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ORIGIN OF *DERMACENTOR ALBIPICTUS* (ACARI: IXODIDAE) ON ELK IN THE YUKON, CANADA

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ABSTRACT: Winter ticks (*Dermacentor albipictus*) on elk (*Cervus elaphus canadensis*) have recently increased in numbers in the Yukon, Canada, potentially posing risks to other indigenous host species in the region. To evaluate the regional source of winter ticks in the Yukon, we sequenced one nuclear (ITS-2) and two mitochondrial (16SrRNA and COI) genes, and genotyped 14 microsatellite loci from 483 winter tick specimens collected across North America. We analyzed genetic variation across the geographic and host ranges of this tick species with the use of variance partitioning, Bayesian clustering, and standard population genetic analyses. Based on our results, winter ticks on elk in the Yukon could have originated either by translocation from central Alberta or by northward range expansion of more geographically proximate populations in northern Alberta and British Columbia. Although there was some genetic structuring of winter ticks on different hosts in the same region, we found little evidence of host specificity in winter ticks from five ungulate host species, suggesting that the winter ticks on elk in the Yukon could potentially become established on other locally available host species such as moose (*Alces alces*).

Key words: *Dermacentor albipictus*, genetics, host specificity, invasive species, parasites.

INTRODUCTION

The winter tick, *Dermacentor albipictus* (Packard, 1869) is a North American ectoparasite of large ungulates (Mooring and Samuel 1998; Samuel 2004). The tick is a wildlife management concern because of its association with hair loss and mortality in various cervid species, particularly moose (*Alces alces*; Samuel 2004; Musante 2006). It was originally assumed that the winter tick is unable to survive north of the 60th parallel in western Canada (Wilkinson 1967). However, a controlled translocation experiment by Zarnke et al. (1990) showed that winter ticks could potentially become established in regions of Alaska. In addition, trappers and indigenous hunters in the Yukon have historically, although infrequently, observed the kind of late-winter sequential hair damage on moose (Samuel 1989; Kutz et al. 2009) that is normally associated with winter tick infestations. However, since the mid 1990s, reports of winter tick infestations and hair loss on elk (*Cervus elaphus canadensis*) in the Yukon have increased substantially (Environment Yukon 2011). Winter ticks have also recently been recovered from hunter-killed moose and mule deer (*Odocoileus hemionus*) in regions occupied by tick-infested elk (W.M.S. unpubl.; Rick Ward, Environment Yukon, pers. comm.). The origin of these expanding winter tick populations in the Yukon remains unclear.

Between 1951 and 1994, 168 elk were introduced to southern Yukon near Whitehorse (Yukon Elk Management Planning Team 2008). Eighty-one of these elk were from farms in the Yukon, and the remaining 87 (49 in 1951 and 1954, and 38 in March 1991) originated from Elk Island National Park in central Alberta. In 1991 and 1993, *D. albipictus* were reportedly collected from some of the elk translocated in 1991 (Al Shostak, University of Alberta, pers. comm.). Given the history of translocations and timing of adult tick discovery on elk in the Yukon, it is possible that the current winter tick population on

elk in the Yukon originated with the introduction of cervids from Elk Island National Park. It has also been suggested that ticks may have been carried into the region via range expansion of infested ungulate populations across the Yukon border (Environment Yukon 2011). Neither hypothesis is supported by definitive evidence.

We investigated the regional origin of *D. albipictus* on elk in the Yukon. If these winter ticks originated from Elk Island National Park, we would expect to observe the greatest genetic similarity between ticks from the Yukon and those from within the park. If the presence of these ticks is the result of natural northward range expansion, we would instead expect to find greater genetic similarity between Yukon ticks and populations close to the Yukon border. Because winter ticks are able to complete their life cycle on a single host, a trait that should predispose them to host race formation, we also examined these ticks for genetic evidence of host specificity (De Meeus et al. 2010). Greater host specificity would suggest a reduced risk of host shifts by winter ticks to ungulates other than elk in the Yukon.

MATERIALS AND METHODS

Specimens, DNA extraction, sequencing, and genotyping

Dermacentor albipictus specimens were obtained from various host species and geographic regions across North America (Table 1). Efforts were made to sample only one tick per host individual to avoid sampling closely related individuals (Table 1). Genomic DNA was extracted using QIAamp DNA mini kits (Qiagen, Valencia, California, USA). Tick vouchers are stored in 95% ethanol at −20 C in the E. H. Strickland Entomological Museum, University of Alberta, Edmonton, Alberta, Canada. We sampled multiple genetic markers in each tick, including 14 species-specific microsatellite loci (Leo et al. 2012) and three genes: mitochondrial 16S ribosomal RNA (16SrRNA), mitochondrial cytochrome oxidase I (COI), and nuclear internal transcribed spacer 2 (ITS-2). Descriptions of PCR amplification and sequencing protocols are available (Leo et al. 2010, 2012).

Variance partitioning analyses

Variance partitioning analyses were performed to determine the extent to which genetic variation among tick populations was associated with geographic localities or host species. All variance partitioning analyses were performed with the use of analysis of molecular variance (AMOVA) in Arlequin ver. 3.5 (Excoffier and Lischer 2010) with the use of standard computations and 1,000 permutations. Gene sequences were grouped into lineages (Leo et al. 2010). Only molecular markers that showed significant associations were used in subsequent analyses on spatial genetic structure or host race formation.

Winter ticks were first partitioned based on their combination of host species and collection location (Table 1). To ensure representative sampling of genetic variability, any population represented by less than five specimens was discarded and ticks collected within 200 km and on the same host were amalgamated and treated as a single population (Table 1). Basic descriptive statistics of allele frequency distributions in each population were obtained with the use of the Microsatellite Toolkit for Excel (Park 2001), and the inbreeding coefficient (F_{IS}) for each population of ticks was determined via Arlequin ver. 3.5 (Excoffier and Lischer 2010).

Populations of ticks were subsequently grouped by host species or geographic regions for analysis of genetic differentiation among host species and geographic regions (Table 1). Each population simultaneously belonged to both a host group and a regional group.

Spatial genetic structure analyses (microsatellite data)

We examined the spatial genetic structure of tick populations across North America by performing analyses separately on each host group (elk, horses, and moose) in an attempt to control for any host species associations. No spatial genetic structuring tests were performed on ticks from mule deer and white-tailed deer (*Odocoileus virginianus*), as they were all collected within a single geographic region (eAB) and were therefore uninformative about spatial genetic variation among regions.

Presence and amount of genetic structuring among tick populations within in each host and regional group were estimated with the use of Wright's *F*-statistics (Wright 1951) and tests of genotypic differentiation. Pairwise *F*-statistics and genotypic differentiation analyses were performed under default parameters using AMOVA in Arlequin ver. 3.5 and GENEPOP (Rousset 2008).

TABLE 1. Fourteen regional populations of winter ticks (*Dermacentor albipictus*) surveyed for 14 microsatellite loci, partitioned by host. *P* values significant after Bonferroni correction ($P<0.00357$) are underlined. Locality names within regional populations in Alberta are shown in Figure 1.[a]

Population	*N*	Collection localities	Host species (*n*)	Regional group	$n_a \pm SE$	$H \pm SE$	$H_O \pm SE$	F_{IS}	*P*
EL_cAB	10	Elk Island National Park, Alberta	Elk (10)	Central Alberta	2.23±0.48	0.301±0.089	0.285±0.098	−0.077	0.742
EL_sAB	17	Waterton, Alberta	Elk (17)	Southern Alberta	4.07±0.92	0.487±0.081	0.403±0.074	0.202	0.021
EL_YT	16	Takhini River Valley & Braeburn Lake, Yukon Territory	Elk (16)	Yukon	3.00±0.52	0.350±0.086	0.289±0.097	0.070	0.346
HO_cAB	10	Edmonton, Alberta	Horse (10)	Central Alberta	3.29±0.79	0.358±0.093	0.235±0.080	0.262	0.029
HO_sAB	8	Crowsnest Pass, Alberta	Horse (8)	Southern Alberta	3.07±0.63	0.389±0.094	0.351±0.096	0.388	0.005
MO_cAB	38	Elk Island National Park, Alberta	Moose (28)	Central Alberta	5.21±1.13	0.429±0.082	0.358±0.074	0.117	0.036
MO_nAB	81	Peace River, Whitburn & Grande Prairie, Alberta	Moose (45)	Northern Alberta	5.43±1.28	0.367±0.085	0.225±0.069	0.195	<u>0.000</u>
MO_ID	32	Moose Ridge, Idaho	Moose (32)	Western USA	6.00±1.11	0.447±0.088	0.207±0.047	0.025	0.418
MO_MI	11	Isle Royale National Park, Michigan	Moose (11)	Eastern USA	2.50±0.45	0.327±0.086	0.235±0.070	0.058	0.397
MO_MN	20	Lake County, Minnesota	Moose (20)	Eastern USA	3.71±1.05	0.368±0.098	0.261±0.088	−0.037	0.722
MO_NH	13	Coos County, New Hampshire	Moose (13)	Eastern USA	1.79±0.38	0.104±0.059	0.083±0.040	−0.091	1.000
MO_WY	20	Near Jackson, Wyoming	Moose (20)	Western USA	3.64±1.10	0.358±0.098	0.233±0.075	0.332	<u>0.000</u>
MD_eAB	183	Oyen, Chauvin & Dillberry Lake Provincial Park, Alberta	Mule deer (97)	Eastern Alberta	5.50±1.35	0.357±0.091	0.267±0.078	−0.058	0.991
WT_eAB	24	Oyen, Chauvin & Dillberry Lake Provincial Park, Alberta	White-tailed deer (13)	Eastern Alberta	4.14±0.89	0.369±0.088	0.271±0.074	0.119	0.031

[a] *N*=number of ticks sampled per population; *n*=number of host individuals from which ticks were sampled; n_a=average number of alleles per locus; H=Nei's gene diversity; H_O=observed heterozygosity; SE=standard error.

Individual-based clustering analyses were performed on microsatellite data in *structure* ver. 2.3 (Pritchard et al. 2000), with the use of the admixture ancestral model and correlated allele frequency model. Ten iterations for each k value (i.e., number of genetic clusters) were analyzed with Markov chain Monte Carlo (MCMC) running for 100,000 generations and initial burn-in of 10,000 generations. The most likely k value was determined by the method described by Evanno et al. (2005), after which a more thorough run was performed with an initial burn-in of 50,000 generations and 500,000 subsequent MCMC generations with k defined.

Host race formation (microsatellite data)

The formation of host associations in winter ticks was investigated with the use of the genetic diversity of ticks collected from multiple host species existing in sympatry within a sampled region (i.e., regional groups of tick populations). We compared average allele numbers and gene diversity among host species with the use of the Wilcoxon two-sample analyses (Wilcoxon 1945) and t-tests. Genetic structuring among populations was performed in GENEPOP and Arlequin, as described above, for spatial structure.

RESULTS

A summary of average allele counts per microsatellite locus, allele frequency distributions, and inbreeding coefficient (F_{IS}) for each tick population is provided in Table 1.

Variance partition analyses

Variance analyses revealed that host species did not significantly account for variation observed among COI (% variance=10.81, P=0.403), 16SrRNA (% variance=0.00, P=0.840), or ITS-2 (% variance=21.61, P=0.095) sequence lineages. However, host association significantly accounted for variation observed in the microsatellite data (% variance=7.37, P=0.000). Similarly, collection locality did not have significant association with mtDNA sequence lineages (COI: % variance=10.01, P=0.194; 16SrRNA: % variance=10.54, P=0.352) or ITS-2 variation (% variance=2.59, P=0.077). Nonetheless, collection locality did account for a significant amount of the variation observed in microsatellite data (% variance=10.04, P=0.007). Variation in COI, 16SrRNA, and ITS-2 was not highly concordant with clusters derived from *structure* analysis of microsatellite data although the association was significant (COI: % variance=6.87, P=0.000; 16SrRNA: % variance=4.96, P=0.001; ITS-2: % variance=4.79%, P=0.035). Because the microsatellite loci were the only molecular markers for which observed variation was associated with both geographic localities and host species, all subsequent analyses were performed on that dataset alone.

Spatial genetic structuring and origin of winter ticks (microsatellite data)

Our results indicated that tick populations from different geographic regions, regardless of host species parasitized, exhibited significant genetic differentiation in the elk host group (combined test, χ^2=infinity, df=22, P=0.0000; F_{ST} = 0.156, P=0.000), horse host group (combined test, χ^2=40.38, df=18, P=0.0019; F_{ST}=0.111, P=0.000), and moose host group (combined test, χ^2=infinity, df=28, P=0.0000; F_{ST}= 0.182, P=0.000).

Structure analyses showed that winter ticks in the Yukon primarily belong to the same genetic cluster as those from northern Alberta (Fig. 1). This indication of genetic similarity is supported by the lack of significant F_{ST} differences between winter tick populations from the Yukon and Peace River in northern Alberta ($F_{ST\ Yukon\ vs.\ Peace\ River}$=0.00161, P=0.17). However, pairwise comparisons of genetic differentiation among winter tick populations also revealed that winter ticks on elk in the Yukon are not genetically distinct from ticks collected from elk and moose within Elk Island National Park ($F_{ST\ Yukon\ vs.\ EINP}$=0.00348, P=0.14).

Host race formation in winter ticks (microsatellite data)

Wilcoxon two-sample analyses and t-tests revealed no significant differences in

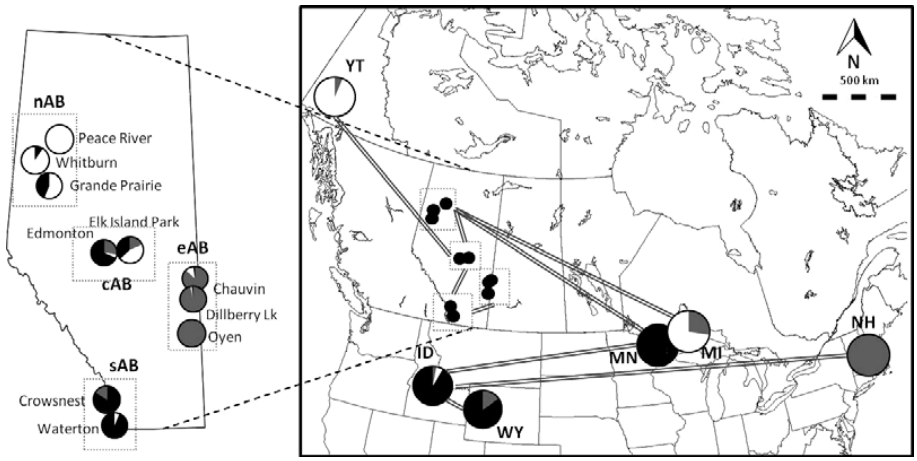

FIGURE 1. Collection localities for winter tick (*Dermacentor albipictus*) populations. Pie charts show proportions of specimens per locality assigned to each of three genetic clusters obtained from *structure* analysis of microsatellite data. Grey double lines indicate a minimum spanning tree (based on allele frequencies) connecting all populations in the figure. Regional codes are as in Table 1.

tick average allele numbers and gene diversity among host species (W=184.0–202.5, P=0.395–1.000; t-test =−0.613–0.687, P=0.545–0.924). F-statistics and genotypic differentiation tests revealed varying levels of genetic differences among ticks sampled from sympatric host species. Ticks collected from mule deer and white-tailed deer in eastern Alberta were not genetically distinct (combined test, χ^2=9.03, df=22, P=0.144; F_{ST}=0.007, P=0.569). However, we found evidence of genetic differences among ticks from elk, horses, and moose in central Alberta (combined test, χ^2=infinity, df=24, P=0.000; F_{ST}=0.096, P=0.000). Ticks on horses and elk from southern Alberta also exhibited genetic differences between host species (combined test, χ^2=105.76, df=22, P=0.000; F_{ST}=0.139, P 0.000).

DISCUSSION

We employed multiple genetic markers that provided differing amounts of information about the origin of the winter tick in the Yukon. Variance partitioning found that microsatellite markers, on the whole, were more informative than sequences for revealing genetic signals of host and regional associations in winter ticks. This is unsurprising, as microsatellite markers generally have higher mutation rates compared to more conserved genetic markers like ITS-2, COI, and 16SrRNA (Schlötterer 2000) and are more likely to provide signals of evolutionary events over ecologic time scales. DNA sequences, on the other hand, may be more suited to investigating older evolutionary processes (e.g., Kempf et al. 2009). The results from our variance partitioning analyses on DNA sequences and microsatellite markers suggest that regional differentiation of winter tick populations is a relatively recent phenomenon. This structuring may have occurred over the time scale of historic ecologic changes on the continent, as suggested by the presence of moderate regional and host-associated genetic structuring for horses (*Equus ferus caballus*) in Alberta, where they have been present for at most a few hundred years. Postcolonization anthropogenic disturbances (i.e., deforestation, overexploitation, urban development, or climate change) may also have caused geographic range contractions

and population size decreases in moose, elk, and mule deer populations across North America (Laliberte and Ripple 2004).

Our primary objective was to investigate the geographic origin of the current population of winter ticks on elk in the Yukon. Current hypotheses suggest that these ticks either originated from infested elk translocated from Elk Island National Park in the 1950s–90s or by natural northward range expansion on hosts in northern Alberta and British Columbia. Pairwise comparisons of microsatellite differentiation among localities in our study indicated that winter ticks on elk in the Yukon are genetically similar to winter ticks collected from Elk Island National Park. Thus human-aided introduction of infested elk may have contributed to establishing a population of winter ticks in the Yukon. However, minimum spanning tree analysis and visual inspection of *structure* clusters showed that Yukon ticks are also genetically very similar to ticks from the Peace River region of northern Alberta (Fig. 1). This suggests that the presence of winter ticks in the Yukon could be the result of natural northward range expansion, in which spatial movement by ungulate host species in response to ecologic factors like climate change (e.g., Harding and McCallum 1997) may have contributed to northward tick dispersal (as suggested by Kutz et al. 2009). Warming climatic conditions could have opened up new habitats previously unsuitable for tick survival and thus enabled successful establishment of winter tick populations in the north.

Given the one-host life history of the winter tick, the species should exhibit a stronger relationship with its reproductive host compared to other multihost tick species that tend to be host generalists (e.g., *Ixodes scapularis* Say [Ostfeld 2011]). As a result, we expected to find evidence for host race formation (i.e., host species association) in winter tick populations similar to those observed in other one-host or nidicolous tick species (e.g., Dietrich et al. 2012). However, genetic markers in our study revealed that host-associated genetic variation in winter ticks (F-statistics: 0.007–0.139) is generally lower than that associated with geographic regions (F-statistics: 0.111–0.182). Possible reasons for this low level of host species association include overlapping host distributions, indiscriminate host-seeking behavior (e.g., McPherson et al. 2000), and both natural and human-mediated long-distance movement (e.g., Mauer 1998; Parks Canada 2010) of infested hosts that can potentially weaken isolation-by-distance effects between both host and tick populations.

We used new genetic data to determine the origin(s) of the winter tick population in the Yukon and investigate host race formation among winter tick populations. We found little evidence of host race formation in the winter tick, indicating that gene flow among winter tick populations is not limited by the host species they parasitize. The genetic structure found in this study raises the possibility that winter ticks on elk in the Yukon could potentially parasitize other host species such as caribou (*Rangifer tarandus*), mule deer, and moose. Such occurrences have already been noted anecdotally in the Yukon (Samuel 1989; Kutz et al. 2009).

Although the source of the winter ticks infesting mule deer and moose in the Yukon remains unknown (because our study lacks specimens from these host species), our results suggest that winter ticks on elk in the Yukon may have originated from either infested hosts translocated from Elk Island National Park or via natural northward range expansion from northern British Columbia and Alberta, or both. Additional in-depth research is needed to definitively determine the origin of the winter ticks that first seeded the population now established in the region. One approach would be to understand better the mechanisms by which winter ticks are invading the

region. For example, examination of winter ticks from northern British Columbia and the Northwest Territories could provide useful additional information regarding the spatial distribution of winter tick genetic diversity along the northern edge of the species range. A multitaxa integrated landscape genetic approach (James et al. 2011) that compares similarities in winter tick spatial genetic patterns and those of their ungulate hosts relative to the landscape could further identify biotic and abiotic variables driving winter tick movement across the landscape. Additional modeling based on historic and future climate scenarios may also be a useful tool for quantifying and comparing the role of climate-driven tick range expansion, relative to human-aided translocation, in the original establishment of winter ticks in the Yukon.

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