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Received: 10 June 2024 | Revised: 21 October 2024 | Accepted: 13 November 2024

DOI: 10.1002/ecs2.70129

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE
Disease Ecology

Winter tick sharing between ungulates in the Greater Yellowstone Ecosystem and implications for apparent competition

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Funding information
USGS Northern Rocky Mountain Science Center; Wyoming Game and Fish Department; Teton County Government; USGS National Climate Adaptation Science Center; Wyoming Governor's Big Game License Coalition; Montana State University; Veterinary Initiative for Endangered Wildlife; Teton Conservation District

Handling Editor: Whitney C. Preisser

Abstract

Host species heterogeneity can drive parasite dynamics through variation in host competency as well as host abundance. We explored how elk (*Cervus canadensis*) with apparent subclinical infestations of winter tick (*Dermacentor albipictus*) may be a cryptic reservoir and drive winter tick dynamics, impacting moose (*Alces alces*) populations. We found that winter tick infestation loads did not vary remarkably between both host species and winter ticks sourced from elk and moose produced similar numbers of larvae which activated within 5 days of each other. We also found similar larval densities in habitats predominately used by elk, moose, and both host species. Our analysis of 2793 informative single-nucleotide polymorphisms showed genetic differentiation among tick populations that were only ~75 km apart, but fewer differences among ticks from elk or moose in the same locality, suggesting sharing of winter ticks across host species. Despite the clinical signs of high winter tick infestations being most apparent on moose, elk may be critical drivers of winter tick population dynamics and indirectly compete with moose in areas where they outnumber moose populations, a common characteristic of

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ungulate communities in western North America. Management interventions aimed at addressing winter tick issues on moose may wish to consider the movement patterns and abundance of cryptic reservoirs like elk.

KEYWORDS
Alces alces, apparent competition, *Cervus canadensis*, *Dermacentor albipictus*, elk, Greater Yellowstone Ecosystem, host competency, moose, parasite sharing, winter tick

INTRODUCTION

Parasites can impact host population dynamics by directly influencing survival or reproduction and indirectly by altering host community structure via parasite sharing (Gibb et al., 2020; Gottdenker et al., 2014; Hudson & Greenman, 1998; Ostfeld et al., 2006; Ostfeld & Keesing, 2020). Parasite sharing can have stabilizing or destabilizing effects on host communities depending on variability in host competency, abundance, susceptibility to disease, and niche overlap between host species (Cronin et al., 2010; Downs et al., 2019; Gilbert et al., 2001; LoGiudice et al., 2003; Marm Kilpatrick et al., 2006). Parasite-mediated apparent competition, whereby one host species indirectly reduces the fitness of another host by sharing a common parasite, could lead to the decline of vulnerable host populations. Theoretically, declines can occur when a highly competent host is capable of supporting large broods of a parasite while also being less susceptible to the negative health outcomes of infestation. Conversely, if susceptibility is similar across host species for a given parasite, sharing may reduce dominant host populations and lead to overall stabilizing host population dynamics (Gilbert et al., 2001). Though several studies have examined pathogen dynamics associated with host competency, few have empirically investigated the extent to which a less competent but highly abundant host serves as a cryptic reservoir driving parasite dynamics (Buhnerkempe et al., 2015; Downs et al., 2019; Gilbert et al., 2001; Grosholz, 1992; Levine et al., 2016).

We refer to cryptic reservoirs as host species with mostly invisible parasite infestations such that typical disease surveillance strategies miss infestations, yet individual hosts may still be infested at rates high enough to influence overall parasite population dynamics (Aliee et al., 2021). With increasing land-use change, competent hosts associated with anthropogenic activities may dominate disturbed landscapes and indirectly compete with rarer species through shared pathogens and parasites even if they do not directly interact via predation or compete for common resources (Gibb et al., 2020). The competency of a certain host for a given parasite is often described as binary, the host being either "competent/noncompetent," but competency exists on a spectrum. Competency is often unique to a host–parasite community and can be measured using observations on parasite–host interactions, like host-associated parasite reproductive output or phenology (Cronin et al., 2010; Wojdak et al., 2014). In this study, we examine evidence that elk (*Cervus canadensis*) may be highly competent for a multi-host parasite, the winter tick (*Dermacentor albipictus*), and potentially serve as a cryptic reservoir affecting moose (*Alces alces*).

The winter tick is an *Ixodidae* tick species that can complete its lifecycle by parasitizing a single host (i.e., a one-host tick) and is commonly cited for its relationship with moose (Chenery et al., 2023). One-host ticks, like the winter tick, can have a wide host species range (Chenery et al., 2023) despite the possibility of host specialization given they complete their lifecycle on a single host. Winter ticks are most commonly cited in the literature as contributors to declines in moose populations during epizootic years when tick infestation loads are exceedingly high. Though the specific drivers of winter tick epizootics are debated across their range, several studies have found correlations between early spring snow melt, mild summers, and late snow fall in autumn and tick loads or hair loss on moose during the following on-host seasons (DeCesare et al., 2024; Dunfey-Ball, 2017; Pouchet et al., 2024; Rosenblatt et al., 2021; Ruprecht et al., 2020). Milder winter conditions are expected across much of moose range in North America under anthropogenic climate change, increasing the risk environmentally transmitted parasites like winter ticks pose to moose in the future (Kutz et al., 2009). Moose can accumulate large numbers of winter ticks during epizootic years, exceeding 30,000 ticks per animal, resulting in hair loss (often described as "ghost" moose), anemia due to blood loss, and sometimes death, especially in calves (Jones et al., 2017, 2019; McLaughlin & Addison, 1986). Winter tick epizootics have been documented with increasing frequency in the southern periphery of moose range in North America, reducing calf survival, cow pregnancy rates, and ultimately leading to population declines or dampening recoveries (DeCesare et al., 2024; Jones et al., 2017; Murray et al., 2006; Nadeau et al., 2017;

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Ruprecht et al., 2020; Samuel, 1989; Timmerman & Rodgers, 2017; Wunschmann et al., 2015). While many other ungulate species such as elk, white-tailed deer (*Odocoileus virginianus*), and caribou (*Rangifer tarandus*) are also known to be infested by winter ticks, widespread population declines associated with winter tick epizootics have yet to be observed in these species though clinical signs from high infestations and some incidental deaths have been reported (Bondo et al., 2019; Calvente et al., 2020; Machtinger et al., 2021; Normandeau et al., 2022). One hypothesis for observed differences in winter tick infestation rates and susceptibility between moose and other ungulate species is that moose are "stimulus" groomers which attempt to remove ticks when they begin to irritate the host as adult ticks engorge in the spring versus "programmed" groomers like elk which may periodically groom throughout the year, thus decreasing tick burden throughout the winter season (Mooring & Samuel, 1998, 1999; Normandeau et al., 2022; Welch et al., 1991). These differences in grooming behaviors could partially explain why health complications from high winter tick infestations, like early hair loss and anemia, are primarily reported in moose versus other ungulate hosts. However, in regions where winter ticks, moose, and other ungulate species are present, moose are often dramatically outnumbered. If ungulates like elk are infested at lower rates than moose, they may still contribute to overall winter tick population dynamics on the landscape through their comparatively higher abundances versus moose. Few studies have explicitly considered non-moose ungulate hosts as potential drivers of winter tick dynamics on the landscape (DeCesare et al., 2024; Drew & Samuel, 1985; Welch et al., 1991).

Winter tick life cycles and activation timing vary across its wide range from northern Canada to southern Mexico (Chenery et al., 2023; Glines, 1983). In the northern portion of winter tick range (Northern United States to northern Canada) where they overlap with moose, winter tick larvae become active and seek out a host during the fall (early or mid-September until snow impedes attachment or larvae deplete energy reserves). Upon attaching to a host, larvae engorge on the host animal and molt into nymphs, remaining on host throughout winter (Figure 1). Nymphs engorge and molt into adults between January and February, with adult female ticks feeding in early spring from March through May. Fed adult female ticks then drop off their host and move on average <1 m from their drop-off site to a location where they can deposit their eggs. Eggs hatch during the spring or early summer (May–June) and clutches of larvae remain dormant throughout the summer until questing season begins in the fall. Sharing of ticks among ungulate species and movement of ticks across the landscape is most likely to occur during the fall and spring, corresponding with larvae questing and adult female drop off seasons respectively (Figure 1). These seasons can broadly align with ungulate migration timing in western North America which creates ample opportunity for habitat overlap between host species.

The Jackson region of the Greater Yellowstone Ecosystem (GYE), encompassing Grand Teton National Park, Bridger-Teton National Forest, the National Elk Refuge (NER), and the urban areas surrounding Jackson, Wyoming, supports a large elk herd, varying between 9500 and 11,500 individuals over the past decade (Wyoming Game and Fish Department, 2021). In comparison, the moose population in this same area and time period has fluctuated between 250 and 350 individuals. Elk concentrations on winter ranges peak from December to March, especially on the NER where elk have been given supplemental feed since the early 1900s (Appendix S1: Figure S2) (Dean et al., 2004). In late March–May, elk migrate from the NER and other low elevation winter habitats across the Jackson region, allowing adult female winter ticks from elk to be deposited into a wide range of habitats, including those used by moose (Figure 2).

Considering the relative abundance of elk populations within moose range in western North America and their potential spatial overlap with moose during migration and winter tick transmission seasons, elk may serve as a cryptic reservoir for winter ticks, resulting in negative impacts on moose also known as parasite-mediated apparent competition. The degree to which winter ticks from elk represent an exposure risk to moose depends on the overlap of moose and elk habitats during transmission seasons as well as the level of competency elk exhibit toward winter ticks versus moose and the degree of specialization winter tick subpopulations may exhibit toward either host. We examined several aspects of elk and moose relationships with winter ticks to explore the possibility of parasite sharing and apparent competition in the Jackson region. We hypothesized that although moose are highly competent winter tick hosts, the higher abundance of elk despite their weaker per capita competency for winter ticks would cause equal net contributions to overall tick abundance between elk and moose. First, because host competency may affect parasite phenology and reproduction, we evaluated the reproduction rates and activation timing of winter ticks that were collected from moose and elk. Second, we collected data on winter tick densities on moose and elk to determine relative tick burdens across host species. Third, we estimated the abundance of questing winter ticks in the fall in

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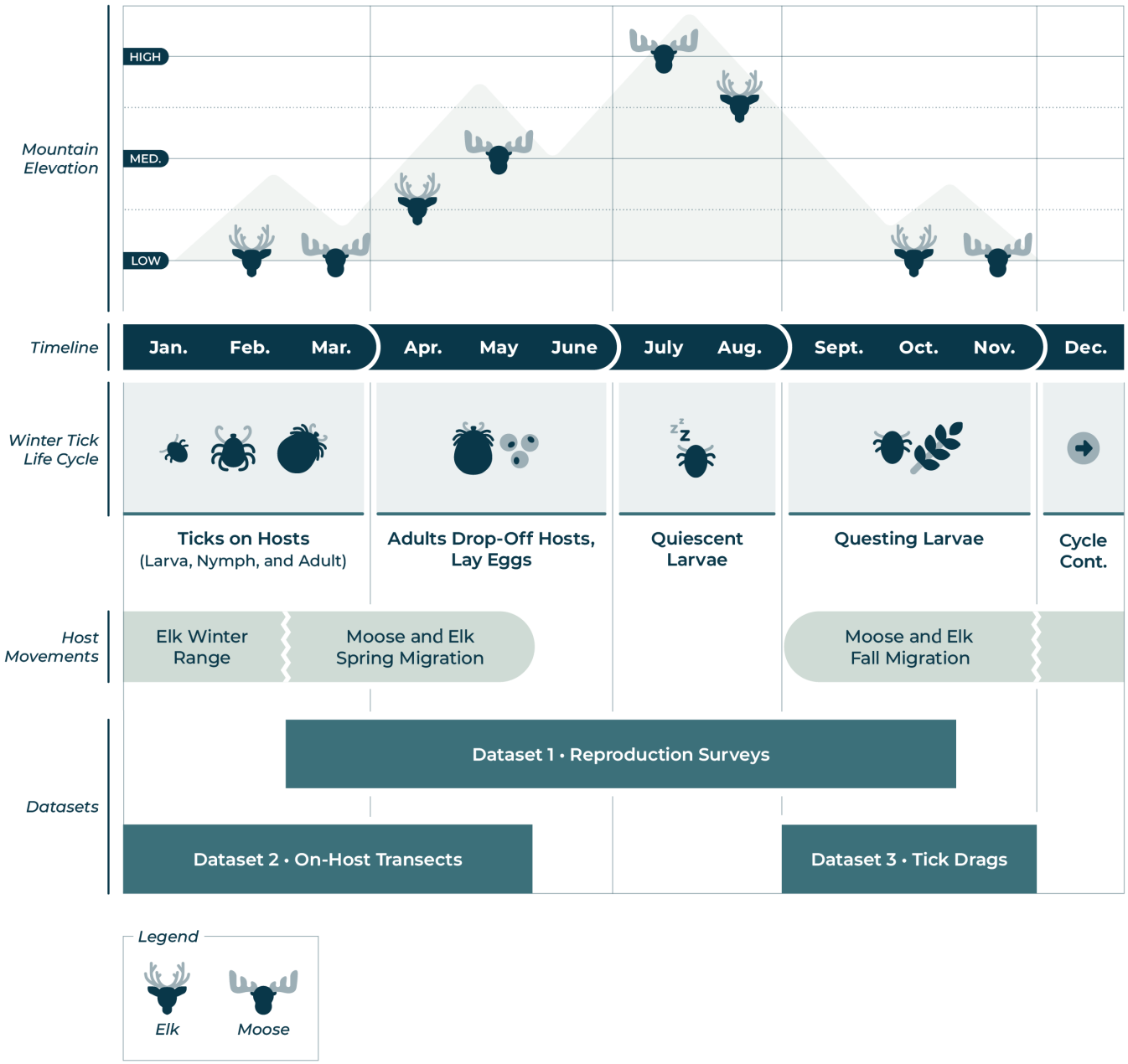


FIGURE 1 Conceptual diagram displaying the overlap of major portions of elk and moose seasonal activities and the winter tick (*Dermacentor albipictus*) life cycle with temporal alignment of studies employed in this project. Top panel depicts classical elk (*Cervus canadensis*) and moose (*Alces alces*) seasonal movements from lower elevation areas (~2000 m) like the National Elk Refuge during winter months to higher elevation areas (2200–2400 m) like the Yellowstone Plateau in summer months. The next panel depicts the general timing of the winter tick life cycle with the following sections depicting elk and moose migration timing and alignment with the three studies described in this manuscript. Graphic credit: Tory Kirkeby.

habitats that are predominantly used by moose, elk, or both hosts in the preceding spring as determined with GPS collar data. Finally, because specialization may involve evolutionary adaptation in favor of a specific host, we used genome-wide single-nucleotide polymorphisms (SNPs) to assess the level of genetic structuring in winter ticks across different spatial locations compared with the structuring across host species.

MATERIALS AND METHODS

Study area

Our study took place in northwestern Wyoming, south of Yellowstone National Park and within the boundaries of Grand Teton National Park, Bridger-Teton National Forest, NER, and the areas surrounding Jackson, USA

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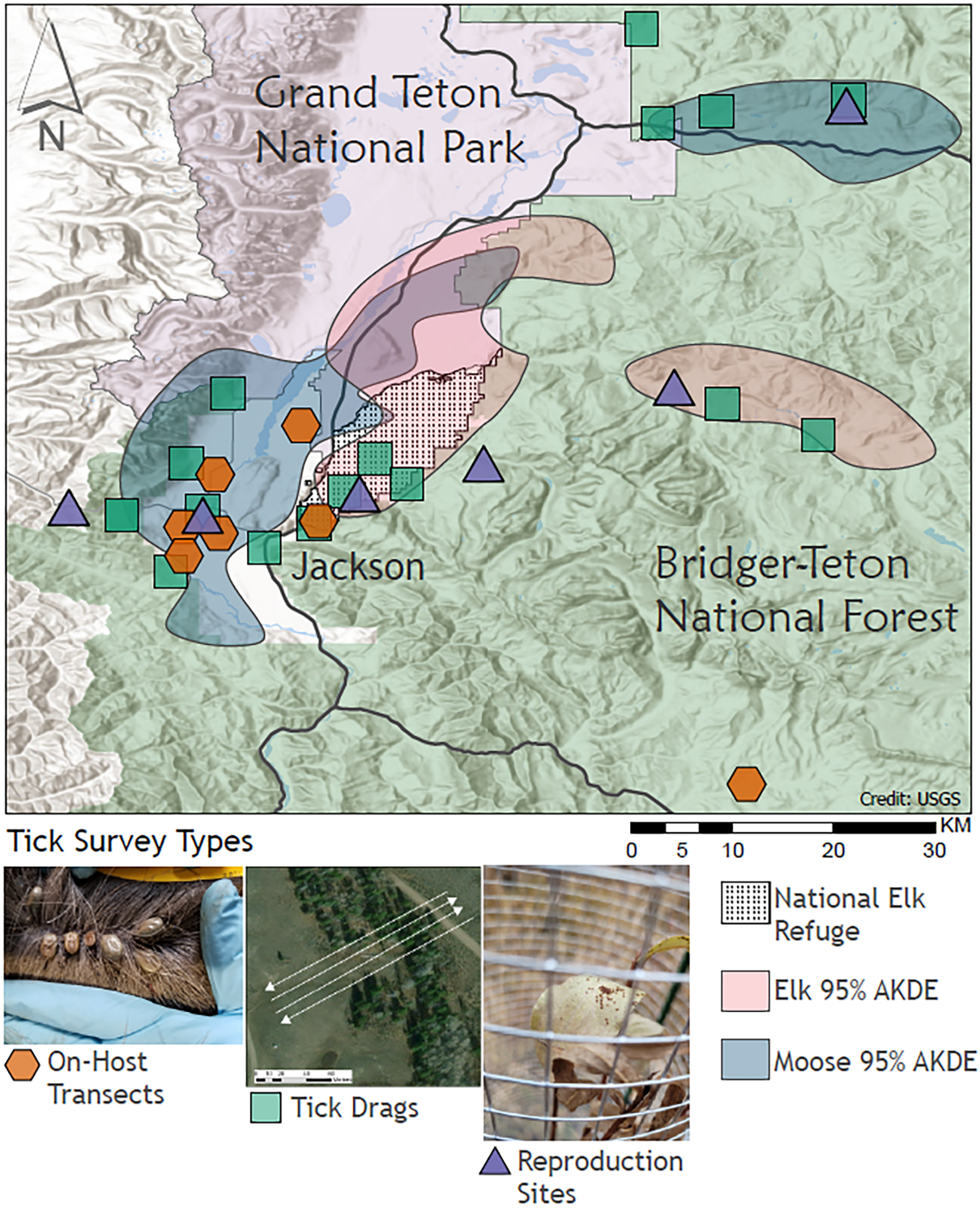


FIGURE 2 Map depicting generalized locations of elk and moose winter tick survey locations in Jackson Hole, Wyoming. Symbols with colors denote different experiment sites. Pink polygons represent smoothed autocorrelated kernel density estimates (AKDEs) of 2022 elk spring ranges using $n = 66$ collar datasets while blue polygons represent spring AKDEs from $n = 12$ moose collar datasets (2022) and $n = 22$ historical moose collar datasets (2006). Graphic credit: Emma Tomaszewski, U.S. Geological Survey.

(Figure 2). Vegetation at lower elevations is dominated by sagebrush (*Artemisia* spp.) communities with willow (*Salex* spp.) and cottonwood (*Populus angustifolia*) galleries in riparian areas. Mixed conifer and aspen forests dominate at mid-elevations including lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*). Spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are common at

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mid-high elevations. Many moose and elk in this ecosystem are migratory, spending the winter at low elevations and migrating to higher elevations in the summer. However, some moose are resident, living year-round near human development on private lands. Likewise, the elk population is shifting to more short-distance migrants and residents over time (Cole et al., 2015).

Winter tick reproduction surveys (Dataset 1)

The reproductive output of ticks that feed on moose and elk can serve as a measure of their overall competency as winter tick hosts. We recovered fed adult female winter ticks from moose ($n = 50$ ticks, $n = 34$ moose sites) and elk ($n = 48$ ticks, $n = 29$ elk sites) at bedding and necropsy sites from April to May 2022. Fed adult female ticks were weighed and deployed in reproduction monitoring stations (one tick per station) in the Blackrock and Jackson districts of Bridger-Teton National Forest, the NER, and along the banks of the Snake River. Each station consisted of a circular enclosure of wire mesh with a 50-cm radius and organdy mesh along the first 10 cm of fencing above ground or snow level to prevent ticks from escaping. Monitoring stations were stratified across open and closed habitats and along an elevational gradient (Appendix S1: Figure S3). After deployment, we monitored stations weekly for survival and oviposition (i.e., egg laying) until the end of May by which time all adult ticks were presumed dead or were confirmed or suspected to have oviposited underneath the available leaf litter layer. We returned to monitoring stations in mid-September 2022 and conducted weekly surveys to identify larval activity timing and abundance by visually inspecting vegetation for questing larvae within the enclosure, then dragging a 1-m^2 flannel cloth across vegetation for quantification.

Winter tick on-host infestation load surveys (Dataset 2)

One sign of host competency, infestation burden, can be measured in the winter tick system via on-host surveys. We surveyed individual adult moose ($n = 19$ live, $n = 11$ dead) and elk ($n = 12$ live, $n = 22$ dead) hides for winter ticks in the Jackson region from 2020 to 2023 during the months of January–March using the line transect method developed by Sine et al. (2009). This sampling window was chosen to occur after questing larvae (first life stage) have attached to a host, but before fed adult female ticks drop off their host in spring. Briefly, line transects were surveyed by recording winter tick numbers and life stages along four parallel 10-cm hide transects along the withers, shoulders, and rump of both sides of the animal if available. Samples of winter ticks were collected from each animal and stored in 75% EtOH to be identified via dichotomous key (Brinton et al., 1965). Live moose and elk tick surveys were opportunistically undertaken alongside existing Wyoming Game and Fish Department (WGFD) collaring initiatives or health sampling and recently deceased animals were surveyed within an estimated 6 h of death, the time after which winter ticks have been observed detaching from deceased hosts (Drew & Samuel, 1985). Moose and elk that were sampled for ticks were in the southern portion of the study area (Figure 2).

Larval winter tick drag surveys in host-associated habitats (Dataset 3)

We acquired GPS collar information for elk ($n = 66$) and moose ($n = 12$) in the Jackson region and used an autocorrelated kernel density estimation (AKDE) method to construct spring (April–May) 2022 utilization distributions then stratified a total of 200 transects of 250 m in length tick drag transects in habitats likely dominated by elk, moose, and both species (Silva et al., 2022). Designations for transect locations as "elk," "moose," or "elk and moose" were based primarily on the AKDEs of collared animals in 2022 (Figure 2). Telemetry data from 22 collared moose in the spring of 2006 were also used to approximate winter tick drop-off locations in the northern region of our study area (Becker, 2011). Tick drags were conducted at least twice between September 20 and November 12, 2022. We surveyed a transect by dragging a 1-m^2 flannel cloth across the prescribed area and checking for any attached larvae approximately every 10 paces. If larvae were found, they were extracted from the drag cloth using a lint roller and placed into a plastic bag for quantification. We then dragged the flannel cloth across nearby vegetation in a spiral pattern up to 10 m away from the original detection event to ensure any nearby larvae were also collected. After completing a spiral drag, we would continue along the original 250-m transect. Transects were not sampled on days where heavy rain or winds exceeding 32 km/h were expected.

Genome-wide SNPs

We collected winter ticks from live (ground darting and corral trap capture events) and dead (road-killed and necropsies) moose and elk from 2020 to 2023 to compare

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genetic structuring within winter tick populations based on sampling location versus host association. Ticks were collected from 40 elk and 27 moose from areas around Jackson, Wyoming, and 12 elk and 7 moose from areas near Pinedale, Wyoming. Winter ticks ($n = 16$) were also sourced from Idaho and Maine to serve as genetic outgroups for comparison with northwestern Wyoming ticks (Appendix S1: Section S1). Although at least five ticks were collected from each animal sampled, only a single tick sample (one tick if adults or nymphs or 10 larvae) was submitted for sequencing to avoid sampling-related ticks from the same clutch.

Tick samples ($n = 102$) were sent to Diversity Arrays Technology Pty Ltd. (DArT), Canberra, Australia, for DNA extraction and DArTseq sequencing. Briefly, DArTseq can be used for genome-wide diversity studies where no reference genome exists as is the case for *D. albipictus*. Samples were digested with restriction enzymes *PstI* and *SphI* and sequenced on an Illumina HiSeq 2500. SNPs were filtered and reported using proprietary DArT software.

SNPs were further filtered in *RStudio* (RStudio Team, 2023) using the package *dartR* (Gruber et al., 2018). A total of 88,506 individual SNPs were identified and were filtered according to the following quality control criteria: (1) more than one SNP found per locus (minor allele removed), (2) the SNP locus has more than 10% missing data, (3) individuals have more than 10% missing data, and (4) minimum allele frequency (MAF) was lower than 0.05 (Ferrante et al., 2022; Georges et al., 2018).

Statistical analyses

We analyzed the three presented datasets using three models, each investigating variable impacts on three responses: larvae production, on-host infestation load, and tick drag larval abundance. We used generalized linear and mixed-effects models (GLM and GLMMs) to analyze the effect of host species associations on dependent variables while accounting for other variables known to affect winter tick abundances (Appendix S1: Table S1) (Bergeron & Pekins, 2014; Chenery et al., 2020). Total larval abundance per reproduction monitoring station was regressed against host species of origin (elk or moose), mothers' mass, canopy cover (open or closed), elevation (in meters), and site (NER, Bridger-Teton National Forest, Snake River bank) as a random effect with intercepts varying across sites. Infestation density (in tick counts per surveyed unit in square centimeter) as determined by on-host hide transects was regressed against host species (elk or moose) and host status (alive or dead) nested within sampling year (2020:2023). Larval abundance per tick drag transect was regressed against likely dominant host species in spring (elk, moose, or both) and site as a random effect which allowed intercepts to vary across sites. We also used a GLM to investigate the effect of host association (elk or moose) on tick mass (scaled, in milligrams) using a GLM with a lognormal distribution. The tick drag abundance and on-host transect count models were fit with a negative binomial distribution while the reproduction model was fit with a quasi-Poisson distribution using the *lme4*, *MASS*, and *glmer* packages due to overdispersion in the data (Bates et al., 2009; Faraway, 2016; Ripley et al., 2013).

We visually assessed population genetic structuring in the filtered SNP dataset using a principal coordinates analysis (PCA) in the package *adegenet* (Jombart, 2008). We also estimated population genetic structure using the *LEA* package to identify the number of ancestral populations (Frichot & François, 2015). *LEA* can be used to estimate admixture coefficients assuming K ancestral populations using latent factor mixed modeling technique. Optimal K was estimated using locus-specific p and z scores for K ranging from 1 to 10 clusters. We calculated the fixation index (F_{ST}) values between populations using the *StAMPP* package with 999 bootstrap replicates (Pembleton et al., 2013). The fixation index is a coefficient of inbreeding that measures genetic differentiation among subpopulations with values ranging from 0 to 1, with zero indicating complete panmixia of two groups (no genetic distinction, groups are interbreeding) and 1 indicating groups do not share any genetic diversity.

RESULTS

While winter ticks that fed on elk produced on average fewer larvae (elk: mean = 241, median = 50, 95% CI = 158–323) than those fed on moose (moose: mean = 309, median = 97, 95% CI = 214–405), this difference was not significant given the variability observed ($\beta = 0.310$, SE = 0.255, $t = 1.217$, $p = 0.227$, df = 97) (Figure 3a, Appendix S1: Tables S1 and S2). Larvae from both hosts began questing between September 26 and September 29, 2022. We also looked at evidence for an effect of host association on tick mass and found none ($\beta = 0.046$, SE = 0.068, $z = 0.677$, $p = 0.499$, df = 97). We observed no clear differences between infestation loads on moose (mean = 66, median = 44, 95% CI = 44–87) and elk (mean = 66, median = 65, 95% CI = 53–79) with a small expected increase of 0.064 in log expected counts of winter ticks on moose compared with elk ($\beta = 0.064$, SE = 0.191, $z = 0.335$, $p = 0.738$, df = 63) (Figure 3b, Appendix S1:

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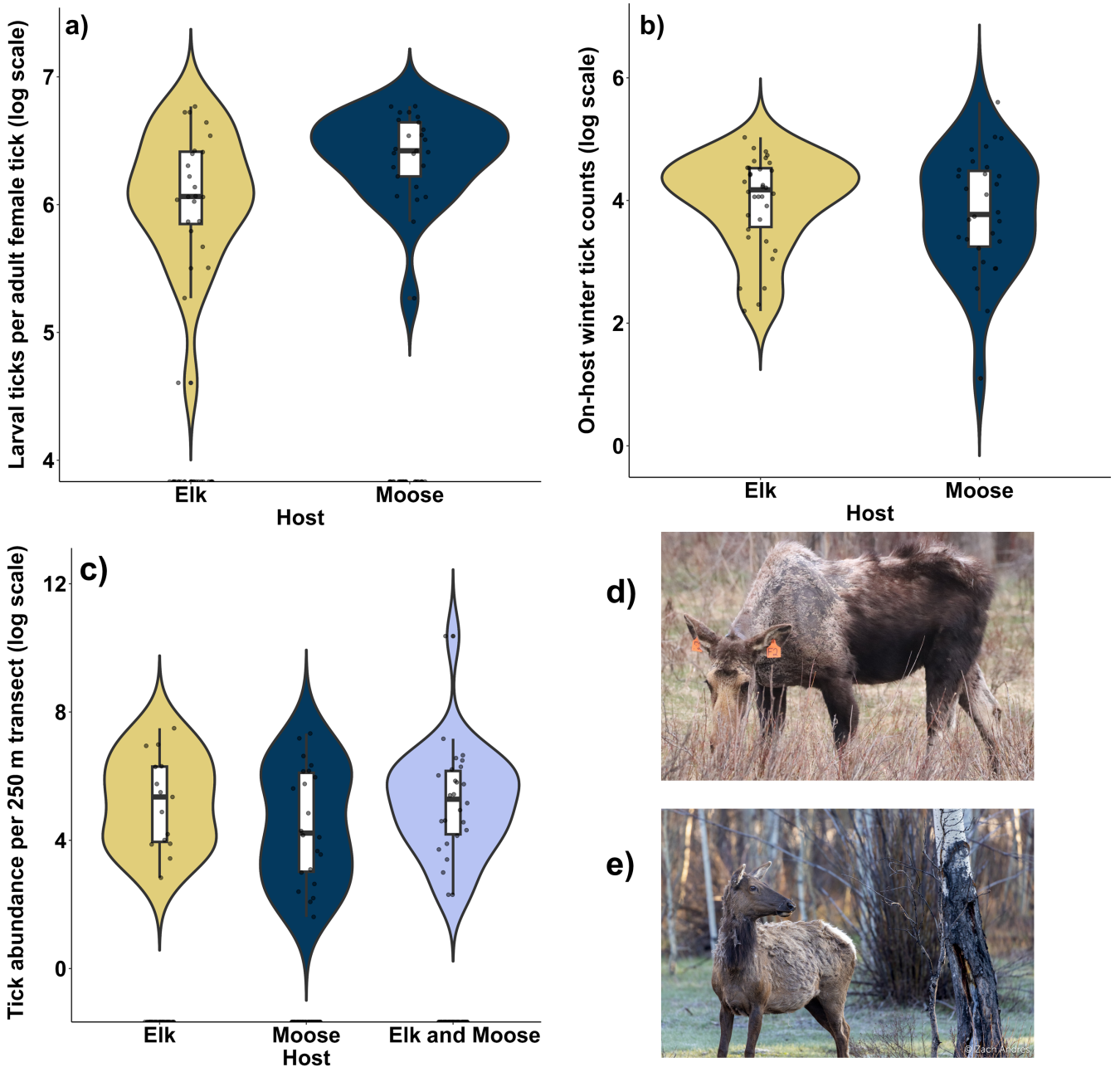


FIGURE 3 Differences in (a) larvae production of winter ticks (*Dermacentor albipictus*) from elk (*Cervus canadensis*) and moose (*Alces alces*). (b) Total tick counts on elk and moose using the Sine et al. (2009) transect method. (c) Questing larval winter tick abundance at sites predominately used by elk, moose, or both species during the spring drop-off period. Responses are presented on the log scale for easier visualization. (d) Photograph taken in May 2022 of an adult cow moose in Jackson, Wyoming, displaying hair loss along the withers and shoulders. Photograph taken by Troy Koser. (e) Photograph of an adult cow elk taken during the spring season in Jackson, Wyoming. Photo credit: Zach Andres.

Tables S1 and S2). We found variability in the average abundance of winter tick larvae found in spring habitats dominated by elk (mean = 101, 95% CI = 22–180), moose (mean = 50, 95% CI = 15–85), or both species (mean = 320, 95% CI = 0–836) but no statistical differences in the expected log counts of winter ticks between these groups ($\beta = -1.761{:}0.001$, SE = 1.314:1.285, $z \sim 0.001$, $p > 0.1$, df = 199) (Figure 3c; Appendix S1: Tables S1 and S2).

Genetic analyses using DArTseq identified 88,506 SNPs from 88 winter tick samples from elk and moose hosts. Our filtering criterion yielded 2793 informative SNPs from 65 winter tick samples (Jackson: $n = 51$, Pinedale: $n = 14$). The PCA explained 6.5% of the

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observed genetic variation in SNPs, with two overlapping groups: Jackson versus Pinedale winter ticks (Figure 4a). Individual ticks appeared to cluster together in the PCA based on location (Jackson and Pinedale) as opposed to host species (elk and moose). The genetic structuring across geographic locations was nearly 10 times stronger than any observed structuring between host species within a region (F_{ST} between hosts: 0.0013, df = 1/64, F_{ST} between sampling locations: 0.0238, df = 1/64). Cross-entropy criterion calculations supported $K = 3$ clusters with population structure analyses representing two populations as Jackson and Pinedale (Figures 4b and 5; Appendix S1: Figure S4).

DISCUSSION

We found that winter tick host competency metrics were similar between elk and moose. Given the abundance of elk relative to moose in the Western United States, elk

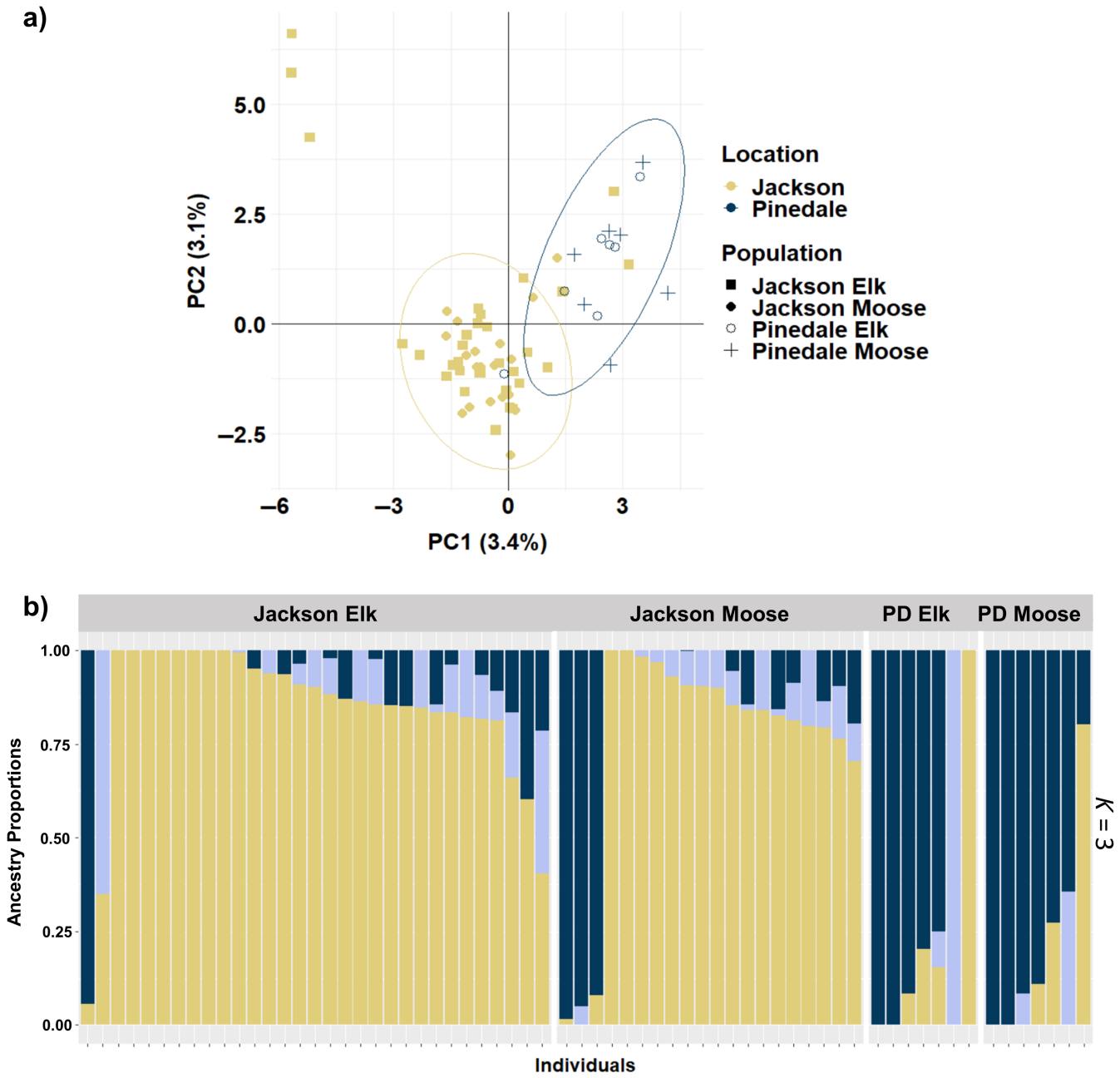


FIGURE 4 (a) Principal coordinates analysis (PCA) results using genomic single nucleotide polymorphisms from winter tick (*Dermacentor albipictus*) extracted from elk (*Cervus canadensis*) and moose (*Alces alces*) in Jackson and Pinedale, Wyoming. (b) Results of the ancestry proportions analysis using the *LEA* package. Support was found for $K = 3$ clusters (Appendix S1: Figure S4).

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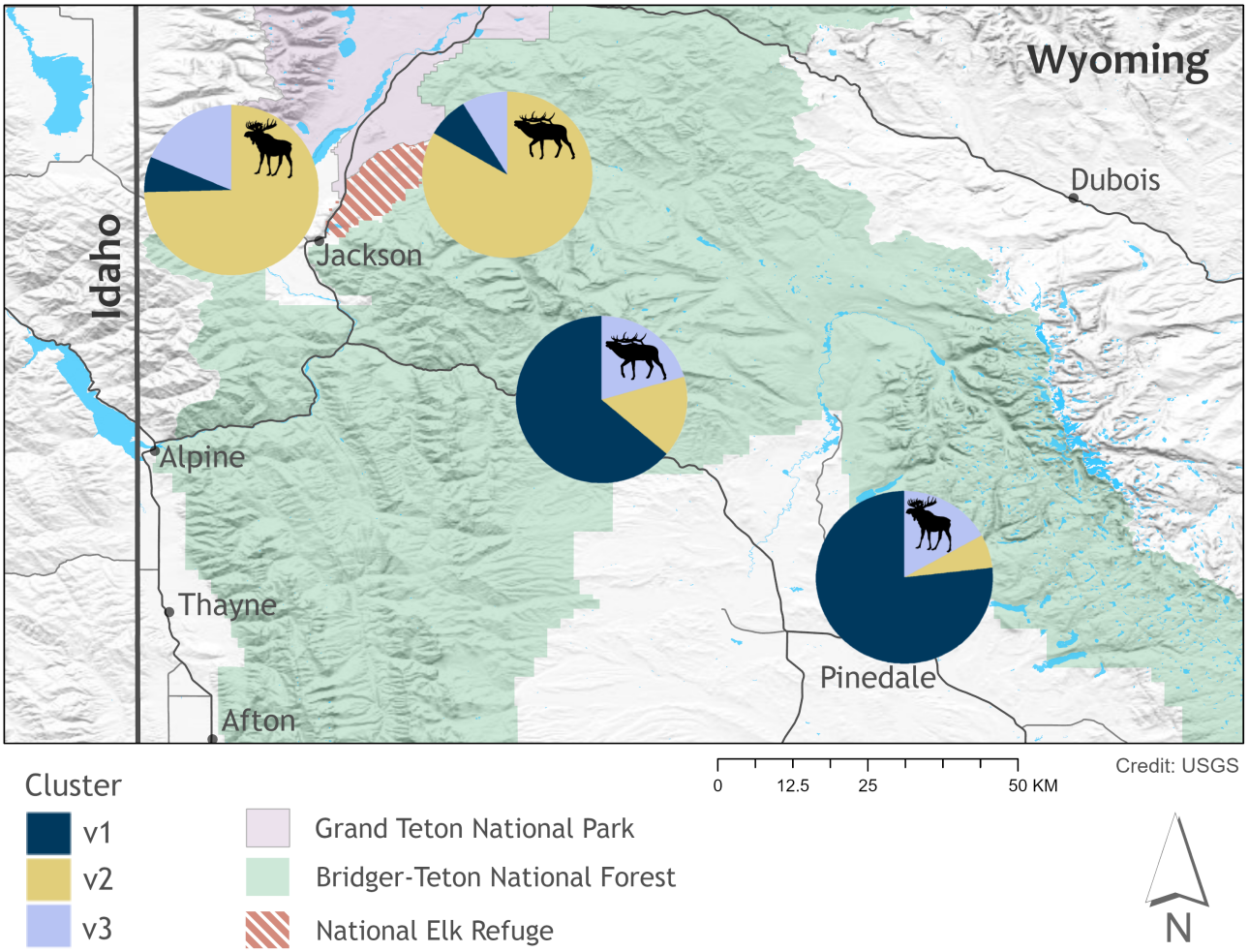


FIGURE 5 Map of northwestern Wyoming with pie charts representing aggregate ancestry proportions (see Figure 4a) for winter ticks (*Dermacentor albipictus*) from elk (*Cervus canadensis*) and moose (*Alces alces*) sampled near Jackson and Pinedale, Wyoming, with colors and proportions representing averaged results from *LEA* estimated ancestry probability proportions. Graphic credit: Emma Tomaszewski, U.S. Geological Survey.

are likely to play an important role in winter tick population dynamics in this region. Elk had similar infestation rates and supported similar tick reproduction rates as moose, even though moose have received disproportionate research attention on this issue (Figure 3a,b). We also found similar larval abundance and activation timing when we examined habitats used predominately by elk, moose, and both species during winter tick drop-off periods (Figure 3c). Furthermore, we found greater population structuring based on sampling location within the Jackson region as opposed to structuring based on host association (Figure 5), implying gene flow between winter ticks from differing hosts and supporting our hypothesis that winter ticks mix between hosts. Together, these results suggest that elk and moose share similar competency as winter tick hosts and implicates elk abundance and movement patterns as potentially critical drivers of winter tick dynamics in the Jackson region.

Our results differ from previous work on winter tick reproduction rates that demonstrated higher survival rates and faster engorgement rates when fed on moose compared with mule deer, elk, and white-tailed deer (Drew, 1984; Welch et al., 1991). These studies nicely control for differences in tick exposure, but our field data suggest that winter tick encounter rates may differ between moose and elk such that infestation loads appear similar between the two host species. In addition, other work suggests a coupling of tick and moose populations, implying that moose may be an especially competent host and disproportionately drive winter tick populations (Welch et al., 1991). However, the degree of affinity between winter tick and moose populations may differ across regions in North America since the availability of different competent host species varies. Specifically, the higher abundances and densities of moose in the Northeastern United States and parts of Canada may

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result in a tighter relationship between winter tick and moose compared with systems in the Western United States with lower moose densities and relatively higher elk or mule deer populations. In addition, the winter tick's broad distribution and wide host range may have led to unique population-specific attributes, which could explain why different regions in North America could see variations in parasite–host competency metrics.

Future studies could explore additional measurements of host competency by comparing elk and moose immune responses to infestation as well as differences between moose subspecies immunological profiles, which may illuminate some reasons why moose in the Western United States seem to be infested at lower rates than Midwest and Northeastern moose but still experience negative health outcomes, albeit at much lower population proportions (Debow et al., 2021; DeCesare et al., 2024; Dunfey-Ball, 2017; Jones et al., 2017; Ruprecht et al., 2020). While we did examine several aspects of winter tick biology in relation to host association, we do not have data on the rates at which ticks from one host attach to another within a transmission season. We also lack comprehensive winter tick datasets on other common ungulate hosts, such as mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*), which may play important roles in moving winter ticks between moose and elk habitats. Given the data presented here, we would hypothesize that winter ticks on other ungulate hosts are likely similarly structured spatially, but not by host species.

If winter ticks in the diverse ungulate community of the Jackson region infest a wide range of similarly competent hosts, then the population levels and movement patterns of a more-abundant host like elk may indirectly impact moose populations via apparent competition. Moose population declines have been reported across the Western United States, but causes are still unclear (Nadeau et al., 2017). Research on the major drivers of western moose population decline and dampening recovery rates is still needed, but our results suggest that parasite-mediated apparent competition from much larger non-moose ungulate populations may be a contributing factor. We expect parasite-mediated competitive interactions may increase in the future as long-distance elk migrations decline and more elk become residents or short-distance migrants, potentially creating more overlap between elk and moose during key times of parasite lifecycles (Cole et al., 2015). Additionally, warmer and drier spring and fall seasons may lengthen parasite transmission seasons, therefore increasing the window of opportunity for migrating ungulates to disperse parasites like winter ticks across shared ranges (Pouchet et al., 2024; Weiskopf et al., 2020). These same conditions could also increase abundances the winter tick and affect the life cycles of other moose parasites like the meningeal worm (*Parelaphostrongylus tenuis*) and arterial worm (*Elaeophora schneideri*) (DeCesare et al., 2024; Drew & Samuel, 1985; Dunfey-Ball, 2017; Healy et al., 2020; Holmes et al., 2018; Jones et al., 2017; Lankester, 2018; Nadeau et al., 2017; Pouchet et al., 2024; Samuel, 2007). Cold-adapted moose in ecosystems like the GYE are also near the southern extent of their range, potentially exacerbating disease issues by reducing energy budgets available for immune defenses or defensive behaviors like grooming (Molnár et al., 2013). Rising temperatures under climate change are likely to only exacerbate thermal stress for moose at the lower latitudes of their range.

Managers concerned with winter tick infestations on vulnerable hosts like moose may wish to consider management options to reduce elk abundance and overlap between spring elk and fall moose habitats. These management actions, such as increased elk hunting in targeted areas, may align with management plans for other diseases like brucellosis or chronic wasting disease (Proffitt et al., 2015; Williams et al., 2002). Future research on winter tick dynamics in western North America would ideally consider non-moose hosts alongside known drivers like climate and moose density (Dunfey-Ball, 2017; Holmes et al., 2018; Rosenblatt et al., 2021). As parasite-tolerant hosts continue to dominate disturbed landscapes, we may expect shared parasites to dampen the recovery of rare or specialized hosts and must continue to explore consequences for parasite–host coevolution.

AUTHOR CONTRIBUTIONS

Troy Koser collected and analyzed data and lead manuscript writing. Alyson Courtemanch, Benjamin Wise, Sarah Dewey, Amy Girard, Jared Rogerson, Brandon Scurlock, and Gary Fralick provided data as well as fieldwork logistical help. Paul Cross, Laura Thompson, Kennan Oyen, and Alynn Martin provided analysis advice. Paul Cross, Laura Thompson, Kennan Oyen, Alynn Martin, Alyson Courtemanch, Amy Girard, and Brandon Scurlock provided manuscript review comments and edits.

ACKNOWLEDGMENTS

This research was supported by the U.S. Geological Survey (USGS) National Climate Adaptation Science Center, USGS Northern Rocky Mountain Science Center, and Montana State University-Bozeman. Funding for live moose captures was provided by Teton County Government, Teton Conservation District, Wyoming Game and Fish Department, Wyoming Governor's Big Game License Coalition, and Veterinary

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Initiative for Endangered Wildlife. Winter tick samples from moose were provided by generous collaborators without whom this study would not be possible: Lee Kantar (Maine Department of Inland Fisheries & Wildlife), Janet Rachlow (University of Idaho), and Holly Miyazaki (Idaho Department of Fish and Game). We thank our lab technician Anna DeCann and field technicians Zach Andres and Eva Laubach. We are grateful to the logistic and support staff at Grand Teton National Park, National Elk Refuge, Jackson Hole Land Trust, Teton County Parks and Recreation Department, and Bridger-Teton National Forest for providing research permits, lodging, emergency support, and technical assistance. We thank the Jackson Hole Wildlife Foundation and Teton County Weed & Pest District for connecting the authors to private landowners and for other support. Troy Koser would like to thank his academic advisors, David McWethy and Raina Plowright, for academic support and encouragement. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are sensitive, and data sharing agreements used to facilitate this study preclude public data sharing for host telemetry datasets. Inquiries on the moose or elk telemetry data can be directed to Wyoming Game and Fish Department https://wgfd.wyo.gov/contact-us. Data (Koser et al., 2024) for analyses of winter tick reproduction rates, infestation rates, and abundance surveys are available from the USGS ScienceBase-Catalog: https://doi.org/10.5066/P13RAIEZ. Data for genetic analyses are available from GenBank via the National Center for Biotechnology Information BioProject Accession PRJNA1165274: https://www.ncbi.nlm.nih.gov/bioproject/?term=PRJNA1165274.

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REFERENCES

Aliee, M., M. J. Keeling, and K. S. Rock. 2021. "Modelling to Explore the Potential Impact of Asymptomatic Human Infections on Transmission and Dynamics of African Sleeping Sickness." *PLoS Computational Biology* 17: e1009367.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, and P. Green. 2009. "Package 'lme4'." cran-r. http://lme4.r-forge.r-project.org.

Becker, S. 2011. "Spatial and Temporal Characteristics of Moose Highway Crossings during Winter in the Buffalo Fork Valley, Wyoming." *Alces* 47: 69–81.

Bergeron, D. H., and P. J. Pekins. 2014. "Evaluating the Usefulness of Three Indices for Assessing Winter Tick Abundance in Northern New Hampshire." *Alces* 50: 1–15.

Bondo, K. J., B. Macbeth, H. Schwantje, K. Orsel, D. Culling, B. Culling, M. Tryland, I. H. Nymo, and S. Kutz. 2019. "Health Survey of Boreal Caribou (*Rangifer tarandus caribou*) in Northeastern British Columbia, Canada." *Journal of Wildlife Diseases* 55: 544–562.

Brinton, E. P., D. E. Beck, and D. M. Allred. 1965. "Identification of the Adults, Nymphs and Larvae of Ticks of the Genus Dermacentor Koch (Ixodidae) in the Western United States." *Brigham Young University Science Bulletin, Biological Series* 5: 1.

Buhnerkempe, M. G., M. G. Roberts, A. P. Dobson, H. Heesterbeek, P. J. Hudson, and J. O. Lloyd-Smith. 2015. "Eight Challenges in Modelling Disease Ecology in Multi-Host, Multi-Agent Systems." *Epidemics* 10: 26–30.

Calvente, E., S. Pelletier, J. Banfield, J. Brown, and N. Chinnici. 2020. "Prevalence of Winter Ticks (*Dermacentor albipictus*) in Hunter-Harvested Wild Elk (*Cervus canadensis*) from Pennsylvania, USA (2017–2018)." *Veterinary Sciences* 7: 177.

Chenery, E. S., N. J. Harms, H. Fenton, N. E. Mandrak, and P. K. Molnár. 2023. "Revealing Large-Scale Parasite Ranges: An Integrated Spatiotemporal Database and Multisource Analysis of the Winter Tick." *Ecosphere* 14: e4376.

Chenery, E. S., N. J. Harms, N. E. Mandrak, and P. K. Molnár. 2020. "First Records of *Dermacentor albipictus* Larvae Collected by Flagging in Yukon, Canada." *Parasites & Vectors* 13: 565.

Cole, E. K., A. M. Foley, J. M. Warren, B. L. Smith, S. R. Dewey, D. G. Brimeyer, W. S. Fairbanks, H. Sawyer, and P. C. Cross. 2015. "Changing Migratory Patterns in the Jackson Elk Herd." *The Journal of Wildlife Management* 79: 877–886.

Cronin, J. P., M. E. Welsh, M. G. Dekkers, S. T. Abercrombie, and C. E. Mitchell. 2010. "Host Physiological Phenotype Explains Pathogen Reservoir Potential." *Ecology Letters* 13: 1221–32.

Dean, R., M. Gocke, B. Holz, S. Kilpatrick, T. J. Kreeger, B. M. Scurlock, S. Smith, E. T. Thorne, and S. Werbelow. 2004. *Elk Feedgrounds in Wyoming*. Cheyenne, WY: Wyoming Game and Fish Department.

Debow, J., J. Blouin, E. Rosenblatt, C. Alexander, K. Gieder, W. Cottrell, J. Murdoch, and T. Donovan. 2021. "Effects of Winter Ticks and Internal Parasites on Moose Survival in Vermont, USA." *The Journal of Wildlife Management* 85: 1423–39.

DeCesare, N. J., R. B. Harris, M. P. Atwood, E. J. Bergman, A. B. Courtemanch, P. C. Cross, G. L. Fralick, K. R. Hersey, M. A. Hurley, and T. M. Koser. 2024. "Warm Places, Warm Years, and Warm Seasons Increase Parasitizing of Moose by Winter Ticks." *Ecosphere* 15: e4799.

Downs, C. J., L. A. Schoenle, B. A. Han, J. F. Harrison, and L. B. Martin. 2019. "Scaling of Host Competence." *Trends in Parasitology* 35: 182–192.

Drew, M. L. 1984. *Reproduction and Transmission of the Winter Tick, Dermacentor albipictus (Packard) in Central Alberta*. Edmonton, Alberta: University of Alberta.

Drew, M. L., and W. M. Samuel. 1985. "Factors Affecting Transmission of Larval Winter Ticks, *Dermacentor albipictus*

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(Packard), to Moose, *Alces alces* L., in Alberta, Canada." *Journal of Wildlife Diseases* 21: 274–282.

Dunfey-Ball, K. R. 2017. *Moose Density, Habitat, and Winter Tick Epizootics in a Changing Climate*. Durham, New Hampshire: University of New Hampshire.

Faraway, J. J. 2016. *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Boca Raton, FL: CRC Press.

Ferrante, J. A., C. H. Smith, L. M. Thompson, and M. E. Hunter. 2022. "Genome-Wide SNP Analysis of Three Moose Subspecies at the Southern Range Limit in the Contiguous United States." *Conservation Genetics* 23: 109–121.

Frichot, E., and O. François. 2015. "LEA: An R Package for Landscape and Ecological Association Studies." *Methods in Ecology and Evolution* 6: 925–29.

Georges, A., B. Gruber, G. B. Pauly, D. White, M. Adams, M. J. Young, A. Kilian, X. Zhang, H. B. Shaffer, and P. J. Unmack. 2018. "Genomewide SNP Markers Breathe New Life into Phylogeography and Species Delimitation for the Problematic Short-Necked Turtles (Chelidae: Emydura) of Eastern Australia." *Molecular Ecology* 27: 5195–5213.

Gibb, R., D. W. Redding, K. Q. Chin, C. A. Donnelly, T. M. Blackburn, T. Newbold, and K. E. Jones. 2020. "Zoonotic Host Diversity Increases in Human-Dominated Ecosystems." *Nature* 584: 398–402.

Gilbert, L., R. Norman, K. Laurenson, H. W. Reid, and P. J. Hudson. 2001. "Disease Persistence and Apparent Competition in a Three-Host Community: An Empirical and Analytical Study of Large-Scale, Wild Populations." *Journal of Animal Ecology* 70: 1053–61.

Glines, M. V. 1983. *The Winter Tick, Dermacentor albipictus (Packard, 1869): Its Life History, Development at Constant Temperatures and Physiological Effects on Moose, Alces alces L.* Edmonton, Alberta: University of Alberta.

Gottdenker, N. L., D. G. Streicker, C. L. Faust, and C. Carroll. 2014. "Anthropogenic Land Use Change and Infectious Diseases: A Review of the Evidence." *EcoHealth* 11: 619–632.

Grosholz, E. D. 1992. "Interactions of Intraspecific, Interspecific, and Apparent Competition with Host-Pathogen Population Dynamics." *Ecology* 73: 507–514.

Gruber, B., P. J. Unmack, O. F. Berry, and A. Georges. 2018. "Dartr: An r Package to Facilitate Analysis of SNP Data Generated from Reduced Representation Genome Sequencing." *Molecular Ecology Resources* 18: 691–99.

Healy, C., P. J. Pekins, S. Atallah, and R. G. Congalton. 2020. "Using Agent-Based Models to Inform the Dynamics of Winter Tick Parasitism of Moose." *Ecological Complexity* 41: 100813.

Holmes, C. J., C. J. Dobrotka, D. W. Farrow, A. J. Rosendale, J. B. Benoit, P. J. Pekins, and J. A. Yoder. 2018. "Low and High Thermal Tolerance Characteristics for Unfed Larvae of the Winter Tick *Dermacentor albipictus* (Acari: Ixodidae) with Special Reference to Moose." *Ticks and Tick Borne Diseases* 9: 25–30.

Hudson, P., and J. Greenman. 1998. "Competition Mediated by Parasites: Biological and Theoretical Progress." *Trends in Ecology & Evolution* 13: 387–390.

Jombart, T. 2008. "Adegenet: A R Package for the Multivariate Analysis of Genetic Markers." *Bioinformatics* 24: 1403–5.

Jones, H., P. J. Pekins, L. E. Kantar, M. O'Neil, and D. Ellingwood. 2017. "Fecundity and Summer Calf Survival of Moose during 3 Successive Years of Winter Tick Epizootics." *Alces* 53: 85–98.

Jones, H., P. Pekins, L. Kantar, I. Sidor, D. Ellingwood, A. Lichtenwalner, and M. O'Neal. 2019. "Mortality Assessment of Moose (*Alces alces*) Calves during Successive Years of Winter Tick (*Dermacentor albipictus*) Epizootics in New Hampshire and Maine (USA)." *Canadian Journal of Zoology* 97: 22–30.

Koser, T. M., E. M. Tomaszewski, A. B. Courtemanch, K. Oyen, J. Rogerson, A. Girard, B. Wise, B. Scurlock, and P. C. Cross. 2024. "Winter Tick Host Competency Data from Elk and Moose the Southern Greater Yellowstone Ecosystem 2020–2023." U.S. Geological Survey Data Release. https://doi.org/10.5066/P13RAIEZ.

Kutz, S. J., E. J. Jenkins, A. M. Veitch, J. Ducrocq, L. Polley, B. Elkin, and S. Lair. 2009. "The Arctic as a Model for Anticipating, Preventing, and Mitigating Climate Change Impacts on Host-Parasite Interactions." *Veterinary Parasitology* 163: 217–228.

Lankester, M. W. 2018. "Considering Weather-Enhanced Transmission of Meningeal Worm, *Parelaphostrongylus tenuis*, and Moose Declines." *Alces* 54: 1–13.

Levine, R. S., D. G. Mead, G. L. Hamer, B. J. Brosi, D. L. Hedeen, M. W. Hedeen, J. R. McMillan, D. Bisanzio, and U. D. Kitron. 2016. "Supersuppression: Reservoir Competency and Timing of Mosquito Host Shifts Combine to Reduce Spillover of West Nile Virus." *The American Journal of Tropical Medicine and Hygiene* 95: 1174–84.

LoGiudice, K., R. S. Ostfeld, K. A. Schmidt, and F. Keesing. 2003. "The Ecology of Infectious Disease: Effects of Host Diversity and Community Composition on Lyme Disease Risk." *Proceedings of the National Academy of Sciences of the United States of America* 100: 567–571.

Machtinger, E. T., H. R. Springer, J. E. Brown, and P. U. Olafson. 2021. "Sudden Mortality in Captive White-Tailed Deer with Atypical Infestation of Winter Tick." *Journal of Medical Entomology* 58: 1962–65.

Marm Kilpatrick, A., P. Daszak, M. J. Jones, P. P. Marra, and L. D. Kramer. 2006. "Host Heterogeneity Dominates West Nile Virus Transmission." *Proceedings of the Royal Society B: Biological Sciences* 273: 2327–33.

McLaughlin, R. F., and E. M. Addison. 1986. "Tick (*Dermacentor albipictus*)-Induced Winter Hair-Loss in Captive Moose (*Alces alces*)." *Journal of Wildlife Diseases* 22: 502–510.

Molnár, P. K., S. J. Kutz, B. M. Hoar, and A. P. Dobson. 2013. "Metabolic Approaches to Understanding Climate Change Impacts on Seasonal Host-Macroparasite Dynamics." *Ecology Letters* 16: 9–21.

Mooring, M. S., and W. M. Samuel. 1998. "The Biological Basis of Grooming in Moose: Programmed Versus Stimulus-Driven Grooming." *Animal Behaviour* 56: 1561–70.

Mooring, M. S., and W. M. Samuel. 1999. "Premature Loss of Winter Hair in Free-Ranging Moose (*Alces alces*) Infested with Winter Ticks (*Dermacentor albipictus*) Is Correlated with Grooming Rate." *Canadian Journal of Zoology* 77: 148–156.

Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006.

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"Pathogens, Nutritional Deficiency, and Climate Influences on a Declining Moose Population." *Wildlife Monographs* 166: 1–30.

Nadeau, M. S., N. J. DeCesare, D. Brimeyer, E. J. Bergman, R. B. Harris, K. R. Hersey, K. K. Huebner, P. E. Matthews, and T. P. Thomas. 2017. "Status and Trends of Moose Populations and Hunting Opportunity in the Western United States." *Alces* 53: 3.

Normandeau, J., C. Cassady St, S. J. Clair, M. H. Kutz, and E. H. Merrill. 2022. "What Makes Elk Tick: Winter Tick (*Dermacentor albipictus*) Grooming Behavior in Wild Elk (*Cervus canadensis*)." *Journal of Mammalogy* 103: 373–382.

Ostfeld, R. S., and F. Keesing. 2020. *Species that Can Make Us Ill Thrive in Human Habitats*. London: Nature Publishing Group.

Ostfeld, R. S., C. D. Canham, K. Oggenfuss, R. J. Winchcombe, and F. Keesing. 2006. "Climate, Deer, Rodents, and Acorns as Determinants of Variation in Lyme-Disease Risk." *PLoS Biology* 4: e145.

Pembleton, L. W., N. O. Cogan, and J. W. Forster. 2013. "St AMPP: An R Package for Calculation of Genetic Differentiation and Structure of Mixed-Ploidy Level Populations." *Molecular Ecology Resources* 13: 946–952.

Pouchet, C., C. Fernandez-Prada, C. Dussault, M. Leclerc, J. P. Tremblay, and S. D. Côté. 2024. "Linking Weather Conditions and Winter Tick Abundance in Moose." *The Journal of Wildlife Management* 88: e22551.

Proffitt, K. M., N. Anderson, P. Lukacs, M. M. Riordan, J. A. Gude, and J. Shamhart. 2015. "Effects of Elk Density on Elk Aggregation Patterns and Exposure to Brucellosis." *The Journal of Wildlife Management* 79: 373–383.

Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, D. Firth, and M. B. Ripley. 2013. "Package 'Mass'." cran r 538, 113–20.

Rosenblatt, E., J. DeBow, J. Blouin, T. Donovan, J. Murdoch, S. Creel, W. Rogers, K. Gieder, N. Fortin, and C. Alexander. 2021. "Juvenile Moose Stress and Nutrition Dynamics Related to Winter Ticks, Landscape Characteristics, Climate-Mediated Factors and Survival." *Conservation Physiology* 9: coab048.

RStudio Team. 2023. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. http://www.rstudio.com/.

Ruprecht, J. S., D. N. Koons, K. R. Hersey, N. T. Hobbs, and D. R. MacNulty. 2020. "The Effect of Climate on Population Growth in a Cold-Adapted Ungulate at Its Equatorial Range Limit." *Ecosphere* 11: e03058.

Samuel, W. M. 1989. "Locations of Moose in Northwestern Canada with Hair Loss Probably Caused by the Winter Tick, *Dermacentor albipictus* (Acari: Ixodidae)." *Journal of Wildlife Diseases* 25: 436–39.

Samuel, W. M. 2007. "Factors Affecting Epizootics of Winter Ticks and Mortality of Moose." *Alces* 43: 10.

Silva, I., C. H. Fleming, M. J. Noonan, J. Alston, C. Folta, W. F. Fagan, and J. M. Calabrese. 2022. "Autocorrelation-Informed Home Range Estimation: A Review and Practical Guide." *Methods in Ecology and Evolution* 13: 534–544.

Sine, M., K. Morris, and D. Knupp. 2009. "Assessment of a Line Transect Field Method to Determine Winter Tick Abundance on Moose." *Alces* 45: 143–46.

Timmerman, H. R., and A. R. Rodgers. 2017. "The Status and Management of Moose in North America – Circa 2015." *Alces* 53: 23.

Weiskopf, S. R., M. A. Rubenstein, L. G. Crozier, S. Gaichas, R. Griffis, J. E. Halofsky, K. J. W. Hyde, et al. 2020. "Climate Change Effects on Biodiversity, Ecosystems, Ecosystem Services, and Natural Resource Management in the United States." *Science of the Total Environment* 733: 137782.

Welch, D. A., W. M. Samuel, and C. J. Wilke. 1991. "Suitability of Moose, Elk, Mule Deer, and White-Tailed Deer as Hosts for Winter Ticks (*Dermacentor albipictus*)." *Canadian Journal of Zoology* 69: 2300–2305.

Williams, E. S., M. W. Miller, T. J. Kreeger, R. H. Kahn, and E. T. Thorne. 2002. "Chronic Wasting Disease of Deer and Elk: A Review with Recommendations for Management." *The Journal of Wildlife Management* 66: 551–563.

Wojdak, J. M., R. M. Edman, J. A. Wyderko, S. A. Zemmer, and L. K. Belden. 2014. "Host Density and Competency Determine the Effects of Host Diversity on Trematode Parasite Infection." *PLoS One* 9: e105059.

Wunschmann, A., A. G. Armien, E. Butler, M. Schrage, B. Stromberg, J. B. Bender, A. M. Firshman, and M. Carstensen. 2015. "Necropsy Findings in 62 Opportunistically Collected Free-Ranging Moose (*Alces alces*) from Minnesota, USA (2003-13)." *Journal of Wildlife Diseases* 51: 157–165.

Wyoming Game and Fish Department. 2021. Big Game Job Completion Report. Cheyenne, WY.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Koser, Troy, Alynn Martin, Alyson Courtemanch, Laura Thompson, Benjamin Wise, Gary Fralick, Sarah Dewey, et al. 2025. "Winter Tick Sharing between Ungulates in the Greater Yellowstone Ecosystem and Implications for Apparent Competition." *Ecosphere* 16(1): e70129. https://doi.org/10.1002/ecs2.70129

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