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Tick species infesting humans in the United States

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Abstract

The data for human tick encounters in the United States (US) presented in this paper were compiled with the goals of: (i) presenting quantitative data across the full range of native or recently established human biting ixodid (hard) and argasid (soft) tick species with regards to their frequency of infesting humans, based on published records of ticks collected while biting humans or crawling on clothing or skin; and (ii) providing a guide to publications on human tick encounters. Summary data are presented in table format, and the detailed data these summaries were based on are included in a set of Supplementary Tables. To date, totals of 36 ixodid species (234,722 specimens) and 13 argasid species (230 specimens) have been recorded in the published literature to infest humans in the US. Nationally, the top five ixodid species recorded from humans were the blacklegged tick, *Ixodes scapularis* (n=158,008 specimens); the lone star tick, *Amblyomma americanum* (n=36,004); the American dog tick, *Dermacentor variabilis* (n=26,624); the western blacklegged tick, *Ixodes pacificus* (n=4,158); and the Rocky Mountain wood tick, *Dermacentor andersoni* (n=3,518). Additional species with more than 250 ticks recorded from humans included *Ixodes cookei* (n=2,494); the Pacific Coast tick, *Dermacentor occidentalis* (n=809); the brown dog tick, *Rhipicephalus sanguineus* sensu lato (n=714); the winter tick, *Dermacentor albipictus* (n=465); and the Gulf Coast tick, *Amblyomma maculatum* (n=335). The spinose ear tick, *Otobius megnini* (n=69), and the pajaroello tick, *Ornithodoros coriaceus* (n=55) were the argasid species most commonly recorded from humans. Additional information presented for each of the 49 tick species include a breakdown of life stages recorded from humans, broad geographical distribution in the US, host preference, and associated human pathogens or medical conditions. The paper also provides a history of publications on human tick encounters in the US, with tables outlining publications containing quantitative data on human tick encounters as well as other notable publications on human-tick interactions. Data limitations are discussed. Researchers and public health professionals in possession of unpublished human tick encounter data are strongly encouraged to publish this information in peer-reviewed scientific journals. In future papers, it would be beneficial if data consistently were broken down by tick species and life stage as well as host species and ticks found biting versus crawling on clothing or skin.

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Disclaimer
The findings and conclusions of this study are by the author and do not necessarily represent the views of the Centers for Disease Control and Prevention.

Supplementary materials
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Keywords

Tick; Human biting; United States

1. Background

Tick-borne diseases represent a growing problem in the United States (US). Increasing incidence of reported human disease cases have been documented over the last two decades for multiple tick-borne infections, including anaplasmosis, babesiosis, ehrlichiosis, Lyme disease, and spotted fever group rickettsiosis (Rosenberg et al., 2018). Root causes include geographic range expansion and population increase of key tick vector species - including *Amblyomma americanum* (lone star tick), *Amblyomma maculatum* (Gulf Coast tick), and *Ixodes scapularis* (blacklegged tick or deer tick, including the junior synonym, *Ixodes dammini*) – together with human encroachment on natural tick habitat presumably resulting in more frequent human tick encounters (Sonenshine, 2018). A long-term data set for human encounters with ticks of different species is lacking for the public at the national scale. However, such data sets have been generated at the state scale via passive tick collection initiatives where residents or health care facilities submit encountered ticks for species identification and in some cases also pathogen detection. Examples of geographical areas with human tick encounter data sets spanning a decade or more include California/Oregon/Washington (Xu et al., 2019), Connecticut (Little et al., 2019), Maine (Rand et al., 2007; Elias et al., 2020), Michigan (Walker et al., 1998), Mississippi (Goddard, 2002), New Jersey (Jordan and Egizi, 2019), and Rhode Island (Johnson et al., 2004). Such data sets have generated information of direct relevance to public health in the target areas, for example by: (i) quantifying the relative contribution of different species to human tick encounters, and how this may change over time; (ii) documenting seasonal trends in human encounters with ticks of different species and life stages; and (iii) presenting species and life stage specific tick encounter data broken down by human age group or bite location on the body. Such information can be of value both to the public, to help guide decisions about use of personal protection measures, and medical practi-tioners, to help understand the health risks associated with a tick bite, including when the tick is not available for species identification. Additionally, the Centers for Disease Control and Prevention (CDC) launched a national initiative in 2017 aiming to summarize data on human tick bites via keyword searches of electronic records from emergency department settings (CDC, 2022). Information is presented for a range of important topics, including interannual and seasonal tick bite trends, geographical tick bite patterns, and human demographic tick bite patterns, but the data have the limitation of not accounting for tick species. Tick species are associated with different suites of human tick-borne infections, and bites by some species also can cause other types of medical conditions such as tick paralysis or red meat allergy (Table 1). It therefore is important to know which tick species are the locally most important human biters, and which species parasitized a person seeking care for a tick bite.

Sources for published data on human encounters with ixodid (hard) or argasid (soft) tick species in the US include medical case reports, research studies including collection of ticks from humans, information from passive tick collection initiatives, host records from curated tick collections, and host records included in monographs on ticks in the US or individual states. Data on human tick encounters from tick bite prevention or tick control intervention studies were included if ticks were encountered during normal recreational or occupational activities but excluded if tick encounters were based solely on experimentally prescribed behaviors. To compile human tick encounter data, published literature from the US was initially queried by searching the Scopus database using different combinations of key words for abstracts: “tick” and “human” together with “bite”, “bites” or “biting”. The snowball technique, which identifies additional publications based on referenced materials, was then employed to identify additional publications of interest. To avoid subjective assessments of data quality, the information compilation was restricted to data presented in peer-reviewed journals or in monographs, and does not include information presented only on websites. Information on human encounters with ixodid ticks in the US, for the period up to 2018, can also be found within the excellent compilation of records for global human encounters with ixodid ticks presented by Guglielmone and Robbins (2018). The intent of this paper was to complement Guglielmone and Robbins (2018) by providing information specific to the US in table formats, adding a set of studies published after 2018 that present massive data sets from passive tick collections initiatives (Jordan and Egizi, 2019; Little et al., 2019; Pak et al., 2019; Porter et al., 2019; Salkeld et al., 2019; Smith et al., 2019; Xu et al., 2019, 2021; Hart et al., 2022), and include human encounters with both argasid and ixodid ticks.

Bearing in mind the limitations inherent in compiling data from varied sources spanning a long time period, I found it of interest to quantify the total number of tick specimens recorded to infest humans, by species and life stage, in the US. This was done with the goals of: (i) presenting quantitative data across the full range of native or recently established human biting tick species in the US with regards to their frequency of infesting humans, based on published records of ticks collected from humans while biting or crawling on clothing or skin (summarized in Table 1 for ixodid ticks and Table 2 for argasid ticks); and (ii) providing a guide to publications on human tick encounters in the US, including information for tick species and the geographical area and time period of data collection (summarized in Table 3 for publications containing quantitative data for human tick encounters, and in Table 4 for other notable publications on human-tick interactions). The detailed information the quantitative data summaries are based on is presented in Supplementary Tables 1 to 36 for ixodid tick species and 37 to 49 for argasid tick species. The data compilation does not include records of infestation by exotic tick species of travelers returning to the US after spending time abroad (see for example, Merten and Durden, 2000; Keirans and Durden, 2001; Burridge, 2011; Stafford et al., 2022) or infestation by tick species native to the US of foreign nationals discovering ticks upon returning home after spending time in the US (see for example, Okino et al., 2007; Heath and Hardwick, 2011; McGarry, 2011; Gillingham et al., 2020; Faccini-Martínez et al., 2021).

Section 2 of this paper outlines the history of publications for human tick encounters in the US; Section 3 focuses on the main findings of the data compilation; Section 4 provides a discussion of data limitations; and Section 5 briefly outlines future directions. It also should be noted that some of the identified data sources clearly state that all recorded ticks were biting (attached), whereas other sources do not make a clear distinction between ticks that were collected while biting versus crawling on clothing or skin. Distinguishing between ticks found biting versus crawling on clothing or skin is important because tick species vary in their host preferences and the likelihood of a tick encounter resulting in a human bite therefore can be assumed to differ across tick species. In this paper, the phrases "human tick encounter(s)", "ticks infesting humans" and "ticks recorded from humans" are used to indicate that the ticks may have been either biting or crawling on clothing or skin when collected from a human. For information regarding specific bite sites on the bodies of human hosts for different tick species and life stages, I refer to a previous review paper (Eisen, 2022).

2. History of publications on human tick encounters in the US

The recorded history of humans encountering ticks in the US spans more than 250 years (summarized in Tables 3 and 4). The naturalist Pehr Kalm noted the following (translated into English by J.R. Forster) while traveling from New Jersey to Pennsylvania in April of 1749: "There were vast numbers of woodlice [ticks] in the woods about this time; they are a very disagreeable insect; for as soon as a person sits down on an old stump of a tree, or on a tree which is cut down, or on the ground itself, a whole army of woodlice creep upon his clothes, and insensibly come upon the naked body" (Kalm, 1772). Specimens of ticks collected by Kalm were classified by Carl Linnaeus as *Am. americanum* (=*Acarus americanus*), which agrees with Kalm's mention of wooded habitat and description of their active host-seeking behavior (see review by Rochlin et al., 2022). More than a century then passed before additional human tick encounters were described. Packard (1869) described one case of an *Am. americanum* tick (=*Ixodes unipunctata*) biting a girl in Pennsylvania, albeit the species identification was made from a drawing of the tick; and Fitch (1872) noted that the previously abundant human biting *Am. americanum* (=*Ixodes americanus*) had declined to become nearly extinct in parts of the Northeast due to forest clearing whereas it was still abundant in sparsely settled parts of the country further west and south. Moreover, Fitch (1872) described human bites in New York State by *Ixodes cookei* (=*Ixodes cruciarius*) (see review by Keirans and Barnes, 1987). The list of ticks biting humans in the US was expanded to five species two decades later as Curtice (1892) added the blacklegged tick, *Ixodes scapularis*, and the American dog tick, *Dermacentor variabilis* (=*Dermacentor americanus*), in the eastern US, and the Pacific Coast tick, *Dermacentor occidentalis*, in the far western US.

The recognition shortly thereafter that ticks can transmit disease agents affecting livestock and humans – based on seminal work by Smith and Kilborne (1893) demonstrating transmission of the parasite now called *Babesia bigemina* by cattle ticks, and Ricketts (1906) demonstrating transmission of the Rocky Mountain spotted fever agent, *Rickettsia rickettsii,* by *Dermacentor* ticks – spurred increased interest in ticks biting humans. A suite of monographs and journal articles published from 1901 to 1920 (Neumann, 1901; Simpson and Wheeler, 1901; Hunter and Hooker, 1907; Banks, 1908; Stiles, 1910; Hunter and Bishopp, 1911a, b; Nuttall et al., 1911; Hooker et al, 1912; Cooley, 1915; Herms, 1917) further expanded the list of tick species considered to bite humans in the US by adding three species of argasid ticks (the pajaroello tick, *Ornithodoros coriaceus*; the relapsing fever tick, *Ornithodoros turicata*; and the spinose ear tick, *Otobius megnini* [=*Argas* *megnini, Ornithodoros megnini*]) and four species of ixodid ticks (*Am. maculatum*; the Rocky Mountain wood tick, *Dermacentor andersoni* (=*Dermacentor venustus*); *Dermacentor parumapertus*; and the cattle tick *Rhipicephalus annulatus* [=*Margaropus annulatus*]). These publications either reported on a single or a few cases of human tick infestation, or did not specify numbers of ticks recorded infesting humans, with two notable exceptions. Hunter and Bishopp (1911a) reported 800 *De. andersoni* (=*De. venustus*), comprising 400 female and 400 male ticks, infesting humans in a Rocky Mountain spotted fever endemic area in Montana. Hooker et al. (1912) noted 16 specimens of *De. occidentalis* infesting humans together with nine *Am. americanum*, two *De. variabilis*, two *Ot. megnini* (=*Or. megnini*) and single specimens of *Am. maculatum* and *De. parumapertus*.

The period from 1921 to 1940 included a limited number of publications describing tick species infesting humans in the US, typically with small numbers of recorded ticks (Bassoe, 1924; Bruce, 1934; Hamilton, 1934; Bishopp and Hixson, 1936; Barnett, 1937; Chamberlin, 1937; Kohls, 1937; Bradley and Connell, 1938; Cooley, 1938; Cooley and Kohls, 1938; Philip and Davis, 1940). Three species were added as human biters in the US during this time period: one argasid species, *Ornithodoros hermsi* (Philip and Davis, 1940); and two ixodid species, *Ixodes angustus* and the western blacklegged tick, *Ixodes pacificus* (=*Ixodes californicus*; see also Cooley and Kohls, 1943) (Chamberlin, 1937). Knowledge of human biting ticks then increased dramatically in the 1940s through an increasing number of publications (see Tables 3 and 4) including a series of notable compilations on the ticks of the US, which not only recorded the species infesting humans but also quantified numbers of ticks collected from human hosts by species and life stage (Cooley and Kohls, 1944a, 1944b, 1945; Bequaert, 1945; Bishopp and Trembley, 1945; Cooley, 1946a; Carpenter et al., 1946). During the 1940s, the first mention or records of human infestation in the US was published for three argasid tick species (*Argas miniatus, Ornithodoros parkeri*, and *Ornithodoros stageri*) and nine ixodid tick species (the Cay-enne tick, *Amblyomma cajennense* [most likely representing misidentified specimens of *Amblyomma mixtum*, as indicated below]; the winter tick, *Dermacentor albipictus*; the bird tick, *Haemaphysalis chordeilis*; the rabbit tick, *Haemaphysalis leporispalustris; Ixodes dentatus; Ixodes muris, Ixodes sculptus, Ixodes spinipalpis*, and the brown dog tick, *Rhipicephalus sanguineus* sensu lato [s.l.]) (Bishopp and Trembley, 1945; Carpenter et al., 1946; Collins et al., 1949)

Information for ticks infesting humans were included in a large number of US publications from 1950 to 1999 (see Tables 3 and 4), as well as a global reference compilation by Doss et al. (1974) and a global review (Estrada-Peña and Jongejan, 1999). From 1950 to 1980, only three species of ixodid ticks were added to the list of human biters in the US: *Amblyomma tenellum* (=*Amblyomma imitator*) (Kohls, 1958), *Dermacentor hunteri* (Brinton and Kohls, 1963), and *Ixodes marxi* (Snetsinger, 1968). The period from 1980 to 1999 was more fruitful, with numerous publications on human tick infestation (see Tables 3 and 4) and the addition as human biters in the US of four species of argasid ticks (*Argas monolakensis* [initially described as *Argas cooleyi*; see Schwan et al., 1992], *Argas sanchezi, Ornithodoros concanensis*, and *Ornithodoros kelleyi*) and seven species of ixodid ticks (*Ixodes baergi, Ixodes banksi, Ixodes brunneus, Ixodes rugosus, Ixodes texanus, Ixodes uriae*, and *Ixodes woodi*) (Easton, 1983; Furman and Loomis, 1984; Schwan and Winkler, 1984; Robbins, 1989; Hall et al., 1991; Keirans and Lacombe, 1998, Walker et al., 1998; Williams et al., 1999).

In a notable achievement, Merten and Durden (2000) then provided a summary of records for ticks recorded from humans in the US based on data retrieved from the Smithsonian Institution's Tick Database. This database contained information for tick specimens identified by curators of the United States National Tick Collection (housed at Georgia Southern University, Statesboro, GA, USA) and then accessioned into the collection. Using this resource, Merten and Durden (2000) presented data on >2,500 specimens of native ticks infesting humans, broken down by tick species, life stage, number of specimens, and region and state of collection. This included the first records as human biters in the US for two argasid species (*Ornithodoros capensis* and *Otobius lagophilus*) and three ixodid species (*Amblyomma inornatum, Amblyomma tuberculatum*, and *Ixodes kingi*). Overall, the vast majority (98%) of the ticks included in the data compilation by Merten and Durden (2000) were ixodid species and the most common life stage was adult females (44%), followed by adult males (31%), nymphs (15%) and larvae (10%). The tick species most frequently recorded from humans and included in the National Tick Collection by the end of the 20th century was *De. andersoni* (39% of all tick specimens), followed by *Am. americanum* (20%), *De. variabilis* (12%), and *Ix. scapularis* (8%).

A notable recent development is that among publications from 2001 to present on human tick encounters (Tables 3 and 4), there is an increase in presentations of large data sets for human tick encounters, including summaries for passive tick collection initiatives conducted at national scale (Nieto et al., 2018; Porter et al., 2019; Xu et al., 2021) or for regions or individual states (Goddard, 2002; Johnson et al., 2004; Rand et al., 2007; Williamson et al., 2010; Rossi et al., 2015; Gleim et al., 2016; Mitchell et al., 2016; Xu et al., 2016, 2019; Egizi et al., 2017; Oliver et al., 2017; Jordan and Egzi, 2019; Little et al., 2019; Salkeld et al., 2019; Elias et al., 2020; Little and Molaei, 2020; Lyons et al., 2021; Rounsville et al., 2021; Dowling, et al., 2022; Hart et al., 2022; Pasternak and Palli, 2022). The only new additions after 2000 to the list of tick species recorded to infest humans in the US are *Amblyomma triste* (Mertins et al., 2010; Herrick et al., 2016), *Ixodes affinis* (Xu et al., 2021), and the invasive but now established Asian longhorned tick, *Haemaphysalis longicornis* (Beard et al., 2018; Bickerton and Toledo, 2020; Wormser et al., 2020; Molaei et al., 2021). Information for native tick species in the US infesting humans were also included in two global reviews (Guglielmone and Robbins, 2018; Guglielmone et al., 2020).

3. Summary of human tick encounter data from the US

Summaries of human tick encounter data from the published literature for the US are provided in Table 1 for 36 ixodid species (based on the detailed data presented in Supplementary Tables 1 to 36) and Table 2 for 13 argasid species (Supplementary Tables 37 to 49). These summaries should be interpreted with some caveats in mind. Human tick encounters recorded in the published literature undoubtedly underestimate actual tick encounters by several orders of magnitude. Data presented in Tables 1 and 2 for total number of specimens of a given species recorded to infest humans are rather intended to provide a picture of the relative contribution of each species to overall recorded human tick encounters. For example, the number of *Ix. scapularis* recorded to infest humans is four-fold higher than for any other ixodid species and more than 10,000-fold higher than for 15 of the 35 other ixodid species recorded to infest humans in the US (Table 1).

Moreover, many of the studies included in the data summaries did not make a clear statement that all ticks recorded from humans were biting, rather than collected while either biting or crawling on clothing or skin. The data therefore should be viewed as representing human tick encounters, including but not exclusive to tick bites. As noted previously, not distinguishing between ticks found biting versus crawling on clothing or skin is unfortunate as the likelihood of a tick encounter resulting in a human bite most likely differs across tick species. As one example, a recent human skin bioassay revealed that nymphs of the invasive *Ha. longicornis* voluntarily dropped off shortly after being introduced onto a human arm whereas *Ix. scapularis* nymphs uniformly remained on the arm and started moving toward a bite location (Foster et al., 2020). In addition, not all publications provide a breakdown for life stages of the tick species recorded from humans. Tables 1–2 therefore present summaries for all ticks of a given species recorded from humans regardless of life stage as well as a breakdown of numbers presented by life stage. It would be beneficial if all future studies present data for both tick species and life stages.

It also should be noted that the data compilation spans a long time period and includes studies from a large number of investigators with variable expertise in tick taxonomy and access to species identification resources (including molecularly based tick species identification), likely resulting in uneven quality of tick species identification across studies. As indicated by the variety of synonyms used for tick species names in the publications listed in Tables 3 and 4, especially in the early literature, tick taxonomy is an evolving research field. The reader should also keep in mind that recovery of ticks from humans can be biased to specific geographical areas and tick species during a given time period. For example, the frequent records of *De. andersoni* as a human biting tick in a national data compilation from the 1940s (Bishopp and Trembley, 1945) and a later national data compilation including early records (Merten and Durden, 2000) may in part be explained by that the early recognition of this species as a vector of the Rocky Mountain spotted fever agent spurred investigations of how often it bites humans. Similarly, the recognition of *Ix. scapularis* as the primary vector of pathogens causing Lyme disease, babesiosis, and anaplasmosis in the 1980s and 1990s (Eisen and Eisen, 2018) led to both research and passive tick collection initiatives focusing specifically on the role of this species as a human biter. Additional data limitations are discussed in Section 4.

The taxonomic nomenclature for ixodid tick species follows Guglielmone et al. (2014, 2020), Nava et al. (2014a, 2014b, 2015), and Guglielmone and Robbins (2018). In the last decade, several poorly resolved ixodid tick species complexes have been recognized, including *Am. cajennense* s.l. (Nava et al., 2014a) and *Rh. sanguineus* s.l. (Nava et al., 2015). Some ixodid species included in the data compilations presented in the present paper merit special mention based on recent taxonomic developments. There are unresolved questions regarding identification of *Am. cajennense* versus *Am. mixtum* in the US (Nava et al., 2014a; Guglielmone and Robbins, 2018), and Guglielmone et al. (2020) considers *Am. mixtum* to be the only member of the *Am. cajennense* s.l. complex established in the US.

Data for these closely related species, which both are known to bite humans (Guglielmone and Robbins, 2018), are therefore presented as *Am. cajennense* s.l. in this paper. Moreover, *Am. imitator* was relegated to a junior synonym of *Am. tenellum* by Nava et al. (2014b). Human biting ticks from far southwestern Texas and southern Arizona previously identified as *Am. maculatum* were reclassified as *Am. triste* by Mertins et al. (2010), and additional collections of *Am. triste* from humans in Arizona were presented by Herrick et al. (2016). Recently, *De. variabilis* from the disjunct population in the far western US was proposed to be a separate species, *Dermacentor similis* n. sp. (Lado et al., 2021). Finally, data are presented for *Rh. sanguineus* s.l. due to unresolved taxonomic issues for species within this complex (Nava et al., 2015).

The taxonomic nomenclature for argasid tick species follows Guglielmone et al. (2010) and Nava et al. (2017). Some argasid species included in the data compilations in the present paper merit special mention in this regard. Due to ongoing taxonomic debate, four of the included *Ornithodoros* species (*Or. capensis, Or. concanensis, Or. kelleyi*, and *Or. stageri*) are referred to as belonging to genus *Carios* by some authors (see Mans et al., 2019). Moreover, ticks from Mono Lake in California initially described as *Ar. cooleyi* by Schwan and Winkler (1984) were later redescribed as a new species, *Ar. monolakensis* (Schwan et al., 1992). Finally, as noted by Kohls et al. (1970), there is confusion in the early literature with regards to North American records for the new world species *Ar. miniatus* (present across the southern US) and *Ar. sanchezi* (present in the western US) in relation to the cosmopolitan fowl tick, *Argas persicus* (collected only sporadically in the US). All three species commonly infest domestic fowl. Prior to the resurrection by Kohls et al. (1970) of *Ar. miniatus* and *Ar. sanchezi* as valid species names, they were considered synonyms of *Ar. persicus* by some authors (e.g., Nuttall et al., 1911; Cooley and Kohls, 1944a). For example, geographical collection records for *Ar. persicus*, explicitly including the synonyms *Ar. miniatus* and *Ar. sanchezi*, reported by Cooley and Kohls (1944a) across the southern US (not including any human infestation records) most likely predominantly represented *Ar. miniatus* and *Ar. sanchezi*. The human infestation records for *Ar. miniatus* and *Ar. sanchezi* included in the data compilation in the present paper (see Supplementary Tables 37 and 39) were all described under these two species names.

3.1. Ixodid tick species

Human infestation has been recorded in the US for 36 native or recently established species of ixodid ticks (Table 1), including 18 *Ixodes* species, seven *Amblyomma* species, six *Dermacentor* species, three *Haemaphysalis* species, and two *Rhipicephalus* species. Information in Table 1 for each of the 36 tick species include the total number of specimens recorded to infest humans, a breakdown of records by life stage, broad geographical distribution in the US, host preference, and associated human pathogens or medical conditions.

3.1.1. Human tick encounters by species—At the national scale, only one tick species has >100,000 recorded human encounters: *Ix. scapularis* with 158,008 specimens documented to infest humans, accounting for 67% of all recorded human encounters with ixodid ticks (Table 1). Unfortunately, this notorious human biter is a primary vector of seven human pathogens causing Lyme disease (*Borrelia burgdorferi* sensu stricto [s.s.] and *Borrelia mayonii*), hard tick-borne relapsing fever (*Borrelia miyamotoi*), anaplasmosis (*Anaplasma phagocytophilum*), ehrlichiosis (*Ehrlichia muris eauclairensis*), babesiosis (*Babesia microti*), and Powassan encephalitis (Powassan virus) (Eisen et al., 2017). The second and third species most commonly recorded infesting humans are *Am. americanum* (n=36,004 specimens) and *De. variabilis* (n=26,624). This top three species list, which accounts for 94% of all recorded human tick encounters, is not surprising as these species have vast geographical ranges in the eastern US, can be locally abundant in and around human population centers, readily infest mammals, and quest openly from vegetation in at least one life stage which facilitates contact with humans. *Amblyomma americanum* is a primary vector of pathogens causing ehrlichiosis (*Ehrlichia chaffeensis, Ehrlichia ewingii*, and Panola Mountain *Ehrlichia*) and arboviral diseases (Bourbon virus and Heartland virus), and bites by this tick have been linked to Alpha-gal syndrome/red meat allergy (Childs and Paddock, 2003; Eisen and Paddock, 2021; Mitchell et al., 2020a). Based on ongoing northward range expansion for *Am. americanum* in the eastern US (Sonenshine, 2018), it would not be surprising if this species increased its share of recorded human bites in the future at the national scale. *Dermacentor variabilis* is a primary vector of pathogens causing Rocky Mountain spotted fever (*Rickettsia rickettsii*) and tularemia (*Francisella tularensis*), and bites by this tick can cause tick paralysis (Edlow and McGillicuddy, 2008; Eisen et al., 2017). Due to variable tick population densities within the ranges of the top three human biting species, their habitat preferences, and different questing behavior of *Ix. scapularis* in the northern versus southern part of its range, the regionally dominant human biting tick is *Ix. scapularis* in the Northeast and Upper Midwest, whereas it is *Am. americanum* in the southern part of the eastern US and *De. variabilis* in the Great Plains (see state level data presented by Merten and Durden, 2000; and Supplementary Tables 1, 13, and 29).

Five additional species have more than 500 recorded human encounters: *Ix. pacificus* (n=4,158 specimens); *De. andersoni* (n=3,518); *Ix. cookei* (n=2,494); *De. occidentalis* (n=809); and *Rh. sanguineus* s.l. (n=714). Based on their geographical distributions, *Ix. pacificus* and *De. occidentalis* are the tick species most commonly recorded from humans in the Pacific Coast states, and the same distinction goes to *De. andersoni* in the Rocky Mountain region. All three species readily infest a wide range of mammals, quest openly from vegetation in at least one life stage, and serve as primary vectors of human pathogens in their distributional areas: *Bo. burgdorferi* s.s., *Bo. miyamotoi*, and *An. phagocytophilum* for *Ix. pacificus*; the Pacific Coast tick fever agent, *Rickettsia philipii* for *De. occidentalis*; and *Fr. tularensis, Ri. rickettsii*, and Colorado tick fever virus for *De. andersoni*, the bite of which also can cause tick paralysis (Edlow and McGillicuddy, 2008; Eisen et al., 2017). Frequent human encounters with *Rh. sanguineus* s.l., which occurs across the continental US and is a primary vector of *Ri. rickettsii* in the Southwest, are not surprising as this tick primarily parasitizes dogs and can be found in and around human habitations (Dantas-Torres, 2010; Eisen et al., 2017). Of note for *Ix. cookei*, which has a broad distribution in the eastern US and is a vector of Powassan virus (Ebel, 2010), roughly 70% of the human infestation records come from Maine in the far Northeast (Rand et al., 2007; Smith et al., 2019). Common human exposure to *Ix. cookei* in some areas may be related, in part, to animal trapping as this species commonly infest mustelids; and it also parasitizes cats and dogs (Rand et al., 2007).

Rounding out the top 10 tick species recorded to infest humans in the US are *De. albipictus* (n=465) and *Am. maculatum* (n=335). *Amblyomma maculatum* is of increasing concern, as its distribution in the Southeast appears to be expanding northward, it infests a wide range of mammals, quests openly for hosts in the adult stage, and is a vector of *Rickettsia parkeri* causing spotted fever group rickettsiosis (Paddock and Goddard, 2015). Human infestation with the one-host tick *De. albipictus*, which is widely distributed in the US and preferentially parasitizes moose and deer, is in large part related to hunter exposures or people encountering clumps of questing larval ticks (Rand et al., 2007). *Dermacentor albipictus* was recently incriminated as a potential vector of *Babesia duncani*, causing babesiosis in the northwestern US (Swei et al., 2019).

Another grouping of eight species each have 100 to 250 recorded human tick encounters (Table 1). This includes five species known to be associated with *Bo. burgdorferi* s.l. spirochetes: *Ix. angustus, Ix. dentatus, Ix. muris, Ix. spinipalpis*, and *Ix. uriae* (Eisen, 2020). The eight species have variable host preferences and modes of human exposure. Three of the species feed primarily on seabirds (*Ix. uriae*), tortoises (*Am. tuberculatum*), or lagomorphs (*Ix. dentatus*) and therefore present risk mostly for people handling these animals or spend time in places where they congregate. Four other widely distributed species (*Ix. angustus, Ix. marxi, Ix. muris*, and *Ix. spinipalpis*) are found most commonly on rodents, shrews, and carnivores, but can occasionally be encountered questing openly near host burrows or nests. There is no obvious reason for any of these seven tick species to become more important as human biters in the future. The eight species, *Am. cajennense* s.l., infests medium-sized and large mammals but is presently found only in southern Texas in the US. Should climate-driven northward expansion occur for *Am. cajennense* s.l. in the future, then additional human populations will be placed at risk for bites by this species in the US.

A final grouping of ticks includes 18 species with <50 specimens recorded to infest humans (Table 1). These include ticks primarily infesting rodents or carnivores (*Ix. banksi, Ix. kingi, Ix. rugosus, Ix. sculptus, Ix. texanus*, and *Ix. woodi*); ticks preferentially feeding on birds (*Ha. chordeilis, Ix. baergi*, and *Ix. brunneus*), lagomorphs (*De. parumapertus* and *Ha. leporispalustris*) or wild sheep (*De. hunteri*); and ticks found only in southern Texas in the US (*Am. inornatum, Am. tenellum, Rh. annulatus*). However, three other species (*Am. triste, Ha. longicornis*, and *Ix. affinis*) from this grouping deserve special mention as they may rise in the ranks of human biting ticks in the future. As noted previously, human biting records for *Am. maculatum* may in certain areas represent misidentified *Am. triste*, which similarly to *Am. maculatum* is considered a vector of *Ri. parkeri* (Herrick et al., 2016). Moreover, records for *Ix. scapularis* in the southeastern US could potentially include misidentified *Ix. affinis*, as these two vector species of *Bo. burgdorferi* s.l. spirochetes (Eisen, 2020) are very difficult to distinguish morphologically in the immature life stages (Wright et al., 2014). Although the invasive *Ha. longicornis* does not appear to be an aggressive human biter, it is already widely distributed along the Eastern Seaboard, can reach very high local population densities, and will quest openly from vegetation in all life stages which facilitates contact with humans.

It would therefore not be surprising if this tick species rose sharply in the ranks of human biting ticks in the US in coming decades. Of note, additional records of human infestation for *Ha. longicornis* not yet presented in the peer-reviewed literature are included in the United States Department of Agriculture, National *Haemaphysalis longicornis* (Asian longhorned tick) Situation Report (https://www.aphis.usda.gov/animal_health/animal_diseases/tick/downloads/longhorned-tick-sitrep.pdf), which lists humans as hosts for 54 *Ha. longicornis* of unspecified life stage, presumably including some of the 32 ticks included in Table 1 and Supplementary Table 16. The potential for *Ha. longicornis* to serve as a natural vector of human pathogens in the US is still under investigation.

It is also worth noting that a few ixodid species with established populations in the US but not recorded to bite humans in this country have been found to infest humans elsewhere. *Amblyomma dissimile* and *Amblyomma rotundatum*, which occur in Florida and parasitize reptiles and amphibians (Keirans and Durden, 1998), have been recorded on very rare occasions from humans in other parts of the Americas (Serra-Freire et al., 1995; Quintero and Ramírez, 2008; Guzmán-Cornejo et al., 2011; Guglielmone and Robbins, 2018). *Ixodes soricis*, which occurs in the western US and infests shrews (Durden and Keirans, 1996), was recorded biting a human on a single occasion in British Columbia, Canada (Spencer, 1963). The southern cattle tick, *Rhipicephalus microplus*, which can be found in southernmost Texas (Osbrink et al., 2020), has been recorded to infest humans in Mexico, Central America, and South America (Rodríguez-Vivas et al., 2016; Guglielmone and Robbins, 2018). For general overviews of the ixodid tick species recorded to infest humans in the neighboring countries of Canada and Mexico, I refer to the following publications: Gregson (1956), Guzmán-Cornejo et al. (2007, 2011, 2016), Guzmán-Cornejo and Robbins (2010), Lindquist et al. (2016), and Guglielmone and Robbins (2018).

3.1.2. Human tick encounters by life stage—Breakdowns for life stages recorded to infest humans (Table 1) generally mirror previously described patterns for commonly human biting tick species but a few observations are merited here. Encounters with the most commonly human biting *Ixodes* species (*Ix. scapularis, Ix. pacificus*, and *Ix. cookei*) involve all life stages, with larvae accounting for a small proportion (1 to 6%) of recorded specimens. For *Ix. scapularis*, the contribution to recorded encounters is 55% for adults and 42% for nymphs. However, it should be noted that bites by the smaller, more inconspicuous nymphs most likely go undetected more often than for adults. Encounters with adult ticks predominate for *Ix. pacificus* (84%) with a smaller contribution by nymphs (15%), whereas for *Ix. cookei* the situation is reversed with nymphs predominating (75%) and adults having a smaller contribution (19%). Human infestation by *De. andersoni* and *De. variabilis* almost exclusively (>99% of all recorded human encounters) involve adult ticks, whereas for *De. occidentalis* adults still account for the majority of human encounters (81%) but with recovery of nymphs being more common (18%). Human infestation by the one-host tick, *De. albipictus* involve all life stages, most commonly (66%) adults but also the free-living larval stage (26%). Notable *Amblyomma* species have variable infestation patterns across life stages. For *Am. americanum*, humans most commonly are recorded encountering nymphs (49%) and adults (43%), but larval infestation also occurs (9%). In contrast, the vast majority (94%) of *Am. maculatum* recorded from humans are adults, with the remaining 6% made up by nymphs. All life stages of the brown dog tick. *Rh. sanguineus* s.l. have been recorded to infest humans, most commonly adults (53%) followed by nymphs (42%) and larvae (5%). Finally, human infestation by different life stages of the invasive *Ha. longicornis* is not yet clear but seems to involve all life stages and perhaps especially larvae (Table 1).

Understanding which life stages of a given tick species bite humans is important because pathogen infection prevalence can vary across life stages. Bites by host-seeking larval ticks pose a risk for human infection only for transovarially passed pathogens, such as *Borrelia miyamotoi* and viral agents (Bourbon virus, Heartland virus, and Powassan virus) transmitted by *Ix. scapularis* or *Am. americanum*, both species with larval stage ticks known to bite humans (Godsey et al., 2016, 2021; Eisen and Paddock, 2021). For horizontally maintained pathogens, either of the nymphal or adult stages can pose a risk for human infection. However, for some pathogens, such as *B. burgdorferi* s.s., the infection prevalence is distinctly higher in the adult stage (Lehane et al., 2021) as an adult tick have had two chances to acquire the agent while feeding as larva and nymph. To assess the risk for human infection following a tick bite, it is important to determine both the species and life stage of the tick, ideally combined with information on how long the tick was attached before being removed as this can influence the likelihood of transmission for some pathogens (Eisen, 2018).

3.2. Argasid tick species

Human infestation has been recorded in the US for 13 native species of argasid ticks (Table 2 and Supplementary Tables 37 to 49), including eight *Ornithodoros* species, three *Argas* species, and two *Otobius* species. Information in Table 2 for each of the 13 tick species include the total number of specimens recorded to infest humans, a breakdown of records by life stage, broad geographical distribution in the US, host preference, and associated human pathogens or medical conditions. The overall recorded human encounters with argasid ticks include only 230 specimens, but this very likely is a gross underestimate of actual human encounters. With the notable exception of the one-host *Otobius* ticks, the argasid species listed in Table 2 are multi-host ticks that retreat to a crack, crevice, or animal nest or burrow after the completed blood meal to molt to the next developmental stage, or lay eggs as females. Blood meals tend to be of short duration for nymphal stages (<1 h) and females (1 to 2 h), whereas larvae of species specializing on bats or birds can feed over several days (Sonenshine, 1991). With the exception of *Ot. megnini* as noted below, recovering argasid ticks while biting (including for a sleeping human host) therefore is far less likely than for ixodid ticks with feeding durations uniformly ranging from several days for immatures to 1 to 2 wk for adults. Argasid species are likely to encounter humans under very specific circumstances, reflecting their preferred natural hosts. Host preferences for the argasid species listed in Table 2 as recorded to infest humans range from ungulates (*Or. coriaceus* and *Ot. megnini*) to lagomorphs (*Ot. lagophilus*), rodents, (*Or. hermsii* and *Or. parkeri*), rodents and reptiles (*Or. turicata*), bats (*Or. concanensis, Or. kelleyi*, and *Or. stageri*), and birds (*Ar. monolakensis, Ar. miniatus, Ar. sanchezi*, and *Or. capensis*). With regards to pathogen transmission, *Or. hermsii, Or. parkeri*, and *Or. turicata* each serves as the vector of a relapsing fever spirochete: *Borrelia hermsii, Borrelia parkeri*, and *Borrelia turicatae*, respectively (Lopez et al., 2016).

The spinose ear tick, *Ot. megnini*, is the argasid species most commonly recorded from humans in the US (n=69 specimens), likely due to the discomfort this tick causes while feeding in the external ear canal and because the larval and nymphal stages of this one-host tick remain in the ear for a prolonged period of time (days to months). All life stages have been recorded from human hosts (Table 2). Most likely, bites by *Ot. megnini* result in recovery of the offending tick far more frequently than for any other human biting argasid species in the US. This tick is a parasite of ungulates in the western US, including cattle which helps to explain why it occasionally comes into contact with humans. *Ornithodoros coriaceus*, another species associated with ungulates, including cattle, in the western US, has yielded 55 specimens recorded to infest humans (Table 2). Together, *Ot. megnini* and *Or. coriaceus* account for 54% of the argasid ticks recorded from human hosts in the US.

The majority (34%) of the remaining argasid tick records from humans came from researchers studying gulls on islands in Mono Lake, California, during the summers of 1981 and 1982, with recovery of 41 *Ar. monolakensis* and 34 *Or. hermsi* (Schwan and Winkler, 1984). The researchers were sleeping on a partially enclosed wooden platform on one of the islands and engorged ticks were collected from their sleeping bags. Based on the host preferences of these two tick species, the researchers likely acquired the bird tick, *Ar. monolakensis*, while working in the gull colonies and the tick infesting mammals, *Or. hermsi*, at the camp site. A few (n=4) additional *Or. hermsi* have been recorded to infest humans (Philip and Davis, 1940; Merten and Durden, 2000). As shown in Table 2, only a few specimens (1 to 5) have been recorded to infest humans for each of the nine remaining argasid species (*Ar. miniatus, Ar. sanchezi, Or. capensis, Or. concanensis, Or. kelleyi, Or. parkeri, Or. stageri, Or. turicata*, and *Ot. lagophilus*), collectively accounting for 12% of all human encounters with argasid ticks.

It is also worth noting that two argasid species with established populations in the US but not recorded to bite humans in this country have been found to infest humans elsewhere. As noted by Keirans and Durden (2001), *Ar. persicus* was introduced to the US at some time in the past, presumably via infested chickens, and has been collected sporadically from various states, with most collection records from Maryland and Pennsylvania. This species also occurs in Mexico (Guzmán-Cornejo et al., 2019) and is known to bite humans on rare occasions in other parts of the world (Hoogstraal, 1985; Estrada-Peña and Jongejan, 1999). Moreover, *Ornithodoros talaje* (also referred to as *Carios talaje* by some authors), which occurs in the western and southcentral US and parasitizes rodents, has been recorded to infest humans in Mexico and Central America (Cooley and Kohls, 1944a; Lopez et al., 2016; Guzmán-Cornejo et al., 2019). Notably, *Or. talaje* is a vector of the relapsing fever spirochete, *Borrelia mazzottii* which causes disease in humans (Lopez et al., 2016). For general overviews of the argasid tick species recorded to infest humans in the neighboring countries of Canada and Mexico, I refer to the following publications: Cooley and Kohls (1944a), Gregson (1956), Kohls et al. (1957), Lindquist et al. (2016), Lopez et al. (2016), and Guzmán-Cornejo et al. (2019).

4. Data limitations

Two fundamental limitations of the data were already discussed in some detail in Section 3: the still ongoing evolution of tick taxonomy and variable accuracy over time and across studies for tick species identification. Additional data limitations are addressed in Sections 4.1 to 4.4.

4.1. Completeness of the data

Despite my best efforts to track down all potentially relevant publications, there may be published data for human tick encounters that were overlooked. Not all relevant publications are included in electronic databases, and individual tick encounter records can be phrased in a variety of ways to indicate the host, including "*Homo sapiens*", "*H. sapiens*", "human", "man", "woman", "child", "boy", "girl", or "clothing". Numerous older publications presented information about tick species infesting humans but without enumerating the numbers of specimens recorded. This information could not be included in the quantitative data compilation forming the basis for Tables 1 and 2 and Supplementary Tables 1 to 49, but due to their historical significance the relevant findings of such publications are presented in Table 4. An additional issue leading to loss of data is that some publications based on passive tick collection initiatives have presented large data sets (totaling >10,000 tick specimens across studies) broken down by tick species but where the subset of tick encounters accounted for specifically by humans, rather than pets, is not quantified. Results from these publications are summarized in Table 4 as they nevertheless provide information about the tick species most commonly recorded from humans or pets combined. Other publications, including passive tick collection initiatives and tick bite prevention or tick control intervention studies, have presented data for human tick encounters but without a breakdown for tick species (totaling >25,000 tick specimens across studies). These publications also are mentioned in Table 4, as the study locations can provide the basis for reasonable assumptions about which tick species were most likely to contribute to the human tick encounters. Another issue of note is that a limited amount of data may have been included in multiple publications, for example in original publications and then as accessioned ticks in curated collections.

4.2. Biases for data on human biting ticks

The most notable bias for the data on human tick encounters is a focus on specific species of medical importance, which is location specific and also can change over time. As vectors of the agents causing Rocky Mountain spotted fever and tularemia, *De. andersoni* and *De. variabilis* were considered the medically most important tick species in the US up to the 1970s. A strong focus on *De. andersoni* in the early 1900s explains why this was the tick species most frequently recorded to infest humans and included in the National Tick Collection by the end of the 20th century (Merten and Durden, 2000). However, the proportion of overall human encounters with ixodid ticks accounted for by *De. andersoni* has fallen from 40% in the national data compilation by Merten and Durden (2000) to 2% in the present data compilation (Table 1), which included the records from Merten and Durden (2000). This is in stark contrast to *De. variabilis*, for which the proportion of overall human tick encounters is 12% in Merten and Durden (2000) and 11% in the present data compilation (Table 1). One explanation for this discrepancy between *De. andersoni* and *De. variabilis* is that the latter species co-occurs with *Ix. scapularis* in areas of the Northeast and Upper Midwest that emerged as endemic for Lyme disease, babesiosis, and anaplasmosis from the 1980s onward. Over the last half-century, *Ix. scapularis* has experienced dramatic population growth and geographical spread, most likely in response to reforestation, increasing deer populations and a warming climate (Spielman, 1994; Sonenshine, 2018). The intense focus on *Ix. scapularis* as a human biter since the 1980s have led to common recovery also of other co-occurring human biting species, including *De. variabilis*. One driver for the accumulation of records for human encounters specifically with *Ix. scapularis*, rather than broadly for human biting ticks, is publications based on passive tick collection in the context of pathogen testing services focusing primarily or exclusively on *Ix. scapularis* (Xu et al., 2016; Little et al., 2019; Little and Molaei, 2020). Consequently, the proportion of overall human encounters with ixodid ticks accounted for by *Ix. scapularis* has risen from 7% in the national data compilation by Merten and Durden (2000) to 67% in the present data compilation (Table 1). Another tick species with rising interest for its role as a human biter is *Am. americanum*, which has long been recognized as a major nuisance biting tick in the southeastern and south-central US but more recently also was incriminated as a vector of human pathogens and associated with red meat allergy. The proportion of overall human encounters with ixodid ticks accounted for by *Am. americanum* was 20% in the national data compilation by Merten and Durden (2000) and 15% in the present data compilation (Table 1). This change may in part be related to the strong focus in recent decades on human biting *Ix. scapularis* in areas of the US where this species co-occurs with *De. variabilis* but where *Am. americanum* is absent or rare, leading to an underestimate of the national importance of *Am. americanum* as a human biting tick, relative to *Ix. scapularis* and *De. variabilis*. Moreover, due to ongoing northward expansion of *Am. americanum* into heavily populated areas in the Northeast and increasing concern about red meat allergy in areas of the eastern US where this species is highly abundant, it would not be surprising to see its share of recorded human tick encounters rise sharply in the future. The long-term study by Jordan and Egizi (2019) from Monmouth County in central coastal New Jersey is perhaps a harbinger of this, as *Am. americanum* was found during the study period to overtake *Ix. scapularis* as the tick species most commonly recorded to infest humans.

4.3. Records of ticks collected while biting humans versus crawling on skin or clothing

Many of the publications included in the data compilation in the present paper did not make a clear statement that all ticks recorded from humans were biting, rather than either biting or crawling on clothing or skin. Although understandable based on lack of information for this from original tick encounter descriptions, this may lead to an over-emphasis of some tick species or life stages as human biters. Some species questing from vegetation may be less inclined than other species to bite a human after contact is made, and therefore would be less prom-inent when considering only biting ticks rather than also including ticks collected while crawling on clothing or skin in a broader tick encounter classification. One example of this is the invasive *Ha. longicornis*, a mobile tick that effectively makes contact with drags/flags during tick sampling in the field (Sherpa et al., 2021), but was observed in the laboratory to voluntary disengage from human skin (Foster et al., 2020). Consequently, this tick species may have a lower ratio of encounters resulting in bites compared to notorious native human biters, such as *Am. americanum, De. variabilis*, and *Ix. scapularis*. For species with both immature and adult life stages commonly infesting humans, it also is possible that the larger, more easily spotted and recognized adults are overrepresented when reported as crawling ticks compared to biting ticks. For example, compared to the overall breakdown for *Ix. scapularis* recorded from humans in this data compilation, with 55% adults and 45% immatures (Table 1), two individual studies restricted to data for biting ticks and presenting data sets exceeding 200 ticks included a higher proportion (53 to 59%) of *Ix. scapularis* immatures (Sood et al., 1997; Nadelman et al., 2001). Moreover, less than 60% of surveyed members of the public recognized *Ix. scapularis* nymphs (embedded in resin blocks) as ticks, whereas more than 75% recognized adults of *Am. americanum, De. variabilis*, and *Ix. scapularis* as ticks in a recent study from the Upper Midwest (Bron et al., 2021).

4.4. Tick encounter locations

Ticks recorded to infest humans come with the challenge of travel potentially masking the actual location where the tick encounter occurred. This problem is most pronounced at finer spatial scales, including counties, but as cautioned in Tables 3 to 4 and the Supplementary Tables, state level records may include tick exposures resulting from out-of-state travel within the US. A few examples of this include records of *De. andersoni* and *Ix. pacificus* in Michigan (Walker et al., 1998), *Am. americanum* in California (Lang, 1999; Salkeld et al., 2019), and *Am. americanum, De. andersoni, De. variabilis*, and *Ix. scapularis* in Alaska (Hahn et al., 2020).

5. Future directions

Researchers and public health professionals in possession of unpublished human tick encounter data are strongly encouraged to publish this information in peer-reviewed scientific journals. For future papers including information on human tick encounters, it would be beneficial if data consistently were broken down by tick species and life stage in addition to specifying the geographical area covered and the time period of collection. Moreover, providing data for the subset of ticks infesting humans is important if the overall data set also includes ticks from pets or other sources. When possible, it also is of value to provide a breakdown for ticks collected while biting humans versus crawling on clothing or skin, and to provide information on travel histories of those encountering ticks. Biases toward collection of certain tick species are generally easy to elucidate from the stated purpose of a publication and the methods used. With the ongoing increase in passive tick collection initiatives, it seems likely that data on human tick encounters will amass rapidly in coming decades, hopefully accounting for the above considerations to maximize the usefulness of the gathered information. Another issue to consider in the future is how to deal with the increasing volume of data on human tick encounters available only from various websites.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Data availability

Data included in Supplementary Tables

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Table 1

Native or recently established ixodid tick species documented to bite humans in the United States (US).

Tick species[a]	Total tick specimens recorded to infest humans[f]		Number (%) of ticks recorded to infest humans by life stage for a given species[g]			Geographical distribution in the US	Primary host preference	Selected associated human pathogens or medical conditions
	Number	%	Adult	Nymph	Larva			
Ixodes scapularis [b]	158,008	67.3	60,426 (55)	46,481 (42)	2,796 (3)	Eastern	Wide range of mammals, Birds, Lizards	*Anaplasma phagocytophilum* *Babesia microti* *Borrelia burgdorferi* s.s.[h] *Borrelia mayonii* *Borrelia miyamotoi* Powassan virus
Amblyomma americanum	36,004	15.4	5,605 (43)	6,396 (49)	1,137 (9)	Eastern	Ungulates, Carnivores, Birds	Bourbon virus *Ehrlichia chaffeensis* *Ehrlichia ewingii* Heartland virus Red meat allergy
Dermacentor variabilis [c]	26,624	11.3	19,391 (99.6)	73 (0.4)	11 (<0.1)	Eastern, Far Western[c]	Rodents, Carnivores	*Francisella tularensis* *Rickettsia rickettsii* Tick paralysis
Ixodes pacificus [b]	4,158	1.8	2,187 (84)	384 (15)	26 (1)	Far Western	Wide range of mammals, Birds, Lizards	*Anaplasma phagocytophilum* *Borrelia burgdorferi* s.s. *Borrelia miyamotoi*
Dermacentor andersoni [b]	3,518	1.5	2,970 (99.6)	10 (0.3)	3 (0.1)	Western	Wide range of mammals	Colorado tick fever virus *Francisella tularensis* *Rickettsia rickettsii* Tick paralysis
Ixodes cookei [b]	2,494	1.1	130 (19)	513 (75)	38 (6)	Eastern	Rodents, Carnivores	Powassan virus
Dermacentor occidentalis	809	0.3	562 (81)	126 (18)	10 (1)	Far Western	Wide range of mammals	*Rickettsia philipii*
Rhipicephalus sanguineus s.l.[d]	714	0.3	175 (53)	138 (42)	18 (5)	Widely in the US	Dogs	*Rickettsia rickettsii*
Dermacentor albipictus [b]	465	0.2	31 (66)	4 (8)	12 (26)	Widely in the US	Ungulates	*Babesia duncani*
Amblyomma maculatum	335	0.1	237 (94)	14 (6)	0 (0)	Southeastern	Wide range of mammals, Birds	*Rickettsia parkeri*
Ixodes marxi	232	0.1	19 (41)	25 (54)	2 (4)	Eastern	Rodents, Carnivores	None
Ixodes uriae	224	0.1	2 (29)	5 (71)	0 (0)	Maine, Oregon, Alaska	Seabirds	*Borrelia garinii*
Amblyomma cajennense s.l.[d]	222	<0.1	122 (55)	85 (38)	14 (6)	Southern Texas	Wide range of mammals, Birds	None
Ixodes muris	213	<0.1	27 (66)	13 (32)	1 (2)	Eastern	Rodents, Shrews, Birds	*Borrelia burgdorferi* s.s.

Tick species[a]	Total tick specimens recorded to infest humans[f]		Number (%) of ticks recorded to infest humans by life stage for a given species[g]			Geographical distribution in the US	Primary host preference	Selected associated human pathogens or medical conditions
	Number	%	Adult	Nymph	Larva			
Ixodes dentatus	165	<0.1	7 (7)	91 (92)	2 (2)	Eastern	Lagomorphs, Birds	*Borrelia burgdorferi* s.s.
Ixodes angustus	132	<0.1	53 (72)	21 (28)	0 (0)	Widely in the US	Rodents, Shrews, Carnivores	*Borrelia burgdorferi* s.s.
Ixodes spinipalpis	110	<0.1	13 (28)	34 (72)	0 (0)	Western	Rodents, Lagomorphs, Birds	*Borrelia burgdorferi* s.s.
Amblyomma tuberculatum	109	<0.1	0 (0)	0 (0)	109 (100)	Southeastern	Tortoises	None
Haemaphysalis longicornis [e]	32	<0.1	2 (9)	3 (13)	18 (78)	Eastern	Ungulates, Carnivores, Birds	Under investigation
Haemaphysalis leporispalustris	30	<0.1	1 (17)	5 (83)	0 (0)	Widely in the US	Lagomorphs	None
Dermacentor hunteri	25	<0.1	24 (96)	1 (4)	0 (0)	Southwestern	Ungulates (wild sheep)	None
Amblyomma triste	9	<0.1	9 (100)	0 (0)	0 (0)	Arizona/Texas	Wide range of mammals, Birds	*Rickettsia parkeri*
Dermacentor parumapertus	7	<0.1	5 (71)	2 (29)	0 (0)	Western	Lagomorphs	None
Ixodes texanus	6	<0.1	1 (17)	0 (0)	5 (83)	Widely in the US	Rodents, Lagomorphs, Carnivores	None
Amblyomma tenellum [b]	5	<0.1	2 (50)	2 (50)	0 (0)	Southern Texas	Wide range of mammals, Birds	None
Haemaphysalis chordeilis	5	<0.1	1 (100)	0 (0)	0 (0)	Widely in the US	Birds	None
Ixodes kingi	5	<0.1	1 (25)	3 (75)	0 (0)	Widely in the US	Rodents, Carnivores	None
Ixodes sculptus	5	<0.1	1 (25)	3 (75)	0 (0)	Widely in the US	Rodents, Carnivores	None
Amblyomma inornatum	4	<0.1	1 (100)	0 (0)	0 (0)	Southern Texas	Wide range of mammals, Birds	None
Ixodes woodi	3	<0.1	0 (0)	2 (100)	0 (0)	Widely in the US	Rodents	None
Rhipicephalus annulatus [b]	3	<0.1	3 (100)	0 (0)	0 (0)	Southern Texas	Ungulates	None
Ixodes affinis	2	<0.1	—	—	—	Southeastern	Wide range of mammals, Birds	*Borrelia burgdorferi* s.s.
Ixodes banksi	2	<0.1	1 (100)	0 (0)	0 (0)	Eastern	Rodents	None
Ixodes baergi	1	<0.1	—	—	—	Eastern	Birds	None
Ixodes brunneus	1	<0.1	1 (100)	0 (0)	0 (0)	Widely in the US	Birds	None
Ixodes rugosus	1	<0.1	1 (100)	0 (0)	0 (0)	Far Western	Carnivores	None

[a] Based on taxonomic nomenclature presented by Guglielmone et al. (2014, 2020), Nava et al. (2014a, 2014b, 2015), and Guglielmone and Robbins (2018).

[b] Including synonyms for the following species: *Amblyomma tenellum* (=*Amblyomma imitator*); *Dermacentor albipictus* (=*Dermacentor nigrolineatus*); *Dermacentor andersoni* (=*Dermacentor venustus*); *Ixodes cookei* (=*Ixodes cruciarius*); *Ixodes pacificus* (=*Ixodes ricinus californicus, Ixodes californicus*); *Ixodes scapularis* (=*Ixodes ricinus scapularis, Ixodes dammini*); and *Rhipicephalus annulatus* (=*Margaropus annulatus, Boophilus annulatus*).

[c] Records for *Dermacentor variabilis* in the far western US may in part or entirely represent the recently described *Dermacentor similis* n. sp. (Lado et al., 2021).

[d] As noted by Nava et al. (2014a, 2015) and Guglielmone and Robbins (2018), there are unresolved questions regarding species within the *Rhipicephalus sanguineus* sensu lato and *Amblyomma cajennense* sensu lato complexes, including identification of *Am. cajennense* versus *Amblyomma mixtum* in the US, and data for these two closely related species are therefore presented as *Am. cajennense* s.l. Guglielmone et al. (2020) consider *Am. mixtum* to be the only member of the *Am. cajennense* s.l. complex established in the US.

[e] The invasive *Haemaphysalis longicornis* is now established in the US and therefore merits inclusion here. Additional records of human infestation not yet presented in the peer-reviewed literature are included in the United States Department of Agriculture, National *Haemaphysalis longicornis* (Asian longhorned tick) Situation Report (https://www.aphis.usda.gov/animal_health/animal_diseases/tick/downloads/longhorned-tick-sitrep.pdf).

[f] All life stages combined, based on data presented in Supplementary Tables 1–36. Percentages refer to contribution to human encounters across tick species. The data refer broadly to human tick encounters, as not all publications make it clear if ticks recorded to infest humans were biting or still crawling on clothing or skin.

[g] Excluding specimens for which life stage was not defined (see Supplementary Tables 1–36). Percentages refer to contribution to human encounters across life stages for a given tick species.

[h] *Borrelia burgdorferi* sensu stricto.

Table 2

Native argasid tick species documented to bite humans in the United States (US).

Tick species[a]	Total tick specimens recorded to infest humans[c]		Number (%) of ticks recorded to infest humans by life stage for a given species[d]			Geographical distribution in the US	Primary host preference	Associated human pathogens or medical conditions
	Number	%	Adult	Nymph	Larva			
Otobius megnini [b]	69	30.0	9 (17)	36 (69)	7 (14)	Western	Ungulates, including cattle	Damage at external ear canal bite site
Ornithodoros coriaceus	55	23.9	4 (40)	4 (40)	2 (20)	Far Western	Ungulates, including cattle	None
Argas monolakensis [b]	41	17.8	23 (56)	18 (44)	0 (0)	Western	Birds	None
Ornithodoros hermsi	38	16.5	5 (13)	33 (87)	0 (0)	Western	Rodents	*Borrelia hermsii*
Ornithodoros turicata	5	2.2	0 (0)	4 (80)	1 (20)	Southern[e]	Rodents, Reptiles	*Borrelia turicatae*
Ornithodoros parkeri	4	1.7	3 (100)	0 (0)	0 (0)	Western	Rodents, Lagomorphs	*Borrelia parkeri*
Argas sanchezi	3	1.3	1 (33)	2 (67)	0 (0)	Western	Birds, including domestic fowl	None
Ornithodoros capensis	3	1.3	0 (0)	3 (100)	0 (0)	Southeast, Hawaii	Seabirds	None
Ornithodoros concanensis	3	1.3	2 (100)	0 (0)	0 (0)	Western	Bats, Birds	None
Ornithodoros kelleyi	3	1.3	0 (0)	2 (100)	0 (0)	Widely in the US	Bats	None
Ornithodoros stageri	3	1.3	1 (100)	0 (0)	0 (0)	Southern	Bats	None
Argas miniatus	2	0.9	0 (0)	2 (100)	0 (0)	Southern	Birds, including domestic fowl	None
Otobius lagophilus	1	0.4	0 (0)	0 (0)	1 (100)	Western	Lagomorphs	None

[a]Based on taxonomic nomenclature presented by Guglielmone et al. (2010) and Nava et al. (2017). Some other authors (see Mans et al., 2019) place four of the *Ornithodoros* species (*Or. capensis, Or. concanensis, Or. kelleyi*, and *Or. stageri*) included in this table in the genus *Carios*.

[b]Including synonyms for the following species: *Argas monolakensis* (=*Argas cooleyi*) and *Otobius megnini* (=*Argas megnini, Ornithodoros megnini*).

[c]All life stages combined, based on data presented in Supplementary Tables 37–49. Percentages refer to contribution to human encounters across tick species. The data refer broadly to human tick encounters, as not all publications make it clear if ticks recorded to infest humans were biting/had bitten or were still crawling on clothing or skin.

[d]Excluding specimens for which life stage was not defined (see Supplementary Tables 37–49). Percentages refer to contribution to human encounters across life stages for a given species.

[e]Mainly southwestern, with a disjunct population in Florida.

Table 3

Publications presenting quantitative data (included in the data compilations presented in Tables 1–2 and Supplementary Tables 1–49) for records of crawling or biting tick specimens collected from humans for tick species with established populations in the United States (US).

Reference	Geographical area[a]	Time period	Tick species recorded to infest humans (synonym for species used in the publication)[b]
Fitch (1872)	NY	1857–1868	*Ixodes cookei* (=*Ixodes cruciarius)*
Simpson and Wheeler (1901)	AZ	1900	*Otobius megnini* (=*Argas megnini)*
Hunter and Hooker (1907)	TX	Up to 1907	*Otobius megnini* (=*Ornithodoros megnini*), *Rhipicephalus annulatus* (=*Margaropus annulatus)*
Stiles (1910)	MT, WY	1902–1904	*Dermacentor andersoni*
Hunter and Bishopp (1911a)	US	Up to 1911	*Dermacentor andersoni* (=*Dermacentor venustus)*
Hooker et al. (1912)	US	Up to 1912	*Amblyomma americanum, Amblyomma maculatum, Dermacentor occidentalis, Dermacentor variabilis, Otobius megnini* (=*Ornithodoros megnini*)
Herms (1917)	CA	1915	*Otobius megnini* (=*Ornithodoros megnini*)
Bassoe (1924)	CO	1923	*Dermacentor andersoni* (=*Dermacentor venustus*)
Hamilton (1934)	NY	1931	*Ixodes cookei* (=*Ixodes hexagenia* var. *cookei)*
Kohls (1937)	CA	1936	*Dermacentor occidentalis*
Barnett (1937)	ID	1936	*Dermacentor andersoni*
Bradley and Connell (1938)	NJ	Not stated	*Amblyomma americanum*
Cooley and Kohls (1938)	NY	Not stated	*Ixodes cookei*
Philip and Davis (1940)	ID	1937	*Ornithodoros hermsi*
Katz (1941)	OH	1937	*Dermacentor variabilis*
Augustson (1942)	CA	1940	*Dermacentor andersoni*
Parker et al. (1943)	TX	1942	*Amblyomma americanum*
Cooley and Kohls (1944a)	CA, NV, OR	1935–1939	*Ornithodoros parkeri, Ornithodoros stageri, Otobius megnini*
Cooley and Kohls (1944b)	AR, MO, MS, OK, TX	1937–1942	*Amblyomma americanum, Amblyomma maculatum*
Riley (1944)	MN, OH	1939–1942	*Amblyomma americanum*
Bequaert (1945)	US	Up to 1945	*Amblyomma americanum, Dermacentor variabilis, Ixodes cookei, Ixodes scapularis*
Cooley and Kohls (1945)	CA, MO, MT, OR, VT, WA	1935–1944	*Ixodes angustus, Ixodes cookei, Ixodes pacificus, Ixodes scapularis, Ixodes spinipalpis*
Bishopp and Trembley (1945)	US	1910–1945	*Amblyomma americanum, Amblyomma cajennense* sensu lato (s.l.)[e], *Amblyomma maculatum, Argas miniatus, Dermacentor albipictus, Dermacentor andersoni, Dermacentor occidentalis, Dermacentor variabilis, Haemaphysalis chordeilis, Ixodes angustus, Ixodes cookei, Ixodes muris, Ixodes pacificus* (=*Ixodes ricinus californicus), Ixodes scapularis* (=*Ixodes ricinus scapularis*), *Ixodes sculptus, Otobius megnini, Rhipicephalus sanguineus* sensu lato (s.l.)
MacCreary (1945)	DE	1939–1944	*Amblyomma americanum*
Carpenter et al. (1946)	AL, FL, GA, MS, NC, SC	1943–1945	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Haemaphysalis leporispalustris, Ixodes scapularis* (=*Ixodes ricinus scapularis*), *Rhipicephalus sanguineus* s.l.
Cooley (1946b)	OR, WA	1931–1945	*Ixodes angustus*
Anastos (1947)	NY	1946	*Ixodes muris, Ixodes scapularis*
Knipping et al. (1950)	WI	1925–1949	*Dermacentor variabilis*

Reference	Geographical area[a]	Time period	Tick species recorded to infest humans (synonym for species used in the publication)[b]
Holdenried et al. (1951)	CA	1940–1945	*Ixodes pacificas*
Edmunds (1951)	UT	1938–1945	*Ixodes pacificus*
Helms (1952)	NE	1951	*Rhipicephalus sanguineus* s.l.
Philip (1952)	AZ, IA	1942–1950	*Rhipicephalus sanguineus* s.l.
Rehn (1953)	NY	1952	*Amblyomma americanum*
Beck (1955a)	UT	1953	*Ixodes pacificus*
Ryckman et al. (1955)	CA	1952	*Ornithodoros coriaceus* (same record also presented by Waldron, 1962)
Sollers (1955)	DC	1954	*Ixodes dentatus*
Eads et al. (1956)	TX	1937–1955	*Amblyomma maculatum, Dermacentor variabilis, Ixodes cookei, Ixodes scapularis, Otobius megnini, Rhipicephalus sanguineus* s.l.
Roscoe (1956)	UT	1955	*Dermacentor parumapertus*
Allred et al (1960)	UT	1955	*Ixodes pacificus*
Waldron (1962)	CA	1952–1958	*Ornithodoros coriaceus*
Brinton and Kohls (1963)	MT, UT	1952–1955	*Dermacentor hunteri*
Sonenshine et al. (1965)	VA	1912–1963	*Amblyomma americanum, Dermacentor albipictus, Dermacentor variabilis*
Johnson (1966)	UT	1951–1966	*Dermacentor albipictus, Dermacentor parumapertus, Ixodes pacificus*
Arthur and Snow (1968)	CA, OR, UT, WA	Not stated	*Ixodes pacificus*
Snetsinger (1968)	PA	Up to 1968	*Amblyomma maculatum, Dermacentor albipictus*
Nelson (1969)	US	1942–1968	*Rhipicephalus sanguineus* s.l.
Cooney and Hays (1972)	AL	1963–1966	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Rhipicephalus sanguineus* s.l.
Good (1973)	NY	1971	*Amblyomma americanum, Ixodes muris*
Burgdorfer et al. (1975)	SC	1973–1974	*Amblyomma americanum, Dermacentor variabilis, Rhipicephalus sanguineus* s.l.
Benach et al. (1977)	NY	1975–1976	*Dermacentor variabilis*
Loving et al. (1978)	SC	1974–1976	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Steere et al. (1978)	CT	1977	*Ixodes scapularis*
Wallis et al. (1978)	CT	1977	*Dermacentor variabilis, Ixodes scapularis*
Magnarelli et al. (1979)	CT	1976–1977	*Dermacentor variabilis*
Spielman et al. (1979)	MA	1930–1971	*Ixodes scapularis* (=*Ixodes dammini*)
Steere and Malawista (1979)	Eastern US	1975–1979	*Ixodes scapularis* (=*Ixodes dammini*)
Terry and Williams (1980)	IN	1977	*Dermacentor variabilis*
Jones (1981)	NC	1980	*Amblyomma americanum*
Jensen et al. (1982)	UT	1981	*Otobius megnini*
Lane et al. (1982)	CA	1979	*Ixodes pacificus*
McKeon et al. (1982)	NY	1954–1981	*Amblyomma americanum*
Easton (1983)	SD	1937–1967	*Dermacentor andersoni, Dermacentor variabilis, Ornithodoros concanensis*
Eads and Campos (1984)	NM	Not stated	*Otobius megnini*

Reference	Geographical area[a]	Time period	Tick species recorded to infest humans (synonym for species used in the publication)[b]
Furman and Loomis (1984)	CA	1915–1982	*Argas sanchezi, Dermacentor andersoni, Dermacentor hunteri, Dermacentor occidentalis, Dermacentor parumapertus, Dermacentor variabilis, Haemaphysalis leporispalustris, Ixodes pacificus, Ixodes rugosus, Ixodes sculptus, Ornithodoros coriaceus, Ornithodoros parkeri, Otobius megnini, Rhipicephalus sanguineus* s.l.
Schwan and Winkler (1984)	CA	1981–1982	*Argas monolakensis* (=*Argas cooleyi*), *Ornithodoros hermsi*
Keirans (1985)	MT	1903	*Dermacentor andersoni*
Demaree (1986)	IN	1980–1984	*Amblyomma americanum, Dermacentor variabilis, Ixodes cookei, Rhipicephalus sanguineus* s.l.
Bode et al. (1987)	TX	Not stated	*Amblyomma americanum*
Falco and Fish (1988)	NY	1985	*Amblyomma americanum, Dermacentor variabilis, Ixodes scapularis* (=*Ixodes dammini*)
Costello et al. (1989)	CT	1986	*Ixodes scapularis* (=*Ixodes dammini)*
Damrow et al. (1989)	WA	1987	*Ixodes angustus*
Goddard (1989)	OK, TX	1986–1988	*Rhipicephalus sanguineus* s.l.
Magnarelli and Anderson (1989)	CT	1983–1988	*Dermacentor variabilis, Ixodes cookei, Ixodes scapularis* (=*Ixodes dammini*)
Robbins (1989)	AK, OR, WA, WY	1932–1977	*Ixodes angustus, Ixodes woodi*
Carpenter et al. (1990)	FL, OK, TX	1980–1989	*Rhipicephalus sanguineus* s.l.
Hall et al. (1991)	VW	1987–1990	*Ixodes cookei, Ixodes dentatus, Ixodes texanus*
Monsen et al. (1992)	CA	1989–1990	*Ixodes pacificus*
Shapiro et al. (1992)	CT	1989–1991	*Ixodes scapularis* (=*Ixodes dammini*)
Smith et al. (1992)	ME	1989–1990	*Dermacentor albipictus, Dermacentor variabilis, Ixodes cookei, Ixodes marxi, Ixodes muris, Ixodes scapularis* (=*Ixodes dammini*)
Walker et al. (1992)	MI	1992	*Ixodes dentatus*
Schwartz et al. (1993)	NY	1988–1990	*Dermacentor variabilis, Ixodes scapularis* (=*Ixodes dammini*)
Slaff and Newton (1993)	NC	1989–1991	*Amblyomma americanum, Dermacentor variabilis, Rhipicephalus sanguineus* s.l.
Campbell and Bowles (1994)	US	1989–1992	*Amblyomma americanum, Dermacentor andersoni, Dermacentor variabilis, Ixodes cookei, Ixodes pacificus, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Clover and Lane (1995)	CA	1989–1991	*Ixodes pacificus*
Yeh et al. (1995)	PA, RI	Not stated	*Ixodes scapularis*
Anderson et al. (1996)	CT, NJ, NY	1990–1992	*Ixodes dentatus, Ixodes scapularis*
Falco et al. (1996)	NY	1985–1989	*Ixodes scapularis*
Felz et al. (1996)	GA, SC	1990–1995	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Harrison et al. (1997)	NC	1973–1995	*Amblyomma maculatum, Haemaphysalis leporispalustris, Ixodes cookei, Ixodes dentatus, Otobius megnini, Rhipicephalus sanguineus* s.l.
Sood et al. (1997)	NY	1992–1993	*Amblyomma americanum, Dermacentor variabilis, Ixodes cookei, Ixodes dentatus, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Keirans and Lacombe (1998)	ME	1990–1995	*Amblyomma americanum, Ixodes dentatus, Ixodes uriae*
Walker et al. (1998)	MI	1985–1996	*Amblyomma americanum, Dermacentor albipictus, Dermacentor andersoni, Dermacentor variabilis, Haemaphysalis leporispalustris, Ixodes angustus, Ixodes baergi, Ixodes banksi, Ixodes cookei, Ixodes dentatus, Ixodes marxi,*

Reference	Geographical area[a]	Time period	Tick species recorded to infest humans (synonym for species used in the publication)[b]
			Ixodes muris, Ixodes pacificas, Ixodes scapularis, Ixodes sculptus, Ornithodoros kelleyi, Otobius megnini, Rhipicephalus sanguineus s.l.
Dworkin et al. (1999)	WA	1947–1996	*Dermacentor andersoni*
Felz and Durden (1999)	GA, SC	1995–1998	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Ixodes scapularis*
Lacombe et al. (1999)	ME	1989–1999	*Ixodes muris*
Lang (1999)	CA	1992–1993	*Amblyomma americanum, Dermacentor hunteri, Dermacentor occidentalis, Dermacentor variabilis, Ixodes pacificus*
Felz et al. (2000)	GA	Not stated	*Dermacentor variabilis*
Merten and Durden (2000)	US (including data broken down for 49 states)	Up to 2000	*Amblyomma americanum, Amblyomma cajennense* s.l.[e], *Amblyomma inornatum, Amblyomma maculatum, Amblyomma tenellum* (=*Amblyomma imitator*), *Amblyomma tuberculatum, Argas miniatus, Argas sanchezi, Dermacentor albipictus, Dermacentor andersoni, Dermacentor hunteri, Dermacentor occidentalis, Dermacentor parumapertus, Dermacentor variabilis, Ixodes angustus, Ixodes banksi, Ixodes brunneus, Ixodes cookei, Ixodes dentatus, Ixodes kingi, Ixodes marxi, Ixodes muris, Ixodes pacificus, Ixodes scapularis, Ixodes sculptus, Ixodes spinipalpis, Ixodes texanus, Ixodes uriae, Ixodes woodi, Ornithodoros capensis, Ornithodoros concanensis, Ornithodoros coriaceus, Ornithodoros hermsi, Ornithodoros kelleyi, Ornithodoros parkeri, Ornithodoros stageri, Ornithodoros turicata, Otobius lagophilus, Otobius megnini, Rhipicephalus annulatus* (=*Boophilus annulatus*), *Rhipicephalus sanguineus* s.l.
Armstrong et al. (2001)	MD	1994–1996	*Amblyomma americanum, Dermacentor variabilis, Ixodes dentatus, Ixodes scapularis* (=*Ixodes dammini*)
James et al. (2001)	Not clear	1999	*Amblyomma americanum*
Love et al. (2001)	US	2000	*Amblyomma americanum*
Nadelman et al. (2001)	NY	1987–1996	*Ixodes cookei, Ixodes scapularis*
Stromdahl et al. (2001)	Eastern US	1997	*Amblyomma americanum, Dermacentor variabilis, Ixodes scapularis*
Goddard (2002)	MS	1990–1999	*Amblyomma americanum, Amblyomma maculatum, Amblyomma tuberculatum, Dermacentor albipictus, Dermacentor variabilis, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Stromdahl et al. (2003)	VA	2000–2002	*Amblyomma americanum*
Gill et al. (2004)	IA	Not stated	*Ornithodoros kelleyi* (=*Carios kelleyi*)
Wormser et al. (2005)	MO	2001–2003	*Amblyomma americanum*
James et al. (2006)	US	1903–2001	*Dermacentor andersoni*
Schulze et al. (2006)	NJ	2001–2005	*Amblyomma americanum, Dermacentor variabilis, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Smith et al. (2006)	ME	1996–2005	*Ixodes uriae*
Billeter et al. (2007)	NC	2006	*Amblyomma americanum*
Rand et al. (2007)	ME	1989–2006	*Amblyomma americanum, Amblyomma maculatum, Dermacentor albipictus, Dermacentor variabilis, Haemaphysalis leporispalustris, Ixodes cookei, Ixodes dentatus, Ixodes marxi, Ixodes muris, Ixodes scapularis, Ixodes uriae, Rhipicephalus sanguineus* s.l.
Reeves et al. (2007)	NC, TN	2001	*Dermacentor variabilis*
Loftis et al. (2008)	Eastern US	1998–2006	*Amblyomma americanum*
Reeves et al. (2008)	GA	2005	*Amblyomma americanum*
Cohen et al. (2009)	GA	2005–2006	*Amblyomma americanum, Amblyomma maculatum*

Reference	**Geographical area**[a]	**Time period**	**Tick species recorded to infest humans (synonym for species used in the publication)**[b]
Murphree et al. (2009)	KY	2005–2007	*Amblyomma americanum, Dermacentor variabilis*
Jiang et al. (2010)	Eastern US	2005	*Amblyomma americanum*
Mertins et al. (2010)	AZ	1942–1992	*Amblyomma triste*
Williamson et al. (2010)	TX	2004–2008	*Amblyomma americanum, Amblyomma cajennense* s.l.[e], *Amblyomma maculatum, Dermacentor albipictus, Dermacentor andersoni, Dermacentor variabilis, Ixodes scapularis, Otobius megnini, Rhipicephalus sanguineus* s.l.
Feder et al. (2011)	CT	2009	*Amblyomma americanum*
Stromdahl et al.(2011) [c]	US	1994–2009	*Dermacentor variabilis, Rhipicephalus sanguineus* s.l.
Willen et al. (2011)	AL	Not stated	*Amblyomma americanum*
Jiang et al. (2012)	AL, FL, GA, KS, KY, LA, MD, MS, NC, OK, VA	2000–2009	*Amblyomma maculatum*
Cortinas and Spomer (2014)	NE	1911–2011	*Amblyomma americanum, Amblyomma maculatum, Dermacentor andersoni, Dermacentor variabilis, Ixodes kingi, Otobius megnini, Rhipicephalus sanguineus* s.l.
Lee et al. (2014)	NC	2011–2012	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Ixodes scapularis*
Russart et al. (2014)	ND	2010	*Amblyomma americanum*
Stromdahl et al. (2014) [c]	Eastern US	1997–2012	*Ixodes scapularis*
Richards et al. (2015)	KY, NC, OH, TN, VA	2013	*Amblyomma americanum, Dermacentor variabilis, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Stromdahl et al. (2015) [d]	US	1997–2010	*Amblyomma americanum, Ixodes pacificus*
Stromdahl et al. (2015)	AL, AR, DE, FL, GA, KS, KY, MD, MO, NC, NJ, PA, RI, SC, TN, VA	2013	*Amblyomma americanum*
Carter et al. (2016)	US	Not stated	*Dermacentor variabilis*
Durden et al. (2016)	AK	2011–2016	*Amblyomma americanum, Dermacentor andersoni, Dermacentor variabilis, Haemaphysalis leporispalustris, Ixodes angustus, Rhipicephalus sanguineus* s.l.
Gleim et al. (2016)	GA	2005–2006	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Ixodes scapularis*
Herrick et al. (2016)	AZ	2015	*Amblyomma triste*
McAllister et al. (2016)	AR	1910–1993	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Ixodes scapularis*
Mitchell et al. (2016)	TX	2008–2014	*Amblyomma americanum, Amblyomma cajennense* s.l.[e], *Amblyomma inornatum, Amblyomma maculatum, Amblyomma tenellum* (=*Amblyomma imitator*), *Dermacentor albipictus* (including *Dermacentor nigrolineatus*), *Dermacentor andersoni, Dermacentor variabilis, Ixodes scapularis, Ixodes woodi, Otobius megnini, Rhipicephalus sanguineus* s.l.
Padgett et al. (2016)	CA	1971–2011	*Dermacentor occidentalis*
Xu et al. (2016)	MA	2006–2012	*Ixodes scapularis*
Cavanaugh et al. (2017)	US	Not stated	*Ixodes scapularis*
Goddard (2017)	MS	2016	*Amblyomma americanum*
Herman-Giddens and Herman-Giddens (2017)	NC	2001–2014	*Amblyomma americanum, Dermacentor variabilis, Ixodes scapularis*
Karki et al. (2017)	US	Not stated	*Dermacentor variabilis*
Soghigian et al. (2017)	CT	2015	*Ixodes scapularis*

Reference	Geographical area[a]	Time period	Tick species recorded to infest humans (synonym for species used in the publication)[b]
Beard et al. (2018)	Eastern US	2017–2018	*Haemaphysalis longicornis*
Jordan and Egizi (2019)	NJ	2006–2016	*Amblyomma americanum, Dermacentor variabilis, Ixodes cookei, Ixodes dentatus, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Oliver et al. (2017)	IA	1990–2013	*Ixodes scapularis*
Little et al. (2019)	CT	1996–2017	*Ixodes scapularis*
Little and Molaei (2020)	CT	2018	*Ixodes scapularis*
Pak et al. (2019)	PA	1900–2017	*Amblyomma americanum, Amblyomma maculatum, Dermacentor albipictus, Dermacentor variabilis, Ixodes angustus, Ixodes cookei, Ixodes dentatus, Ixodes marxi, Ixodes muris, Ixodes scapularis, Rhipicephalus sanguineus* s.l.
Porter et al. (2019)	CT, MA, ME, NH, NJ, NY, RI, PA, VT	2016–2017	*Amblyomma americanum, Dermacentor variabilis, Ixodes scapularis*
Salkeld et al. (2019)	CA	2016–2017	*Amblyomma americanum, Dermacentor occidentalis, Dermacentor variabilis, Ixodes pacificus, Ixodes spinipalpis, Otobius megnini, Rhipicephalus sanguineus* s.l.
Smith et al. (2019)	ME	2009–2013	*Ixodes cookei, Ixodes scapularis*
Xu et al. (2019)	CA, OR, WA	2006–2017	*Ixodes angustus, Ixodes cookei, Ixodes pacificus, Ixodes scapularis, Ixodes spinipalpis*
Bickerton and Toledo (2020)	NJ	2019	*Haemaphysalis longicornis*
Hahn et al. (2020)	AK	1909–2019	*Amblyomma americanum, Dermacentor andersoni, Dermacentor variabilis, Haemaphysalis leporispalustris, Ixodes angustus, Ixodes scapularis, Ixodes uriae, Rhipicephalus sanguineus* s.l.
Wormser et al. (2020)	NY	2018	*Haemaphysalis longicornis*
Feder et al. (2021)	CT	2019	*Ixodes scapularis* (=*Ixodes dammini*)
Hook et al. (2021)	CT, MD	2011–2012	*Amblyomma americanum, Dermacentor variabilis, Ixodes scapularis*
Molaei et al. (2021)	CT	2018–2020	*Haemaphysalis longicornis*
Xu et al. (2021)	US	2013–2019	*Amblyomma americanum, Amblyomma cajennense* s.l.[e], *Amblyomma maculatum, Dermacentor andersoni, Dermacentor occidentalis, Dermacentor variabilis, Haemaphysalis leporispalustris, Haemaphysalis longicornis, Ixodes affinis, Ixodes angustus, Ixodes cookei, Ixodes dentatus, Ixodes marxi, Ixodes muris, Ixodes pacificus, Ixodes scapularis, Ixodes spinipalpis, Rhipicephalus sanguineus* s.l.
Kerr et al. (2022)	AL	2018–2021	*Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Ixodes scapularis*
Hart et al. (2022)	NY	2020	*Amblyomma americanum, Dermacentor variabilis, Haemaphysalis chordeilis, Ixodes cookei, Ixodes marxi, Ixodes muris, Ixodes scapularis*
Khalil et al. (2022)	CT	2021	*Ixodes scapularis*

[a]Geographical area listed by state(s), or a larger geographical area if state level data were not provided. State level records may include tick exposures resulting from travel within the US.

[b]Based on taxonomic nomenclature presented by Guglielmone et al. (2010, 2014, 2020), Nava et al. (2014a, 2014b, 2015, 2017), and Guglielmone and Robbins (2018). Some other authors (see Mans et al., 2019) place four of the *Ornithodoros* species (*Or. capensis, Or. concanensis, Or. kelleyi*, and *Or. stageri*) included in this table in the genus *Carios*.

[c]Including data also presented by Stromdahl et al. (2001) for *Dermacentor variabilis* or *Ixodes scapularis* collected from humans and submitted to the Department of Defense, Human Tick Testing Program for parts of the overall time period.

[d]Including data also presented by Stromdahl et al. (2001, 2003) and Jiang et al. (2010) for *Amblyomma americanum* collected from humans and submitted to the Department of Defense, Human Tick Testing Program for parts of the overall time period.

[e]As noted by Nava et al. (2014a, 2015) and Guglielmone and Robbins (2018), there are unresolved questions regarding species within the *Rhipicephalus sanguineus* sensu lato and *Amblyomma cajennense* sensu lato complexes, including identification of *Am. cajennense* versus *Amblyomma mixtum* in the US, and data for these two closely related species are therefore presented as *Am. cajennense* s.l. Guglielmone et al. (2020) consider *Am. mixtum* to be the only member of the *Am. cajennense* s.l. complex established in the US.

Table 4

Notable information on human encounters with native tick species in the United States (US) not included in the quantitative data compilation.

Reference	Geographical area[a]	Time period	Notes on human tick encounters in the US (synonyms for species used in the publication)[b]
Kalm (1772)	Northeast US	1749	Report of human infestation by ticks (wood lice), most likely belonging to *Amblyomma americanum* as collected specimens later were classified as *Acarus americanus* by Linneus.
Packard (1869)	PA	Not stated	Report of a human bite by *Amblyomma americanum* (=*Ixodes unipunctata*), but the species identification is uncertain as it was made from a drawing of the tick.
Curtice (1892)	US	Up to 1892	Mention in general terms of the following species infesting humans: *Amblyomma americanum* (=*Amblyomma unipunctata), Dermacentor occidentalis, Dermacentor variabilis* (=*Dermacentor americanus),* and *Ixodes scapularis*.
Neumann (1901)	US	Up to 1901	Mention in general terms of the following species as present in the US and as associated with humans: *Amblyomma americanum, Argas miniatus, Dermacentor parumapertus, Dermacentor variabilis* (=*Dermacentor electus),* and *Ornithodoros turicata*.
Cary (1907)	US	Up to 1907	Mention in general terms of the following species infesting humans: *Amblyomma americanum, Dermacentor occidentalis* (=*Dermacentor reticulatus*), *Dermacentor variabilis* (=*Dermacentor electus), Ixodes cookei* (=*Ixodes hexagonus),* and *Ixodes scapularis* (=*Ixodes ricinus*).
Hunter and Hooker (1907)	US	Up to 1907	Mention in general terms of the following species infesting humans: *Amblyomma americanum, Amblyomma maculatum, Dermacentor occidentalis*, and *Dermacentor parumapertus*. Also includes quantitative data for *Otobius megnini* (=*Ornithodoros megnini)* and *Rhipicephalus annulatus* (=*Margaropus annulatus);* see Table 3.
Banks (1905, 1908)	US	Up to 1908	Mention in general terms of the following species infesting humans: *Amblyomma americanum, Amblyomma maculatum, Dermacentor andersoni* (=*Dermacentor venustus*), *Dermacentor parumapertus, Dermacentor variabilis, Ixodes cookei, Ixodes scapularis, Ornithodoros coriaceus, Ornithodoros turicata*, and *Otobius megnini* (=*Ornithodoros megnini)*.
Hunter and Bishopp (1911b)	US	Up to 1911	Mention in general terms of the following species infesting humans: *Amblyomma americanum, Amblyomma maculatum, Dermacentor andersoni* (=*Dermacentor venustus*), *Dermacentor occidentalis, Dermacentor variabilis,* and *Otobius megnini* (=*Ornithodoros megnini*).
Nuttall et al. (1911)	US	Up to 1911	Mention in general terms of the following species infesting humans: *Ixodes scapularis* (=*Ixodes ricinus* var. *scapularis*), *Ornithodoros turicata*, and *Otobius megnini* (=*Ornithodoros megnini*).
Mohler (1914)	US	Up to 1914	Mention in general terms of the following species infesting humans: *Amblyomma americanum, Dermacentor albipictus, Dermacentor variabilis, Ixodes cookei* (=*Ixodes hexagonus*), and *Ixodes scapularis* (=*Ixodes ricinus*).
Cooley (1915)	MT	Up to 1915	Mention in general terms of *Dermacentor andersoni* (=*Dermacentor venustus*) infesting humans.
Parker and Wells (1917)	MT	Up to 1917	Mention in general terms of the following species infesting humans: *Dermacentor andersoni* (=*Dermacentor venustus*) and *Dermacentor variabilis*.
Bruce (1934)	TX	1930	Report of human infestation by *Ornithodoros turicata* after visiting a cave.
Bishopp and Hixson (1936)	US	Up to 1936	Mention in general terms of *Amblyomma maculatum* infesting humans.
Chamberlin (1937)	OR	Up to 1937	Mention in general terms of the following species infesting humans: *Dermacentor andersoni, Dermacentor occidentalis, Ixodes angustus*, and *Ixodes pacificus* (=*Ixodes californicus*).
Cooley (1938)	US	Up to 1938	Mention in general terms of the following species infesting humans: *Dermacentor andersoni, Dermacentor occidentalis, Dermacentor parumapertus*, and *Dermacentor variabilis*.
Brunet (1939)	US	1932–1934	Report of two cases of human tick infestation, presumably with *Dermacentor andersoni*.
Bishopp (1941)	US	Up to 1941	Mention in general terms of *Argas miniatus* biting humans.

Reference	Geographical area[a]	Time period	Notes on human tick encounters in the US (synonyms for species used in the publication)[b]
Davis et al. (1941)	CA	1940	Report of human bites by numerous ticks at a sandstone cliff with small caves, where *Ornithodoros parkeri* ticks subsequently were collected.
Travis (1941)	FL	1936–1937	Mention in general terms of the following species infesting humans: *Amblyomma americanum, Amblyomma maculatum*, and *Ixodes scapularis (Ixodes ricinus scapularis*).
Parker et al. (1943)	OK, SC, TX	1941–1942	Report of ticks infesting humans developing Rocky Mountain spotted fever, with *Amblyomma americanum* collected around case premises.
Woodland et al. (1943)	TX	1942	Mention in general terms of *Amblyomma americanum* infesting humans.
Archer (1944)	TN	Up to 1944	Mention in general terms of the following species infesting humans: *Amblyomma americanum* and *Dermacentor variabilis*.
Cooley and Kohls (1944a)	US	Up to 1944	Mention in general terms of the following species infesting humans or found in homes or cabins of tick bite victims: *Ornithodoros coriaceus, Ornithodoros hermsi,* and *Ornithodoros turicata*. Also includes quantitative data for *Ornithodoros parkeri, Ornithodoros stageri,* and *Otobius megnini;* see Table 3.
Brennan (1945)	TX	1943–1944	Mention in general terms of the following species infesting humans: *Amblyomma americanum* and *Ixodes scapularis*.
MacCreary (1945)	DE	1939–1944	Mention in general terms of *Dermacentor variabilis* infesting humans. Also includes quantitative data for *Amblyomma americanum;* see Table 3.
Cooley (1946a)	US	Up to 1946	Mention in general terms of *Rhipicephalus sanguineus* sensu lato (s.l.) infesting humans.
Bequaert (1947)	NH	1947	Mention in general terms of *Dermacentor variabilis* infesting humans.
Collins et al. (1949)	NY	Up to 1949	Mention in general terms of the following species infesting humans: *Dermacentor variabilis, Ixodes dentatus,* and *Ixodes scapularis*.
Holdenried et al. (1951)	CA	1940–1945	Mention in general terms of the following species infesting humans (field workers): *Dermacentor occidentalis* (adults and immatures) and *Ornithodoros turicata* (several larvae after probing a ground squirrel burrow by hand). Also includes quantitative data for *Ixodes pacificus;* see Table 3.
Tibbetts (1953)	NC	1952	Mention in general terms of the following species infesting humans: *Amblyomma americanum* and *Ixodes scapularis*.
Coffey (1954)	UT	Up to 1954	Mention in general terms of *Dermacentor andersoni* infesting humans.
Beck (1955b)	UT	Up to 1955	Mention in general terms of *Dermacentor andersoni* infesting humans.
White (1955)	MS	1947–1949	Mention in general terms of the following species infesting humans: *Amblyomma americanum* (adults, nymphs, and larvae), *Amblyomma maculatum* (adults), *Dermacentor variabilis* (adults), and *Ixodes scapularis* (adults).
Kohls et al. (1957)	US	Up to 1957	Mention in general terms of the following species infesting humans or found in homes of tick bite victims: *Ornithodoros capensis, Ornithodoros concanensis, Ornithodoros coriaceus, Ornithodoros kelleyi, Ornithodoros parkeri, Ornithodoros turicata,* and *Otobius megnini*.
Kohls (1958)	TX	Up to 1958	Mention in general terms of *Amblyomma tenellum* (=*Amblyomma imitator)* infesting humans.
Clifford et al. (1961)	Eastern US	Up to 1961	Mention in general terms of the following species infesting humans: *Amblyomma americanum* (AL, LA, VA) and *Ixodes muris* (NY).
Johnson (1962)	CO	1961	Mention in general terms of *Dermacentor andersoni* infesting humans.
Clark (1964)	GA	1961–1962	Mention in general terms of the following species infesting humans: *Amblyomma americanum* and *Dermacentor variabilis*.
Allred (1968)	ID	1966–1967	Mention in general terms of *Dermacentor andersoni* (adults) infesting humans.
Snetsinger (1968)	PA	Up to 1968	Mention in general terms of the following species infesting humans: *Amblyomma americanum, Dermacentor albipictus, Dermacentor variabilis, Ixodes angustus, Ixodes cookei, Ixodes marxi*, and *Rhipicephalus sanguineus* s. l. Also includes quantitative data for *Amblyomma maculatum;* see Table 3.
Duckworth et al. (1985)	VA	1982–1983	Mention in general terms of *Amblyomma americanum* (larvae) infesting humans.

Reference	Geographical area[a]	Time period	Notes on human tick encounters in the US (synonyms for species used in the publication)[b]
Goddard (1990)	AR	1988	Report of numerous tick bites during military training, most likely predominantly by *Amblyomma americanum*.
Webb et al. (1990)	CA	Up to 1990	Mention in general terms of *Ixodes pacificus* infesting humans.
Robbins and Keirans (1992)	North America	Up to 1992	Mention in general terms of the following species infesting humans in North America: *Ixodes angustus, Ixodes soricis*, and *Ixodes woodi*.
Durden and Kollars (1992)	TN	Up to 1992	Mention in general terms of the following species infesting humans: *Amblyomma americanum* and *Dermacentor variabilis*.
Durden and Keirans (1996)	US	Up to 1996	Mention in general terms of the following species infesting humans in North America: *Ixodes angustus, Ixodes cookei, Ixodes dentatus, Ixodes pacificus, Ixodes scapularis, Ixodes spinipalpis* (=*Ixodes neotomae*), *Ixodes texanus,* and *Ixodes woodi*.
Lavender and Oliver (1996)	GA	1984–1985	Mention in general terms of *Ixodes scapularis* infesting humans.
Williams et al. (1999)	SC	Up to 1999	Mention in general terms of the following species infesting humans: *Amblyomma americanum, Amblyomma maculatum, Dermacentor variabilis, Ixodes brunneus,* and *Ixodes scapularis*.
Johnson et al. (2004)	Ri	1991–200	Report of human infestation by *Ixodes scapularis* in Rhode Island. Data were collected from 1991 to 2000 via a passive tick collection initiative. The paper includes 1,033 submitted *I. scapularis* nymphs but it is not clearly stated if they all were collected from humans (rather than pets or other sources).
Fisher et al. (2006)	KY	Not stated	Report of multiple larval bites by *Amblyomma* ticks, presumably *Amblyomma americanum*.
Nelder et al. (2009)	SC	2004–2007	Mention in general terms of the following species infesting humans in zoos: *Amblyomma americanum* and *Dermacentor variabilis*.
Lubelczyk et al. (2010)	ME, VT	2008	Report of tick bites in cabins subsequently found to be infested with *Ixodes cookei* and *Ixodes marxi*.
Vaughn and Meshnick (2011)	NC	2008	Report of 74 tick bites in a tick bite prevention intervention study in North Carolina, but without specifying the tick species. Based on the study location, the majority of the biting ticks likely were *Amblyomma americanum*.
Vaughn et al. (2014) / Wallace et al. (2016)	NC	2011–2012	Report of 1,045 human tick bites in a tick bite prevention intervention study, with *Amblyomma americanum* accounting for >90% of a subset of 867 ticks identified to species, and with additional recorded species including *Amblyomma maculatum, Dermacentor variabilis*, and *Ixodes scapularis*.
Rossi et al. (2015)	Eastern US	2006–2012	Report of 11,282 ticks (including *Amblyomma americanum, Dermacentor variabilis*, and *Ixodes scapularis*) collected from patients at Military Treatment Facilities in the eastern US, but without a breakdown in the paper allowing for calculation of numbers by tick species.
Xu et al. (2016)	US	2006–2012	Report of 3,551 ticks (3,127 *Ixodes scapularis*, 231 *Dermacentor variabilis*, 159 *Amblyomma americanum*, 26 *Ixodes pacificus,* 5 *Rhipicephalus sanguineus* s.l., 1 *Dermacentor occidentalis*, and 1 *Haemaphysalis leporispalustris*) collected from humans and domestic animals via a passive tick collection initiative but without a breakdown of numbers by tick species collected specifically from humans, with the exception that quantitative data were presented for a subset of 1,962 *Ixodes* scapularis collected from humans in Massachusetts (see Table 3).
Hinckley et al. (2016)	CT, MD, NY	2011–2013	Report of ticks found crawling on or attached to humans in a tick control intervention study in Connecticut, Maryland, and New York, but without providing information either for number of ticks or tick species. Based on the study locations, it appears likely the majority of the biting ticks were *Ixodes scapularis, Dermacentor variabilis*, and *Amblyomma americanum*.
Egizi et al. (2017)	NJ	2006–2015	Report of human infestation by thousands of *Amblyomma americanum* and *Ixodes scapularis* via a passive tick collection initiative in Monmouth County, New Jersey from 2006 to 2015, presented only graphically without specifying exact numbers.
Mead et al. (2018)	CT	2013	Report of ticks found crawling on or attached to humans in a tick control intervention study in Connecticut, but without providing information either for number of ticks or tick species. Based on the study locations, it appears likely the majority of the biting ticks were *Ixodes scapularis* and *Dermacentor variabilis*.
Nieto et al. (2018)	US	2016–2017	Report of 11,486 ticks collected from humans and submitted via a nationwide passive tick collection initiative, but without a breakdown of numbers by tick species collected specifically from humans. Quantitative data for subsets of ticks,

Reference	Geographical area[a]	Time period	Notes on human tick encounters in the US (synonyms for species used in the publication)[b]
			by species, recorded from humans were later presented by Porter et al. (2019) for the northeastern US and Salkeld et al. (2019) for California; see Table 3.
Nigrovic et al. (2019)	DE, MA, PA, RI, WI	2015–2018	Report of 167 tick bites in children diagnosed with Lyme disease in Delaware, Massachusetts, Pennsylvania, Rhode Island, and Wisconsin, but without specifying the tick species. Based on the study locations, it appears likely the majority of the biting ticks were *Ixodes scapularis* and *Dermacentor variabilis*.
Elias et al. (2020)	ME	1990–2013	Report of *Ixodes scapularis* collected from humans via a passive surveillance initiative in Maine from 1990 to 2013. Data from 1990 to 2006 were previously included in Rand et al. (2007) and the paper does not include information specifically for the subsequent period from 2007 to 2013.
Mitchell et al. (2020b)	MA, RI	2016–2018	Report of 226 tick bites in a tick bite prevention intervention study in Massachusetts and Rhode Island, but without specifying the tick species. Based on the study locations, it appears likely the majority of the biting ticks were *Ixodes scapularis* and *Dermacentor variabilis*.
Bechtel et al. (2021)	NV	2017–2018	Report of tick-borne relapsing fever in scientists following exposure to argasid ticks, most likely *Ornithodoros turicata*, associated with tortoise burrows.
Hinckley et al. (2021)	CT	2012–2016	Report of ticks found crawling on or attached to humans in a tick control intervention study in Connecticut, but without providing information for either number of ticks or tick species. Based on the study location, it appears likely the majority of the ticks were *Ixodes scapularis* and *Dermacentor variabilis*.
Lyons et al. (2021)	IL	2018	Report of 261 *Dermacentor variabilis* (all adults), 150 *Amblyomma americanum* (78 adults and 72 nymphs), 21 *Ixodes scapularis* (16 adults and 5 nymphs), and 4 *Amblyomma maculatum* (all adults) collected from humans and pets, but without a breakdown for the number of ticks recorded specifically from humans.
Rounsville et al. (2021)	ME	2019	Report of 2,016 *Ixodes scapularis* (1413 females, 30 males, 553 nymphs, and 20 larvae) submitted via a passive tick collection initiative in Maine, but without a clear statement of the proportion of ticks recorded from humans versus pets or other animals.
Dowling et al. (2022)	AR	2017–2018	Report of 9,002 ticks collected from humans, pets and livestock and submitted via a passive tick collection initiative in Arkansas. This included 6,854 *Amblyomma americanum*, 1,357 *Dermacentor variabilis*, 282 *Ixodes scapularis*, 257 *Amblyomma maculatum*, 242 *Rhipicephalus sanguineus* s.l., 8 *Dermacentor albipictus*, 1 *Haemaphysalis leporispalustris*, and 1 *Ixodes cookei,* but it is not clear from the paper which proportion of these ticks were recorded from humans versus pets or livestock.
Keesing et al. (2022)	NY	2017–2020	Report of 1,664 human encounters with ticks in a tick control intervention study in New York, but without specifying the tick species. Based on the study location, it appears likely the majority of the ticks were *Ixodes scapularis* and *Dermacentor variabilis*.
Pasternak and Palli (2022)	KY	2019–2020	Report of 336 *Ixodes scapularis* (330 adults, 5 nymphs, and 1 larva) collected from humans and pets, but without a breakdown for the number of ticks recorded specifically from humans.

[a]Geographical area listed by state(s), or a larger geographical area if state level data were not provided. State level records may include tick exposures resulting from travel within the US.

[b]Based on taxonomic nomenclature presented by Guglielmone et al. (2010, 2014, 2020), Nava et al. (2014a, 2014b, 2015, 2017), and Guglielmone and Robbins (2018). Some other authors (see Mans et al., 2019) place four of the *Ornithodoros* species (*Or. capensis, Or. concanensis, Or. kelleyi*, and *Or. stageri*) included in this table in the genus *Carios*.