



Original article

Establishing a baseline for tick surveillance in Alaska: Tick collection records from 1909-2019



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ABSTRACT

The expanding geographic ranges of tick species that are known pathogen vectors can have implications for human, domestic animal, and wildlife health. Although Alaska is home to several hard tick species, it has historically been outside of the range of the most common medically important ticks in the contiguous United States and western Canada. To assess the status of tick species establishment in the state and to provide a baseline for tracking future change in the distribution of ticks, we reviewed and compiled historical tick records and summarized recent tick occurrence records collected through the development of the Alaska Submit-A-Tick Program and through tick drag sampling at sentinel sites in southcentral Alaska. Between 1909–2019, there were 1190 tick records representing 4588 individual ticks across 15 species in Alaska. The majority of ticks were species historically found in Alaska: *Haemaphysalis leporispalustris*, *Ixodes angustus*, *Ixodes auritulus*, *Ixodes howelli*, *Ixodes signatus*, and *Ixodes uriae*. Over half of all tick records in the state were collected in the last 10 yr. During this time, the number of tick records and the number of tick species recorded in Alaska each year has increased substantially. Between 2010–2019, there were 611 tick records representing 1921 individual ticks. The most common hosts for reported ticks were domestic animals ($n = 343$, 56 %) followed by small wild mammals ($n = 147$, 24 %), humans ($n = 49$, 8%), and wild birds ($n = 31$, 5%). Less than 5% of records ($n = 25$) were of unattached ticks found in the environment. Since 2007, non-native tick species have been documented in the state every year, including *Amblyomma americanum*, *Dermacentor andersoni*, *Dermacentor occidentalis*, *Dermacentor variabilis*, *Ixodes pacificus*, *Ixodes ricinus*, *Ixodes scapularis*, *Ixodes texanus*, and *Rhipicephalus sanguineus sensu lato* (s.l.). Almost half of the records ($n = 68$, 48 %) of non-native tick species from 2010 to 2019 represented ticks found on a host (usually a dog or a human) that had traveled outside of Alaska in the two weeks prior to collection. However, *A. americanum*, *D. variabilis*, *I. pacificus*, *I. texanus*, and *R. sanguineus* s.l. have been found on humans and domestic animals in Alaska without reported recent travel. In particular, there is evidence to suggest that there is local establishment of *R. sanguineus* s.l. in Alaska. A tick species historically found in the state, *I. angustus* was frequently found on human and dogs, suggesting a potential role as a bridge vector of pathogens. Given the inconsistency of tick monitoring in Alaska over the past century, it is difficult to draw many conclusions from temporal trends in the data. Continued monitoring through the Alaska Submit-A-Tick Program will allow a more accurate assessment of the changing risk of ticks and tick-borne diseases in the state and provide information for setting clinical and public health guidelines for tick-borne disease prevention.

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1. Introduction

Ecological systems are changing rapidly in Alaska (Markon et al., 2018), raising concern about the potential emergence of vector-borne disease threats to human and wildlife health (Yoder et al., 2018). There is recent evidence that several medically-important tick species that are endemic in the contiguous United States and western Canada, but previously unknown in Alaska, are being introduced into the state (Durden et al., 2016). Additionally, several other Arctic nations have reported an expanding geographic range of ticks, potentially facilitated by rapidly warming temperatures at northern latitudes (Alfredsson et al., 2017; Jaenson et al., 2016; Tokarevich et al., 2011). In order to evaluate the present and future risk of tick-borne diseases in Alaska, it is essential to have baseline information on the range of tick species.

Although there are records of six tick species in Alaska from the early to mid-20th century, little is known about the distribution, abundance, or vector potential of these species (Deardorff et al., 2013; Fay and Rausch, 1969; Goethert et al., 2006). Limited evidence suggests that *Ixodes angustus* Neumann may be present mostly in southern coastal areas of the state (Deardorff et al., 2013; Fay and Rausch, 1969; Goethert et al., 2006; Murrell et al., 2003). Murrell et al. (2003) found that 20 percent of small mammals were parasitized by at least one *I. angustus*, but the prevalence ranged from 0 to 57 percent by host species. There are published reports of the rabbit tick, *Haemaphysalis leporispalustris* (Packard) collected mostly in interior Alaska, but also on the Kenai Peninsula in the southcentral part of the state (Philip, 1938). Approximately 27 percent of the hares trapped in the study were parasitized by *H. leporispalustris* (Philip, 1938). Most of the research on the seabird ticks, *Ixodes signatus* Birula and *Ixodes uriae* White is from islands in the Aleutian chain or off the west coast of Alaska (Choe and Kim, 1987; Olsen et al., 1995). In a study of the parasite community on seabirds on the Pribilof Islands, Choe and Kim (1987) found that the prevalence of tick infestation was approximately 28 percent for *I. signatus* and 91 percent for *I. uriae*, although this ranged from 10 to 50 percent and 80 to 97 percent, respectively, by bird species. Regarding other bird-associated ticks that have been found in Alaska, reports of *Ixodes howelli* (Cooley and Kohls) and *Ixodes auritulus* (Neumann) are limited to a handful of a presence records with no information on sampling effort associated with these records.

A recent study of ticks collected from humans and pets in Alaska showed that several non-native tick species have been brought into the state through out-of-state travel (Durden et al., 2016). However, there was no conclusive evidence of establishment or long-term survival of the species identified in the study: *Amblyomma americanum* (Linnaeus), *Dermacentor andersoni* Stiles, *Dermacentor variabilis* (Say), *Ixodes ricinus* (Linnaeus), *Ixodes scapularis* Say, and *Rhipicephalus sanguineus* (Latreille) *sensu lato* (s.l.).

The ability to document changes in tick vector distributions relies on accurate information about where tick species have occurred in the past, as well as continuously updated contemporary records of tick occurrence. The active collection of ticks through repeated tick drag sampling or small mammal trapping is useful for geographically targeted investigations, but these methods are too resource intensive to maintain consistently at a large scale (Cull et al., 2018). Alternatively, national or state-wide passive surveillance systems are designed to accept ticks from voluntary reporting as they are found (Cull et al., 2018; Johnson et al., 2004; Ogden et al., 2006b; Rand et al., 2017). This tick surveillance strategy can be implemented continuously, for a long period of time, over a broad area with relatively low human or financial resources (Cull et al., 2018; Johnson et al., 2004; Rand et al., 2017). Additionally, tick data collected through passive surveillance have been used to provide information about tick phenology and host associations (Rand et al., 2017), identify environmental risk factors for tick presence (Ogden et al., 2006b), and as an indicator of the area where vector-borne disease transmission risk is a concern (Johnson et al., 2004).

Here we review historical tick records in Alaska and summarize

recent tick occurrence records collected through the development of the Alaska Submit-A-Tick Program and through tick drag sampling at sentinel sites in southcentral Alaska. The development of a passive tick surveillance program in Alaska, as presented here, coupled with baseline information on the abundance and diversity of ticks will facilitate an ongoing assessment of the risk of tick-borne diseases in human, domestic animal, and wildlife populations in the state.

2. Materials and methods

2.1. Historical tick records in Alaska, 1909–2018

Historical tick occurrence records were retrieved from the Arctos database (<http://arctos.database.museum/>, accessed 9 September 2019). We used ‘Alaska’ as the search term for “State/Province” and used the following keywords under “Taxon name”: ‘tick’ or ‘Ixodes’ or ‘Amblyomma’ or ‘Dermacentor’ or ‘Haemaphysalis’ or ‘Rhipicephalus’. Individual results were reviewed to ensure that they referred to tick specimens. The scientific names of the tick species and host if applicable, text description of the location of the collection, the date of collection, and assigned coordinates and location accuracy were extracted for each valid record.

Since 2010, the Alaska Department of Fish and Game and the Alaska Office of the State Veterinarian have been cataloging ticks submitted to the state by veterinarians, biologists, and the public. Ticks were identified morphologically using standard guides and archived in the University of Alaska Museum of the North in Fairbanks (Durden et al., 2016). Raw data files from each of the agencies were crosschecked against the Arctos database. Duplicate entries were removed. The submitter information, tick host, text description of the location of the collection, the date the tick was received, and the tick species, life stage, and sex were extracted from each record.

We also performed a literature review to identify additional tick records that were in neither the Arctos database nor the state tick records. We searched Web of Science, PubMed, and Research Gate to identify studies that contained tick occurrence records in Alaska between 1900 and 2019. We limited the language to English. We used the following keywords: ‘Alaska’ AND ‘Ixodes’ or ‘Amblyomma’ or ‘Dermacentor’ or ‘Haemaphysalis’ or ‘Rhipicephalus’. We reviewed titles and abstracts to identify studies that took place in Alaska. Records were included in our database if the descriptions of the tick identification, collection location, and time period in the article were sufficient to determine the species, city or borough of collection, and year of collection. When available, we also extracted tick host information to the species level.

2.2. Development of the Alaska Submit-A-Tick program

In 2019, we established a systematic, statewide passive surveillance system to collect ticks in Alaska, similar to those in other jurisdictions (Cull et al., 2018; Johnson et al., 2004; Ogden et al., 2006b; Rand et al., 2017). Through the “Alaska Submit-A-Tick Program,” the public, veterinarians, clinicians, and biologists can voluntarily submit ticks that they find on themselves, a family member, a pet, in the environment, or on wildlife to the Office of the State Veterinarian for species identification and pathogen testing. Submitters have the option to request species identification results. With each tick submission, we request information on the date of tick collection, tick host, probable location of tick encounter, and history of travel inside or outside of Alaska of anyone or any pet within a submitter’s household within the two weeks prior to submission. Contact information is optional, if submitter would like to receive tick identification results. Submitted ticks are morphologically identified to species, life stage, and sex.

Key components of the surveillance program include 1) a program website where the public can access information on how to identify ticks, how to safely remove a tick, and how to submit a tick to the

program (<https://dec.alaska.gov/eh/vet/ticks>), 2) a standardized surveillance form that accompanies tick submissions, and 3) targeted outreach materials to increase awareness of the program. Tick submissions can be dropped off or mailed to the Office of the State Veterinarian in Anchorage. They can also be submitted to local Alaska Department of Fish and Game offices. This approach was essential for ensuring a broad geographic reach across Alaska.

2.3. Geocoding

Both the historical and contemporary tick occurrence records collected through passive surveillance had varying levels of specificity regarding the location of the collection. In order to standardize the location information, we developed a geocoding scheme. Using the described location associated with each tick record (e.g., city, hiking area, game management unit), we assigned GPS coordinates and an accuracy range of the assigned coordinates depending on the precision of the location information. For records that were associated with recent travel history, the city of residence of the tick host in Alaska was used for the location information.

2.4. Active surveillance for ticks

We selected 10 recreational sites in southcentral Alaska to conduct drag sampling for ticks. This region is characterized by a mild coastal climate, with average summer temperatures between 12–14 °C, average winter temperatures between -7 and -8 °C, and approximately 42–46 cm of annual precipitation (Köppen Dfc). We chose parks and campgrounds with trails, off-leash dog parks, and forested areas in order to target locations with substantial overlap between human, dog, and wildlife activity. The five sites in Anchorage were Far North Bicentennial Park, University Lake Park, Ruth Arcand Park, Connors Lake Park, and Kincaid Park. On the Kenai Peninsula, we sampled Centennial Park in Soldotna, Hidden Lake Campground in the Kenai National Wildlife Refuge, Slidehole Campground in Anchor Point, and Jack Gist Park in Homer. The tick sampling location within each recreational site was selected through discussion with the natural resources manager in each jurisdiction who was familiar with high-use forested areas in the parks. All sampling sites were located in deciduous or mixed deciduous / coniferous forest with dense vegetation in the understory.

We drag sampled for ticks every two weeks between 24 May and 28 September 2019. We chose these dates to coincide with a likely peak in questing activity of the multi-host hard tick species previously reported in Alaska. We sampled for ticks by dragging a 1-m² cloth made of rubber-bonded cotton fabric with a rope attached to a 1.2 m dowel inside the top edge. Weighted “fingers” were sewn to the bottom half of the drag in order to sample near the ground. We dragged 1000 m² in each recreational site.

2.5. Tick handling, identification, and classification

All ticks were morphologically identified to species and life stage at Georgia Southern University using standard guides (Brinton et al., 1965; Cooley, 1946a; Cooley and Kohls, 1944; Durden and Keirans, 1996; Estrada-Peña et al., 2017; Keirans and Clifford, 1978; Robbins and Keirans, 1992; Yamaguti et al., 1971) and stored in vials of 80–100% ethanol at -20 to -70 °C. Ticks were pooled by host, species, and life stage for analysis (e.g., if a vole was found with 15 adult female *I. angustus*, it is recorded as one record). References to tick diversity refer to the number of tick species recorded. We used boroughs, the Alaskan equivalent to counties, as the geographic boundaries for assessing tick species establishment. We considered only contemporary tick records (2010–2019) for species establishment because host travel history was available for tick records consistently after 2010. For each tick species, we extracted records where ticks were either found in the

Table 1

Number of records and ticks recorded in Alaska between 1909–2019. Data compiled from a review of historical records as well as contemporary records collected through the Alaska Submit-A-Tick Program.*.

Species	No. records	Total ticks
Tick species with historical presence records in Alaska		
<i>Haemaphysalis leporispalustris</i>	78	2205
<i>Ixodes angustus</i>	695	1207
<i>Ixodes auritulus</i>	7	7
<i>Ixodes howelli</i>	1	1
<i>Ixodes signatus</i>	46	164
<i>Ixodes uriae</i>	196	699
Non-native tick species		
<i>Amblyomma americanum</i>	21	37
<i>Dermacentor andersoni</i>	6	6
<i>Dermacentor occidentalis</i>	1	1
<i>Dermacentor variabilis</i>	57	59
<i>Ixodes pacificus</i>	3	3
<i>Ixodes ricinus</i>	4	4
<i>Ixodes scapularis</i>	11	15
<i>Ixodes texanus</i>	2	6
<i>Rhipicephalus sanguineus</i> s.l.	44	87

*An additional 15 records (comprising 41 ticks) that were identified only to *Ixodes* genus and 3 records (comprising 46 ticks) that were identified only to *Haemaphysalis* genus in the historical records were excluded from this table.

environment or on a host without reported travel outside of Alaska in the prior two weeks (i.e. wildlife hosts, humans who reported they had not traveled, or domestic animals whose owners reported that the pets had not traveled). We considered a tick species “established” in a borough if at least six ticks, or two or more life stages, were collected in a single borough in a single year (Dennis et al., 1998; Eisen et al., 2016; Hahn et al., 2016). We considered a tick species “reported” if there were records in the borough but they did not meet either of these criteria. While these criteria were originally created for *I. scapularis* and *I. pacificus*, they have been utilized recently to develop distribution maps for *D. variabilis* and *A. americanum* in the contiguous U.S (Lehane et al., 2020; Springer et al., 2015).

3. Results

3.1. Overview of tick occurrence records

Between 1909–2019, there were 1190 tick records representing 4588 individual ticks across 15 species in Alaska (Table 1). The majority of ticks were species that have historically been found in the state: *H. leporispalustris*, *I. angustus*, *I. auritulus*, *I. howelli*, *I. signatus*, and *I. uriae* accounted for 86 % (n = 1026) of all records (Fig. 1). *Ixodes angustus* was the most commonly recorded tick, representing 58 % (n = 695) of the tick records, followed by *I. uriae* (n = 196, 16 %) and

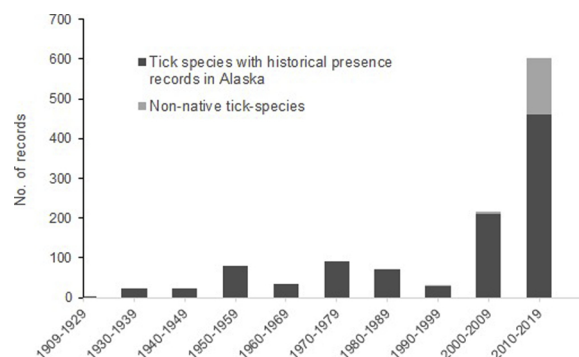


Fig. 1. Number of tick records in Alaska between 1909–2019 from a compilation of secondary data and records from ticks submitted through the Alaska Submit-A-Tick Program.

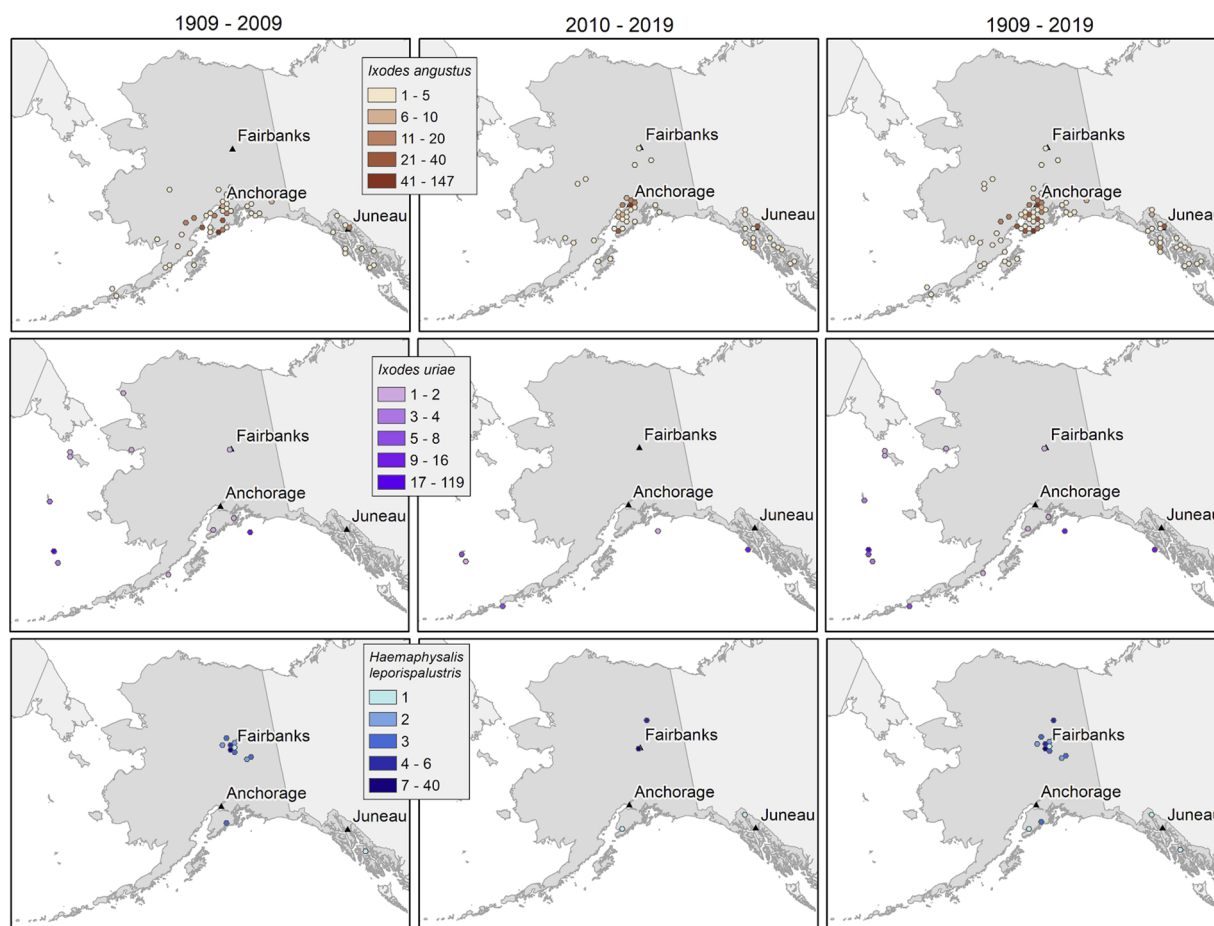


Fig. 2. Maps of the historical (1909-2009), contemporary (2010-2019), and cumulative (1909-2019) number of presence records of *Ixodes angustus*, *Ixodes uriae*, and *Haemaphysalis leporispalustris*, the three most commonly reported tick species in Alaska, at 1000 km² resolution.

H. leporispalustris (n = 78, 7%). The first record of a non-native tick found in Alaska occurred in 1997 when an adult male and a nymphal *A. americanum* were found on a person recently traveling from Oklahoma. Since 2007, non-native tick species have been documented in the state every year, including *D. andersoni*, *Dermacentor occidentalis*, *D. variabilis*, *Ixodes pacificus*, *I. ricinus*, *I. scapularis*, *Ixodes texanus*, and *R. sanguineus* s.l.

3.2. Geographic distribution of tick species

The most commonly reported tick species in the state between 1909 and 2019 were *I. angustus*, *I. uriae*, and *H. leporispalustris*, although there were also reports of *I. signatus*, *I. auritulus*, and *I. howelli*. *Ixodes angustus* was most commonly reported from southcentral and southeastern Alaska, with a few contemporary records in the interior (Fig. 2). *Ixodes uriae* has been reported sporadically from the coasts of the Kenai Peninsula. The vast majority of the *I. uriae* presence records are from seabirds on the western coast of the state and on islands in the Bering Sea (St. George, St. Paul, St. Lawrence, and St. Matthew), Aleutians (Amchitka, Aiktak, Buldir, Great Sitkin, Kasatochi, and Tanadag), in the Gulf of Alaska (Middleton), and in the southeast (St. Lazaria). *Haemaphysalis leporispalustris* has been reported primarily from the interior of Alaska, in the Fairbanks area, with sporadic reports from the Kenai Peninsula and southeast Alaska. The majority of *I. signatus* records are from St. Paul Island, but there are also records from the Aleutian Islands (Shemya and Amak Islands) and Kachemak Bay at the southern end of the Kenai Peninsula. *Ixodes auritulus* records are from southeast Alaska, near Juneau, Wrangell, and Sitka, and the *I. howelli* record is from western Alaska, near Kokechik Bay. Given the inconsistency of tick

monitoring in the state over the last century and the reliance on inquisitive biologists and members of the public to turn in found ticks, it is difficult to draw conclusions regarding changes in the distribution of these ticks over time. The presence records presented here likely represent the general distribution of these species, but these ranges could be refined with further environmental sampling.

3.3. Contemporary tick occurrence records (2010-2019)

Over half of all tick records in the state were collected in the last 10 years (Fig. 1). The majority of tick submissions were clustered around major population centers, including Anchorage and the Matanuska-Susitna Valley, Kenai Peninsula, Fairbanks, and Juneau, with submissions from all boroughs except North Slope, Wade Hampton, and Yakutat. During this time, the number of tick records and the diversity of tick species recorded in Alaska each year has increased substantially, although much of this trend is likely due to increased awareness of ticks and collection effort (Fig. 3). Between 2010-2019, there were 611 tick records representing 1921 individual ticks. The number of tick records each year has ranged from 3 (in 2010) to 232 (in 2019). Non-native ticks (including *A. americanum*, *D. andersoni*, *D. variabilis*, *I. pacificus*, *I. ricinus*, *I. scapularis*, *I. texanus*, and *R. sanguineus* s.l.) accounted for 23 % (n = 143) of the records (Table 2). In 2019, the first year of the Alaska Submit-A-Tick Program, we received specimens of 13 tick species found in the state.

Beginning in 2010, ancillary data on submitter, tick host, and host travel history are available for the majority of tick records. The majority of contemporary tick records were submitted by the public (n = 283, 46 %) followed by veterinarians (n = 185, 30 %) and biologists

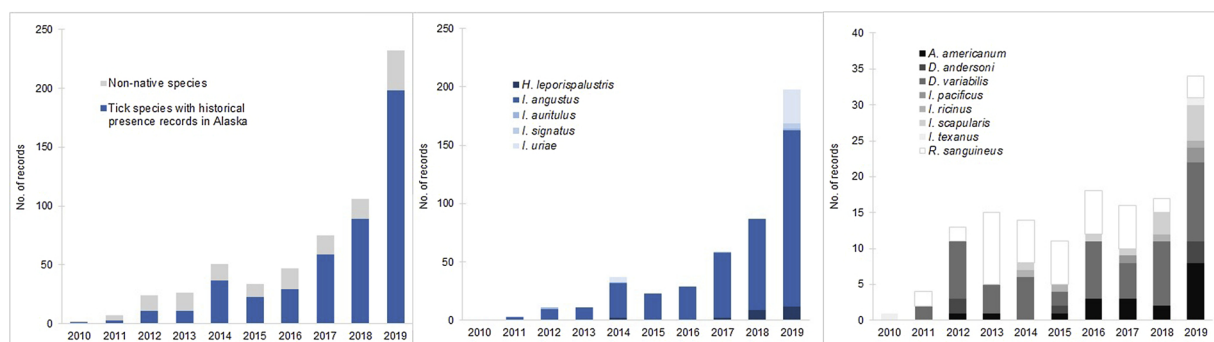


Fig. 3. Number of tick records in Alaska between 2010–2019, by species (left panel: all tick records, middle panel: records of tick species that have historically been found in Alaska, right panel: non-native tick species records).

($n = 113$, 19 %). Human health professionals submitted 6 records (1%). Two adult *I. angustus* ticks were collected through drag sampling in 2019 at Kinkaid Park (female; collected in June) and Hidden Lake Campground (male; July). No other ticks were collected via drag sampling.

Most ticks were submitted between May and September, with a distinct peak from June to August (Fig. 4). However, ticks were submitted throughout the year. In most months, the majority of submissions were of tick species that have historically been found in Alaska. In January and April, while we received three *I. angustus* ticks in each of these months, more non-native ticks were submitted during these time periods. The peak of travel-related tick submissions was slightly earlier in the year compared to overall tick submissions (Fig. 5). Travel-related tick submissions occurred in all months except February and October with the largest number of submissions from April to June, with waning numbers in July and August.

3.4. Tick host associations

The most common host for reported ticks was domestic animals ($n = 343$, 56 %) followed by small wild mammals ($n = 147$, 24 %), humans ($n = 49$, 8%), and wild birds ($n = 31$, 5%) (Table 2). A small number of ticks were found off-host (25 records, 4%) in places like a bed, on the ground, on a health clinic counter, or in nesting materials of bird colonies. Less than 3% of records ($n = 16$) either lacked information on the host or listed more than one potential host (e.g., human or dog).

Ixodes angustus was found on a wide variety of wildlife hosts including northern red-backed voles (*Myodes rutilus*), meadow voles (*Microtus pennsylvanicus*), red squirrels (*Sciurus vulgaris*), hares (*Lepus* spp.) martens (*Martes* spp.), shrews (*Sorex* spp.), rabbits, and a porcupine (*Erethizon dorsatum*). Of note, this tick species was commonly recorded on domestic animals (dogs [*Canis lupus familiaris*] ($n = 158$, 41 %); cats [*Felis catus*] ($n = 73$, 19 %), and frequently found on humans ($n = 17$, 4%).

Unsurprisingly, the majority of *H. leporispalustris* records were from snowshoe hares (*Lepus americanus*, $n = 19$, 66 %) and the Alaskan hare (*Lepus othus*, $n = 1$, 3%), reflecting their known feeding preference for lagomorphs. Immature stages of *H. leporispalustris* feed on a wide variety of bird species, and in this study, larvae were found on two wild birds (American robin [*Turdus migratorius*], 1 record, 4%; Slate-colored Junco [*Junco hyemalis*], 1 record, 4%). This tick was also found on dogs (2 records, 7%), cats (3 records, 10 %), and a human (1 record, 4%).

Ixodes uriae were found mainly on seabirds, although 2 records (6%) came from humans. *Ixodes uriae* were found on least auklets (*Aethia pusilla*), fork-tailed storm petrels (*Hydrobates furcatus*), Leach's storm petrels (*Oceanodroma leucorhoa*), thick-billed murre (*Uria lomvia*), and tufted puffins (*Fratercula cirrhata*). Almost a third of the records of this species ($n = 10$) came from burrows or nesting areas of tufted puffins.

There were only five contemporary *I. signatus* records. Four of these

(80 %) were from black-legged kittiwakes (*Rissa tridactyla*), and the other record (20 %) was from a red-faced cormorant (*Phalacrocorax urile*). Three of the four *I. auritulus* records had definitive information on the host. Of these, one was from a crow (*Corvus* spp.), one from a dog (*Canis lupus familiaris*), and one in the environment in a backyard.

3.5. Non-native ticks records

Almost half of the records ($n = 68$, 48 %) of non-native tick species from 2010 to 2019 were found on a host (usually a dog or a human) that had traveled outside of Alaska in the two weeks prior. About 16 % ($n = 23$) of the records were missing host information. Despite the large number of travel-associated tick collections, there was a substantial number of non-native tick records where the host reportedly had not recently traveled outside the state ($n = 52$, 36 %). In 2016, an adult male *A. americanum* was found on the counter in a health clinic in Kotzebue, and in 2017, another was found on a dog in Palmer. Two adult female *I. pacificus* have been found on dogs in Anchorage with no recent travel history (2017 and 2019). There also have been six adult female *I. texanus* found on two different martens in Ketchikan (2010 and 2019).

There were 21 *D. variabilis* records, comprising 21 ticks that have been found in the state between 2010–2019 either in the environment or on a host without recent reported travel history (Fig. 6). All of these were adults, and they were found across a wide area of the state, including southcentral, interior, southeast, and the West Aleutians. There were no boroughs where more than six individual ticks were found in a single year. Therefore, *D. variabilis* does not meet the criteria for establishment in Alaska based on available presence records as of 2019.

There were 25 *R. sanguineus* s.l. records, comprising 65 ticks that have been found in the state between 2010–2019 either in the environment or on a host without recent reported travel history (Fig. 6). They were found across a wide area of the state, including southcentral, interior, southeast, and southwest. In 2013, 47 *R. sanguineus* s.l. were found on four different hosts without recent travel history in Fairbanks North Star borough, including 46 adults and a single nymph. There were no other boroughs where more than six individual ticks or more than one life stage were found in a single year. Therefore, there is evidence to suggest that *R. sanguineus* s.l. is established in Fairbanks North Star borough, although additional records would strengthen this classification.

4. Discussion

Accurate and timely records of the distribution of tick species and host associations are critical for developing clinical, public health, and veterinary guidelines for tick-borne disease prevention. In areas where ticks are an emerging concern, surveillance efforts should focus on establishing a baseline for tick species distributions and guidelines for updating tick establishment maps regularly. In particular, areas at

Table 2

Number of records and ticks recorded in Alaska between 2010-2019 by species, host, and life stage.*.

Tick species with historical presence records in Alaska	Host	No. records	Adults	Nymphs	Larvae	Total ticks
<i>Haemaphysalis leporispalustris</i>	Domestic animal	5	2	12	8	22
	Human	1		1		1
	Wild mammal	21	862	10	5	877
	Wild bird	2			13	13
	Environment	0				0
	Unknown	0				0
<i>Ixodes angustus</i>	TOTAL	29	864	23	26	913
	Domestic animal	238	224	31	4	259
	Human	17	15	2		17
	Wild mammal	121	221	49	16	286
	Wild bird	0				0
	Environment	7	8			8
<i>Ixodes auritulus</i>	Unknown	5	5			5
	TOTAL	388	473	82	20	575
	Domestic animal	1	1			1
	Human	0				0
	Wild mammal	0				0
	Wild bird	1	1			1
<i>Ixodes signatus</i>	Environment	1	1			1
	Unknown	1	1			1
	TOTAL	4	4	0	0	4
	Domestic animal	0				0
	Human	0				0
	Wild mammal	0				0
<i>Ixodes uriae</i>	Wild bird	5	3	4	4	11
	Environment	0				0
	Unknown	0				0
	TOTAL	5	3	4	4	11
	Domestic animal	0				0
	Human	2	1	1		2
<i>Amblyomma americanum</i>	Wild mammal	0				0
	Wild bird	0				0
	Environment	1	1			1
	Unknown	0				0
	TOTAL	19	27	8	0	35
	Domestic animal	4	4			4
<i>Dermacentor andersoni</i>	Human	1	1			1
	Wild mammal	0				0
	Wild bird	0				0
	Environment	1	1			1
	Unknown	0				0
	TOTAL	6	6	0	0	6
<i>Dermacentor variabilis</i>	Domestic animal	36	37			37
	Human	16	15	1		16
	Wild mammal	0				0
	Wild bird	0				0
	Environment	2	2			2
	Unknown	1	1			1
<i>Ixodes pacificus</i>	TOTAL	55	55	1	0	56
	Domestic animal	3	3			3
	Human	0				0
	Wild mammal	0				0
	Wild bird	0				0
	Environment	0				0
<i>Ixodes ricinus</i>	Unknown	0				0
	TOTAL	3	3	0	0	3
	Domestic animal	3	3			3
	Human	1		1		1
	Wild mammal	0				0
	Wild bird	0				0
<i>Ixodes scapularis</i>	Environment	0				0
	Unknown	0				0
	TOTAL	4	3	1	0	4
	Domestic animal	7	11			11
	Human	3	2			2
	Wild mammal	0				0

(continued on next page)

Table 2 (continued)

Tick species with historical presence records in Alaska	Host	No. records	Adults	Nymphs	Larvae	Total ticks
<i>Ixodes texanus</i>	Wild bird	0	1			1
	Environment	1				0
	Unknown	0				0
	TOTAL	11	14	0	0	14
	Domestic animal	0				0
	Human	0				0
	Wild mammal	2	6			6
	Wild bird	0				0
	Environment	0				0
<i>Rhipicephalus sanguineus</i> s.l.	Unknown	0				0
	TOTAL	2	6	0	0	6
	Domestic animal	35	36			36
	Human	1	1			1
	Wild mammal	0				0
	Wild bird	0				0
	Environment	0				0
	Unknown	7	45	1		46
	TOTAL	43	82	1	0	83

*An additional 8 records (comprising 10 ticks: 3 *H. leporispalustris*, 2 *I. angustus*, 1 *D. variabilis*, 1 *I. scapularis*, and 3 *R. sanguineus* s.l.) that were missing life stage information were excluded from the life stage columns in this table. An additional 7 records (comprising 32 ticks) that were identified only to *Ixodes* genus and 2 records (comprising 45 ticks) that were identified only to *Haemaphysalis* genus were excluded from this table.

Northern latitudes that are experiencing rapid warming are most likely to see new tick species records and expanding ranges of ticks that are already established (Alfredsson et al., 2017; Gray et al., 2009; Jääskeläinen et al., 2010; Jaenson et al., 2016; Lindgren and Gustafson, 2001; Ogden et al., 2006a; Tokarevich et al., 2011).

The number of tick records in Alaska has increased substantially over the last decade, likely largely due to an increase in public awareness of ticks. Most of the tick submissions from the first year of the Alaska Submit-A-Tick Program were from the public, followed by veterinarians, and biologists. Targeted outreach to veterinary clinics and small mammal and bird biologists through e-mails and clinic visits with informational posters likely boosted submissions from these groups. Future outreach efforts could include clinical care providers, which may be the first point of contact for people who find a tick on their self or a family member or pet (Dantas-Torres et al., 2012). A higher proportion of non-native tick species were submitted in January and April, likely due to increased holiday and spring break travel outside of the state. Travel-related tick submissions occurred throughout the year, peaking in late spring and early summer. This has implications for targeting seasonal messaging about tick prevention and tick checks when traveling versus when to check for ticks while spending time outside in Alaska.

There are several tick species that have been found in Alaska, many of which have an unknown vector potential for human and animal pathogens. In addition, imported ticks entering the state on people and pets traveling from tick and tick-borne disease endemic regions are a substantial concern due to the possibility of establishing local

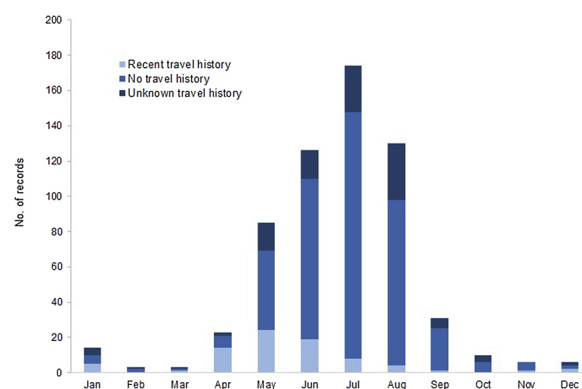


Fig. 5. Seasonality of travel-related tick submissions in Alaska between 2010-2019.

populations of these vectors. Relying solely on incidence of tick-borne disease in regions where ticks are an emerging concern will likely underestimate the risk of transmission due to lack of familiarity of these diseases among the clinicians. Enhanced surveillance for ticks and pathogen testing in collected ticks can provide an early indicator of changing tick and tick-borne pathogen distributions. While environmental surveillance through tick drag sampling or small mammal trapping is a more direct method for verifying tick establishment, we only collected two ticks through a full summer season of drag sampling. This is likely due to the low density of ticks, lack of phenological

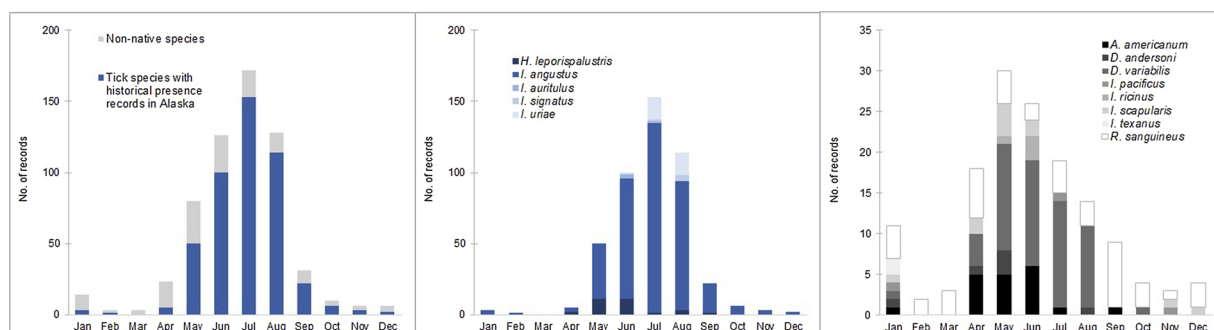


Fig. 4. Seasonality of tick records in Alaska between 2010-2019 (left panel: all tick records, middle panel: records of tick species that have historically been found in Alaska, right panel: non-native tick species records).

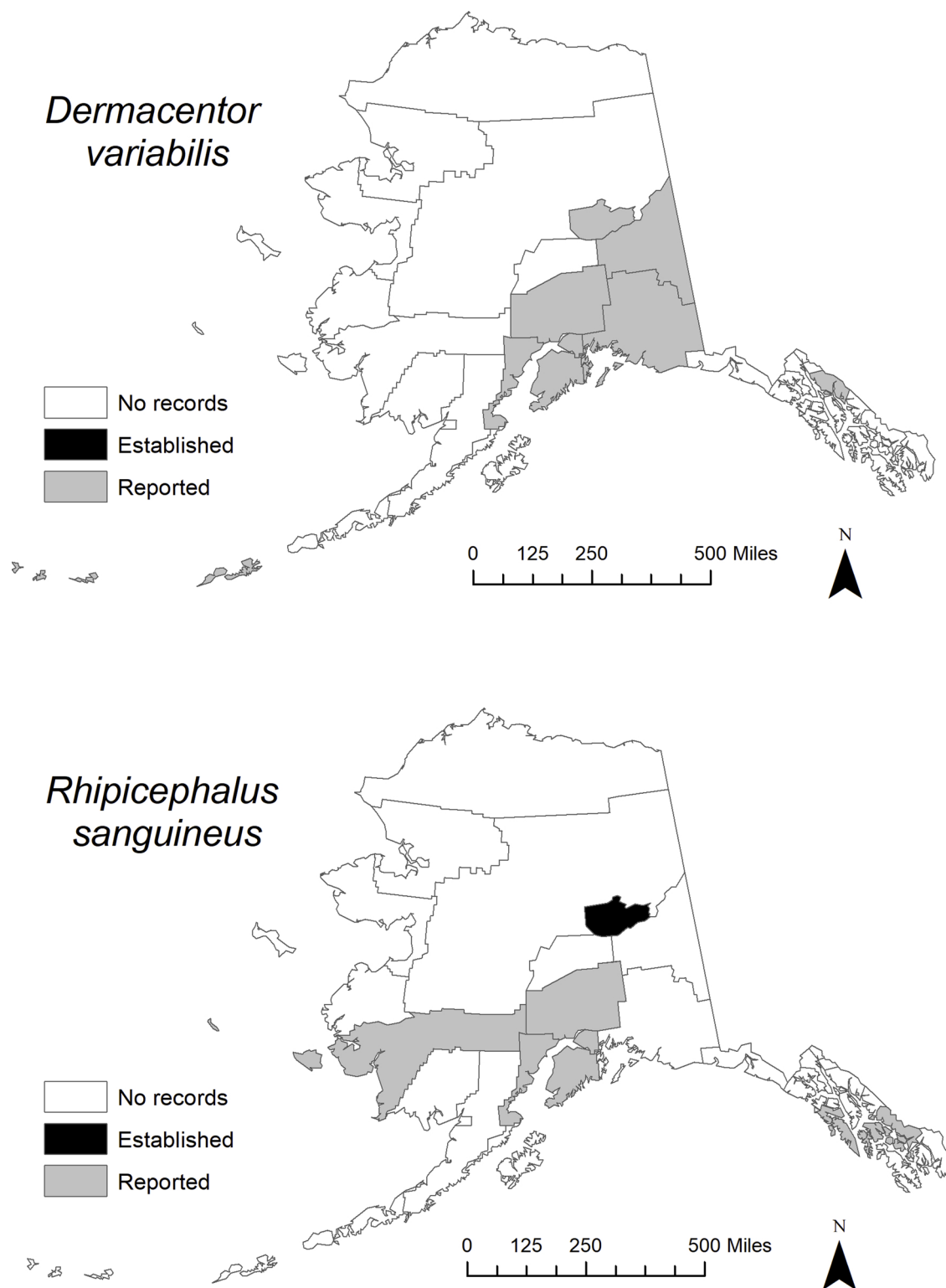


Fig. 6. Maps depicting boroughs where *D. variabilis* (top) and *R. sanguineus* s.l. (bottom) have been reported and are likely established. Only records where ticks were found in the environment or on a host without recent reported travel history are shown.

information for ticks in an Alaskan climate to time sampling efforts, and/or the nidicolous tendency of *I. angustus* (Foley et al., 2011). Passive surveillance through public tick submissions is a more cost-effective method to track a wide variety of ticks throughout a large region (Cull et al., 2018; Laaksonen et al., 2017; Nelder et al., 2014). In addition, passive surveillance records can identify potentially important sites for follow-up environmental surveillance. The records of *I.*

pacificus in Anchorage or *R. sanguineus* s.l. in Fairbanks on hosts without recent travel history point to key areas for enhanced surveillance. Continuous updates of maps that show reported and established tick populations throughout the state would likewise support targeted surveillance efforts (Eisen et al., 2016; Hahn et al., 2016).

Ixodes angustus, *H. leporispalustris*, and *I. uriae* were the most commonly reported tick species in this study. *Ixodes angustus* is reported

mostly in cool, Northern latitude areas (Robbins and Keirans, 1992), and has been found on a wide variety of mammalian hosts (Cooley, 1946b; Murrell et al., 2003; Robbins and Keirans, 1992; Sorensen and Moses, 1998; Spencer, 1963). Most of the host associations for these ticks in Alaska were in line with the published literature. Notably, a high proportion of *I. angustus* was found on domestic animals, which is uncommon for this nidicolous tick, which tends not to quest far from the host nest (Stephenson et al., 2016). This may represent a potential transmission route of tick-borne pathogens from sylvatic cycles to pets or humans. *Ixodes angustus* is capable of transmitting the causative bacterial agent of Lyme disease, *Borrelia burgdorferi* sensu stricto (Peavey et al., 2000), and there has been a documented case of Lyme disease in Washington state that was associated with this tick (Damrow et al., 1989). However, a study in California in areas where there was a high prevalence of infection with tick-borne pathogens in *I. pacificus* found that *I. angustus* was rarely infected (Stephenson et al., 2016). These authors suggest that *I. angustus* could play an important role in the ecology of zoonotic tick-borne disease by maintaining infection among small mammal hosts or as a vector to humans in areas lacking other vectors that more commonly bite humans. Given the widespread distribution of *I. angustus* in Alaska, its adaptation to cool weather climates, and the propensity of the tick to feed on a wide variety of hosts, it may be an important, understudied tick in the region. In coastal Alaska, there is evidence of *Babesia microti* transmission to rodents by *I. angustus* suggesting its role as a vector of bacterial pathogens (Goethert et al., 2006). *Ixodes uriae* is the only hard tick (Ixodidae) with both an Arctic and Antarctic circumpolar distribution (Dietrich et al., 2012, 2011; Muñoz-Leal and González-Acuña, 2015). It parasitizes over 60 different seabird species, the majority of which roost in colonies (Dietrich et al., 2012, 2011). *Ixodes uriae* has extreme cold hardiness and exploits seabird nesting sites as an additional microhabitat refuge (Lee and Baust, 1987; Muñoz-Leal and González-Acuña, 2015). This tick harbors a variety of viral and bacterial pathogens (Muñoz-Leal and González-Acuña, 2015), and there is evidence to suggest that seabirds may be an important reservoir and means of transport for pathogens across hemispheres (Dietrich et al., 2011; Olsen et al., 1995).

Although *I. texanus* was presented here as a non-native tick, it is possible that it has been present in Alaska historically. *Ixodes texanus* has been collected in large numbers on wildlife in Michigan and Ontario, Canada (Hamer et al., 2010; Smith et al., 2019). Information on its life history, distribution, and role as a vector of tick-borne pathogens is sparse, but this tick species has historically been found in southern British Columbia, Canada (Cooley and Kohls, 1945; Keirans and Clifford, 1978; Lindquist et al., 2016). Similarly, although *I. auritulus* and *I. howelli* have historically been found in Alaska, it is difficult to say whether these ticks have long-term established populations due to the small number of presence records. *Ixodes auritulus* was found on three different avian host species, in three different locations, in 1945, 1946, and 1953, providing evidence of a local population. There was only one record of *I. howelli* in the state from 1963 which merely alludes to the presence of this tick and does not provide sufficient information to conclude that there are local populations of *I. howelli*, only that this tick has historically been found in the area.

The most commonly imported non-native ticks were *A. americanum*, *D. variabilis*, and *R. sanguineus* s.l. In order for these ticks to establish local populations in Alaska, an adventitious gravid female would need to fall off the host and lay eggs in the environment (or inside for *R. sanguineus*) that hatch into larvae. Alternatively, either multiple immature ticks (larvae or nymphs) or both male and female adventitious ticks could arrive in the state on a single host. Migratory birds entering Alaska are a likely source of tick importation (Cohen et al., 2015; Morshed et al., 2005; Ogden et al., 2008). The lifecycle of each of these three-host hard ticks varies slightly in terms of seasonality, but in general, either the adult female, eggs, or newly hatched larvae would need to overwinter. Two ecological niche modeling studies of *A. americanum* under future climate scenarios show northward expansion

of the tick, which has historically been limited to regions east of the 100th western meridian and south of the 45th northern parallel (Raghavan et al., 2019; Springer et al., 2015). Under an extreme emissions scenario, small pockets of high model agreement show potentially climatically suitable habitat on the margins of Western Canada and on the Kenai and Alaska Peninsulas in the late 21st century (Raghavan et al., 2019). Establishment of this species under present-day climate is unlikely. Recent climate suitability modeling for *D. variabilis* shows a substantial shift of the potential range of the tick into north-west Canada by 2050 under low to extreme emissions scenarios (Minigan et al., 2018). Our results show that *D. variabilis* has been reported in interior, southcentral, and southeastern Alaska. This tick may currently be limited by cold winter temperatures in much of the state, but sufficient insulating snowpack could provide a suitable microclimate for overwintering (McEnroe, 1984; Yunik et al., 2015). Continued surveillance for this tick species is warranted. *Rhipicephalus sanguineus* s.l. has historically spread from its native Afrotropical distribution, mostly on domestic dogs, and now has a vast worldwide range extending from about 50°N to 30°S (Walker et al., 2000). This tick can survive indoors and has been shown to complete one-host or three-host life cycles, demonstrating its ability to adapt to a variety of living conditions (Dantas-Torres, 2010). Here we show evidence that *R. sanguineus* s.l. is likely established in Alaska based on tick presence records. Although this tick species met the broad establishment criteria used here, it is important to note that these data likely represent local infestations in households that could be controlled with targeted acaricide treatment to prevent the broader establishment of *R. sanguineus* s.l. populations.

Our study shows that three medically important *Ixodes* spp. ticks have been found in Alaska: *I. scapularis*, *I. pacificus*, and *I. ricinus*. Importation of these species will likely continue, particularly of the two blacklegged ticks (*I. scapularis* and *I. pacificus*) due to frequent human and pet travel between Alaska and endemic areas in the continental United States and Canada (Mak et al., 2010). In addition to climate considerations, suitable land cover and reservoir hosts for each stage of their lifecycle are also pre-requisites for establishment of newly introduced ticks. *Ixodes pacificus* has been collected from British Columbia, near the Alaskan border (Mak et al., 2010), and *I. ricinus* is widely distributed across Europe and has been expanding into high latitude areas of Sweden and Iceland (Alfredsson et al., 2017; Medlock et al., 2013; Talleklint and Jaenson, 1998), indicating that the Alaskan climate is likely not a limiting factor for these tick species. Many of the coastal regions of Alaska have a mild, humid climate with less extreme winter temperatures than areas in the interior U.S. and Canada where *I. scapularis* is established (Brunner et al., 2012; Robbin Lindsay et al., 1995). In general, *Ixodes* tick habitat is characterized by forested areas with leaf litter or vegetation with sufficient humidity to prevent tick desiccation (Diuk-Wasser et al., 2010; Killilea et al., 2008; Medlock et al., 2013; Talleklint-Eisen and Lane, 2000). While much of Alaska's forests are boreal, almost seven percent of the state's 1.7 million km² of land area is classified as deciduous or mixed forest (Selkowitz and Stehman, 2011). Immature stages of *Ixodes* ticks tend to feed on small mammals and birds and rely on larger wildlife for bloodmeals in their adult stage (Gray, 1998). Although deer are an important host for *I. scapularis* and *I. ricinus* adults in areas where these ticks are currently endemic (Rand et al., 2003; Sprong et al., 2018), large wildlife such as bears, moose, lynx, and coyotes in Alaska may serve as a sufficient bloodmeal source for this life stage (Bloemer and Zimmerman, 1988; Brillhart et al., 1994; Castro and Wright, 2007; Zolnik et al., 2015). Of note, these wildlife species are found in urban areas throughout the state that abut vast regions of wilderness, indicating the possibility of overlap between areas where ticks are most frequently imported due to human and pet travel and native wildlife populations.

Although the results presented here represent the most comprehensive assessment of ticks in Alaska to date, there are important limitations to the interpretation of these data. We relied on the accuracy of

the historical records retrieved from databases and published literature. In many cases, historical tick records were submitted by biologists who found ticks incidentally during their fieldwork. We assume that they either had familiarity with tick species identification methods or collaborated with an entomologist to identify their specimens. While the contemporary public submissions were morphologically identified by an entomologist/acarologist using standard guides, it is possible that people submitted incorrect ancillary information, such as the location of collection, date, or recent travel history of the host. In cases where there was missing or confusing information on a tick submission form, we followed up with a phone call to the submitter to clarify.

All records presented here except for the two ticks collected on tick drags in summer 2019 were obtained through voluntary submissions. These data must be interpreted cautiously. In some cases, similar tick passive surveillance programs have found that the number of samples they receive is related to the distribution of potential reporters, i.e. they receive more ticks from highly populated areas, and fewer ticks from regions that are more sparsely populated (Laaksonen et al., 2017; Nelder et al., 2014). On the other hand, the Tick Surveillance Scheme in the United Kingdom found that they received the highest number of *I. ricinus* samples from the region of England with the lowest population density, implying that the tick records are not biased towards areas of high human population density and may be a reasonable indicator of the tick distribution (Cull et al., 2018). In the present study, the origin of most tick submissions was near major population centers, particularly those specimens associated with recent travel history of the host. The key point is that a region that does not have any tick presence records may not be devoid of ticks. This highlights the importance of outreach to rural communities in Alaska about ticks, particularly because of the prevalence of hunting and trapping in these areas. Conversely, it should be noted that the opposite is also true – the presence of a tick in the state does not necessarily represent an expansion of its range. In the context of the Alaska Submit-A-Tick Program, many of the submitted ticks were associated with recent travel of the host outside of the state. We relied on self-reported travel history for all members of the household, which may lead to misclassification of a locally-acquired tick. But even among those ticks submitted that were accurately classified as locally-acquired, individual tick records may represent adventitious ticks that were transported by migratory birds into the state (Ogden et al., 2006c) that will not be able to survive due to lack of suitable vegetation, hosts, or climatic limitations as discussed above. Nonetheless, data collected through the passive surveillance program may serve as an early indicator of the introduction and potential for establishment of medically-important tick species in Alaska, particular as climate change continues to make temperatures more suitable for tick survival.

We found no records of *Dermacentor albipictus*, the winter tick, in this study. This tick has been found in western Canada (Leo et al., 2014) and has caused severe morbidity and mortality in moose in the north-eastern United States (Jones et al., 2019). A decrease in the Alaskan moose population would negatively impact an important food resource for many residents, particularly those living in rural areas who collectively harvest approximately 70 pounds of wild game meat per capita each year (Fall, 2016). Outreach to hunters and trappers with information on where to look for ticks on a variety of mammalian wildlife such as moose, wolves, foxes, bears, and caribou may provide an early warning of newly imported tick species.

By combining tick presence records from multiple data sources, we have established a baseline from which to track the range expansion of ticks in Alaska. Despite the limitations of passive surveillance, it will likely be the most resource-effective method for continued tick monitoring in the state. Given the rapid rate of climatic change in Arctic and sub-Arctic regions, and evidence of tick spread in other northern regions, it is likely that the tick population in Alaska will continue to change. Proactive, consistent monitoring and increasing tick awareness among clinicians and residents, particularly pet owners and those

traveling out of state, are important public health activities in areas where ticks are an emerging concern. Collaborative surveillance and education programs that involve public health, human medicine, veterinary, and wildlife expertise and agencies can be an effective model for simultaneously, and synergistically, protecting human and animal health.

CRediT authorship contribution statement

Micah B. Hahn: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization, Supervision, Project administration, Funding acquisition. **Gale Disler:** Investigation, Data curation, Writing - review & editing. **Lance A. Durden:** Investigation, Writing - review & editing. **Sarah Coburn:** Resources, Data curation, Writing - review & editing. **Frank Witmer:** Software, Visualization. **William George:** Investigation, Data curation. **Kimberlee Beckmen:** Conceptualization, Resources, Writing - review & editing. **Robert Gerlach:** Conceptualization, Resources, Writing - review & editing.

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References

- Alfredsson, M., Olafsson, E., Eydal, M., Unnsteinsdottir, E.R., Hansford, K., Wint, W., Alexander, N., Medlock, J.M., 2017. Surveillance of *Ixodes ricinus* ticks (Acari: Ixodidae) in Iceland. *Parasit. Vectors* 10, 466. <https://doi.org/10.1186/s13071-017-2375-2>.
- Bloemer, S.R., Zimmerman, R.H., 1988. Ixodid ticks on the coyote and gray fox at land between the lakes, Kentucky-Tennessee, and implications for tick dispersal. *J. Med. Entomol.* 25, 5–8. <https://doi.org/10.1093/jmedent/25.1.5>.
- Brillhart, D.B., Fox, L.B., Upton, S.J., 1994. Ticks (Acari: ixodidae) collected from small and medium-sized Kansas mammals. *J. Med. Entomol.* 31, 500–504. <https://doi.org/10.1093/jmedent/31.3.500>.
- Brinton, E., Beck, D., Allred, D., 1965. Identification of the adults, nymphs and larvae of ticks of the genus *Dermacentor* Koch (Ixodidae) in the western United States. *Biol. Ser.* 5.
- Brunner, J.L., Killilea, M., Ostfeld, R.S., 2012. Overwintering survival of nymphal *Ixodes scapularis* (Acari: ixodidae) under natural conditions. *J. Med. Entomol.* 49, 981–987. <https://doi.org/10.1603/me12060>.
- Castro, M.B., Wright, S., 2007. Vertebrate hosts of *Ixodes pacificus* (Acari: ixodidae) in California. *J. Vector Ecol.* 32, 140–149. [https://doi.org/10.3376/1081-1710\(2007\)32](https://doi.org/10.3376/1081-1710(2007)32).
- Choe, J., Kim, K., 1987. Community structure of arthropod ectoparasites on Alaskan seabirds. *Can. J. Zool.* 65, 2998–3005. <https://doi.org/10.1139/z87-454>.
- Cohen, E.B., Auckland, L.D., Marra, P.P., Hamer, S.A., 2015. Avian migrants facilitate invasions of neotropical ticks and tick-borne pathogens into the United States. *Appl. Environ. Microbiol.* 81, 8366–8378. <https://doi.org/10.1128/AEM.02656-15>.
- Cooley, R., 1946a. The genera *Boophilus*, *Rhipicephalus*, and *Haemaphysalis* (Ixodidae) of the New World. *Natl. Inst. Heal. Bull.* 187.
- Cooley, R., 1946b. Note on the tick, *Ixodes angustus* Neumann. *J. Parasitol.* 32, 210. <https://doi.org/10.2307/3272601>.
- Cooley, R., Kohls, G., 1944. The genus *Amblyomma* (Ixodidae) in the United States. *J. Parasitol.* 30, 77–111. <https://doi.org/10.2307/3272571>.
- Cooley, R., Kohls, G., 1945. The Genus *Ixodes* in North America. US Government Printing

- Office.
- Cull, B., Pletzsch, M.E., Hansford, K.M., Gillingham, E.L., Medlock, J.M., 2018. Surveillance of British ticks: An overview of species records, host associations, and new records of *Ixodes ricinus* distribution. *Ticks Tick. Dis.* 9, 605–614. <https://doi.org/10.1016/j.ttbdis.2018.01.011>.
- Damrow, T., Freedman, S.H., Washington, R., Lane, R.S., California, B., Preston, K.L., Redmond, W., 1989. Is *Ixodes (Ixodopsis) angustus* a vector of Lyme disease in Washington state? *West. J. Med.* 150, 580–582.
- Dantas-Torres, F., 2010. Biology and ecology of the brown dog tick, *Rhipicephalus sanguineus*. *Parasit. Vectors* 3, 26. <https://doi.org/10.1186/1756-3305-3-26>.
- Dantas-Torres, F., Chomel, B.B., Otranto, D., 2012. Ticks and tick-borne diseases: a one Health perspective. *Trends Parasitol.* 28, 437–446. <https://doi.org/10.1016/J.PT.2012.07.003>.
- Deardorff, E.R., Nofchissey, R.A., Cook, J.A., Hope, A.G., Tsvetkova, A., Talbot, S.L., Ebel, G.D., 2013. Powassan virus in mammals, Alaska and new mexico, USA, and Russia, 2004–2007. *Emerg. Infect. Dis.* 19.
- Dennis, D.T., Nekomoto, T.S., Victor, J.C., Paul, W.S., Piesman, J., 1998. Reported distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: ixodidae) in the United States. *J. Med. Entomol.* 35, 629–638.
- Dietrich, M., Gómez-Díaz, E., McCoy, K.D., 2011. Worldwide distribution and diversity of seabird ticks: implications for the ecology and epidemiology of tick-borne pathogens. *Vector-Borne Zoonotic Dis.* 11, 453–470. <https://doi.org/10.1089/vbz.2010.0009>.
- Dietrich, M., Kempf, F., Gómez-Díaz, E., Kitaysky, A.S., Hipfner, J.M., Boulenger, T., McCoy, K.D., 2012. Inter-oceanic variation in patterns of host-associated divergence in a seabird ectoparasite. *J. Biogeogr.* 39, 545–555. <https://doi.org/10.1111/j.1365-2699.2011.02620.x>.
- Diuk-Wasser, M.A., Vourc'h, G., Cislo, P., Hoen, A.G., Melton, F., Hamer, S.A., Rowland, M., Cortinas, R., Hickling, G.J., Tsao, J.I., Barbour, A.G., Kitron, U., Piesman, J., Fish, D., 2010. Field and climate-based model for predicting the density of host-seeking nymphal *Ixodes scapularis*, an important vector of tick-borne disease agents in the eastern United States. *Glob. Ecol. Biogeogr.* 19, 504–514. <https://doi.org/10.1111/j.1466-8238.2010.00526.x>.
- Durden, L.A., Keirans, J.E., 1996. Nymphs of the Genus *Ixodes* (Acari: Ixodidae) of the United States: Taxonomy, Identification Key, Distribution, Hosts, and medical/veterinary Importance, Monographs of the Thomas Say Foundation. Entomological Society of America, Lanham, MD.
- Durden, L.A., Beckmen, K.B., Gerlach, R.F., 2016. New records of ticks (Acari: ixodidae) from dogs, cats, humans, and some wild vertebrates in Alaska: invasion potential. *J. Med. Entomol.* 53, 1391–1395. <https://doi.org/10.1093/jme/tjw128>.
- Eisen, R.J., Eisen, L., Beard, C., 2016. County-scale distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: ixodidae) in the continental United States. *J. Med. Entomol.* 53, 349–386.
- Estrada-Peña, A., Mihalca, A., Petney, T., 2017. Ticks of Europe and North Africa: a Guide to Species Identification. Springer International Publishing, Cham, Switzerland. <https://doi.org/10.1007/978-3-319-63760-0>.
- Fall, J.A., 2016. Regional patterns of fish and wildlife harvests in contemporary Alaska. *Arctic* 69, 47–64.
- Fay, F., Rausch, R., 1969. Parasitic organisms in the blood of Arvicoline rodents in Alaska. *J. Parasitol.* 55, 1258–1265.
- Foley, J., Rejmanek, D., Fleer, K., Nieto, N., 2011. Nidicolous ticks of small mammals in *Anaplasma phagocytophilum*-enzootic sites in northern California. *Ticks Tick. Dis.* 2, 75–80. <https://doi.org/10.1016/j.ttbdis.2011.03.003>.
- Goethert, H., Cook, J., Lance, E., Telford, S., 2006. Fay and Rausch 1969 revisited: *Babesia microti* in Alaskan small mammals. *J. Parasitol.* 92, 826–831.
- Gray, J.S., 1998. The ecology of ticks transmitting Lyme borreliosis. *Exp. Appl. Acarol.* 22, 249–258. <https://doi.org/10.1023/A:1006070416135>.
- Gray, J.S., Dautel, H., Estrada-Peña, A., Kahl, O., Lindgren, E., 2009. Effects of climate change on ticks and tick-borne diseases in Europe. *Interdiscip. Perspect. Infect. Dis.* 1–12. <https://doi.org/10.1155/2009/593232>.
- Hahn, M.B., Jarnevich, C.S., Monaghan, A.J., Eisen, R.J., 2016. Modeling the geographic distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: ixodidae) in the contiguous United States. *J. Med. Entomol.* 53, 1176–1191.
- Hamer, S.A., Tsao, J.I., Walker, E.D., Hickling, G.J., 2010. Invasion of the Lyme disease vector *Ixodes scapularis*: implications for *Borrelia burgdorferi* endemicity. *Ecohealth* 7, 47–63. <https://doi.org/10.1007/s10393-010-0287-0>.
- Jääskeläinen, A.E., Sironen, T., Murueva, G.B., Subbotina, N., Alekseev, A.N., Castrén, J., Alitalo, I., Vaheri, A., Vapalahti, O., 2010. Tick-borne encephalitis virus in ticks in Finland, Russian Karelia and Buryatia. *J. Gen. Virol.* 91, 2706–2712. <https://doi.org/10.1099/vir.0.023663-0>.
- Jaenson, T.G.T., Värvi, K., Fröjdman, I., Jääskeläinen, A., Rundgren, K., Versteirt, V., Estrada-Peña, A., Medlock, J.M., Golovljova, I., 2016. First evidence of established populations of the taiga tick *Ixodes persulcatus* (Acari: Ixodidae) in Sweden. *Parasit. Vectors* 9, 377. <https://doi.org/10.1186/s13071-016-1658-3>.
- Johnson, J., Ginsberg, H.S., Zhou, E., Whitworth, U., Markowski, D., Hyland, K., Hu, R., 2004. Passive tick surveillance, dog seropositivity, and incidence of human Lyme disease. *Vector-borne Zoonotic Dis.* 4, 137–142.
- Jones, H., Pekins, P., Kantar, L., Sidor, I., Ellingwood, D., Lichtenwalner, A., O'Neal, M., 2019. Mortality assessment of moose (*Alces alces*) calves during successive years of winter tick (*Dermacentor albipictus*) epizootics in New Hampshire and Maine (USA). *Can. J. Zool.* 97, 22–30. <https://doi.org/10.1139/cjz-2018-0140>.
- Keirans, J., Clifford, C., 1978. The genus *Ixodes* in the United States: A scanning electron microscope study and key to the adults. *J. Med. Entomol.* 15 (Suppl.2), 1–38. <https://doi.org/10.1093/jmedent/15.suppl2.1>.
- Killilea, M.E., Swei, A., Lane, R.S., Briggs, C.J., Ostfeld, R.S., 2008. Spatial dynamics of Lyme disease: a review. *Ecohealth* 5, 167–195. <https://doi.org/10.1007/s10393-008-0171-3>.
- Laaksonen, M., Sajanti, E., Sormunen, J.J., Penttinen, R., Hänninen, J., Ruohomäki, K., Sääksjärvi, I., Vesterinen, E.J., Vuorinen, I., Hytönen, J., Klemola, T., 2017. Crowdsourcing-based nationwide tick collection reveals the distribution of *Ixodes ricinus* and *I. persulcatus* and associated pathogens in Finland. *Emerg. Microbes Infect.* 6, 1–7. <https://doi.org/10.1038/emi.2017.17>.
- Lee Jr, R., Baust, J., 1987. Cold-hardiness in the Antarctic tick, *Ixodes uriae*. *Physiol. Zool.* 60, 499–506.
- Lehane, A., Parise, C., Evans, C., Beati, L., Nicholson, W.L., Eisen, R.J., 2020. Reported county-level distribution of the American dog tick (Acari: ixodidae) in the contiguous United States. *J. Med. Entomol.* 57, 131–155. <https://doi.org/10.1093/jme/tjz119>.
- Leo, S.S.T., Samuel, W.M., Pybus, M.J., Sperling, F.A.H., 2014. Origin of *Dermacentor albipictus* (Acari: ixodidae) on elk in the Yukon. Canada. *J. Wildl. Dis.* 50, 544–551. <https://doi.org/10.7589/2013-03-078>.
- Lindgren, E., Gustafson, R., 2001. Tick-borne encephalitis in Sweden and climate change. *Lancet* 358, 16–18. [https://doi.org/10.1016/S0140-6736\(00\)05250-8](https://doi.org/10.1016/S0140-6736(00)05250-8).
- Lindquist, E.E., Galloway, T.D., Artsob, H., Lindsay, L.R., Drebot, M., Wood, H., Robbins, R.G., 2016. A handbook to the ticks of Canada. *Biol. Survey of Canada Monograph Series*.
- Mak, S., Morshed, M., Henry, B., 2010. Ecological niche modeling of Lyme disease in British Columbia. Canada. *J. Med. Entomol.* 47, 99–105. <https://doi.org/10.1603/033.047.0114>.
- Markon, C., Gray, S., Berman, M., Eerkes-Medrano, L., Hennessy, T., Huntington, H.P., Littell, J., McCammon, M., Thoman, R., Trainor, S.F., 2018. Chapter 26 : Alaska. Impacts, Risks, and Adaptation in the United States: The Fourth National Climate Assessment, Volume II. Washington, DC. <https://doi.org/10.7930/NCA4.2018.CH26>.
- McEnroe, W., 1984. The effect of snowcover on an American Dog Tick, *Dermacentor variabilis* (say) (Acari, Ixodidae) population under a harsh winter environment. *J. Appl. Entomol.* 97, 481–484. <https://doi.org/10.1111/j.1439-0418.1984.tb03778.x>.
- Medlock, J.M., Hansford, K.M., Bormane, A., Derdakova, M., Estrada-Peña, A., George, J.-C., Golovljova, I., Jaenson, T.G., Jensen, J.-K., Jensen, P.M., Kazimirova, M., Oteo, C.A., Papa, A., Pfister, K., Plantard, O., Randolph, S.E., Rizzoli, A., Santos-Silva, M.M., Sprong, H., Vial, L., Hendrickx, G., Zeller, H., Van Bortel, W., 2013. Driving forces for changes in geographical distribution of *Ixodes ricinus* ticks in Europe. *Parasit. Vectors* 6, 1. <https://doi.org/10.1186/1756-3305-6-1>.
- Minigan, J.N., Hager, H.A., Peregrine, A.S., Newman, J.A., 2018. Current and potential future distribution of the American Dog Tick (*Dermacentor variabilis*, say) in North America. *Ticks Tick. Dis.* 9, 354–362. <https://doi.org/10.1016/j.ttbdis.2017.11.012>.
- Morshed, M.G., Scott, J.D., Fernando, K., Beati, L., Mazerolle, D.F., Geddes, G., Durden, L.A., Fernandez, K., Beati, L., Geddes, G., Durden, L.A., 2005. Migratory songbirds disperse ticks across Canada, and first isolation of the Lyme disease spirochete, *Borrelia burgdorferi*, from the avian tick, *Ixodes auritulus*. *J. Parasitol.* 91, 780–790.
- Muñoz-Leal, S., González-Acuña, D., 2015. The tick *Ixodes uriae* (Acari: ixodidae): hosts, geographical distribution, and vector roles. *Ticks Tick. Dis.* 6, 843–868. <https://doi.org/10.1016/j.ttbdis.2015.07.014>.
- Murrell, B.P., Durden, L.A., Cook, J.A., 2003. Host associations of the tick, *Ixodes angustus* (Acari: ixodidae), on Alaskan mammals. *J. Med. Entomol.* 40, 682–685.
- Nelder, M.P., Russell, C., Lindsay, L.R., Dhar, B., Patel, S.N., Johnson, S., Moore, S., Kristjansson, E., Li, Y., Ralevski, F., 2014. Population-based passive tick surveillance and detection of expanding foci of blacklegged ticks *Ixodes scapularis* and the Lyme disease agent *Borrelia burgdorferi* in Ontario, Canada. *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0105358>.
- Ogden, N.H., Maarouf, A., Barker, I.K., Bigras-Poulin, M., Lindsay, L.R., Morshed, M.G., O'Callaghan, C.J., Ramay, F., Walther-Toews, D., Charron, D.F., 2006a. Climate change and the potential for range expansion of the Lyme disease vector *Ixodes scapularis* in Canada. *Int. J. Parasitol.* 36, 63–70. <https://doi.org/10.1016/j.ijpara.2005.08.016>.
- Ogden, N.H., Trudel, L., Artsob, H., Barker, I.K., Beauchamp, G., Charron, D.F., Drebot, M.A., Galloway, T.D., O'handley, R., Thompson, R.A., Lindsay, L.R., 2006b. Ticks collected by passive surveillance in Canada: analysis of geographic distribution and infection with Lyme borreliosis agent *Borrelia burgdorferi*. *J. Med. Entomol.* 43, 600–609. <https://doi.org/10.1093/jmedent/43.3.600>.
- Ogden, N.H., Trudel, L., Artsob, H., Barker, I.K., Beauchamp, G., Charron, D.F., Drebot, M.A., Galloway, T.D., O'handley, R., Thompson, R.A., Lindsay, L.R., 2006c. *Ixodes scapularis* ticks collected by passive surveillance in Canada: analysis of geographic distribution and infection with Lyme borreliosis agent *Borrelia burgdorferi*. *J. Med. Entomol.* 43, 600–609. <https://doi.org/10.1093/jmedent/43.3.600>.
- Ogden, N.H., Lindsay, L.R., Hanincová, K., Barker, I.K., Bigras-Poulin, M., Charron, D.F., Heagy, A., Francis, C.M., O'Callaghan, C.J., Schwartz, I., Thompson, R.A., 2008. Role of migratory birds in introduction and range expansion of *Ixodes scapularis* ticks and of *Borrelia burgdorferi* and *Anaplasma phagocytophilum* in Canada. *Appl. Environ. Microbiol.* 74, 1780–1790. <https://doi.org/10.1128/AEM.01982-07>.
- Olsen, B., Duffy, D., Jaenson, T., Gylfe, A., Bonnedahl, J., Bergstrom, S., 1995. Transhemispheric exchange of Lyme disease spirochetes by seabirds. *J. Clin. Microbiol.* 33, 3.
- Peavey, C.A., Lane, R.S., Damrow, T., 2000. Vector competence of *Ixodes angustus* (Acari: ixodidae) for *Borrelia burgdorferi* sensu stricto. *Exp. Appl. Acarol.* 24, 77–84.
- Philip, C.B., 1938. A parasitological reconnaissance in Alaska with particular reference to varying hares. *J. Parasitol.* 24, 483–488.
- Raghavan, R.K., Townsend Peterson, A., Cobos, M.E., Ganta, R., Foley, D., 2019. Current and future distribution of the Lone Star Tick, *Amblyomma americanum* (L.) (Acari: Ixodidae) in North America. *PLoS One* 14. <https://doi.org/10.1371/journal.pone.0209082>.
- Rand, P.W., Lubelczyk, C., Lavigne, G.R., Elias, S., Holman, M.S., Lacombe, E.H., Smith, R.P., 2003. Deer density and the abundance of *Ixodes scapularis* (Acari: ixodidae). *J. Med. Entomol.* 40, 179–184. <https://doi.org/10.1603/0022-2585-40.2.179>.

- Rand, P.W., Lacombe, E.H., Dearborn, R., Cahill, B., Elias, S., Lubelczyk, C.B., Beckett, G.A., Smith, R.P., 2017. Passive surveillance in Maine, an area emergent for tick-borne diseases. *Vector-borne Dis. Surveillance, Prev.* 44, 1118–1129.
- Robbin Lindsay, L., Barker, I.K., Surgeoner, G., McEwen, S.A., Gillespie, T., Robinson, J., 1995. Survival and development of *Ixodes scapularis* (Acari: ixodidae) under various climatic conditions in Ontario, Canada. *J. Med. Entomol.* 32, 143–152. <https://doi.org/10.1093/jmedent/32.2.143>.
- Robbins, R., Keirans, J., 1992. Systematics and Ecology of the Subgenus *Ixodiopsis* (Acari: Ixodidae: ixodes), Monographs of the Thomas Say Foundation. Entomological Society of America, Lanham, MD.
- Selkowitz, D.J., Stehman, S.V., 2011. Thematic accuracy of the National Land Cover Database (NLCD) 2001 land cover for Alaska. *Remote Sens. Environ.* 115, 1401–1407. <https://doi.org/10.1016/j.rse.2011.01.020>.
- Smith, K.A., Oesterle, P.T., Jardine, C.M., Dibbernardo, A., Huynh, C., Lindsay, R., Pearl, D.L., Nemeth, N.M., 2019. Tick infestations of wildlife and companion animals in Ontario, Canada, with detection of human pathogens in *Ixodes scapularis* ticks. *Ticks Tick. Dis.* 10, 72–76. <https://doi.org/10.1016/j.ttbdis.2018.08.018>.
- Sorensen, T.C., Moses, R.A., 1998. Host preferences and temporal trends of the tick *Ixodes angustus* in North-Central Alberta. *J. Parasitol.* 84, 902–906. <https://doi.org/10.2307/3284617>.
- Spencer, G., 1963. Attacks on humans by *Ixodes angustus* Neumann, the coast squirrel tick, and *I. Soricis* Gregson, the shrew tick. *J. Entomol. Soc.* 60.
- Springer, Y.P., Jarnevich, C.S., Barnett, D.T., Monaghan, A.J., Eisen, R.J., 2015. Modeling the present and future geographic distribution of the Lone Star Tick, *Amblyomma americanum* (Ixodida: ixodidae), in the continental United States. *Am. J. Trop. Med. Hyg.* 93, 875–890. <https://doi.org/10.4269/ajtmh.15-0330>.
- Sprong, H., Azagi, T., Hoomstra, D., Nijhof, A.M., Knorr, S., Baarsma, M.E., Hovius, J.W., 2018. Control of Lyme borreliosis and other *Ixodes ricinus*-borne diseases. *Parasit. Vectors.* <https://doi.org/10.1186/s13071-018-2744-5>.
- Stephenson, N., Wong, J., Foley, J., 2016. Host, habitat and climate preferences of *Ixodes angustus* (Acari: ixodidae) and infection with *Borrelia burgdorferi* and *Anaplasma phagocytophilum* in California. USA. *Exp. Appl. Acarol.* 70, 239–252. <https://doi.org/10.1007/s10493-016-0068-8>.
- Talleklint, L., Jaenson, T.G.T., 1998. Increasing geographical distribution and density of *Ixodes ricinus* (Acari: Ixodidae) in Central and Northern Sweden. *J. Med. Entomol.* 35, 521–526. <https://doi.org/10.1093/jmedent/35.4.521>.
- Talleklint-Eisen, L., Lane, R.S., 2000. Spatial and temporal variation in the density of *Ixodes pacificus* (Acari: ixodidae) nymphs. *Environ. Entomol.* 29, 272–280. <https://doi.org/10.1093/ee/29.2.272>.
- Tokarevich, N.K., Tronin, A.A., Blinova, O.V., Buzinov, R.V., Boltenkov, V.P., Yurasova, E.D., Nurse, J., Tokarevich, N.K., Tronin, A.A., Blinova, O.V., Buzinov, R.V., 2011. The impact of climate change on the expansion of *Ixodes persulcatus* habitat and the incidence of tick-borne encephalitis in the north of European Russia. *Glob. Health Action* 4, 9448. <https://doi.org/10.3402/gha.v4i0.8448>.
- Walker, J., Keiran, J., Horak, I., 2000. The Genus *Rhipicephalus* (Acari, Ixodidae): A Guide to the Brown Ticks of the World. Cambridge University Press, Cambridge, UK.
- Yamaguti, N., Tipton, V.J., Keegan, H.L., Toshioka, S., 1971. Ticks of Japan, Korea, and the Ryukyu Islands. Brigham Young University Science Bulletin.
- Yoder, S., Deglin, S., Pachoe, M., Hamade, A., Anderson, P., Springer, Y., McLaughlin, J., Castrodale, L., 2018. Assessment of the potential health impacts of climate change in Alaska. *State Alaska, Epidemiol. Bull.* 20.
- Yunik, M.E.M., Galloway, T.D., Lindsay, L.R., 2015. Ability of unfed *Dermacentor variabilis* (Acari: ixodidae) to survive a second winter as adults in Manitoba, Canada, near the northern limit of their range. *J. Med. Entomol.* 52, 138–142. <https://doi.org/10.1093/jme/tju061>.
- Zolnik, C.P., Makkay, A.M., Falco, R.C., Daniels, T.J., 2015. American black bears as hosts of blacklegged ticks (Acari: Ixodidae) in the northeastern United States. *J. Med. Entomol.* 52, 1103–1110. <https://doi.org/10.1093/jme/tjv092>.