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Research

Sampling, Distribution, Dispersal

Dermacentor variabilis is the Predominant *Dermacentor* spp. (Acari: Ixodidae) Feeding on Dogs and Cats Throughout the United States

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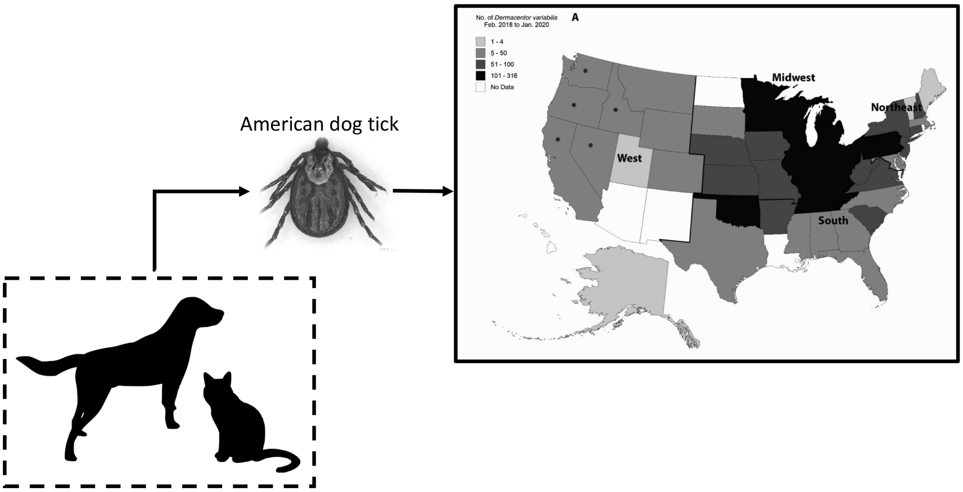
Abstract

Throughout North America, *Dermacentor* spp. ticks are often found feeding on animals and humans, and are known to transmit pathogens, including the Rocky Mountain spotted fever agent. To better define the identity and distribution of *Dermacentor* spp. removed from dogs and cats in the United States, ticks submitted from 1,457 dogs (*n* = 2,924 ticks) and 137 cats (*n* = 209 ticks) from veterinary practices in 44/50 states from February 2018-January 2020 were identified morphologically (*n* = 3,133); the identity of ticks from regions where *Dermacentor andersoni* (Stiles) have been reported, and a subset of ticks from other regions, were confirmed molecularly through amplification and sequencing of the ITS2 region and a 16S rRNA gene fragment. Of the ticks submitted, 99.3% (3,112/3,133) were *Dermacentor variabilis* (Say), 0.4% (12/3,133) were *D. andersoni*, and 0.3% (9/3,133) were *Dermacentor albipictus* (Packard). While translocation of pets prior to tick removal cannot be discounted, the majority (106/122; 87%) of *Dermacentor* spp. ticks removed from dogs and cats in six Rocky Mountain states (Montana, Idaho, Wyoming, Nevada, Utah, and Colorado) were *D. variabilis*, suggesting this species may be more widespread in the western United States than is currently recognized, or that *D. andersoni*, if still common in the region, preferentially feeds on hosts other than dogs and cats. Together, these data support the interpretation that *D. variabilis* is the predominant *Dermacentor* species found on pets throughout the United States, a finding that may reflect recent shifts in tick distribution.

Graphical Abstract



Key words: American dog tick, dog, cat, *Dermacentor*

Dermacentor spp. are some of the most common ticks found on dogs and cats in North America (Dryden and Payne 2004, Thomas et al. 2016, Little et al. 2018, Saleh et al. 2019). A national survey of pets across the United States showed that, of pets infested with ticks, 17.9% of cats and 35.6% of dogs are infested with *D. variabilis* (Saleh et al. 2019). In addition to being a primary parasite, *D. variabilis* can cause tick paralysis in pets and people, is an important vector of *Rickettsia rickettsii* and *Francisella tularensis*, and has been implicated as a primary or secondary vector associated with transmission of several other tick-borne pathogens (Dryden and Payne 2004, Jongejan and Uilenberg 2004). Historically, *D. variabilis* was thought to be present primarily in southcentral and southeastern Canada, the eastern half of the United States, and in Mexico, with a second population found along the West Coast, but was considered largely absent from the Rocky Mountain region (Bishop and Trembley 1945, Dryden and Payne 2004, Dergousoff et al. 2013, Guzmán-Cornejo et al. 2016, CDC 2020). Instead, a related species (*D. andersoni),* appropriately called the Rocky Mountain wood tick, was widely thought to predominate in this higher elevation area of the continent (Dryden and Payne 2004, CDC 2020).

In recent years, the geographic distributions of several tick species in North America have expanded due to a variety of factors, such as climate change and habitat change, that have made new areas supportive of tick populations. Human and animal-mediated introductions then facilitate expansion into these regions (Little 2013, MacDonald 2018, Sonenshine 2018). Northward and westward expansion of *D. variabilis* is well documented in Canada, and recent models indicate habitat suitability for this tick is expected to increase dramatically in those regions in future decades (Dergousoff et al. 2013, Yunik et al. 2015, Wood et al. 2016, Minigan et al. 2018). A similar shift may be occurring in the Rocky Mountain region of the United States, but recognizing the change could be delayed by morphologic similarities between *D. variabilis* and *D. andersoni* (Dryden and Payne 2004, Dergousoff and Chilton 2007). Some recent publications have identified *Dermacentor* species from the Rocky Mountain region by 'incorporat[ing] information on geographic range to allow species identification,' an approach that may lead to confusion about the current distribution of a given species, particularly given that the importance of *D. variabilis* is thought to be under-recognized in some areas (Nieto et al. 2018, Lehane et al. 2020). The aim of the present study was to confirm the identity of *Dermacentor* spp. ticks removed from dogs and cats across the United States, with a particular focus on *Dermacentor* spp. submitted from the western and central regions, to more accurately confirm the current geographic distribution and host preferences of members of this genus.

Materials and Methods

Ticks used in the current study were obtained through an ongoing national survey of ticks on pets as previously described (showusyourticks.org; Saleh et al. 2019) following collection and submission to Oklahoma State University by veterinarians across the United States. Ticks were collected from February 2018 to January 2020 and include those collected in 2018 and published in an earlier report (Saleh et al. 2019) and a second year of ticks collected in 2019 and reported in the present paper for the first time. Ticks were submitted together with information about pet species, age, weight, estimated percent time spent outside as reported by the owner, sex, and spay/neuter status. Upon receipt, all ticks were identified to species using standard morphologic keys and then stored in 70% ethanol at −20°C until further work was performed (USDA 1976, Lindquist et al. 2016).

The identity of all *Dermacentor* spp. ticks from the western United States (*n* = 188), all *Dermacentor* spp. ticks from states bordering the western United States (*n* = 122), and a subset of remaining ticks from the Midwest (*n* = 163), South (*n* = 147), and Northeast (*n* = 42) United States were confirmed molecularly. To achieve a broadly representative subsampling, up to 13 ticks (if available) were randomly selected for molecular confirmation from each state. Molecular confirmation was made using two nucleic acid targets, namely, fragments of the mitochondrial 16S rRNA gene and the nuclear ribosomal second internal transcribed spacer (ITS-2), as previously described (Dergousoff and Chilton 2007, Nadolny et al. 2011). Nucleic acid was extracted with a commercial kit (Illustra GenomicPrep Kit, GE Healthcare) and polymerase chain reaction (PCR) was used to amplify the two genetic markers. Following confirmation of amplification on a 2% agarose gel, products were column-purified and sequenced directly with an ABI 3730 capillary sequencer (Applied Biosystems, Foster City, CA) at the Oklahoma State University Molecular Core Facility (Stillwater, OK). Upon verification of high-quality electropherograms by visual inspection and routine editing, sequences were compared to those published for *Dermacentor* spp. and to all available sequences in GenBank (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Descriptive statistics (mean, range, proportion, and exact binomial 95% CI were calculated with Microsoft Excel (Microsoft Office Professional Plus 2016). Geographic regions used in comparisons were determined as previously described (Blagburn et al. 1996).

Results

A total of 3,133 *Dermacentor* spp. were examined, including 2,924 collected from 1,457 dogs and 209 from 137 cats. Age, weight, estimated time outside, sex, and spay/neuter status of dogs and cats infested with *Dermacentor* spp. are summarized in Table 1. An average of 1.5 and 1.2 ticks (median = 1) were collected from each dog and cat, respectively, with as many as 23 or 4 *Dermacentor* spp. on a single dog or cat, respectively.

Morphologic identification confirmed the identity of ticks as 3,112 *D. variabilis* (99.3%, 95% CI 99.0–99.6), 12 *D. andersoni* (0.4%, 95% CI 0.2–0.7), and 9 *D. albipictus* (0.3%, 95% CI 0.1–0.6). Molecular identification using two genetic markers on a subset (*n* = 662) confirmed the identity of 641 *D. variabilis*, 12 *D. andersoni*, and 9 *D. albipictus*. Of the submissions that included state of origin on the pet information form, the *Dermacentor* spp. primarily originated from the Midwest (*n* = 1,660; 53.0%), followed by the South (*n* = 853; 27.2%), the Northeast (*n* = 430; 13.7%), and the West (*n* = 188; 6.0%); two ticks were submitted without a state of origin. Only *D. variabilis* were submitted from the Northeast; both *D. variabilis* and *D. albipictus* were received from the South and Midwest; and *D. variabilis*, *D. andersoni*, and *D. albipictus* were submitted from the West (Table 2).

Every state with *Dermacentor* spp. submitted (*n* = 44 states) had *D. variabilis* collected from pets (Fig. 1A); *D. andersoni* was submitted from only six western states (Montana, Colorado, Idaho, Wyoming, Oregon, and Washington) and in lower numbers (Fig. 1B). Out of the 188 ticks submitted from the West, the majority (90.4%, 170/188, 95% CI 85.3–93.9) were *D. variabilis*. More specifically, 106 of the 122 ticks (86.9%, 95% CI 79.7–91.9) submitted from six Rocky Mountain states (Montana, Idaho, Wyoming, Nevada, Utah,

Table 1. Age, weight, estimated time spent outside, and sex and spay/neuter status for dogs and cats infested with *Dermacentor* spp. from across the United States

	Dogs	Cats
Age (yr), mean (range)	5.3 (0.1–19) 95% CI 5.1–5.5	5.4 (0.1–18) 95% CI 4.6–6.2
Weight (kg), mean (range)	21.1 (0.2–90.9) 95% CI 20.3–21.8	4.2 (0.2–11.4) 95% CI 3.8–4.5
Estimated time outside (%), mean (range)	44.0 (0–100) 95% CI 42.1–45.9	73.0 (0–100) 95% CI 65.7–80.2
Total female (*n*, %)	660 (46.5%) 95% CI 43.9–49.1	56 (42.8%) 95% CI 34.6–51.3
Female intact (*n*, %)	203 (30.8%) 95% CI 27.4–34.4	22 (39.3%) 95% CI 27.6–52.4
Female spayed (*n*, %)	457 (69.2%) 95% CI 65.6–72.7	34 (60.7%) 95% CI 47.6–72.4
Total male (*n*, %)	759 (53.5%) 95% CI 51.0–56.1	75 (57.3%) 95% CI 48.7–65.4
Male intact (*n*, %)	280 (36.9%) 95% CI 33.5–40.4	26 (34.7%) 95% CI 24.9–46.0
Male neutered (*n*, %)	479 (63.1%) 95% CI 59.6–66.5	49 (65.3%) 95% CI 54.0–75.1

kg, kilograms.

Table 2. Number of *Dermacentor variabilis* and *Dermacentor andersoni* adult and nymphal ticks collected from dogs and cats by species, stage, and geographic region

Species	Stage	Region			
		Northeast	South	Midwest	West
Dermacentor variabilis	Female	284	493	964	103
	Male	146	359	689	62
	Nymph	0	0	5	5
Dermacentor andersoni	Female	0	0	0	8
	Male	0	0	0	4
	Nymph	0	0	0	0
Dermacentor albipictus	Female	0	1	1	1
(Duncan et al. 2020)	Male	0	0	0	1
	Nymph	0	0	1	4
Total		430	853	1,660	188

No *Dermacentor* spp. larvae were submitted from pets over the 2-yr period. The *Dermacentor albipictus* listed here were reported in an earlier, multi-institutional paper (Duncan et al. 2020).

and Colorado) were *D. variabilis* while *D. andersoni* accounted for 10 out of 122 ticks (8.2%, 95% CI 4.4–14.6) submitted from these six states. Sequence analysis (16S rRNA gene) revealed *D. variabilis* submitted from California, Oregon, Washington, Idaho, and Nevada were most closely related (~99.5–100% similarity) to *D. variabilis* from California, or the 'western' *D. variabilis* population (GenBank Accession MG834237 and MG834234). Sequence of all other submitted *D. variabilis* from the western United States (Colorado, Utah, Wyoming, Montana) were identical (100%) to that of *D. variabilis* from Colorado and Indiana, or the 'eastern' *D. variabilis* population (GenBank Accession MG834244 and MG834241).

Adult *D. variabilis* was the stage of *Dermacentor* most often submitted (n = 3,102), and the time of collection peaked in the warmer, summer months in every region (Fig. 2). In the Northeast, Midwest, and West, tick collection was highest in May and June but collections declined in July, and reached almost zero by September (Fig. 2A, C, and D). In the South, tick collection increased in May, remained high through July, and then numbers declined in August, reaching zero by October (Fig. 2B). More female ticks were collected than male (n = 1,846 (59.5%) and n = 1,256 (40.5%), respectively), and the peak time of collection for each stage was similar for each region. However, in the Northeast, South, and Midwest, more male ticks than female ticks were collected in April just prior to the peak of female ticks in the summer months (Fig. 2).

Discussion

Dermacentor variabilis was the predominant *Dermacentor* species recovered from dogs and cats in every region in the present study. In each of the 44 states from which *Dermacentor* spp. ticks were submitted, including those in the Rocky Mountain region, more *D. variabilis* were submitted than *D. andersoni* as confirmed both morphologically and molecularly. Indeed, 10-fold more *D. variabilis* than *D. andersoni* were submitted from dogs and cats examined by veterinarians in Rocky Mountain states, a finding that is surprising

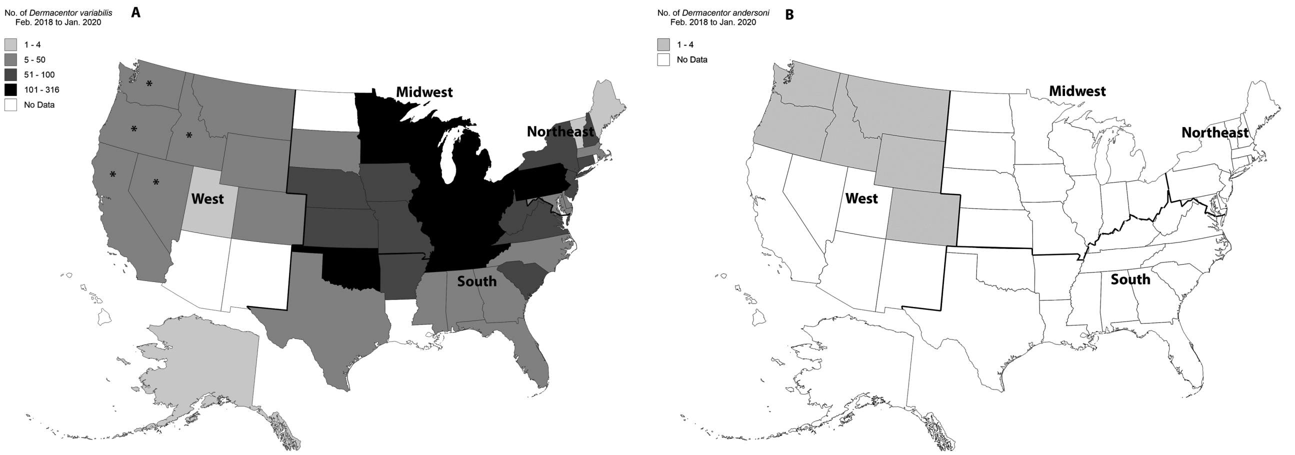


Fig. 1. Number of *Dermacentor variabilis* (A) and *Dermacentor andersoni* (B) collected from dogs and cats in different states in the United States, February 2018 to January 2020. Identification was confirmed molecularly for all ticks in the western United States and for a representative subset of ticks in other regions. Analysis showed distinct sequences indicating 'western' *D. variabilis* only in the five western states denoted with an asterisk (*); all other *D. variabilis* sequences were identical to those previously reported from the 'eastern' populations of *D. variabilis*.

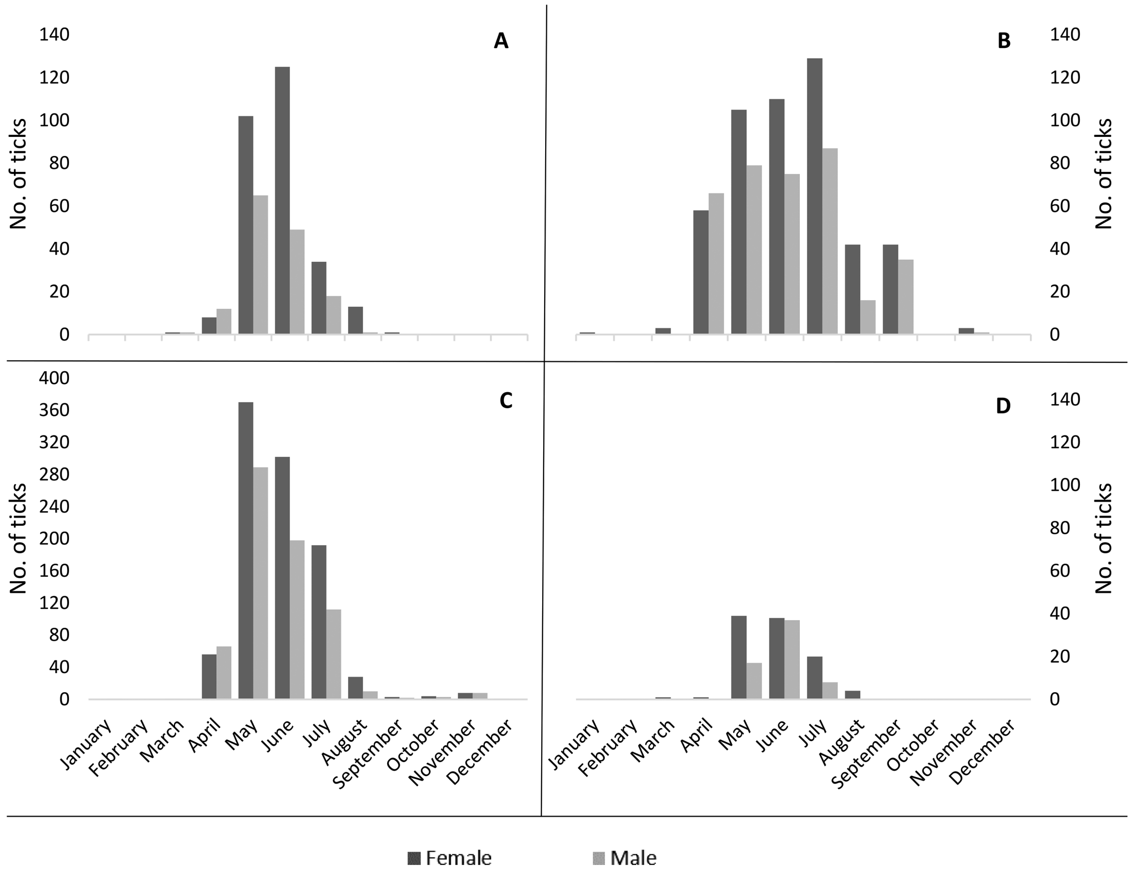


Fig. 2. Month of collection of adult *Dermacentor variabilis* from dogs and cats in the Northeast (A), South (B), Midwest (C), and West (D) regions of the United States. Due to the large number of *Dermacentor variabilis* ticks submitted from the Midwest, the scale of the *y*-axis for Fig. 2C is adjusted.

in light of current distribution maps for these two species (CDC 2020). A few *D. albipictus* were also identified and are reported elsewhere (Duncan et al. 2020). Of the 1,594 dogs and cats with *Dermacentor* spp. included in the present study, 1,330 (83.4%) were only infested with a single species of *Dermacentor*; *D. variabilis* was not found co-infesting any pets with other *Dermacentor* spp., although 264 animals (16.6%) had a co-infestation with ticks of a different genus, including *Amblyomma americanum* (59.1%), *Ixodes scapularis* (30.3%), *Amblyomma maculatum* (6.8%), *Rhipicephalus sanguineus* (2.3%), *Haemaphysalis longicornis* (1.1%), and *I. pacificus* (0.4%; data not shown).

Translocation is sometimes found to account for unexpected geographic distribution of ticks removed from pets or people that have recently traveled (Jones et al. 2017, Xu et al. 2019).

However, in the present study, sequence analysis revealed that every *D. variabilis* collected from the far western United States was placed in the 'western *D. variabilis*' phylogenetic group, and all *D. variabilis* from the eastern side of the Rocky Mountain range were 'eastern *D. variabilis*,' suggesting geographic expansion of the eastern population is more likely, and that, to the extent that translocation of *D. variabilis* on pets occurs, it is more common within regions rather than between regions. A shift in the distribution of *D. andersoni* and *D. variabilis* has been suggested by others and indicates that, should the findings in the present paper be confirmed by direct collection of questing ticks in the region, tick distribution maps for *Dermacentor* spp. may benefit from reconsideration and updating (James et al. 2015, Minigan et al. 2018, CDC 2020). Alternatively, *D. andersoni* may still be present and abundant in the Rocky Mountain region but sympatric with *D. variabilis*, and the latter species preferentially feeds on the hosts—dogs and cats—surveyed in the present paper. Host preferences for the different *Dermacentor* spp. have been reported although both *D. variabilis* and *D. andersoni* readily feed on pets (Cooley 1938, Dryden and Payne 2004).

Our data demonstrate the distribution of *D. andersoni* and *D. variabilis* likely overlaps over a much larger area than originally reported. Historically, sympatric populations of these two species were known to occur in the western Great Plains region of the United States and in southern Saskatchewan (Gibbons 1939, Bishop and Trembley 1945, Dergousoff et al. 2013), with *D. andersoni* reportedly more common in areas with hot and dry summers and *D. variabilis* restricted to regions with humid summers (Wilkinson 1967). Further complicating matters, hybridization has long been known to occur among several closely related *Dermacentor* spp., including *D. andersoni* and *D. variabilis* (Cooley 1938, Oliver et al. 1972, Goddard et al. 2020). Indeed, laboratory hybrids of *D. andersoni*, *D. occidentalis*, and *D. variabilis* are described although subsequent generations have not been demonstrated (Oliver et al. 1972). Determining the extent to which *D. variabilis* may be displacing *D. andersoni* in this region, if at all, will require direct surveys for questing ticks from the field and identification of ticks on larger domestic and wildlife hosts in the region. However, the present study and work in other tick systems underscore that, given ongoing shifts in distribution, geographic origin should not be used as a deciding factor in tick identification, particularly when morphologically similar species are likely present (Mertins et al. 2010, Nieto et al. 2018, Xu et al. 2019, Goddard et al. 2020).

As has been reported by others, very few immature stages of *Dermacentor* spp. were submitted from dogs and cats in the present study; these stages preferentially feed on rodents and other small mammals in nature and are rarely found on domestic animals (Bishop and Trembley 1945, Dryden and Payne 2004). It is unlikely that these smaller stages were simply overlooked, as larvae or nymphs of other ixodid tick species, including *Amblyomma americanum*, *Ixodes scapularis*, and *Rhipicephalus sanguineus*, are routinely collected and submitted from pets (Little et al. 2018, Saleh et al. 2019). However, all *D. andersoni* recovered in the present study, and almost all *D. variabilis* (99.7%), were adults. In contrast, nymphs of the one-host tick *D. albipictus* are occasionally reported from pets in both the United States and Canada (Duncan et al. 2020). Adults—both male and female—of *D. variabilis* and *D. andersoni* are known to feed on a wide array of medium and large domestic and wild mammals, including horses, cattle, sheep, dogs, and cats, as well as deer and other wild cervids, coyotes, and bears, questing almost entirely in the warmer months throughout their range (Cooley 1938, Harwood and James 1979, Burg 2001, Kollars et al. 2000, Dryden and Payne 2004, Eisen et al. 2007). In the present study, collection of *D. variabilis* from dogs and cats similarly peaked in the summer months (Fig. 2).

While *Dermacentor* spp. ticks feeding on pets can cause direct harm, including blood loss and tick paralysis, members of this genus are also important vectors of pathogens capable of causing severe disease, including *R. rickettsii* and other spotted fever group *Rickettsia* spp. (SFGR; Burgdorfer 1975, McDade and Newhouse 1986, Dryden and Payne 2004, Parola et al. 2013). The expansion of *D. variabilis* populations suggested by other recent publications and supported by the findings in the present study further underscores the need to better understand the role of this tick as a vector of disease agents (Minigan et al. 2018, Lehane et al. 2020). *Rickettsia rickettsii*, the causative agent of Rocky Mountain spotted fever, is infrequently detected in *D. variabilis,* with surveys identifying the pathogen in 0.1% or fewer of ticks tested, if at all (Hecht et al. 2019, Luedtke et al. 2020, Occi et al. 2020). Recent work suggests that *R. rickettsii* also may be transmitted by ticks of other genera, including *R. sanguineus* sensu lato, *A. americanum,* and *Haemaphysalis longicornis* (Labruna et al. 2008, Levin et al. 2017, Stanley et al. 2020). Other SFGR, including *R. montanensis* and *R. bellii*, are more often identified in *D. variabilis* although they are widely suspected to have milder or unknown pathogenicity compared to *R. rickettsii* (Hecht et al. 2019, Sanchez-Vicente et al. 2019, Trout Fryxell et al. 2015, McQuiston et al. 2012, Stromdahl et al. 2011, Macaluso et al. 2002). Further research is warranted to better understand the veterinary and public health implications and the pathogenic potential of *D. variabilis* as a commonly encountered tick that appears to be more geographically widespread than is current recognized (Lehane et al. 2020). Together, our findings reinforce the need to accurately identify ticks both morphologically and molecularly and to continue to monitor distribution of *D. variabilis* as a critical aspect of tick-borne disease control (Lehane et al. 2020).

Acknowledgments

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