is on the rise in the United States. One root cause is that several human-biting tick species serving as pathogen vectors, including the blacklegged tick and the lone star tick, have expanded their geographic ranges in recent decades, with many areas in the U.S. now harboring multiple species of vector ticks. As currently used, personal tick bite prevention and environmental tick control have not succeeded in stemming the rising tide of humans being bitten by ticks. A national strategy to prevent and control vector-borne diseases provides a blueprint to solve the problem, but this will require sustained investments in tick bite prevention and tick control. Efforts are needed to: (i) stimulate industry engagement in development of novel technologies and products; (ii) intensify research to clarify the benefit of using different tick bite prevention and tick control methods, and clarify barriers to their adoption and use; (iii) establish publicly-funded local organizational structures to support individuals and communities in their efforts to prevent tick bites; and (iv) strengthen the workforce in public health, academia, and industry with expertise in ticks and tick-borne diseases. Solving the problem with ticks in the U.S. will be challenging but is worth pursuing because the alternative is for the public to accept that illness associated with tick bites now is simply a fact of life and that the problem is likely to get worse over time. This perspective paper includes “take home messages” and a conclusions section for an abbreviated read.

Keywords

Ticks; Bite prevention; Control; United States

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CRediT authorship contribution statement

Lars Eisen: Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

Given my role as Section Editor, I had no involvement in the peer-review of this article and had no access to information regarding its peer-review. Full responsibility for the editorial process for this article was delegated to another journal editor.

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1. The ticks are winning

There is a clear winner in the ongoing contest between humans and ticks. And it is not us. In recent decades, there have been dramatic range expansions in the United States (U.S.) for three tick species that commonly bite humans and serve as vectors of human pathogens: *Amblyomma americanum* (lone star tick), *Amblyomma maculatum* (Gulf Coast tick), and *Ixodes scapularis* (blacklegged tick or deer tick) (Paddock and Yabsley, 2007; Paddock and Goddard, 2015; Eisen et al., 2016; Sonenshine, 2018; Molaei et al., 2021; Rochlin et al., 2022; Wikel, 2022; Eisen and Eisen, 2023). Five other notable human-biting vector tick species, with wide geographic distributions in the U.S. documented already in the 1940s (Bishopp and Trembley, 1945), have either shown moderate expansion of their ranges or still occupy the same ranges as in the 1940s; these include *Dermacentor andersoni* (Rocky Mountain wood tick), *Dermacentor occidentalis* (Pacific Coast tick), *Dermacentor variabilis* (American dog tick), *Ixodes pacificus* (western blacklegged tick), and *Rhipicephalus sanguineus* sensu lato (brown dog tick) (James et al., 2006, 2015; Sonenshine, 2018; Wikel, 2022; Grant et al., 2023; Eisen et al., 2024). Every state in the contiguous U.S. now harbors at least two of these eight species of ixodid (hard) human-biting vector ticks, and most states have as many as five species present (Table 1; Fig. 1). Having multiple species of human-biting ticks present within the same area can lead to a longer period of the year with risk for human tick bites as well as a wider range of habitats where ticks can be encountered (Table 2). Crafting of informative messages to the public about their risk for tick bites therefore requires local knowledge of which tick species are present, which of their life stages bite humans, and in which habitats and during what parts of the year these ticks are questing for hosts.

Each of the eight mentioned species are three-host ticks. They take single blood meals from different host individuals in each of the larval, nymphal, and adult stages, and they leave the host at the completion of the blood meal to molt to the next life stage (larvae and nymphs) or lay eggs (females). Based on total numbers for different tick species recorded to infest humans in the U.S. (Eisen, 2022a), the top three human-biters are ticks with wide geographic distributions in the eastern part of the country: *I. scapularis, Am. americanum*, and *D. variabilis* (Fig. 1). In the western part of the U.S., the two species most commonly recorded to infest humans are *D. andersoni* in the Intermountain West (the area extending westward from the Rocky Mountains to the Cascades and Sierra Nevada mountain ranges) and *I. pacificus* along the Pacific Coast (Fig. 1; Eisen, 2022a). Both nymphs and adults are commonly recorded to infest humans for *I. scapularis* in the northern part of the eastern U.S. and for *Am. americanum* and *Rh. sanguineus* s.l. (Table 2; Eisen, 2022a, 2025). The adult stage dominates for other species, with contributions to human infestations by adults reaching 80 to 85 % for *D. occidentalis* and *I. pacificus*, 90 to 95 % for *I. scapularis* in the southern part of the eastern U.S. and for *Am. maculatum*, and more than 99 % for *D. andersoni* and *D. variabilis* (Table 2; Eisen, 2022a, 2025). Human infestation by larval ticks also occurs for some species, especially *Am. americanum* and *I. scapularis*, but is recorded much less frequently than for nymphs and adults (Eisen, 2022a). The combination of expanding geographic ranges of human-biting tick species and increasing

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human encroachment on tick habitats for housing and recreation sets the stage for increasing numbers of people encountering and being bitten by ticks in the coming decades.

Human-biting ixodid tick species collectively serve as vectors to humans of a wide range of disease agents, including viruses causing Bourbon virus disease, Colorado tick fever, Heartland virus disease, and Powassan virus disease; bacteria causing anaplasmosis (*Anaplasma phagocytophilum*), ehrlichiosis (*Ehrlichia chaffeensis, Ehrlichia ewingii*, and *Ehrlichia muris euclairensis*), hard tick relapsing fever (*Borrelia miyamotoi*), Lyme disease, also known as Lyme borreliosis (*Borrelia burgdorferi* sensu stricto and *Borrelia mayonii*), spotted fever rickettsioses (*Rickettsia parkeri* and *Rickettsia rickettsii*), and tularemia (*Francisella tularensis*); and parasites causing babesiosis (*Babesia duncani* and *Babesia microti*) (Table 3; Eisen and Paddock, 2021; Wikel, 2022). Some of these pathogens can be transmitted by multiple human-biting tick species, and a single tick species can serve as a vector for multiple human pathogens (see Table 3). For example, in the U.S., the causative agent of Rocky Mountain spotted fever (*Ri. rickettsii*) is transmitted by at least three different tick species: *D. andersoni, D. variabilis*, and *Rh. sanguineus* s.l. (Macaluso and Paddock, 2014). Conversely, *I. scapularis* is a vector of seven human pathogens including a virus (Powassan virus), five bacterial agents (*An. phagocytophilum, Bo. burgdorferi* s.s., *Bo. mayonii, Bo. miyamotoi*, and *E. muris eauclairensis*), and a parasite (*Ba. microti*) (Eisen and Eisen, 2018). Individual nymphal or adult *I. scapularis* can be co-infected with two or more of these disease agents (Lehane et al., 2021). Transmission occurs via bites by nymphs and adults for all tick-borne pathogens mentioned above, whereas larval bites only present risk for transmission of pathogens that can be passed transovarially from an infected female to her offspring: these include Bourbon virus, Heartland virus, Powassan virus, *Bo. miyamotoi, Ri. parkeri*, and *Ri. rickettsii* (Table 3; Burgdorfer, 1963; Ebel, 2010; Rollend et al., 2013; Macaluso and Paddock, 2014; Wright et al., 2015; Godsey et al., 2016, 2021).

The incidence of tick-borne diseases has increased in recent decades (CDC, 2025a). From 2004 to 2016, the number of reported cases doubled or increased even more for anaplasmosis/ehrlichiosis, babesiosis, Lyme disease, Powassan virus disease, and spotted fever rickettsioses (Rosenberg et al., 2018). Tick-borne disease cases are reported across the U.S. but concentrated in the Upper Midwest and Northeast regions, together with parts of the South, Southeast, and Ohio Valley regions (Fig. 2). This geographic pattern is driven by human population density in conjunction with abundant populations of the pre-eminent vectors of tick-borne disease agents: northern populations of *I. scapularis* in the Upper Midwest and Northeast, and *Am. americanum* in the South, Southeast, and Ohio Valley regions (Springer et al., 2014, 2015; Foster et al., 2024; Holcomb et al., 2025). Additional health conditions associated with human tick bites include tick paralysis (caused by toxins in tick saliva and primarily associated with bites by *D. andersoni* and *D. variabilis*) and the recently described alpha-gal syndrome or red meat allergy (an allergic condition that can occur when food products made from mammals and containing the galactose-α-1,3-galactose carbohydrate are consumed after a person is bitten by ticks, primarily in association with bites by *Am. americanum*) (Edlow and McGillicuddy, 2008; Mitchell et al., 2020; Eisen, 2022a; Kersh et al., 2023; CDC, 2025b).

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In addition to the previously mentioned long established human-biting ticks, invasive species are of concern. *Haemaphysalis longicornis* (Asian longhorned tick), which originated in eastern Asia and later spread to Australia, New Zealand, and islands in the western Pacific (Hoogstraal et al., 1968), is a case in point. This tick was found to infest a sheep in New Jersey in the summer of 2017 (Rainey et al., 2018) and a mere eight years later, by 2025, it had been documented as far south as South Carolina and Georgia, as far north as Massachusetts, and as far west as Oklahoma and Iowa (Table 1; USDA, 2025). Retrospective studies of earlier *Haemaphysalis* collections revealed that specimens of *H. longicornis* had been recovered in West Virginia in 2010; in New Jersey, New York, and Pennsylvania from 2013 to 2015; and in Kentucky, New Jersey, New York, Pennsylvania, Virginia, and West Virginia in the spring of 2017 (USDA, 2025). Modeling exercises suggest that suitable environment for *H. longicornis* occurs in most parts of the contiguous U.S. (Raghavan et al., 2019; Rochlin, 2019; Namgyal et al., 2020). In the coming years, this tick may therefore expand its range westward into the Great Plains, the Intermountain West, and the Pacific Coast states. *Haemaphysalis longicornis* poses a major threat to cattle due to heavy infestations and transmission of parasites causing bovine theileriosis (Dinkel et al., 2021). The tick also bites humans (Eisen, 2022a). It is an experimental vector of human disease agents, including Heartland virus, Powassan virus, and *Ri. rickettsii* (Stanley et al., 2020; Raney et al., 2022a, b), but evidence for natural infection of *H. longicornis* with these pathogens is rare (Soliman et al., 2025).

Take home message: In the U.S., geographic ranges of human-biting tick species are expanding and the incidence of human illness associated with tick bites is increasing. Section 2 outlines the root causes for why the ticks are winning, and Section 3 explores what can be done to counter the rising tide of ticks and illness associated with tick bites.

2. Why are the ticks winning?

In stark contrast to mosquitoes, ixodid tick species that commonly bite humans in the U.S. have very limited capacity for locomotion while questing for a host (5 to 20 m depending on species) and long generation times (1 to 3 years). Despite these limitations in their potential for host acquisition and population growth, the ticks have proven difficult to control even at the fine spatial scale of residential properties, and they are most likely impossible to eradicate at large geographic scales. To compound the problem, there are substantial challenges with adoption and use of personal protection measures to prevent tick bites.

2.1. Extensive geographic distributions

Most of the ixodid tick species mentioned in Section 1 have wide climate tolerances, allowing for establishment across large geographic areas in the U.S. (Table 1; Fig. 1; CDC, 2025c). *Dermacentor variabilis* and *I. scapularis* have the most extensive distributions in the eastern U.S. Both species occur from Florida in the south to Maine in the north along the Eastern Seaboard and extend as far west as Texas in the south to North Dakota in the north (Fig. 1; James et al., 2015; Eisen et al., 2016; Eisen and Eisen, 2023). At the western edges of their distributions, *D. variabilis* extends further into the Great Plains than the

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strongly forest-associated *I. scapularis* which is limited to especially humid riparian areas in the open plains (Maestas et al., 2018; Nielsen et al., 2020). Established populations of *D. variabilis* were recently discovered to also occur along the Front Range of the Rocky Mountains in Colorado, at the far western edge of the Great Plains (Fig. 1; Freeman and Salkeld, 2022). *Amblyomma americanum* also has a wide distribution in the eastern U.S. but does not extend as far north in the Upper Midwest and Northeast regions as *D. variabilis* and *I. scapularis* (Fig. 1; Springer et al., 2014; Rochlin et al., 2022; Wojahn et al., 2026). *Amblyomma maculatum* has a narrower distribution in the eastern U.S., largely restricted to the South and Southeast regions but extending along the Atlantic Seaboard as far north as Connecticut (Fig. 1; Paddock and Goddard, 2015; Molaei et al., 2021). Both *Amblyomma* species appear to be in the process of extending their geographic distributions northward in the U.S. (Sonenshine, 2018; Molaei et al., 2021; Rochlin et al., 2022; Wikel, 2022).

Dermacentor andersoni has a wide distribution in the Intermountain West, from the Canadian border to the northern parts of New Mexico and Arizona (Fig. 1; James et al., 2006). In the far west, *I. pacificus* occurs in the Pacific Coast states from southern California to northern Washington, with additional outlier populations in Arizona and Utah (Fig. 1; Furman and Loomis, 1984; Eisen et al., 2016, 2024). Two other species – *Dermacentor similis* (previously considered a far western outlier population of *D. variabilis*) and *D. occidentalis* – also occur in the Pacific Coast states from California to Washington, with additional outlier populations of *D. similis* in Idaho (Table 1; Furman and Loomis, 1984; Lado et al., 2021; Paddock et al., 2024). Also worth noting here is the one-host tick *Dermacentor albipictus* (winter tick or moose tick), which has a wide distribution in the U.S. (Koser et al., 2025) and has been implicated as a vector of *Ba. duncani* in the Pacific Coast states (Table 3; Swei et al., 2019). This tick preferentially parasitizes moose and deer, and human tick exposures primarily involve encounters with clumps of questing larval ticks or infestation of hunters by adult ticks resulting from handling of dead animals (Eisen, 2022a).

The primarily dog-associated *Rh. sanguineus* s.l. is a special case as it occurs across the contiguous U.S. as well as in Alaska and Hawaii (Table 1; CDC, 2025c) but is found in domestic and peridomestic settings rather than across the landscape (Dantas-Torres, 2010; Gray et al., 2013). The geographic distribution of the invasive *H. longicornis* currently encompasses states in the South, Southeast, Ohio Valley, and Northeast regions (Table 1; USDA, 2025) but, as noted in Section 1, this tick is expected to continue expanding its range westward.

Take home message: Extensive geographic tick distributions result in many areas having several species of human-biting vector ticks present. Every state in the contiguous U.S. now harbors at least two notable human-biting ixodid vector tick species, and most states have five or more species present. The geographic ranges of the most prominent human-biting vector tick species are either expanding or holding steady in the U.S., and there is no reason to believe this will change in the near future, either from natural causes or human agency.

2.2. Broad host ranges

Nearly all of the tick species addressed in this paper are generalists that infest a wide variety of wildlife hosts (Table 4). The immature larval and nymphal stages infest vertebrates

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ranging in size from shrews, rodents, lizards, and birds to lagomorphs, carnivores (various wildlife species within Order Carnivora), and cervids. Shrews are not always commonly recovered in trapping efforts targeting rodents, and their contribution as hosts for immature ticks is likely underestimated. Adult female ticks feed on larger sized hosts, including large rodents (e.g., marmots, woodchucks, woodrats, and porcupines), large birds (e.g., turkeys), lagomorphs, carnivores, and cervids. The exception to this pattern of broad host ranges for medically important ixodid three-host ticks is *Rh. sanguineus* s.l., which primarily parasitizes dogs (Table 4).

Table 4 provides an overview of wildlife serving as primary and secondary hosts for immature and adult life stages across tick species (see also the table for references). It should be noted, however, that existing data on host infestation by ticks come primarily from compilations of individual studies with strong biases in the selection of targeted host animals, rather than studies aiming specifically to determine the relative contribution of a wide range of host species (shrews, rodents, lizards, birds, lagomorphs, carnivores and cervids) to tick feeding. With this limitation in mind, *Am. americanum* primarily infests birds and cervids in the immature stages and cervids as adults, whereas immatures of *Am. maculatum* primarily utilize birds and rodents, and the adults feed extensively on both carnivores and cervids. All four mentioned three-host *Dermacentor* species (*D. andersoni, D. occidentalis, D. similis*, and *D. variabilis*) utilize rodents as the primary hosts for the immature stages, whereas adult ticks predominantly feed on cervids for *D. occidentalis*, carnivores for *D. variabilis*, and a variety of hosts for *D. andersoni*. Both *Ixodes* species (*I. pacificus* and *I. scapularis*) primarily infest cervids as adults, whereas the immature stages feed primarily on lizards and rodents for *I. scapularis* in the southern part of the eastern U.S. and for *I. pacificus*, and primarily on rodents and shrews for *I. scapularis* in the northern part of the eastern U.S. Secondary hosts for immatures of *I. pacificus* and *I. scapularis* include deer and birds. Wild pigs have been documented to serve as secondary hosts for adults of some species, including *Am. americanum, Am. maculatum, D. variabilis*, and *I. scapularis*. Data on wildlife host associations of the invasive *H. longicornis* are still accumulating but this tick appears to feed commonly on carnivores and cervids, and has also been recorded from birds, rodents, and lagomorphs as immatures (Tufts et al., 2019, 2021; White et al., 2020; Pandey et al., 2022; Thompson et al., 2021, 2022; Butler et al., 2024; USDA, 2025).

Despite the differences in host preference across the human-biting generalist tick species, they are all able to feed on a wide range of hosts (Table 4) and therefore can persist in environments with variable host communities. The broad range of host options also makes these ticks challenging to eliminate by means of host-targeted control methods, such as host reduction or exclusion or use of topical or oral acaricides that are self-applied by the tick hosts (see also Section 2.6.2). Host-targeted approaches are especially challenging when targeting the immature tick stages, which have the broadest host ranges. The greatest potential for strong impact on tick populations with a host-targeted approach most likely lies in targeting key reproductive host species that provide blood meals to the majority of female ticks (see also Section 2.6.2). None of the generalist tick species addressed in this paper are exclusively reliant on a single reproductive host species, however, and it is very challenging to simultaneously target multiple species of medium-sized and large mammals (e.g., both raccoons and deer) with potential to serve as reproductive hosts.

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Take home message: Most human-biting ixodid vector tick species are generalists that infest a wide variety of wildlife hosts. Due to their broad host ranges, these ticks are resilient to changes in host community composition resulting from natural causes or human agency. On-host targeting of the immature stages is challenging due to larval and nymphal ticks being able to feed on a wide range of wildlife host animals. Tick population suppression based on host-targeted control is more likely to succeed when focusing on the narrower range of hosts that the adult female tick must rely on for her bloodmeal.

2.3. Spread via wildlife hosts

Ixodid ticks have limited ability for locomotion, with lateral movement while questing for a host ranging from a few meters in *Ixodes* ticks with a "sit-and-wait" host finding strategy (Gray, 1985; Falco, 1987; Daniels and Fish, 1990; Stafford, 1992; Goddard, 1993; Curtis et al., 2020) to <5 to 20 m, depending on life stage, in *Amblyomma* ticks that use a "hunting" strategy to find a host (Wilson et al., 1972; Koch and McNew, 1982; Kensinger and Allan, 2011; Marshall et al., 2025). Spread of ticks across the landscape is therefore primarily a result of host movement. Ixodid ticks remain attached to their hosts for several days to complete their bloodmeal; for example, attachment durations for *Ixodes* ticks range from 2 to 4 days for larvae to 3 to 5 days for nymphs and 7 to 10 days for adult females (Balashov, 1972; Kahl and Gray, 2023; Kahl et al., 2023). The distances over which feeding ticks are transported depend on the home range sizes and movement patterns of their hosts together with drop-off rhythms of fully fed ticks, which in some cases are synchronized to coincide with host resting periods (Matuschka et al., 1990; Vredevoe et al., 1997).

Transport of feeding ticks via hosts will occur only over short distances for animals with small home ranges, such as rodents and lizards, but can occur over longer distances for mammals with larger home ranges, such as carnivores and cervids. Tick transport via birds can range from short distances to very long distances during periods of migration. Generalist tick species that infest birds as immatures include *Am. americanum* (Durden et al., 2001; Loss et al., 2016; Roselli et al., 2022), *Am. maculatum* (Durden et al., 2001; Loss et al., 2016; Roselli et al., 2022), *H. longicornis* (Pandey et al., 2022; USDA, 2025), *I. pacificus* (Wright et al., 2000; Eisen et al., 2004; Castro and Wright, 2007; Dingler et al., 2014), and *I. scapularis* (Anderson and Magnarelli, 1984; Weisbrod and Johnson, 1989; Battaly and Fish, 1993; Stafford et al., 1995; Rand et al., 1998; Hyland et al., 2000; Durden et al., 2001; Loss et al., 2016).

Studies from both Europe and North America indicate that migrating birds collectively transport large numbers of ticks during their spring and fall migrations (Olsén et al., 1995; Smith et al., 1996; Scott et al., 2001; Ogden et al., 2008). The local seasonal activity pattern of a given tick species and life stage will determine the likelihood of the ticks being transported long distances during bird migration periods. In the case of *Am. americanum*, for example, birds migrating northward in the spring will primarily carry nymphs whereas birds migrating southward in the fall will be infested mostly by larvae. The scenario is more complex for *I. scapularis* because seasonal activity patterns for larvae and nymphs differ across its geographical range (Eisen, 2025): spring migrating birds can acquire both larvae

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and nymphs in the southern part of the eastern U.S. and the Upper Midwest but primarily nymphs in the Northeast; fall migrating birds are most likely to be infested by larvae.

Tick species that feed on a wide range of animals with different sized home ranges and variable movement patterns can effectively spread to and establish in new areas. Spread can occur via diffusion dispersal outward from the edges of an area where a tick species is established. One such example is transport of *I. scapularis* adults via deer some distance beyond the edge of an area where the tick already was established. Detached fed females will then give rise to large numbers of *I. scapularis* larvae, which readily feed on ubiquitous animals such as rodents. Knowing this, it is not difficult to envision how the gradual spread of deer from tick-infested areas in the Upper Midwest and Northeast in the latter part of the 1900s resulted in diffusion dispersal of *I. scapularis* across the landscape (Eisen and Eisen, 2023; see also Section 2.6.2.2).

Spread of ticks can also occur via long-distance jump dispersal, primarily via migrating birds. Ticks transported in this manner are sometimes referred to as adventitious ticks, and they are occasionally detected via passive surveillance from humans and pets in areas without known established tick populations (Ogden et al., 2006, 2008; Nelder et al., 2019). Jump dispersal has the potential to lead to local establishment of a tick species, assuming suitable climate, photoperiod, and habitat conditions, and presence of hosts for all life stages. However, it remains unclear how often all these conditions favor tick population establishment following a jump dispersal event (Gray et al., 2021). Moreover, if immatures are introduced via jump dispersal this ultimately requires a female and male to find each other, off or on host, and mate for potential local establishment to occur. The invasive *H. longicornis* is an exception to this rule as North American populations of this tick can reproduce parthenogenetically (Egizi et al., 2020), which means that a single larval tick transported by a bird to a location where this tick species was not present could give rise to a local population if climate, photoperiod, and habitat conditions are suitable and hosts are present for both immatures and adults.

Take home message: Human-biting vector tick species with broad host preferences are effective in spreading to new areas because they are transported over variable distances by a wide range of wildlife hosts. Once established, some of the most prominent human-biting tick species become ubiquitous in suitable habitats (throw a rock in the Northeast woods and you stand a good chance of hitting a blacklegged tick). Moreover, should these ticks be eliminated from an area, they are highly likely to reinvade if the control effort leading to their elimination is not sustained.

2.4. Risk for tick bites in multiple habitat types during extensive parts of the year

The habitat types and times of the year presenting risk for human tick bites in a given area depend on the tick species present, which of their life stages bite humans, and local climate conditions influencing when ticks can be active. Table 2 provides a general overview of habitat associations and seasonal activity patterns of the primary human-biting life stages of medically important tick species in the U.S. Additionally, the University of Rhode Island TickEncounter website (URI, 2025a) provides an excellent interactive online resource with graphical depictions of seasonal activity patterns of the life stages of medically important

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ticks in different regions of the U.S., together with information about the habitat preferences of the ticks (URI, 2025b).

In general, tick questing activity is limited by periods of the year that are too cold for ticks to seek hosts and influenced by periods where hot and dry conditions lead to increased mortality of questing ticks (Kahl and Gray, 2023). For example, the human-biting adult stage of *I. pacificus* in California and *I. scapularis* in the southeastern U.S. can be actively questing throughout the mild winters typical of these areas, whereas low temperatures and snow can prevent questing activity by *I. scapularis* adults in the winter months in the northern part of the eastern U.S. (L. Eisen, 2025). However, even in colder areas ticks may become active during warm spells in the winter when the ground is not covered by snow. Such winter activity has been observed for *I. scapularis* adults in Maryland in the U.S. (Carroll and Kramer, 2003) and the closely related *Ixodes ricinus* (castor bean tick) in Germany (Dautel et al., 2008) and Sweden (Kjellander et al., 2023). Both warm spells in the winter and warmer temperatures in early spring, resulting in earlier activation of overwintering ticks, can lead to an increase in the length of the season presenting risk for human tick bites in the northern part of the U.S.

It is instructive to consider examples from different geographic areas in the U.S. of habitat-associated and seasonal tick bite risk patterns that range from better-case to worse-case scenarios. Colorado represents a better-case scenario for seasonal tick bite risk where until recently only adults of *D. andersoni* commonly infested humans, with peak activity of these ticks in the spring (Table 2; Eisen, 2007, 2022a; URI, 2025b). Recent spread of *D. variabilis* to the Front Range area in central Colorado (Freeman and Salkeld, 2022) added another human-biting tick to this part of the state but did not lead to a major change in the time of the year with human risk for tick bites because the human-biting adults of this species are active predominantly from spring to early summer (Table 2; URI, 2025b). However, the addition of *D. variabilis* did increase the geographical area with risk for tick exposure in the Front Range. *Dermacentor andersoni* occurs primarily at elevations above where the main population centers along the Front Range are located (Eisen et al., 2007), and this tick therefore poses a risk mostly during recreational activities in the foothills and mountains. Urban areas at the base of the foothills were essentially free of human-biting ticks until the recent emergence of *D. variabilis*, which is now widespread and abundant in natural areas in the main human population centers along the Front Range (L. Eisen, personal observation).

Florida in the Southeast is an example of a worse-case scenario. Although the adults of *I. scapularis* is the only stage of this species commonly infesting humans in that part of the U.S., the state also harbors *Am. americanum, Am. maculatum*, and *D. variabilis* (Tables 1–2). Elevated activity of the human-biting stages of these ticks occurs in spring and summer for *Am. americanum, Am. maculatum*, and *D. variabilis*, and from fall through winter to spring for *I. scapularis* (Table 2; Eisen, 2025; URI, 2025b). People are therefore at risk for tick bites throughout the year in forested habitats (*Am. americanum* and *I. scapularis*) and in spring and summer in more open grassy and brushy habitats (*Am. maculatum* and *D. variabilis*).

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New Jersey represents another worse-case scenario, with established populations of *Am. americanum, D. variabilis, H. longicornis*, and *I. scapularis* (Table 1; Occi et al., 2019), and ongoing incursion by *Am. maculatum* (Musnoff et al., 2024). In this area, both nymphs and adults of *I. scapularis* commonly bite humans (Table 2; Jordan and Egizi, 2019; Eisen, 2022a). Across the tick species present in New Jersey, human-biting life stages show elevated activity from March to November (Jordan and Egizi, 2019; Bickerton et al., 2022; URI, 2025b), thus spanning the entire period from spring through fall. Moreover, the multiple tick species present in New Jersey collectively present risk for tick exposure both in forested habitats (spring through fall) and more open grassy and brushy habitats (spring and summer) (Table 2).

Northern populations of *I. scapularis* merit additional mention here because, in contrast to southern populations, all three active life stages climb vegetation while questing for hosts (Arsnoe et al., 2015, 2019). This questing behavior facilitates contact with humans and leads to bites by all three life stages, albeit human bites by larvae are much less frequently reported than for nymphs and adults (Eisen, 2022a). Moreover, pathogen infection prevalence for questing nymphs and adults of *I. scapularis* is generally higher for northern compared to southern population ticks (Ginsberg et al., 2021; Lehane et al., 2021). The highest level of activity for northern population *I. scapularis* occurs from April to May and October to November for adults, May to July for nymphs, and July to September for larvae (Jordan and Egizi, 2019; Eisen, 2025; URI, 2025b). Spread of *I. scapularis* in recent decades to areas in the northern part of the eastern U.S. where *D. variabilis* previously was the dominant human-biting tick (with peak risk for exposure to the adult human-biting stage of *D. variabilis* limited to spring and early summer in open areas) therefore substantially extended the period of the year presenting risk for human tick bites in those areas, as well as adding forested areas to the environments with risk for tick exposure. It also should be noted that human bites by *I. scapularis* can occur commonly in the peridomestic environment for residential properties that include a wooded portion or border on a forested area where ticks are present (Falco and Fish, 1988a; Stafford, 2007; Stafford et al., 2017; Hahn et al., 2018; Mead et al., 2018; Fischhoff et al., 2019a; Jordan and Egizi, 2019; Salkeld et al., 2019; Keesing et al., 2022; Dill et al., 2025). Based on the considerations outlined above, it is concerning that northern populations of *I. scapularis* appear to be spreading from the Northeast into West Virginia, Virginia, and North Carolina where previously only southern populations of this species occurred (see review by Eisen and Eisen, 2023).

Take home message: Humans are at risk for encountering ticks throughout the year or from spring through fall in large parts of the U.S. (Tables 1–2). The risk of encountering pathogen-infected ticks is greatest in the Upper Midwest and Northeast regions, together with portions of the South, Southeast, and Ohio Valley regions (Fig. 2). Many areas harbor multiple human-biting vector tick species with different habitat associations, leading to risk for tick exposure in both forested and more open grassy and brushy areas. People also need to be aware that they can encounter ticks in a variety of settings including residential properties, greenspaces in a neighborhood, and public lands ranging from small local parks to national forests.

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2.5. Difficulty in keeping up with personal protection measures against tick bites

Depending on where people live, work, and recreate, spending time in tick habitat may happen only occasionally, such as while hiking on public land, or may be an everyday occurrence when going into the backyard or walking the dog in the neighborhood. In addition to avoiding tick habitat when possible, personal protection measures to reduce the risk of tick bites include: (i) wearing untreated protective clothing such as long pants tucked into socks and a long-sleeved shirt tucked into pants (to increase the chance of spotting a tick while it is still crawling on clothing in search of skin); (ii) wearing permethrin-treated clothing (to make ticks fall off the clothing due to the irritant effect of permethrin); (iii) using tick repellents labeled for application to skin and clothing (to either make ticks fall off the host if they make initial contact with treated skin or clothing, or to prevent ticks making first contact with untreated portions of skin or clothing from walking onto treated skin, which increases the likelihood of the ticks falling off or being detected before finding a bite site); (iv) conducting cursory tick checks while outdoors (to increase the chance of spotting a tick while it is still crawling on clothing or skin in search of a bite site); and (v) doing a more thorough tick check after coming inside, which can include removing outdoor clothing articles and running them in a dryer on high heat (to kill undetected ticks still on the clothing) and taking a shower/bath (to aid in detecting ticks that are crawling on the skin or in the process of attaching) (Table 5; Fig. 3). It also is important to promptly remove attached ticks when they are discovered because the likelihood of pathogen transmission increases with the duration a tick is attached for most pathogens (Eisen, 2018). Key characteristics of currently available and potential future personal protection measures to prevent tick bites or tick-borne infections are summarized in Table 5.

Personal tick bite prevention measures are not consistently/routinely used by most people even in areas with high incidence of tick-borne diseases (Hook et al., 2015; Butler et al., 2016; Niesobecki et al., 2019; Nawrocki and Hinckley, 2021; Kopsco and Mather, 2022; Cuadera et al., 2023; Ernst et al., 2024; Zembsch et al., 2025). A review of the published literature by Eisen (2022b) showed that the most frequently used personal protection measures were wearing untreated protective clothing or conducting tick checks (done routinely by 30 to 70 % of respondents in most studies of the public), followed by using repellents on skin/clothing or showering/bathing after being outdoors (15 to 40 % range), and wearing permethrin-treated clothing (<5 to 20 % range). Frequently cited reasons for not using tick bite prevention measures such as tick checks or repellents include forgetting to do it or that it is too much trouble or effort (Bowser et al., 2025; Hansen et al., 2025). Being diligent about using personal protection measures to prevent tick bites becomes more challenging with increased frequency of having to carry them out, to the point of requiring what may amount to unrealistic effort if ticks are present in your backyard and throughout your neighborhood during many months of the year. In this context, Bowser et al. (2025) further noted that: “To avoid alienating individuals whose residence or occupation puts them at very high risk for tick exposure, it is worthwhile acknowledging that consistent tick bite prevention is not as straightforward as is often implied through communication campaigns.”.

As noted in recent reviews by Eisen (2022b) and Schwartz et al. (2022), the evidence base for the above-mentioned personal protection measures to reduce human tick bites and tick-

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borne disease is weak and studies conducted to date have not been sufficiently detailed to clarify the circumstances under which protection is most likely to be achieved, for example with regards to which parts of the body typically are protected with clothing or repellents. Eisen (2022b) also noted that analyses of the impact of personal protection measures on tick bites or tick-borne disease cases should be based on information from each study participant on the full range of personal protection measures used, to avoid the pitfall for assessments of single measures that individuals not taking a given protective action (such as wearing long pants tucked into socks and a long-sleeved top tucked into pants) chose to do so because they took another action with the same purpose (in this case, applying repellent to exposed skin on the arms and legs).

With regards to tick checks while outdoors, a recent study by Zembsch et al. (2025) found that *I. scapularis* ticks positioned on a mannequin were three times more likely to be detected on white-colored clothing compared to dark-colored clothing; ticks above the waistline were three times more likely to be detected than those below the waistline; and adult females were three to four times more likely to be detected compared to nymphs. There are general recommendations for how to conduct a thorough tick check when coming indoors (CDC, 2025d) but very little knowledge of how people actually conduct tick checks while outdoors or when coming inside, or how effective they are in detecting biting ticks (Eisen, 2022b; Bowser et al., 2025). There also is an important issue to consider with variable effectiveness of marketed repellent products against ticks (see review by Eisen, 2024). Tick repellent products registered by the Environmental Protection Agency (EPA) are safe to use and will effectively repel ticks for a label-specified duration of time (EPA, 2025). There are, however, additional unregulated tick repellent products (typically based on botanical oils) on the market; these are referred to as minimum risk products and although they are safe to use consumers should be aware that there may be substantial variability among these products in their ability to repel ticks (Burtis et al., 2024a; Eisen, 2024).

Human vaccines against tick-borne pathogens are also personal protection measures, but against infection rather than tick bites (Fig. 3). Lyme disease is the most commonly reported tick-borne disease in the U.S. with nearly half a million cases estimated to occur each year (Kugeler et al., 2021). A human Lyme disease vaccine is likely the only personal protection measure with potential to dramatically reduce the incidence of this disease in the next 5–10 years. A candidate Lyme disease vaccine is currently undergoing phase III trials (see Plotkin and Shapiro, 2024) and may become available for use in the near future. An effective human Lyme disease vaccine would have great value to public health (Shen et al., 2011; Embers and Narasimhan, 2013; Gomes-Solecki et al., 2020; Plotkin and Shapiro, 2024), but less attention has been given to how a new human Lyme disease vaccine would fit into the overall picture of personal protection measures against tick bites and tick-borne infections once it is commercially available (see Eisen, 2021). Although beneficial in protecting against infection with Lyme disease spirochetes, the vaccine would have no impact on the frequency of human tick bites and would provide no protection against other bacterial, viral, or parasitic disease agents transmitted by species of *Amblyomma, Dermacentor, Haemaphysalis, Ixodes*, or *Rhipicephalus* infesting humans. The latter is obvious but nevertheless worth noting because the *Ixodes* vector species that transmit Lyme disease spirochetes in the U.S. also carry several other less commonly occurring

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agents of human disease, including *An. phagocytophilum* (*I. pacificus* and *I. scapularis*), *Bo. miyamotoi* (*I. pacificus* and *I. scapularis*), *Ba. microti* (*I. scapularis*) and Powassan virus (*I. scapularis*) (Table 3; Eisen and Paddock, 2021). It therefore is important that future public health recommendations for use of a new human Lyme disease vaccine are accompanied by messaging to clarify that use of personal protection measures to prevent tick bites is still needed, together with the vaccine, because the same tick species that transmit Lyme disease spirochetes also transmit other human disease agents.

Take home message: Despite efforts from federal and state public health agencies to promote the use of personal protection measures to prevent tick bites, cases of tick-borne disease and other medical conditions associated with tick bites have increased in recent decades. There are still gaps in the knowledge of how personal protection measures such as tick checks, repellents, and permethrin-treated clothing need to be used (e.g., frequency of use and parts of the body protected or inspected) in order to be most protective against tick bites. This makes it difficult to assess the true potential of these personal protection measures to reduce tick bites, and it also complicates messaging to the public about the value of different personal protection measures to prevent tick bites and how they need to be used in order to be most protective. There is a need for studies to better understand the potential for recommended personal protection measures to prevent tick bites as well as the barriers for their adoption and use.

2.6. Tick control options are falling short

From a public health perspective, the purpose of tick control is to reduce the number of human tick bites in order to reduce the number of cases of tick-borne disease and other medical conditions associated with tick bites. Achieving this goal requires both access to control methods and products capable of reducing the number of questing ticks (reviewed by Ginsberg and Stafford, 2005; Schulze and Jordan, 2006; Stafford, 2007; Eisen and Dolan, 2016; Stafford and Williams, 2017; White and Gaff, 2018; Rochlin et al., 2019; Eisen, 2021, 2023; Eisen and Stafford, 2021; Ost et al., 2025) and effective implementation of these tick control methods and products by stakeholders ranging from homeowners to pest control operators and public health professionals (see Eisen, 2020; Egizi and Jordan, 2020; Roy, 2021; Eisen and Stafford, 2021; Burtis et al., 2024b; Jordan et al., 2024). However, there are also other factors that influence the extent to which reduction in questing ticks translates to reduction in human tick bites (see Ginsberg, 1993; Poland, 2001; Eisen and Eisen, 2016; McClure and Diuk-Wasser, 2018; Hook et al., 2021; Ostfeld and Keesing, 2023, 2026). The only thing that is certain is that no ticks will bite humans in areas where there are no questing ticks present. Beyond that, the relationship between density of questing ticks and incidence of human tick bites remains unclear and a target threshold for tick control to achieve in terms of a density of questing ticks that is likely to translate into reduced numbers of human tick bites is still lacking. Factors expected to influence the incidence of human tick bites in areas where ticks are present include: (i) the density of questing ticks, with variable host finding strategies and levels of mobility across tick species and life stages also influencing their likelihood of making contact with humans; (ii) human activities and behaviors, which can influence the likelihood of coming into contact with questing ticks in an area where they are present (Carroll and Kramer, 2001; Lane et al., 2004); and (iii) use

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of personal protection measures to prevent tick contact from resulting in bites (Section 2.5; Table 5; Fig. 3).

Key characteristics of currently available and potential future methods to control ticks and their associated human pathogens in the environment are summarized in Table 6. As outlined in Sections 2.6.1 to 2.6.3, and discussed further in Sections 2.7 and 2.8, there are several challenges for these tick control tactics to substantially reduce human tick bites and tick bite-associated infections and other medical conditions. Factors that influence the impact of environmental tick control include: (i) limited public acceptability for use of some existing tick control methods or types of products; (ii) inadequate knowledge of how to operationally implement tick control products in order to maximize their effectiveness; (iii) emergence of unregulated acaricide products (based on minimum risk active and inert ingredients and therefore exempt from EPA registration) with highly variable tick killing efficacy; (iv) lack of publicly-funded local tick management programs; (v) inadequate industry engagement in the development of novel tick control methods and products; and (vi) a weak evidence base for environmental tick control to result not only in reduction in the density of questing ticks but also in the incidence of human tick bites and tick-borne disease. Another factor worth mentioning here is the public's willingness to pay for tick control (Gould et al., 2008; Niesobecki et al., 2022; Cuadera et al., 2023; Schiffman et al., 2025), which appears to generally involve lower sums of money than what tick control actually costs (Jordan and Schulze, 2020a; Schulze et al., 2023). However, a recent study by Enriquez et al. (2025) demonstrated that willingness to pay for tick control (in the form of broadcast acaricide spraying) is not static but can be influenced by factors such as control effectiveness (higher cost was acceptable for a more effective tick control product) and type of product (higher cost was acceptable for an organic versus a synthetic broadcast acaricide). Additional studies are encouraged to better understand the nuances of the public's willingness to pay for tick control.

Take home message: Controlling ticks in the environment is a challenging undertaking and the potential for tick control to reduce human tick bites remains poorly understood. Tick management guidance tends to outline the potential options that can be used to suppress ticks in the environment (e.g., Stafford, 2007; CDC, 2025d) but does little to help stakeholders decide which options are best suited for their own particular circumstances (see Fig. 4 for a homeowner stakeholder example). The following sections outline different types of tick control approaches based on targeting of ticks while they are questing or infesting hosts.

2.6.1. Broadcast of acaricides and landscaping/vegetation management:

Interventions targeting ticks off-host, such as hardscaping/xeriscaping, brush and leaf litter removal, or broadcast of acaricides or biological control agents should only be assumed to be effective within the specific areas where they are implemented (Table 6; Fig. 3). In the context of evaluating the impact of this type of tick control intervention on the incidence of human tick bites, it is very important to consider the extent of the treatment area in relation to the human activity space. For example, the practice of restricting broadcast application of synthetic acaricides to the lawn-woods ecotone on residential properties can result in only a portion of the tick habitat present on the properties being treated. Such ecotone applications

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tend to cover areas extending only a short distance into the woods (up to 6 m) and the lawn (up to 3 m) from the edge between these habitats (Stafford, 2007; Hinckley et al., 2016). In the absence of evidence for the majority of tick bites linked to exposures on residential properties resulting specifically from contact with ticks in this lawn-woods ecotone area, the potential for using this tick control tactic as a stand-alone method to reduce human tick bites in the peridomestic environment is uncertain. A strong impact on human tick bites would be expected only if the treated area represents the majority of tick habitat on the property where the residents spend time during the tick season, the treatment is highly effective in killing questing ticks, and the residents encounter ticks primarily on their own property. However, this best-case scenario may not be representative of most residential properties: Hinckley et al. (2016) found that a roughly 60 % reduction in the density of questing *I. scapularis* nymphs within the lawn-woods ecotone area on residential properties where additional tick habitat was left untreated failed to impact human tick encounters. It is not clear to what extent this lack of observed impact resulted from a moderately effective tick control intervention versus tick exposures commonly occurring in the untreated portions of the properties, on other properties or greenspaces in the neighborhood, or elsewhere. There is also an educational aspect to consider on the side of the tick control applicator. If residents of a property where a lawn-woods ecotone area was treated with broadcast acaricide are under the impression that the treated area, or the entire property, is now completely free of ticks they may relax their efforts to take personal protection measures while spending time in: (i) treated areas of the property where tick numbers in reality were only reduced by some percentage from an unknown starting point (e.g., the number of questing ticks was reduced by 60 % from 50 to 20 ticks) or (ii) untreated portions of the property where the tick numbers were not impacted at all.

There is strong evidence from research studies for EPA-registered synthetic acaricides to effectively suppress questing ticks (reviewed by Eisen and Dolan, 2016; White and Gaff, 2018; Ost et al., 2025). However, little is known about how this translates to operational effectiveness when the implementation is done by homeowners, pest control firms, or public health professionals. This is in stark contrast to mosquito control, where operational use of insecticides has evolved over the last century via continual evaluation and optimization by publicly-funded mosquito control programs (Mulla, 1994; Patterson, 2016), and the knowledge gained is made available to stakeholders via the American Mosquito Control Association, including in its flagship journal (Journal of the American Mosquito Control Association). Questions that already have been addressed for operational mosquito control remain unanswered for operational tick control. For example, there is not an adequate understanding of how the effectiveness of a broadcast application of synthetic acaricide against ticks is impacted by: (i) the level of knowledge of product application techniques and tick biology of the implementer, who could be a homeowner, pest control operator, or public health professional; (ii) the type of acaricide formulation and mode of application used, which may include granules distributed via different types of mechanical spreaders or sprays applied using different types of equipment and spray pressures (e.g., via ready-to-use hose end products, backpack/knapsack low-pressure sprayers, or truck-mounted high-pressure sprayers); (iii) the structure of the vegetation, which influences penetration to the microhabitats where the ticks are found and therefore need to be considered in the

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choice of acaricide formulation and mode of application; and (iv) the seasonal timing and frequency of acaricide applications, balancing the need to effectively suppress human-biting ticks with negative impacts on non-target organisms, including pollinators. Finally, it is important to consider the spatial extent of areas that realistically can be protected via broadcast of synthetic acaricides. Areawide broadcast of synthetic acaricides across a range of tick habitats at large scale on public lands is not common practice, due in large part to environmental concerns (Ginsberg et al., 2017).

In recent decades, broadcast products based on natural active ingredients such as botanical oils or entomopathogenic fungi, rather than synthetic chemical active ingredients, have emerged for killing of questing ticks in the environment. Such natural products tend to have higher acceptability by the public (Niesobecki et al., 2022; Schiffman et al., 2025) but appear to require more frequent reapplications compared to synthetic acaricides to maintain a high level of tick suppression (Table 6; Schulze and Jordan, 2021), which increases the cost of the intervention. Some products based on botanical oils are classified as minimum risk products, exempt from EPA registration. Such products are increasingly used by pest control firms (Jordan and Schulze, 2020a), but substantial variability has been documented across products in their ability to kill ticks (Dyer et al., 2021, Eisen, 2024). In a worst-case scenario, homeowners could pay for an application of a product with minimal tick killing efficacy and relax their vigilance with personal protection measures in the belief that ticks were no longer a problem on the property, paradoxically enhancing their risk for tick bites.

Landscaping techniques aiming to reduce the suitability of the peridomestic environment for desiccation-sensitive ticks (e.g., tree canopy thinning, brush clearing, leaf litter removal, keeping lawn grass short, and xeriscaping; Table 6; Fig. 3; see also Stafford, 2007) share the issue outlined above for broadcast application of acaricides of only being impactful for the area where they are implemented. While there is substantial evidence for broadcast application of synthetic acaricides to effectively kill questing ticks, there is very limited evidence in the literature for landscaping and vegetation management to reduce the density of questing ticks on residential properties (Jordan and Schulze, 2020b; Fischhoff et al., 2019b; Linske and Williams, 2024). Although landscaping and vegetation management intuitively should help to reduce tick numbers, these approaches may not be effective enough for use as stand-alone solutions for tick control.

Take home message: Broadcast of acaricides can be used to suppress questing ticks in spatially limited settings with frequent human use, such as on residential properties or in high-use portions of public lands. However, efforts to date have fallen short both in evaluating the ability of this tick control tactic to reduce the density of questing ticks when applied by real life stakeholders (homeowners, pest control professionals, and public health personnel) and to optimize application techniques and timing schedules in order to improve tick killing efficacy while also taking impacts on non-target organisms into consideration.

2.6.2. Host-targeted tick control: Tick or pathogen control targeting wildlife hosts focus on rodents and deer. Rodents are important hosts for the immature life stages of numerous tick species (*Am. maculatum, D. andersoni, D. occidentalis, D. similis, D. variabilis, I. pacificus*, and *I. scapularis*) and serve as reservoirs for a large number of

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human pathogens (*An. phagocytophilum, Ba. microti, Bo. burgdorferi* s.s., *Bo. mayonii, Bo. miyamotoi, F. tularensis, Ri. parkeri, Ri. rickettsii*, Colorado tick fever virus, and Powassan virus) (Tables 2–3; Eisen et al., 2017; Tsao et al., 2021). Deer are important reproductive hosts for numerous tick species (*Am. americanum, Am. maculatum, D. andersoni, D. occidentalis, H. longicornis, I. pacificus*, and *I. scapularis*) and also serve as reservoirs for some human pathogens (*E. chaffeensis* and *E. ewingii*) (Tables 2–3; Rochlin et al., 2025). Rodent-targeted tick or pathogen control methods, together with deer fencing, are suited for implementation on residential properties (Eisen 2021, 2023), whereas other methods targeting deer (deer population reduction and self-treatment of deer with topical or oral acaricides) are suitable for implementation at neighborhood or community scales (Stafford and Williams, 2017; Telford, 2017). Host-targeted tick control has the benefit of potentially impacting ticks throughout the home ranges of the targeted hosts (see Table 6) and thus having an effect over a larger portion of the human activity space compared to highly focal broadcast of acaricides. Methods based on tick hosts self-treating with acaricide also have the environmental benefit of the pesticide being confined to delivery devices, rather than being spread openly in the environment and potentially impacting non-target species such as pollinators (Ginsberg et al., 2017). Key characteristics of specific tick control methods targeting rodents or deer are summarized in Table 6.

Take home message: Host-targeted interventions aim to impede tick population growth, by targeting animals such as deer which are key hosts for the adult tick stage, or to reduce production of pathogen-infected ticks, by targeting hosts such as rodents which are heavily infested by immatures and serve as pathogen reservoirs (see Fig. 3).

2.6.2.1. Rodent-targeted tick/pathogen control. It has long been understood that rodents play an important role in natural transmission of human disease agents vectored by fleas and ticks, motivating the development of methods and products to attack these vectors while they are feeding on rodent hosts (Gage et al., 1995). Rodent-targeted tick or pathogen control methods, such as self-application of topical or oral acaricides and oral vaccination against Lyme disease spirochetes, and the outcomes of intervention studies using these methods were reviewed previously by Eisen (2023). These methods are suited for implementation on residential properties: with strategic placement of treatment delivery devices, it should be possible to impact all individuals of targeted rodent species with home ranges falling completely or in part within the boundary of a single property (Table 6). Targeting of rodents with acaricide has the potential to directly reduce tick infestation, in turn leading to reduced abundance of questing ticks, as well as indirectly reducing pathogen infection in rodent reservoirs through a decrease in feeding by infected ticks, ultimately also leading to reduced prevalence of infection in questing ticks.

There are, however, drawbacks to the use of rodent-targeted control methods. For *I. scapularis* in the northeastern U.S., impact on acarological risk for human exposure to pathogen-infected questing nymphs, which are considered to account for the majority of pathogen transmission to humans by this tick species, is not expected to occur until the year after the intervention is first put in place (Table 6). Rodent-targeted acaricides or vaccines also have the inherent weakness of their impact being related to the proportion of all fed ticks that are produced by the host species they target. If this proportion is on the low side,

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the intervention can succeed in reducing production of infected ticks by the targeted rodent species without having a significant impact on the public health relevant metric of density of questing infected ticks (see Eisen, 2023). Tick tubes containing permethrin-treated cotton offered as nesting material will primarily impact production of fed ticks by mice whereas bait boxes for topical or oral acaricide treatment will impact production of fed ticks by a broader range of rodents that occur commonly in peridomestic settings, including mice as well as chipmunks (Jordan and Schulze, 2019). However, neither method will impact shrews, which can be abundant in some settings and are heavily infested by ticks as well as effective pathogen reservoirs (Brisson et al., 2008; Goethert et al., 2025). Variation in local tick host communities is most likely a key contributing factor to why interventions with rodent-targeted acaricides have shown wildly different results in impacting the density of questing *I. scapularis* nymphs, ranging from near complete suppression of questing nymphs in some studies to moderate reduction or no significant reduction in nymphal density in other studies (see reviews by Eisen and Dolan, 2016; Eisen, 2023). The poor understanding of the circumstances under which currently available rodent-targeted tick control products succeed or fail to suppress questing *I. scapularis* ticks makes it difficult to predict how the products will perform on a given individual residential property. It is also important to note that studies to evaluate if deployment of rodent-targeted acaricides can reduce human tick encounters have to date failed to document such an impact (Hinckley et al., 2021; Keesing et al., 2022; Ostfeld and Keesing, 2026).

Take home message: The tactic of targeting rodents, which serve both as important hosts for immature ticks and key pathogen reservoirs, remains a logical complement to methods that are based on attacking ticks while they are actively seeking a host, such as broadcast of acaricides. Based on the highly variable outcomes for studies conducted to date on rodent-targeted tick control methods, additional studies are needed to optimize their implementation and to determine if it is possible to ensure robust impact across a wide range of environmental settings and tick host communities. Due to the sensitivity of rodent-targeted control methods to the presence of alternative tick hosts and pathogen reservoirs not impacted by these interventions, they are best suited as components of integrated tick management approaches rather than being used as stand-alone interventions (see also Section 2.6.3).

2.6.2.2. Deer-targeted tick control. A number of tick species feed on cervids in the adult stage (Table 4) but here the focus is on two of the species that are most dependent on cervids as reproductive hosts: *Am. americanum* and *I. scapularis* (Paddock and Yabsley, 2007; Stafford and Williams, 2017; Telford, 2017; Rochlin et al., 2025). White-tailed deer (*Odocoileus virginianus*) are considered the dominant hosts for adults of both tick species and the immatures also infest deer, with larvae and nymphs of *Am. americanum* feeding on deer more commonly than for *I. scapularis* (Clymer et al., 1970; Piesman et al., 1979; Bloemer et al., 1988; Telford et al., 1988). There are well-founded hypotheses of *Am. americanum* and *I. scapularis* being widely distributed in the eastern U.S. prior to the European colonization, whereafter deforestation and decimation of white-tailed deer populations resulted in range contraction for both tick species culminating in the early 1900s (Paddock and Yabsley, 2007; Rochlin et al., 2022; Eisen and Eisen, 2023). The decline

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of white-tailed deer was most dramatic in the northern part of the eastern U.S., where this animal had become scarce to absent across most of the Northeast, Upper Midwest, and Ohio Valley regions by the late 1800s to early 1900s (McCabe and McCabe, 1984). White-tailed deer nevertheless did persist in some geographically limited refugia sites in these regions. This included locations that were very sparsely populated by or mostly inaccessible to humans, or where the landowners purposefully managed the deer population. Following the nadir of the white-tailed deer in the early 1900s, reforestation and new deer management practices (e.g., restocking programs and legislation to protect deer) led to the white-tailed deer rebounding and ultimately reclaiming its historical range in the eastern U.S., where it has now reached population levels considered similar to those before the European colonization (McDonald and Miller, 2004; Adams and Hamilton, 2011). This comeback by the white-tailed deer was followed by re-emergence of *Am. americanum* and *I. scapularis* in the northern part of the eastern U.S. over the last half-century, with spread of *Am. americanum* from south to north (Sonenshine, 2018; Wikel, 2022; Rochlin et al., 2022) and of *I. scapularis* in all cardinal directions from refugia sites in the coastal Northeast and in the Upper Midwest (Eisen and Eisen, 2023).

There is no doubt that deer were the engine driving population increases and spread of *Am. americanum* and *I. scapularis* over the last half-century. The historical circumstantial evidence for the dependence of these ticks on deer as the primary reproductive host (Rochlin et al., 2022; Eisen and Eisen, 2023) is complemented by the outcomes of experimental studies on *I. scapularis* where white-tailed deer were reduced or completely eliminated from peninsulas on or islands off the Atlantic coast in the Northeast (reviewed by Stafford, 2007; Eisen and Dolan, 2016; Telford, 2017). For example, complete removal of deer from Monhegan Island off the coast of Maine from 1996 to 1999 resulted in the population of *I. scapularis* being reduced to very low levels by 2002 and this trend was documented to be sustained until 2008 (Rand et al., 2004; Elias et al., 2011, 2021a). An ecological follow-up study suggested that *I. scapularis* immatures were reintroduced to the island annually via birds, but that the tick was unable to complete its life cycle due to lack of deer as a reproductive host (Elias et al., 2011). Two important conclusions can be drawn: (i) *I. scapularis* can be reduced to very low densities following complete removal of deer in settings without alternative reproductive hosts (such as carnivores); and (ii) continual importation of immatures via other hosts, such as birds, sets the stage for rapid tick population growth should deer or other reproductive hosts be introduced.

Having established that *I. scapularis* can be driven to near elimination if prevented access to deer in a setting where other wildlife capable of serving as reproductive hosts are lacking or scarce, the question arises whether there is an opportunity to achieve this more broadly in the eastern U.S. to reduce the risk of human bites by *I. scapularis* and *Am. americanum*. The ability of these ticks to make contact with and successfully feed on deer can be targeted in different ways (summarized in Table 6), including by reduction in the number of deer (reviewed by Stafford, 2007; Eisen and Dolan, 2016; Kugeler et al., 2016; Telford, 2017) or self-treatment by deer with topical acaricides (reviewed by Stafford, 2007; Curtis et al., 2011; Eisen and Dolan, 2016; Stafford and Williams, 2017), or oral acaricides (Pound et al., 1996; Rand et al., 2000; Poché et al., 2023a, b; Williams et al., 2023a; Brown et al., 2026). Exclusion of deer via fencing has a different primary purpose: to prevent deer from

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introducing fed female ticks to the fenced area (reviewed by Stafford, 2007; Eisen and Dolan, 2016).

Deer fencing is most suitable for small areas, such as individual residential properties, whereas deer reduction and treatment of deer with acaricides are suited for implementation at larger spatial scales such as neighborhoods or communities. As outlined in Table 7, all deer-targeted approaches come with sets of challenges that complicate their practical implementation or potentially impact their efficacy in suppressing tick populations. For example, all of the methods share the drawback that they need to be sustained in perpetuity to prevent a tick resurgence. Deer reduction and treatment of deer with acaricides also share the drawback of a long time-lag from implementation to impact on questing nymphs and adults (up to 1 year for *Am. americanum* and 1–2 years for *I. scapularis*; see Table 6). Moreover, both deer population reduction and exclusion of deer by fencing may result in a temporary increase in density of questing ticks, especially adults, in the first 1–2 years after implementation due to the reduced number of hosts moving around in the environment and removing ticks from the questing population (Ginsberg et al., 2002).

In terms of impact on questing *I. scapularis* and *Am. americanum*, several studies have documented reduction in density of questing ticks within fenced areas (Bloemer et al., 1990; Daniels et al., 1993; Stafford, 1993; Daniels and Fish, 1995), but it appears the impact may be greater for fenced areas larger than 2–3 ha compared to smaller fenced areas (Table 7; Perkins et al. 2006; Connally et al., 2025). Deer reduction and self-application by deer of topical acaricides also have been shown to reduce the density of questing *I. scapularis* and *Am. americanum* (see reviews by Eisen and Dolan, 2016; Stafford and Williams, 2017; Telford, 2017; White and Gaff, 2018), but the evidence for their impact on the frequency of human tick encounters or incidence of tick-borne disease is weak (Garnett et al., 2011; Kilpatrick et al., 2014; Kugeler et al., 2016). It stands to reason that the impact of deer reduction on questing ticks should depend on the deer density achieved after the cull. However, the relationship between deer density and host acquisition and feeding success by *I. scapularis* and *Am. americanum* adults may be non-linear, such that a threshold deer density exists above which deer reduction has little impact on the tick population dynamics, but below which deer reduction likely is accompanied by time-lagged reduction in the density of questing ticks. Moderate culling in areas with high deer density may consequently not be sufficient to meaningfully impact tick populations, and it could also potentially divert immature *I. scapularis* to feed more commonly on rodent pathogen reservoirs. Moreover, reduction of deer populations to the low densities that have been suggested to severely impact tick populations (<8 deer per km^2) or potentially disrupt enzootic pathogen transmission (<3 deer per km^2) (Stafford, 2007; Telford, 2017) would in many areas require logistically challenging and costly culling programs that remove the vast majority of the deer and therefore may not be acceptable to the public or managers of public lands.

Implementation of large-scale efforts for treatment of deer with acaricides appear to be more acceptable (Nawrocki et al., 2023), but is currently hampered by logistical and regulatory issues (Stafford and Williams, 2017; Connally et al., 2022) as well as a dearth of publicly-funded local vector management programs that include a focus on tick control and could

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assume the responsibility for managing such interventions (Eisen, 2020; Roy, 2021; Burtis et al., 2024b; Jordan et al., 2024). There is also the issue of a long time-lag until maximum impact of the intervention is reached. Field studies on self-application by deer of topical acaricides, via 4-Poster devices, have shown a gradual impact on the density of host-seeking *I. scapularis* nymphs over time, approaching a 50 % reduction only by the third year after the intervention began and not reaching 60 % and 70 % reduction until the fourth and sixth years, respectively (Brei et al., 2009, Pound et al., 2009).

One critical challenge going forward is to deliver a topical or oral acaricide to a large proportion of the deer present in an area (by providing an untreated food bait to attract deer to a station where a topical acaricide is self-applied or offering a treated food bait to deliver an oral acaricide) while minimizing deer aggregation and the potential for contact transmission of disease agents, such as the prions causing chronic wasting disease. Another challenge specifically for targeting of *I. scapularis* on deer via acaricide treatment is that the peak infestation period for the adult ticks in the fall coincides with the deer hunting season in the Northeast and Upper Midwest, which potentially can be addressed in the future by using an acaricide with a short withdrawal period in deer tissues (Williams et al., 2023a).

Take home message: Areawide suppression of *Am. americanum* and *I. scapularis* is not possible without preventing their ability to infest and feed successfully on the key reproductive deer host. A weak evidence base for impact not only on questing ticks but also on human tick bites and tick-borne disease, combined with logistical and regulatory challenges of implementing deer-targeted tick control, makes it difficult to assess if the currently available deer-targeted tactics and tools operationally can achieve tick suppression at a level that translates to reduction in human tick bites. Due to the long lag-time required for deer-targeted tick control methods to result in a high level of suppression of questing ticks, they initially need to be combined with other actions to reduce the risk of tick bites (see also Section 2.6.3).

2.6.3. Integrated tick management: All individual tick control methods addressed in Sections 2.6.1 and 2.6.2 have strengths as well as weaknesses when considering tick killing efficacy (Eisen and Dolan, 2016; White and Gaff, 2018; Eisen, 2023) together with spatial extent of protection (Tables 5–6), time from implementation to impact (Tables 5–6), intervention cost (Schulze et al., 2023), willingness to pay (Niesobecki et al., 2022; Cuadera et al., 2023; Enriquez et al., 2025; Schiffman et al., 2025), environmental impact (see Ginsberg et al., 2017), and public acceptability (Niesobecki et al., 2019; Beck et al., 2022; Kopsco and Mather, 2022; Nawrocki et al., 2023; Blossey et al., 2025; Enriquez et al., 2025; Hansen et al., 2025). Vegetation management checks the boxes for low intervention cost, low environmental impact, high public acceptability, and a relatively short time to impact, but has a low tick killing efficacy and will only impact the managed areas, which are likely to be of limited spatial extent. Broadcast of acaricides is characterized by moderate to high tick killing efficacy (depending on the type of acaricide used), short time to impact, and low intervention cost, but has a higher environmental impact and confer protection only within treated areas (e.g., along woods-lawn ecotones on residential properties); the level of public acceptability tends to be higher for natural product-based acaricides than for synthetic acaricides.

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Rodent-targeted acaricide has low environmental impact but is characterized by variable tick killing efficacy (ranging from low to high across research studies), limited spatial extent of protection (reflecting the rodent home range), low to high intervention cost (depending on the product used), and a long time to impact on questing ticks; public acceptability is not well understood. Deer population reduction and self-application by deer of acaricide are more complex to characterize: the main strength of these tactics is the potential for moderate to high tick killing efficacy across large areas (reflecting the deer home range) while the long time to full impact on questing ticks is a notable weakness. The intervention cost is high (Schulze et al., 2023) but this is offset by protection of neighborhoods or communities rather than individual properties. The environmental impact and public acceptability will depend on the type of deer-targeted intervention. Self-application by deer of acaricide has a low environmental impact and appears to be well accepted by the public (Nawrocki et al., 2023). For deer population reduction, the level of environmental impact will depend on the severity of the deer cull, which also may influence public acceptability together with perceived benefits of a deer cull such as lower risk of deer collisions and reduced likelihood of tick-borne disease (Blossey et al., 2025).

Due to the drawbacks of individual tick control methods, it is clear that no single method can become a universal solution. However, bearing in mind if the goal is to suppress ticks within a limited area (e.g., an individual residential property) or over a more extensive area (e.g., a community), combinations of methods with complementary strengths can be considered in an integrated tick management (ITM) approach (for further discussion of integrated pest management and ITM, see Ginsberg and Stafford, 2005; Stafford et al., 2017; Eisen and Stafford, 2021; Ost et al., 2025). A recent modeling exercise comparing the effectiveness of single versus integrated control methods for *I. scapularis* concluded that a three-treatment combination (broadcast of entomopathogenic fungus, rodent-targeted acaricide, and deer population reduction) performed better than each method implemented singly (Ruiz-Carrascal et al., 2024).

Options to consider for inclusion in an ITM targeting a small area, such as a single residential property, range from hardscaping/xeriscaping and vegetation management to broadcast of acaricides or biological control agents, implementation of rodent-targeted acaricide, and installation of a deer fence. Unfortunately, this laundry list of options for methods to potentially include leaves homeowners with a difficult and bewildering task in deciding on an ITM approach that is suitable for their particular setting as well as affordable and acceptable (Fig. 4; Piesman and Eisen, 2008; Eisen, 2021). A study by Hornbostel et al. (2021) underscored the need for creative educational methods to help homeowners identify the riskiest areas on their properties for exposure to ticks and then use appropriate tick control actions together with personal protection measures to reduce their risk of tick bites.

The task of selecting tick control options for an ITM approach is complicated by some tick control methods impacting all human-biting tick species (e.g., broadcast of acaricides), whereas other methods either have variable impact across tick species (e.g., removal of leaf litter and lawn mowing should have a stronger impact on desiccation-sensitive species such as *I. scapularis* compared with hardier species such as *Am. americanum* and *D. variabilis*) or no impact on certain tick species due to their host preferences (e.g., deer

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fencing will not impact *D. variabilis* and rodent-targeted acaricides will not impact *Am. americanum*). ITM approaches for residential properties also need to be designed bearing in mind that broadcast of acaricides will suppress questing ticks very quickly (within a few days) whereas vegetation management acts over weeks to months and host-targeted methods (e.g., rodent-targeted acaricides or a deer fence) may not reduce the density of questing ticks until the following year. Moreover, ITM approaches for tick control may not easily fit within existing pest control company business practices (Jordan and Schulze, 2020a), and also may exceed what most individual homeowners are willing to pay for tick control (Niesobecki et al., 2022; Cuadera et al., 2023; Schiffman et al., 2025). High cost could similarly be an issue for a community-based ITM approach if it was operated by a publicly-funded vector control program and included a deer-targeted component to achieve areawide tick suppression (Schulze et al., 2023).

Studies on ITM approaches for residential properties or high use portions of public lands are scarce (see Eisen and Dolan, 2016; Ost et al., 2025). An early study by Bloemer et al. (1990) focusing on *Am. americanum* in a campground setting showed strong suppression (≥87 % across years) of questing nymphs and adults using broadcast of synthetic pesticide together with vegetation management (mowing, leaf litter removal, and selective removal of overstory and midstory vegetation) and deer fencing. A later study by Schulze et al. (2007), 2008) demonstrated strong suppression (86–87 %) in the second year after implementation for questing *I. scapularis* nymphs and adults on residential properties using an ITM approach that included self-application of topical acaricide by deer (areawide) and rodents (on residential properties) combined with ecotone broadcast of synthetic acaricide on residential properties. This strategy is intriguing as it presented a staggered approach where a less environmentally friendly method without a time-lag for impact on *I. scapularis* (broadcast of acaricide) was used as a short-term solution for protection of a key habitat on residential properties until the more environmentally friendly host-targeted methods took effect on residential properties (rodent-targeted acaricide) or across the landscape (deer-targeted acaricide) in the following years. More recent studies (Williams et al., 2018; Keesing et al., 2022; Ostfeld et al. 2023; Ostfeld and Keesing, 2026) explored the impact of combinations of delivery of rodent-targeted acaricide and broadcast of entomopathogenic fungus on questing *I. scapularis* nymphs in residential settings in the Northeast. Williams et al. (2018) reported a 75 % reduction of questing *I. scapularis* nymphs for this ITM approach in a small-scale study in Connecticut, whereas a larger-scale study in New York (Keesing et al., 2022; Ostfeld et al. 2023; Ostfeld and Keesing, 2026) found no statistically signficant reduction in the density of questing *I. scapularis* nymphs for the same type of ITM approach. The study in New York also included human-based outcome measures: no statistically signficant reduction was observed for either human tick encounters or tick-borne disease cases.

Rocky Mountain spotted fever associated with bites by brown dog ticks (*Rh. sanguineus* s.l.) is a rare success story for a tick-borne disease, where an ITM approach combining dog-targeted acaricide treament with spray application of acaricide in peridomestic settings resulted in reduction of tick infestations and human infections (Drexler et al., 2014; Straily et al., 2016; Brophy et al., 2025). This is, however, an outlier case because brown dog ticks feed primarily on dogs in all life stages and are concentrated in peridomestic environments

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while off-host. ITM approaches are far more challenging to implement when targeting tick species that have broad host ranges and are distributed across the landscape.

Take home message: Suppression of questing ticks to densities low enough to translate to reductions in human tick bites and tick-borne disease cases will most likely require use of ITM approaches. For tick species that have broad host ranges and are widely distributed in the environment, it remains unclear whether or not existing tick control methods can be combined into ITM approaches capable of reducing human tick bites and tick-borne disease cases. Additional studies on promising ITM approaches are therefore needed.

2.7. Weak engagement by industry in development of novel technologies and new products for tick control and personal tick bite prevention

Industry has multiple roles in the context of environmental tick control and personal protection against tick bites: (i) production of already marketed products; (ii) development of new technologies and products; and (iii) services provided by landscaping and pest management professionals (Graf et al., 2004; Jordan and Schulze, 2020a). As evidenced by product availability, there has been strong industry engagement in development of tick repellents applied to human skin, treatment of clothing with permethrin, and topically or orally applied systemic acaricides to control ticks on pets (Blagburn and Dryden, 2009; Pfister and Armstrong, 2016; Stafford, 2017; Smith and Starkey, 2024; EPA, 2025). Industry engagement has been weaker for development of novel technologies and new commercial products aiming to kill ticks when they are questing for hosts (e.g., effective and long-lasting formulations of natural product acaricides), infesting wildlife hosts (e.g., oral acaricides or anti-tick vaccines for rodents or deer), or while they are biting humans but go undetected while attached (e.g., skin lotions containing acaricides, oral acaricides, or anti-tick vaccines). This may in part be related to the tick control market being less predictable than the mosquito control market, as the tick control market is driven by homeowner demand (whether they do it themselves or hire professionals to implement tick control) while publicly-funded mosquito control programs perhaps constitute a more stable and predictable consumer base for control technologies and products targeting mosquitoes.

Development of novel tick or pathogen control technologies requires long-term research followed by commercial product development with associated costs, patent or licensing issues, registration approvals, marketing, and finally acceptance and use by the public or pest management professionals (Graf et al. 2004). As it currently stands, federal funding awarded to private industry is often instrumental in moving novel technologies and new products for tick control through initial proof-of-concept studies and early-stage efficacy evaluations in the laboratory and field. Moreover, based on the example of a rodent reservoir-targeted vaccine against *Bo. burgdorferi* s.s., the process of moving from proof-of-concept to commercialized product can take more than a decade (Gomes-Solecki et al., 2006; Stafford et al., 2020; van Oosterwijk, 2021). Such a long timeline may not be realistic for small businesses exploring novel tick control technologies, unless they can partner with a larger company partway through the process.

Take home message: Novel technologies and new products for tick bite prevention and tick control are needed to reduce human tick bites. However, this cannot be achieved in a timely

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manner without stronger involvement by industry in the development and commercialization of such technologies and products.

2.8. Lack of involvement by publicly-funded vector control programs in support, delivery and evaluation of tick control

Piesman and Eisen (2008) noted that: “Mosquito control is a community responsibility; tick control is an individual homeowner responsibility. This may explain why currently in the United States, several thousand people are dedicated to mosquito control, whereas only a few dozen are dedicated to public-health related tick control.” Although there has been increasing interest in tick control over the last two decades, involvement by publicly-funded vector control programs in the support, delivery and evaluation of tick control remains rare (Eisen, 2020; Egizi and Jordan, 2020; Mader et al., 2021; Roy, 2021; Dye-Braumuller et al., 2022; Burtis et al., 2024b; Jordan et al., 2024; Roy et al., 2024). Recent surveys indicate that local public health and vector control agencies are interested in becoming involved in tick control, but that lack of funding is a major obstacle for taking on this responsibility (Burtis et al., 2024b; Jordan et al., 2024). The critical importance of adequate and sustainable funding for an added responsibility of tick control, together with realistic expectations for what can be achieved by a local program in terms of tick control and tick bite prevention, was previously noted by Egizi and Jordan (2020).

In the case of mosquito control in the U.S., publicly-funded programs play an important role in development of mosquito control technologies (in partnership with industry) as well as in delivery and evaluation of mosquito control. These publicly-funded programs employ skilled personnel and have a strong imperative to ensure that mosquito control is both effective and deployed in a manner that minimizes environmental impacts. They are also a tremendous resource for field evaluations of the performance of mosquito control equipment and products across different environments and targeting different mosquito species, which provides critical information to optimize local mosquito control. To further facilitate mosquito control in the U.S., the American Mosquito Control Association serves to connect local mosquito control programs with each other and with industry partners (AMCA, 2025).

This is in stark contrast to tick control in the U.S., with the vast majority of control interventions carried out either by homeowners or commercial pest control or landscaping firms (Eisen, 2020; Jordan and Schulze, 2020a). One major drawback of the lack of involvement of local publicly-funded programs in tick control is a paucity of information from field evaluations of the performance of operationally implemented tick control, as homeowners and private firms are unlikely to generate and/or share data on control efficacy for landscaping/vegetation management, broadcast of acaricides, or use of rodent-targeted tick control products. Such data are generated almost exclusively through research studies, and it is not clear how representative they are of the efficacy of operational tick control conducted by homeowners or commercial pest control or landscaping firms. A related issue is that the lack of local public health professionals with knowledge of tick control can make it challenging for homeowners to seek out sound and objective advice regarding tick control methods that are appropriate for their specific residential properties. It is also

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worth noting that, in addition to conducting and evaluating tick control and providing support to community members regarding personal tick bite prevention measures and locally appropriate tick control methods, a local publicly-funded vector control program would most likely also engage in surveillance of ticks and the pathogens they carry (Burtis et al., 2024b; Jordan et al., 2024; Roy et al., 2024). Challenges unique to community-based tick control, relative to mosquito control, were discussed previously (Eisen, 2020); notable differences include that: (i) ticks of all life stages have diffuse distributions in the environment, rather than some life stages being concentrated in distinct settings that readily can be surveilled and targeted for control, such as aquatic development sites for mosquito larvae; and (ii) physical access to individual residential properties is needed for acaricide application to control ticks in the peridomestic environment, whereas mosquito control can be achieved with spraying of insecticides from trucks or airplanes without the need to access each residential property to be treated.

Take home message: Involvement by publicly-funded vector control programs in tick control remains rare in the U.S. This is detrimental to the support, delivery, and evaluation of operational tick control, and it also makes it difficult for homeowners to seek out sound and objective advice regarding locally appropriate tick control on their properties.

3. What can we do about it?

From a population level perspective, the re-emergence of a Lyme disease vaccine has the potential to reverse the national trend of increasing tick-borne disease cases because Lyme disease accounts for the majority of reported tick-borne infections in the U.S. The same is true for individual states where Lyme disease accounts for the majority of tick-borne infections (see CDC, 2025a), but not in states where *Ixodes* vectors are scarce or absent and other tick bite-associated illnesses (e.g., alpha-gal syndrome, ehrlichiosis, or rickettsiosis) are more prevalent than Lyme disease. It also should be noted that: (i) many areas harbor multiple species of human-biting ticks collectively carrying a wide range of disease agents (see Tables 1 and 3) and (ii) the *Ixodes* species serving as vectors of Lyme disease spirochetes also carry other pathogens causing anaplasmosis, babesiosis, hard tick relapsing fever, and Powassan virus disease (Table 3). Even if a person is vaccinated against Lyme disease, every tick bite therefore still has the possibility to lead to an infection (as it may not be known if the tick carried a pathogen causing another disease). Consequently, the need for personal tick bite prevention is unchanged even though the risk of infection specifically with Lyme disease is reduced in vaccinated individuals.

In addition to illness associated with tick bites, concerns about tick-bites may negatively impact people's well-being, for example by individuals avoiding to spend time recreating in natural environments or experiencing anxiety about tick bites while being outdoors (Cuadera et al., 2023; Potes et al., 2023; Bowser et al., 2025). There is a multitude of internet-based sources providing information about personal tick bite protection measures and tick control methods, but limited guidance on best practices for how to assess personal risk and make informed decisions about actions that can reduce the risk of tick bites. For example, there is still limited knowledge of which combinations of habitats found on residential properties (e.g., open lawn, a section of the lawn bordering on a wooded area, the wooded part of the

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same ecotone, a continuous wooded area, and ornamental plantings) and human activities (e.g., gardening, other yard work, and play involving children or pets) that commonly result in tick encounters. The lack of support for informed decision-making by members of the public regarding prevention of tick bites and tick-borne disease was noted nearly two decades ago by Piesman and Eisen (2008), and only limited progress has been made to remedy the situation. One noteworthy decision support initiative is the TickSmart™ concept promoted via the University of Rhode Island TickEncounter website (URI, 2025c).

Take home message: Even with the re-emergence of a Lyme disease vaccine, there would still be a need for individuals to prevent tick bites. This underscores the point that, as currently used, existing options for personal tick bite prevention and environmental tick control have not been successful in stemming the rising tide of illness associated with tick bites. Sections 3.1 to 3.5 explore what may be done to remedy this situation.

3.1. Recent national initiatives to prevent tick bites and control ticks in the environment

In response to the increasing problem with tick-borne diseases, Congress established a Tick-Borne Disease Working Group in 2016, as part of the 21st Century Cures Act. This working group produced three reports, published from 2018 to 2022 (TBDWG, 2018, 2020, 2022). With respect to personal tick bite prevention and environmental tick control, the final report (TBDWG, 2022) recommended that efforts be made to (i): increase funding for development, evaluation, and deployment of tick bite prevention and tick control approaches and strategies; (ii) minimize roadblocks and streamline the regulatory process for getting new tick bite prevention and tick control products to market; and (iii) increase adoption and expand knowledge of tick bite prevention and tick control methods across all affected population groups. Congress also passed the Kay Hagan Tick Act in 2019 to broadly address tick-borne diseases, including to provide continued support for CDC-funded regional Centers of Excellence in Vector-Borne Diseases (first established in 2017 as part of CDC's Zika virus disease response; CDC, 2025e) and to also establish regional Training and Evaluation Centers focused on vector-borne diseases (CDC, 2025f). These Centers of Excellence and Regional Training and Evaluation Centers focus on research/evaluation, training, and partnership building to strenghten the nation's capacity to address vector-borne disease threats. Special focus has been on rebuilding medical entomology expertise in the U.S., which had become eroded by 2015 when the Zika virus disease epidemic started (Wilson, 2020; Harrington and Mader, 2023). In the second funding cycle for the Centers of Excellence in Vector-Borne Diseases (from 2022 to 2027), there is special emphasis on applied research aiming to prevent vector bites and to suppress vectors and their associated human pathogens in the environment.

There also has been a recognized need for improved local knowledge of where and when during the year people are at risk for bites by ticks of different species, in order to inform the use of personal protection measures against tick bites and provide the medical community with information about locally occurring tick species and their associated human pathogens (TBDWG, 2018). A national tick and tick-borne pathogen surveillance program was launched in 2018 to address this need by supporting systematic and standardized tick and pathogen surveillance efforts (Eisen and Paddock, 2021). As part of this program, CDC

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developed guidelines for active surveillance of ticks and the pathogens they carry (CDC, 2025g, h) and provides funding for tick and pathogen surveillance efforts to state health departments and other public health entities via the Epidemiology and Laboratory Capacity Program. Information resulting from the national tick and tick-borne pathogen surveillance program is available online (CDC, 2025i) and has also been described in a suite of recent publications (Fleshman et al., 2022; Eisen and Eisen, 2023; Foster et al., 2023, 2024, 2025; Eisen et al., 2024, 2025; Osikowicz et al., 2024). Additional information on where and when during the year people are exposed to ticks of different species and life stages in the U.S. are generated via passive tick surveillance efforts, most often conducted by state or local public health entities or universities, where ticks or images of ticks collected from people or pets are submitted for identification by professional entomologists (Walker et al., 1998; Rand et al., 2007; Xu et al., 2016; Jordan and Egizi, 2019; Little et al., 2019; Porter et al., 2019; Salkeld et al., 2019; Bron et al., 2021; Eisen and Eisen, 2021; Kopsco et al., 2021; Dowling et al., 2022; Hart et al., 2022; Kache et al., 2023; Sack et al., 2023; Dill et al., 2025).

To further address the increasingly severe and complex problems with tick-borne and mosquito-borne diseases (Beard et al., 2019; Petersen et al., 2019), federal agencies developed a national strategy to prevent and control human vector-borne diseases (VBDs) (DHHS-CDC, 2024). The national strategy document outlines a vision (“A nation where VBDs no longer threaten the health of people”) and a mission (“Protect people from illness, suffering and death due to VBDs”), together with specific goals for reductions in impact of selected VBDs (Lyme disease, Rocky Mountain spotted fever, dengue, and West Nile virus neuroinvasive disease). The document also outlines challenges and opportunities relating to the stated mission together with specific goals, strategic priorities, and objectives. However, to complement this blueprint for moving forward to reduce tick bites and illness associated with tick bites in the U.S., there is a need to consider how the stated mission practicably can be achieved. Key issues to consider include reliance on personal tick bite prevention measures versus implementation of environmental tick control (Section 3.2), the thorny problem of achieving increased adoption and use of personal tick bite prevention measures and environmental tick control (Section 3.3), strengthening of the involvement of industry in the development of tick bite prevention and tick control products (Section 3.4), and how public health efforts to prevent tick bites and control ticks in the environment can be organized (Section 3.5).

Take home message: The national strategy to prevent and control human vector-borne diseases (DHHS-CDC, 2024) provides a blueprint for reducing illness associated with tick bites, and specific CDC initiatives such as the launch of a national tick and tick-borne pathogen surveillance program and funding of regional Centers of Excellence in Vector-Borne Diseases provide frameworks for moving toward this goal. The devil is now in the details of how to translate the blueprint and its associated initiatives into practical actions taken at state and local levels, and by individual members of the public, to reduce illness associated with tick bites.

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3.2. Use of personal protection measures versus environmental tick control

There is a fundamental question of whether to rely solely on personal protection measures or to also implement environmental tick control in order to prevent human illness associated with tick bites. As noted by Eisen and Gray (2016), tick-borne disease prevention in Europe has consisted of providing information and education for the public in order to promote personal protection measures, complemented by the emergence of a vaccine against the potentially debilitating tick-borne encephalitis virus. Most tick exposures in Europe are considered to result from recreational or occupational activities on public lands, and there are concerns about implementation of tick control over large areas of public land from the standpoints of cost and logistical feasibility as well as environmental impact (Eisen and Gray, 2016; Sprong et al., 2018; Černý et al., 2020).

The European scenario can perhaps be interpreted as accepting that ticks are part of the natural environment, combined with a view that prevention of tick bites and illness associated with tick bites is an individual responsibility that should be based on use of personal protection measures rather than implementation of environmental tick control over large areas. In contrast, efforts in the U.S. to prevent tick bites and human illness associated with tick bites have since the 1980s progressed along parallel tracks of developing both personal protection measures and methods to control ticks in the environment. This two-pronged approach stems from the early recognition in the northeastern U.S. that *I. scapularis* ticks infected with Lyme disease spirochetes were commonly encountered in the peridomestic environment (Falco and Fish, 1988a, b; Maupin et al., 1991). There is no doubt that implementation of tick control is more readily achieved over a limited area, such as a residential property, compared to the extensive public lands where most tick exposures are thought to occur in Europe.

Ixodes scapularis and its associated pathogens have been the main drivers for the development of methodologies and products to prevent tick bites and human illness associated with tick bites in the U.S. Moreover, there has been a strong focus on the suburban residential landscapes where Lyme disease emerged in the 1970s and 1980s in the Northeast (Steere, 2024). Since then, the threat posed by human-biting ticks in the U.S. has increased both in severity and complexity. The geographic areas where people are at risk for tick bites in the eastern U.S. have expanded; settings with risk for tick bites have been recognized to include residential properties as well as neighborhood greenspaces, parks, and other public recreation areas; and tick bites are now known to be a problem in urban as well as suburban and rural settings. Moreover, the overall problem has grown increasingly complex with many areas now harboring multiple human-biting tick species with their associated suites of pathogens.

Going forward, it will be useful to consider the circumstances under which it is reasonable to rely solely on personal protection measures to prevent tick bites versus complementing this with environmental tick control. There are several factors to consider, including: (i) whether the area with risk for tick exposure is located on private property or public land; (ii) whether the issue is viewed from the perspective of an individual or a population; (iii) variable acceptability by individuals or communities of risk of health impacts resulting

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from a tick bite; and (iv) who should bear the responsibility and cost of environmental tick control.

Take home message: Short of recreating the deforestation and decimation of deer populations that led to elimination of *Am. americanum* and *I. scapularis* from large parts of the eastern U.S. in the 1800s, there is no escaping the fact that human-biting ticks are now part of the natural environment. All indications point to the problem with ticks becoming even worse in the future. There is a need to address the question of when it is reasonable to rely solely on personal protection measures versus also implementing environmental tick control in order to prevent human illness associated with tick bites, based on the current understanding of when and where people are at risk for tick bites and the effectiveness of personal tick bite prevention measures versus tick control in reducing human tick bites.

3.2.1. Relying solely on personal protection measures: One main argument for use of personal protection measures as the primary option to prevent human illness associated with tick bites is that protection is universal across the landscape where ticks are present. Additionally, most of these approaches have a low cost. However, it is important for people to understand the strengths and weaknesses of existing and potential future personal protection strategies (see Table 5 and Fig. 3). Disease-specific vaccines for humans impact the one disease they protect against, but will not impact any other disease or medical condition associated with tick bites. It appears likely that a human Lyme disease vaccine will re-emerge in the near future, but prospects are bleak for vaccines against other important tick-borne diseases in the U.S. Other approaches that would be convenient to use (i.e., not requiring daily action) if ongoing development efforts result in safe and effective commercial products approved by the U.S. Food and Drug Administration for use in humans include pathogen transmission-blocking anti-tick vaccines (Merino et al., 2013; Rego et al., 2019; van Oosterwijk and Wikel, 2021; Narasimhan et al., 2023) or oral acaricides similar to those used in pets (Tarsus, 2025). Depending on the range of impacted tick species, these approaches have potential to protect against multiple or even all tick-borne diseases if they act rapidly enough on biting ticks to disrupt pathogen transmission.

Currently available personal protection measures (see Table 5) all have the drawback of requiring daily use when spending time in tick habitat, and none of them is a magic bullet when used singly. These measures should be viewed as a suite of complementary approaches that need to be used in combination for comprehensive protection. Wearing non-treated or permethrin-treated protective clothing, or using repellents, should be combined with conducting cursory tick checks while outside, running the outdoor clothing in a dryer at high heat and taking a shower combined with a thorough tick check when coming inside, and promptly removing attached ticks. As noted by Bowser et al. (2025), it is important to acknowledge that maintaining comprehensive tick bite prevention in daily life is not always simple and straightforward but rather can be very challenging for those whose residence or occupation puts them at high risk for tick exposure. The decision of whether or not to take precautions, and which measures to use to protect against tick bites, likely will depend on the perceived health risk from a tick bite in relation to the time to be spent in tick habitat (e.g., during a hike versus a short venture into the backyard), the level of inconvenience in using a given personal protection measure, and the confidence in the

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measure actually reducing the risk of tick bites. Use of personal protection measures despite their inconvenience may be more likely if people venture into tick habitat only rarely or occasionally. Spending time in tick habitat on a daily basis over extended time periods, for example in the backyard, undoubtedly presents a higher risk of tick bites, but the level of inconvenience in taking precautions every day may erode the vigilance in doing so. There is a clear need to better understand the main motivating factors for and against day-to-day decisions regarding the use of personal protection measures to prevent tick bites when venturing into tick habitat (see also Bowser et al., 2025). Another related need, to help guide the use of personal protection measures, is to better understand which types of activities (e.g., walking through different habitat types, yard work, or play involving children or pets) most commonly result in tick encounters on residential properties or elsewhere.

Take home message: Personal protection measures should be viewed as a primary option to prevent tick bites and human illness associated with tick bites, in part because their protection is universal across the landscape where ticks are present. Behavioral studies are needed to better understand motivations for and against the use of currently available personal protection measures to prevent tick bites. The critical issue of how to improve adoption and use of personal tick bite prevention measures is discussed in Section 3.3.

3.2.2. Complementing personal protection measures with environmental tick control: Environmental tick control should be viewed as a complement to rather than replacement for the use of personal protection measures. The protection awarded by environmental tick control is limited to the specific intervention area for landscaping/vegetation management and broadcast acaricide application to kill questing ticks, or to the home ranges for rodents or deer targeted with acaricides to kill ticks feeding on these animals (see Table 6). Moreover, it should not be assumed that an area impacted by environmental tick control is free of ticks because such interventions most likely will reduce the abundance of ticks rather than killing all questing and non-questing ticks present in the area. It is instructive to consider this using the example of *I. scapularis*, which is the tick species studied most intensively with regards to impact of experimental control interventions. Based on published studies (see references in Section 2.6), the level of reduction in density of questing *I. scapularis* nymphs following a control intervention is expected to be low for landscaping/vegetation management; low to moderate for deer fencing, rodent-targeted acaricides, and broadcast of natural product acaricides or entomopathogenic fungal agents; moderate for deer-targeted acaricides; moderate to high for broadcast of synthetic acaricides; and highly variable for deer population reduction depending on the population size after the cull.

Considering the control effectiveness together with the spatial extent of protection and the potential for suppressing questing ticks of different species, no single control approach is effective enough across the full range of important human-biting tick species to remove the need for use of personal protection measures. Broadcast of synthetic acaricides comes closest in terms of effectiveness (high level of impact on all tick species) but this method is restricted to very limited spatial scales. Deer-targeted control methods are the closest to magic bullets for tick suppression at the spatial scales of neighborhoods or communities, but they are challenging to implement (see Table 7) and will not impact all human-biting tick

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species (see Table 6). Data for ITM approaches are still too scarce to assess the level of protection against tick bites that can be achieved by using combinations of complementary tick control methods. Moreover, ITM approaches will no doubt be costly.

Scenarios where environmental tick control has the greatest potential for impact include high-use portions of public land and residential properties. Tick control on high-use portions of public land may be justified from a population-level perspective, as well as potentially being cost-effective, as many people would be spending time in the same area with risk for tick exposure. Recent surveys indicate willingness of local vector control or public health agencies to engage in tick control on public lands (Burtis et al., 2024b; Jordan et al., 2024). Tick control on residential properties is rather driven by the desire of the residents to reduce the risk of encountering ticks in an environment where they spend time on a daily basis. The only methods that potentially could suppress ticks on residential properties without physical access to each property are area-wide deer population reduction and acaricide self-treatment by deer, but it is not clear how uniform the level of tick suppression would be across properties within an impacted area. All other tick control methods require physical access to each property, which is one reason local vector control or public health agencies are reluctant to consider engaging in tick control on residential properties (Burtis et al., 2024b; Jordan et al., 2024). Commercial pest control firms, together with homeowners, will therefore likely continue to be the primary parties responsible for tick control on residential properties, with potential support from publicly-funded local tick management programs or other public health entities in the form of objective guidance regarding best practices for residential tick control and how to assess the efficacy of tick suppression efforts. When a pest control firm is contracted to conduct tick control, it is important that the residents understand which portions of the property received treatment and which areas with tick habitat remained untreated.

Take home message: Environmental tick control should be viewed as a complement to, rather than replacement for, the use of personal protection measures. Scenarios where environmental tick control has the greatest potential for impact include high-use portions of public land (from a population perspective) and residential properties (from an individual perspective). The knowledge base for impact of various tick control interventions in ecologically diverse settings still has notable gaps for *I. scapularis* and *Am. americanum* (the two most studied tick species) and is weak for all other human-biting vector tick species. It therefore remains challenging to produce relevant guidelines for environmental tick control on public lands or residential properties that go beyond listings of potential control methods.

3.2.3. Alternative community-based solutions to reduce human-tick contact in residential settings: The classic residential setting presenting risk for tick exposure is a property with a backyard that includes a lawn bordering on a wooded back portion of the property, which in turn is adjacent to a larger wooded area (Diuk-Wasser et al., 2021; Gregory et al., 2022). This essentially presents a situation where a natural area providing opportunities for proliferation of forest-associated ticks, such as *I. scapularis* and *Am. americanum*, and enzootic transmission of the pathogens they carry extends all the way up to the lawn behind the residence. Potential (but perhaps not realistic) strategies to reduce human contact with ticks therefore include community planning efforts aiming to

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either avoid building new residential developments in settings that will promote contact with forest-associated ticks or to design developments in a way that creates “anti-tick buffers” such as non-forested impervious surfaces between residential yards and prime tick habitat (Jackson et al., 2006; Kaup, 2018; MacDonald et al., 2019).

3.3. Messaging to increase adoption and use of personal tick bite prevention measures and environmental tick control

Access to effective tick bite prevention and tick control methods and products will only make a difference if they are used, and how much of a difference depends on whether or not they are used regularly and correctly. There is a recognized need to improve public health communication around the use of personal tick bite prevention measures and environmental tick control (TBDWG, 2022; DHHS-CDC, 2024), but there is no doubt that promoting behavior change in order to reduce the risk of tick bites is a challenging undertaking. Different theories and models have been put forth to explain what drives human action in different contexts (Eyster et al., 2022), and the communication and messaging landscape is highly complex due to the numerous information platforms now available on the internet (e.g., government websites, wiki websites, social media sites, and blogs). A large number of sources provide information specifically on tick bite prevention and tick control; these range from federal, state, and local public health entities to academic institutions, commercial businesses (e.g., manufacturers of tick bite prevention and tick control products, landscaping firms, and pest control firms), special interest groups, and individual influencers. There is also considerable variability among members of the public in how they respond to a message based on their level of trust in the source of the information, the format and content of a message (use of images or video versus text, and personal narratives versus factual information), how the message is framed (focusing on benefit/gain versus cost/loss), whether the information process is based on one-way or two-way communication, and if the communication involves actual interaction with a person.

Relatively few published studies from the U.S. have explored whether delivery of information on tick bite prevention and tick control methods results not only in improved knowledge but also in behavior change. Such studies have focused on education of school-age children (Lawless et al., 1997; Fox, 2008; Shadick et al., 2016; Torbert, 2024) or information provided to adults representing the general population (Malouin et al., 2003; Daltroy et al., 2007; Gould et al., 2008; Hornbostel et al., 2021) or outdoor workers (Jones et al., 2015). All studies showed increased knowledge following education sessions or provision of information. However, results were mixed for increased knowledge translating to improved use of tick bite prevention or tick control measures, and few studies explored how long increased motivation for taking action persisted. Although informative, these studies do not necessarily reflect the current, internet-dominated information landscape with ready access to a multitude of sources containing information of variable quality. Considering the numerous competing internet sources providing information on personal tick bite prevention and environmental tick control, together with variable preferences for members of the public regarding how messages are designed and delivered, there is a strong need for research studies to explore how trusted sources for information most effectively can

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reach their audiences and deliver evidence-based messages, in different variations of format and content, capable of leading to behavior change.

Take home message: Messaging around the use of personal tick bite prevention measures and environmental tick control is challenging in today's internet-dominated and fluid information landscape. There is a need for trusted information sources to deliver evidence-based messages based on contents and formats capable of leading to behavior change and, ultimately, reduced risk of tick bites.

3.4. Novel technologies and products to control ticks, prevent tick bites, or reduce the risk of illness following the bite of an infected tick

Previous publications (Hayes and Piesman, 2003; Eisen et al., 2012) raised the question of whether or not existing tick control strategies and tools are adequate to reduce Lyme disease if they are implemented properly. More than a decade later we still do not have a clear answer to that question but based on large-scale studies with epidemiological outcomes (Hinckley et al., 2016, 2021; Keesing et al., 2022; Ostfeld et al., 2023; Ostfeld and Keesing, 2026) the answer is leaning towards that we do not. To counter this, there has been initiatives to develop new tools (products) for strategies that are considered to have merit despite disappointing intervention study outcomes, such as moving from topical to oral application of acaricides targeting rodents (Poché et al., 2020; Williams et al., 2023b; Pelletier et al., 2025) and deer (Poché et al., 2023a, b; Williams et al., 2023a). However, such efforts need to be intensified to move forward in a timely manner. It also should be noted that our understanding of the environments (e.g., in different habitats within your own residential property, on other residential properties or in greenspaces in your neighborhood, or in more distantly located public access areas) in which people most commonly encounter ticks of different species is limited and based primarily on data from the northeastern U.S. focused on *I. scapularis* (Falco and Fish, 1988a; Stafford et al. 2017; Mead et al., 2018; Jordan and Egizi, 2019; Dill et al., 2025). This makes it difficult to assess the potential value of novel environmental tick control methods that provide only limited spatial protection.

Getting novel products to control ticks or pathogens in the environment to market has proven to be a very slow-moving process (Eisen and Stafford, 2021) and there have been recent calls for strengthened industry engagement in the development of novel technologies and new products for both tick bite prevention and tick control (TBDWG, 2022; DHHS-CDC, 2024; see also Section 2.7 and Table 5). One problem is the lack of an effective path to connect early-stage research and development, often conducted in academic settings or by small companies, with the later stage, more costly and time-consuming efforts needed to bring the product development process to completion and secure the regulatory approvals needed to bring a new tick bite prevention or tick control product to market. This disconnect could result in potentially game-changing products stalling out after the proof-of-concept phase. To solve the problem, there is a need for more effective mechanisms to either support promising product concepts developed by academia or small companies all the way through regulatory product approval, or to more effectively connect academia/small companies with larger industry partners capable of bearing the cost of bringing promising products to

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market. This is one area where the emergence of a national association focused on tick management could be of value.

Take home message: More effective mechanisms are needed to ensure that promising concepts for tick bite prevention and tick control products proceed all the way to marketed products. It also should be clarified why industry is not engaging more in development of novel products for environmental tick control.

3.5. Organization of public health efforts to prevent tick bites and control ticks in the environment

The current lack of publicly-funded local tick management programs is an impediment to achieving the vision of a nation where ticks no longer threaten the health of people. Communities of medically important ticks differ in their species composition across the U.S. (see Sections 2.1 and 2.4). Efforts to prevent tick bites via personal protection measures and control of ticks in the environment therefore requires knowledge of local tick communities and the local ecology of the tick species that are present, as well as an understanding of state and local regulations related to tick control. Local tick management programs are best placed to support such efforts, with potential assistance from state and federal government entities.

Despite the limitations to our knowledge of what existing options for tick bite prevention and tick control can achieve in terms of reducing human tick bites, local tick management programs have the potential to serve as trusted sources of information for their communities and to provide a range of important services. Cornerstones of a local tick management program could include: (i) surveillance of ticks and their associated pathogens, with the aim to inform the public and medical community of which species of ticks and pathogens occur locally and when and where the tick encounter risk is greatest; (ii) outreach to the public and outdoor workers regarding personal tick bite prevention measures; (iii) implementation and evaluation of tick control on public lands, for example targeted to high-use trails and the perimeters of campgrounds, picnic areas, and sports fields; and (iv) support for tick control on residential properties, with potential services ranging from provision of objective guidance for locally suitable tick control methods and products (tier 1) to evaluation of the efficacy of tick control conducted by homeowners or pest control firms (tier 2), or perhaps even to limited implementation of tick control in special circumstances (tier 3). It also could be beneficial if local tick management programs were linked to each other and other stakeholders via a national association.

Few studies have posed questions to the public regarding who should be responsible for management of tick control to address tick-borne diseases or how community-based tick control should be funded if implemented (Elias et al., 2021b; Ernst et al., 2024). One survey focusing on islands off the coast of Maine and conducted primarily in the context of deer population reduction found that a higher percentage of respondents agreed town governments were obligated to manage tick control on their islands (79 %) compared to the state government (70 %), individuals/groups of individuals (66 %), or the U.S. government (40 %) (Elias et al., 2021b). Another study from the northeastern U.S. explored the question of who should be responsible for control of ticks and tick-borne diseases in two different

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settings: the densely populated Staten Island, a borough of New York City, with around 500,000 residents and Block Island off the coast of Rhode Island with a population of less than 1500 residents (Ernst et al., 2024). The main difference between these settings was that respondents from Block Island, compared to Staten Island, were more likely to view control of ticks and tick-borne diseases as the responsibility of individuals and the community but less likely to consider it the responsibility of state and federal agencies. Additional surveys in different geographic regions of the U.S. could better define the opinions of the U.S. public regarding the respective responsibilities of individuals versus local, state, or federal government for environmental tick control.

There also is a need to better understand the existing landscape of involvement by different local and state entities in tick surveillance, tick control, and education/outreach. This may differ in organizational structure among states, for example based on whether or not there has been a long history of publicly organized vector control focused on mosquitoes, such as in Florida, California, and New Jersey. In parallel, there is a need to study how vector-related activities currently are funded, and to explore how this would need to change with introduction of local tick management programs (see Egizi and Jordan, 2020). Unlike mosquito-borne diseases, which at the local level in the U.S. tend to be characterized by outbreak years requiring emergency resources interspersed with years of lower activity, the burden of tick-borne diseases and the resources needed to address them are more stable from year to year.

The fact that every year is a bad year for tick-borne diseases in endemic areas underscores the importance of adequate and sustainable funding for local tick management programs, whether they are created as stand-alone programs or become part of broader vector management programs that also address mosquitoes. Eisen (2020) noted that tick management cannot be incorporated into an existing mosquito management program as an unfunded activity or mandate, and Egizi and Jordan (2020) voiced concern that if tick management is incorporated into an existing mosquito management program, there is a risk for tick-related resources being redirected during a mosquito-borne disease outbreak. Egizi and Jordan (2020) further observed that tick management programs lacking adequate and stable budgets, or being burdened with unrealistic expectations for what they can achieve, run the risk of undermining public trust and willingness to sustain their funding. These sentiments were confirmed by recent surveys indicating that local public health and vector control agencies are interested in becoming involved in tick control, but that lack of funding is a major obstacle for taking on this responsibility (Burtis et al., 2024b; Jordan et al., 2024). Although there is no guarantee that the establishment of publicly-funded local tick management programs will turn the rising tide of human tick bites and tick-borne infections, it is clear that the educational efforts made by federal and state governments over the last decades to promote personal tick bite prevention measures and tick control have not been sufficient to stop the increase in illness associated with tick bites.

Take home message: Publicly-funded local tick management programs are rare in the U.S. but have the potential to serve as trusted sources of information for their communities and provide a range of important services with the overarching goal of reducing tick bites. However, the views of the public and other stakeholder groups at local and state

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levels about the value of such programs, and how they should be financed, are poorly understood. Because every year is a bad year for tick-borne diseases in endemic areas, it is critically important that publicly-funded local tick management programs are adequately and sustainably funded if they are created.

4. Conclusions

Human-biting vector tick species are expanding their geographic ranges in the U.S. and currently available methods to control them in the environment have fallen short in preventing their spread and curbing their population growth. Moreover, widely recommended personal protection measures to prevent tick bites have not stemmed the rising tide of tick bite-associated illness. All indications point to the situation continuing to worsen unless actions are taken to counter the public health threat posed by ticks. The re-emergence of a safe and effective Lyme disease vaccine would be of great benefit, both for individuals concerned about this disease and from a population level standpoint due to reduced numbers of tick-borne disease cases, but it will not reverse the broader threat posed by ticks because this vaccine would address only a single of the many illnesses associated with tick bites in the U.S.

The recently developed national strategy to prevent and control vector-borne diseases in the U.S. (DHHS-CDC, 2024) provides a blueprint to make real a vision of a nation where vector-borne diseases no longer threaten the health of people. Reaching this goal in practice, however, will require investments to stimulate product development, promote applied and behavioral research, develop local organizational structures to address tick bite prevention and tick control, and strengthen the workforce in public health, academia, and industry with expertise in ticks and illness associated with tick bites. Specific actions to make this happen could include:

- Continuation of support for major ongoing CDC initiatives, including the national tick and tick-borne pathogen surveillance program and the regional Centers of Excellence in Vector-Borne Diseases;
- Improvement of industry engagement in development of novel technologies and new products for environmental tick control, prevention of tick bites, and reduction in the risk of pathogen transmission from the bite of infected ticks;
- Support for applied research to evaluate and optimize the effectiveness of existing and emerging methods to control ticks in the environment or to prevent tick bites;
- Support for behavioral research to better understand motivations for and barriers to use of personal tick bite prevention and tick control, with the goal to develop messaging strategies with potential for not only improving knowledge but also leading to behavior change;
- Strengthening of the evidence base for what personal protection measures against tick bites and environmental tick control (especially integrated tick management

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strategies) can achieve in terms of reducing the incidence of tick bites and illness associated with tick bites;

- Establishment of publicly-funded local organizational structures for tick management (including training of the workforce to staff them) with capacity to:
  - conduct tick surveillance;
  - conduct and evaluate environmental tick control, with a primary focus on public access land;
  - provide objective information to individuals and communities about when and where people are at risk for tick bites, actions that can be taken to reduce the risk of tick bites, and locally appropriate methods to control ticks on residential properties.
- Consideration of formation of a national association for tick management serving to bring together stakeholders with interest in tick bite prevention and tick control, including publicly-funded local vector management programs, pest management industry, academic researchers, and federal, state, and local public health agencies. Such a national association for tick management could be a stand-alone entity or become part of an existing related entity, for example the American Mosquito Control Association.

Turning the rising tide of human illness associated with tick bites is a massive undertaking that cannot succeed without investments that remain stable over time. And there is no guarantee of success. It is nevertheless a challenge worth pursuing because the alternative is for the public to accept that tick bites and illness associated with tick bites now is simply a fact of life in the U.S. and that the problem is likely to get worse over time. The clock has not yet struck the hour when we should wave the white flag of surrender and concede that the ticks, indeed, have won.

Acknowledgments

Michelle Allerdice, Bryan Ayres, Rebecca Eisen, and William Nicholson of the Centers for Disease Control and Prevention provided helpful advice and assistance with the content of tables and figures.

Data availability

No data was used for the research described in the article.

References

Adams KP, Hamilton RJ, 2011. Management history. In: Hewitt DG (Ed.), Biology and Management of White-Tailed Deer. CRC Press, New York, NY, USA, pp. 355–377.

Allan SA, Simmons L-A, Burridge MJ, 2001. Ixodid ticks on white-tailed deer and feral swine in Florida. J. Vector. Ecol 26, 93–102. [PubMed: 11469190]

AMCA (American Mosquito Control Association), 2025. Welcome to the American Mosquito Control Association. Accessed 19 August, 2025, https://www.mosquito.org/.

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Anderson JF, Magnarelli LA, 1984. Avian and mammalian hosts for spirochete-infected ticks and insects in a Lyme disease focus in Connecticut USA. Yale J. Biol. Med 57, 627–641. [PubMed: 6516460]

Arsnoe IM, Hickling GJ, Ginsberg HS, McElreath R, Tsao JI, 2015. Different populations of blacklegged tick nymphs exhibit differences in questing behavior that have implications for human Lyme disease risk. PLoS. One 10, e0127450. [PubMed: 25996603]

Arsnoe I, Tsao JI, Hickling GJ, 2019. Nymphal *Ixodes scapularis* questing behavior explains geographic variation in Lyme borreliosis risk in the eastern United States. Ticks. Tick. Borne Dis 10, 553–563. [PubMed: 30709659]

Balashov YS, 1972. Bloodsucking ticks (Ixodoidea), vectors of diseases of man and animals. Misc. Publ. Entomol. Soc. Am 8, 161–376.

Battaly GR, Fish D, 1993. Relative importance of bird species as hosts for immature *Ixodes dammini* (Acari: Ixodidae) in a suburban residential landscape of southern New York State. J. Med. Entomol 30, 740–747. [PubMed: 8360897]

Beard CB, Visser SN, Petersen LR, 2019. The need for a national strategy to address vector-borne disease threats in the United States. J. Med. Entomol 56, 1199–1203. [PubMed: 31505668]

Beck A, Bjork J, Biggerstaff BJ, Eisen L, Eisen RJ, Foster E, Signs K, Tsao JI, Kough E, Peterson M, Schiffman E, Muganda CP, Osborn R, Wozniak R, Bron GM, Phaneuf D, Smith D, Bartholomay L, Paskewitz S, Hinckley AF, 2022. Knowledge, attitudes, and behaviors regarding tick-borne disease prevention in Lyme disease-endemic areas of the Upper Midwest, United States. Ticks. Tick. Borne Dis 13, 101925. [PubMed: 35255349]

Bickerton M, Rochlin I, González J, McSorley K, Toledo A, 2022. Field applications of granular and liquid pyrethroids, carbaryl, and IGRs to control the Asian longhorned tick (*Haemaphysalis longicornis*) and impacts on nontarget invertebrates. Ticks. Tick. Borne Dis 13, 102054. [PubMed: 36215766]

Bishopp FC, Trembley HL, 1945. Distribution and hosts of certain North American ticks. J. Parasitol 31, 1–54.

Blagburn BL, Dryden MW, 2009. Biology, treatment, and control of flea and tick infestations. Vet. Clin. Small Anim 39, 1173–1200.

Bloemer SR, Zimmerman RH, Fairbanks K, 1988. Abundance, attachment sites, and density estimators of lone star ticks (Acari: Ixodidae) infesting white-tailed deer. J. Med. Entomol 25, 295–300. [PubMed: 3404547]

Bloemer SR, Mount GA, Morris TA, Zimmerman RH, Barnard DR, Snoddy EL, 1990. Management of lone star ticks (Acari: Ixodidae) in recreational areas with acaricide applications, vegetative management, and exclusion of white-tailed deer. J. Med. Entomol 27, 543–550. [PubMed: 1696994]

Blossey B, Brice E, Dalaba J, Hare D, 2025. Perspectives of New York State residents on deer management, hunting, and predator reintroduction. Sci. Rep 15, 6123. [PubMed: 39971768]

Bowser N, Bouchard C, Robertson M, Hongoh V, Richard L, Leighton P, Carabin H, Aenishaenslin C, 2025. You adapt, and you try not to resent it': a qualitative study exploring impacts of living with ticks and barriers to adopting preventive measures in Canada. BMC. Public Health 25, 2845. [PubMed: 40830443]

Brei B, Brownstein JS, George JE, Pound JM, Miller JA, Daniels TJ, Falco RC, Stafford KC III, Schulze TL, Mather TN, Carroll JF, Fish D, 2009. Evaluation of the United States Department of Agriculture northeast area-wide tick control project by meta-analysis. Vector. Borne Zoonotic. Dis 9, 423–430. [PubMed: 19650737]

Brisson D, Dykhuizen DE, Ostfeld RS, 2008. Conspicuous impacts of inconspicuous hosts on the Lyme disease epidemic. Proc. R. Soc. B 275, 227–235.

Bron GM, Fernandez MDP, Bartholomay LC, Diuk-Wasser MA, Paskewitz SM, Tsao JI, 2021. Benefits and drawbacks of citizen science to complement traditional data gathering approaches for medically important hard ticks (Acari: Ixodidae) in the United States' regarding the Tick App and research-based citizen science. J. Med. Entomol 58, 991–993. [PubMed: 33399210]

Brophy MK, Drexler NA, Stone NE, Busch JD, Ballard R, Bourgeois RM, Pemberton GL, Paddock CD, Horiuchi K, Biggerstaff BJ, Blocher BH, Kersh GJ, Bendle H, Wagner DM, Nicholson

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WL, Salzer JS, 2025. Ecologic risk factors for infestation of *Rhipicephalus sanguineus* s.l. in a Rocky Mountain spotted fever-endemic area of eastern Arizona. Am. J. Trop. Med. Hyg 113, 156. [PubMed: 40328244]

Brown JE, Linske MA, DeNicola AJ, DeNicola VL, Boulanger JR, Tamez C, Williams SC, 2026. Oral delivery of the systemic acaricide moxidectin to a confined *Odocoileus virginianus* (Artiodactyla: Cervidae) herd parasitized by *Ixodes scapularis* (Ixodida: Ixodidae). J. Med. Entomol 63 tjag022.

Burgdorfer W, 1963. Investigation of "transovarial transmission" of *Rickettsia rickettsii* in the wood tick, *Dermacentor andersoni*. Exp. Parasitol 14, 152–159.

Burtis JC, Ford SL, Parise CM, Eisen RJ, Eisen L, 2024a. Efficacy of unregulated minimum risk tick repellent products evaluated with *Ixodes scapularis* nymphs in a human skin bioassay. Parasit. Vectors 17, 50. [PubMed: 38303091]

Burtis JC, Foster E, Eisen RJ, Eisen L, 2024b. Willingness and capacity of publicly-funded vector control programs in the United States to engage in tick management. Parasit. Vectors 17, 316. [PubMed: 39039577]

Butler AD, Sedghi T, Petrini JR, Ahmadi R, 2016. Tick-borne disease preventive practices and perceptions in an endemic area. Ticks. Tick. Borne Dis 7, 331–337. [PubMed: 26704290]

Butler RA, Muller LI, Grove D, Trout Fryxell RT, 2024. Ecological relationships of *Haemaphysalis longicornis* Neumann with other tick species on wildlife hosts at cow–calf farms implementing integrated pest management in eastern Tennessee. Parasitology. 151, 1001–1011. [PubMed: 39540321]

Campbell H, Loftin K, Szalanski A, Steinkraus D, Smith E, 2022. Tick (Acarina: Ixodidae) species and life stages collected from Arkansas wild pigs. Fla Entomol 105, 194–199.

Carroll JF, Kramer M, 2001. Different activities and footwear influence exposure to host-seeking nymphs of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). J. Med. Entomol 38, 596–600. [PubMed: 11476342]

Carroll JF, Kramer M, 2003. Winter activity of *Ixodes scapularis* (Acari: Ixodidae) and the operation of deer-targeted tick control devices in Maryland. J. Med. Entomol 40, 238–244. [PubMed: 12693854]

Casher LE, Lane RS, Barrett RH, Eisen L, 2002. Relative importance of lizards and mammals as hosts for ixodid ticks in northern California. Exp. Appl. Acarol 26, 127–143. [PubMed: 12475082]

Castro MB, Wright SA, 2007. Vertebrate hosts of *Ixodes pacificus* (Acari: Ixodidae) in California. J. Vector. Ecol 32, 140–149. [PubMed: 17633435]

CDC (Centers for Disease Control and Prevention), 2025a. Tickborne Disease Surveillance Data Summary. Accessed 19 August, 2025, https://www.cdc.gov/ticks/data-research/facts-stats/tickborne-disease-surveillance-data-summary.html.

CDC (Centers for Disease Control and Prevention), 2025b. About Alpha-gal Syndrome. Accessed 19 August, 2025, https://www.cdc.gov/alpha-gal-syndrome/about/index.html.

CDC (Centers for Disease Control and Prevention), 2025c. Where Ticks Live. Accessed 19 August, 2025, https://www.cdc.gov/ticks/about/where-ticks-live.html.

CDC (Centers for Disease Control and Prevention), 2025d. Preventing Tick Bites. Accessed 19 August, 2025, https://www.cdc.gov/ticks/prevention/index.html.

CDC (Centers for Disease Control and Prevention), 2025e. Centers of Excellence in Vector-Borne Diseases. Accessed 19 August, 2025, https://www.cdc.gov/vector-borne-diseases/what-cdc-is-doing/centers-of-excellence-in-vector-borne-diseases.html.

CDC (Centers for Disease Control and Prevention), 2025f. Regional Training and Evaluation Centers. Accessed 19 August, 2025, https://www.cdc.gov/vector-borne-diseases/what-cdc-is-doing/regional-training-and-evaluation-centers-1.html.

CDC (Centers for Disease Control and Prevention), 2025g. Blacklegged Tick (Ixodes scapularis) Surveillance. Accessed 19 August, 2025, https://www.cdc.gov/ticks/resources/TickSurveillance_Iscapularis-P.pdf.

CDC (Centers for Disease Control and Prevention), 2025h. Guide to the Surveillance of Metastriate Ticks (Acari: Ixodidae) and their pathogens in the United States. Accessed 19 August, 2025, https://www.cdc.gov/ticks/pdfs/Tick_surveillance-P.pdf.

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

CDC (Centers for Disease Control and Prevention), 2025i. Tick Surveillance Data Sets. Accessed 19 August, 2025, https://www.cdc.gov/ticks/data-research/facts-stats/tick-surveillance-data-sets.html.

Černý J, Lynn G, Hrnková J, Golovchenko M, Rudenko N, Grubhoffer L, 2020. Management options for *Ixodes ricinus*-associated pathogens: a review of prevention strategies. Int. J. Environ. Res. Public Health 17, 1830. [PubMed: 32178257]

Childs JE, Paddock CD, 2003. The ascendancy of *Amblyomma americanum* as a vector of pathogens affecting humans in the United States. Annu. Rev. Entomol 48, 307–337. [PubMed: 12414740]

Clymer BC, Howell DE, Hair JA, 1970. Animal hosts of economically important ticks (Acarina) in east-central Oklahoma. Ann. Entomol. Soc. Am 63, 612–614.

Connally NP, Rowe A, Kaufman A, Meek JI, Niesobecki SA, Hansen AP, White J, Nawrocki C, Foster E, Hinckley AF, Eisen L, 2022. Designing an intervention trial of human-tick encounters and tick-borne diseases in residential settings using 4-Poster devices to control *Ixodes scapularis* (Acari: Ixodidae): challenges for site selection and device placement. J. Med. Entomol 59, 911–921. [PubMed: 35294011]

Connally NP, Hornbostel VL, Dyer MC, Hojgaard A, Osikowicz LM, Christopher DA, Mather TN, 2025. The impact of deer exclusion fencing on host-seeking blacklegged ticks on suburban residential properties in southern New England. J. Med. Entomol 62, 1208–1220. [PubMed: 40580545]

Cooley RA, 1938. The Genera Dermacentor and Otocentor (Ixodidae) in the United States, With Studies in variation. Bulletin No. 171 Public Health Service, National Institute of Health, Washington, DC, USA.

Cooley RA, 1946. The Genera Boophilus, Rhipicephalus, and Haemaphysalis (Ixodidae) of the New World. Bulletin No.187 United States Public Health Service, National Institute of Health, Washington, DC, USA.

Cooley RA, Kohls GM, 1944. The genus *Amblyomma* (Ixodidae) in the United States. J. Parasitol 30, 77–111.

Cooley RA, Kohls GM, 1945. The Genus Ixodes in North America. Bulletin No. 184 United States Public Health Service, National Institute of Health, Washington, DC, USA.

Cooney JC, Burgdorfer W, 1974. Zoonotic potential (Rocky Mountain spotted fever and tularemia) in the Tennessee Valley Region. I. Ecologic studies of ticks infesting mammals in Land Between the Lakes. Am. J. Trop. Med. Hyg 23, 99–108. [PubMed: 4204030]

Cuadera MK, Mader EM, Greiner Safi A, Harrington LC, 2023. Knowledge, attitudes, and practices for tick bite prevention and tick control among residents of Long Island, New York, USA. Ticks. Tick. Borne Dis 14, 102124. [PubMed: 36764054]

Curtis PD, Walker SM, Gilrein DO, 2011. Shelter Island and Fire Island 4-Poster Deer and Tick Study: Final Report. Cornell University & Cornell Cooperative Extension, Ithaca, NY, USA.

Curtis TR, Shi M, Qiao X, 2020. Patience is not always a virtue: effects of terrain complexity on the host-seeking behaviour of adult blacklegged ticks, *Ixodes scapularis*, in the presence of a stationary host. Med. Vet. Entomol 34, 309–315. [PubMed: 32227497]

Daltroy LH, Phillips C, Lew R, Wright E, Shadick NA, Liang MH, 2007. A controlled trial of a novel primary prevention program for Lyme disease and other tick-borne illnesses. Health Educ. Behav 34, 531–542. [PubMed: 17468463]

Daniels TJ, Fish D, 1990. Spatial distribution and dispersal of unfed larval *Ixodes dammini* (Acari: Ixodidae) in southern New York. Environ. Entomol 19, 1029–1033.

Daniels TJ, Fish D, 1995. Effect of deer exclusion on the abundance of immature *Ixodes scapularis* (Acari: Ixodidae) parasitizing small and medium-sized mammals. J. Med. Entomol 32, 5–11. [PubMed: 7869342]

Daniels TJ, Fish D, Schwartz I, 1993. Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) and Lyme disease risk by deer exclusion. J. Med. Entomol 30, 1043–1049. [PubMed: 8271246]

Dantas-Torres F, 2010. Biology and ecology of the brown dog tick, *Rhipicephalus sanguineus*. Parasit. Vectors 3, 26. [PubMed: 20377860]

Dautel H, Dippel C, Kämmer D, Werkhausen A, Kahl O, 2008. Winter activity of *Ixodes ricinus* in a Berlin forest. Int. J. Med. Microbiol 298 (Suppl. 1), 50–54.

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

DHHS-CDC (U.S. Department of Health and Human Services and U.S. Centers for Disease Control and Prevention), 2024. The National Public Health Strategy to Prevent and Control Vector-Borne Diseases in People. Accessed 19 August, 2025: https://www.cdc.gov/vector-borne-diseases/php/data-research/national-strategy/index.html.

Dill GM, Rounsville TF, Bryant AM, Gardner AM, 2025. Patterns of demographic and behavioral factors associated with tick encounters in Maine (USA) using passive surveillance data. Ticks. Tick. Borne Dis 16, 102573. [PubMed: 41275585]

Dingler RJ, Wright SA, Donohue AM, Macedo PA, Foley JE, 2014. Surveillance for *Ixodes pacificus* and the tick-borne pathogens *Anaplasma phagocytophilum* and *Borrelia burgdorferi* in birds from California's Inner Coast Range. Ticks. Tick. Borne Dis 5, 436–445. [PubMed: 24690191]

Dinkel KD, Herndon DR, Noh SM, Lahmers KK, Todd SM, Ueti MW, Scoles GA, Mason KL, Fry LM, 2021. A U.S. isolate of *Theileria orientalis*, Ikeda genotype, is transmitted to cattle by the invasive Asian longhorned tick, *Haemaphysalis longicornis*. Parasit. Vectors 14, 157. [PubMed: 33726815]

Diuk-Wasser MA, VanAcker MC, Fernandez MP, 2021. Impact of land use changes and habitat fragmentation on the eco-epidemiology of tick-borne diseases. J. Med. Entomol 58, 1546–1564. [PubMed: 33095859]

Dowling APG, Young SG, Loftin K, 2022. Collaborating with community scientists across Arkansas to update tick distributions and pathogen prevalence of spotted fever group *Rickettsia* and *Ehrlichia*. J. Med. Entomol 59, 565–575. [PubMed: 34850921]

Drexler N, Miller M, Gerding J, Todd S, Adams L, Dahlgren FS, Bryant N, Weis E, Herrick K, Francies J, Komatsu K, Piontkowski S, Velascosoltero J, Shelhamer T, Hamilton B, Eribes C, Brock A, Sneezy P, Goseyun C, Bendle H, Hovet R, Williams V, Massung R, McQuiston JH, 2014. Community-based control of the brown dog tick in a region with high rates of Rocky Mountain spotted fever, 2012–2013. PLoS. One 9, e112368. [PubMed: 25479289]

Durden LA, Oliver JH Jr., Kinsey AA, 2001. Ticks (Acari: Ixodidae) and spirochetes (Spirochaetaceae: Spirochaetales) recovered from birds on a Georgia Barrier Island. J. Med. Entomol 38, 231–236. [PubMed: 11296828]

Durden LA, Oliver JH Jr., Banks CW, Vogel GN, 2002. Parasitism of lizards by immature stages of the blacklegged tick, *Ixodes scapularis* (Acari, Ixodidae). Exp. Appl. Acarol 26, 257–266. [PubMed: 12537298]

Dye-Braumuller KC, Gordon JR, Johnson D, Morrissey J, McCoy K, Dinglasan RR, Nolan MS, 2022. Needs assessment of southeastern United States vector control agencies: capacity improvement is greatly needed to prevent the next vector-borne disease outbreak. Trop. Med. Infect. Dis 7, 73. [PubMed: 35622700]

Dyer MC, Requintina MD, Berger KA, Puggioni G, Mather TN, 2021. Evaluating the effects of minimal risk natural products for control of the tick, *Ixodes scapularis* (Acari: Ixodidae). J. Med. Entomol 58, 390–397. [PubMed: 33044507]

Ebel GD, 2010. Update on Powassan virus: emergence of a North American tick-borne flavivirus. Annu. Rev. Entomol 55, 95–110. [PubMed: 19961325]

Edlow JA, McGillicuddy DC, 2008. Tick paralysis. Infect. Dis. Clin. North Am 22, 397–413. [PubMed: 18755381]

Egizi A, Jordan RA, 2020. Stemming the rising tide of human-biting ticks and tickborne diseases, United States. Emerg. Infect. Dis 26, 2534–2535. [PubMed: 32946730]

Egizi A, Bulaga-Seraphin L, Alt E, Bajwa WI, Bernick J, Bickerton M, Campbell SR, Connally N, Doi K, Falco RC, Gaines DN, Greay TL, Harper VL, Heath ACG, Jiang J, Klein TA, Maestas L, Mather TN, Occi JL, Oskam CL, Pendleton J, Teator M, Thompson AT, Tufts DM, Umemiya-Shirafuji R, VanAcker MC, Yabsley MJ, Fonseca DM, 2020. First glimpse into the origin and spread of the Asian longhorned tick, *Haemaphysalis longicornis*, in the United States. Zoonoses. Public Health 67, 637–650. [PubMed: 32638553]

Eisen L, 2007. Seasonal pattern of host-seeking activity by the human-biting adult life stage of the Rocky Mountain wood tick, *Dermacentor andersoni* (Acari: Ixodidae). J. Med. Entomol 44, 359–366. [PubMed: 17427709]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Eisen L, 2018. Pathogen transmission in relation to duration of attachment by *Ixodes scapularis* ticks. Ticks. Tick. Borne Dis 9, 535–542. [PubMed: 29398603]

Eisen L, 2020. Stemming the rising tide of human-biting ticks and tickborne diseases, United States. Emerg. Infect. Dis 26, 641–647. [PubMed: 32186484]

Eisen L, 2021. Control of ixodid ticks and prevention of tick-borne diseases in the United States: the prospect of a new Lyme disease vaccine and the continuing problem with tick exposure on residential properties. Ticks. Tick. Borne Dis 12, 101649. [PubMed: 33549976]

Eisen L, 2022a. Tick species infesting humans in the United States. Ticks. Tick. Borne Dis 13, 102025. [PubMed: 35973261]

Eisen L, 2022b. Personal protection measures to prevent tick bites in the United States: knowledge gaps, challenges, and opportunities. Ticks. Tick. Borne Dis 13, 101944. [PubMed: 35364518]

Eisen L, 2023. Rodent-targeted approaches to reduce acarological risk of human exposure to pathogen-infected *Ixodes* ticks. Ticks. Tick. Borne Dis 14, 102119. [PubMed: 36680999]

Eisen L, 2024. Efficacy of unregulated minimum risk products to kill and repel ticks. Emerg. Infect. Dis 30, 1–7.

Eisen L, 2025. Seasonal activity patterns of *Ixodes scapularis* and *Ixodes pacificus* in the United States. Ticks. Tick. Borne Dis 16, 102433. [PubMed: 39764925]

Eisen L, Dolan MC, 2016. Evidence for personal protective measures to reduce human contact with blacklegged ticks and for environmentally based control methods to suppress host-seeking blacklegged ticks and reduce infection with Lyme disease spirochetes in tick vectors and rodent reservoirs. J. Med. Entomol 53, 1063–1092. [PubMed: 27439616]

Eisen L, Eisen RJ, 2016. Critical evaluation of the linkage between tick-based risk measures and the occurrence of Lyme disease cases. J. Med. Entomol 53, 1050–1062. [PubMed: 27330093]

Eisen L, Eisen RJ, 2021. Benefits and drawbacks of citizen science to complement traditional data gathering approaches for medically important hard ticks (Acari: Ixodidae) in the United States. J. Med. Entomol 58, 1–9. [PubMed: 32772108]

Eisen L, Eisen RJ, 2023. Changes in the geographic distribution of the blacklegged tick, *Ixodes scapularis*, in the United States. Ticks. Tick. Borne Dis 14, 102233. [PubMed: 37494882]

Eisen L, Gray JS, 2016. Lyme borreliosis prevention strategies: United States versus Europe. In: Braks MAH, Van Wierer SE, Takken W, Sprong H (Eds.), Ecology and Prevention of Lyme Borreliosis. Wageningen Academic Publishers, Wageningen, The Netherlands, pp. 429–450.

Eisen L, Stafford KC III, 2021. Barriers to effective tick management and tick-bite prevention in the United States (Acari: Ixodidae). J. Med. Entomol 58, 1588–1600. [PubMed: 32372075]

Eisen L, Eisen RJ, Lane RS, 2004. The roles of birds, lizards, and rodents as hosts for the western black-legged tick *Ixodes pacificus*. J. Vector. Ecol 29, 295–308. [PubMed: 15709249]

Eisen L, Meyer AM, Eisen RJ, 2007. Climate-based model predicting acarological risk of encountering the human-biting adult life stage of *Dermacentor andersoni* (Acari: Ixodidae), in a key habitat type in Colorado. J. Med. Entomol 44, 694–704. [PubMed: 17695027]

Eisen L, Saunders M, Kramer VL, Eisen RJ, 2024. History of the geographic distribution of the western blacklegged tick, *Ixodes pacificus*, in the United States. Ticks. Tick. Borne Dis 15, 102325. [PubMed: 38387162]

Eisen RJ, Eisen L, 2018. The blacklegged tick, *Ixodes scapularis*: an increasing health concern. Trends. Parasitol 34, 295–309. [PubMed: 29336985]

Eisen RJ, Paddock CD, 2021. Tick and tickborne pathogen surveillance as a public health tool in the United States. J. Med. Entomol 58, 1490–1502. [PubMed: 32440679]

Eisen RJ, Piesman J, Zielinski-Gutierrez E, Eisen L, 2012. What do we need to know about disease ecology to prevent Lyme disease in the Northeastern United States? J. Med. Entomol 49, 11–22. [PubMed: 22308766]

Eisen RJ, Eisen L, Beard CB, 2016. County-scale distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae) in the Continental United States. J. Med. Entomol 53, 349–386. [PubMed: 26783367]

Eisen RJ, Kugeler KJ, Eisen L, Beard CB, Paddock CD, 2017. Tick-borne zoonoses in the United States: persistent and emerging threats to human health. ILAR. J 58, 319–335. [PubMed: 28369515]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Eisen RJ, Foster E, Kjemtrup A, Saunders ME, Brown J, Green L, Cervantes K, Prusinski MA, White J, Barbarin AM, Williams C, 2025. Perspectives from federal and state public health departments on their participation in and the utility of *Ixodes scapularis* (Acari: Ixodidae) and *Ixodes pacificus* tick and tick-borne pathogen surveillance in the United States. J. Med. Entomol 62, 289–300. [PubMed: 39657826]

Elias SP, Smith RP Jr., Morris SR, Rand PW, Lubelczyk C, Lacombe EH, 2011. Density of *Ixodes scapularis* ticks on Monhegan Island after complete deer removal: a question of avian importation? J. Vector. Ecol 36, 11–23. [PubMed: 21635637]

Elias SP, Stone BB, Rand PW, Lubelczyk CB, Smith RP, 2021a. History of deer herd reduction for tick control on Maine's offshore islands. Maine Policy Rev 30, 10–19.

Elias SP, Rand PW, Rickard LN, Stone BB, Maasch KA, Lubelczyk CB, Smith RP Jr., 2021b. Support for deer herd reduction on offshore islands of Maine, U.S.A. Ticks. Tick. Borne Dis 12, 101634. [PubMed: 33370715]

Embers ME, Narasimhan S, 2013. Vaccination against Lyme disease: past, present, and future. Front. Cell Infect. Microbiol 3, 6. [PubMed: 23407755]

Enriquez AJ, Berry K, del Pilar Fernandez M, Gregory N, Ernst KC, Hayden MH, Diuk-Wasser M, 2025. Simple stated preference questions can enhance transdisciplinary projects: linking perceived risks with willingness to spray and pay. Environ. Resour. Econ 88, 81–124.

EPA (Environmental Protection Agency), 2025. Find the Repellent that is Right for You. Accessed 19 August, 2025; https://www.epa.gov/insect-repellents/find-repellent-right-you.

Ernst KC, Fernandez P, Diuk-Wasser M, Enriquez AJ, Berry K, Hayden MH, 2024. Contrasting perceptions, knowledge, and actions around Lyme disease in an urban area of emerging Lyme disease and an area of endemic Lyme disease in the Northeastern United States. Am. J. Trop. Med. Hyg 111, 865–879. [PubMed: 39043173]

Eyster HN, Satterfield T, Chan KM, 2022. Why people do what they do: an interdisciplinary synthesis of human action theories. Annu Rev. Environ. Resour 47, 725–751.

Falco RC, 1987. Abundance of the Deer Tick, Ixodes dammini (Acari: Ixodidae), in a Lyme Disease Endemic Area of Southern New York State. Ph.D. Thesis, Fordham University, Bronx, N.Y., USA.

Falco RC, Fish D, 1988a. Ticks parasitizing humans in a Lyme disease endemic area of southern New York State. Am. J. Epidemiol 128, 1146–1152. [PubMed: 3189288]

Falco RC, Fish D, 1988b. Prevalence of *Ixodes dammini* near the homes of Lyme disease patients in Westchester County, New York. Am. J. Epidemiol 128, 826–830.

Fischhoff IR, Bowden SE, Keesing F, Ostfeld RS, 2019a. Systematic review and meta-analysis of tick-borne disease risk factors in residential yards, neighborhoods, and beyond. BMC. Infect. Dis 19, 861. [PubMed: 31623574]

Fischhoff IR, Keesing F, Pendleton J, DePietro D, Teator M, Duerr STK, Mowry S, Pfister A, LaDeau SL, Ostfeld RS, 2019b. Assessing effectiveness of recommended residential yard management measures against ticks. J. Med. Entomol 56, 1420–1427. [PubMed: 31120510]

Fleshman AC, Foster E, Maes SE, Eisen RJ, 2022. Reported county-level distribution of seven human pathogens detected in host-seeking *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae) in the contiguous United States. J. Med. Entomol 59, 1328–1335. [PubMed: 35583265]

Foster E, Maes SA, Holcomb KM, Eisen RJ, 2023. Prevalence of five human pathogens in host-seeking *Ixodes scapularis* and *Ixodes pacificus* by region, state, and county in the contiguous United States generated through national tick surveillance. Ticks. Tick. Borne Dis 14, 102250. [PubMed: 37703795]

Foster E, Holcomb KM, Eisen RJ, 2024. Density of host-seeking *Ixodes scapularis* nymphs by region, state, and county in the contiguous United States generated through national tick surveillance. Ticks. Tick. Borne Dis 15, 102316. [PubMed: 38325243]

Foster E, Maes SA, Osikowicz LM, Hojgaard A, Parise CM, Holcomb KM, Eisen RJ, 2025. Geographic trends in acarological risk reporting for *Ixodes scapularis* (Acari: Ixodidae)-borne infections across the eastern United States based on data submissions to the ArboNET Tick Module, 2004 to 2023. J. Med. Entomol 62, 1540–1552. [PubMed: 40907973]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Fox NN, 2008. Tick-Borne Diseases: An Evaluation of Lyme Disease Prevention Education Program for Eight, Nine-, and Ten-Year Olds. Ph.D. Thesis. Wilmington University, New Castle, Delaware, USA. Available from ProQuest (#3342827).

Freeman EA, Salkeld DJ, 2022. Surveillance of Rocky Mountain wood ticks (*Dermacentor andersoni*) and American dog ticks (*Dermacentor variabilis*) in Colorado. Ticks. Tick. Borne Dis 13, 102036. [PubMed: 36274450]

Furman DP, Loomis EC, 1984. The ticks of California (Acari: Ixodida). Bull. Calif. Insect Surv 25, 1–239.

Gage KL, Ostfeld RS, Olson JG, 1995. Nonviral vector-borne zoonoses associated with mammals in the United States. J. Mammal 76, 695–715.

Garnett JM, Connally NP, Stafford KC III, Cartter ML, 2011. Evaluation of deer targeted interventions on Lyme disease incidence in Connecticut. Public Health Rep 126, 446–454. [PubMed: 21553675]

Ginsberg HS, 1993. Transmission risk of Lyme disease and implications for tick management. Am. J. Epidemiol 138, 65–73. [PubMed: 8333428]

Ginsberg HS, Stafford KC III, 2005. Management of ticks and tick-borne diseases. In: Goodman JL, Dennis DT, Sonenshine DE (Eds.), Tickborne Diseases of Humans. ASM Press, Washington, D.C., USA, pp. 65–86.

Ginsberg HS, Butler M, Zhioua E, 2002. Effect of deer exclusion by fencing on abundance of *Amblyomma americanum* (Acari: Ixodidae) on Fire Island, New York, USA. J. Vector. Ecol 27, 215–221. [PubMed: 12546457]

Ginsberg HS, Bargar TA, Hladik ML, Lubelczyk C, 2017. Management of arthropod pathogen vectors in North America: minimizing adverse effects on pollinators. J. Med. Entomol 54, 1463–1475. [PubMed: 28968680]

Ginsberg HS, Hickling GJ, Burke RL, Ogden NH, Beati L, LeBrun RA, Arsnoe IM, Gerhold R, Han S, Jackson K, Maestas L, Moody T, Pang G, Ross B, Rulison EL, Tsao JI, 2021. Why Lyme disease is common in the northern US, but rare in the south: the roles of host choice, host-seeking behavior, and tick density. PLoS. Biol 19, e3001066. [PubMed: 33507921]

Goddard J, 1993. Ecological studies of *Ixodes scapularis* (Acari: Ixodidae) in central Mississippi: lateral movement of adult ticks. J. Med. Entomol 30, 824–826. [PubMed: 8360912]

Godsey MS Jr., Savage HM, Burkhalter KL, Bosco-Lauth AM, Delorey MJ, 2016. Transmission of Heartland virus (Bunyaviridae: *Phlebovirus*) by experimentally infected *Amblyomma americanum* (Acari: Ixodidae). J. Med. Entomol 53, 1226–1233. [PubMed: 27330103]

Godsey MS Jr., Rose D, Burkhalter KL, Breuner N, Bosco-Lauth AM, Kosoy OI, Savage HM, 2021. Experimental infection of *Amblyomma americanum* (Acari: Ixodidae) with Bourbon virus (Orthomyxoviridae: *Thogotovirus*). J. Med. Entomol 58, 873–879. [PubMed: 33710315]

Goethert H, O'Callahan A, Johnson R, Roden-Reynolds P, Telford S III, 2025. Minor hosts have a major impact on the enzootic transmission of *Borrelia burgdorferi*. Am. J. Trop. Med. Hyg 112, 101–110. [PubMed: 39531726]

Gomes-Solecki MJC, Brisson DR, Dattwyler RJ, 2006. Oral vaccine that breaks the transmission cycle of the Lyme disease spirochete can be delivered via bait. Vaccine 24, 4440–4449. [PubMed: 16198456]

Gomes-Solecki M, Arnaboldi PM, Backenson PB, Benach JL, Cooper CL, Dattwyler RJ, Diuk-Wasser M, Fikrig E, Hovius JW, Laegreid W, Lundberg U, Marconi RT, Marques AR, Molloy P, Narasimhan S, Pal U, Pedra JHF, Plotkin S, Rock DL, Rosa P, Telford SR III, Tsao J, Yang XF, Schutzer SE, 2020. Protective immunity and new vaccines for Lyme disease. Clin. Infect. Dis 70, 1768–1773. [PubMed: 31620776]

Gould LH, Nelson RS, Griffith KS, Hayes EB, Piesman J, Mead PS, Cartter ML, 2008. Knowledge, attitudes, and behaviors regarding Lyme disease prevention among Connecticut residents, 1999–2004. Vector. Borne Zoonotic. Dis 8, 769–776. [PubMed: 18637724]

Graf J-F, Gogolewski R, Leach-Bing N, Sabatini GA, Molento MB, Bordin EL, Arantes GJ, 2004. Tick control: an industry point of view. Parasitology. 129, S427–S442. [PubMed: 15938522]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Grant AN, Lineberry MW, Sundstrom KD, Allen KE, Little SE, 2023. Geographic distribution and seasonality of brown dog tick lineages in the United States. J. Med. Entomol 60, 102–111. [PubMed: 36342085]

Gray JS, 1985. A carbon dioxide trap for prolonged sampling of *Ixodes ricinus* populations. Exp. Appl. Acarol 1, 35–44. [PubMed: 3939717]

Gray J, Dantas-Torres F, Estrada-Peña A, Levin M, 2013. Systematics and ecology of the brown dog tick, *Rhipicephalus sanguineus*. Ticks. Tick. Borne Dis 4, 171–180. [PubMed: 23415851]

Gray J, Kahl O, Zintl A, 2021. What do we still need to know about *Ixodes ricinus*? Ticks. Tick. Borne Dis 12, 101682. [PubMed: 33571753]

Gregory N, Fernandez MP, Diuk-Wasser M, 2022. Risk of tick-borne pathogen spillover into urban yards in New York City. Parasit. Vectors 15, 288. [PubMed: 35948911]

Hahn MB, Bjork JKH, Neitzel DF, Dorr FM, Whitemarsh T, Boegler KA, Graham CB, Johnson TL, Maes SE, Eisen RJ, 2018. Evaluating acarological risk for exposure *to Ixodes scapularis* and *Ixodes scapularis*-borne pathogens in recreational and residential settings in Washington County. Minnesota. Ticks Tick Borne Dis 9, 340–348. [PubMed: 29195857]

Hahn MB, Disler G, Durden LA, Coburn S, Witmer F, George W, Beckmen K, Gerlach R, 2020. Establishing a baseline for tick surveillance in Alaska: tick collection records from 1909–2019. Ticks. Tick. Borne Dis 11, 101495. [PubMed: 32723642]

Hansen AP, Wilkinson MM, Niesobecki S, Rutz H, Meek JI, Niccolai L, Hinckley AF, Hook S, 2025. Barriers to the uptake of tickborne disease prevention measures: Connecticut, Maryland 2016–2017. J. Public Health Manage Pract 31, E52–E60.

Harrington LC, Mader EM, 2023. Northeast Regional Center for Excellence in Vector-Borne Diseases' Master of Science training program: a curriculum to support future capacity in public health entomology. J. Med. Entomol 60, 865–874. [PubMed: 37531091]

Harris EK, Foy BD, Ebel GD, 2023. Colorado tick fever virus: a review of historical literature and research emphasis for a modern era. J. Med. Entomol 60, 1214–1220. [PubMed: 37862094]

Hart CE, Bhaskar JR, Reynolds E, Hermance M, Earl M, Mahoney M, Martinez A, Petzlova I, Esterly AT, Thangamani S, 2022. Community engaged tick surveillance and *tick*MAP as a public health tool to track the emergence of ticks and tick-borne diseases in New York. PLOS. Glob. Public Health 2, 0000215.

Hayes EB, Piesman J, 2003. Current concepts - how can we prevent Lyme disease? N. Engl. J. Med 348, 2424–2430. [PubMed: 12802029]

Hinckley AF, Meek JI, Ray JAE, Niesobecki SA, Connally NP, Feldman KA, Jones EH, Backenson PB, White JL, Lukacik G, Kay AB, Miranda WP, Mead PS, 2016. Effectiveness of residential acaricides to prevent Lyme and other tick-borne diseases in humans. J. Clin. Dis 214, 182–188.

Hinckley AF, Niesobecki SA, Connally NP, Hook SA, Biggerstaff BJ, Horiuchi KA, Hojgaard A, Mead PS, 2021. Prevention of Lyme and other tickborne diseases using a rodent-targeted approach: a randomized controlled trial in Connecticut. Zoonoses. Public Health 68, 578–587. [PubMed: 34050628]

Holcomb KM, Foster E, Eisen RJ, 2025. Estimating the density of questing *Ixodes scapularis* nymphs in the eastern United States using climate and land cover data. Ticks. Tick. Borne Dis 16, 102446. [PubMed: 40057413]

Hoogstraal H, Roberts FH, Kohls GM, Tipton VJ, 1968. Review of *Haemaphysalis* (*Kaiseriana*) *longicornis* Neumann (resurrected) of Australia, New Zealand, New Caledonia, Fiji, Japan, Korea, and Northeastern China and USSR, and its parthenogenetic and bisexual populations (Ixodoidea, Ixodidae). J. Parasitol 54, 1197–1213. [PubMed: 5757695]

Hook SA, Nelson CA, Mead PS, 2015. U.S. public's experience with ticks and tick-borne diseases: results from national HealthStyles surveys. Ticks. Tick. Borne Dis 6, 483–488. [PubMed: 25887156]

Hook SA, Nawrocki CC, Meek JI, Feldman KA, White JL, Connally NP, Hinckley AF, 2021. Human-tick encounters as a measure of tickborne disease risk in Lyme disease endemic areas. Zoonoses. Public Health 68, 384–392. [PubMed: 33554467]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Hornbostel VL, Krall RK, Reid JJ, Schappach JL, Volpe S, Connally NP, 2021. *Spray safe, play safe:* story-based films increase homeowner confidence about backyard tick management. J. Med. Entomol 58, 857–865. [PubMed: 33225365]

Hyland KE, Bernier J, Markowski D, MacLachlan AB, Amr Z, Pitocchelli J, Myers JE, Hu R, 2000. Records of ticks (Acari: Ixodidae) parasitizing birds (Aves) in Rhode Island, USA. Int. J. Acarol 26, 183–192.

Jackson LE, Hilborn ED, Thomas JC, 2006. Towards landscape design guidelines for reducing Lyme disease risk. Int. J. Epidemiol 35, 315–322. [PubMed: 16394113]

James AM, Freier JE, Keirans JE, Durden LA, Mertins JW, Schlater JL, 2006. Distribution, seasonality, and hosts of the Rocky Mountain wood tick in the United States. J. Med. Entomol 43, 17–24. [PubMed: 16506443]

James AM, Burdett C, McCool MJ, Fox A, Riggs P, 2015. The geographic distribution and ecological preferences of the American dog tick, *Dermacentor variabilis* (Say), in the USA. Med. Vet. Entomol 29, 178–188. [PubMed: 25684582]

Jones EH, Chanlongbutra A, Wong D, Cunningham F, Feldman KA, 2015. Knowledge, attitudes, and practices regarding Lyme disease prevention among employees, day visitors, and campers at Greenbelt Park. Park. Sci 32, 46–53.

Jordan RA, Egizi A, 2019. The growing importance of lone star ticks in a Lyme disease endemic county: passive tick surveillance in Monmouth County, NJ, 2006–2016. PLoS. One 14, e0211778. [PubMed: 30753233]

Jordan RA, Schulze TL, 2019. Ability of two commercially available host-targeted technologies to reduce abundance of *Ixodes scapularis* (Acari: Ixodidae) in a residential landscape. J. Med. Entomol 56, 1095–1101. [PubMed: 30984975]

Jordan RA, Schulze TL, 2020a. Availability and nature of commercial tick control services in three Lyme disease endemic states. J. Med. Entomol 57, 807–814. [PubMed: 31794013]

Jordan RA, Schulze TL, 2020b. Artificial accumulation of leaf litter in forest edges on residential properties via leaf blowing is associated with increased numbers of host-seeking *Ixodes scapularis* (Acari: Ixodidae) nymphs. J. Med. Entomol 57, 1193–1198. [PubMed: 32186344]

Jordan RA, Eisen L, Schulze TL, 2024. Willingness and ability of existing mosquito control and public health agencies in New Jersey to assume responsibilities for management of ticks and tick-borne disease. J. Med. Entomol 61, 1051–1063.

Kache PA, Bron GM, Zapata-Ramirez S, Tsao JI, Bartholomay LC, Paskewitz SM, Diuk-Wasser MA, del Pilar Fernandez M, 2023. Evaluating spatial and temporal patterns of tick exposure in the United States using community science data submitted through a smartphone application. Ticks. Tick. Borne Dis 14, 102163. [PubMed: 37001417]

Kahl O, Gray JS, 2023. The biology of *Ixodes ricinus* with emphasis on its ecology. Ticks. Tick. Borne Dis 14, 102114. [PubMed: 36603231]

Kahl O, Levin M, Beard CB, 2023. An Annotated Reprint of Yu. S. Balashov's 1972 Book Bloodsucking Ticks (Ixodoidea) - Vectors of Diseases of Man and Animals. Entomological Society of America, Annapolis, MD, USA.

Kaup B, 2018. The making of Lyme disease: a political ecology of ticks and tick-borne illness in Virginia. Environ. Sociol 4, 381–391.

Keesing F, Mowry S, Bremer W, Duerr S, Evans AS Jr., Fischhoff IR, Hinckley AF, Hook SA, Keating F, Pendleton J, Pfister A, Teator M, Ostfeld RS, 2022. Effects of tick-control interventions on tick abundance, human encounters with ticks, and incidence of tickborne diseases in residential neighborhoods, New York, USA. Emerg. Infect. Dis 28, 957–966. [PubMed: 35447066]

Keirans JE, Hutcheson HJ, Durden LA, Klompen JSH, 1996. *Ixodes* (*Ixodes*) *scapularis* (Acari: Ixodidae): redescription of all active stages, distribution, hosts, geographical variation, and medical and veterinary importance. J. Med. Entomol 33, 297–318. [PubMed: 8667375]

Kensinger BJ, Allan BF, 2011. Efficacy of dry ice-baited traps for sampling *Amblyomma americanum* (Acari: Ixodidae) varies with life stage but not habitat. J. Med. Entomol 48, 708–711. [PubMed: 21661336]

Kersh GJ, Salzer J, Jones ES, Binder AM, Armstrong PA, Choudhary SK, Commins GK, Amelio CL, Kato CY, Singleton J, Biggerstaff BJ, 2023. Tick bite as a risk factor for alpha-gal–specific

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

immunoglobulin E antibodies and development of alpha-gal syndrome. Ann. Allergy Asthma Immunol 130, 472–478. [PubMed: 36574585]

Kilpatrick HJ, LaBonte AM, Stafford KC III, 2014. The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community. J. Med. Entomol 51, 777–784. [PubMed: 25118409]

Kjellander P, Bergvall UA, Chirico J, Ullman K, Christensson M, Lindgren PE, 2023. Winter activity of *Ixodes ricinus* in Sweden. Parasit. Vectors 16, 229. [PubMed: 37430316]

Koch HG, McNew RW, 1982. Sampling of lone star ticks (Acari: Ixodidae): dry ice quantity and capture success. Ann. Entomol. Soc. Am 75, 579–582.

Kollars TM Jr., Oliver JH Jr., Durden LA, Kollars PG, 2000a. Host associations and seasonal activity of *Amblyomma americanum* (Acari: Ixodidae) in Missouri. J. Parasitol 86, 1156–1159. [PubMed: 11128501]

Kollars TM Jr., Oliver JH Jr., Masters EJ, Kollars PG, Durden LA, 2000b. Host utilization and seasonal occurrence of *Dermacentor* species (Acari: Ixodidae) in Missouri, USA. Exp. Appl. Acarol 24, 631–643. [PubMed: 11201355]

Kopsco HL, Mather TN, 2022. Tick-borne disease prevention behaviors among participants in a tick surveillance system compared with a sample of master gardeners. J. Community Health 47, 246–256. [PubMed: 34727297]

Kopsco HL, Duhaime RJ, Mather TN, 2021. Crowdsourced tick image-informed updates to U.S. county records of three medically important tick species. J. Med. Entomol 58, 2412–2424. [PubMed: 33973636]

Koser TM, Déry F, Spitz B, Chenery ES, 2025. Gaps and opportunities in on-host winter tick (*Dermacentor albipictus*) surveillance in North America. J. Wildl. Manage 89, e22726.

Kugeler KJ, Jordan RA, Schulze TL, Griffith KS, Mead PS, 2016. Will culling white-tailed deer prevent Lyme disease? Zoonoses. Public Health 63, 337–345. [PubMed: 26684932]

Kugeler KJ, Schwartz AM, Delorey MJ, Mead PS, Hinckley AF, 2021. Estimating the frequency of Lyme disease diagnoses, United States, 2010–2018. Emerg. Infect. Dis 27, 616–619. [PubMed: 33496229]

Lado P, Glon MG, Klompen H, 2021. Integrative taxonomy of *Dermacentor variabilis* (Ixodida: Ixodidae) with description of a new species, *Dermacentor similis* n. sp. J. Med. Entomol 58, 2216–2227. [PubMed: 34378782]

Lane RS, Steinlein DB, Mun J, 2004. Human behaviors elevating exposure to *Ixodes pacificus* (Acari: Ixodidae) nymphs and their associated bacterial zoonotic agents in a hardwood forest. J. Med. Entomol 41, 239–248. [PubMed: 15061284]

Lavender DR, Oliver JH Jr., 1996. Ticks (Acari: Ixodidae) in Bulloch County. Georgia. J. Med. Entomol 33, 224–231. [PubMed: 8742526]

Lawless KA, Brown SW, Cartter M, 1997. Applying educational psychology and instructional technology to health care issues: combating Lyme disease. Int. J. Instr. Media 24, 287–297.

Lehane A, Maes SE, Graham CB, Jones E, Delorey M, Eisen RJ, 2021. Prevalence of single and coinfections of human pathogens in *Ixodes* ticks from five geographical regions in the United States, 2013–2019. Ticks. Tick. Borne Dis 12, 101637. [PubMed: 33360805]

Lindquist EE, Galloway TD, Artsob H, Lindsay LR, Drebot M, Wood H, Robbins RG, 2016. A Handbook to the Ticks of Canada (Ixodida: Ixodidae, Argasidae). Biological Survey of Canada, Victoria, Canada.

Linske MA, Williams SC, 2024. Evaluation of landscaping and vegetation management to suppress host-seeking *Ixodes scapularis* (Ixodida: Ixodidae) nymphs on residential properties in Connecticut, USA. Environ. Entomol 53, 268–276. [PubMed: 38376061]

Little EAH, Anderson JF, Stafford KC III, Eisen L, Eisen RJ, Molaei G, 2019. Predicting spatiotemporal patterns of Lyme disease incidence from passively collected surveillance data for *Borrelia burgdorferi* sensu lato-infected *Ixodes scapularis* ticks. Ticks. Tick. Borne Dis 10, 970–980. [PubMed: 31101553]

Loss SR, Noden BH, Hamer GL, Hamer SA, 2016. A quantitative synthesis of the role of birds in carrying ticks and tick-borne pathogens in North America. Oecologia 182, 947–959. [PubMed: 27670413]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Macaluso KR, Paddock CD, 2014. Tick-borne spotted fever group rickettsiosis and *Rickettsia* species. In: Sonenshine DE, Roe RM (Eds.), Biology of Ticks, Biology of Ticks, 2. Oxford University Press, New York, NY, USA, pp. 211–250 second ed.

MacDonald AJ, Larsen AE, Plantinga AJ, 2019. Missing the people for the trees: identifying coupled natural–human system feedbacks driving the ecology of Lyme disease. J. Appl. Ecol 56, 354–364.

Mader EM, Ganser C, Geiger A, Harrington LC, Foley J, Smith RL, Mateus-Pinilla N, Teel PD, Eisen RJ, 2021. A survey of tick surveillance and control practices in the United States. J. Med. Entomol 58, 1503–1512. [PubMed: 34270770]

Maestas LP, Mays SE, Britten HB, Auckland LD, Hamer SA, 2018. Surveillance for *Ixodes scapularis* (Acari: Ixodidae) and *Borrelia burgdorferi* in eastern South Dakota State Parks and nature areas. J. Med. Entomol 55, 1549–1554. [PubMed: 29939293]

Malouin R, Winch P, Leontsini E, Glass G, Simon D, Hayes EB, Schwartz BS, 2003. Longitudinal evaluation of an educational intervention for preventing tick bites in an area with endemic Lyme disease in Baltimore County, Maryland. Am. J. Epidemiol 157, 1039–1051. [PubMed: 12777368]

Marshall DS, Poh KC, Reichard MV, Starkey LA, Owen JP, 2025. Spatial and temporal activity patterns of *Amblyomma americanum*. Parasit. Vectors 18, 12. [PubMed: 39819362]

Matuschka FR, Richter D, Fischer P, Spielman A, 1990. Time of repletion of subadult *Ixodes ricinus* ticks feeding on diverse hosts. Parasitol. Res 76, 540–544. [PubMed: 2381897]

Maupin GO, Fish D, Zultowsky J, Campos EG, Piesman J, 1991. Landscape ecology of Lyme disease in a residential area of Westchester County. Am. J. Epidemiol 133, 1105–1113. [PubMed: 2035514]

McCabe RE, McCabe TR, 1984. Whitetail biology and ecology: of slings and arrows - an historical retrospection. In: Halls LK (Ed.), White-Tailed Deer: Ecology and Management. Stackpole Books, Harrisburg, PA, USA, pp. 19–72.

McClure M, Diuk-Wasser M, 2018. Reconciling the entomological hazard and disease risk in the Lyme disease system. Int. J. Environ. Res. Public Health 15, 1048. [PubMed: 29789489]

McDonald JS, Miller KV, 2004. A History of White-tailed Deer Restocking in the United States 1878 to 2004. Quality Deer Management Association, Bogart, GA, USA.

Mead P, Hook S, Niesobecki S, Ray J, Meek J, Delorey M, Prue C, Hinckley A, 2018. Risk factors for tick exposure in suburban settings in the northeastern United States. Ticks. Tick. Borne Dis 9, 319–324. [PubMed: 29174449]

Merino O, Alberdi P, Pérez de la Lastra JM, de la Fuente J, 2013. Tick vaccines and the control of tick-borne pathogens. Front. Cell Infect. Microbiol 3, 30. [PubMed: 23847771]

Merrill MM, Boughton RK, Lord CC, Sayler KA, Wight B, Anderson WM, Wisely SM, 2018. Wild pigs as sentinels for hard ticks: a case study from south-central Florida. Int. J. Parasitol.: Parasit. Wildl 7, 161–170.

Mitchell CL, Lin F-C, Vaughn M, Apperson CS, Meshnick SR, Commins SC, 2020. Association between lone star tick bites and increased alpha-gal sensitization: evidence from a prospective cohort of outdoor workers. Parasit. Vectors 13, 470. [PubMed: 32928302]

Molaei G, Little EAH, Khalil N, Ayres BN, Nicholson WL, Paddock CD, 2021. Established population of the Gulf Coast tick, *Amblyomma maculatum* (Acari: Ixodidae), infected with *Rickettsia parkeri* (Rickettsiales: Rickettsiaceae), in Connecticut. J. Med. Entomol 58, 1459–1462. [PubMed: 33458776]

Mulla MS, 1994. Mosquito control then, now, and in the future. J. Am. Mosquito Contr. Assoc 10, 574–584.

Musnoff BL, Cuadera MKQ, Birney MR, Zipper L, Nicholson W, Ayres B, Cervantes K, Woell D, Occi JL, 2024. The first record of an established population of *Amblyomma maculatum* (Acari: Ixodidae) in New Jersey, USA. J. Med. Entomol 61, 1081–1085. [PubMed: 38712431]

Namgyal J, Couloigner I, Lysyk TJ, Dergousoff SJ, Cork SC, 2020. Comparison of habitat suitability models for *Haemaphysalis longicornis* Neumann in North America to determine its potential geographic range. Int. J. Environ. Res. Public Health 17, 8285. [PubMed: 33182472]

Narasimhan S, Fish D, Pedra JH, Pal U, Fikrig E, 2023. A ticking time bomb hidden in plain sight. Sci. Transl. Med 15, eadi7829.

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Nawrocki CC, Hinckley AF, 2021. Experiences with tick exposure, Lyme disease, and use of personal prevention methods for tick bites among members of the U.S. population, 2013–2015. Ticks. Tick. Borne Dis 12, 101605. [PubMed: 33217712]

Nawrocki CC, Piedmonte N, Niesobecki SA, Rowe A, Hansen AP, Kaufman A, Foster E, Meek JI, Niccolai L, White J, Backenson B, Eisen L, Hook SA, Connally NP, Hornbostel VL, Hinckley AF, 2023. Acceptability of 4-poster deer treatment devices for community-wide tick control among residents of high Lyme disease incidence counties in Connecticut and New York, USA. Ticks. Tick. Borne Dis 14, 102231. [PubMed: 37531890]

Nelder MP, Russell CB, Clow KM, Johnson S, Weese JS, Cronin K, Ralevski F, Jardine CM, Patel SN, 2019. Occurrence and distribution of *Amblyomma americanum* as determined by passive surveillance in Ontario, Canada (1999–2016). Ticks. Tick. Borne Dis (10), 146–155. [PubMed: 30337263]

Nielsen LE, Cortinas R, Fey PD, Iwen PC, Nielsen DH, 2020. First records of established populations of *Ixodes scapularis* (Acari: Ixodidae) collected from three Nebraska counties. J. Med. Entomol 57, 939–941. [PubMed: 31776568]

Niesobecki S, Hansen A, Rutz H, Mehta S, Feldman K, Meek J, Niccolai L, Hook S, Hinckley A, 2019. Knowledge, attitudes, and behaviors regarding tick-borne disease prevention measures in endemic areas. Ticks. Tick. Borne Dis 10, 101264. [PubMed: 31431351]

Niesobecki S, Rutz H, Niccolai L, Hook S, Feldman K, Hinckley A, 2022. Willingness to pay for select tick-borne disease prevention measures in endemic areas. J. Public Health Manage. Pract 28, E37–E42.

NIH (National Institutes of Health), 2025. An Efficacy, Safety, Tolerability, Immunogenicity, and Lot-Consistency Clinical Trial of a 6-Valent OspA-Based Lyme Disease Vaccine (VLA15) (VALOR). Accessed 19 August, 2025. https://www.clinicaltrials.gov/study/NCT05477524.

NOAA (National Oceanic and Atmospheric Administration), 2025. U.S. Climate Regions Accessed 19 August, 2025, https://www.ncei.noaa.gov/access/monitoring/reference-maps/us-climate-regions.

Occi JL, Egizi AM, Robbins RG, Fonseca DM, 2019. Annotated list of the hard ticks (Acari: Ixodida: Ixodidae) of New Jersey. J. Med. Entomol 56, 589–598. [PubMed: 30753552]

Ogden NH, Trudel L, Artsob H, Barker IK, Beauchamp G, Charron D, Drebot MA, Galloway TD, O'Handley R, Thompson RA, Lindsay LR, 2006. Ixodes scapularis ticks collected by passive surveillance in Canada: analysis of geographic distribution and infection with the Lyme borreliosis agent *Borrelia burgdorferi*. J. Med. Entomol 43, 600–609. [PubMed: 16739422]

Ogden NH, Lindsay LR, Hanincova K, Barker IK, Bigras-Poulin M, Charron DF, Heagy A, Francis CM, O'Callaghan CJ, Schwartz I, Thompson RA, 2008. Role of migratory birds in introduction and range expansion of *Ixodes scapularis* ticks, and *Borrelia burgdorferi* and *Anaplasma phagocytophilum* in Canada. Appl. Environ. Microbiol 74, 1780–1790. [PubMed: 18245258]

Olsén B, Jaenson TGT, Bergström S, 1995. Prevalence of *Borrelia burgdorferi* sensu lato-infected ticks on migrating birds. Appl. Environ. Microbiol 61, 3082–3087. [PubMed: 7487041]

Osikowicz LM, Rizzo MR, Hojgaard A, Maes SE, Eisen RJ, 2024. Detection of *Borrelia burgdorferi* sensu lato species in host-seeking *Ixodes* species ticks in the United States. Ticks. Tick. Borne Dis 15, 102270. [PubMed: 37813001]

Ost K, Norman M, Dumas A, Corrin T, Waddell L, Schryer R, Duguay C, Facchin O, Zinszer K, Rocheleau J-P, Bouchard C, Aenishaenslin C, Krentel A, Feng C, Kulkarni MA, 2025. A systematic review of the effectiveness and utility of Lyme disease prevention measures in Canada, the United States, and Europe. BMC. Infect. Dis 25, 889. [PubMed: 40604446]

Ostfeld RS, Keesing F, 2023. Does experimental reduction of blacklegged tick (*Ixodes scapularis*) abundance reduce Lyme disease incidence? Pathogens. 12, 714. [PubMed: 37242384]

Ostfeld RS, Keesing F, 2026. Ecological and epidemiological consequences of tick-control interventions in residential neighborhoods: a synthesis of The Tick Project. Transbound. Emerg. Dis, 4940832, 2026.

Ostfeld RS, Mowry S, Bremer W, Duerr S, Evans AS, Fischhoff IR, Hinckley AF, Hook SA, Keating F, Pendleton J, Pfister A, Teator M, Keesing F, 2023. Impacts over time of neighborhood-scale interventions to control ticks and tick-borne disease incidence. Vector. Borne Zoonotic. Dis 23, 89–105. [PubMed: 36848248]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Paddock CD, Goddard J, 2015. The evolving medical and veterinary importance of the Gulf Coast tick (Acari: Ixodidae). J. Med. Entomol 52, 230–252. [PubMed: 26336308]

Paddock CD, Yabsley MJ, 2007. Ecological havoc, the rise of white-tailed deer, and the emergence of *Amblyomma americanum*-associated zoonoses in the United States. Curr. Topics Microbiol. Immunol 315, 289–324.

Paddock CD, Zambrano ML, Clover JR, Ladd-Wilson S, Dykstra EA, Salamone A, Kangiser D, Ayres BN, Shooter SL, Karpathy SE, Kjemtrup AM, 2024. *Rickettsia* species identified in adult, host-seeking *Dermacentor occidentalis* (Acari: Ixodidae) from Baja California, Mexico, and Oregon and Washington, United States. J. Med. Entomol 61, 781–790. [PubMed: 38408183]

Paddock CD, Karpathy SE, Henry A, Ryle L, Hecht JA, Hacker JK, Padgett KA, Kjemtrup AM, Bullock H, Lane RS, Ladner JT, 2025. *Rickettsia rickettsii* subsp *californica* subsp nov, the etiologic agent of Pacific Coast tick fever. J. Infect. Dis 231, 849–858. [PubMed: 39432903]

Pandey M, Piedmonte NP, Vinci VC, Falco RC, Daniels TJ, Clark JA, 2022. First detection of the invasive Asian longhorned tick (Acari: Ixodidae) on migratory passerines in the Americas. J. Med. Entomol 59, 2176–2181. [PubMed: 36166571]

Patterson GM, 2016. Looking backward, looking forward: the long, torturous struggle with mosquitoes. Insects. 7, 56. [PubMed: 27775554]

Pelletier J, Rocheleau J-P, Bouchard C, Baron G, Coatsworth H, Dibernardo A, Fernandez-Prada C, Ogden NH, Potes L, Leighton PA, Aenishaenslin C, 2025. Rodent-targeted fluralaner baiting reduces the density of *Borrelia burgdorferi*-infected questing *Ixodes scapularis* ticks in a peri-urban setting in southern Canada. Ticks. Tick. Borne Dis 16, 102467. [PubMed: 40086203]

Perkins SE, Cattadori IM, Tagliapietra V, Rizzoli AP, Hudson PJ, 2006. Localized deer absence leads to tick amplification. Ecology. 87, 1981–1986. [PubMed: 16937637]

Petersen LR, Beard CB, Visser SN, 2019. Combatting the increasing threat of vector-borne disease in the United States with a national vector-borne disease prevention and control system. Am. J. Trop. Med. Hyg 100, 242–245. [PubMed: 30499427]

Pfister K, Armstrong R, 2016. Systemically and cutaneously distributed ectoparasiticides: a review of the efficacy against ticks and fleas on dogs. Parasit. Vectors 9, 436. [PubMed: 27502490]

Piesman J, Eisen L, 2008. Prevention of tick-borne diseases. Annu. Rev. Entomol 53, 323–343. [PubMed: 17877457]

Piesman J, Spielman A, 1979. Host-associations and seasonal abundance of immature *Ixodes dammini* in southeastern Massachusetts. Ann. Entomol. Soc. Am 72, 829–832.

Piesman J, Spielman A, Etkind P, Ruebush II TK, Juranek DD, 1979. Role of deer in the epizootiology of *Babesia microti* in Massachusetts USA. J. Med. Entomol 15, 537–540. [PubMed: 544828]

Plotkin SA, Shapiro ED, 2024. The current and future state of vaccines for Lyme disease. Clin. Infect. Dis 81, 687–692.

Poché DM, Franckowiak G, Clarke T, Tseveenjav B, Polyakova L, Poché RM, 2020. Efficacy of a low dose fipronil bait against blacklegged tick (*Ixodes scapularis*) larvae feeding on white-footed mice (*Peromyscus leucopus*) under laboratory conditions. Parasit. Vectors 13, 391. [PubMed: 32736585]

Poché DM, Wagner D, Green K, Smith Z, Hawthorne N, Tseveenjav B, Poché RM, 2023b. Development of a low-dose fipronil deer feed: evaluation of efficacy against two medically important tick species parasitizing white-tailed deer (*Odocoileus virginianus*) under pen conditions. Parasit. Vectors 16, 94. [PubMed: 36894942]

Poché DM, Wagner D, Hawthorne N, Tseveenjav B, Poché RM, 2023a. Development of a low-dose fipronil deer feed: bait-screening and range-finding to determine the optimal formulation to control blacklegged ticks *(Ixodes scapularis)* feeding on white-tailed deer *(Odocoileus virginianus)*. J. Vector. Ecol 48, 103–112. [PubMed: 37843452]

Poland GA, 2001. Prevention of Lyme disease: a review of the evidence. Mayo Clin. Proc 76, 713–724. [PubMed: 11444404]

Porter WT, Motyka PJ, Wachara J, Barrand ZA, Hmood Z, McLaughlin M, Pemberton K, Nieto NC, 2019. Citizen science informs human-tick exposure in the Northeastern United States. Int. J. Health Geogr 18, 9. [PubMed: 31064416]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Potes L, Bouchard C, Rocheleau J-P, Richard L, Leighton P, Pelletier J, Baron G, Aenishaenslin C, 2023. Evaluation of a community-based One Health intervention to reduce the risk of Lyme disease in a high-incidence municipality. CABI One Health 2, ohcs202300017.

Pound JM, Miller JA, George JE, Oehler DD, Harmel DE, 1996. Systemic treatment of white-tailed deer with ivermectin-medicated bait to control free-living populations of lone star ticks (Acari: Ixodidae). J. Med. Entomol 33, 385–394. [PubMed: 8667385]

Pound JM, Miller JA, George JE, Fish D, Carroll JF, Schulze TL, Daniels TJ, Falco RC, Stafford KC III, Mather TN, 2009. The United States Department of Agriculture's northeast area-wide tick control project: summary and conclusions. Vector. Borne Zoonotic. Dis 9, 439–448. [PubMed: 19650739]

Raghavan RK, Barker SC, Cobos ME, Barker D, Teo EJM, Foley DH, Nakao R, Lawrence K, Heath ACG, Peterson AT, 2019. Potential spatial distribution of the newly introduced long-horned tick, *Haemaphysalis longicornis* in North America. Sci. Rep 9, 498. [PubMed: 30679711]

Rainey T, Occi JL, Robbins RG, Egizi A, 2018. Discovery of *Haemaphysalis longicornis* (Ixodida: Ixodidae) parasitizing a sheep in New Jersey, United States. J. Med. Entomol 55, 757–759. [PubMed: 29471482]

Rand PW, Lacombe EH, Smith RP Jr., Ficker J, 1998. Participation of birds (Aves) in the emergence of Lyme disease in southern Maine. J. Med. Entomol 35, 270–276. [PubMed: 9615546]

Rand PW, Lacombe EH, Holman MS, Lubelczyk C, Smith RP Jr., 2000. Attempt to control ticks (Acari: Ixodidae) on deer on an isolated island using ivermectin-treated corn. J. Med. Entomol 37, 126–133. [PubMed: 15218916]

Rand PW, Lubelczyk C, Holman MS, Lacombe EH, Smith RP Jr., 2004. Abundance of *Ixodes scapularis* (Acari: Ixodidae) after the complete removal of deer from an isolated offshore island, endemic for Lyme disease. J. Med. Entomol 41, 779–784. [PubMed: 15311475]

Rand PW, Lacombe EH, Dearborn R, Cahill B, Elias S, Lubelczyk CB, Beckett GA, Smith RP Jr., 2007. Passive surveillance in Maine, an area emergent for tick-borne diseases. J. Med. Entomol 44, 1118–1129. [PubMed: 18047214]

Raney WR, Herslebs EJ, Langohr IM, Stone MC, Hermance ME, 2022a. Horizontal and vertical transmission of Powassan virus by the invasive Asian longhorned tick, *Haemaphysalis longicornis*, under laboratory conditions. Front. Cell Infect. Microbiol 12, 923914. [PubMed: 35846754]

Raney WR, Perry JB, Hermance ME, 2022b. Transovarial transmission of Heartland virus by invasive Asian longhorned ticks under laboratory conditions. Emerg. Infect. Dis 28, 726–729. [PubMed: 35202534]

Rego ROM, Trentelman JJA, Anguita J, Nijhof AM, Sprong H, Klempa B, Hajdusek O, Tomás-Cortázar J, Azagi T, Strnad M, Knorr S, Sima R, Jalovecka M, Fumačová Havlíková S, Ličková M, Slaviková M, Kopacek P, Grubhoffer L, Hovius JW, 2019. Counterattacking the tick bite: towards a rational design of anti-tick vaccines targeting pathogen transmission. Parasit. Vectors 12, 229. [PubMed: 31088506]

Rochlin I, 2019. Modeling the Asian longhorned tick (Acari: Ixodidae) suitable habitat in North America. J. Med. Entomol 56, 384–391. [PubMed: 30544234]

Rochlin I, Ninivaggi DV, Benach JL, 2019. Malaria and Lyme disease - the largest vector-borne US epidemics in the last 100 years: success and failure of public health. BMC. Public Health 19, 804. [PubMed: 31234827]

Rochlin I, Egizi A, Lindström A, 2022. The original scientific description of the lone star tick (*Amblyomma americanum*, Acari: Ixodidae) and implications for the species' past and future geographic distributions. J. Med. Entomol 59, 412–420. [PubMed: 35024845]

Rochlin I, Kenney J, Little E, Molaei G, 2025. Public health significance of the white-tailed deer (*Odocoileus virginianus*) and its role in the eco-epidemiology of tick- and mosquito-borne diseases in North America. Parasit. Vectors 18, 43. [PubMed: 39915849]

Rollend L, Fish D, Childs JE, 2013. Transovarial transmission of *Borrelia* spirochetes by *Ixodes scapularis*: a summary of the literature and recent observations. Ticks. Tick. Borne Dis 4, 46–51. [PubMed: 23238242]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Roselli MA, Noden BH, Loss SR, 2022. Tick infestation of birds across a gradient of urbanization intensity in the United States Great Plains. Urban. Ecosyst 25, 379–391.

Rosenberg R, Lindsey NP, Fischer M, Gregory CJ, Hinckley AF, Mead PS, Paz-Bailey G, Waterman SH, Drexler NA, Kersh GJ, Hooks H, Partridge SK, Visser SN, Beard CB, Petersen LR, 2018. Vital signs: trends in reported vectorborne disease cases — United States and Territories, 2004–2016. Morb. Mortal. Wkly. Rep 67, 496–501.

Roy A, 2021. Examining mosquito and tick surveillance and control capacity at the local level. J. Public Health Manage Pract 27, 618–620.

Roy A, Gridley-Smith C, Patel K, Garofalini C, McCall TC, 2024. Vector Surveillance and Control at the Local Level: Findings from the 2023 Vector Control Assessment. National Association of County and City Health Officials, Washington, DC, USA. https://bit.ly/2023VectorReport.

Ruiz-Carrascal D, Bastard J, Williams SC, Diuk-Wasser M, 2024. Modeling platform to assess the effectiveness of single and integrated *Ixodes scapularis* tick control methods. Parasit. Vectors 17, 339. [PubMed: 39135071]

Sack A, Naumova EN, Price LL, Xu G, Rich SM, 2023. Passive surveillance of human-biting *Ixodes scapularis* ticks in Massachusetts from 2015–2019. Int. J. Environ. Res. Public Health 20, 4306. [PubMed: 36901316]

Salkeld DJ, Porter WT, Loh SM, Nieto NC, 2019. Time of year and outdoor recreation affect human exposure to ticks in California, United States. Ticks. Tick. Borne Dis 10, 1113–1117. [PubMed: 31201125]

Schiff P, Cumbie AN, Roberts A, Riley J, Eastwood G, 2025. Eastern cottontails (*Sylvilagus floridanus*) as hosts for ticks infected with *Borrelia burgdorferi, Anaplasma phagocytophilum*, and Powassan virus in Virginia, USA. J. Med. Entomol 62, 610–620. [PubMed: 39945387]

Schiffman EK, Bjork J, Phaneuf D, Beck A, Foster E, Tsao JI, Osborn R, Eisen R, Paskewitz S, Hook SA, Hinckley AF, 2025. Willingness to pay for residential property-based and community-based tick control methods in Lyme disease-endemic areas of the Upper Midwest, United States. Ticks. Tick. Borne Dis 16, 102531. [PubMed: 40773902]

Schulze TL, Jordan RA, 2006. Assessment and Management of Vector Tick Populations in New Jersey: A Guide For Pest Management Professionals, Land Managers, and Public Health Officials. Freehold Township Health Department, Freehold, New Jersey, USA.

Schulze TL, Jordan RA, 2021. Synthetic pyrethroid, natural product, and entomopathogenic fungal acaricide product formulations for sustained early season suppression of host-seeking *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae) nymphs. J. Med. Entomol 58, 814–820. [PubMed: 33215212]

Schulze TL, Jordan RW, Schulze CJ, Healy SP, Jahn MB, Piesman J, 2007. Integrated use of 4-poster passive topical treatment devices for deer, targeted acaricide applications, and Maxforce TMS bait boxes to rapidly suppress populations of *Ixodes scapularis* (Acari: Ixodidae) in a residential landscape. J. Med. Entomol 44, 830–839. [PubMed: 17915516]

Schulze TL, Jordan RW, Dolan MC, Dietrich G, Healy SP, Piesman J, 2008. Ability of 4-poster passive topical treatment devices for deer to sustain low population levels of *Ixodes scapularis* (Acari: Ixodidae) after integrated tick management in a residential landscape. J. Med. Entomol 45, 899–904. [PubMed: 18826033]

Schulze TL, Eisen L, Russell K, Jordan RA, 2023. Community-based integrated tick management programs: cost and feasibility scenarios. J. Med. Entomol 60, 1048–1060. [PubMed: 37540592]

Schwartz AM, Mackeprang JM, Mead PS, Hinckley AF, 2022. Effectiveness of personal protection measures against Lyme disease: a review of epidemiologic studies from the United States. Zoonoses. Public Health 69, 777–791. [PubMed: 35791092]

Scott JD, Fernando K, Banerjee SN, Durden LA, Byrne SK, Banerjee M, Mann RB, Morshed MG, 2001. Birds disperse ixodid (Acari: Ixodidae) and *Borrelia burgdorferi*-infected ticks in Canada. J. Med. Entomol 38, 493–500. [PubMed: 11476328]

Shadick NA, Zibit MJ, Nardone E, Demaria A, Iannaccone CK, Cui J, 2016. A school-based intervention to increase Lyme disease preventive measures among elementary school-aged children. Vector. Borne Zoonotic. Dis 16, 507–515. [PubMed: 27248436]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Shen AK, Mead PS, Beard CB, 2011. The Lyme disease vaccine - a public health perspective. Clin. Infect. Dis 52, S247–S252. [PubMed: 21217171]

Smith RC, Starkey LA, 2024. Ticks and Tick-Transmitted Diseases in cats. Today's Vet, 14. Pract, pp. 26–32. November/December.

Smith RP Jr., Rand PW, Lacombe EH, Morris SR, Holmes DW, Caporale DA, 1996. Role of bird migration in the long-distance dispersal of *Ixodes dammini*, the vector of Lyme disease. J. Infect. Dis 174, 221–224. [PubMed: 8656000]

Soliman M, Williams GM, Ali MM, Preidel A, Cervantes K, Bickerton M, Woell D, Yadav U, Castellanos MM, Nicholson WL, Ayres BN, 2025. First finding of *Rickettsia rickettsii* in Haemaphysalis longicornis (Acari: Ixodidae) in North America. J. Med. Entomol 62, 1635–1639. [PubMed: 40986409]

Sonenshine DE, 1993. Biology of Ticks, 2. Oxford University Press, New York, NY, USA.

Sonenshine DE, 2018. Range expansion of tick disease vectors in North America: implications for spread of tick-borne disease. Int. J. Environ. Res. Public Health 15, 478. [PubMed: 29522469]

Sonenshine DE, Ratzlaff RE, Troyer J, Demmerle S, Demmerle ER, Austin WE, Tan S, Annis BA, Jenkins S, 1995. *Borrelia burgdorferi* in eastern Virginia: comparison between a coastal and inland locality. Am. J. Trop. Med. Hyg 53, 123–133. [PubMed: 7677212]

Spielman A, Clifford CM, Piesman J, Corwin MD, 1979. Human babesiosis on Nantucket Island, USA: description of the vector, *Ixodes* (*Ixodes*) *dammini*, n. sp. (Acarina: Ixodidae). J. Med. Entomol 15, 218–234. [PubMed: 439119]

Springer YP, Eisen L, Beati L, James AM, Eisen RJ, 2014. Spatial distribution of counties in the continental United States with records of *Amblyomma americanum* (L.). J. Med. Entomol 51, 342–351. [PubMed: 24724282]

Springer YP, Jarnevich CS, Barnett DT, Monaghan AJ, Eisen RJ, 2015. Modeling the present and future geographic distribution of the lone star tick, *Amblyomma americanum* (Ixodida: Ixodidae), in the continental United States. Am. J. Trop. Med. Hyg 93, 875–890. [PubMed: 26217042]

Sprong H, Azagi T, Hoornstra D, Nijhof AM, Knorr S, Baarsma ME, Hovius JW, 2018. Control of Lyme borreliosis and other *Ixodes ricinus*-borne diseases. Parasit. Vectors 11, 145. [PubMed: 29510749]

Stafford KC III, 1992. Oviposition and larval dispersal of *Ixodes dammini* (Acari: Ixodidae). J. Med. Entomol 29, 129–132. [PubMed: 1552522]

Stafford KC III, 1993. Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) with exclusion of deer by electric fencing. J. Med. Entomol 30, 986–996. [PubMed: 8271257]

Stafford KC III, 2007. Tick Management Handbook: An Integrated Guide for Homeowners, Pest Control Operators, and Public Health Officials for the Prevention of Tick-Associated Disease, 2nd Edition. The Connecticut Agricultural Experiment Station, New Haven, CT, USA. Bull. No. 1010.

Stafford KC III, 2017. Prevention of Ticks and Tick-Associated Disease in Companion Animals. Connecticut Agricultural Experiment Station Fact Sheet, New Haven, CT, p. 9. https://portal.ct.gov/CAES/Publications.

Stafford KC III, Williams SC, 2017. Deer-targeted methods: a review of the use of topical acaricides for the control of ticks on white-tailed deer. J. Integr. Pest Manage 8, 19.

Stafford KC III, Bladen VC, Magnarelli LA, 1995. Ticks (Acari: Ixodidae) infesting wild birds (Aves) and white-footed mice in Lyme, CT. J. Med. Entomol 32, 453–466. [PubMed: 7650706]

Stafford KC III, Williams SC, Molaei G, 2017. Integrated pest management in controlling ticks and tick-associated diseases. J. Integr. Pest Manage 8, 28.

Stafford KC III, Williams SC, van Oosterwijk JG, Linske MA, Zatechka S, Richer LM, Molaei G, Przybyszewski C, Wikel SK, 2020. Field evaluation of a novel oral reservoir-targeted vaccine against *Borrelia burgdorferi* utilizing an inactivated whole-cell bacterial antigen expression vehicle. Exp. Appl. Acarol 80, 257–268. [PubMed: 31898760]

Stanley HM, Ford SL, Snellgrove AN, Hartzer K, Smith EB, Krapiunaya I, Levin ML, 2020. The ability of the invasive Asian longhorned tick *Haemaphysalis longicornis* (Acari: Ixodidae) to acquire and transmit *Rickettsia rickettsii* (Rickettsiales: Rickettsiaceae), the agent of Rocky

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Mountain spotted fever, under laboratory conditions. J. Med. Entomol 57, 1635–1639. [PubMed: 32338290]

Steere AC, 2024. Lyme arthritis: a 50-year journey. J. Infect. Dis 230, S1–S10. [PubMed: 39140724]

Straily A, Drexler N, Cruz-Loustaunau D, Paddock CD, Alvarez-Hernandez G, 2016. Notes from the field: community-based prevention of Rocky Mountain spotted fever - Sonora, Mexico, 2016 Morb. Mortal. Wkly. Rep 65, 1302–1303.

Swei A, O'Connor KE, Couper LI, Thekkiniath J, Conrad PA, Padgett KA, Burns J, Yoshimizu MH, Gonzales B, Munk B, Shirkey N, Konde L, Lane RS, Kjemtrup A, 2019. Evidence for transmission of the zoonotic apicomplexan parasite *Babesia duncani* by the tick *Dermacentor albipictus*. Int. J. Parasitol 49, 95–103. [PubMed: 30367862]

Tarsus, 2025. TP-05: An Investigational Therapeutic for the Prevention of Lyme Disease. Accessed 19 August, 2025, https://tarsusrx.com/pipeline/tp-05/.

TBDWG (Tick-Borne Disease Working Group), 2018. Tick-Borne Disease Working Group 2018 Report to Congress. Accessed 19 August, 2025; https://www.hhs.gov/sites/default/files/tbdwg-report-to-congress-2018.pdf.

TBDWG (Tick-Borne Disease Working Group), 2020. Tick-Borne Disease Working Group 2020 Report to Congress. Accessed 19 August, 2025; https://health.gov/sites/oash/files/2025-02/tbdwg-2020-report_to-ongress-final.pdf.

TBDWG (Tick-Borne Disease Working Group), 2022. Tick-Borne Disease Working Group 2022 Report to Congress. Accessed 19 August, 2025; https://health.gov/sites/oash/files/2025-02/tbdwg-2022-report-to-congress.pdf.

Teel PD, Ketchum HR, Mock DE, Wright RE, Strey OF, 2010. The Gulf Coast tick: a review of the life history, ecology, distribution, and emergence as an arthropod of medical and veterinary importance. J. Med. Entomol 47, 707–722. [PubMed: 20939363]

Telford SR III, 2017. Deer reduction is a cornerstone of integrated deer tick management. J. Integr. Pest Manage 8, 25.

Telford SR III, Goethert HK, 2020. Ecology of *Francisella tularensis*. Annu. Rev. Entomol 65, 351–372. [PubMed: 31600457]

Telford SR III, Mather TN, Moore SI, Wilson ML, Spielman A, 1988. Incompetence of deer as reservoirs of the Lyme disease spirochete. Am. J. Trop. Med. Hyg 39, 105–109. [PubMed: 3400797]

Thompson AT, White SA, Shaw D, Garrett KB, Wyckoff ST, Doub EE, Ruder MG, Yabsley MJ, 2021. A multi-seasonal study investigating the phenology, host and habitat associations, and pathogens of *Haemaphysalis longicornis* in Virginia. U.S.A. Ticks Tick Borne Dis 12, 101773. [PubMed: 34229999]

Thompson AT, White SA, Doub EE, Sharma P, Frierson K, Dominguez K, Shaw D, Weaver D, Vigil SL, Bonilla DL, Ruder MG, Yabsley MJ, 2022. The wild life of ticks: using passive surveillance to determine the distribution and wildlife host range of ticks and the exotic *Haemaphysalis longicornis*, 2010–2021. Parasit. Vectors 15, 331. [PubMed: 36127708]

Torbert LH, 2024. The Blast Away Ticks Lyme Disease Prevention Program: Can Education Increase Students' Knowledge And Modify Their Behavior To Reduce Lyme Disease? Ph.D. Thesis. Wilmington University, New Castle, Delaware, USA. Available from ProQuest (#31561785).

Tsao JI, Hamer SA, Han S, Sidge JL, Hickling GJ, 2021. The contribution of wildlife hosts to the rise of ticks and tick-borne diseases in North America. J. Med. Entomol 58, 1565–1587. [PubMed: 33885784]

Tufts DM, VanAcker MC, Fernandez MP, Denicola A, Egizi A, Diuk-Wasser MA, 2019. Distribution, host-seeking phenology, and host and habitat associations of *Haemaphysalis longicornis* ticks, Staten Island, New York, USA. Emerg. Infect. Dis 25, 792–796. [PubMed: 30681071]

Tufts DM, Goodman LB, Benedict MC, Davis AD, VanAcker MC, Diuk-Wasser M, 2021. Association of the invasive *Haemaphysalis longicornis* tick with vertebrate hosts, other native tick vectors, and tick-borne pathogens in New York City, USA. Int. J. Parasitol 51, 149–157. [PubMed: 33130214]

URI (University of Rhode Island), 2025a. TickEncounter. Accessed 19 August, 2025, 2025. https://web.uri.edu/tickencounter/.

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

URI (University of Rhode Island), 2025b. Field Guide to Ticks. Accessed 19 August, 2025, 2025. https://web.uri.edu/tickencounter/fieldguide/.

URI (University of Rhode Island), 2025c. TickSmart Prevention – Everyday Practices for TickSafe Living. Accessed 19 August, 2025, 2025. https://web.uri.edu/tickencounter/ticksmart/.

USDA (United States Department of Agriculture), 2025. National Haemaphysalis longicornis (Asian Longhorned Tick) Situation Report, as of April 22, 2025. United States Department of Agriculture, Animal and Plant Health Inspection Service, Riverdale, Maryland, USA.

van Oosterwijk JG, 2021. Anti-tick and pathogen transmission blocking vaccines. Parasite Immunol 43, e12831. [PubMed: 33704804]

van Oosterwijk JG, Wikel SK, 2021. Resistance to ticks and the path to anti-tick and transmission blocking vaccines. Vaccines. (Basel) 9, 725. [PubMed: 34358142]

Vredevoe LK, Richter RJ, Kimsey RB, 1997. Temporal drop-off pattern of juvenile *Ixodes pacificus* (Acari: Ixodidae). Can. J. Zool 75, 613–617.

Walker ED, Stobierski MG, Poplar ML, Smith TW, Murphy AJ, Smith PC, Schmitt SM, Cooley TM, Kramer CM, 1998. Geographic distribution of ticks (Acari: Ixodidae) in Michigan, with emphasis on *Ixodes scapularis* and *Borrelia burgdorferi*. J. Med. Entomol 35, 872–882. [PubMed: 9775623]

Weisbrod AR, Johnson RC, 1989. Lyme disease and migrating birds in the St. Croix River Valley. Appl. Environ. Microbiol 55, 1921–1924. [PubMed: 2782872]

Westrom DR, 1975. The Population Dynamics and Distribution of Ectoparasites on Black-Tailed Deer (Odocoileus hemionus columbianus) in Mendocino County, California. Ph.D. Thesis. University of California, Berkeley, CA, USA.

Westrom DR, Lane RS, Anderson JR, 1985. *Ixodes pacificus* (Acari: Ixodidae): population dynamics and distribution on Columbian black-tailed deer (*Odocoileus hemionus columbianus*). J. Med. Entomol 22, 507–511. [PubMed: 4045944]

White A, Gaff H, 2018. Application of tick control technologies for blacklegged, lone star, and American dog ticks. J. Integr. Pest Manage 9, 12.

White SA, Bevins SN, Ruder MG, Shaw D, Vigil SL, Randall A, Deliberto TJ, Dominguez K, Thompson AT, Mertins JW, Alfred JT, 2020. Surveys for ticks on wildlife hosts and in the environment at Asian longhorned tick (*Haemaphysalis longicornis*)-positive sites in Virginia and New Jersey, 2018. Transbound. Emerg. Dis 68, 605–614. [PubMed: 32639639]

Wikel SK, 2022. Changing geographic ranges of human biting ticks and implications for tick-borne zoonoses in North America. Zoonotic Dis 2, 126–146.

Williams SC, Stafford KC III, Molaei G, Linske MA, 2018. Integrated control of nymphal *Ixodes scapularis*: effectiveness of white-tailed deer reduction, the entomopathogenic fungus *Metarhizium anisopliae*, and fipronil-based rodent bait boxes. Vector. Borne Zoonotic. Dis 18, 55–64. [PubMed: 29173127]

Williams SC, Linske MA, Denicola AJ, Denicola VL, Boulanger JR, 2023a. Experimental oral delivery of the systemic acaricide moxidectin to free-ranging white-tailed deer (Artiodactyla: Cervidae) parasitized by *Amblyomma americanum* (Ixodida: Ixodidae). J. Med. Entomol 60, 733–741. [PubMed: 37208791]

Williams SC, Linske MA, Stafford KC III, 2023b. Orally delivered fipronil-laced bait reduces juvenile blacklegged tick (*Ixodes scapularis*) burdens on wild white-footed mice (*Peromyscus leucopus*). Ticks. Tick. Borne Dis 14, 102189. [PubMed: 37156086]

Wilson JG, Kinzer DR, Sauer JR, Hair JA, 1972. Chemo-attraction in the lone star tick (Acarina: Ixodidae): I. Response of different developmental stages to carbon dioxide administered via traps. J. Med. Entomol 9, 245–252. [PubMed: 5057498]

Wilson N, 2020. Medical entomologists: a vanishing species. Bioscience 70, 281–288.

Wojahn B, Black H, Warner M, Britten HB, 2026. Range expansion of *Amblyomma americanum* and *Ixodes scapularis* ([Ixodida]: [Ixodidae]) in South Dakota, and new record for *Amblyomma maculatum*. J. Med. Entomol 63, tjaf154.

Wright CL, Gaff HD, Sonenshine DE, Hynes WL, 2015. Experimental vertical transmission of *Rickettsia parkeri* in the Gulf Coast tick, *Amblyomma maculatum*. Ticks. Tick. Borne Dis 6, 568–573. [PubMed: 25958197]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Wright SA, Thompson MA, Miller MJ, Knerl KM, Elms SL, Karpowicz JC, Young JF, Kramer VL, 2000. Ecology of *Borrelia burgdorferi* in ticks (Acari: Ixodidae), rodents, and birds in the Sierra Nevada foothills, Placer County, California. J. Med. Entomol 37, 909–918. [PubMed: 11126549]

Xu G, Mather TN, Hollingsworth CS, Rich SM, 2016. Passive surveillance of *Ixodes scapularis* (Say), their biting activity, and associated pathogens in Massachusetts. Vector. Borne Zoonotic. Dis 16, 520–527. [PubMed: 27248292]

Zembsch T, Jansen D, Lee X, Oberle E, Philip R, Bartholomay L, Paskewitz S, 2025. Tick spotting: using mannequins to evaluate individual efficacy at detecting *Ixodes scapularis* (Acari: Ixodidae). J. Med. Entomol 62, 961–969. [PubMed: 40384496]

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Fig. 1.

Generalized geographic distributions of selected ixodid tick species of medical importance in the contiguous United States (https://www.cdc.gov/ticks/about/where-ticks-live.html). Tick populations in the far western U.S. previously considered to be outlier populations of *Dermacentor variabilis* were recently designated as a new species, *Dermacentor similis* (Lado et al., 2021). Tick photos courtesy of CDC (Lauren Bishop, James Gathany, William Nicholson, and Christopher Paddock).

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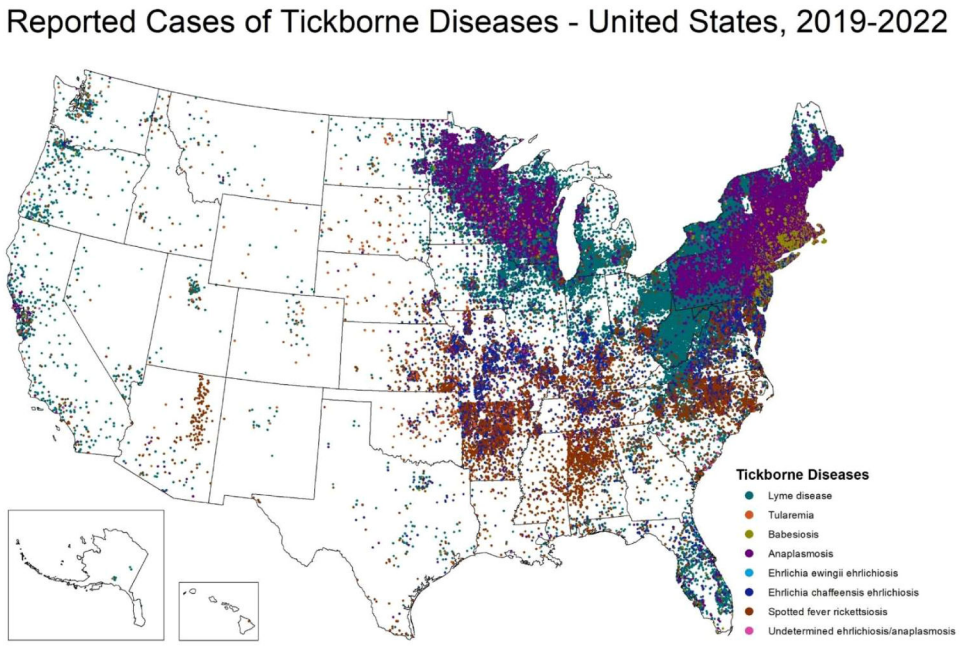


Fig. 2.

Geographic distribution of reported cases of tick-borne diseases in the United States from 2019 to 2022 (https://www.cdc.gov/ticks/media/images/2024/06/TBD-Consolidated-Map_Static_6.21.24.JPG). An interactive version of this map can be found on the following webpage: https://www.cdc.gov/ticks/data-research/facts-stats/geographic-distribution-of-tickborne-disease-cases.html.

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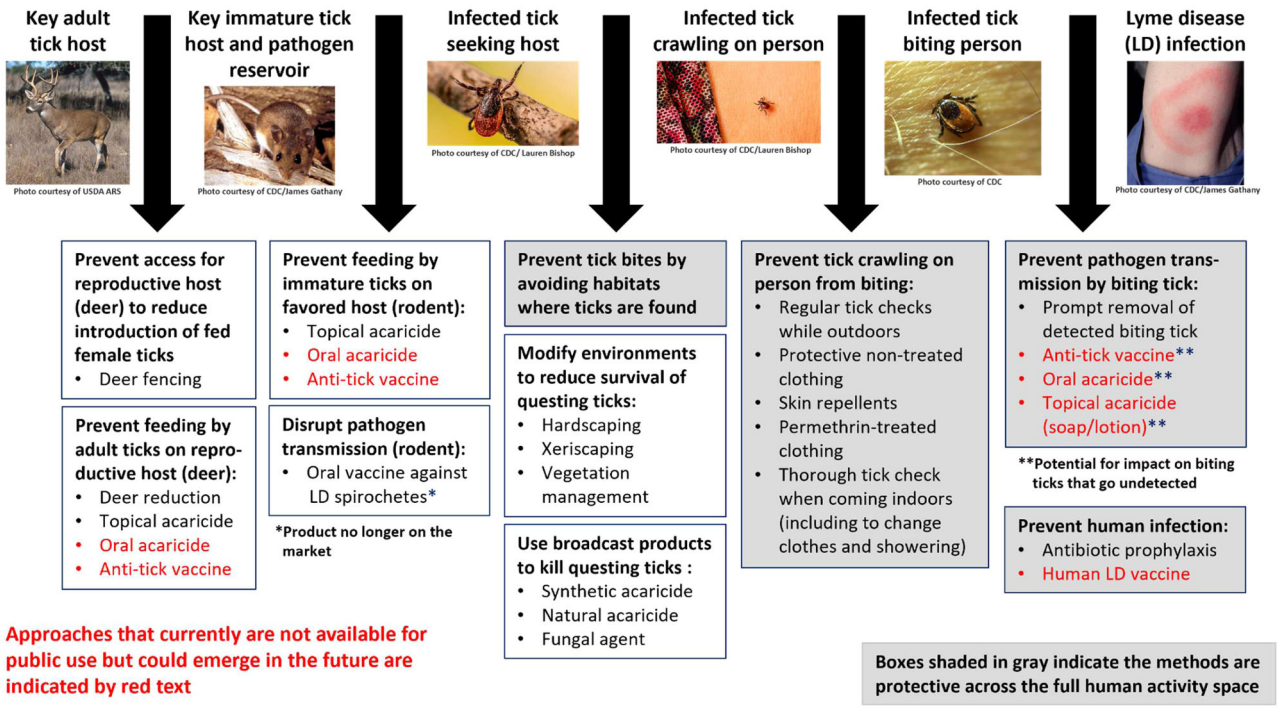


Fig. 3.

Chain of events leading to infection with a tick-borne disease, using Lyme disease as an example, with intervention points for approaches aiming to suppress ticks in the environment, reduce the risk of tick bites, or reduce the risk of infection following a bite by an infected tick.

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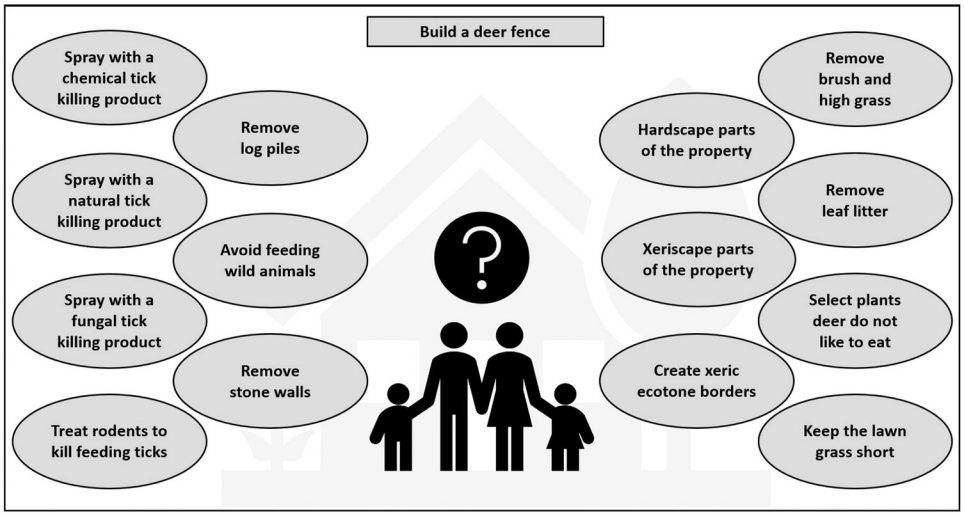


Fig. 4.

The bewildering choices facing homeowners trying to create tick-free residential properties. Previously published by Eisen (2021).

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Table 1

Geographic distributions of selected ixodid tick species of medical importance, by state in the contiguous United States.

Region[a] and State	*Amblyomma americanum*	*Amblyomma maculatum*	*Dermacentor andersoni*	*Dermacentor occidentalis*	*Dermacentor similis* [b]	*Dermacentor variabilis*	*Haemaphysalis longicornis* [c]	*Ixodes pacificus*	*Ixodes scapularis*	*Rhipicephalus sanguineus* sensu lato[d]
Southeast										
Alabama	●	●				●			●	●
Florida	●	●				●			●	●
Georgia	●	●				●	●		●	●
North Carolina	●	●				●	●		●	●
South Carolina	●	●				●	●		●	●
Virginia	●	●				●	●		●	●
Northeast										
Connecticut	●	●				●	●		●	●
Delaware	●	●				●	●		●	●
Maine	●					●			●	●
Maryland	●	●				●	●		●	●
Massachusetts	●					●	●		●	●
New Hampshire						●			●	●
New Jersey	●	●				●	●		●	●
New York	●	●				●	●		●	●
Pennsylvania	●	●				●	●		●	●
Rhode Island	●					●	●		●	●
Vermont						●			●	●
South										
Arkansas	●	●				●	●		●	●
Kansas	●	●				●	●		●	●
Louisiana	●	●				●			●	●
Mississippi	●	●				●			●	●
Oklahoma	●	●				●	●		●	●
Texas	●	●				●			●	●
Ohio Valley										
Illinois	●	●				●	●		●	●

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Region[a] and State	*Amblyomma americanum*	*Amblyomma maculatum*	*Dermacentor andersoni*	*Dermacentor occidentalis*	*Dermacentor similis* [b]	*Dermacentor variabilis*	*Haemaphysalis longicornis* [c]	*Ixodes pacificus*	*Ixodes scapularis*	*Rhipicephalus sanguineus* sensu lato[d]
Indiana	●	●				●	●		●	●
Kentucky	●	●				●	●		●	●
Missouri	●	●				●	●		●	●
Ohio	●	●				●	●		●	●
Tennessee	●	●				●	●		●	●
West Virginia	●	●				●	●		●	●
Upper Midwest										
Iowa	●					●	●		●	●
Michigan	●	●				●	●		●	●
Minnesota	●					●			●	●
Wisconsin	●					●			●	●
Northern Rockies and Plains										
Montana			●			●				●
Nebraska	●	●	●			●			●	●
North Dakota	●		●			●			●	●
South Dakota	●		●			●			●	●
Wyoming			●			●				●
Southwest										
Arizona			●					●		●
Colorado			●			●				●
New Mexico			●							●
Utah			●					●		●
West										
California			●	●	●			●		●
Nevada			●							●
Northwest										
Idaho			●		●					●
Oregon			●	●	●			●		●
Washington			●	●	●			●		●

[a]Based on climate regions for the contiguous U.S. as defined by the National Oceanic and Atmospheric Administration (NOAA, 2025).

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[b] Outlier populations of *Dermacentor variabilis* in the far western U.S. were recently designated as a new species, *Dermacentor similis* (Lado et al., 2021).

[c] Geographic distribution based on data from USDA (2025)), with additional state records for Iowa and Michigan based on reports by the Iowa Department of Agriculture & Land Stewardship and the Michigan Department of Agriculture and Rural Development in 2025.

[d] The only tick species included in the table that may be considered established outside of the contiguous U.S. in Alaska and Hawaii is *Rhipicephalus sanguineus* sensu lato (Hahn et al., 2020; Grant et al., 2023).

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Table 2

Habitat associations of selected ixodid tick species of medical importance in the United States, and peak seasonal activity periods of the key human-biting life stages.

Tick species	Life stages that most commonly bite humans[a]	Primary habitats for human tick encounters[b]		Peak periods for questing activity[c]	
		Nymph	Adult	Nymph	Adult
Amblyomma americanum	Nymph and adult[d]	Primarily forest and forested edges, but also open grassy and brushy areas	Primarily forest and forested edges, but also open grassy and brushy areas	Spring and summer	Spring and early summer
Amblyomma maculatum	Adult	N/A[e]	Open grassy areas and forested edges	N/A	Spring and summer
Dermacentor andersoni	Adult	N/A	Forested, brushy, and grassy areas	N/A	Spring
Dermacentor occidentalis	Nymph and adult[f]	Forested areas	Forested, brushy, and grassy areas	Summer	Winter and spring
Dermacentor variabilis	Adult	N/A	Open grassy and brushy areas, and forested edges	N/A	Spring and early summer
Haemaphysalis longicornis	TBD[g]	Forested, brushy, and grassy areas	Forested, brushy, and grassy areas	Spring	Late spring and summer
Ixodes pacificus	Nymph and adult[f]	Dense forest with limited emergent vegetation	Forested, brushy, and grassy areas	Spring	Late fall and winter
Ixodes scapularis (South, Southeast)[h]	Adult	N/A	Forest and forested edges	N/A	Fall and winter
Ixodes scapularis (Upper Midwest, Northeast)[h]	Nymph and adult[d]	Forest and forested edges	Forest and forested edges	Late spring and early summer	Early spring and fall
Rhipicephalus sanguineus sensu lato	Nymph and adult[d]	Indoors and peridomestic environment	Indoors and peridomestic environment	Late spring, summer, and early fall	Spring, summer, and fall

[a] Based on Eisen (2022a). Included life stages account for >10 % of the total number of ticks of a given species recorded to infest humans.

[b] Habitats where nymphal or adult ticks are abundant and where they quest for hosts in a manner that facilitates contact with humans.

[c] Winter, January to March; Spring, April to June; Summer, July to September; Fall, October to December. Based on L. Eisen (2025) and URI (2025b).

[d] Similar contributions (40–60 %) by nymphs and adults to recorded human infestations.

[e] Not applicable as nymphs of this species only rarely are encountered crawling on or biting humans.

[f] Adults account for most (>80 %) recorded human infestations with nymphs having a smaller contribution (11–20 %).

[g] To be determined when more data become available for human bites. All three life stages have been reported to infest humans (Eisen 2022a, USDA, 2025).

[h] *Ixodes scapularis* is broken down by regions due to geographic differences in the life stages that commonly bite humans and seasonal activity patterns.

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Table 3

Tick-borne disease agents impacting humans in the United States, and characteristics of their natural transmission cycles.

Pathogen	Disease	Primary human-biting tick vectors for the pathogen	Experimental evidence of transovarial transmission in tick vector	Primary wildlife pathogen reservoirs	Domestic animal pathogen reservoirs
Viral					
Bourbon virus	Bourbon virus disease	*Amblyomma americanum*	Yes	Not determined	
Colorado tick fever virus	Colorado tick fever	*Dermacentor andersoni*	Contradictory[a]	Rodents	
Heartland virus	Heartland virus disease	*Amblyomma americanum*	Yes	Not determined	
Powassan virus	Powassan virus disease	*Ixodes scapularis*	Yes	Rodents	
Bacterial					
Anaplasma phagocytophilum	Anaplasmosis	*Ixodes pacificus* *Ixodes scapularis*	No	Rodents Insectivores	
Borrelia burgdorferi sensu stricto	Lyme disease	*Ixodes pacificus* *Ixodes scapularis*	No	Rodents Insectivores	
Borrelia mayonii	Lyme disease	*Ixodes scapularis*	No	Rodents Insectivores	
Borrelia miyamotoi	Hard tick relapsing fever	*Ixodes pacificus* *Ixodes scapularis*	Yes	Rodents	
Ehrlichia chaffeensis	Ehrlichiosis	*Amblyomma americanum*	No	Deer	
Ehrlichia ewingii	Ehrlichiosis	*Amblyomma americanum*	No	Deer	Dogs
Ehrlichia muris euclairensis	Ehrlichiosis	*Ixodes scapularis*	No	Rodents	
Francisella tularensis	Tularemia	*Amblyomma americanum* *Dermacentor andersoni* *Dermacentor variabilis*	Contradictory[a]	Rodents Lagomorphs	
Rickettsia parked	*Rickettsia parkeri* rickettsiosis	*Amblyomma maculatum*	Yes	Rodents	
Rickettsia rickettsii	Rocky Mountain spotted fever	*Dermacentor andersoni* *Dermacentor variabilis* *Rhipicephalus sanguineus* sensu lato	Yes	Rodents	Dogs
Rickettsia rickettsii californica[b]	Pacific Coast tick fever	*Dermacentor occidentalis*	No[c]	Not determined	
Parasitic					
Babesia duncani	Babesiosis	*Dermacentor albipictus*	No[c]	Deer	
Babesia microti	Babesiosis	*Ixodes scapularis*	No	Rodents Insectivores	

[a]Results from experimental studies are contradictory for Colorado tick fever virus (Harris et al., 2023) and *Francisella tularensis* (Telford and Goethert, 2020).

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[b] Previously referred to as *Rickettsia* 364D and *Rickettsia philipii* (Paddock et al., 2025).

[c] Disease agent has been detected in field-collected larval ticks but experimental studies to demonstrate passage from female to offspring are still lacking.

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Table 4

Wildlife hosts of selected ixodid tick species of medical importance in the United States.

Tick species	Hosts for larvae and nymphs[a,b]		Hosts for adults[a,b]		Selected references
	Primary hosts	Secondary hosts	Primary hosts	Secondary hosts	
Amblyomma americanum	Birds Cervids	Carnivores Lagomorphs	Cervids	Carnivores Lagomorphs Large birds[c] Wild pigs	Cooley and Kohls (1944); Bishopp and Trembley (1945); Cooney and Burgdorfer (1974); Kollars et al. (2000a); Childs and Paddock (2003); Campbell et al. (2022); Thompson et al. (2022)
Amblyomma maculatum	Birds Rodents	Carnivores Cervids Lagomorphs	Carnivores Cervids	Lagomorphs Wild pigs	Cooley and Kohls (1944); Bishopp and Trembley (1945); Allan et al. (2001); Teel et al. (2010); Paddock and Goddard (2015); Merrill et al. (2018); Thompson et al. (2022)
Dermacentor andersoni	Rodents	Carnivores Cervids Lagomorphs	Not clear[d]	Carnivores Cervids Lagomorphs Large rodents[e] Wild goats/sheep	Cooley (1938); Bishopp and Trembley (1945); James et al. (2006); Lindquist et al. (2016)
Dermacentor occidentalis	Rodents	Carnivores Cervids Lagomorphs	Cervids	Carnivores Lagomorphs Large rodents[e]	Cooley (1938); Bishopp and Trembley (1945); Westrom (1975); Furman and Loomis (1984); Casher et al. (2002)
Dermacentor variabilis	Rodents	Carnivores Lagomorphs	Carnivores	Lagomorphs Large rodents[e] Wild pigs	Cooley (1938); Bishopp and Trembley (1945); Cooney and Burgdorfer (1974); Kollars et al. (2000b); Allan et al. (2001); Lindquist et al. (2016); Campbell et al. (2022); Thompson et al. (2022)
Ixodes scapularis (South, Southeast, southern Ohio Valley)[f]	Lizards Rodents	Birds Carnivores Cervids Lagomorphs Shrews	Cervids	Carnivores Lagomorphs Wild pigs	Cooley and Kohls (1945); Bishopp and Trembley (1945); Sonenshine et al. (1995); Keirans et al. (1996); Lavender and Oliver (1996); Allan et al. (2001); Durden et al. (2002); Loss et al. (2016); Thompson et al. (2022); Schiff et al. (2025)
Ixodes scapularis (northern Ohio Valley, Upper Midwest, Northeast)[f]	Rodents Shrews	Birds Carnivores Cervids Lagomorphs Lizards	Cervids	Carnivores Lagomorphs	Piesman and Spielman (1979); Piesman et al. (1979); Spielman et al. (1979); Keirans et al. (1996); Loss et al. (2016); Thompson et al. (2022)
Ixodes pacificus	Lizards Rodents	Birds Carnivores Cervids Lagomorphs Shrews	Cervids	Carnivores Lagomorphs Large rodents[e]	Cooley and Kohls (1945); Furman and Loomis (1984); Westrom et al. (1985); Casher et al. (2002); Castro and Wright (2007)
Rhipicephalus sanguineus sensu lato	Dogs[g]	Birds Rodents Carnivores	Dogs[g]	Carnivores	Cooley (1946); Dantas-Torres (2010)

[a]Existing data on host infestation by ticks come primarily from compilations of individual studies with strong biases in the selection of targeted host animals, rather than studies aiming specifically to determine the relative contribution of a wide range of host species to tick feeding.

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[b] Host species are grouped as follows: rodents (Order Rodentia), shrews (Order Eulipotyphla), lagomorphs (Order Lagomorpha), carnivores (Order Carnivora), cervids (Order Artiodactyla), birds (Class Aves), and lizards (Order Squamata). Additional species (dogs, bighorn sheep, wild pigs, and mountain goats) are noted as special cases.

[c] Adults have been collected from large birds (e.g., turkey), but the level of feeding success for female ticks on these hosts is not clear.

[d] The dominant hosts for the adult stage of *Dermacentor andersoni* among lagomorphs, carnivores, cervids, and wild goats or sheep (bighorn sheep, mountain goats) are not clear from the published literature.

[e] Adults have been collected from large rodents (e.g., ground squirrels, woodchucks, marmots, woodrats, tree squirrels, and porcupines) for *Dermacentor* and *Ixodes* species, but the level of feeding success for female ticks on these hosts is not clear.

[f] *Ixodes scapularis* is broken down by region due to geographic differences in the use of lizards by the immature stages.

[g] Dogs are the dominant hosts for *Rhipicephalus sanguineus* sensu lato, with wildlife playing only a secondary role.

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Table 5

Characteristics of personal protection measures to prevent tick bites or tick-borne infections in humans.

Method	Rationale	Lag-time from implementation to protection against bites or infection	Spatial extent of protection	Temporal extent of protection	Potentially impacted tick species or pathogens	Currently available for use
Prevention of tick bites						
Avoidance of tick habitat[a]	Reduced chance of contact with ticks	None	Avoided area	When used	All ticks	Yes
Regular cursory tick checks while outdoors in tick habitat	Increased chance of spotting ticks crawling on clothing or skin before they bite	None	Unlimited	When used	All ticks	Yes
Protective non-treated clothing: long pants tucked into socks and long-sleeved shirt tucked into pants[b]	Increased chance of ticks falling off the clothing or being spotted while crawling on clothing before reaching skin and biting	None	Unlimited	When used	All ticks	Yes
Repellents for use on skin and clothing	Reduced risk of ticks making contact with clothing or skin being able to locate a bite site[c]	None	Unlimited	1–14 hours after application of EPA-registered products[d]	All ticks	Yes
Permethrin-treated clothing: spray-on application	Reduced risk of ticks making contact with clothing being able to locate a bite site[e]	None	Unlimited	2–6 weeks after application of EPA-registered product to clothing[f]	All ticks	Yes
Permethrin-treated clothing: pre-treated commercially available clothing	Reduced risk of ticks making contact with clothing being able to locate a bite site[e]	None	Unlimited	Up to 70 launderings for the treated clothing	All ticks	Yes
Thorough tick check when coming indoors, including to change clothing and take shower or bath[g]	Increased chance of spotting ticks crawling on clothing or skin before they bite	None	Unlimited	When used	All ticks	Yes
Prevention of tick-borne infections						
Prompt removal of attached ticks[h]	Reduced chance of pathogens being transmitted by infected biting ticks, through active removal of detected ticks	None	Unlimited	When used	All ticks / tick-borne pathogens	Yes
Topical acaricide for human use[i]	Reduced chance of pathogens being transmitted by infected biting ticks, through killing of undetected ticks	None	Unlimited	Likely less than 24 hours	All ticks / tick-borne pathogens	No
Oral acaricide for human use[j]	Reduced chance of pathogens being transmitted by infected biting ticks, through killing of undetected ticks	Likely less than 1 week[j]	Unlimited	Would likely require monthly dosing[j]	All ticks / tick-borne pathogens	No
Anti-tick vaccine for human use[k]	Reduced chance of pathogens being transmitted by infected biting ticks, through disruption of feeding by undetected ticks	To be determined	Unlimited	To be determined	To be determined[l]	No

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Method	Rationale	Lag-time from implementation to protection against bites or infection	Spatial extent of protection	Temporal extent of protection	Potentially impacted tick species or pathogens	Currently available for use
Lyme disease vaccine for human use	Reduced chance of infection with Lyme disease spirochetes following a bite by an infected tick	To be determined[m]	Unlimited	To be determined[m]	*Borrelia burgdorferi* sensu lato	No

[a]Avoidance of tick habitat during times of the year when ticks are active can include actions such as refraining from entering tick habitat while recreating on public lands, selecting routes that do not include tick habitat while walking dogs in the neighborhood, and minimizing the time spent in high-quality tick habitat on the residential property (e.g., by staying away from the sections of the property that are wooded or have wooded edges, and moving play structures and seating areas to open lawn portions of the yard).

[b]Light-colored clothing creates contrast with dark-colored ticks and makes them easier to spot on clothing during a cursory tick check (Zembsch et al., 2025).

[c]Repellents labeled for use on skin and clothing are intended to prevent ticks from moving onto a treated area but will not kill them. The effectiveness of using repellents depends on their coverage; ticks making first contact with treated skin or clothing will try to get away from the repellent, including by dislodging and falling off the person, but ticks that instead make contact with untreated parts of the body or clothing may still be able to navigate to an untreated bite site. For example, if a person wearing shorts only has part of the leg below the knee treated with repellent, a tick that makes first contact with an untreated thigh will be able to crawl up and bite in the groin area.

[d]Protection time differs among EPA-registered products depending on type and/or concentration of active ingredient (EPA, 2025).

[e]Exposure to permethrin-treated clothing causes ticks to actively try to dislodge from the garment (due to contact irritancy they experience after getting on the treated clothing) and if they remain on the permethrin-treated clothing they will first lose their ability to move and ultimately perish. The effectiveness of using permethrin-treated clothing depends on the parts of the body covered. For example, if a person only wears permethrin-treated socks, there is no protection against ticks that make first contact on the legs above the socks.

[f]Protection time differs among EPA-registered products, for example depending on concentration of permethrin. Protection time can be reduced by washing of the treated clothing.

[g]It is important to conduct a thorough tick check after coming inside, including to remove outdoor clothing articles and run them in a dryer on high heat (to kill undetected ticks still on the clothing) and take a shower or bath (to aid in detecting ticks crawling on the skin or in the process of attaching, and potentially also dislodge crawling ticks that go undetected).

[h]Ticks can be removed with tweezers (fine-tipped ones are best but other types work too), other similar tools, or as a last option your fingers (preferably covered with something - e.g., tissue, a candy wrapper, part of a plastic bag, or a shirt sleeve - in case the tick bursts open when it is removed). Prompt removal of detected ticks is important because the risk for transmission of disease agents increases with the length of time an infected tick is allowed to remain attached for most pathogens.

[i]For example using a lotion containing an active ingredient that is safe for humans but toxic to ticks.

[j]Similar to oral acaricides available for pets. Oral acaricides are typically effective within a few days after the first dose and require monthly doses thereafter.

[k]Vaccine intended to disrupt tick feeding and thus reduce the risk of pathogen transmission from infected ticks.

[l]The range of tick species potentially impacted by anti-tick vaccines is still to be determined.

[m]In an ongoing phase III trial with the VLA15 Lyme disease vaccine (see NIH, 2025), the participants receive a 3-dose primary vaccination series at about 0, 2, and 5 to 9 months, and then receive a booster dose about 12 months after the end of primary vaccination series. Levels of protection at different time-points after the first dose are still to be determined.

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Table 6

Characteristics of methods to control ticks or tick-borne pathogens in the environment.

Method	Rationale	Lag-time from implementation to protection against questing ticks	Spatial extent of protection	Temporal extent of protection	Potentially impacted tick species or pathogens	Currently available for use
Habitat alteration						
Hardscaping[a]	Reduce the amount of area with tick habitat	None	Hardscaped area	Permanent	All ticks	Yes
Xeriscaping[a]	Reduce the amount of area with optimal tick habitat	Weeks to months[b]	Xeriscaped area	Permanent	All ticks	Yes
Vegetation management[c]	Reduce the amount of area with optimal tick habitat	Weeks to months[b]	Managed area	Weeks to years[d]	All ticks	Yes
Burning	Reduce the amount of area with optimal tick habitat	None	Burned area	Months to years[e]	All ticks	Yes
Broadcast of acaricides or biological control agents						
Synthetic acaricide	Reduce the abundance of questing ticks	<1 day	Treated area	6–8 weeks for single application	All ticks	Yes
Natural product acaricide	Reduce the abundance of questing ticks	<1 day	Treated area	1−3 weeks for single application	All ticks	Yes
Entomopathogenic fungal agent	Reduce the abundance of questing ticks	1−2 weeks	Treated area	1−3 weeks for single application	All ticks	Yes
Targeting of rodents serving as tick hosts and pathogen reservoirs [f]						
Remove rodent harborage[g]	Reduce abundance of rodents acting as tick hosts and pathogen reservoirs	Months	Rodent home range[h]	Permanent	Ticks/pathogens that infest/infect rodents[f]	Yes
Topical acaricide	Reduce production by rodents of infected ticks	Months to 1 year for questing nymphs[i] and adults[j] depending on tick species and geographic area	Rodent home range[h]	1 year; requires annual application	Ticks/pathogens that infest/infect rodents[f]	Yes
Oral acaricide	Reduce the production by rodents of infected ticks	Months to 1 year for questing nymphs[i] and adults[j] depending on tick species and geographic area	Rodent home range[h]	1 year; requires annual application	Ticks/pathogens that infest/infect rodents[f]	No
Anti-tick vaccine	Reduce the production by rodents of infected ticks	Months to 1 year for questing nymphs[i] and adults[j] depending on tick species and geographic area	Rodent home range[h]	1 year; requires annual application	Ticks/pathogens that infest/infect rodents[f]	No
Oral vaccine against Lyme disease spirochetes	Reduce production by rodents of ticks infected with Lyme disease spirochetes	1 year for questing nymphs; months for questing adults[k]	Rodent home range[h]	1 year; requires annual application	*Borrelia burgdorferi* sensu stricto	No[l]
Targeting of deer serving as reproductive tick hosts, and in a few cases also pathogen reservoirs [m]						

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Method	Rationale	Lag-time from implementation to protection against questing ticks	Spatial extent of protection	Temporal extent of protection	Potentially impacted tick species or pathogens	Currently available for use
Deer fencing	Prevent deer from introducing fed female ticks into the fenced area	1–2 years depending on tick species and life stage[n]	Fenced area	Permanent	Ticks/pathogens that infest/infect deer[m]	Yes
Deer population reduction	Reduce access for ticks to reproductive hosts	1–2 years depending on tick species and life stage[n]	Deer home range[o]	1 year; requires annual management	Ticks/pathogens that infest/infect deer[m]	Yes
Topical acaricide	Reduce production of ticks or infected ticks by deer	1–2 years depending on tick species and life stage[n]	Deer home range[o]	1 year; requires annual application	Ticks/pathogens that infest/infect deer[m]	Yes
Oral acaricide	Reduce production of ticks or infected ticks by deer	1–2 years depending on tick species and life stage[n]	Deer home range[o]	1 year; requires annual application	Ticks/pathogens that infest/infect deer[m]	No
Anti-tick vaccine	Reduce production of ticks or infected ticks by deer	1–2 years depending on tick species and life stage[n]	Deer home range[o]	1 year; requires annual application	Ticks/pathogens that infest/infect deer[m]	No

[a] Hardscaping or xeriscaping can include larger areas as well as narrow barriers (e.g., a 1-meter strip covered by gravel or mulch) located along the lawn/woods ecotone on residential properties, or along trail edges on public lands.

[b] Impact on ticks via decreased humidity leading to mortality over time.

[c] Including various methods such as tree trimming, removal of brush and high grass/weeds, leaf litter removal, and keeping lawn grass short.

[d] Temporal extent of protection depends on the pace of vegetation regeneration, ranging from weekly for lawn mowing to annual for brush and leaf litter removal, and potentially to several years for tree trimming.

[e] Temporal extent of protection depends on burn intensity (influencing the proportion of ticks that perish) and the pace of vegetation regeneration (recovery of high-quality tick microhabitat).

[f] Potential for impact on multiple tick species (*Amblyomma maculatum, Dermacentor andersoni, Dermacentor occidentalis, Dermacentor similis, Dermacentor variabilis, Ixodes pacificus*, and *Ixodes scapularis*) and multiple human pathogens (*Anaplasma phagocytophilum, Babesia microti, Borrelia burgdorferi* sensu stricto, *Borrelia mayonii, Borrelia miyamotoi, Francisella tularensis, Rickettsia parkeri, Rickettsia rickettsii*, Colorado tick fever virus, and Powassan virus).

[g] Features providing harborage for rodents can, for example, include wood piles and stonewalls.

[h] Variable across habitats, rodent species, and sexes but typically in the range of 0.1 to 1.0 ha for white-footed mice.

[i] The lag-time before impact on questing nymphs can vary both across species and within species in different geographic areas. For example, reduced production by rodents of fed, pathogen-infected *Ixodes scapularis* larvae in the summer of a given year in the Northeast and Upper Midwest will not result in reduction of molted, infected questing nymphs until spring of the following year, whereas reduced production by rodents of fed, pathogen-infected *Dermacentor variabilis* larvae in the spring in the Southeast will result in result in reduction of molted, infected questing nymphs in the summer of the same year (Sonenshine, 1993).

[j] The lag-time before impact on questing adults also can vary across species and within species in different geographic areas. For example, reduced production by rodents of fed, pathogen-infected *Ixodes scapularis* nymphs in the spring of a given year in the Northeast and Upper Midwest will result in result in reduction of molted, infected questing adults in the fall of the same year, whereas *Dermacentor variabilis* nymphs having fed on pathogen-infected hosts in the summer in the Northeast will molt in the same year but enter diapause and not emerge as questing adults until the spring of the following year (Sonenshine, 1993).

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[k] Reduced production by rodents of fed, *Borrelia burgdorferi* sensu stricto-infected *Ixodes pacificus* or *Ixodes scapularis* larvae in the spring/summer of a given year will not result in reduction of molted, infected questing nymphs until spring of the following year, whereas reduced production of infected nymphs in the spring will result in reduction of molted, infected questing adults already in the fall of the same year.

[l] Commercial product no longer on the market.

[m] Potential for impact on multiple tick species (*Amblyomma americanum, Amblyomma maculatum, Dermacentor andersoni, Dermacentor occidentalis, Haemaphysalis longicornis, Ixodes pacificus*, and *Ixodes scapularis*) and a few human pathogens (*Ehrlichia chaffeensis* and *Ehrlichia ewingii*).

[n] The lag-time before impact depends on the tick species and life stage. *Amblyomma americanum* infests deer heavily in all life stages and impacts on questing nymphs and adults can be expected within 1 year. For *Ixodes scapularis*, only the adults feed predominantly on deer and the lag-time before impact on questing nymphs and adults is therefore 1 to 2 years.

[o] Variable across habitat types and sexes but in the range of 10 to >100 ha for white-tailed deer.

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Table 7

Challenges for deer-targeted methods to control *Amblyomma americanum* and *Ixodes scapularis*.

Method[a,b] and challenges
Deer population reduction via hunting
• Multi-year time lag from implementation to impact on questing nymphs and adults of *Ixodes scapularis*.
• Impact can be influenced by the presence of alternative reproductive hosts.
• Needs to be sustained in perpetuity to prevent a tick resurgence.
• Lethal method (which may limit public acceptance).
• Depending on the starting deer density in a given area, removal of very large numbers of deer may be required for the method to be effective in reducing questing ticks (which may limit public acceptance).
• The relationship between densities of deer and questing ticks is not fully understood, which complicates the setting of targets for deer density to achieve following a cull. Stafford (2007) noted that observational studies and computer models suggest that a reduction of deer density to less than 20 animals per square mile (~8 per km^2) may suppress the density of *Ixodes scapularis* to levels resulting in reduced tick bite risk for humans, and that an even lower deer density of less than 8 animals per $mile^2$ (~3 per km^2) needs to be achieved to dramatically impact the enzootic transmission cycle for Lyme disease spirochetes and thus effectively reduce the risk of human infection.
• Removal of deer can temporarily result in higher density of questing ticks in the first 1–2 years after implementation (due to a reduced number of hosts moving around in the environment and removing ticks from the questing population).
• The method is not suitable to protect individual residential properties.
Deer exclusion via fencing
• Multi-year time lag from implementation to impact on questing nymphs and adults of *Ixodes scapularis*.
• Impact can be influenced by the presence of alternative reproductive hosts which are not impeded by the fence (e.g., raccoons).
• Needs to be sustained in perpetuity to prevent a tick resurgence.
• Limitation of the size of the area that reasonably can be protected via fencing restricts the usefulness of this method to individual properties or small groups of properties.
• Protection depends on the height of the fence (must be high enough to prevent deer from jumping over) and the completeness of coverage along the perimeter of the area of interest (to prevent deer from coming in through gaps in the fence).
• The size of the fenced area may influence the level of reduction in tick density, potentially with a greater impact on tick density within fenced areas larger than 2–3 ha.
• Exclusion of deer can temporarily result in higher density of questing ticks in the first 1–2 years after implementation (due to a reduced number of hosts moving around within the fenced area and removing ticks from the questing population).
Treatment of deer with topical acaricides via the 4-Poster system [c]
• Multi-year time lag from implementation to impact on questing nymphs and adults of *Ixodes scapularis*.
• Impact can be influenced by the presence of alternative reproductive hosts.
• Needs to be sustained in perpetuity to prevent a tick resurgence.
• Deer are attracted to 4-Poster devices using corn as bait, potentially leading to deer aggregation and increased risk for contact transmission of disease agents (e.g., prions causing chronic wasting disease).
• The corn bait can attract non-target species (e.g., rodents, raccoons, and bears).

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Method[a,b] and challenges
• Treatment efficacy may be impacted by level of access for deer to other food sources. • The topical acaricide (permethrin) is delivered to deer via rollers that can be accessed by people, requiring a low fence to be erected around the 4-Poster device in some locations to reduce the risk of accidental acaricide exposure to children. • Some states have additional specific regulations for 4-Poster device placement that limits the usefulness of the approach in residential neighborhoods. • Due to the withdrawal period for permethrin in deer, use against *Ixodes scapularis* is complicated by that the fall activity period of the adult tick stage coincides with the deer hunting season (which may limit public acceptance). • The method is not suitable to protect individual residential properties.
Treatment of deer with oral acaricides
• Multi-year time lag from implementation to impact on questing nymphs and adults of *Ixodes scapularis*. • Impact can be influenced by the presence of alternative reproductive hosts. • Needs to be sustained in perpetuity to prevent a tick resurgence. • Deer are attracted using a bait containing acaricide, potentially leading to deer aggregation and increased risk for contact transmission of disease agents. However, the bait can be distributed in the environment in ways to minimize deer aggregation. • The treated bait may attract non-target species (e.g., rodents, raccoons, and bears). • Treatment efficacy may be impacted by level of access for deer to other food sources. • Depending on the withdrawal period for the active acaricide ingredient in the bait, use against *Ixodes scapularis* may be complicated by that the fall activity period of the adult tick stage coincides with the deer hunting season (which may limit public acceptance). • The method is not suitable to protect individual residential properties. • There is currently no approved product on the market for oral acaricide treatment of deer.

[a] For general overviews of deer-targeted tick control methods, see Stafford (2007), Kilpatrick et al. (2014), Eisen and Dolan (2016), Kugeler et al. (2016), Stafford and Williams (2017), Telford (2017), and White and Gaff (2018)).

[b] See Schulze et al. (2023) for cost estimates of deer-targeted methods.

[c] See Stafford and Williams (2017) and Connally et al. (2022) for descriptions of how the 4-Poster acaricide treatment system works.