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Tick and Tickborne Pathogen Surveillance as a Public Health Tool in the United States

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Abstract

In recent decades, tickborne disease (TBD) cases and established populations of medically important ticks have been reported over expanding geographic areas, and an increasing number of tickborne bacteria, viruses, and protozoans have been recognized as human pathogens, collectively contributing to an increasing burden of TBDs in the United States. The prevention and diagnosis of TBDs depend greatly on an accurate understanding by the public and healthcare providers of when and where persons are at risk for exposure to human-biting ticks and to the pathogens these ticks transmit. However, national maps showing the distributions of medically important ticks and the presence or prevalence of tickborne pathogens are often incomplete, outdated, or lacking entirely. Similar deficiencies exist regarding geographic variability in host-seeking tick abundance. Efforts to accurately depict acarological risk are hampered by lack of systematic and routine surveillance for medically important ticks and their associated human pathogens. In this review, we: 1) outline the public health importance of tick surveillance; 2) identify gaps in knowledge regarding the distributions and abundance of medically important ticks in the United States and the presence and prevalence of their associated pathogens; 3) describe key objectives for tick surveillance and review methods appropriate for addressing those goals; and 4) assess current capacity and barriers to implementation and sustainability of tick surveillance programs.

Key words: tick, surveillance, United States, *Ixodes*, *Amblyomma*

The last several decades have witnessed a steady and continued rise in the number of notifiable tickborne disease (TBD) cases, which now account for more than 75% of vector-borne infections reported in the United States annually, and represent persistent and emerging threats to public health (Eisen and Eisen 2018, Rosenberg et al. 2018). Since the early 1900s, when the bacterium eventually described as *Rickettsia rickettsii* was identified as the first tickborne human pathogen in the United States (Ricketts 1906, 1909), 18 additional tickborne human pathogens have been recognized; remarkably, more than 40% of these agents have been described since 1980 (Paddock et al. 2016, Eisen et al. 2017) (Fig. 1). The accelerated pace of tickborne pathogen discovery can be explained, in part, by increased clinician awareness of TBDs and improved diagnostic methods, particularly molecular techniques that have revolutionized the ability and capacity to detect novel disease-causing agents (Tijsse-Klasen et al. 2014). Another key factor in the emergence and recognition of these diseases has been the rapid expansion of geographic ranges and abundance of multiple medically relevant, human-biting tick species during the last several decades (Paddock and Yabsley 2007, Teel et al. 2010, Springer et al. 2014, Paddock and Goddard 2015, Eisen et al. 2016a, Sonenshine 2018, Molaei et al. 2019). In this context, human-tick encounter rates have increased considerably the likelihood of human infections with these pathogens, particularly those infrequently or rarely found in ticks, and those distributed focally or regionally (e.g., *Borrelia miyamotoi*, *Borrelia mayonii*, *Ehrlichia muris eauclairensis*, *Rickettsia* 364D, and Heartland virus) (Gugliotta et al. 2013, Padgett et al. 2016, Pritt et al. 2016a, Pritt et al. 2016b, Brault et al. 2018). Many protozoa, bacteria, and viruses have been identified infecting ticks for which pathogenicity in humans remains unknown, suggesting that the trend of discovery of new tickborne pathogens will continue (Tijsse-Klasen et al. 2014, Bonnet et al. 2017).

The prevention and diagnosis of TBDs depend greatly on an accurate understanding by the public and healthcare providers of when and where persons are at risk for exposure to human-biting ticks and to the pathogens transmitted by these species. However, national maps showing the distributions of medically important ticks and the presence or prevalence of tickborne pathogens are often incomplete,

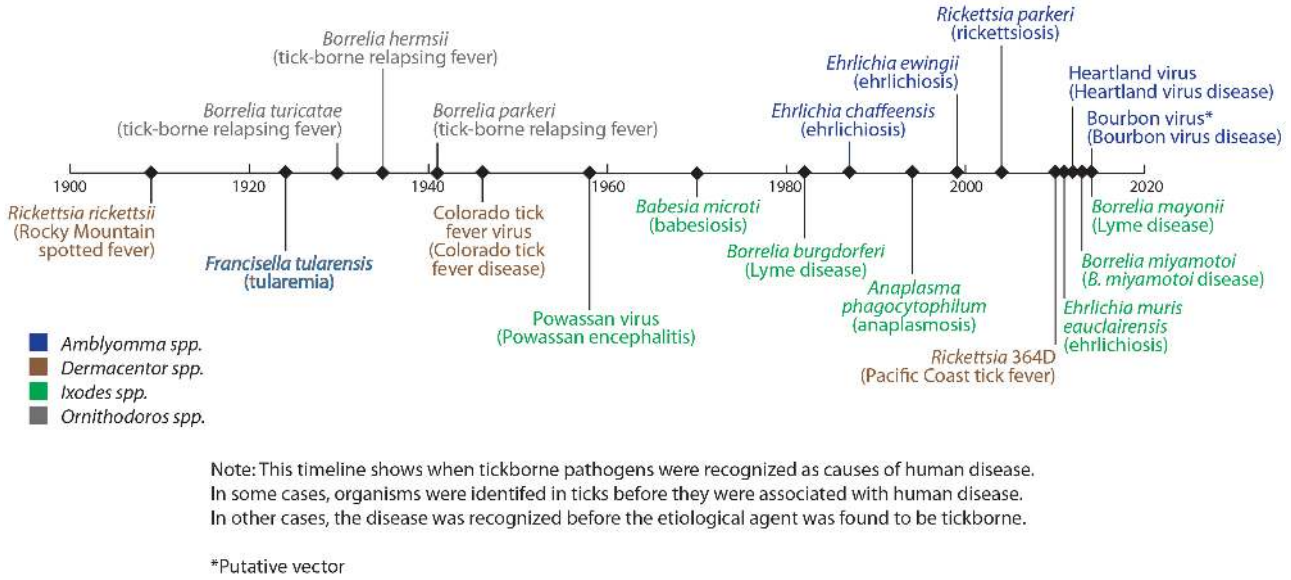

Fig. 1. Discovery of tickborne pathogens as causes of human disease in the United States, 1900 to present.

outdated, or lacking entirely. Similar deficiencies exist regarding geographic variability in host-seeking tick abundance. In this review, we: 1) outline the public health importance of tick surveillance; 2) identify gaps in knowledge regarding distributions and abundance of medically important ticks in the United States and the presence and prevalence of their associated pathogens; 3) describe key objectives for tick surveillance and review methods appropriate for addressing those goals; and 4) assess current capacity and barriers to implementation and sustainability of tick surveillance programs. Although soft ticks (Argasidae) represent important vectors of borrelioses, particularly in the western United States (Donaldson et al. 2016, Sage et al. 2017), this review focuses exclusively on hard ticks (Acari: Ixodidae) of medical importance.

Public Health Importance of Tick Surveillance

Public health surveillance can be defined as the ongoing, systematic collection, analysis, and interpretation of health-related data essential to planning, implementation, and evaluation of public health practice. Surveillance data for TBDs provide critically important information to identify where cases have occurred but can be inaccurate when exposure occurs outside the county or state of residence. Additionally, reporting practices can vary spatially and temporally for some TBDs that are not nationally notifiable, such as *B. miyamotoi* disease and babesiosis. Tick surveillance complements TBD surveillance by generating representative estimates of the distribution and abundance of ticks and the presence and prevalence of their associated pathogens. These data serve several crucial public health functions, including 1) providing local information on when and where persons are at risk for exposure to ticks and tickborne pathogens as well as clarifying misperceptions of risk; 2) explaining epidemiological trends and predicting changes in risk for TBDs; and 3) informing tickborne pathogen discovery efforts.

Surveillance for ticks and tickborne pathogens bridges gaps in TBD surveillance by providing an independent data source for assessing the risk of human encounters with infected ticks. Currently, nearly all environmental interventions designed to reduce human risk of exposure to ticks and tickborne pathogens have proven inadequate to reduce the increasing rates of TBD cases (Eisen and Dolan 2016, Eisen and Gray 2016, Hinckley et al. 2016, Stafford et al. 2017, Eisen and Eisen 2018), and all strategies face inherent challenges of cost and acceptability (Gould et al. 2008, Connally et al. 2009, Hook et al. 2015, Eisen and Gray 2016, Niesobecki et al. 2019). As a result, recommendations for the prevention of TBDs focus primarily on preventing tick bites by avoiding tick habitats when ticks are active and using personal protective measures including EPA-registered repellents or permethrin-treated clothing, as well as early detection and removal of feeding ticks by daily tick checks (Piesman and Eisen 2008). In addition to clinical symptoms, diagnosis relies, in part, on assessing the probability of exposure to ticks and their associated human pathogens (Moore et al. 2016). Lack of accurate data on the distribution of ticks and pathogens impedes these prevention and diagnostic strategies. Moreover, if a vaccine for any TBD becomes commercially available, tick surveillance data could be a useful component for identifying recipient populations at high risk for TBDs. For example, when the Lymerix Lyme disease vaccine was introduced two decades ago, recommendations on who should be vaccinated were made based on assessments of a person's likelihood of being bitten by tick vectors infected with *Borrelia burgdorferi*. In the absence of reliable tick surveillance data, risk maps were generated based on 1) smoothed estimates of the distributions of vector species that were based primarily on non-standardized methods for assessing tick distributions (Dennis et al. 1998), 2) predicted *B. burgdorferi* infection prevalence estimates based on tick-host distributions, and 3) reported cases of Lyme disease (CDC 1999).

Tick surveillance data are useful for explaining and predicting epidemiological trends. For example, although *Ixodes scapularis* Say, the primary vector of Lyme disease spirochetes in the United States, is broadly distributed throughout the eastern states, Lyme disease cases are reported primarily from the Northeast, Mid-Atlantic, and North-Central regions where the density of host-seeking *B. burgdorferi* sensu stricto-infected nymphs is significantly greater than in other parts of the tick's range (Diuk-Wasser et al. 2012, Stromdahl and

Hickling 2012, Arsnoe et al. 2015, Adams et al. 2016, Eisen et al. 2016a). Lyme disease cases have been reported among residents from all 50 states, including those where infected vector ticks have not been reported, and many of these cases have been associated with travel to high incidence areas (Forrester et al. 2015). Recognizing that the distribution of vector ticks can change substantially over time (Eisen et al. 2016a) and that the host-seeking behavior of the tick varies in ways that alter the risk of human exposure to infected ticks across the tick's range (Diuk-Wasser et al. 2010, Diuk-Wasser et al. 2012, Stromdahl and Hickling 2012, Arsnoe et al. 2015), accurate data on the distribution of host-seeking infected ticks aids in identifying areas posing a risk of local exposures. Combining data on where Lyme disease cases have been reported with tick surveillance data might be used to predict trends in the expansion of Lyme disease-endemic areas (Bisanzio et al. 2020), but the accuracy of such models is dependent on access to high quality epidemiological and acarological surveillance data (Kugeler and Eisen 2020).

Tick surveillance can provide information to better explain trends or temporal shifts in the epidemiological characteristics of various TBDs. For example, national surveillance data for spotted fever rickettsiosis (SFR) show marked increases in incidence and decreased severity of reported cases during the last several decades, and these trends are believed to be due, in part, to infections with tickborne *Rickettsia* species of lower pathogenicity than *R. rickettsii*. During this same period, the range of *Amblyomma americanum* L. (the lone star tick), a species associated with spotted fever group rickettsiae of low or undetermined pathogenicity, has expanded considerably in the United States (see *Amblyomma americanum* section below). When incidence, hospitalization and case fatality rates of SFR during this period were regressed against the presence of *A. americanum*, the decade of onset of symptoms and the county of residence, an association was demonstrated between the expansion of lone star tick populations and increasing incidence and decreasing severity of reported case of SFR in the United States (Dahlgren et al. 2016).

Tick surveillance can provide objective and quantifiable data that reconcile misperceptions of risk and refocus attention to underrecognized vector species of increasing public health importance. As an example, based on a study conducted in the mid-1990s, tick surveillance in a small coastal community of Maryland with an exaggerated perception of Lyme disease risk identified a surprising predominance of *A. americanum* ticks, accounting for >90% of all ticks saved by residents and comprising the majority of host-seeking specimens collected from vegetation. These results were supported by a cross-sectional study that showed Lyme disease was rare in this community and disproportionally low compared to the perceived risk (Armstrong et al. 2001). Similar surveillance data can be used to quantify changing acarological risk. For example, investigators evaluated 11 yr of passive tick surveillance data from Monmouth County, NJ that included 7,722 specimens and identified a marked shift in the predominant species submitted over time. During 2006–2011, *I. scapularis* made up most of the submissions (49.5 ± 3.0%), followed by *A. americanum* (30.9 ± 3.9%). However, during the period from 2012 to 2016, lone star ticks replaced blacklegged ticks as the most frequently submitted species (45.1 ± 2.1 % for *A. americanum* vs. 33.9 ± 4.0% for *I. scapularis*), indicating increasing human encounter rates with ticks other than *I. scapularis* in this county (Jordan and Egizi 2019). From a public health perspective, these data can forecast increasing risk of lone star tick-associated infections such as ehrlichiosis, which is possibly underrecognized in Monmouth County by as much as two orders of magnitude, despite high reported incidence rates of Lyme disease (Egizi et al. 2017).

Tick surveillance can aid in rapidly identifying introduced species of potential public health significance. For example, *Haemaphysalis longicornis* Newman (the Asian longhorned tick) is native to East Asia and is an invasive agricultural pest in New Zealand, Australia and several Pacific Islands. *Haemaphysalis longicornis* has been implicated in the transmission of *Rickettsia japonica* (the cause of Japanese spotted fever) and the bunyavirus causing Severe Fever with Thromocytopenia Syndrome. Although its role in enzootic transmission of other human pathogens remains unclear, *Anaplasma* spp., *Ehrlichia* spp. and *Borrelia* spp. have been identified in field-collected ticks from China and Korea (Hoogstraal et al. 1968, Beard et al. 2018, Rainey et al. 2018). The Asian longhorned tick had been intercepted previously on imported animals at U.S. ports of entry, but recognition of multiple life stages of this tick infesting a sheep in Hunterdon County, NJ, in August 2017 raised significant concerns of its establishment in the United States (Rainey et al. 2018). This led to extensive coordination among federal, state, and local public health and agriculture agencies and university partners to assess the distribution of the tick in the United States. In the absence of a national tick surveillance program at that time, these efforts were largely Ad hoc but revealed that within 1 yr of initial recognition, the tick had been found in 546 counties across nine eastern states (Beard et al. 2018). Notably, retrospective review of archived specimens revealed that the tick had been present, but not detected for at least several years. Specifically, *H. longicornis* was collected from a deer in West Virginia in 2010 and from a dog in New Jersey in 2013 (Beard et al. 2018). Surveillance efforts continue to 1) better define the distribution of *H. longicornis* in the United States; 2) detect recognized or potential pathogens associated with this species; 3) determine its public health significance; and 4) assess its impact on native vector tick populations.

Effective tick surveillance programs can be leveraged to provide data that rapidly assess the distribution and prevalence of newly recognized pathogens by retrospective analysis of archived specimens. Although most tickborne human pathogens were discovered after description of the clinical syndrome, an increasing number of tickborne pathogens, including *B. miyamotoi*, *Rickettsia parkeri*, and *Rickettsia* 364D, were identified in ticks several decades before being associated with a TBD (Parker et al. 1939, Cory et al. 1975, Telford and Goethert 2004, Branda and Rosenberg 2013, Tijsse-Klasen et al. 2014). Knowledge gained through the use of advanced molecular detection methods that better characterize microorganisms found in ticks, coupled with laboratory vector competence studies that demonstrate which organisms are transmissible by ticks, could be used to guide pathogen (microorganisms causing illness in hosts) discovery efforts. Specifically, knowledge of the prevalence of such microorganisms in ticks could be used to define minimum sample sizes of humans per area needed to detect candidate pathogens in clinical specimens. Finally, tick surveillance efforts can assist in assessing risk for tick-associated health concerns not linked to a specific tickborne pathogen, including tick paralysis (Dworkin et al. 1999, Morshed et al. 2017) and alpha-gal (galactose-α-1,2-galactose) red meat allergy (Commins et al. 2011, Crispell et al. 2019).

Gaps in Knowledge of the Distribution and Abundance of Medically Important Ticks and the Presence and Prevalence of Their Associated Human Pathogens

Medically important ticks are present in each of the 48 states in the contiguous United States; however, their regional abundance

varies considerably, and their geographic ranges can change dramatically over relatively short periods of time. The absence of ongoing and systematic sampling efforts and national tick surveillance databases hamper efforts to develop accurate depictions of the distributions and relative risks associated with these medically important ticks. In the absence of such resources, tick distribution maps have been generated based on data found through review of published peer-reviewed literature, public health agency reports, and personal communications. Many tick occurrence records have been lost because adequate data on collection methods and numbers of ticks collected by life stage often have not been included in the published literature (Gilliam et al. 2019, Lehane et al. 2020). Moreover, tick collection and pathogen detection methods differ considerably, which limits the ability to compare records over time and across sampling areas.

National data on the distribution and prevalence of tickborne pathogens in ticks and on tick abundance is sparse and often fragmentary. Although infection prevalence in ticks are described at various scales, including state, county or local levels, comprehensive distribution maps showing the presence or prevalence of tickborne pathogens found in field-collected vector ticks across the United States have not been published. Only one study, conducted almost a decade ago, used systematic sampling methods to estimate the density of host-seeking, *B. burgdorferi*-infected *I. scapularis* nymphs across the tick's geographic range (Diuk-Wasser et al. 2010, Diuk-Wasser et al. 2012). Recent efforts to catalog tick distribution records, usually at the county level, and to develop species range maps or models, indicate that the distributions of several medically important ticks have expanded in the United States. Overall, the range of suitable habitat where ticks could become established is more widely distributed than the reported ranges of established populations, suggesting there is either potential for range expansion or that the current reported distributions under-estimate true ranges (James et al. 2015; Springer et al. 2015; Hahn et al. 2016, 2017). Below we summarize trends in the distributions of medically important ticks and prevalence of human pathogens found in them.

Ixodes scapularis

Historical changes in the geographic distribution of the blacklegged tick have been described by multiple investigators (Spielman et al. 1985, Lane et al. 1991, Eisen and Eisen 2018). As of 2016, *I. scapularis* was documented in 1,420 counties (45.7% of U.S. counties in the contiguous United States) from 37 states spanning from the Atlantic coastline to the eastern edge of the Great Plains. The tick was considered established (6 or more ticks or 2 or more life stages collected per county within a 12-mo period) in 842 counties distributed across 35 eastern states (Eisen et al. 2016a). This more than doubled the number of counties classified as having established populations compared with records published nearly two decades prior (Dennis et al. 1998). Models of habitat suitability for this woodland-associated tick indicated that it could become more broadly established in forested areas across the eastern United States, or may be under-reported currently (Hahn et al. 2016, 2017).

Ixodes scapularis transmits seven pathogens of humans, including *Babesia microti* (Spielman 1976, Piesman and Spielman 1980), *B. burgdorferi* sensu stricto, (Burgdorfer et al. 1982, Piesman et al. 1987), *Anaplasma phagocytophilum* (Telford et al. 1996), Powassan virus (Costero and Grayson 1996), *E. muris eauclairensis* (Karpathy et al. 2016b), *B. miyamotoi* (Scoles et al. 2001), and *B. mayonii* (Dolan et al. 2016). Data describing the prevalence of these pathogens in host-seeking ticks is incomplete, but overall indicate that pathogen prevalence varies regionally and by life stage. With the exception of *B. miyamotoi* and Powassan virus, which can be transmitted transovarially (Costero and Grayson 1996, Rollend et al. 2013), larvae are not infected. In the absence of zooprophylactic hosts, infection rates are usually higher in each progressive life stage as opportunities to acquire infection increase with each bloodmeal.

Borrelia burgdorferi s.s. is the most commonly detected pathogen in host-seeking *I. scapularis*. Although infection prevalence can vary greatly among sampling locations, in general in the Northeast and North-Central regions, *B. burgdorferi* infection rates in nymphs and adults are commonly in the 15–30% and 35–60% ranges, respectively (Prusinski et al. 2014; Johnson et al. 2018; New York State Department of Health 2020a,b). Detection of *A. phagocytophilum* and *Ba. microti*, which are among the most prevalent infections in *I. scapularis*, appears to be more geographically focal than *B. burgdorferi* and local establishment of these agents in ticks typically lags temporally behind *B. burgdorferi* (Prusinski et al. 2014, Diuk-Wasser et al. 2016, Johnson et al. 2018). Within sites in New York and Minnesota, prevalence in host-seeking nymphs averaged from 5 to 8% for *A. phagocytophilum* and 3–6% for *Ba. microti* (Prusinski et al. 2014, Johnson et al. 2018). *Borrelia miyamotoi* is generally detected in *I. scapularis* over broad geographic areas, but often at low prevalence (typically <2% in host-seeking nymphs) (Crowder et al. 2014; Johnson et al. 2018; New York State Department of Health 2020a,b). Thus far, *E. muris eauclairensis* and *B. mayonii* have been detected only in the North-Central region and prevalence of infection in host-seeking nymphs is typically less than 2% (Johnson et al. 2018). Powassan virus was detected in less than 1% of host-seeking nymphs in Minnesota and less than 4% of host-seeking adults in New York (Aliota et al. 2014, Johnson et al. 2018). Host-seeking nymphs are seldomly encountered by drag sampling or found on people in the southeastern United States and *B. burgdorferi* infection rates are comparatively lower in adults relative to the Northeast and North-Central regions (Diuk-Wasser et al. 2010, Diuk-Wasser et al. 2012, Stromdahl and Hickling 2012, Arsnoe et al. 2015, Hickling et al. 2018).

Ixodes pacificus

Recent assessments of the distribution of the western blacklegged tick, *I. pacificus* Cooley and Kohls, which is established primarily in Pacific Coast states, showed a modest increase in the numbers of counties reporting the presence of this tick from 1995 through 2015 (Dennis et al. 1998, Eisen et al. 2016a), and models indicate that the tick is already established in most areas classified as environmentally suitable (Hahn et al. 2016). *Ixodes pacificus* transmits multiple pathogens, including *B. burgdorferi* sensu stricto (Lane et al. 1994) and *A. phagocytophilum* (Teglas and Foley 2006), and is a presumed vector of *B. miyamotoi* (Padgett et al. 2014, Krause et al. 2015). Infection prevalence varies by pathogen, geographic region, and by life stage. In California, prevalence of *B. burgdorferi* s.l. infection is typically higher in north-coastal counties compared with southern counties (California Department of Public Health 2019), and infection prevalence is usually higher in nymphs compared with adults, because nymphs commonly feed on lizards that clear *B. burgdorferi* s.s. infection during blood-feeding (Lane and Quistad 1998). In Mendocino county, an average of 5% of host-seeking nymphs were infected with *B. burgdorferi*, whereas within the same generational cohort, adult infection rates were often four-fold lower (Eisen et al. 2004, Eisen et al. 2010). Prevalence of *A. phagocytophilum* in host-seeking western blacklegged ticks in California ranged from 0.4 to

4.3% in adults to 0–0.2% in nymphs collected from three northern or central coastal counties in 2018 (California Department of Public Health 2019). Of 5,428 individually tested *I. pacificus* adults and 615 individually tested nymphs collected in California in 2018, 0.7 and 1.3%, respectively, were infected with *B. miyamotoi* (California Department of Public Health 2019).

Amblyomma americanum

Changes to the geographical range of the lone star tick during the last century provide a salient example of the distributional fluidity that can occur for medically important tick species over relatively short periods of time (Springer et al. 2014). In this respect, the boundaries for the northern limits of *A. americanum* have undergone remarkable changes since the beginning of the 20th century. In 1912, the northern range of the lone star tick included southern Michigan and much or all of New York, Connecticut, and Massachusetts (Hooker et al. 1912). By 1945, *A. americanum* was no longer recognized in any of these states, and its northern distributional limit extended from Missouri to Virginia, and along the Atlantic seaboard to southern New Jersey (Bishopp and Trembley 1945). These changes have been attributed, in part, to various anthropogenic influences, including the near extirpation of white-tailed deer (*Odocoileus viginianus*) during the late 19th and early 20th Century (Paddock and Yabsley 2007). However, the last several years have witnessed a steady and pronounced northward expansion of lone star tick populations that now extend into southern counties of Wisconsin and Michigan, throughout most of New York, and into several northeastern states (Springer et al. 2014, Christenson et al. 2017, Sonenshine 2018, Stafford et al. 2018). The dynamic range expansion of *A. americanum* also is evidenced by its westward establishment throughout most counties of Kansas and Oklahoma and parts of southeastern Nebraska (Cortinas and Spomer 2013, Barrett et al. 2015, Noden and Dubie 2017). As of 2014, *A. americanum* was considered established in 653 counties spanning 32 states, mainly spanning southwest from southern Iowa through southern Texas and southeast from southern Illinois through central Florida. Although *A. americanum* continues to expand its distribution further north (Paddock and Yabsley 2007, Springer et al. 2014, Molaei et al. 2019), its northern limit is currently further south compared with *I. scapularis*; nonetheless, suitability models indicate the potential for northerly range expansion (Springer et al. 2014, Springer et al. 2015). Simulation modeling to estimate minimum temperature conditions for the survival of *A. americanum* indicate that continued climatic changes during the 21st century could create favorable conditions for this species as far north as the densely populated areas of south-central and southeastern Canada, reinforcing the importance of systematic surveillance for lone star ticks in this region (Nelder et al. 2019, Sagurova et al. 2019).

Remarkably, the recognized public health importance of the lone star tick was relatively minimal until the early 1990s, when investigators used nascent PCR technology to implicate this species as the most likely vector of *E. chaffeensis* (Anderson et al. 1993). Since that time, other studies have established its role as a vector of *Ehrlichia ewingii* (Anziani et al. 1990), Heartland virus (Godsey et al. 2016), and has been implicated as a vector of Bourbon virus (Savage et al. 2017). Estimates of infection prevalence of adult *A. americanum* ticks with *E. chaffeensis* or *E. ewingii* vary considerably by region, generally ranging between 2–19% and 1–16%, respectively (Cohen et al. 2010, Maegli et al. 2016, Sayler et al. 2016, Hudman and Sargentini 2018). Data for Heartland and Bourbon virus infections are sparse, but current estimates derived from pooled adult ticks are approximately 0.1 and 0.03%, respectively (Savage et al. 2016, Savage et al. 2017). Lone star ticks also are implicated as the cause of medical conditions not yet associated with a specific pathogen, including Southern Tick-Associated Rash Illness (Masters et al. 1998) and alpha-gal allergy (Commins et al. 2011, Crispell et al. 2019). The role of *A. americanum* in the ecology and epidemiology of Rocky Mountain spotted fever is unclear; however, DNA of *R. rickettsii* occasionally is detected in specimens of this species (Berrada et al. 2011, Egizi et al. 2017), and lone star ticks can effectively transmit *R. rickettsii* in laboratory experiments (Parker et al. 1933, Levin et al. 2017). In a similar manner, infections with *Rickettsia parkeri* are detected occasionally in lone star ticks in areas where these ticks are sympatric with *Amblyomma maculatum* Koch (the Gulf Coast tick) (Cohen et al. 2009, Wright et al. 2015). Finally, lone star ticks commonly are infected with *Rickettsia amblyommatis* (Karpathy et al. 2016a), a spotted fever group *Rickettsia* species of undetermined importance as a pathogen of humans (Apperson et al. 2008), that nonetheless could profoundly affect human seroprevalence to spotted fever rickettsioses and dramatically impact surveillance estimates for these diseases in the United States (Straily et al. 2020).

Amblyomma maculatum

Until the middle of the 20th century, the core distribution of *A. maculatum* in the United States was identified as a relatively narrow band extending 100–150 miles inland from the Gulf Coast of Texas, across to Florida, and northward along the Atlantic Coast to South Carolina (Hooker et al. 1912, Bishopp and Trembley 1945, Paddock and Goddard 2015, Maestas et al. 2020, Phillips et al. 2020). Established populations of *A. maculatum* are now recognized in several land-locked states where few or no records of this species existed during the first half of the 20th Century, including Arkansas, Kentucky, Illinois, and Tennessee, as well as coastal regions of North Carolina, Virginia, and Delaware (Paddock and Goddard 2015, Maestas et al. 2020, Phillips et al. 2020). The largest and best-characterized inland incursion occurred in the southern Great Plains. Incidental collection records for *A. maculatum* in southeastern Oklahoma were first documented during the early 1940s (Bishopp and Trembley 1945). By the early 1970s, the distribution of *A. maculatum* had expanded considerably to include multiple counties of northeastern and south-central Oklahoma as well as parts of southeastern Kansas. During the following 30 yr, Gulf Coast ticks were collected from 65% of Oklahoma counties and 18% of Kansas counties, reflecting a contiguous inland distribution involving thousands of square miles of upland prairie (Teel et al. 2010).

Rickettsia parkeri has been detected in Gulf Coast ticks collected in almost every state included within the range of the vector. Current estimates of infection among questing adults vary from 8 to 56% and rates of 20 to 40% are not unusual (Paddock and Goddard 2015). Some inland populations of *A. maculatum* in the central United States are disproportionately infected with *Candidatus* 'Rickettsia andeanae', a *Rickettsia* species of undetermined pathogenicity that could diminish the frequency and limit distribution of *R. parkeri* in this region. Nonetheless, this could reflect a dynamic process and be subject to change over time. As an example, none of 122 Gulf Coast ticks collected from 9 counties in Oklahoma during 2011–2014 contained DNA of *R. parkeri* (Paddock et al. 2015). However, a subsequent survey conducted during 2017–2018 identified *R. parkeri* in approximately 3% of 172 ticks collected near Oklahoma City, indicating that persons in this metropolitan center are at now risk of acquiring this infection (Noden et al. 2020).

Dermacentor variabilis

The American dog tick, *D. variabilis* Say, is one of the most widely distributed ticks and is considered to be established in 42 states within the contiguous United States (Lehane et al. 2020). Suitable habitat for this tick is focused predominantly in the eastern United States, within Pacific coast states, and in western states along the Canadian border (James et al. 2015). The current range boundaries for *D. variabilis* could expand considerably based on climate change models for North America, indicating a northward expansion by this species throughout most of Canada during the next 50 yr (Minigan et al. 2018). *Dermacentor variabilis* is a vector of *R. rickettsii* (Levin et al. 2020) and *Francisella tularensis* (Reese et al. 2011). These pathogens characteristically are distributed unevenly among populations of *D. variabilis* and infection rates can be quite low in areas not otherwise recognized as enzootic foci. Contemporary estimates of infection among adult ticks range from <0.1 to 1.7% for *R. rickettsii* (Stromdahl et al. 2011, Kakumanu et al. 2018, Hecht et al. 2019) and <1 to 4.1% for *F. tularensis* (Goethert and Telford 2009, Whitten et al. 2019).

Dermacentor andersoni

As of 2006, the Rocky Mountain wood tick, *D. andersoni* Stiles, was reported in 87 counties and considered established in 180, for a total of 267 counties having records of the tick's presence. The tick was found primarily in the Mountain west and Pacific Northwest. Although the records included in this survey spanned from 1903 through 2001, the majority were derived from collections from 1921 to 1940, highlighting the opportunistic nature of tick collections informing distribution maps (James et al. 2006). *Dermacentor andersoni* is a vector of Colorado tick fever virus (Florio et al. 1950) and *R. ricketsii* (Burgdorfer 1975). In the Bitterroot Valley in Montana, where Colorado tick fever virus and *R. rickettsii* are both established, infection rates in adults are approximately 7 and 1%, respectively. However, Rocky Mountain spotted fever cases are reported more commonly in that area, likely owing to greater severity of the disease compared with Colorado tick fever (Gage et al. 1994, Williamson et al. 2019).

Dermacentor occidentalis

The Pacific Coast tick, *Dermacentor occidentalis* Marx, is among the most widely distributed and frequently encountered tick species along the Pacific Coast of the United States and occurs throughout much of California, the southwestern counties of Oregon, and parts of south-central Washington. This species has been implicated as a vector of *F. tularensis* (Parker et al. 1929), *R. rickettsii* (Ricketts 1906), and Colorado tick fever virus (Kohls 1955). However, the primary public health importance of the Pacific Coast tick is its suspected role in the transmission of *Rickettsia* 364D, the etiological agent of Pacific Coast tick fever (Padgett et al. 2016). This pathogen is distributed sporadically and focally among California populations of *D. occidentalis* and may be entirely absent among hundreds of adult specimens collected from multiple locations in one county, yet present at rates of 3 to 8% in ticks collected from adjacent or nearby counties (Padgett et al. 2016, Paddock et al. 2018).

Rhipicephalus sanguineus

The brown dog tick, *R. sanguineus* sensu lato, is distributed broadly across the United States and its range is inextricably linked to the occurrence of domesticated dogs which serve as principal host for this species. The brown dog tick is anthropophilic and well-adapted to survive and reproduce in peridomestic settings, contributing to challenges associated with control or eradication of vector populations in settings of known transmission of a TBD (Dantas-Torres 2008). *Rhipicephalus sanguineus* s.l., effectively transmits *R. rickettsii* (Parker et al. 1933) and is responsible for outbreaks of Rocky Mountain spotted fever in the southwestern United States (Demma et al. 2005, Nicholson et al. 2006). As with other vector species of *R. rickettsii*, infections with this pathogen are distributed unevenly among populations of *R. sanguineus* s.l.; however, an infection rate of 3% has been reported from one hyperendemic focus of this disease (Demma et al. 2005).

Key Objectives for Tick Surveillance and Associated Field Methods

Tick surveillance is intended as a long-term effort that characterizes changes in the distribution and abundance of medically important ticks and the presence and prevalence of tickborne pathogens to provide actionable, evidence-based information to the public, healthcare providers and public health policy makers (CDC 2018a,b). In 2018, the Centers for Disease Control and Prevention initiated a national surveillance program focused on *I. scapularis* and *I. pacificus* and their associated pathogens. Many surveillance guidelines for these tick species are transferable to other medically important ixodid ticks in the United States, although further guidance for metastriate ticks (i.e., *Amblyomma*, *Dermacentor*, and *Rhipicephalus* spp.) has been developed (CDC 2020). National surveillance efforts typically focus on the county as the smallest spatial unit to align with the spatial scale at which TBD case data are reported.

Identification of those counties with reported or established populations of medically important tick species represents the most fundamental goal of tick surveillance; nonetheless, tick presence alone has limited value in assessing risk of human exposure to tickborne pathogens or for triggering interventions. For example, *I. scapularis* is distributed widely across the eastern United States, but detection of Lyme disease spirochetes in ticks is far more common in the Northeast, Mid-Atlantic, and North-Central states compared with the Southeast (Diuk-Wasser et al. 2012). Classifying county status for the presence of specific pathogens in ticks provides additional information needed to accurately evaluate the potential for TBD in that region following exposure to a vector species. Other goals, which require increased cost and effort to achieve, aim to better characterize the acarological risk by describing the abundance of host-seeking ticks by life stage, prevalence of pathogens within vector species, and ultimately estimate the density of host-seeking infected nymphs or adults. Density estimates of host-seeking *B. burgdorferi* s.s. infected nymphs (i.e., numbers of host-seeking infected ticks per area dragged) are superior predictors of the likelihood of Lyme disease occurrence than tick or pathogen presence or abundance alone (Mather et al. 1996, Pepin et al. 2012). This relationship is likely transferable to other TBDs of lower incidence. Because risks of human-tick encounters vary by season, an additional objective aims to describe the host-seeking phenology of medically important ticks by life stages. Although differences in host-seeking phenology have been described across the range of a tick species, phenology is generally consistent within geographic regions, and therefore, this measure does not need to be assessed for individual counties. For example, the life cycle of *I. scapularis* spans 2 to 4 yr and the timing and duration of the seasonal peaks in host-seeking activity differ depending on regional climatic conditions (Eisen et al. 2016b).

Many methods can be used to collect ticks, but some are better suited for achieving specific surveillance objectives than others. Important considerations include 1) the spatial precision of the method relative to the surveillance objective; 2) the efficiency of the method for detecting the tick species and life stage of interest; and 3) the reliability of pathogen infection rates associated with the method. In general, infection prevalence derived from host-collected or blood-fed ticks is not representative of infection rates in questing or host-seeking specimens. Therefore, methods targeting questing or host-seeking ticks should be used for objectives related to assessing pathogen prevalence or estimating the risk of infection from the bites by host-seeking infected ticks. Moreover, laboratory diagnostic methods used to detect known pathogens in ticks should be sufficiently specific to differentiate pathogenic organisms from genetically similar, but nonpathogenic organisms occurring in ticks.

Drag sampling or flagging are the most universal tick collection methods and can be used for any of the outlined surveillance objectives. Drag sampling has been identified as the single most reliable method for quantifying the density of host-seeking (infected) *I. scapularis* nymphs (Falco and Fish 1992). Dragging and flagging are similar methods used to collect host-seeking ticks (Daniels and Fish 1990, Carroll and Schmidtmann 1992, Falco and Fish 1992). Both methods use standard sized (typically 1 m wide by 1 m long) flannel, denim, corduroy, or other sturdy white material sufficiently textured to allow ticks to adhere to the fabric. Light-colored fabric is essential for facilitating detection of dark-colored ticks on a contrasting colored surface. Weights, such as metal washers or chains, may be sewn into the trailing edge of the fabric, or strips may be cut into the weighted edges to increase contact between the fabric and vegetation.

Although the designs of collection devices may differ slightly, the primary difference between drag sampling and flagging is in the contact between the fabric and vegetation. When drag sampling, the fabric is usually moved horizontally along the vegetation for fixed distances or times, whereas flagging more commonly uses a sweeping motion, making an arc over sampled vegetation. When using either of these methods for assessing the density of host-seeking ticks, it is critical to 1) sample a large enough area to accurately estimate abundance (≥750 m^2), 2) check the fabric frequently before ticks dislodge (typically ≤15 m), 3) to sample on two or more occasions during the estimated seasonal peak of the life stage of interest. The peak of host-seeking activity can be estimated based on regular drag sampling of the same area, with sampling conducted weekly or bi-weekly, or from epidemiological data. If using case occurrence data to estimate seasonal peaks, it is important to account for disease incubation periods to discern the peak of tick activity.

Walking sampling, which entails an investigator walking through tick habitat and checking their clothing and body for crawling ticks (Carey et al. 1980, Schulze et al. 1986), is likely to be more accurate in assessing human-tick encounter rates compared with other tick collection methods, but accuracy varies among vegetation types, tick species or life stages. For example, walking sampling was similar in efficiency to flagging or dragging for adult ticks, but yielded fewer nymphs for species that generally seek hosts in the leaf litter, such as *I. scapularis* (Ginsberg and Ewing 1989). Therefore, walking sampling is not recommended for assessing the density of infected host-seeking nymphs of *I. scapularis* or *I. pacificus*. When using this method for density estimates, similar to dragging or flagging, light-colored clothing is recommended to increase detection of ticks, the distance walked should be standardized, consistent enough to detect ticks before they drop off, and conducted during the presumed peak of host-seeking activity of the life stage of interest.

Carbon dioxide-baited tick traps can be useful for each of the stated surveillance objectives, but their effective implementation depends largely on the particular species and surveillance goal. Similar to dragging, flagging, and walking, these traps provide high spatial precision for documenting where host-seeking ticks were collected, but their success is dependent on host-seeking behavior of the target tick species. Based on the premise that ticks have well-developed chemoreceptors and are attracted to carbon dioxide to find a host, the traps consist of a solid insulated base that holds dry ice. The base is surrounded by sticky tape to capture ticks attracted to the carbon dioxide that is released as the dry ice sublimates (Wilson et al. 1972). This method was developed originally to collect feeding stages of *A. americanum*, which display more aggressive and mobile host-seeking behavior compared with many other tick species. Although this method may be useful for estimating the density of host-seeking *A. americanum*, it is less efficient at collecting *I. scapularis* and therefore is not recommended for estimating the density of host-seeking *I. scapularis*. Given its inefficiency, narrow collection range per trap and the number of ticks required to accurately estimate infection rates in ticks, it is not recommended for estimating infection rates in *I. scapularis*. Nonetheless, it may be convenient for documenting infection presence in any tick species.

Deer serve as important bloodmeal hosts for several tick species, including *I. scapularis*, *I. pacificus*, and *A. americanum*. Inspection of hunter-killed deer is a cost-effective method of detecting changes in the distribution of ticks, particularly in areas where a tick species is emerging. It, therefore, is an acceptable method of documenting establishment of ticks in a county. However, because of the moderate home range of deer (<150 ha; Kilpatrick et al. 2001), abundance estimates obtained from deer may not correlate well with estimates of host-seeking tick densities obtained through drag sampling (French et al. 1992, Bouchard et al. 2013, Lee et al. 2013, Raizman et al. 2013). If human pathogens are detected in ticks collected from deer, this is sufficient evidence to document the presence of a pathogen in the county in which the deer was collected but is not sufficient for estimating pathogen prevalence.

Small- and medium-sized mammals, birds, and lizards often serve as hosts for immature ticks, but host preferences differ among tick species. Therefore, typical tick-host associations in particular geographic regions should be considered in determining the utility of this method for achieving surveillance goals. Trapping and inspecting these animals for ticks can provide useful information on the presence and abundance of ticks and the presence of their associated human pathogens and can be particularly useful in assessing host-seeking phenology, particularly in areas where some life stages may not host-seek openly.

Using ticks found on people or pets is increasingly being used to monitor changes in tick and pathogen distributions, particularly with the rise of citizen science (Nieto et al. 2018, Chauhan et al. 2019, Lee et al. 2019). Such methods can be useful and cost-effective. However, because people and pets often travel long distances, data derived from them should only be used for tick surveillance when travel histories are assessed, and it is found that the person or animal did not leave the county where the tick encounter occurred within 10 d of discovering the tick.

Current Capacity and Barriers to Implementation and Sustainability of Tick Surveillance Programs

Shortly before CDC issued guidance for the surveillance of *I. scapularis* and *I. pacificus* and their associated pathogens (CDC

2018a,b), a survey was administered to 140 vector-borne disease professionals across the United States to assess tick surveillance practices at state and sub-state level jurisdictions (Mader et al. 2020). Overall, the survey revealed that approximately two-thirds of respondents were engaged in passive tick surveillance, but fewer than half reported that their jurisdiction was engaged in routine, active surveillance. Most of those conducting some form of tick surveillance were focused on the most basic surveillance goal of identifying tick presence. Considerably fewer jurisdictions assessed pathogen presence or prevalence or quantified acarological risk based on densities of infected host-seeking ticks. Among those aiming to detect pathogens in ticks, the majority were focused on identifying pathogens associated with *Ixodes* spp., or *Rickettsia* spp. in metastriate ticks. Although respondents expressed a desire to expand their capacity to conduct tick surveillance, stated barriers to doing so included a lack of consistent funding, limited infrastructure and training, and a need for guidance on best practices.

In their 2018 report to Congress, the national Tickborne Diseases Working Group recommended funding studies and activities on tick biology and TBD ecology, including systematic tick surveillance efforts, particularly in regions beyond the Northeast and Upper Midwest (Tickborne Diseases Working Group 2018). Beginning in 2018, the Centers for Disease Control and Prevention increased funding to state health departments, including those beyond the Northeast and Upper Midwest, to support tick surveillance efforts and issued guidance on surveillance for medically important ticks and their associated human pathogens. Improving the efficiency and cost-effectiveness of such programs is paramount to their sustainability. Given resource limitations, it is not surprising that many jurisdictions focus on the most basic objective of documenting tick presence by county. Efforts aimed at quantifying densities of host-seeking ticks and infection rates in ticks add considerable cost and effort, but addressing these surveillance objectives also provides more robust estimates of TBD risk.

Additional research is needed to provide data-driven recommendations for reducing the cost of surveillance programs while maximizing the collection of actionable public health data. Some obvious operational research questions include the following. Once a tick or tickborne pathogen becomes established in a given location, how much variation is typically observed in tick densities or infection prevalence from year to year? Is there a predictable period between introduction of a tick species and its associated pathogen(s) before a stable infection prevalence or tick density is observed to allow scaled-back surveillance following establishment? What level of variability in tick densities or pathogen prevalence is acceptable and are there thresholds that would engage public health mitigation? How frequently should sites be sampled to obtain accurate information on risk of TBDs while minimizing costs for maintaining a surveillance program? How many sites should be sampled per county to accurately assess TBD risk and how does environmental variability in the county impact those estimates? How does passive surveillance data (e.g., tick submissions from the public or from veterinarians) compare with active surveillance (e.g., tick drag sampling) for estimating TBD occurrence or incidence? Can pathogen detection assays or testing strategies be improved to reduce cost while retaining sensitivity and specificity?

Conclusions

Current and accurate information on when and where persons are at risk for TBDs aids in prevention and diagnosis. In the absence of a national tick surveillance program, data from published studies and health departments has been used to develop tick distribution maps, revealing remarkable geographic expansion of several medically important ticks in recent decades. However, such maps are of limited value because collection efforts are not uniform across the country, resulting in maps that likely under-represent the actual distribution of ticks. National maps showing abundance of host-seeking ticks provide improved data for assessing the likelihood of human encounters with medically important ticks; however, depending on the tick species, such maps are either not current or non-existent. Likewise, national maps showing the distribution of TBD agents found in host-seeking ticks are lacking. Being bitten by an infected vector tick is a primary risk factor for TBDs. National tick and tickborne pathogen surveillance efforts can improve our understanding of geographic variation in risk factors for TBDs, and efforts to build such a program have increased in recent years. Nonetheless, sustainability of tick surveillance programs is dependent on improving their fiscal support, efficiency, coordination, and cost-effectiveness.

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