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Ticks infesting dogs and cats in North America: Biology, geographic distribution, and pathogen transmission

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Title: Ticks infesting dogs and cats in North America: Biology, geographic distribution, and pathogen transmission

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Highlights:

- Update on ixodid and argasid tick species infesting dogs and cats in North America

- Up to date summary of recent range expansion of *I. scapularis* and *A. americanum*

- Details introduction of the exotic ticks species *H. longicornis* into North America

- Summarizes understanding of *Rhipicephalus* spp. genetic diversity in North America

- Figures with images to show key features of common tick species in North America

Abstract: A diverse array of ixodid and argasid ticks infest dogs and cats in North America, resulting in skin lesions, blood loss, and disease. The ticks most commonly found on pets in this region are hard ticks of the genera *Amblyomma*, *Dermacentor*, *Ixodes*, and *Rhipicephalus*, as well as the more recently established *Haemaphysalis longicornis*. Soft tick genera, especially *Otobius* and *Ornithodoros*, are also reported from pets in some regions. In this review, we provide a summary of the complex and diverse life histories, distinct morphologies, and questing and feeding behaviors of the more common ticks of dogs and cats in North America with a focus on recent changes in geographic distribution. We also review pathogens of dogs and cats associated with the different tick species, some of which can cause

serious, potentially fatal disease, and describe the zoonotic risk posed by ticks of pets. Understanding

the natural history of ticks and the maintenance cycles responsible for providing an ongoing source of

tick-borne infections is critical to effectively combatting the challenges ticks pose to the health of pets

and people.

Keywords: *Amblyomma*, cat, *Dermacentor*, dog, *Ixodes*, *Haemaphysalis*, *Ornithodoros*, *Otobius*,

Rhipicephalus, tick

1. Introduction

Ticks are common hematophagous ectoparasites of both medical and veterinary importance that readily

infest a variety of vertebrate hosts including dogs, cats, and humans. In contrast to many other

arthropod vectors, where only specific instars imbibe blood, all motile tick stages feed on blood

(Nicholson et al., 2019). In addition to direct effects from attachment and blood feeding, such as trauma

to the skin and anemia, ticks vector a variety of pathogens, many of which are zoonotic (Childs and

Paddock, 2003; Sonenshine et al., 2013; Eisen et al., 2017; Centers for Disease Control and Prevention,

2018). Several tick-borne pathogens are readily transmitted to dogs and cats (Groves et al., 1975; Little

et al., 2010; Nicholson et al., 2010; Little et al., 2018). Clinical disease due to these agents is well-

characterized in dogs (Shaw et al., 2001a), and occurs, although is less well understood, in cats (Shaw, et

al., 2001b; Magnarelli et al., 2005). In North America, vaccines are only available to limit disease due to

Borrelia burgdorferi infection in dogs, thus routine use of effective tick control products and avoiding

tick infestations are crucial to protecting pets. However, the complex biology and diverse array of ticks

active in this region make control and prevention inherently difficult. Ticks are relatively long-lived and

prolific parasites with varying life histories, both among species and within species in differing

geographic locations (Yunik et al., 2015; Ogdon et al., 2018). Further complicating control efforts, most

tick species spend a majority of their life span in the environment and dogs and cats are continually re-

exposed to questing ticks in nature.

Over the past several decades, tick populations have increased and their geographic ranges have

expanded (Paddock et al., 2016; Sonenshine, 2018). These changes are the result of a variety of factors,

many of which are anthropogenic, including climate change, habitat fragmentation, and host availability

(Paddock and Yabsley, 2007; Diuk-Wasser et al. 2010; Paddock and Goddard, 2015). Tick ranges and

populations are dynamic, as are the infestation and disease risk faced by dogs and cats. In addition to

the increases in tick abundance and geographic range, the establishment of a novel tick species in North

America (Beard et al., 2018) provides further evidence that the tick risk facing dogs and cats has shifted

in the last few decades. The objectives of the current review are to (1) describe the species of ticks that

commonly infest dogs and cats in North America and (2) review the biology and current geographic

range of each species and the veterinary and zoonotic pathogens they transmit.

1.1 Ixodid (Hard) Ticks.

Ticks infesting dogs and cats are from two families: Ixodidae (hard ticks) and Argasidae (soft ticks).

Ixodid ticks are characterized by the presence of a distinct hard sclerotized plate on the dorsum called a

scutum, with or without ornamentation, and a capitulum (head) that extends anterior to the idiosoma

(body). The life cycle of ixodid ticks consists of four stages: egg, larva, nymph, and adult, of which the

latter three are motile. In female, nymphal, and larval ticks, the scutum extends from the capitulum

covering the anterior one-third to half of the dorsal body surface; in males the scutum covers the entire

dorsal surface of the idiosoma (Figure 1). The incomplete scutum of females, nymphs, and larvae allows

the posterior portion of the body to greatly expand as the tick imbibes blood, whereas the complete

scutum of males limits the degree of expansion achieved while feeding (Nicholson et al., 2019).

All common species of hard ticks found on dogs and cats in North America have a three-host life

cycle, with each new motile stage feeding on a different host. Eggs laid by adult females hatch and give

rise to six legged larvae, commonly referred to as seed ticks. For sylvatic species, large numbers of unfed

larvae seek hosts in low lying vegetation often utilizing small rodents, lizards, or birds. Larvae will drop

from the host after feeding to repletion and molt to eight-legged nymphs. The unfed nymphs then quest

for a suitable host, feed, drop off of the host, and molt to eight-legged adults. The unfed adults then

seek a third, final host. Although feeding behavior varies between species, both males and females of

the common ixodid species in North America attach and imbibe blood. Adult females will feed and mate,

becoming dramatically engorged before detaching from the host to lay eggs and die. Females in

populations of some species are able to reproduce parthenogenetically. Female ixodid ticks have only a

single gonotrophic cycle, meaning a single clutch containing thousands of eggs are laid at one time

before she dies (Apanaskevich and Oliver, 2013).

The majority of an ixodid tick's life cycle is spent off-host in the environment (Nicholson et al.,

2019). The time to life cycle completion varies greatly depending on climate, particularly temperature

and humidity. In laboratory studies some ixodid species exhibited generation times ranging from 3–4

months while others had longer generation times of up to 8 months (Loomis, 1961; Troughton and

Levin, 2007). Generally speaking ticks in tropical regions develop more quickly and may complete

multiple generations within a single year. However, in areas with both dry and rainy seasons, completion

takes longer as ticks stop host seeking when humidity is low (Nicholson et al., 2019). Ticks inhabiting

areas with colder temperatures also develop more slowly, and can undergo diapause when it is coldest,

extending the time to life cycle completion to two years or more (Nicholson et al., 2019).

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Host-seeking strategies vary among tick species but can largely be categorized as either nidicolous (nest or burrow dwelling) or non-nidicolous (Waladde and Rice, 1982; Carroll et al., 2002). Within the non-nidicolous ticks there are two major "questing" strategies for locating hosts: ambush and hunting (Nicholson et al., 2019). Ambush ticks climb vegetation and passively wait for hosts with their first pair of legs extended to grasp the fur, feathers, or clothing of passing hosts (Nicholson et al., 2019). This first pair of legs contains the Haller's organ, structures with setae that sense humidity, temperature, and carbon dioxide to assist with locating a host (Sonenshine and Roe, 2013; Carr et al., 2017). In contrast, ticks that exhibit hunting behavior actively pursue their host and are located on or very close to the ground, also utilizing the Haller's organ for chemoreception, particularly of carbon dioxide (Sonenshine, 2018; Nicholson et al., 2019). Ticks that ambush hosts include *Ixodes scapularis* and *Dermacentor variabilis* (Carroll et al., 2002), while ticks such as *Amblyomma americanum* are considered hunters (Carroll et al., 2002; Sonenshine, 2018). Once a potential host has been acquired, the ixodid tick determines if the host is appropriate to attach and feed. If the correct host-recognition cues (e.g. odor, heat, and carbon dioxide) are not found, the tick may drop off and resume host seeking (Nicholson et al., 2019). Even after the suitability of the host has been recognized, ixodid ticks may spend several minutes to hours locating a feeding site (Nicholson et al., 2019). Preferred feeding sites for host attachment have been demonstrated for numerous tick species and stages on several different hosts including dogs, cats, cattle, birds, and humans (Koch, 1982; Barnard et al., 1989; Felz et al., 1999; Heylen et al., 2011; Duscher et al., 2013; Beck et al., 2014; Little et al., 2018; Saleh et al., 2019).

After reaching the feeding site the tick uses chelicerae to lacerate the epidermis and insert the chelicerae and hypostome into the dermis (Moorhouse, 1969; Kemp et al., 1982), initiating the attachment process. The first one to two days an adult female tick is attached, the tick prepares the feeding lesion by secreting cement from the salivary glands (Moorhouse, 1969; Sonenshine and Anderson, 2013). The amount of cement produced varies among tick species. Genera with shorter

mouthparts (*Dermacentor*, *Haemaphysalis*, and *Rhipicephalus*) that only penetrate as far as the dermal-epidermal junction secrete more cement, and tick genera with longer mouthparts (*Amblyomma* and *Ixodes*) extending into the dermis produce less cement (Moorhouse, 1969). The cement secretion hardens around the chelicerae and helps secure the feeding position, ensuring the tick is firmly affixed (Sonenshine and Anderson, 2013). Once secure, the tick alternates salivating and imbibing, injecting anticoagulants and immunomodulatory compounds as it salivates, thus enlarging the wound (Ribeiro, 1989; Steen et al., 2006; Wikel, 2013; Nicholson et al., 2019) and enabling the tick to feed slowly from the pooling blood for several days (Suppan et al., 2018). As feeding progresses the tick must produce fresh cuticle to allow for the expansion of the body as it engorges (Lees, 1952; Flynn and Kaufman, 2011). Duration of attachment and time to engorgement range from as little as 2–3 days for larval ticks and from 2 weeks or longer for adult females (USDA APHIS, 1976; Apanaskevich and Oliver, 2013). To allow for prolonged attachment to the host, ticks mute the host immune response by the secretion of numerous pharmacologically active compounds in the tick saliva, including anti-inflammatory and immunosuppressive proteins (Ribeiro, 1987; Steen et al., 2006; Wikel, 2013).

1.2 Argasid (Soft) Ticks. Unlike Ixodidae, Argasidae lack a scutum and as such are commonly referred to as soft ticks. Most species have a rounded body margin, and as adults the capitulum and mouthparts are not visible protruding from the body when the tick is viewed dorsally (Nicholson et al., 2019). In contrast to the life cycles exhibited by ixodid ticks, argasids are more variable with the majority feeding multiple times on multiple hosts. Argasid ticks also develop through the same basic life stages (egg, larva, nymph, and adult) but have several nymphal instars rather than the single nymphal instar of ixodid ticks. The number of argasid nymphal instars varies among species and is influenced by temperature, engorgement status, and number of previous instars (Apanaskevich and Oliver, 2013). Some species of argasid ticks do not take blood meals as larvae or as stage I nymphs, instead directly molting to the next

stage using nutrients stored from their previous stage while others do not feed as adults (Apanaskevich and Oliver, 2013).

Most argasids are long-lived nidicolous ticks, living in caves, burrows, or nests of their hosts and often undergoing several month-long intervals between feedings when nests are vacant (Nicholson et al., 2019). Like ixodid ticks, argasid ticks possess and utilize the specialized sensory Haller's organ to locate their host (Gray et al., 2013). Argasid ticks are relatively rapid feeders, with some active stages feeding in as little as fifteen to thirty minutes (Apanaskevich and Oliver, 2013). With a few exceptions, the majority of soft ticks do not secrete cement. No new cuticle is secreted during feeding, and soft tick engorgement is limited by how far the existing cuticle can stretch (Suppan et al., 2018; Nicholson et al., 2019). Females are able to complete multiple gonotrophic cycles, and usually lay several small batches of a few hundred eggs each after taking a small blood meal, repeating the process sometimes months later. Other species are autogenous and lay eggs without taking a blood meal in the adult stage (Nicholson et al., 2019).

2. Ticks infesting dogs and cats in North America

Ixodid ticks of the most importance to dogs and cats in North America include: *Amblyomma americanum* (lone star tick), *Amblyomma maculatum* (Gulf Coast tick), *Dermacentor variabilis* (American dog tick), *Haemaphysalis longicornis* (longhorned or bush tick), *Ixodes pacificus* (western black-legged tick), *Ixodes scapularis* (eastern black-legged or deer tick), and *Rhipicephalus* spp. (brown dog ticks) (Koch, 1982; Dryden and Payne, 2004; Burroughs et al., 2016; Thomas et al., 2016; Shannon et al., 2017; Little et al., 2018; Saleh et al., 2019). Other less common ixodid tick species may also occasionally be found on dogs and cats in this region (Bishopp and Trembley, 1945; Koch, 1982; Wells et al., 2004; Little et al., 2018; Saleh et al., 2019; Ghosh et al., 2020; Duncan et al., 2020). Additionally, two genera of argasid ticks, *Otobius* spp. and *Ornithodoros* spp., infest dogs and cats in North America (Cooley and

Kohls, 1944; Bishopp and Trembley, 1945; Breitschwerdt et al., 1994; Kelly et al., 2014; Esteve-Gasent et al., 2017; Saleh et al., 2019).

2.1. *Amblyomma americanum* (lone star tick)

2.1.1. Environment

Amblyomma americanum, the lone star tick, is a three-host ixodid tick commonly found in the eastern United States. Historically this tick was primarily restricted to the southeastern and southcentral United States (Bishopp and Trembley, 1945). More recently, the range of *A. americanum* has expanded considerably (Brown et al., 2011; Cortinas and Spomer, 2013; Barrett et al., 2015; Dahlgren et al., 2016) and can now be found in parts of most northeastern and Midwestern states (Springer et al., 2014; Monzon et al., 2016;). Additionally, *A. americanum* is found with increasing frequency in southern Ontario (Nelder et al., 2019). Application of bioclimatic modeling and climate change forecasts to predict future geographical distributions of *A. americanum* suggest continued expansion in the upper Midwest, contraction in areas of coastal Florida, Alabama, Mississippi, Louisiana, and eastern Texas, and no westward expansion beyond the current limit of the 100th meridian (Springer et al., 2015). Others examining the current and future potential distribution of *A. americanum* with ecological niche modelling support continued expansion of the lone star tick northward (Raghavan et al., 2019). Additionally, broad areas in northern California as well as the west coast of Oregon, Washington, and British Colombia are thought to be climactically suitable for *A. americanum* although there is no evidence to suggest populations of lone star ticks have established in these areas (Raghavan et al., 2019).

Amblyomma americanum can be found in a variety of habitats ranging from open grasslands and prairies to mature, climax forest. The greatest number of lone star ticks are found in wooded habitats with dense underbrush or trees < 6 m in height and low-lying branches (Hair and Howell, 1970;

Semtner et al., 1971; Sonenshine et al., 1966). Within its preferred habitat, lone star ticks are not

uniformly distributed and are found most along ecotones (Semtner et al., 1971), within forest openings,

and areas with abundant animal hosts (Hair and Howell, 1970). *Amblyomma americanum* overwinters as

adults and nymphs. Activity of both stages of lone star ticks in the spring are thought largely to be

stimulated by mean and maximum daily temperature, however, temperature and humidity within the

tick's micro-habitat are key for their development and survival (Hair and Howell, 1970). Data collected in

New Jersey noted that *A. americanum* adults did not quest at temperatures below 4.4°C (Schulze et al.,

2001). Across the core range of *A. americanum* in the United States, each feeding stage of the tick

fluctuates seasonally in levels of activity (Sonenshine et al., 1966; Hair and Howell, 1970; Jackson et al.,

1996; Lavender and Oliver Jr, 1996; Kollars Jr et al., 2000; Goddard, 2007). Adults and nymphal *A.*

americanum emerge in early spring and peak in activity in May. Adult *A. americanum* will remain active

through June and July but their activity begins to subside by August. Despite the clear seasonality of *A.*

americanum, adult lone star ticks can be found on preferred hosts, white-tailed deer (*Odocoileus*

virginianus) anytime of the year suggesting they become active during warm weather breaks in colder

months (Hair and Howell, 1970). Nymphal activity also subsides through summer but increases for a

second time in September and into October. Activity of *A. americanum* larvae increases in June and

continues through August and September, but declines rapidly thereafter.

  Amblyomma americanum is euryxenous and will feed on a wide range of vertebrate animals.

When active, lone star ticks aggressively seek hosts and are relatively non-specific when selecting a host.

Nevertheless, larvae, nymphs, and adults of *A. americanum* most commonly infest medium- and large-

sized wild and domestic mammals (Bishopp and Trembley, 1945; Hair and Howell, 1970; Childs and

Paddock, 2003). White-tailed deer are principal hosts to all feeding stages *of A. americanum* (Koch,

1988) and are critical to maintain populations of lone star ticks in natural environments. Ground-

inhabiting birds, such as wild turkey (*Meleagris gallopavo*) and bobwhite quail (*Colinus virginanus*) are

also readily infested with *A. americanum* larvae and nymphs (Bishopp and Trembley, 1945; Hair and

Howell, 1970). Small mammals are rarely to occasionally infested with *A. americanum* larvae and

nymphs (Bishopp and Trembley, 1945; Hair and Howell, 1970; Zimmerman et al., 1987; Kollars Jr et al.,

2000).

2.1.2. Morphology

Amblyomma americanum are medium-sized ticks with females being a little larger than males

(Figure 2). Lone star ticks are reddish brown, ornate, have long mouth parts, eyes, a rectangular basis

capitulum, and festoons. Female *A. americanum* are easily identified by the conspicuous iridescent

white dot on the posterior margin of the scutum. Its designation as the lone star tick is attributed to the

resemblance of the conspicuous dot to the prominent single white star on the Texas state flag, known as

the "Lone Star" flag. Male *A. americanum* are readily identified by having white markings on the margin

of the scutum and flecked on the festoons. Nymphs and larvae of *A. americanum*, like most other

immature ixodids, are more difficult to distinguish from other species of ticks. Nymphal *A. americanum*

are light brown to reddish brown in color and have long mouth parts. Nymphs resemble adult *A.

americanum* but are inornate and approximately half the size. Larval *A. americanum* are commonly

called "seed ticks" because they are about the size of a poppy seed. Larval *A. americanum* are pale in

color and difficult to see on an animal due to their small size. Seed ticks often occur in the 100s or 1000s

on hosts as they migrate very little from where a clutch of eggs was deposited by a female. Keys are

available to aid the identification of adult and immature *A. americanum* (Keirans and Litwak, 1989;

Keirans and Durden, 1998; Coley, 2015)

2.1.3. Feeding and disease transmission

Dogs and cats are both readily infested by larval, nymphal, and adult *A. americanum*. In a national survey of ticks on dogs and cats recovered by veterinarians in the United States (Saleh et al., 2019), *A. americanum* was present on 23.1% of dogs (345 of 1494) with lone star ticks collected every month except February and November. In the same survey, *A. americanum* was collected from 29.5% of cats (99 of 336) with lone star ticks collected every month except January, February, and December. Proportions of dogs and cats infested with lone star ticks will vary depending on geographic region with infestations more common in the southcentral and southeastern United States. Examination of *A. americanum* infested dogs from southeastern Oklahoma and northwestern Arkansas, noted the fewest number of adult lone star ticks on the dorsum with an even distribution over the rest of the body (Koch, 1982). Nymphs were most abundant on the chest and front legs whereas larvae were mostly attached to dogs' ears. Saleh et al. (2019) noted adult *A. americanum* preferred to attach to the abdomen, axillary, and inguinal regions of dogs. On cats, however, significantly more adult *A. americanum* were attached to the tail and perianal region (Saleh et al., 2019).

The bite of lone star ticks is painful and irritating due to their long mouthparts. Despite relatively high tick burdens, levels of *A. americanum* infestation are rarely severe enough on domestic animals to result in debilitating clinical disease from the tick bite alone. However, in white-tailed deer fawns, severe infestations of *A. americanum* may result in the death due to anemia, tissue destruction, and secondary bacterial infection (Bolte et al., 1970; Hair et al., 1992). Lone star ticks are aggressive and annoying. Grossly, the bite of a lone star tick appears superficial and relatively innocuous in contrast to histopathological changes that take place in a tick bite lesion. Compared to pre-infestation levels, the number of immune cells in the bite lesion of an *A. americanum* female increased over the duration of attachment (Thomas et al., 2020). Significantly more neutrophils, eosinophils, lymphocytes, and macrophages were noted 8 days post-infestation in dogs whereas significantly more eosinophils, lymphocytes, and macrophages were noted in cats. Pruritus due to infestation with *A. americanum* on

dogs and cats may result in trauma and secondary bacterial infection; intradermal infestations with *A. americanum* described in red foxes (*Vulpes vulpes*) have not yet been reported in pets in the region (Smith et al., 1986).

Amblyomma americanum are primary vectors for a variety of pathogens to dogs and cats. These pathogens include: *Cytauxzoon felis*, *Ehrlichia chaffeensis*, *Ehrlichia ewingii*, and *Francisella tularensis* (Table 1). Although experimental and limited field evidence suggests *A. americanum* may be a secondary vector of *Rickettsia rickettsii* (Breitschwerdt et al 2011; Levin et al. 2017), more research is needed to explore the relative importance of this tick in transmitting true Rocky Mountain spotted fever (RMSF) agent. *Amblyomma americanum* is a vector for other spotted fever group Rickettsia including *Rickettsia amblyomattis* (Barrett et al. 2014).

2.1.4. Pathogens

Amblyomma americanum has been demonstrated as a vector of *C. felis* to domestic cats (Reichard et al., 2009; Reichard et al., 2010). In addition to adult *A. americanum* transmitting *C. felis*, nymphal lone star ticks have been shown to transmit the piroplasm to domestic cats (Allen et al., 2019). *Dermacentor variabilis* has also been demonstrated as a competent vector for *C. felis* to domestic cats (Blouin et al., 1984) and bobcats (Blouin et al., 1987). Cytauxzoonosis in domestic cats occurs throughout the southcentral and southeastern United States (Sherrill and Cohn, 2015), in an area that overlaps the distribution of both *A. americanum* and *D. variabilis.* In a study conducted in Oklahoma by Reichard et al. (2008), the highest number of cytauxzoonosis cases occurred in May and September when activities of *A. americanum* adults and nymphs were expected to be highest. *Cytauxzoon felis* has been documented in bobcats from two states, North Dakota (Shock et al., 2011) and Pennsylvania (Birkenheuer et al., 2008), in which no known cases of cytauxzoonosis have been reported from domestic cats. The prevalence of *C. felis* in bobcats is higher in states with established populations of *A.*

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americanum (Shock et al., 2011). *Cytauxzoon felis* DNA was present in *A. americanum* nymphs collected from 3 cats with cytauxzoonosis in Missouri (Bondy et al., 2005). In wild-collected, unfed *A. americanum* and *D. variabilis* from Oklahoma, the minimum infection of *C. felis* was 0.5% in male (1 of 153), 0.8% in nymphal (3 of 393), and 1.9% in female (3 of 161) lone star ticks, and 0.0% in female (n=74) and 0.0% in male (n=86) American dog ticks (Reichard et al., 2010). Shock et al., 2014 examined *A. americanum* and *D. variabilis* from Kentucky, Tennessee, Georgia, and Texas and found *C. felis* DNA only in American dog ticks from Tennessee (1.8%; 8 of 442) and Georgia (0.8%; 1 of 125).

   Amblyomma americanum is a primary vector for *E. chaffeensis* (Ewing et al., 1995; Varela-Stokes, 2007) and *E. ewingii* (Anziania et al., 1990). Examination of 8,662 dogs from the southcentral and southeastern United States, where *A. americanum* populations are most abundant, showed a higher percentage of dogs are exposed to *E. ewingii* (5.1%) than *E. chaffeensis* (2.8%) (Beall et al., 2012). Despite dogs being naturally exposed to and infected by *E. chaffeensis*, attempts to infect dogs experimentally by transmission feeding infected *A. americanum* have failed (Ewing et al., 1995). Transovarial transmission of *E. chaffeensis* in *A. americanum* does not appear to take place (Long et al., 2003). Numerous publications exist reporting the presence of *E. chaffeensis* and *E. ewingii* DNA in *A. americanum* throughout the geographic range of the tick, and prevalence generally ranges from <1.0% to approximately 10% (Anderson et al., 1993; Lockhart et al., 1997; Yu et al., 1997; Burket et al., 1998; Murphy et al., 1998; Roland et al., 1998; Steiner et al., 1999; Ijdo et al., 2000; Irving et al., 2000; Whitlock et al., 2000; Wolf et al., 2000; Stromdahl et al., 2001; Steiert and Gilfoy, 2002; Goddard et al., 2003; DeShields et al., 2004; Long et al., 2004; Mixson et al., 2004; Varela et al., 2004a; Schulze et al., 2005; Mixson et al., 2006; Castellaw et al., 2010; Cohen et al., 2010; Yabsley, 2010; Schulze et al., 2011; Fritzen et al., 2011; Fitak et al., 2014; Gaines et al., 2014; Maegli et al., 2016; Sayler et al., 2016; Simpson et al., 2019)) depending on experimental design, detection methodology, and sample size.

Francisella tularensis (subspecies *tularensis*, or type A), causative agent of tularemia, can be vectored by several arthropods including ticks. Transmission of *F. tularensis* through ticks is considered biological whereas transmission through other arthropods is mechanical. It is believed that *D. variabilis* is the primary vector of *F. tularensis* and maintains infections among wild animals, whereas *A. americanum* acts as a bridge vector for human infection (Eisen, 2007; Mani et al., 2015). Information on infection of *F. tularensis* in *A. americanum* is limited to several reports of either natural infections from lone star ticks collected off hosts in Arkansas (Calhoun, 1954), experimental infection and demonstration of transstadial transmission (Hopla, 1953; Hopla and Downs, 1953), and quantification, colonization, and duration of infection (Mani et al., 2015).

2.1.5. Zoonotic concerns

Amblyomma americanum has emerged as a serious parasite and vector of pathogens to humans in the United States (Childs and Paddock, 2003; Paddock and Yabsley, 2007). Larvae, nymphs, and adults of *A. americanum* all can infest and feed on humans. *Amblyomma americanum* is the most commonly recovered tick from humans in the southeastern United States (Merten and Durden, 2000). In surveys, 83% of ticks recovered from humans in Georgia and South Carolina were *A. americanum* (Felz et al., 1996); 63% of ticks collected off humans in Mississippi were *A. americanum* (Goddard, 2002). Along with *D. variabilis* (34.0%), *A. americanum* (34.3%) was the most commonly recovered tick species from United States Air Force personnel (Campbell and Bowles, 1994). *Amblyomma americanum* is either a known or suspected vector for several established or potential pathogens of humans including: *Ehrlichia chaffeensis* (Childs and Paddock, 2003; Paddock and Yabsley, 2007), *E. ewingii* (Childs and Paddock, 2003; Paddock and Yabsley, 2007), Panola mountain *Ehrlichia* (PME) (Loftis et al., 2008; Reeves et al., 2008), *Rickettsia amblyommatis* (Billeter et al., 2007; Jiang et al., 2010; Karpathy et al., 2016), Bourbon virus (Lambert et al., 2015; Savage et al., 2017; Jackson et al., 2019), Heartland virus (Brault et al., 2018),

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and *Borrelia lonestari* (James et al., 2001; Varela et al., 2004b). The bite of *A. americanum* has been associated with development of red meat allergy in humans. This delayed anaphylaxis is believed to be initiated by feeding of *A. americanum* and the production of antibodies against galactose-alpha-1,3-galactose (alpha-gal), a carbohydrate produced in all mammals besides humans, great apes, and new world monkeys (Commins et al., 2001; Steinke et al., 2015).

2.2. *Amblyomma maculatum* (Gulf Coast tick)

2.2.1. Environment

Amblyomma maculatum is an aggressive, three-host species commonly known as the Gulf Coast tick (Paddock & Goddard, 2015; Nadolny and Gaff, 2018). Historically found only as far as 161–257 km (100–160 miles) inland in states bordering the Gulf Coast and southern Atlantic Coast, this tick is now established 402 km (250 miles) inland in coastal states and is endemic in states along the Atlantic Coast into Delaware and in several land-locked Midwestern and southern states (Paddock and Goddard, 2015; Portugal and Goddard, 2016; Lockwood et al., 2018; Nadolny and Gaff, 2018; Maestas et al., 2020; Phillips et al., 2020). Immature Gulf Coast ticks feed on a variety of birds and rodents, while adult *A. maculatum* infest larger mammals including cattle, coyotes (*Canis latrans*), feral swine (*Sus scrofa*), horses, sheep, and white-tailed deer. However, Gulf Coast ticks occasionally feed on domestic dogs and cats (Dryden and Payne 2004; Paddock and Goddard, 2015; Little et al., 2018; Nadolny and Gaff 2018; Saleh et al., 2019).

Gulf Coast ticks are able to tolerate exposed, arid and hot environments. Common habitats include mesquite areas, oak savannah, prairie, and scrublands, especially when adjacent to wetland areas (Goddard and Paddock, 2015; Nadolny and Gaff, 2018; Maestas et al., 2020). The catholic feeding behavior of *A. maculatum*, their ability to thrive in both dry and humid environments, expansion of white-tailed deer and feral swine populations, frequent movement of livestock, and migration patterns

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of avian hosts have all likely contributed to the broadening geographic distribution of this tick species over the past 50–70 years. The establishment and spread of coastal *A. maculatum* populations are also facilitated by anthropogenic disturbances, and inland populations may contract or bloom according to precipitation patterns (Goddard and Paddock, 2015; Nadolny and Gaff, 2018).

Host-seeking adult Gulf Coast ticks are found on vegetation in open, exposed areas, and are able to tolerate harsh summertime conditions in which other common sympatric tick species would languish. Seasonal peak activity of immature *A. maculatum* has not fully been elucidated, and field survey data investigating questing behaviors vary depending on region (Goddard, 2007; Paddock and Goddard, 2015; Portugal and Goddard, 2016; Nadolny and Gaff, 2018). Experimentally, nymphal Gulf Coast ticks quest low on vegetation and migrate horizontally at a slow rate. This questing behavior may be the reason why immature *A. maculatum* are commonly found on ground-dwelling birds and other small animals. Adults of *A. maculatum* are active during March through September, but as with immatures, data differ somewhat with the geographic region surveyed and months of activity (Portugal and Goddard, 2016; Nadolny and Gaff, 2018).

2.2.2. Morphology

Amblyomma maculatum is a member of the *Amblyomma maculatum* group, which also includes *A. neumanni*, *A. parvitarsum*, *A. tigrinum*, and *A. triste*. Within this group, *A. maculatum*, *A. tigrinum*, and *A. triste* are exceptionally difficult to distinguish by morphology during all instars, and therefore misidentifications have likely occurred since their original descriptions (Estrada-Pena et al., 2005; Mertins et al., 2010; Lado et al., 2018). Phylogenetic comparisons have led some researchers to hypothesize that *A. maculatum* and *A. triste* are indeed the same species. However, further studies are needed to support or refute this hypothesis (Lado et al., 2018), and therefore *A. maculatum* is regarded as distinct from *A. triste* in the current review.

Keys are available to aid in species identification of immature and adult *Amblyomma* spp. in the

United States (Cooley and Kohls, 1944; Keirans and Durden, 1998). Like other *Amblyomma* species, *A.*

maculatum have characteristically elongate mouthparts (Figure 3) (Cooley and Kohls, 1944). Because

morphologies are quite similar among immature *Amblyomma* spp., consultation with a diagnostic lab

having specific entomologic expertise may be advisable. Subtle morphologic differences between

immature *Amblyomma* spp. as observed under magnification include characteristic margins of the basis

capitulum with presence/absence of lateral projections, presence/absence of projections on the ventral

basis capitulum, shape and dentition of hypostomes, and presence/absence of spurs on Coxae I–III

(Cooley and Kohls, 1944; Keirans and Durden, 1998).

Amblyomma spp. adults are more easily differentiated. Among other characteristics, female *A.*

maculatum have an ornate scutum with pale markings in an extensive pattern and a very short spur on

the first pair of coxae. Male *A. maculatum* have an ornate scutum with a filigree pattern in white and

brown, and one spur on the second, third, and fourth pair of coxae (Cooley and Kohls, 1944; Lado et al.,

2018). *Amblyomma maculatum* and *D. variabilis* males and females are sometimes confused based on

their large sizes and ornate patterns (Paddock and Goddard, 2015), but careful examination of

mouthpart length and basis capitulum shape can lead to successful species identification (Cooley and

Kohls, 1944).

2.2.3. Feeding and disease transmission

Little is known about the direct effects of feeding *A. maculatum* on cats and dogs, and

attachment site preferences have not been reported. On wildlife hosts, immature *A. maculatum* most

often attach near or on the head region. On cattle, immature *A. maculatum* most often attach to dorsal

body areas (withers, midline, and tail-head) (Ketchum et al., 2005). Adult *A. maculatum* preferentially

feed on inner and outer surfaces of the external ear of livestock (especially cattle), and over time may

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cause the inflammatory, destructive condition dubbed "gotch ear" (Edwards, 2011; Paddock and Goddard, 2015). Other direct effects of feeding Gulf Coast ticks on cattle are well-documented and include abscesses, anemia, edema, and predisposition to myiasis and secondary infection (Nadolny and Gaff, 2018). Similar consequences from *A. maculatum* infestations in dogs and cats may occur but reports are lacking and warrant further consideration.

Amblyomma maculatum is primarily of concern to canine medicine because it is the vector of *Hepatozoon americanum,* the apicomplexan parasite causing American canine hepatozoonosis (ACH; Table 1). Immature *A. maculatum* acquire *H. americanum* via feeding on infected canids; the parasite subsequently develops within ticks during ecdysis, resulting in numerous sporulated oocysts in emerged instars. Dogs become infected with *H. americanum* via ingestion of Gulf Coast ticks harboring the oocysts. Ingestion of ticks may occur through grooming of self or other dogs, or possibly by the incidental ingestion of infected ticks parasitizing prey species (Vincent-Johnson et al., 1997; Mathew et al., 1998; Johnson et al., 2009; Allen et al., 2011). Rarely, the feeding of Gulf Coast ticks has been associated with paralysis in dogs (Gothe et al., 1979; Espinoza-Gimez et al, 2011; Sonenshine, 2014; Paddock and Goddard, 2015).

2.2.4. Pathogens

Experimentally, oocysts of *H. americanum* are found free in the body cavity of *A. maculatum*, and may be abundant. Each oocyst contains numerous sporocysts that are comprised of hundreds of infective sporozoites (Mathew et al., 1998). In enzootic areas, prevalence of *H. americanum* infection in Gulf Coast tick populations is not known but seems low (KE Allen, unpublished data). Coyotes may serve as reservoirs of *H. americanum* to feeding *A. maculatum* in Oklahoma and Texas (Kocan et al., 2000; Garrett et al., 2005; Starkey et al., 2013). Dogs with ACH are typically diagnosed in regions where Gulf

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Coast ticks are established, but infections have been documented in other states due to displacement or travel history (Allen et al., 2008; Li et al., 2008).

DNA of *Anaplasma platys, E. chaffeensis,* and *E. ewingii* has been documented within field-collected *A. maculatum.* These zoonotic canine pathogens transmit via tick feeding and are thought to primarily use other tick vectors in nature (Williamson et al., 2010; Maggi, et al., 2013; Breitschwerdt et al., 2014; Mays et al., 2016; Allerdice et al., 2017; Maestas et al., 2020). Gulf Coast ticks have also been experimentally shown to vector Panola Mountain *Ehrlichia* (PME), which naturally cycles between *A. americanum* and likely white-tailed deer reservoirs in the United States (Paddock and Goddard, 2015; Loftis et al., 2016); DNA of PME was detected in 0.5–4.3% of *A. maculatum* tested from several Gulf Coast states (Loftis et al., 2016). However, the potential role of *A. maculatum* as a natural alternative vector for any of these bacterial organisms is not clear (Williamson et al., 2010; Jiang et al., 2012; Loftis et al., 2016; Allerdice et al., 2017; Maestas et al., 2020).

2.2.5. Zoonotic concerns

Amblyomma maculatum is chiefly recognized as a risk to human health because it is the vector of *Rickettsia parkeri,* an emerging spotted fever rickettsia. Cases have been documented in mid-Atlantic, southeastern, and southern states, and in some regions of Arizona (Hardstone et al., 2018). DNA of *R. parkeri* has been detected in the blood of domestic dogs by PCR; dogs are not known to develop apparent clinical signs with infection, and may serve as potential reservoirs to feeding ticks (Grasperge et al., 2012; Hardstone et al., 2018). Field-collected Gulf Coast ticks have also been shown to harbor DNA of *Rickettsia felis*, an emerging flea-borne infection in humans that is found world-wide. Although the pathogen has been molecularly detected in dogs in Africa, to date it has not been documented in dogs in North America (Moonga et al., 2019).

Gulf Coast ticks may also transmit more poorly understood spotted fever rickettsia to humans including *R. amblyommatis* (formerly *Rickettsia amblyommii* and *Candidatus* Rickettsia amblyommii) and

Rickettsia montanensis (Nadolny et al., 2014; Karpathy et al., 2016; Lee et al., 2017; Harris et al., 2017; Hardstone et al., 2018; Maestas et al., 2020;). Molecular evidence suggests that both of these organisms can infect dogs (Barrett et al., 2014; Hardstone et al., 2018), and therefore possibly Gulf Coast ticks feeding on dogs. Also, as in canine medicine, the role of *A. maculatum* as a vector of *Ehrlichia* spp. to humans is not clear (Williamson et al., 2010; Jiang et al., 2012; Maggi RG, et al., 2013; Breitschwerdt et al., 2014, Paddock and Goddard, 2015; Loftis et al., 2016; Mays et al., 2016; Allerdice et al., 2017; Maestas et al., 2020). Feeding Gulf Coast ticks have also been associated with tick paralysis (Gothe et al., 1979; Espinoza-Gimez et al, 2011; Paddock and Goddard, 2015).

2.3. *Dermacentor variabilis*

A variety of *Dermacentor* spp. occur in North America and infest dogs and cats, including *D. albipictus*, *D. andersoni, D. occidentalis,* and *D. variabilis.* However, *D. variabilis*, the American dog tick, is the most common species recovered from dogs and cats throughout the United States (Little et al., 2018; Saleh et al., 2019). *Dermacentor albipictus,* the winter tick, is found across the United States and Canada and commonly infests large ungulates but has been reported from a few dogs and cats in the Midwestern and western United States and from Alberta and British Columbia in Canada (Lindquist, 2016; Saleh et al., 2019; Duncan et al., 2020). *Dermacentor andersoni* is found in Rocky Mountain states and western Canada. The Pacific Coast tick, *D. occidentalis,* is found from central Oregon to California in the United States; this tick commonly infests humans and has occasionally been reported from dogs (Hooker et al., 1912; Merten and Durden, 2000; Vigil et al., 2013). In Mexico *D. occidentalis* is found in Baja California and Baja California Sur (Guzmán-Cornejo et al., 2016). The most common *Dermacentor* sp. infesting dogs and cats in North America is *D. variabilis* and will be the focus of this review.

2.3.1. Environment

Dermacentor variabilis is one of the most widespread ixodid ticks in North America. Its distribution ranges from Florida to southern Canada in the eastern half of the United States, and extends to the Gulf of Mexico, with isolated populations also occurring along the Pacific Coast in California, Oregon, and Washington, and extending eastward into Idaho (Bishopp and Trembley, 1945; Wilkinson, 1967; Stout et al., 1971; Rotramel et al., 1976; Easton et al., 1977). In Canada *D. variabilis* is present in 8 of 10 provinces and 2 of 3 territories, with the greatest abundance in parts of Nova Scotia as well as southern Manitoba and Ontario. The species has also been documented in Alaska (Dergousoff et al., 2013; Durden et al., 2016; Lindquist et al., 2016). In Mexico, *D. variabilis* has been documented in 18 of 32 states throughout the country (Guzmán-Cornejo et al., 2016). Traditionally, *D. variabilis* has been considered absent from the Rocky Mountain region of North America, with a related species, *D. andersoni,* aptly called the Rocky Mountain wood tick, present in this area. However, as far back as 1939, there have been reports that these two *Dermacentor* spp. overlapped in distribution in eastern California, southern Oregon, in addition to localities in Montana, North and South Dakota, and Nebraska in the United States, and in south-central Saskatchewan in Canada (Gibbons, 1939; Bishopp and Trembley, 1945; Dergousoff et al., 2013). Generally, *D. andersoni* is found in areas with hot and dry summers, while *D. variabilis* is in areas with summers that are more humid (Wilkinson, 1967).

Dermacentor variabilis is commonly found questing in low elevation grasslands and along the forest edge in addition to the boundaries of trails and roadways (Easton et al., 1977; Sonenshine, 1979; Dergousoff et al., 2013). Typical host species for *D. variabilis* range from small mammals such as voles (*Microtus* spp.) and chipmunks (*Tamias* spp.) for immature ticks to medium and larger-sized mammals such as opossums (*Didelphis virginianus*), raccoons (*Procyon lotor*), dogs, white-tailed deer, and humans for adult ticks (Kollars et al., 2000). Populations of American dog ticks in Canada have expanded greatly northward in recent years and it is considered established in portions of Ontario, Saskatchewan, Manitoba, and Nova Scotia (Dergousoff et al., 2013; Yunik et al., 2015; Wood et al., 2016). Recent work

predicting the future range of *D. variabilis* in response to climate change indicated that areas of suitable

habitat could increase by as much as 50% over the next 50 years (Minigan et al., 2018), allowing for even

further northward expansion of the American dog tick into northern parts of Canada. Additionally,

suitable alternate hosts for immature stages of *D. variabilis* (Sonenshine, 2018) are present, supporting

the recent northward expansion.

2.3.2. Morphology

 Dermacentor variabilis is an ornate reddish-brown tick; both males and females have a distinct

lacy silvery-white pattern covering the scutum, a rectangular basis capitulum with the width exceeding

the length, and palps that are relatively broad and short (Figure 4). All life stages of *Dermacentor* spp.

have festoons and eyes, but only adults possess ornate scuta (Brinton et al., 1965). Several species of

Dermacentor have similar appearances making morphologic identification difficult (Goddard et al.,

2020). Geography has traditionally been used to inform specific identification, but recent work has

demonstrated that in areas that were historically considered *D. andersoni* range, *D. variabilis* may be the

more abundant tick (Dergousoff et al., 2013; Duncan et al., 2020). Keys are available to differentiate

adult and immature *Dermacentor* ticks, but in cases where there is uncertainty molecular techniques to

speciate ticks should be utilized.

2.3.3. Feeding and disease transmission

 American dog ticks commonly attach and feed on both dogs and cats throughout their

geographic range. While ticks can be found anywhere on the host, a significant dorsal preference is seen

for attachment, with most ticks being found on the head, neck, ears, and back for both dogs and cats

(Koch 1982; Little et al., 2018; Saleh et al., 2019). An engorged female American dog tick consumes more

than 1.4 mL of blood from a canine host (Koch and Sauer, 1984). Compared to other ixodid ticks when

feeding the mouthparts of *D. variabilis* are restricted to the superficial epidermis, but a large amount of

cement is secreted resulting in marked hypertrophy of the epidermis at the site of attachment

(Moorhouse, 1969).

Dermacentor variabilis transmits a variety of pathogens to dogs and cats via saliva during tick

feeding (Table 1). The most important are *R. rickettsii* and other spotted fever group *Rickettsia* spp., as

well as *F. tularensis* (Philip and Jellison, 1934; Little 2010). However, American dog ticks are considered a

possible secondary or minor vector for a number of other pathogens including *Cytauxzoon felis, E.*

chaffeensis, and *E. ewingii*, which are more commonly transmitted by the lone star tick (Little 2010).

2.3.4. Pathogens

In North America *D. variabilis* is one of the most important vectors of *R. rickettsii,* especially in

the southeastern and central United States (McDade et al., 1986; Hecht et al., 2019). *Rickettsia rickettsii*

is maintained in *D. variabilis* populations transovarially and transstadially, making the tick both the

vector and reservoir of the pathogen (McDade and Newhouse, 1986). Canine serosurveys identified *R.*

rickettsii antibodies in 10.4% of dogs in the United States (Yancey et al., 2014). However, PCR surveys of

D. variabilis often do not detect *R. rickettsii* DNA or detect it at a very low prevalence, less than 1%

(Stromdahl et al., 2011; Hecht 2019), but often detect other spotted fever group *Rickettsii* spp., such as

R. montanensis (Fritzen et al., 2011; Little et al., 2018).

The proportion of *D. variabilis* infected with a pathogen varies depending on the specific

pathogen and the geographic location. *Cytauxzoon felis* is present in the eastern and southern regions of

the United States. The bobcat is considered the historic reservoir, but in recent years domestic cats with

persistent infections have been considered potentially important reservoirs of *C. felis* (Birkenheuer et

al., 2006; Reichard et al., 2010). Reported prevalences of *C. felis* detected via PCR from healthy

asymptomatic cats in the southern United States range from less than 1% up to 30.3% (Haber et al.,

2007; Brown et al., 2010; Rizzi et al., 2015; Nagamori et al., 2016). DNA of *C. felis* was detected in

015.8% of *D. variabilis* tested from the central and southern United States (Bondy et al., 2005; Shock et

al., 2014; Zieman et al., 2017; Little et al., 2018). However, *A. americanum* is now considered an

important vector of *C. felis* and covers a large portion of the geographic region where cytauxzoonosis

occurs most commonly (Reichard et al., 2010; Mueller et al., 2013).

While *D. variabilis* has been shown to transmit *Ehrlichia canis* experimentally, this pathogen has

only been described from field-caught *D. variabilis* in a few reports (Johnson et al., 1998; Sosa-Gutiérrez

et al., 2016). *Ehrlichia chaffeensis* has been documented in 0–6.7% of field-collected *D. variabilis* in

Virginia, Kentucky, and Missouri, while the prevalence of *E. ewingii* in these ticks was slightly lower

ranging from 0–3.3% (Steiert and Gilfoy, 2002; Fritzen et al., 2011; Wright et al., 2014). DNA of *E. ewingii*

has also been recovered from *D. variabilis* removed from an infected dog in Oklahoma (Murphy et al.,

1998).

2.3.5. Zoonotic concerns

Humans and dogs are both susceptible to infection with *R. rickettsii* from *D. variabilis* (Nicholson

et al., 2010). Infection with *R. rickettsii* in cats is considered uncommon (Allison and Little, 2013).

Concurrent infections with *R. rickettsii* and *Ehrlichia* spp. have been documented in humans and their

pet dogs in the United States (Buller et al., 1999; Paddock et al., 2002; Elchos et al., 2003). *Dermacentor*

variabilis is a principal vector of *R. rickettsii* to both dogs and humans in the eastern and central United

States, while in the West, *D. andersoni* is considered the more important vector of *R. rickettsii*. The

majority of Rocky Mountain spotted fever cases reported in humans in the United States originate from

states extending from Oklahoma and Missouri east to North Carolina and Virginia (Drexler et al., 2017;

Centers for Disease Control and Prevention, 2018). *Dermacentor variabilis* is also an important vector of

F. tularensis, and is considered a key source of human infection (Klock et al., 1973; Petersen and

Schriefer, 2005). Dogs and cats are typically infected with *F. tularensis* after contact with or ingestion of

infected tissues from rabbits or other wild mammals; clinical disease is most commonly seen in cats and

is considered rare in dogs (Feldman, 2003). Additionally, the absorption of toxins from *D. variabilis* saliva

can sometimes result in tick paralysis (Lane et al., 1984; Goth and Neitz, 1991; Diaz, 2010).

2.4. *Haemaphysalis longicornis*

2.4.1. Environment

Historically *Haemaphysalis* spp. in North America have been considered ticks of wildlife with

limited medical and veterinary importance, rarely infesting domestic animals and people (Keirans and

Litwak, 1989; Egizi et al., 2019). The rabbit tick, *H. leporispalustris*, has been infrequently found on dogs

in North America, while *H. chordeilis* and *H. juxtakochi* primarily infest birds and ungulates, respectively

(Bishopp and Trembley, 1945; Kohls, 1960; Lindquist et al., 2016). However, in 2017, natural infestations

with the longhorned tick, *H. longicornis,* were identified for the first time in North America from a sheep

in New Jersey, United States (Rainey et al., 2018; USDA, 2020). *Haemaphysalis longicornis* is native to

East Asia and is established in Australia and New Zealand (Hoogstraal et al., 1968), where it is considered

a significant pest of people, livestock, and companion animals (Shimada et al., 2003; Heath et al., 2013;

Heath et al., 2016; Greay et al., 2016). Since the initial report in 2017, *H. longicornis* has been reported

in 15 different states in the eastern and south-central United States and on numerous hosts including

humans, dogs, and cats in addition to domestic livestock (cattle, sheep) and wildlife (white-tailed deer,

coyotes, raccoons, opossums), with its range continuing to increase (Beard et al., 2018; Saleh et al.,

2019; USDA, 2020). Subsequent reexamination of archived samples demonstrated that *H. longicornis*

has been infesting North American wildlife since at least 2010 (USDA, 2018). Introduced populations of

the longhorned tick are parthenogenic (Oliver et al., 1973; Heath, 2013; Rainey et al., 2018).

Haemaphysalis longicornis thrive in humid, warm-temperate conditions but can tolerate

temperatures ranging from -2°C to 40°C and occupy a variety of climates and latitudes (Hoogstraal et al.,

1968; Sutherst and Moorhouse, 1972; Heath, 2013; Heath, 2016). Populations are often found among

long grass and rushes (Heath, 2016), with unfed nymphs surviving longer in areas with long as opposed

to short grass (Sutherst and Bourne, 1991). In the first recognized infestations in New Jersey, United

States, all feeding stages of longhorned ticks were recovered from the sheep, and larvae were found on

vegetation within the sheep paddock, but not outside the paddock where the grass was mowed (Rainey

et al., 2018).

As a recently established species, the seasonality of North American populations of *H.*

longicornis is still being determined, but early work in the northeastern United States found that activity

of adult longhorned ticks peaked in late July, with nymphs peaking from June to July, and larvae having

the highest activity in August (Tufts et al., 2019). This pattern is similar to that seen in populations of *H.*

longicornis in South Korea and China (Zheng et al., 2012; Johnson et al., 2014). The full extent of the

longhorned tick's geographic distribution in North America is currently unknown. Habitat and climate

preferences of *H. longicornis* in other regions have been used to model the potential range of this

species in North America. Although predictions vary, potential ranges include the southeastern United

States, the Pacific Coast extending into Canada, as well as Mexico, and areas of the Great Lakes region in

the United States and Canada (Raghavan et al., 2018; Rochlin, 2018). To date, both models confirm

extensive suitable habitat for *H. longicornis* in the southeastern and central Midwestern United States

(Raghavan et al., 2018; Rochlin, 2018).

2.4.2. Morphology

Adult *H. longicornis* are inornate, reddish-brown ticks with short mouthparts and a rectangular

dorsal basis capitulum with straight lateral margins (Figure 5). The lateral projection of the second palpal

segment is characteristic of the genus; eyes are absent, but festoons are present (Cooley, 1946).

Haemaphysalis longicornis adults are differentiated from its cogeners in North America (*H. chordeilis, H.*

juxtakochi, and *H. leporispalustris*) by the presence of a dorsal spur on the third palpal segment, and keys are available to aid in the identification of adults and immature stages (Cooley, 1946; Egrizi et al., 2019).

2.4.3. Feeding and disease transmission

In parts of the world where *H. longicornis* is established, longhorned ticks readily infest dogs and cats and are commonly removed from pets (Iwakami et al., 2014; Greay et al., 2016; Zhang et al., 2017). On livestock and wildlife hosts, *H. longicornis* was found to infest the head and ears, including the periocular region more commonly than elsewhere on the host (Heath et al., 1987; Zheng et al., 2011; Zheng et al., 2012). This attachment preference was also noted in the recent North American introduction in New Jersey where ticks were concentrated on the face and ears of the infested sheep (Rainey et al., 2018). Attachment site preferences for dogs and cats have not been reported.

2.4.4. Pathogens

Haemaphysalis longicornis is capable of transmitting several pathogens to pets, livestock, and people (Beard et al., 2018). To date, there have been no reports of pathogens recovered from longhorned ticks removed from dogs and cats in North America, and the only pathogen reported from the United States has been *Theileria orientalis* Ikeda genotype in host seeking *H. longicornis* from Virginia (Beard et al., 2018; Thompson et al., 2020). Under experimental conditions, *H. longicornis* failed to transmit *B. burgdorferi* sensu stricto (s.s.), the causative agent of Lyme disease, but it was able to acquire and transmit at a very low frequency between tick generations (Breuner et al., 2020; Stanley et al., 2020). The importance of *H. longicornis* as an experimentally competent vector of *R. rickettsii* in North America is unknown at this time, but highlights the need for additional studies to determine the potential role of longhorned ticks in pathogen transmission in North America.

2.4.5. Zoonotic concerns

In its historic range *H. longicornis* transmits several different pathogens including severe fever with thrombocytopenia syndrome virus (SFTSV), which causes a hemorrhagic fever in people (Luo et al., 2015). However, while *H. longicornis* has been shown to attach and feed on people in North America, to date no human pathogens have been recovered from these ticks (Beard et al., 2018; Wormser et al., 2019; Thompson et al., 2020; Tufts et al., 2020). The apparent rapid spread of *H. longicornis* in North America, specifically in the eastern United States, has been partially attributed to its ability to reproduce parthenogenetically (Stanley et al., 2020). As the longhorned tick becomes further established and more widespread in North America, its involvement in transmission of zoonotic pathogens warrants further consideration.

2.5. *Ixodes scapularis* and *Ixodes pacificus*

Ixodes spp. are ticks of wildlife that readily infest domestic animals and people. Approximately 40 *Ixodes* spp. have been described in North America, and several have been reported from dogs and cats in this region, including *I. affinis, I. angustus*, *I. banksi*, *I. cookei, I. kingi, I. marxi, I. muris*, and *I. texanus* (Rand et al., 2007; Durden et al., 2016; Nadolny et al., 2018; Little et al., 2018; Saleh et al., 2019; Ghosh et al., 2020). However, by far the most common species found on domestic animals, including pets, are *I. scapularis* in the eastern United States and *I. pacificus* in the West; these two species will be the focus of this review.

2.5.1. Environment

Just a few decades ago, *I. scapularis* populations were considered to be somewhat concentrated in fairly focal areas of the upper midwestern and northeastern United States, with additional populations present in the South (Dennis et al., 1998). Apparent changes in habitat, host, and climate in

recent years have allowed this tick to re-establish throughout most of eastern North America, with populations of *I. scapularis* now found from the Atlantic Coast across to central Texas and up into eastern North Dakota and extending as far north as the southern regions of the Western, Central, and Atlantic Provinces of Canada (Eisen et al., 2016, Clow et al., 2017). In contrast, the geographic range of *I. pacificus* in western North America has remained fairly stable and extends from the foothills of the Sierra Nevada in California northward into British Columbia (Eisen et al., 2016).

Ixodes scapularis and *I. pacificus* populations are found in wooded habitats. A dense understory and accumulation of leaf litter provides favorable microclimates for development and survival of immature and adult ticks in the environment (Lindsay et al., 1999). Seasonal activity of the different stages varies by geographic region. In northern North America, adult *I. scapularis* are usually most active in the fall and winter with peak activity in October and November when temperatures are between 5–15°C; a second, smaller peak of adult activity occurs with the onset of spring weather in March and April. In contrast, in Florida and South Carolina, adult *I. scapularis* activity is highest January through March (Ogden et al., 2004, Ogden et al., 2018). In northern regions of North America, immature *I. scapularis* are most commonly found questing in late spring and summer. Nymphs become active at 15–25°C and often emerge a few weeks before the larvae of the next generation (Ogden et al., 2004). The pattern of activity for immature stages in the southern United States is less well defined; immature stages in this region quest below the leaf litter, usually feed on lizards rather than small mammals, and are rarely found on people or pets (Oliver, 1996; Arsnoe et al., 2015; Little et al., 2018; Saleh et al., 2019). In northwestern California, adult *I. pacificus* quest from late October through May with activity peaking in January, nymphs are active January through October, and larvae are found April through June. At the southern extent of the *I. pacificus* range, seasonal activity, particularly of the immature stages, is confined to a much shorter period of time and all three stages are primarily active in the winter (Salkeld et al., 2014; MacDonald and Briggs, 2016).

Recent increases in the distribution of *I. scapularis* in the northern and mid-Atlantic United States have been attributed to re-establishment of the historical range of this tick, continuing a trend seen for the past several decades (Spielman, 1994, Eisen et al., 2016). This range expansion of *I. scapularis* is considered to be a result of the combined influences of habitat change, increase in white-tailed deer populations, and climate change (Eisen et al., 2016, Ogden et al., 2018). In the past two decades, the previously distinct foci of tick populations in the northeastern and upper Midwestern United States have largely converged (Eisen et al., 2016). *Ixodes scapularis* populations have also spread across western New York, western Pennsylvania, and northern Maine, as well as into higher elevations of the Appalachia (Simmons et al., 2015, Herrin et al., 2016, Eddens et al., 2019, Dewage et al., 2019), putting more people and pets at risk of both *I. scapularis* infestation and infection with associated pathogens (Little et al., 2020).

2.5.2. Morphology

Adult *Ixodes* spp. are inornate, reddish brown to black in color, and have mouthparts longer than the basis capitulum (Figure 6). Both eyes and festoons are absent. All stages (larva, nymph, adult) of *Ixodes* spp. bear a distinct anal groove that arches anterior to the anus. Confirming identification to the species level, even for adult ticks, may require consultation with a diagnostic laboratory with specific expertise; for less common species, both morphologic and molecular identification may be preferred. The presence and number of spurs on the coxae, shape of the scutum, and pattern of dentition on hypostome are all helpful in confirming the identity of a given *Ixodes* sp. specimen. Adult *I. scapularis* have prominent internal spurs on the first pair of coxae. Keys are available to aid identification of adult and immature *Ixodes* spp. (Keirans and Litwak, 1989; Durden and Keirans, 1996).

2.5.3 Feeding and disease transmission

Ixodes scapularis and *I. pacificus* have broad host ranges. Larvae, nymphs, and adult *I. scapularis* infest and feed on a diverse array of wild and domestic mammals, birds, and reptiles (Yuval and Spielman, 1990). However, differences are observed in host preference according to geographic location and tick species (Bishopp and Trembley, 1945; Cooley and Kohls, 1945; Keirans et al., 1996; Castro and Wright, 2007). Surveying naturally infested hosts throughout the range of *I. scapularis* demonstrated that immature black-legged ticks in northern areas feed on small mammals (e.g., white-footed mice (*Peromyscus leucopus*), shrews (Soricidae), chipmunks, etc.) followed by ground-dwelling birds (Mather et al., 1989). In southern areas, immature *I. scapularis* prefer to feed on lizards (Oliver Jr et al., 1993a) over small mammals. In comparison to surveys of naturally infested animals, host-selection experiments conducted in the lab (James and Oliver Jr, 1990), demonstrated that when given a choice, immature *I. scapularis*, regardless of whether ticks originated from northern or southern populations, preferentially feed on mice over other hosts. It is likely that natural feeding patterns of *I. scapularis* result from a multitude of variables (e.g., host availability, questing duration, questing height, climate, etc.), many of which have yet to be elucidated in detail (James and Oliver Jr, 1990). Regardless of geographic location, both northern and southern adult *I. scapularis* feed (Oliver Jr et al., 1993b) and rely (Wilson et al., 1990) on white-tailed deer to maintain tick populations. In addition to white-tailed deer, other medium and large-sized mammals are commonly infested with *I. scapularis* adults and nymphs.

In a national survey of ticks on canine and feline companion animals recovered by veterinarians in the United States, *I. scapularis* was present on 27.4% (409 of 1494) of infested dogs and 46.4% (156 of 336) of cats (Saleh et al., 2019). Dogs were mostly infested with adult *I. scapularis* but a few nymphs were also recorded. Cats were also mostly infested with adult *I. scapularis* but a larger proportion of nymphs and larvae were recovered from cats. Proportions of dogs and cats with *I. scapularis* vary depending on geographic region with differences in tick activity based on local climate and weather (Eisen et al., 2016b). Examination of tick infested dogs from southeastern Oklahoma and northwestern

Arkansas (Koch, 1982) noted adult *I. scapularis* attached to the head and neck. Saleh et al. (2019) also demonstrated that *I. scapularis* adults preferentially attached to the head, ears, neck and dorsum of infested dogs. Similarly, *I. scapularis* were commonly recovered from the head, ears, necks, and dorsum of infested cats (Little et al., 2018; Saleh et al., 2019).

In the western United States, *I. pacificus* also infests a diverse array of wild and domestic mammals, birds, and lizards (Padgett and Lane, 2001; Castro and Wright, 2007). Western fence lizards (*Sceloporus occidentalis*) are considered preferred hosts for immature *I. pacificus* and are found more in greater abundance and prevalence on reptiles compared to wild deer mice (*Peromyscus* spp.) and pinyon mice (*P. truei*) (Lane and Loye, 1989). Columbian black-tailed deer (*O. hemionus columbianus*) along with other medium and large-sized mammals are hosts for adult *I. pacificus* (Padgett and Lane, 2001).

In comparison to humans, *I. scapularis* and *I. pacificus* transmit relatively few pathogens to dogs and cats, namely *Anaplasma phagocytophilum* and *B. burgdorferi* (Table 1). *Ixodes scapularis* also transmits *Ehrlichia muris euclairensis* in the upper Midwest. From a public health perspective, *I. scapularis* presents a serious public health concern as this tick vectors seven known pathogens to humans: *Anaplasma phagocytophilum*, *B. burgdorferi*, *Borrelia mayonii*, *Borrelia miyamotoi*, *E. muris euclarensis*, *Babesia microti*, and Powassan virus (Eisen and Eisen, 2018). Nymphal *I. scapularis*, in particular, are an important stage for disease transmission in the Northeast and Upper Midwest of the United States (Mather et al., 1996; Diuk-Wasser et al., 2010). On the West Coast, *I. pacificus* vectors *A. phagocytophilum* and *B. burgdorferi*, and is a presumed vector of *B. miyamotoi* to humans (Eisen and Paddock, 2020). Dogs and cats are not primary hosts for any of these pathogens and humans become infected from spill-over events from wild animal reservoirs.

Pathogens

Anaplasma phagocytophilum was shown to be transmitted by *I. scapularis* in 1996 (Telford et al., 1996), and *I. pacificus* in 2006 (Teglas and Foley, 2006). Ticks become infected by feeding on *A. phagocytophilum* infected wild rodents such as the white-footed mouse and eastern chipmunk in the eastern and Midwestern United States, and dusky-footed woodrats (*Neotoma fuscipes*), gray squirrels (*Sciurus griseus*), and chipmunks in western states (Carrade et al., 2009). Seroprevalence of *A. phagocytophilum* in dogs has been decreasing in mid-Atlantic states (e.g., Connecticut, Maryland, New Jersey, Rhode Island) as well as in Virginia, Minnesota, and Wisconsin (Dewage et al., 2019). However, seroprevalence of *A. phagocytophilum* has continued to increase in Massachusetts, Maine, New Hampshire, and Vermont (Dewage et al., 2019). Cats living in *A. phagocytophilum* endemic areas can be seropositive but clinical disease appears uncommon (Billeter et al., 2007; Lappin et al., 2020).

Prevalence of *A. phagocytophilum* in *I. scapularis* ranges from 0.1–20% in adults and 2.7–13% in nymphs (reviewed by Little and Molaei, 2020). One study suggested that *I. scapularis* were 98% more likely to be infected with *A. phagocytophilum* if infected with *B. burgdorferi* compared to ticks not infected (Little and Molaei, 2020). Prevalence of *A. phagocytophilum* in *I. pacificus* ranges from 0.4–4.3% in adults to 0.0–0.2% in nymphs (Eisen and Paddock, 2020).

Borrelia burgdorferi was first identified as the etiological agent of Lyme disease in 1982 (Burgdorfer et al., 1982). Experimental infections of *B. burgdorferi* in laboratory-reared dogs corroborated observations of naturally infected dogs in that Lyme disease was a multisystemic, polyarthritic condition in canines (Appel et al., 1993). Estimates of *B. burgdorferi* antibodies in dogs across the United States suggests a decrease in seroprevalence in several states along the mid-Atlantic coast and in Wisconsin (Dewage et al., 2019). These numbers are in stark contrast to an increase in the seroprevalence of *B. burgdorferi* antibodies in dogs from other northeastern and Midwestern states

(e.g., Iowa, Michigan, Maine, New York, Pennsylvania) where Lyme borreliosis is endemic or emerging, as well as in a few states in the upper South (e.g., North Carolina, South Carolina, West Virginia) where endemicity has not been established (Dewage et al., 2019). Cats are susceptible to infection with *B. burgdorferi* but little is known about the clinical course of the disease (Hoyt et al., 2018; Lappin et al., 2015; Magnarelli et al., 2005).

In New England and the upper Midwestern United States, the prevalence of *B. burgdorferi* in *I. scapularis* is relatively high compared to other tick-borne pathogens, typically ranging from 24–64% in adults and 10–23% in nymphs (Tilly et al., 2008; Hamer et al., 2010; Turtinen et al., 2015; Little and Molaei, 2020), depending on experimental methodology, sampling strategy, and endemicity of sampling location. In other regions of the United States, the prevalence of *B. burgdorferi* is much lower to non-detectable (Maggi et al., 2019). Although, recent data suggests that prevalence of *B. burgdorferi* is increasing in *I. scapularis* in areas where the tick is expanding in range (Hickling et al., 2018). Ticks become infected when larvae ingest the spirochete while feeding on *B. burgdorferi* infected wild rodents (Mather et al., 1989). Nymphal *I. scapularis* are considered the most important stage for transmitting *B. burgdorferi* to humans and animals (Mather et al., 1996; Diuk-Wasser et al., 2010). Questing nymphs of *I. scapularis* are rarely collected by dragging techniques or found infesting people in the southeastern United States (Arsnoe et al., 2015). The prevalence of *B. burgdorferi* in *I. pacificus* is considerably lower than that of *I. scapularis*, with estimates usually less than 5% (Burgdorfer et al., 1985; MacDonald et al., 2017). Analysis of *I. pacificus* and other ticks in California for infection with *B. burgdorferi* suggest the highest risk of Lyme disease is in north-central and Sierra Nevada foothill regions of the state with little to no risk in southern regions (Rose et al., 2019).

Ehrlichia muris eauclairensis was first identified in human patients in the upper Midwest with most cases occurring in Minnesota and Wisconsin (Pritt et al., 2011; Johnson et al., 2015; Pritt et al., 2017). *Ixodes scapularis* larvae were able to acquire and nymphs were able to transmit *E. muris*

eauclariensis to C57BL/6J mice (Karpathy et al., 2016). Prevalence of *E. muris eauclairensis* was 2.9% (22

of 757) in *I. scapularis* adults and 0.9% (10 of 1150) in nymphs (Murphy et al., 2017). Electron

microscopy demonstrated that *E. muris eauclairensis* exhibits an affinity for epithelial cells, neuronal

cells of the synganglion, salivary glands, and male accessory glands of *I. scapularis* (Lynn et al., 2015).

Infection of *E. muris eauclairensis* in a dog resulted in decreased appetite, lethargy, recurrent bouts of

vomiting, and fever (Hegarty et al., 2012). Dogs seroconvert to infection with *E. muris eauclairensis* and

antibodies to the pathogen are thought to contribute to the rise in seroprevalence to *Ehrlichia* spp. in

the upper Midwest (Little et al., 2014)

Zoonotic concerns

Both *I. scapularis* and *I. pacificus* bite and feed on humans. In addition to the risk of pathogen

transmission (Eisen and Eisen, 2018), tick bites are painful and annoy humans (Merten and Durden,

2000; Nelder et al., 2014; Lindquist et al., 2016). *Borrelia burgdorferi* that causes Lyme disease in

humans is the most commonly reported vector-borne pathogen in the United States (Rosenberg et al.,

2018). All stages of *I. scapularis* are commonly reported from people in the eastern and northern United

States (Merten and Durden, 2000) and eastern Ontario (Nelder et al., 2014). *Ixodes pacificus* are

commonly recovered from humans in far western states (Merten and Durden, 2000). Despite a basic

understanding of the epidemiology of *I. scapularis* and Lyme disease, infestations of black-legged ticks

on humans (Eisen and Eisen, 2018) and companion animals continue to commonly occur (Saleh et al.,

2019). Furthermore, it appears *I. scapularis* is expanding its range in the upper Midwest, northeast and

mid-Atlantic regions, while remaining stable in the southeastern United States (Eisen et al., 2016a).

Risk of infestation with *I. scapularis* is highest for humans in woodland, mixed grassy, brushy, or

ecotones of natural areas located around domestic and peridomestic communities or recreation areas

(Carroll et al., 1992; Stafford, 2007; Hahn et al., 2018). Outdoor recreational activities (Salkeld et al.,

2019) and contact with wood (e.g., sitting on logs, gathering wood, sitting against trees, walking, stirring

and sitting on leaf litter, just sitting on leaf litter) increase the risk of *I. pacificus* infestation (Lane et al.,

2004). Engorgement indices quantifying specific tick morphological measurements at known time

intervals have been developed to estimate duration of attachment as an indirect indicator for risk

ofpathogen transmission (Yeh et al., 1995). Over 60% of infested people removed *I. scapularis* adults by

36 hours of attachment, but only 10% found and removed nymphal blacklegged ticks within the first 24

hours of feeding (Yeh et al., 1995).

2.6. *Rhipicephalus* spp. (brown dog ticks)

2.6.1. Environment

      Brown dog ticks (*Rhipicephalus* spp.) have the widest geographic distribution of any tick in the

world and are now recognized to be a species group comprised of as many as five different species, or

operational taxonomic units (OTUs), including *R. sanguineus* sensu lato (=tropical) and *R*. sp. I – IV

(Dantas-Torres et al., 2013). Because the taxonomy is still under debate, this review will refer to these

ticks as *Rhipicephalus* spp. or brown dog ticks. Two main populations of brown dog ticks have been

identified in North America to date. Commonly referred to as "tropical" and "temperate," these

populations do not mate and produce offspring, and can be distinguished from one another on the basis

of mitochondrial sequences (16S rDNA, 12S rDNA, and cox1), morphology, and through cross-breeding

experiments (Levin et al., 2012; Dantas-Torres et al., 2013; Sanches et al., 2016; Zemstova et al., 2016;

Jones et al., 2017). Intense brown dog tick infestations are more common in warmer areas in the region

including Mexico, the Caribbean, and the southern United States. However, due to the propensity of

these ticks to establish and flourish indoors, populations of brown dog ticks can be found anywhere

there are dogs (Dryden and Payne, 2004).

Brown dog ticks have a strong host preference for dogs and are distinctly endophilic. Accordingly, infestations are commonly associated with kennels or homes where dogs are present, and these ticks are often found crawling on walls, emerging from gaps in the structures, under upholstery cushions, and in carpeted areas where the dogs spend the majority of their time. In warmer areas, these ticks can also survive outdoors so long as cracks and crevices in walls, between rocks, or in the ground are present to provide safe havens for egg deposition by females (Dantas-Torres, 2010). Although translocation events occasionally occur, tropical brown dog ticks are generally found in areas with annual mean temperatures of > 20°C and temperate brown dog ticks are present where annual mean temperatures are less than 20°C (Zemstova et al., 2016; Jones et al., 2017). This disparate species distribution is thought to be related, in part, to poor survival of fed immature stages of tropical brown dog ticks under more severe winter conditions (Labruna et al., 2017).

Survey of dogs has shown infestations with adult brown dog ticks in Oklahoma are most common in July, August, and September, with a second, smaller peak of adult activity in March, April, and May. Larvae were only found on dogs June through September, and nymphs were present in July and again in September and October (Koch, 1980). In Mexico, dogs were found infested with all stages throughout the year although prevalence of infestation was highest spring through fall and lowest in the winter months (Cruz-Vazquez and Garcia-Vazquez, 1999). Brown dog ticks exhibit a strong host preference for domestic dogs in all stages (larvae, nymphs, adults) although specimens are occasionally reported from cats and people (Demma et al., 2005; Thomas et al., 2016; Little et al., 2018; Saleh et al., 2019). In recent years, apparent rapid northward expansion of tropical brown dog ticks has been identified in California and western Arizona (Villarreal et al., 2018).

2.6.2. Morphology

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Adult *Rhipicephalus* spp. are inornate, reddish brown, and have relatively short mouthparts and a hexagonal basis capitulum (Figure 7). Both festoons and eyes are present. The different taxonomic groups are considered morphologically similar although morphology varies, including in the appearance of festoons, Haller's organ, accessory shield, adanal shield, and spiracular plates (Dantas-Torres et al., 2013; Caetano et al., 2017). Short mouthparts that are approximately the length of the hexagonal basis capitulum are also evident on larvae and nymphs (Dantas-Torres, 2010).

2.6.3. Feeding and disease transmission

Brown dog ticks readily attach to and feed on dogs, and the presence of dogs is critical to long-term establishment of a population of these ticks in a given area. Although *Rhipicephalus* spp. ticks may attach and feed anywhere and on any dog, both feeding site preferences and breed preferences have been described. A slight but significant dorsal preference is seen for attachment, and most ticks are found on the head, especially the ears, and the back, but brown dog ticks also readily attach between the toes and in the inguinal and axillary regions (Dantas-Torres, 2010; Saleh et al., 2019). A comparison study using co-housed dogs of different breeds revealed Cocker Spaniel dogs harbored many more ticks than Beagles in the same environment, suggesting ticks were less attracted to Beagles (Louly et al., 2009).

Dogs with brown dog tick infestations often present with very high numbers of ticks, and blood loss anemia — at times severe and life threatening — can occur when infestations are intense (Dantas-Torres, 2010; Herndon and Little, 2015). Bite site reactions may become inflamed and secondary infections occasionally develop, especially with high intensity infestations, but due in part to shorter mouthparts, the trauma caused by brown dog tick feeding is often less severe than that of other tick species. However, brown dog ticks transmit a wide array of pathogens to dogs (Table 1), including *Babesia vogeli*, *E. canis*, *R. rickettsii*, and other spotted fever group *Rickettsia* spp. (Dantas-Torres, 2010).

Most of these agents are transmitted through saliva during tick feeding, but for *Hepatozoon canis* dogs

ingest the tick to become infected (Little et al., 2009). While suspected, tick transmission has not been

confirmed for some *Rhipicephalus* sp.-associated pathogens in North America including *A. platys*,

Cercopithifilaria sp., *H. canis,* and *Babesia gibsoni* (Allen et al., 2008; Dantas-Torres, 2010; Lineberry et

al., 2020). The latter agent is considered more likely to move between dogs in this region via fighting and

bite wounds (Yeagley et al., 2009).

2.6.4. Pathogens

Disease caused by brown dog tick-transmitted pathogens is much more common in the

southern United States, Mexico, and the Caribbean where this tick commonly occurs than in other areas

of North America. Even in regions where disease associated with brown dog ticks is well documented,

the prevalence of a given bacterial or protozoal pathogen in ticks is usually low (not detected or < 1%) in

the absence of active, ongoing transmission among dogs on a given premise. However, when ticks are

removed from infected dogs, and especially when engorged ticks that contain concentrated blood from

several days of feeding are tested, prevalence of infection in ticks may be much higher. For example, in

Yucatan, Mexico, 36% of fed brown dog ticks removed from dogs and 45% of those from an animal

shelter with ongoing *E. canis* transmission were PCR positive for *E. canis* (Pat-Nah et al., 2015). In

contrast, PCR for *Anaplasma* spp. and *Ehrlichia* spp. failed to confirm any infections in 519 engorged

adult brown dog ticks removed from 100 dogs in northern Mexico despite the fact that *A. platys* was

detected in 3 dogs and *E. canis* was found in 4 dogs (Almazan et al., 2015). In another study in southern

California, United States, *E. canis* was not detected in unfed, questing *Rhipicephalus* sp. ticks although *R.*

rickettsii was detected by PCR in one tick (Wikswo et al., 2007).

As the strongly preferred host, dogs serve as the reservoir of pathogens transmitted by brown

dog ticks, and in the absence of tick control, infection of dogs is very likely. Canine serosurveys and PCR

surveys in the Caribbean, where brown dog ticks are common, have documented *E. canis* antibodies or DNA in 25%–50% of dogs and *A. platys* antibodies or DNA in 10%–25% (Yabsley et al., 2008; Qurollo et al., 2014; Starkey et al., 2016). In the southwestern United States, Mexico, and Central America, antibodies reactive to spotted fever group *Rickettsia* spp. are detected in approximately 10% of dogs tested although during an outbreak canine seroprevalence as high as 70% has been reported (Demma et al., 2006; Wikswo et al., 2007; Moreira-Soto et al., 2016; Pieracci et al., 2019).

2.6.5. Zoonotic concerns

Brown dog ticks are an important vector of *R. rickettsii* in the southwestern United States, Mexico, and Central America. Large outbreaks of human disease have been associated with dog overpopulation, dramatic increases in *Rhipicephalus* sp. numbers, and spillover leading to human infection (Demma et al., 2005; Demma et al., 2006; Nicholson et al., 2006; Eremeeva et al., 2011). Human cases are more commonly seen in areas where canine seroprevalence is high, and dogs can be used as sentinels to predict risk in humans (Demma et al., 2005; McQuiston et al., 2011). Dogs can also serve as an amplifying host for *R. rickettsii*, with infection detected in approximately 10% of nymphs and 36% of adults that fed as larvae and nymphs, respectively, on infected dogs (Piranda et al., 2011). *Rhipicephalus* sp. females also pass *R. rickettsii* infection transovarially, but the route appears inefficient, suggesting horizontal transmission would be necessary to maintain a source of infected ticks in a given area (Piranda et al., 2011). *Rickettsia massiliae* has been described in brown dog ticks in North America although the role of this agent as a human pathogen in the region is unclear (Eremeeva et al., 2006; Beeler et al., 2011; Fornadel et al., 2013). Zoonotic infection with *E. canis* has also been described (Perez et al. 2006).

2.7. *Otobius megnini*

Otobius spp. are soft ticks which parasitize a single host during their life cycle, and only the immature stages are parasitic. Two species present in North America are known to infest dogs and cats — *O. megnini* and *O. lagophilus. Otobius megnini* prefers the arid climate of southwestern states, but has extended beyond these regions and infests a variety of animals across the United States including dogs and cats (Soulsby, 1968; Sonenshine vol. 1, 2013; Levin, 2015; Little et al., 2018; Saleh et al., 2019); thus, the species is of primary concern in veterinary medicine. *Otobius lagophilus*, predominantly found in the southwestern United States, infests wild rabbits (*Sylvilagus* spp. and *Lepus* spp.) and rarely cats (Cooley and Kohls, 1944; Bacha, 1957).

2.7.1. Environment

Otobius megnini, commonly called the spinose ear tick, was first described in 1883 under the scientific name *Argas megnini*, was later transferred to the genus *Ornithodoros*, and finally the genus *Otobius* was erected in 1912 (Keirans and Pound, 2003; Niebuhr et al., 2013). The tick species prefers dry, hot environments and was historically limited to the southwestern United States and Mexico. Immature stages of *O. megnini* feed within the external ear canals of a variety of mammals including cattle, goats, horses, sheep, wild ungulates, and less frequently dogs and cats (Soulsby, 1968; Sonenshine vol. 1, 2013; Levin, 2015; Little et al., 2018; Saleh et al., 2019). Infestation occurs more often in winter and spring months, but *O. megnini* can be found on animals year-round (Levin, 2015). Seasonal abundance may vary according to geographic region and annual climactic pattern (Nava et al., 2009; Niebuhr et al., 2013).

Time to life cycle completion of *O. megnini* depends upon humidity and temperature, which influence time of egg incubation, feeding and molting of immatures, oviposition by females, and larval hatch rate (Vial, 2009; Diyes and Rajakaruna, 2017; Rajakaruna and Diyes, 2019). Unfed larvae are quite active; after finding and climbing onto a suitable host, larval spinose ear ticks will migrate to the ears

and locate far within the external acoustic meatus to feed and undergo ecdysis. Although *O. megnini* is generally accepted to have at least two nymphal instars, consensus among all researchers has yet to be reached. Replete nymphs will drop from host ear canals into the environment, seek shelter in protected microenvironments, and molt to adults (Loomis, 1961; Hoogstraal, 1985; Wanchinga and Barker, 1986; Nava et al., 2009; Niebuhr et al., 2013; Diyes and Rajakaruna, 2017; Njaa 2017; Rajakaruna and Diyes, 2019).

Adult *O. megnini* are free-living and thrive in semi-arid climates. They are often found within cracks and crevices of tree bark, log fences, barns, in pasture shelters under accumulated debris, and under logs and fence posts. Unmated females can survive an average of nearly 5 months and a maximum of 18 months under laboratory conditions. Males can live an average of 100 days (Niebuhr et al., 2013; Rajakaruna and Diyes, 2019). Adults mate in the environment, and within approximately two weeks gravid females will produce 4–10 egg clutches comprised of often hundreds of eggs; oviposition occurs during a single, protracted gonotrophic cycle. Larvae may emerge within two-week's time, but this short of a hatch period appears to occur when environmental temperatures are 25–33°C. Emerged *O. megnini* larvae may survive in favorable environmental conditions off-host without a blood meal for nearly three months (Wanchinga and Barker, 1986; Neibuhr et al., 2013; Diyes and Rajakaruna, 2017).

The covert anatomic location that spinose ticks parasitize likely resulted in the inadvertent translocation of infested livestock. Now, in addition to southwestern states previously recognized, the tick species is documented in states bordering the Pacific Coast into British Columbia, in southcentral states, and in several southeastern states. Also, spinose ear ticks are now found in Australia, Africa, Asia, Central and South America, and Europe (Niebuhr et al., 2013; Levin, 2016; Rajakaruna and Diyes, 2019).

A related species, *O. lagophilus* has been rarely reported infesting cats (Cooley and Kohls, 1944; Bacha, 1957). *Otobius lagophilus* is primarily found in the southwestern United States, although isolated reports have occurred in other geographic regions including Canada. *Otobius lagophilus* has a similar

biology to *O. megnini*, but the parasitic phase of *O. lagophilus* most commonly attaches around the face

and ears of hosts, instead of within the ear canals. Adults of *O. lagophilus* are found free in the

environment but can be found within rodent burrows, suggesting rodents may also serve as natural

wildlife hosts. Nymphs of *O. megnini* and *O. lagophilus* are morphologically similar, but can be

differentiated based on integument spine size, hypostome dentition, and spiracular shape. *Otobius*

lagophilus was once suggested as a vector of Colorado tick fever and a poorly characterized spotted

fever group rickettsial agent in the 1950s; however, the tick species is not currently known to vector any

pathogens (Bacha, 1957).

2.7.2. Morphology

Adults of *O. megnini* are non-parasitic and therefore of little clinical significance. Male and

female *O. megnini* possess vestigial mouthparts which are not visible from the dorsal aspect, and their

cuticles are somewhat granular. Males and females are morphologically similar except that females are

typically larger and have a slightly smaller genital aperture. Adults are grayish to dark brown in color

(Diyas and Rijakaruna, 2017). Capitula of nymphs and larvae extend anteriorly when viewed from the

dorsal aspect (Figure 8). Only the nymphal instars have backward-projecting spines that cover the

integument; characteristic spines and preferred anatomic location on hosts earned the tick species its

common name. Typically, nymphs are the stages observed infesting animals.

Engorged nymphs appear greyish-blue in color, and have a midline constriction that confers a

violin-shaped body. Unfed nymphs are less than half the size of engorged nymphs and may appear ivory

or reddish brown in color. Larvae are usually not observed infesting hosts due to their small size and

location deep within the external ear canal. Engorged larvae may appear greyish, pinkish, or ivory in

color. Unfed larvae are minute especially unlikely to be detected within host ear canals or in the

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environment (Sonenshine, 1948 (vol 1); Soulsby, 1982; Diyas and Rajakaruna, 2017; Njaa 2017; Saari, 2019).

2.7.3. Feeding and disease transmission

Otobius megnini larvae feed for up to two weeks (Neibuhr et al., 2013; Diyes and Rajakaruna, 2017). After this feeding period, they molt to nymphs in host ear canals within two-week's time (Loomis, 1961; Neibuhr et al., 2013; Diyes and Rajakaruna, 2017). Nymphs feed intermittently for approximately 2 to 4 months, remaining in the ear of the same host throughout (Loomis, 1961; Vial 2009; Niebuhr et al., 2013; Diyes and Rajakaruna, 2017). However, the collective parasitic phase of *O. megnini* has been documented to exceed 200 days (Nava et al., 2009). As nymphs mature and grow, they can be observed feeding in more shallow portions of the ear canal or attached to the auricular dermis (Njaa, 2017).

Consequences of infestation with *O. megnini* are related to the trauma caused by blood-feeding larvae and nymphs within the ear canal and associated discomfort. Severe irritation leads to otitis externa with a waxy exudate. Local reactions at attachment sites include perivascular to interstitial dermatitis containing abundant eosinophils and neutrophils (Duron et al., 2015; Njaa, 2017). Large numbers of spinose ear ticks can produce ulcerative lesions. Animals may exhibit vigorous head-shaking. Ear scratching and rubbing of the head may lead to excoriation of the ear pinnae (Levin, 2016; Njaa 2017; Saari, 2017).

2.7.4. Pathogens

Infections of *O. megnini* with *Coxiella burnetii* (Q fever), Colorado tick fever virus, *F. tularensis*, and *R. rickettsii* have been reported, but the tick's vector competence for these agents is unknown (Bowman, 2014; Levin, 2016). Investigations into the vector capacity of *O. megnini* for *B. burgdorferi* and *E. canis* have yielded no evidence supporting competence. In general, *O. megnini* is not considered an

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important vector of any known pathogenic agent in North America (Ewing et al., 1990; Fivas et al., 1990; Rajakaruna and Diyes, 2019). The detriment of spinose ear tick infestations seems mainly due to annoyance and direct injury caused by immature instars within the external ear canal (Sonenshine, 2014; Njaa, 2017; Diyes and Rajakaruna, 2017; Levin, 2016).

2.7.5. Zoonotic Concerns

Sparse reports of *O. megnini* infesting humans include immature stages found attached to the conjunctiva of the eye and within the ear canal (Jellison et al., 1948; Naudé et al., 2001; Diyas and Rajakaruna, 2017). Paralysis as a possible result of *O. megnini* infestation has been documented (Peacock, 1958; Nava et al., 2009). The spinose ear tick was once suspected as a potential vector of *C. burnetii* and *F. tularensis* to humans (Jellison et al., 1948; Nava et al., 2009). However, as humans are rarely ever parasitized by *O. megnini*, the risk of pathogen transmission to humans by this tick species is extraordinarily low.

2.8. *Ornithodoros* spp.

2.8.1. Environment

Ornithodoros species are soft ticks that are found worldwide (Mullen and Durden, 2009; Horton, 2015; Elelu, 2018). The two species of concern in companion animal medicine in North America are *O. hermsi* and *O. turicata. Ornithodoros hermsi* is found in coniferous forests at elevations of 1500–8000 feet in Rocky Mountain States, in states west of the Rocky Mountains, and in southern British Columbia. *Ornithodoros turicata* prefers drier habitats at lower elevations; the species is found in southcentral and southwestern states and into Mexico (Dworkin et al., 2008). The subspecies *O. turicata americanus*, only present in Florida, was proposed based on the marked geographic distance from western populations and possible difference in biology (Beck et al., 1986; Lopez et al., 2016; Krishnavahjala et al., 2018).

Ornithodoros hermsi preferentially feeds on deer and diurnal rodents including chipmunks (*Tamias* spp.) and tree squirrels (*Tamiasciurus* spp.), and tends to infest nests or tree cracks and crevices near nests (Fritz et al., 2013; Sage et al., 2017; Talagrand-Reboul et al., 2018). *Ornithodoros turicata* has been collected in association with numerous mammals including cattle, ground squirrels (*Spermophilus* spp.), pigs, and prairie dogs (*Cynomys* spp.) (Donaldson et al., 2016). Coyotes may serve as a natural host of *O. turicata* in Texas. *Ornithodoros turicata* is often found in underground burrows and cavern floors. In Florida, *O. turicata americanus* is consistently found in dens of gopher tortoises (*Gopherus polyphemus*), suggesting they serve as natural hosts of the tick subspecies. Occasionally, *Ornithodoros* spp. infesting shelter-seeking wildlife may be translocated to vacation cabins or rustic residences and there subsist on other hosts present including dogs and humans (Dworkin et al., 2008; Donaldson et al., 2016; Lopez et al., 2016; Krishnavahjala et al., 2018; Talagrand-Reboul et al., 2018).

2.8.2. Morphology

Ornithodoros species possess hypostomes that are well developed and very similar between males, females, and nymphal instars. The integument is comprised of both discs and mammilla which create various patterns that are continuous from dorsal to ventral surfaces. The bodies typically have very flattened appearances except after feeding, in which case the dorsa are markedly convex. As adults, species may be distinguishable by the presence or absence of eyes and tarsal features. *Ornithodoros hermsi* is significantly smaller than *O. turicata*. The integument of *O. turicata* is made up of characteristically conical mammillae, and the tarsi on the first pair of legs have dorsal projections. Nymphal stages can be differentiated from adults by characteristic protuberances on legs, which become more prominent with successive molts (USDA, 1965; Dworkin et al., 2008).

2.8.3. Feeding and disease transmission

The life cycles of *O. hermsi*, *O. turicata*, and *O. turicata americanus* are very similar, despite preferring different natural habitats and associated hosts (Beck et al., 1986; Dworkin et al., 2008). Like other *Ornithodoros* spp., they are endophilic, nidicolous, nocturnal, rapid feeders (≤ 1.5 h until replete), and directly leave hosts after blood meal acquisition. Motile stages include a single larval instar and several successive nymphal instars preceding the molt to females or males. Larvae and younger nymphs require a single blood meal before ecdysis, while larger nymphs feed more than once. Adults feed numerous times during their lifespans, and females oviposit after each blood meal. In the laboratory, nymphs of *O. turicata* can survive prolonged periods without a blood meal. Adults can survive without a blood meal for 5 years, but can live for over 10 years with regular feedings. Based on field studies, natural *Ornithodoros* spp. populations may be similarly hardy and long-lived (Beck et al., 1986; Donaldson et al., 2016; Talagrand-Reboul et al., 2018).

Ornithodoros hermsi and *O. turicata* transmit *Borrelia hermsii* and *Borrelia turicatae*, respectively, which are causative agents of tick-borne relapsing fever (TBRF) (Dworkin et al., 2008; Elelu, 2018; Talagrand-Reboul et al., 2018). Geographically, the *Borrelia* sp. causing TBRF generally corresponds to the distribution of its *Ornithodoros* sp. vector; in Rocky Mountain and western states, TBRF is predominantly caused by *B. hermsii*, while in arid regions of the southern United States, TBRF is predominantly caused by *B. turicatae* (Horton, 2015; Krishnavajhala et al., 2018). *Borrelia hermsii* and *B. turicatae* have been isolated from dogs in Washington and Texas, respectively (Kelly et al., 2014). Additionally, *B. turicatae* was identified in a dog in Florida (Schwan et al., 2005); *O. turicata americanus* is present in Florida, but the natural transmission of *B. turicatae* by the tick subspecies is not well understood (Krishnavajhala et al., 2018). Rodents and other small mammals are regarded as natural wildlife hosts for TBRF spirochetes (Talagrand-Reboul et al., 2018).

2.8.4. Pathogens

Although *Ornithodoros* species tend to stay in protected habitats near or where wildlife hosts reside to support their frequent need for blood meals, they are generalists and will feed on other animals in close proximity. Dogs may become infested with *Ornithodoros* spp. by sleeping in infested cabins or by exploring natural habitats (for example, caves or underground burrows) (Kelly et al., 2014; Elelu, 2016; Talagrand-Reboul et al., 2018). The quick transfer time of *Borrelia* spp. by *Ornithodoros* spp., and also that spirochetes may be secreted in both saliva and coxal fluid, facilitates transmission. *Borrelia* spp. are maintained transstadially in their respective vectors and may transmit transovarially. Despite multiple factors contributing to efficiency of *Borrelia* spp. transmission by *Ornithodoros* spp., the diagnosis of TBRF in dogs is rare. As *Ornithodoros* spp. ticks are fast-feeders, nocturnal, and typically flee hosts after repletion, they are unlikely to be observed by owners. However, TBRF is recognized as an emerging tick-borne disease that is under-diagnosed in veterinary medicine (Dworkin et al., 2008; Elelu, 2016; Talagrand-Reboul et al., 2018).

2.8.5. Zoonotic concerns

Ornithodoros spp. occasionally feed on humans. Cases of human TBRF caused by *B. hermsii* are often seasonal and typically traced back to events in which humans were sleeping in rustic cabins or within sleeping bags in caves in areas of the western United States (Dworkin et al., 2008; Talagrand-Reboul et al., 2018). Human TBRF cases caused by *B. turicatae* have occurred predominantly in Texas, with older reports in Kansas and Oklahoma. Human cases of *B. turicatae* in Florida (potentially transmitted by *O. turicata americanus*) have not been reported (Dworkin et al., 2008). In California, *Borrelia parkeri* was documented as the causative agent of TBRF in a single human patient in 1939, and has since been detected in *Ornithodoros parkeri* collected within the state; the true medical importance of this spirochete remains unclear (Dworkin et al., 2008; Barbour and Miller, 2014; Osborne et al., 2019).

3. Conclusions

Tick species in North America are diverse in ecology, host-seeking behavior, and pathogens they transmit. Ticks are also dynamic and adaptable, as demonstrated by their changing geographic distributions and establishment in new areas. Factors promoting this expansion include anthropogenic disturbances of terrain, climate change, movement of livestock, translocation via migratory bird hosts, and increases in wildlife populations, particularly white-tailed deer. Here we summarized the current geographic distribution, feeding habits and preferences, and known or novel pathogen transmission patterns for important tick species feeding on dogs and cats in North America. The wildlife-associated ixodid ticks of North America, including *A. americanum* (lone star tick), *A. maculatum* (Gulf Coast tick), *D. variabilis* (American dog tick), *I. scapularis* (black-legged tick, deer tick), *I. pacificus* (western black-legged tick), and now *H. longicornis* (longhorned tick), continue to extend beyond their historic geographic ranges. The domestic dog dependent *Rhipicephalus* spp. (brown dog ticks) are now documented to occasionally feed on cats and humans. The argasid *O. megnini* (spinose ear tick), once limited to the southwestern United States, is now found internationally due to movement of infested livestock. *Ornithodoros* spp. vector relapsing fever in humans, a zoonotic infection now considered emerging in dogs. As humans continue to encroach into natural tick habitats, modify landscape, and transport livestock and companion animals long distances, tick species will adapt accordingly and extend into new areas. It is critical to continually reassess where tick species occur and evaluate associated pathogen endemicity. Regular surveillance and geospatial predictive mapping efforts investigating changing tick populations in North America are important to protect the health of pets and owners alike. Understanding the basic biology, life history, distribution, and pathogen transmission systems of the common ticks of dogs and cats in this region is critically important to successfully address the health challenges ticks create.

Availability of data and materials

Not applicable.

Ethics approval and consent to participate

Not applicable.

CRediT authorship contribution statement

Meriam Saleh: Conceptualization, Writing – Original Draft, Writing – Review and Editing, Project administration. **Kelly Allen**: Conceptualization, Writing – Original Draft, Writing – Review and Editing. **Megan Lineberry**: Visualization, Resources. **Susan Little**: Conceptualization, Writing – Original Draft, Writing – Review and Editing. **Mason Reichard**: Conceptualization, Writing – Original Draft, Writing – Review and Editing.

Declaration of Competing Interest

In the past five years, MNS, KEA, MWL, SEL, and MVR have received honoraria or research support from multiple veterinary pharmaceutical companies directly or through their involvement with the National Center for Veterinary Parasitology. These activities were unrelated to the current review and the

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Table 1. Tick species, commonly reported hosts, known canine and feline pathogens, and current distribution of ticks commonly found parasitizing dogs and cats in North America.

Species	Primary hosts (stages)	Disease agents of dogs and cats	Current distribution in North America
Amblyomma americanum	White-tailed deer (L, N, A), large and medium-sized mammals (L, N, A), birds (L, N)	*Cytauxzoon felis* *Ehrlichia ewingii* *Ehrlichia chaffeensis* *Francisella tularensis*	Eastern half of North America from Gulf of Mexico to northern United States
Amblyomma maculatum	Cattle and other large mammals (A), birds and small mammals (L, N)	*Hepatozoon americanum*	Found 402 km inland in states along the Gulf Coast and in states bordering the Atlantic Coast as far northeast as Delaware; also found in several land-locked Midwestern and southern states
Dermacentor variabilis	Dogs, coyotes, cattle, horses, and raccoons (A), small mammals (L, N)	*Rickettsia rickettsii* *Cytauxzoon felis*	Eastern half of North America from Gulf of Mexico to southern Canada; isolated populations along the Pacific Coast in the United States, and extending eastward into Idaho
Haemaphysalis longicornis	White-tailed deer, cattle, raccoon, opossum (L, N, A)	Not known to be a primary vector of any canine or feline disease agents in North America at this time	Reported in 15 eastern states and in Arkansas, but documented distribution continues to spread

Ixodes pacificus	Black-tailed deer (A), lizards, small rodents (L, N)	*Anaplasma phagocytophilum* *Borrelia burgdorferi*	Western United States, California, western Oregon, western Washington and northward to British Columbia; also, in Utah and Nevada
Ixodes scapularis	White-tailed deer (A), small mammals (L, N in northern North America), lizards (L, N in the southern United States)	*Anaplasma phagocytophilum* *Borrelia burgdorferi* *Ehrlichia muris*	Eastern half of United States from Florida to central Texas and northward to eastern North Dakota and Maine; also common in southern Atlantic, Central, and some Western Provinces in Canada
Rhipicephalus spp.	Dogs (L, N, A)	*Anaplasma platys** *Babesia vogeli* *Babesia gibsoni** *Cercopithifilaria* sp.* *Ehrlichia canis* *Hepatozoon canis** *Rickettsia rickettsii*	Considered ubiquitous wherever there are dogs, with populations more intense in the southern United States, Hawaii, Mexico, and in the Caribbean
Otobius megnini	Cattle, goats, horses, sheep, wild ungulates (L, N)	Not a primary vector of any known disease agent	Southwestern and southcentral states, in states bordering the Pacific Coast into British Columbia, and in some southeastern states

Abbreviations: L, larva; N, nymph; A, adult

*Transmission by ticks has not been confirmed in North America

Figure captions

Figure 1. Dorsal and lateral view of non-fed and fed *Amblyomma americanum* female and male.

Figure 2. *Amblyomma americanum*, lone star tick, dorsal and ventral view of each stage and description of key morphologic features.

Figure 3. *Amblyomma maculatum*, Gulf Coast tick, dorsal and ventral view of each stage and description of key morphologic features.

Figure 4. *Dermacentor variabilis,* American dog tick, dorsal and ventral view of each stage and description of key morphologic features.

Figure 5. *Haemaphysalis longicornis,* longhorned tick, bush tick, cattle tick, dorsal and ventral view of each stage and description of key morphologic features.

Figure 6. *Ixodes scapularis,* black-legged tick or deer tick, dorsal and ventral view of each stage and description of key morphologic features.

Figure 7. *Rhipicephalus* sp.*,* brown dog tick, dorsal and ventral view of each stage and description of key morphologic features.

Figure 8. *Otobius megnini*, spinose ear tick, dorsal and ventral view of nymphal and larval stages and description of key morphologic features.

Figure 1. Dorsal and lateral view of non-fed and fed *Amblyomma americanum* female and male.

Figure 2. *Amblyomma americanum*, lone star tick, dorsal and ventral view of each stage and description of key morphologic features.

Dorsal

2.5–4.0 mm in length and 2.0–2.6 mm in width non-fed, yes present, rectangular basis capitulum, palpi longer than basis capitulum (i.e., long mouthparts) scutum with a conspicuous white spot at the posterior margin of the scutum giving its name, lone star tick.

Ventral

Anal groove does not extend anteriorly around anus, coxae II–IV with 1 spur, coxa I with internal spur about ½ the length of external spur.[1]

2.5–4.0 mm in length and 1.5–3.5 mm in width non-fed, eyes present, rectangular basis capitulum, palpi longer than basis capitulum (i.e., long mouthparts), iridescent markings on the posterior margin of the scutum and festoons.

Anal groove does not extend anteriorly around anus, coxa I with internal spur about ½ the length of external spur.[1]

1.3–2.5 mm in length and 1.2–1.3 mm in width when non-fed, palps elongate with second palpal segment at least twice as long as wide, eyes present, 11 festoons, lateral margin of basis capitulum rounded.

Venter of basis without retrograde projections, coxa I with 2 spurs, spur on coxa IV moderately long.[2]

~0.6 mm in length and ~0.5 mm in width non-fed, scutum covers anterior half of dorsum, 3-pair of legs, basis capitulum triangular or square, palps and hypostome long, postero-lateral angles of dorsal basis capitulum rounded.

Palpal segment II much longer than broad, external spur of coxa I pointed and distinctly larger than internal spur.[3]

2 mm

2 mm

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Figure 3. *Amblyomma maculatum*, Gulf Coast tick, dorsal and ventral view of each stage and description of key morphologic features.

Dorsal

Ventral

3.7–5.0 mm in length and 2.4–2.9 mm in width non-fed, eyes present, rectangular basis capitulum, palpi longer than basis capitulum (i.e., long mouthparts), scutum is largely white with some brown streaks and flecks.

Anal groove does not extend anteriorly around anus, coxae II–IV with 1 spur, coxa I with internal spur very short or insignificant.[1]

3.4–6.0 mm in length 2.3–3.0 mm in width non-fed, eyes present, rectangular basis capitulum, palpi longer than basis capitulum (i.e., long mouthparts), scutum is dark brown with interconnected white lines.

Anal groove does not extend anteriorly around anus, coxae II–IV with 1 spur, coxa I with internal spur very short or insignificant.[1]

0.9–1.3 mm in length and 0.8–0.9 mm in width non-fed, palps elongate with second palpal segment at least twice as long as wide, eyes present, 11 festoons, lateral margins of basis capitulum pointed giving the structure a triangular shape.

Venter of basis with prominent retrograde projections on each side, coxa I with a single spur.[2]

~0.6 mm in length and ~0.4 mm in width non-fed, capitulum triangular or square, palps and hypostome short, postero-lateral angles of dorsal basis capituli acute.[3]

Palpal segment II much longer than broad.

2 mm

2 mm

2 mm

Figure 4. *Dermacentor variabilis*, American dog tick, dorsal and ventral view of each stage and description of key morphologic features.

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Dorsal

Ventral

3.7–4.3 mm in length and 2.3–3.0 mm in width non-fed, eyes present, rectangular basis capitulum, palpi about as long as basis capitulum (i.e., short mouthparts), 11 festoons.[1,4] Scutum ornate with lots of white flecked with brown.

Anal groove does not extend anteriorly around anus, spiracular plate with small goblet cells, palpal segment 2 is about as long as broad.[1,4]

3.5–4.5 mm in length and 2.3–2.9 mm in width non-fed, eyes present, rectangular basis capitulum, palpi about as long as basis capitulum 11 festoons.[1,4] Scutum is highly ornate and largely white with flecks of brown.

Anal groove does not extend anteriorly around anus, palpal segment 2 is about as long as broad, spiracular plate with small goblet cells.[1,4]

1.4–1.5 mm in length and 0.9–1.0 mm in width non-fed, width of basis capitulum is roughly equal to width, lateral points of basis capitulum long and slender, palps are long and slender.[4]

Internal spur on coxa I small and relatively indistinct, external spur on coxa I semi-acute, large.[4]

~0.6 mm in length and ~0.5 mm in width non-fed, dorsal length of basis capitulum greater than width, lateral points of basis prominent, palps are somewhat slender.[4]

Coxa I with distantly acute internal spur, coxa II and III with sub-marginal, broad external spurs.[4]

2 mm

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Figure 5. *Haemaphysalis longicornis,* longhorned tick, bush tick, cattle tick, dorsal and ventral view of each stage and description of key morphologic features.

Dorsal

Ventral

2.7–3.4 mm in length and 1.4–2.0 mm in width non-fed, no eyes, palpal segment 2 extends laterally.[1,5,6]

Anal grove does not extend anteriorly around anus, palpal segment 3 dorsally with prominent retrograde spur.[1,5,6]

~1.8 mm in length and ~1.0 mm in width non-fed, basis capitulum ventrally without cornua at postero-lateral margins.[5,6]

Dorsally lateral margins of basis capitulum straight.[5,6]

~0.6 mm in length and ~0.5 mm in width non-fed, basis capitulum ventrally without cornua at postero-lateral margins. [5,6]

Dorsally lateral margins of basis capitulum straight. [5,6]

2 mm

2 mm

Figure 6. *Ixodes scapularis,* black-legged tick or deer tick dorsal and ventral view of each stage and description of key morphologic features.

Dorsal

Ventral

2.3–3.0 mm in length and 1.3–1.9 mm in width non-fed, inornate, lack eyes, lack festoons with long mouthparts, posterior margin of basis capituli straight or nearly so.[1]

Anal grove extends anteriorly around anus, internal spur of coxa I not extremely long; obvious internal spur on coxa I, external spurs present on all coxae, internal spur of coxa I longer than external.[1]

1.8–2.3 mm in length and 1.1–1.5 mm in width non-fed, scutum is black covering entire dorsum, porose areas absent, central area of scutum not deeply punctate, cornua absent.[1]

Anal grove extends anteriorly around anus, spiracular plate long, internal spur of coxa I narrow anteriorly.[1]

0.9–1.5 mm in length and 0.7–0.9 mm in width non-fed, palpi elongate and slender, length:width ratio 3.5:1 or greater, posterior margin of basis capituli dorsally sinuous; hypostome pointed.[7]

Anal grove extends anteriorly around anus; spurs present on one or more coxae; external spurs present or absent on coxae I–IV, internal spurs present on 1 or more coxae.[7]

0.5–0.6 mm in length and 0.4–0.5 mm in width non-fed, palps long and narrow, tip of hypostome pointed, tiny extension (auriculae) present on ventral basis capituli.[3]

Anal grove extends anteriorly around anus, palpal segment 2 not extending anteriorly and posteriorly.[3]
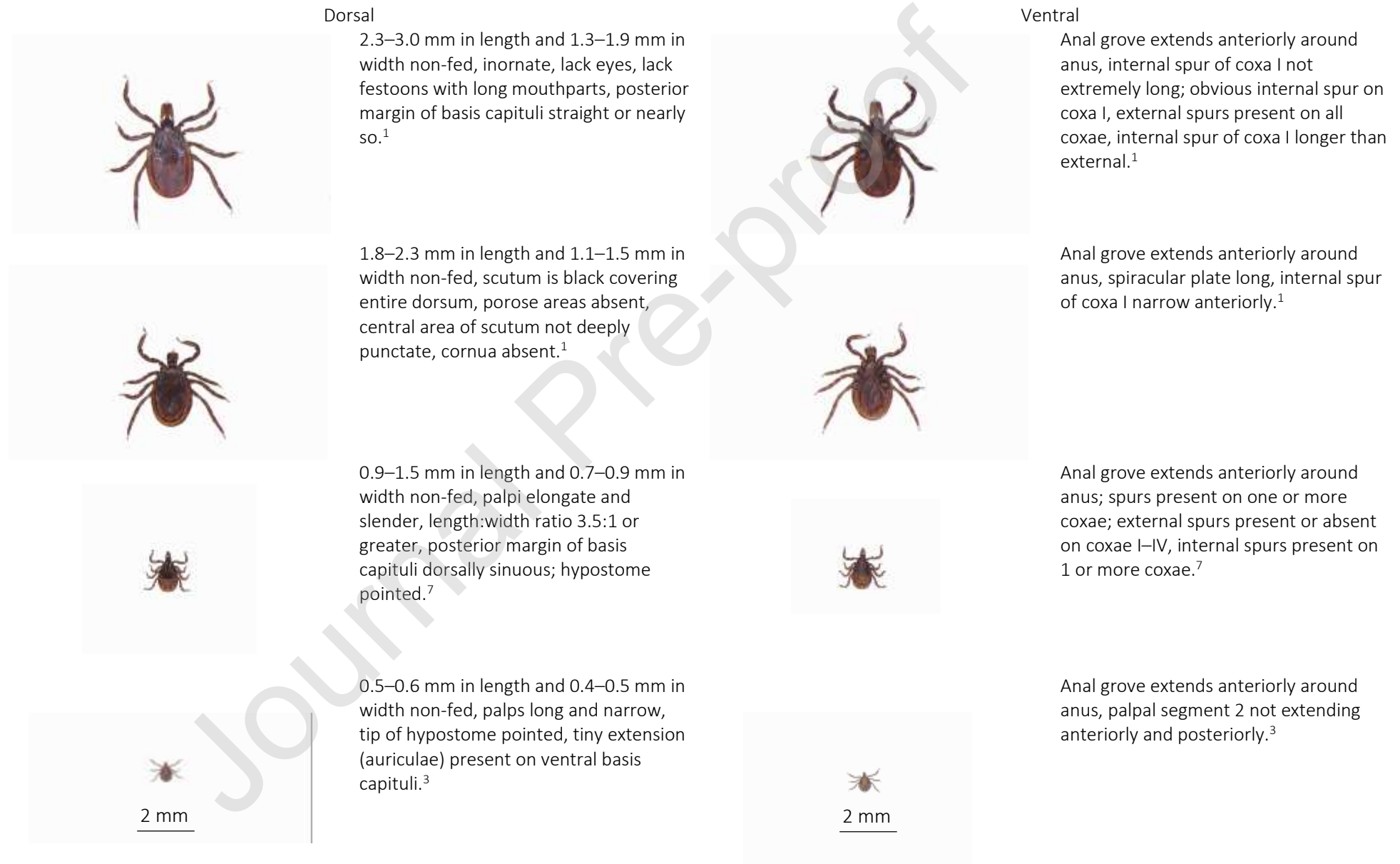
2 mm

2 mm

Figure 7. *Rhipicephalus* sp.*,* brown dog tick dorsal and ventral view of each stage and description of key morphologic features.

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Dorsal

1.5–3.2 mm in length and 1.0–1.3 mm in width non-fed, brown to reddish-brown inornate tick with eyes, festoons, hexagonal basis capitulum, palpi as long as or longer than basis capituli.[1,8]

Ventral

Anal groove does not extend anteriorly around anus.

2.0–3.0 mm in length and 1.3–1.5 mm in width non-fed, brown to reddish-brown inornate tick with eyes, festoons, hexagonal basis capitulum, palpi as long as or longer than basis capituli.[1,8]

Anal groove does not extend anteriorly around anus.

0.9 to 1.4 mm in length and 0.5–0.7 mm in width non-fed, basis capitulum much broader than long, palps short.[8]

Ventral coxae I each with two short, widely separated spurs, external longer than internal, a single rounded external spur decreasing in size on coxae II and II, coxa IV lacks spurs.[8]

~0.5 mm in length and ~0.4 mm in width non-fed, basis capituli almost hexagonal.[3]
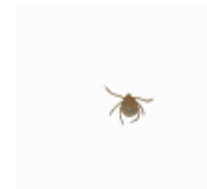
Anal grove not extending anteriorly around anus.[3]

Figure 8. *Otobius megnini,* spinose ear tick dorsal and ventral view of nymphal and larval stages and description of key morphologic features.

Dorsal

2 mm

Soft tick covered in short spines, recovered from the ear canal of infested hosts Two nymphal stages 2.3–3 mm in length and 1.5–2.0 mm in width non-fed,, 2nd nymphal stage is most often encountered by veterinarians and is easily identifiable by: no scutum, mouthparts are not visible from dorsal aspect, narrower posteriorly with constriction beginning between 3rd and 4th pair of legs [9]

One larval stage, 0.6–0.7 mm in length and 0.3 mm in width non-fed. Easily distinguished from nymph by: 3-pair of legs, very long hypostome and palpi that are visible from both ventral and dorsal aspects, integument is thin, striated, and with few bristle-like hairs that are not spines.[9]

Ventral

2 mm

Hypostome well developed that measures 0.36 mm. 1st stage nymphs a smaller with more slender legs and hypostome that measures only 0.19 mm.[9]

In fed larvae, the capitulum extends from a conical anterior projection.

Footnotes

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