EXPLORING RELATIONSHIPS BETWEEN WINTER TICK (*DERMACENTOR ALBIPICTUS*) ECOLOGY, MOOSE (*ALCES ALCES*), AND CLIMATE IN JACKSON HOLE, WYOMING

by

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DEDICATION

This dissertation is dedicated to…

my partner, Tory Kirkeby, who helped ensure my mind, body, and soul would survive graduate school and who held my hand at the hardest of times.

in memory my grandpa, Randy Koser, who has always been proud of my work even when he didn't understand what I do.

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ABSTRACT

Global ecosystem changes are affecting how parasites and their hosts interact. Winter ticks (*Dermacentor albipictus*) are ectoparasites of moose (*Alces alces*) which can cause anemia, hair loss, and even death due to large numbers of hundreds to thousands of ticks feeding. Warming temperatures are expected to increase winter tick abundance and activity windows while habitat loss and other factors diminish moose nutritional conditions making them more susceptible to complications from tick infestations. Though some of these factors are well-studied in parts of Canada and the northeastern U.S., winter tick, moose, and climate interactions are not well understood in the western U.S. We surveyed winter ticks, moose, and elk in Jackson Hole, Wyoming from 2020-2023 and found elk to be feasible reservoirs for winter ticks, potentially impacting moose infestation rates. In 2021 we deployed scent detection dogs to find winter ticks in the field and determined that they are indeed capable of surveying for winter ticks but do not dramatically outperform the traditional tick drag survey. We found that average maximum temperature and vapor pressure deficit over summer affect winter tick occupancy rates but we did not find climate associations with winter tick abundance over three years of surveys in Jackson Hole. We did, however, find temperature to affect winter tick survival and reproduction in monitoring surveys, implying a potential mismatch between extrapolated climate datasets and conditions experienced by ticks. Finally, we found moose that spend more of their fall home range in 'urban' versus 'rural' landscapes and with higher spring and fall seasonal home range overlaps to be in higher hair loss categories. Future research in winter tick-moose systems, and in tick-borne disease research as a whole, should take into account host movement patterns and the potential impacts of multiple competent host species on the landscape.

CHAPTER ONE

INTRODUCTION

Studying Wildlife Disease Ecology in the Anthropocene

Ecosystems around the world are changing rapidly, affecting how pathogens and parasites interact with their hosts and the environment. Changing land-use patterns, increases in human movement and developments, and climate change are among the primary drivers of ecosystem changes threatening wildlife populations via disease (Altizer et al. 2013, Daszak, Cunningham and Hyatt 2000, Daszak, Cunningham and Hyatt 2001, Gottdenker et al. 2014, Polley, Hoberg and Kutz 2010). Species declines and extinctions often stem from a multitude of causes, chief among them can be disease-induced issues due to climate change-associated increases in parasite habitat suitability, increases in reservoir host populations and associated parasites, and novel movements of parasites with human transportation. For example, transportation of equipment and animals can introduce the pathogenic fungal species *Pseudogymnoascus destructans* (causative agent for white-nosed syndrome: WNS) and *Batrachochytrium dendrobatidis* (*i.e., Bd*, causative agent for chytridiomycosis) to susceptible bat and amphibian populations respectively, causing continent-wide population declines and extinctions (Bacigalupe et al. 2017, Hoyt, Kilpatrick and Langwig 2021, Leopardi, Blake and Puechmaille 2015, Reynolds and Barton 2013, Rohr, Halstead and Raffel 2011). Decreases in habitat quality and food availability due to land use changes are responsible for exacerbating disease issues for bat and amphibian populations in North America, reducing energy budgets available to survive high parasite burdens (Berger, Speare and Hyatt 1999, Johnson et al. 2021). Similarly, the northward expansion of white-tailed deer (*Odocoileus virginianus*) in the northern United States, partially due to warmer winters and increased habitat fragmentation and urban forage availability, has resulted in spillover of shared parasites like *Paralaphostrongylus tenuis* (*i.e.*, meningeal worm) to susceptible moose (*Alces alces*) populations (Ditmer et al. 2020, Lankester 2010, Lankester 2018, Schmitz and Nudds 1994). Just as there are rarely one or two primary causes of wildlife population decline, multiple drivers of ecosystem change tend to interact in several ways with wildlife disease systems, necessitating multidisciplinary research approaches to understand key relationships and develop interventions.

Parasite-host interactions under massive ecosystem perturbations like large-scale habitat loss or climate change are not static. In many cases, wildlife hosts have evolved complex relationships with their associated parasites or pathogens, responding to fluctuations in infestation loads or prevalences with systematic defenses like immune response modulation or behavioral defenses like grooming or changes in movement and aggregation behaviors (Altizer, Bartel and Han 2011, Hart and Hart 2018, Waite et al. 2014). As with many co-evolutionary relationships, the interplay between host and parasite can be a fragile one that is quickly destabilized by additional actors on the landscape. Framing parasitic relationships as co-evolutionary interactions turned sour by forces exerting pressure on both host and parasite may allow wildlife stakeholders to better address expectations about wildlife disease ecology in the Anthropocene and teach communities around the globe to accept and prepare for an uncertain future.

A System on the Edge: Winter Ticks, Moose, and Climate

The winter tick (*Dermacentor albipictus*) is a widespread ectoparasite of wildlife hosts in North America, reaching especially high infestation rates on moose (Samuel 2004, Samuel 2007). In the research field of climate change impacting disease in wildlife, the winter tick-moose system is often cited as a prime example due to high environmental sensitivities for winter ticks to conditions like moisture availability and temperature off-host. Though moose are referred to as primary hosts for the winter tick, the winter tick is a generalist tick species feeding on a wide range of host species including other large ungulates like elk (*Cervus canadensis*), white-tailed deer, mule deer (*Odocoileus hemionus*), and caribou (*Rangifer tardus*) as well as domesticated animals such as cattle (*Bos taurus*), among other species (Chenery et al. 2023). Unlike many other tick systems in the United States, winter ticks generally do not impact their host by vectoring pathogens, though they are suspected to be limited vectors for *Babesia duncani* to humans or pets and may play a role in chronic wasting disease and *Anaplasma* spp. transmission (Elliott et al. 2021, Ewing et al. 1997, Haley et al. 2021, Swei et al. 2019). Winter ticks are one-host ticks, spending most of their life cycle and roughly half of a calendar year on an individual host. Winter tick larvae will quest (*i.e.*, search) for a host in fall (September until host attachment or energy reserves are depleted), aggregating in clusters at the tops of vegetation which are thought to help hundreds to thousands of larvae attach to a host via fluid-like adherence chains between individual larva.

Once on-host, winter ticks will take three successive blood meals (one per developmental instar) before becoming an adult tick and dropping off their host in spring (March-May). The process of hundreds to thousands of adult winter ticks feeding synchronously is hypothesized to be the primary cause of pathology in moose, resulting in blood loss due to tick feeding and excess irritation and grooming due to cutaneous inflammation (Addison, Fraser and McLaughlin 2019, Mooring and Samuel 1998, Musante, Pekins and Scarpitti 2007). Highly infested moose in the spring months will display characteristic early spring hair loss, breaking large swaths of winter guard hairs and completely removing coat layers as they attempt to remove engorging ticks, resulting in a silver or drab grey appearance frequently dubbed ‘ghost moose’. Though the specific metabolic impacts of grooming and loss in thermoregulatory ability due to winter coat damage are debated, it is hypothesized that grooming leads to lower predator vigilance, less time foraging, and more time seeking warm and open habitats in highly affected moose (Addison, Fraser and McLaughlin 2019, Mooring and Samuel 1998, Mooring and Samuel 1999, Samuel 2004, Samuel, Mooring and Aalangdong 2000, Samuel and Welch 1991). Exact relationships between winter tick load, degrees of winter coat breakage and loss, and health outcomes remain unclear, but high infestations rates of >30,000 ticks per animal have been correlated to poor health conditions and even death while lower infestations can reduce calf recruitment and survival (Jones et al. 2017, Musante, Pekins and Scarpitti 2007).

Epizootics of winter ticks on moose have been linked to population declines across much of their southern range in North America including the northeastern U.S., midwestern U.S., Ontario, CA, Alberta, CA, and the western U.S (Addison, Johnson and Fyvie 1979, DeCesare et al. 2024, Jones et al. 2019, Jones et al. 2017, Ruprecht et al. 2020, Samuel 1989, Wunschmann et al. 2015). Winter ticks on moose in the western U.S., where the Shiras moose subspecies (*Alces alces shirasi*) is found, are poorly studied when compared to other regions in North America. Blood in moose bedding sites and epizootic years with high prevalences of early spring hair loss on moose have been reported sporadically, but comprehensive scientific studies have been rare save for some recent research (Brimeyer and Thomas 2004, Houston 1967). Evidence of depressed population trends in the core management areas for Shiras moose in the west, including southwestern Montana, eastern Idaho, northwestern Wyoming, and northeastern Utah have raised concerns that predators, human conflict, and parasitic disease could be negatively affecting moose here (Nadeau et al. 2017).

The environmental conditions winter ticks are exposed to in the core of Shiras moose range differ dramatically from many of the areas home to previous research projects. Shiras moose populations in the core of their range are partially migratory, moving from low elevation valley bottoms rich in riparian forage species like *Salex* spp. in winter to high elevation coniferous forests in summer (Burkholder 2012, Houston 1967, Kufeld and Bowden 1996). Some individuals are high desert inhabitants, spending much of their year in arid sagebrush (*Artemesia* spp.) steppe communities, while others are a fixture of fragmented mountain town habitats where urban forage sources allow some moose to remain residents year-round (Becker, Kauffman and Anderson 2010, Burkholder 2012, DeCesare et al. 2019, Houston 1967, Kufeld and Bowden 1996, Van Dyke, Probert and Van Beek 1995). Longer, more severe winters mixed with drier, more desiccating conditions in summer could impact expected relationships between moose, winter ticks, and climate in the Rocky Mountain western states relative to some previous research areas. The presence of large elk herds, also competent winter tick hosts, may influence moose exposure to winter ticks in areas where seasonal home ranges overlap. Finally, the partially migratory behaviors of Shiras moose could affect winter tick exposure and susceptibility to winter tick infestations. In the following dissertation chapters I use multiple approaches to examine previous aspects of winter tick ecology within a western context and investigate novel techniques for researching tick-host relationships. In **Chapter 1** I explore the relative host competencies of moose and elk for winter ticks using a series of surveys and a genome-wide association study. In **Chapter 2** I worked with a scent detection dog team to determine if scent detection dogs could 1) recognize tick scent and distinguish ticks from associated vegetation, 2) be deployed in field surveys for questing winter tick larvae, and 3) outperform the traditional tick drag survey method. The primary goal in **Chapter 3** is to compare previous expectations around the environmental drivers of winter tick abundance and occupancy patterns to what could plausibly be expected to control populations in mountainous areas of the western U.S. Finally, with **Chapter 4** I investigate relationships between types of migration and fall home range characteristics and winter tick infestation rates and hair loss on collared moose alongside landscape variable associations with hair loss in spring for uncollared moose.

My dissertation represents an early exploration into understudied portions of the winter tick-moose relationship like space use and overlap with other host species. The results presented herein demonstrate the importance of considering widespread disease systems within regional contexts and testing novel approaches, even when results do not differ remarkably from previous findings.

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CHAPTER TWO

WINTER TICK SHARING BETWEEN UNGULATES IN THE GREATER YELLOWSTONE ECOSYSTEM AND IMPLICATIONS FOR APPARENT COMPETITION

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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 five days of each other. We also found similar larval densities in habitats predominately used by elk, moose, and both host species. Our analysis of 2,793 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 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.

Introduction

Parasites can impact host population dynamics by directly influencing survival or reproduction and indirectly by altering host community structure via parasite sharing (Hudson and Greenman 1998, Ostfeld et al. 2006, Gottdenker et al. 2014, Gibb et al. 2020, Ostfeld and 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 (Gilbert et al. 2001, LoGiudice et al. 2003, Marm Kilpatrick et al. 2006, Cronin et al. 2010, Downs et al. 2019). 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 (Grosholz 1992, Gilbert et al. 2001, Buhnerkempe et al. 2015, Levine et al. 2016, Downs et al. 2019).

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/non-competent,’ 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 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 (Dunfey-Ball 2017, Ruprecht et al. 2020, Rosenblatt et al. 2021, DeCesare et al. 2024, Pouchet et al. 2024). 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 (McLaughlin and Addison 1986, Jones et al. 2017, Jones et al. 2019). 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 (Samuel 1989, Murray et al. 2006, Wunschmann et al. 2015, Jones et al. 2017, Nadeau et al. 2017, Timmerman and Rodgers 2017, Ruprecht et al. 2020, DeCesare et al. 2024). 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 (Welch et al. 1991, Mooring and Samuel 1998, Mooring and Samuel 1999, Normandeau et al. 2022). 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 (Drew and Samuel 1985, Welch et al. 1991, DeCesare et al. 2024).

Winter tick life cycles and activation timing vary across its wide range from northern Canada to southern Mexico (Glines 1983, Chenery et al. 2023). In the northern portion of winter tick range (northern U.S. 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 meter 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 9,500 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 250-350 individuals. Elk concentrations on winter ranges peak from December-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 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 to the structuring across host species.

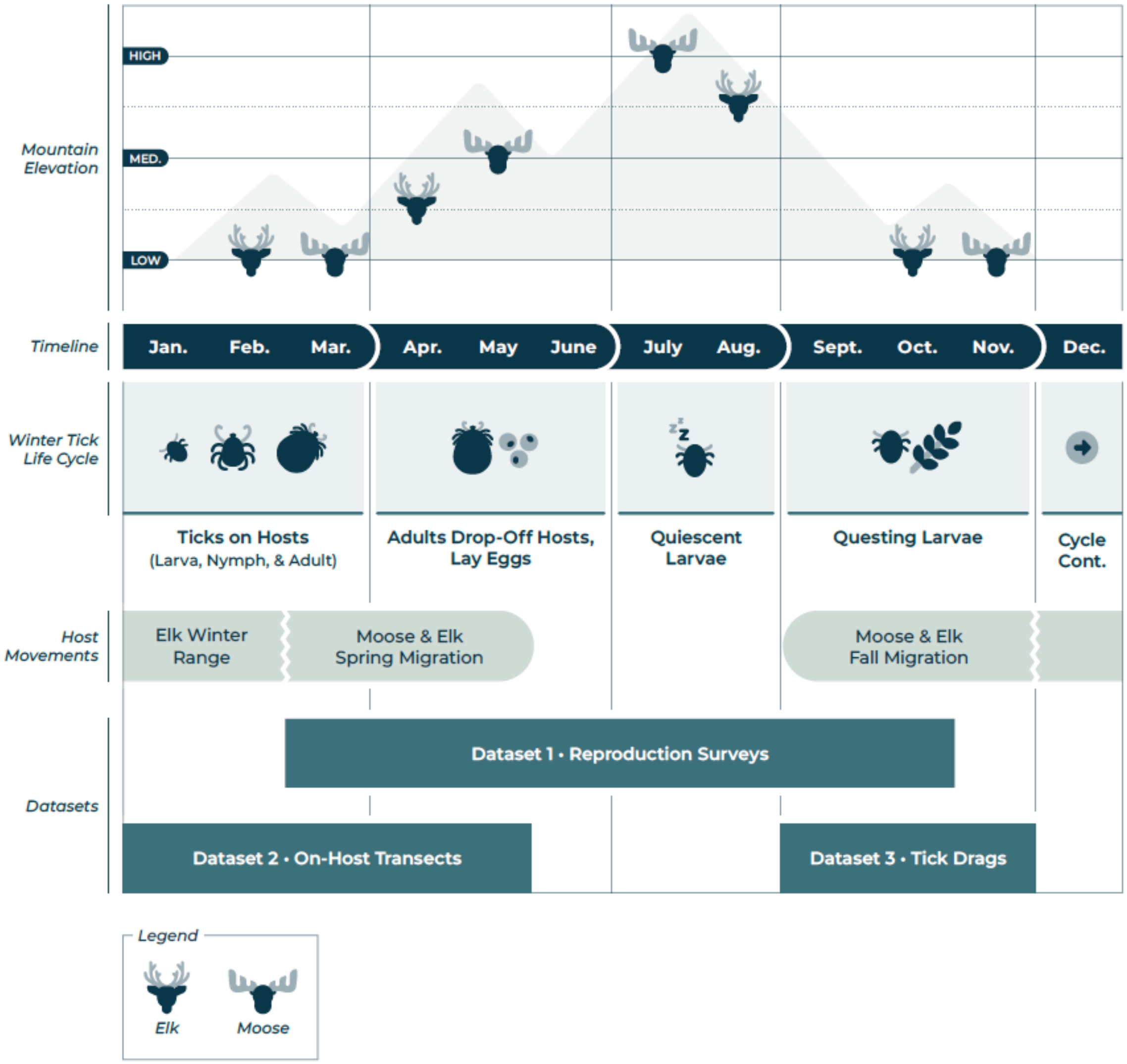

Figure 1: Conceptual diagram displaying the overlap of major portions of elk and moose seasonal activities and the winter tick life cycle with temporal alignment of studies employed in this project. Top panel depicts classical elk and moose seasonal movements from lower elevation areas (~2,000 m) like the National Elk Refuge during winter months to higher elevation areas (2,200 - 2,400 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.

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 (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 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).

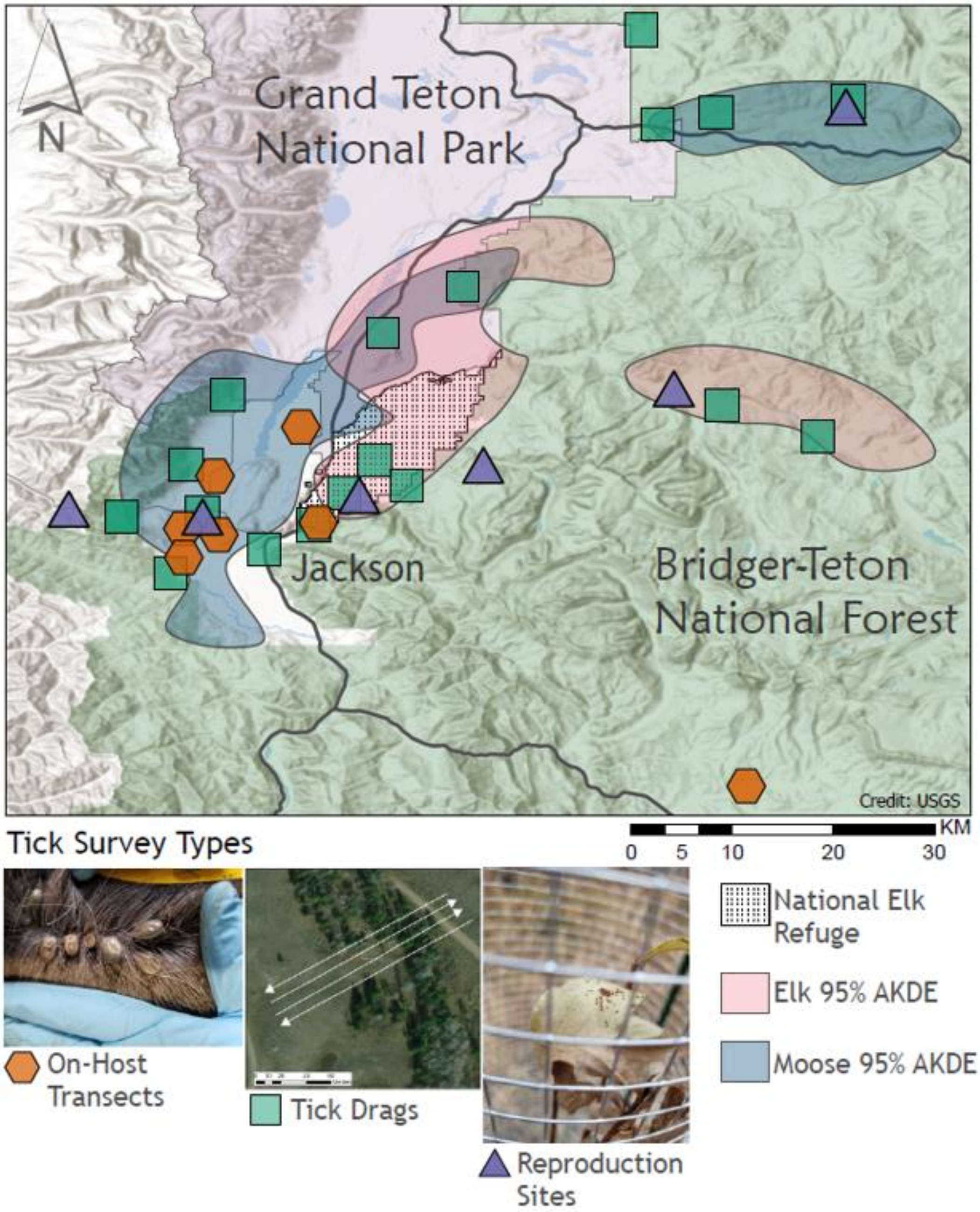

Figure 2: Map depicting generalized locations of elk and moose winter tick survey locations in Jackson Hole, Wyoming. Symbols with colors denote different experiment sites including Dataset 1: reproduction monitoring sites (purple triangle), Dataset 2: on-host transects (orange hexagon), and Dataset 3: tick drag sites (green square). 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.

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-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 2020-2023 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 six hours of death, the time after which winter ticks have been observed detaching from deceased hosts (Drew and Samuel 1984). 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 20th and November 12th, 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 20 miles per hour were expected.

Genome-wide Single Nucleotide Polymorphisms (SNPs)

We collected winter ticks from live (ground darting and corral trap capture events) and dead (road-killed and necropsies) moose and elk from 2020-2023 to compare 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 to northwestern Wyoming ticks (Appendix S1: Section S1). Although at least 5 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 RADseq sequencing. Briefly, DArT employs a proprietary RADseq method that 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. Single nucleotide polymorphisms (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 (Georges et al. 2018, Ferrante et al. 2022).

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 and Pekins 2014, Chenery et al. 2020). Total larval abundance per reproduction monitoring station was regressed against host species of origin (elk or moose), mothers' weight, canopy cover (open or closed), elevation (meters), and site (NER, Bridger-Teton National Forest, Snake River bank) as a random effect with intercepts varying across sites. Infestation density (tick count/surveyed unit in cm^2) 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 generalized linear model to investigate the effect of host association (elk or moose) on tick weight (scaled, milligrams) using a generalized linear model 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 quasipoisson distribution using the *lme4*, *MASS*, and *glmer* packages due to overdispersion in the data (Bates et al. 2009, Ripley et al. 2013, Faraway 2016).

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 and 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 0–1, 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: Table S1, Appendix S1: Table S2). Larvae from both hosts began questing between September 26th and September 29th, 2022. We also looked at evidence for an effect of host association on tick weight and found none

(β = 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 to elk (β = 0.064, SE = 0.191, z = 0.335, p = 0.738, df = 63) (Figure 3b, Appendix S1: Table S1, Appendix S1: Table 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 (β = -1.761:0.001, SE = 1.314:1.285, z ~ 0.001, p > 0.1, df = 199) (Figure 3c, Appendix S1: Table S1, Appendix S1: Table S2).

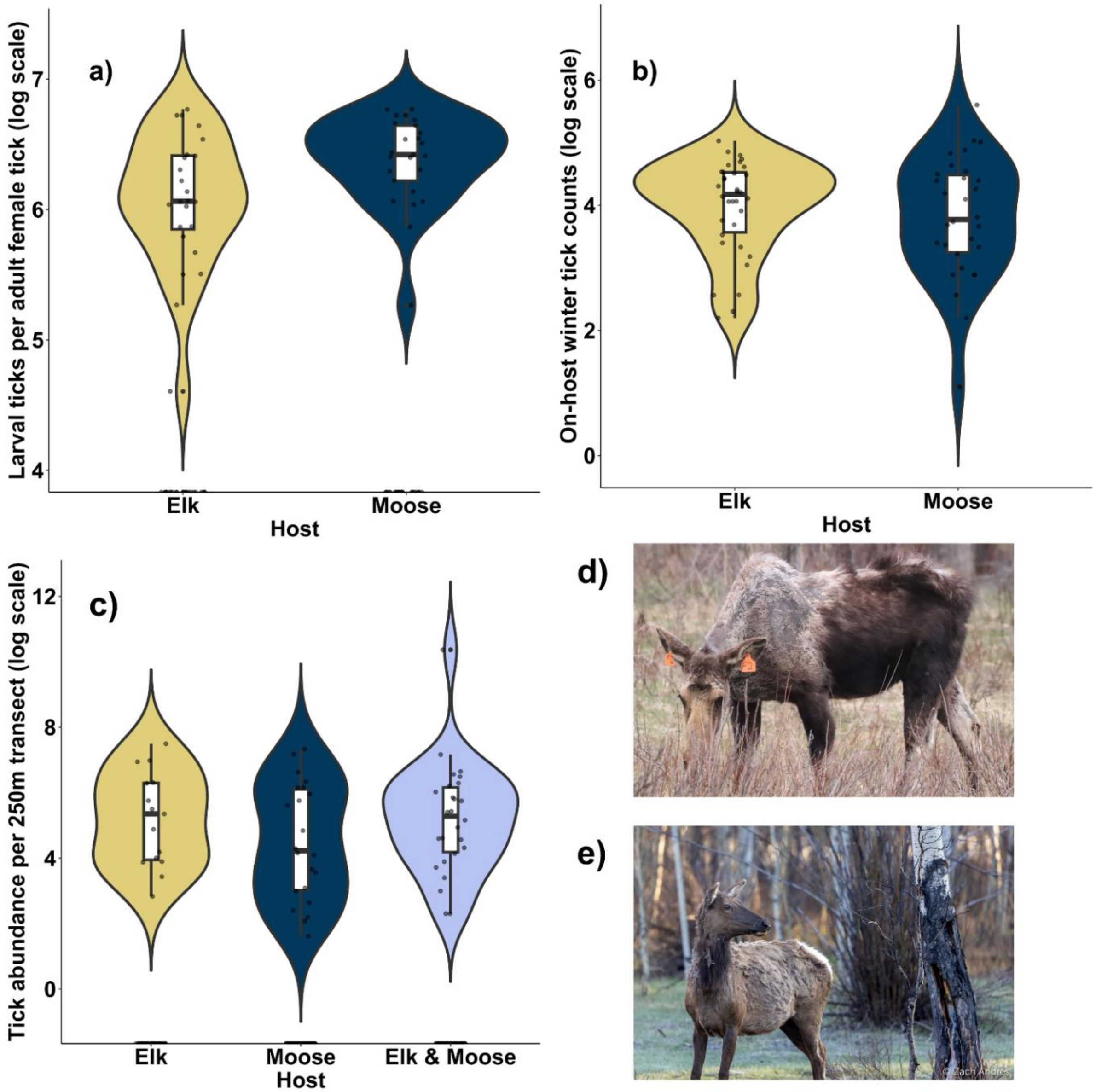

Figure 3: Differences in a) larvae production of winter ticks from elk and moose, b) total tick counts on elk and moose using the Sine et al. 2009 transect method, c) questing larval winter tick abundance at sites predominately used by elk, moose, or both species during the spring drop-off period. Responses are presented on the log scale for better 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. Photograph taken by Zach Andres.

Genetic analyses using DArTseq identified 88,506 SNPs from 88 winter tick samples from elk and moose hosts. Our filtering criterion yielded 2,793 informative SNPs from 65 winter tick samples (Jackson: n = 51, Pinedale: n = 14). The PCA explained 6.5 % of the 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 (Figure 5, Figure 4b, Appendix S1: Figure S4).

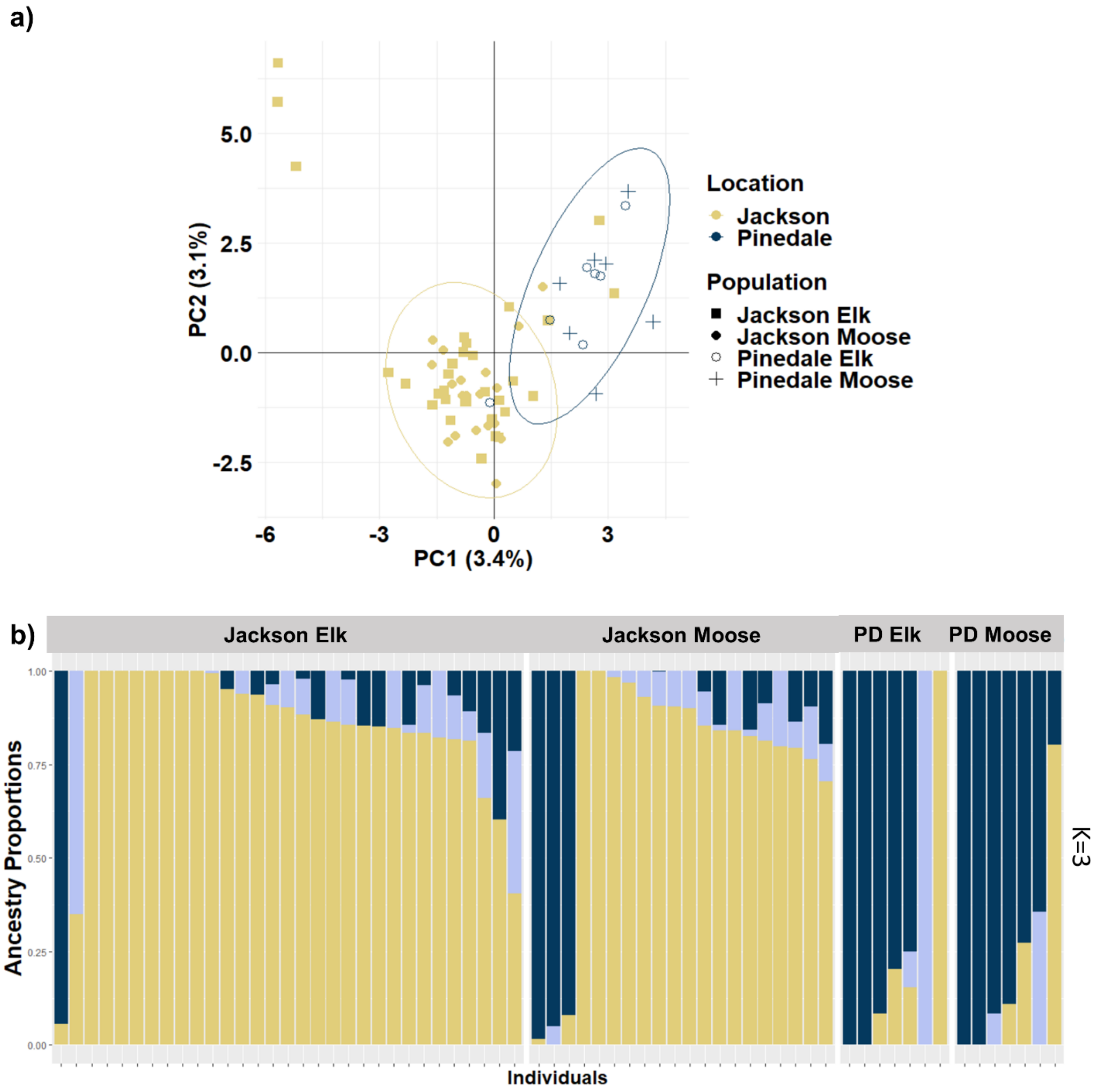

Figure 4. a) Principal coordinates analysis (PCA) results using genomic SNPs from winter tick (*Dermacentor albipictus*) extracted from elk (*Cervus canadensis*) and moose (*Alces alces*) in Jackson and Pinedale, Wyoming. b) Results of the ancestry proportions analysis using the *LEA* package. Support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

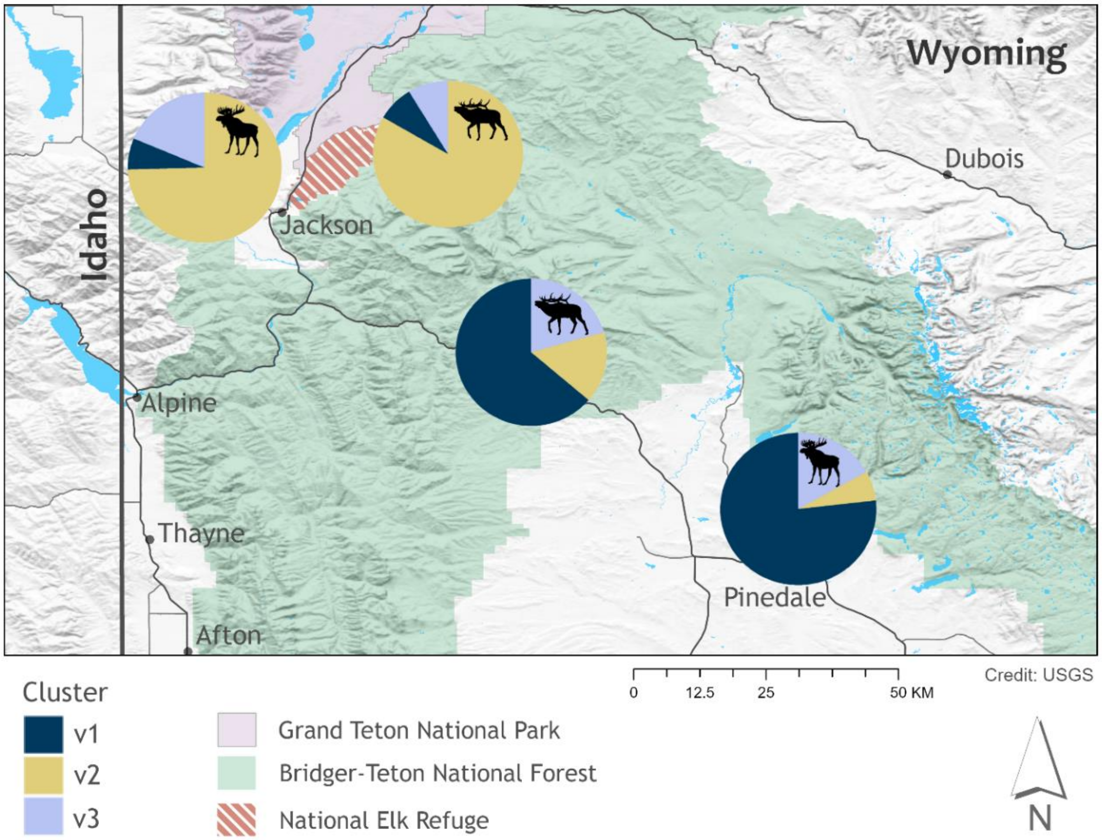

Figure 5: Map of northwestern Wyoming with pie charts representing aggregate ancestry proportions (Figure 4a) for winter ticks from elk and moose sampled near Jackson and Pinedale, Wyoming with colors and proportions representing averaged results from *LEA* estimated ancestry probability proportions.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

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 U.S., elk 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 to mule deer, elk, and white-tailed deer (Drew 1984, Welch, Samuel and Wilke 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 U.S. and parts of Canada may result in a tighter relationship between winter tick and moose compared to systems in the western U.S. 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 U.S. seem to be infested at lower rates than Midwest and Northeastern moose but still experience negative health outcomes, albeit at much lower population proportions (Dunfey-Ball 2017, Jones et al. 2017, Ruprecht et al. 2020, Debow et al. 2021, DeCesare et al. 2024). 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 U.S. 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 (Weiskopf et al. 2020, Pouchet et al. 2024). 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 schneiderii)* (Drew and Samuel 1985, Samuel 2007, Dunfey-Ball 2017, Jones et al. 2017, Nadeau et al. 2017, Holmes et al. 2018, Lankester 2018, Healy et al. 2020, DeCesare et al. 2024, Pouchet et al. 2024). 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 (Williams et al. 2002, Proffitt et al. 2015). 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.

Acknowledgments

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Author Contributions

TK collected and analyzed data and lead manuscript writing. AC, BW, SD, AG, JR, BS, and GF provided data as well as fieldwork logistical help. PC, LT, KO, and AM provided analysis advice. PC, LT, KO, AM, AC, AG, and BS provided manuscript review comments and edits.

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

Data Availability Statement

Data are sensitive and data sharing agreements used to facilitate this study preclude public data sharing for host telemetry datasets. Data (Koser et al. 2024) for analyses of winter tick reproduction rates, infestation rates, and abundance surveys are available from https://www.sciencebase.gov/catalog/item/66f71078d34e98f05fb38049. Data for genetic analyses are available from GenBank via BioProject Accession: PRJNA1165274.

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CHAPTER THREE

SCENT DETECTION DOGS DETECT A SPECIES OF HARD TICK, *DERMACENTOR ALBIPICTUS*, WITH COMPARABLE ACCURACY AND EFFICIENCY TO TRADITIONAL TICK DRAG SURVEYS

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Abstract

Background: Accurate surveillance data are critical for addressing tick and tick-borne pathogen risk to human and animal health. Current surveillance methods for detecting invading or expanding tick species are limited in their ability to scale efficiently to state or national levels. In this study we explored the potential use of scent detection dogs to assist field surveys for a hard tick species: *Dermacentor albipictus*.

Methods: We used a series of indoor and *in situ* training simulations to teach scent detection dogs to recognize *D. albipictus* scent, distinguish tick scent from associated vegetation, and develop a cautious search pattern. After training, we deployed both a scent detection dog survey team and a human-only survey team on transect and surveillance plot surveys then compared the detection rates and efficiency of both methods.

Results: Scent detection dogs required more time and money to train on field surveys but were comparable to traditional tick drags when accounting for cost per unit area surveyed. There was a lack of agreement on positive (ticks present) versus negative (ticks not present) sites between the two methods, implying that neither method is particularly reliable at detecting *D. albipictus*.

Conclusions: Estimating detection bias and false negative rates for tick surveillance methods like tick drags will be important for accurately evaluating tick-borne disease risk across space and into the future. We found scent detection dogs to be a reasonable alternative sampling approach to consider when ticks are at low abundance or patchily distributed such as during tick range expansion or novel invasions. Scent detection dogs may also be useful for sampling for ticks in areas or along surfaces that are difficult to sample with the traditional tick drag technique like at ports of entry or livestock competitions.

Key Words: *Alces alces, Dermacentor albipictus*, Greater Yellowstone Ecosystem, Hard ticks, Moose, Scent detection dogs, Surveillance, Tick drag, Winter ticks

Background

Ticks, specifically ixodid (hard) tick species, pose a significant and growing threat to human and animal health in the United States and around the world. Ticks are responsible for vectoring pathogens causing >90% of nationally notifiable human vector-borne disease cases reported in the U.S. and are major pests in the cattle industry and some wildlife conservation settings (Anderson, Ezenwa and Jolles 2013, Eisen et al. 2017, Samuel 2007, Sonenshine 2018, Tiffin et al. 2022). The recognition of several novel human and animal pathogens in ticks and associated hosts, as well as a wide diversity of potentially pathogenic agents, has increased awareness to the emergence of tick-borne disease threats in the U.S. (Mansfield et al. 2017, Swei et al. 2020, Tsao et al. 2021). Furthermore, climate change has been linked to longer active seasons and increased reproduction rates in important tick vectors like *Ixodes scapularis* and, alongside human movement of ticks and their hosts, creates new opportunities for species invasion or range shifts (Altizer et al. 2013, Cunze et al. 2022, Ogden et al. 2020, Ogden and Lindsay 2016).

Understanding current trends in tick distribution and abundance is critical to estimating tick-borne disease risk and investigating the interactions between ticks, hosts, and the environment. A common technique for surveying tick populations is *in situ* or active surveillance for ticks seeking a host (*i.e.*, ‘questing’) through techniques like dragging a flannel cloth across a prescribed survey path which provides information on tick species presence and density (Newman et al. 2019, Salomon, Hamer and Swei 2020). Pathogen prevalence of infected ticks can be determined from drag surveys if collected ticks are tested for specific disease-causing agents. Dragging for ticks involves relatively low resource investment and has similar detection rates when compared to other methods of tick collection like dry ice-baited traps (Dantas-Torres et al. 2013, Dobson 2013, Holcomb et al. 2023, Kjellander et al. 2021). Though tick drags are by far the most common tick population survey technique, survey effectiveness depends on the spatial scales, tick species attachment behavior(s), and habitat types or other environmental conditions under investigation (Dantas-Torres et al. 2013, Kjellander et al. 2021). For surveys aimed at detecting rare or less conspicuous tick species, as may be the case for an invading or expanding species, techniques for sampling larger areas or with greater detection probabilities may be necessary.

Scent detection dogs have been used to detect several inconspicuous, cryptic, or rare wildlife species including koala (*Phascolarctos cinereus*), Franklin's ground squirrel (*Poliocitellus franklinii*), and brown marmorated stink bugs (*Halyomorpha halys*) (Cristescu et al. 2015, Duggan et al. 2011, Lee et al. 2014). Though resources are needed to train scent detection dogs to find targets in field contexts without destroying or harming remains or animals, survey time per area is often shorter and detection rates higher than other methods (Beebe, Howell and Bennett 2016, Cristescu, Miller and Frère 2020, Orkin et al. 2016, Thompson et al. 2020). For example, overall detection rates and probability of detection (given presence) for black bears (*Ursus americanus*), fishers (*Martes pennanti*), and bobcats (*Lynx rufus*) during scat surveys conducted with scent detection dogs were higher when compared to hair snare and camera surveys (Long et al. 2007). Scent detection dogs may prove a valuable tool in determining tick presence and abundance at previously unfeasible scales and study contexts such as widespread invasive tick surveillance given the variable efficacy of existing detection methods like dragging surveys.

In this study we experimentally trained scent detection dogs to recognize the target scent of a hard tick species, the winter tick (*Dermacentor albipictus*), and conducted field trials to compare accuracy and efficiency to human-conducted surveys. The winter tick is a widespread one-host tick in North America which attaches to a wide range of hosts but reaches high infestation loads on large ungulates like moose (*Alces alces*), elk (*Cervus canadensis*), and caribou (*Rangifer tardus*) [42]. *Dermacentor albipictus* are known for infesting moose at densities high enough to lead to anemia and even death, with winter tick epizootics being linked to moose population declines at the southern end of their range (DelGiudice, Peterson and Samuel 1997, Jones et al. 2017, Samuel 2007, Wunschmann et al. 2015). Tracking *D. albipictus* expansion into the northern reaches of Canada and southern Alaska is of concern for ungulate population managers (Chenery et al. 2020, Leo et al. 2014, Zarnke et al. 1990). Here we present the first documented attempt, to our knowledge, to train and deploy scent detection dogs to survey for a hard tick species, *D. albipictus*, *in situ*. We also provide background on training scent detection dogs to identify tick scent and teaching an appropriate search pattern. Finally, we compared the performance and resource investment of a scent detection dog-assisted survey team to a traditional tick drag survey.

Methods

Preliminary Training

In 2020 two scent detection dogs with Working Dogs for Conservation (WD4C), an adult female Belgian Malinois (Tule) and an adult female Labrador retriever (Lily), began training exercises at the WD4C facility in Turah, Montana to determine their ability to recognize *D. albipictus* scent using wild-caught winter tick larvae. Both dogs demonstrated some ability to recognize *D. albipictus* scent in controlled, indoor settings when trained to identify PVC elbow joints containing ticks versus control joints. Both dogs could also identify containers with ticks present and distinguish from control containers on an outdoor trail. These findings warranted further exploration of their ability to detect questing ticks in the field in Jackson Hole, Wyoming. Lily retired at the end of 2020 thus field training continued with Tule and Frost, an adult male springer spaniel mix. Both Tule and Frost were selected to carry out field training for winter tick surveys because both dogs had experience in relevant field studies. Tule was already exposed to tick scent during preliminary training and feasibility testing in Turah, Montana while Frost had previous experience with hand presentations and searching for targets at head height where clusters of tick larvae were most likely to be present.

Field Training

In 2021 Tule and Frost began target scent recognition training and field exercises for *D. albipictus* surveys with their handler in Jackson Hole, Wyoming. The valley of Jackson Hole is situated in northwestern Wyoming, south of Yellowstone National Park and contains Grand Teton National Park, Bridger-Teton National Forest, the National Elk Refuge, and the residential areas surrounding the towns of Jackson and Wilson. Elevations range from ~ 1,850 m in the Snake

River flood plain to ~ 4,200 m in the Teton Range. Vegetation at lower elevations includes sagebrush (*Artemisia* spp.) communities with willow (*Salex* spp.) and cottonwood (*Populus angustifolia*) galleries in riparian areas. Mixed conifer and aspen forests are present at mid-elevations including lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*). At mid-high elevations, spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are common.

During initial scent-imprinting, dogs were ‘marked’ by the handler with an auditory cue when they smelled target scent and rewarded with either food or toy play. After imprinting of tick scent and dogs showed scent recognition, the dogs were expected to perform a trained final response (TFR), a previously trained behavior which was a sit with either a point at the handler or in the direction of the target scent when they pinpointed the source of target scent. Indoor training used a PVC elbow array where ticks with associated vegetation and three control containers with vegetation were presented to the dogs in various containment systems designed to keep ticks contained but allow air and scent cue to flow (Figure 1). ‘Known’ trials allowed the handler previous knowledge on elbow contents while ‘blind’ trials only allowed the recorder to know elbow contents. During blind trials the handler and dog would stay in a separate room while the recorder organized the trial using gloves to prevent contaminating scent profiles. Once prepared, the recorder would signal to the handler that the trial could commence and record every instance of alert or changes in behavior (CoB) as dictated by the handler. Containment systems included salt and pepper shakers with openings covered by organza, Falcon® tubes with organza coverings, and muslin bags (Figure 1). Falcon tubes and salt and pepper shakers with organza coverings produced the most reliable results while also preventing ticks from escaping the PVC elbows.

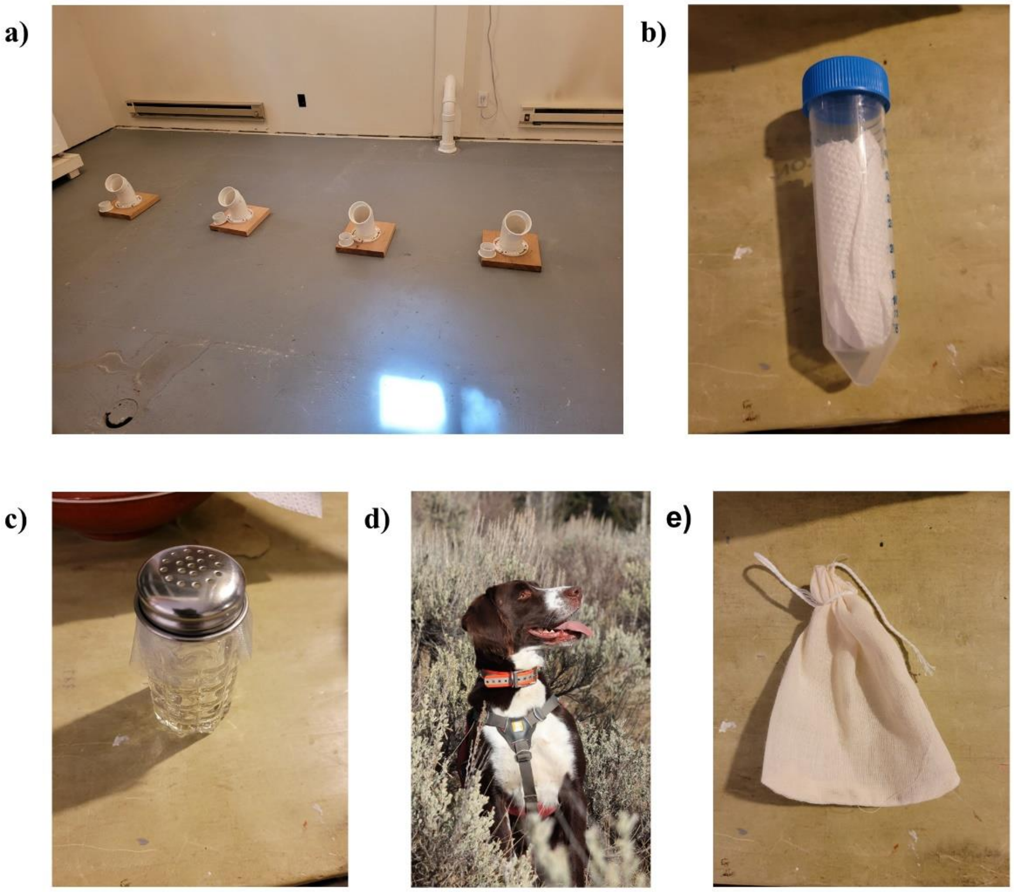

Figure 1: a) PVC elbow array used in indoor training of scent detection dogs to recognize *Dermacentor albipictus* scent and distinguish from associated vegetation. b) 50 ml Falcon® tube with paper towel and holes drilled on top to allow airflow, covered in organza. c) Salt and pepper shaker with organza cloth covering holes. d) Frost, a male Springer spaniel mix at a survey site. e) A muslin bag.

The primary difficulty in progression to *in situ* tick detection was training a search pattern where dogs would carefully search vegetation tips for questing larval clusters without destroying clusters so known clusters could be used for repeated trials. We used a variety of mechanisms surrounding known clusters of questing larval ticks to prevent disturbance by the dogs while searching and to allow for repeated trials, including wrapping vegetation tips in large organza bags and placing 1-cm wire cages around vegetation (Figure 2). Wire mesh cages around known tick clusters proved the best equipment for training target scent context and allowed for repeated trials. Indoor and *in situ* field training required six working days where dogs were actively trained on scent recognition and search patterns. Training also included two rest days where dogs were given time to process their training and technicians could assemble new training courses. The final two days of field training included twelve blind trials where scent detection dog and handler were presented a series of four ‘hot’ cages with tick clusters and four negative control cages along a course. One dog, the springer spaniel mix named Frost, established an effective search pattern and demonstrated the ability to reliably detect known tick clusters and reject controls using training and validation experiments similar to those reported in other scent detection dog studies [23, 24, 25].

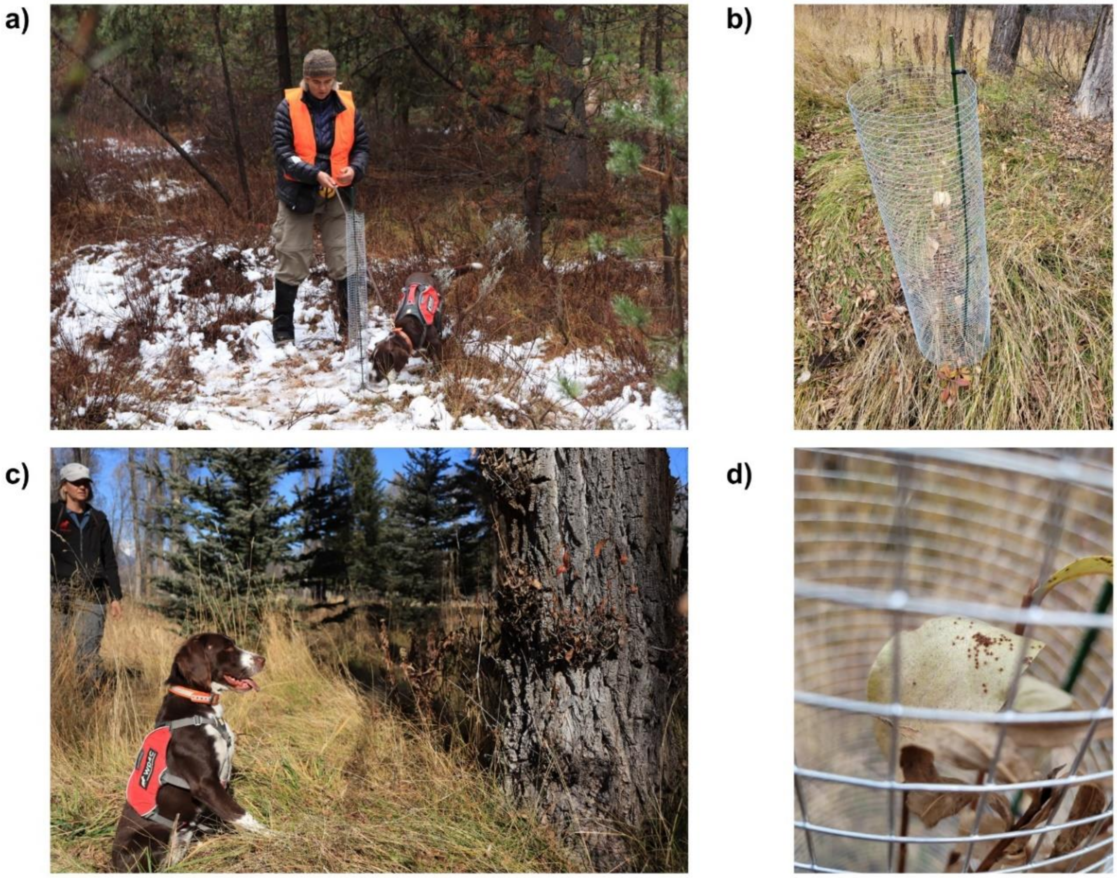

Figure 2: a) Frost, a male Springer spaniel mix, checking a wire mesh cage with handler, Aimee Hurt, during *Dermacentor albipictus* field survey training exercises. b) Wire mesh cage erected around a known cluster of questing *D. albipictus* larvae used in field training exercises. c) Frost performing a Trained Final Response (TFR) during field training. d) Questing larval *D. albipictus* on vegetation within a wire mesh cage.

Field Surveys

We deployed both the scent detection dog-assisted team (Frost, handler, survey guide) and a human-only traditional tick drag team on field surveys for *D. albipictus* over the course of two days. Each survey location was first sampled by the scent detection dog-assisted team to prevent scent contamination and bias from human-only surveys. A technician without knowledge of the dog-assisted survey would then conduct a traditional human-only drag survey, followed finally by a guide from the scent detection dog surveys who dragged or flagged locations marked by the dog-assisted team. Marked locations from the dog-assisted survey were sampled after the traditional drag survey to avoid potential bias in technician drag patterns if they were to notice evidence of previous activity like bent vegetation or flattened grass. Two forms of field trials were undertaken: 250 m transects and 500 x 500 m surveillance plot surveys. The 250m transect surveys are representative of a typical tick abundance and environmental association study where transects are stratified across environmental conditions of interest then sampled (Dantas-Torres et al. 2013, Newman et al. 2019, Salomon, Hamer and Swei 2020). We stratified 32 transects in suitable *D. albipictus* habitats across the Jackson Hole valley in cottonwood/riparian, sagebrush/mixed aspen, mixed forb/grass, and conifer-dominated habitats at low (~1,870m), medium (~1,980m), medium-high (~2,100m) and high elevations (~2,200m) and allowed the scent detection dog and handler to search with a guide to ensure searching was within ~10 m of the transect GPS path. Once the scent detection dog either performed a TFR or demonstrated a 'change of behavior' (CoB), the handler would indicate to the guide which individual plant or cluster of vegetation was likely targeted. The guide would then record a GPS point and take a picture of the site for sampling and recorded the distance from the nearest point on the transect to the indicated vegetation. A change of behavior was called by the handler when the dog changed from standard searching behavior to a set of innate behaviors consistently expressed in the presence of target odor, including a more excited state with exaggerated tail wagging and increased sniffing rate or intensity. After the scent detection dog team completed surveys, a technician with no knowledge of the dog-assisted survey detections would sample the same transects using a traditional human-only drag method. Dragging involved moving a 1m^2 flannel cloth across available vegetation while tracking progress using a GPS device. The surveyor would check the drag cloth for ticks roughly every 10 paces and remove any attached ticks using a lint roller. Ticks were later quantified and ~10 ticks per detection event were preserved in 75% ethanol to confirm species identity using a dichotomous key (Brinton, Beck and Allred 1965). Upon tick detection, the surveyor would retrace their path to find the most likely origin source of ticks and record GPS location, vegetation type, and vegetation height. To ensure all ticks from the identified cluster were collected, the surveyor would then conduct a 10m radius drag by dragging in a spiral away from the focal detection point. All ticks collected during origin-tracing and radius drags were given a 'detection event' label. Once the human surveyor sampled a transect, the guide from the scent detection-assisted surveys then sampled TFR and CoB locations using a 10m radius drag. None of the radius drags from scent detection dog-assisted surveys overlapped within 5m of a human surveyor detection event, but if overlap were to occur, we would count the total tick abundance from an overlapping detection event toward both survey types.

Surveillance plots were designed to simulate a survey type more suited to detect a rare or invading tick species across a large area. We outlined three 500 x 500 m surveillance plots in the northern, middle, and southern portions of Jackson Hole using flagging tape and flags and set a 500m search path within the plot. As above, surveillance plots were first sampled by the scent detection team then a human surveyor and finally the guide from the scent detection team.

Transect results were analyzed using a McNemar's χ^2 test from the *stats* package in R and larvae per cluster, larval density, and larval abundance per transect results were analyzed using a generalized linear model with a "*quasipoisson*" distribution in the package *lme4* (Bates et al. 2009, Team 2023).

The time required to complete transects and surveillance plots was recorded for both methods. Overall costs for training and per transect and surveillance plot were calculated using the 2021 General Schedule (GS) pay rate for a GS-9 Step 1 field technician at $22.08/hour rate for the human-only survey team and $73.75/hour for the dog handler salary, which includes insurance and care for the scent detection dogs (Table 2).

Results

Indoor & Field Training

One scent detection dog, Frost, demonstrated the ability to successfully identify *D. albipictus* larval cluster scent (known trials (n=2) and blind trials (n=4): 100% positive identification rate) and reject control or vegetation-only containers (known trials (n=2): 100% rejection rate for known trials, blind trials (n=4): 80% rejection rate) in controlled indoor trials. Frost was also able to correctly identify all cages containing tick clusters and reject controls in 11/12 field training trials and established a careful search pattern where Frost would search tips of vegetation for tick clusters with minimal disturbance. Field training, including dog handler salary, dog insurance and health care, supplies, lodging, and per diem, required 48 active working hours and cost $4,246. Training for a human tick drag technician required 8 working hours and cost $376.64 including salary, supplies, and lodging (Table 2).

Scent Detection Dog Surveys	Human-only Surveys	
	Positive	Negative
Positive	6	5
Negative	8	13

Table 1: *Dermacentor albipictus* larvae detection results for two survey types: scent detection dog-assisted and human-only traditional tick drag surveys. Both teams surveyed the same thirty-two 250 m transects stratified across Jackson Hole, Wyoming.

Type of Cost	Survey Method	Costs	Cost per unit	Units	Total Cost (USD$)
Training	Human-only Tick Drags	Training in WY	$22.08 per hour	8 hours	176.64
		Supplies	Drag cloth, gear, etc.		150
		Lodging	$50 per day	1 day	50
		TOTAL		**1 day**	**376.64**
	Dog team	Training in Wyo[a]	$73.75 per hour	48 hours	3,540
		Supplies	PVC elbows, etc.		100
		Handler per diem	$51 per day	6 days	306
		Lodging	$50 per day	6 days	300
		TOTAL		**8 days[b]**	**4,246**
32 Transect Surveys	Human-only Tick Drags	Salary	$22.08 per hour	29 hours	640.32
		Lodging	$50 per day	4 days	200
		TOTAL		**4 days**	**840.32**
	Dog team	Handler Service Fee[a]	$73.75 per hour	12 hours	885
		Handler per diem	$51 per day	2 days	102
		Technician Salary	$22.08 per hour	4 hours	88.32
		Lodging (Handler)	$50 per day	2 days	100
		Lodging (Technician)	$50 per day	2 days	100
		TOTAL		**2 days**	**1275.32**
3 Surveillance Plot Surveys	Human-only Tick Drags	Salary	$22.08 per hour	8 hours	176.64
		Lodging	$50 per day	1 day	50
		TOTAL		**1 day**	**226.64**
	Dog team	Handler Service Fee[a]	$73.75 per hour	7 hours	516.25
		Handler per diem	$51 per day	1 day	51
		Technician Salary	$22.08 per hour	2 hours	44.16

	Lodging (Handler)	$50 per day	1 day	50
	Lodging (Technician)	$50 per day	1 day	50
	TOTAL		**1 day**	**711.41**

[a] Handler Service Fee includes handler salary, dog care, insurance, and food as well as operational costs for WD4C.

[b] Scent detection dogs require 2 days of rest for every 5 days of work

Table 2: Estimated costs for training a scent detection dog team to find a hard tick species in the field compared to a human-only tick drag survey. We also compared costs and hours/days worked to survey thirty-two 250 m transects stratified across Jackson Hole, Wyoming and three 500 x 500 m surveillance plots.

Field Surveys

Field surveys were designed to compare a typical *D. albipictus* survey using the tick drag method to a survey by a scent detection dog team. All ticks preserved in ethanol from both survey types were confirmed as *D. albipictus* larvae using a dichotomous key. Ticks were detected on 11 of 32 (34%) transects and in all three surveillance plots surveyed by the scent detection dog team while the traditional tick drag method found ticks on 14 of 32 (44%) transects and in all three surveillance plots. Six transects were found positive for ticks using both methods leaving 13 discordant pairs where dog-assisted and human-only tick drag surveys did not agree on positive versus negative status. Results from the McNemar's χ^2 test did not reveal considerable differences between the predictive accuracies of the two survey methods (Table 1, χ^2=0.308, *df*=31, *P*=0.579).

We found 66% fewer *D. albipictus* larvae in larval clusters in the human-only tick drag surveys (mean=45, 95% CI=17-72) compared to dog-assisted surveys (mean=132, 95% CI=63-201, $t_{(106)}$=-2.70, *P*=0.009, Figure 3a). We observed a small difference of 6% fewer larvae per meter surveyed on human-only tick drag surveys compared to dog-assisted surveys (mean human=0.25 larvae per meter, 95% CI=0-0.54, mean dog=0.24 larvae per meter, 95% CI=0.08-0.39, $t_{(34)}$=0.088, P=0.933, Figure 3b). The scent detection dog-assisted surveys detected a total of 17 larval clusters on 32 transects and 21 clusters on 3 surveillance plots while the traditional tick drag method detected 29 clusters on transects and 21 clusters on surveillance plots.

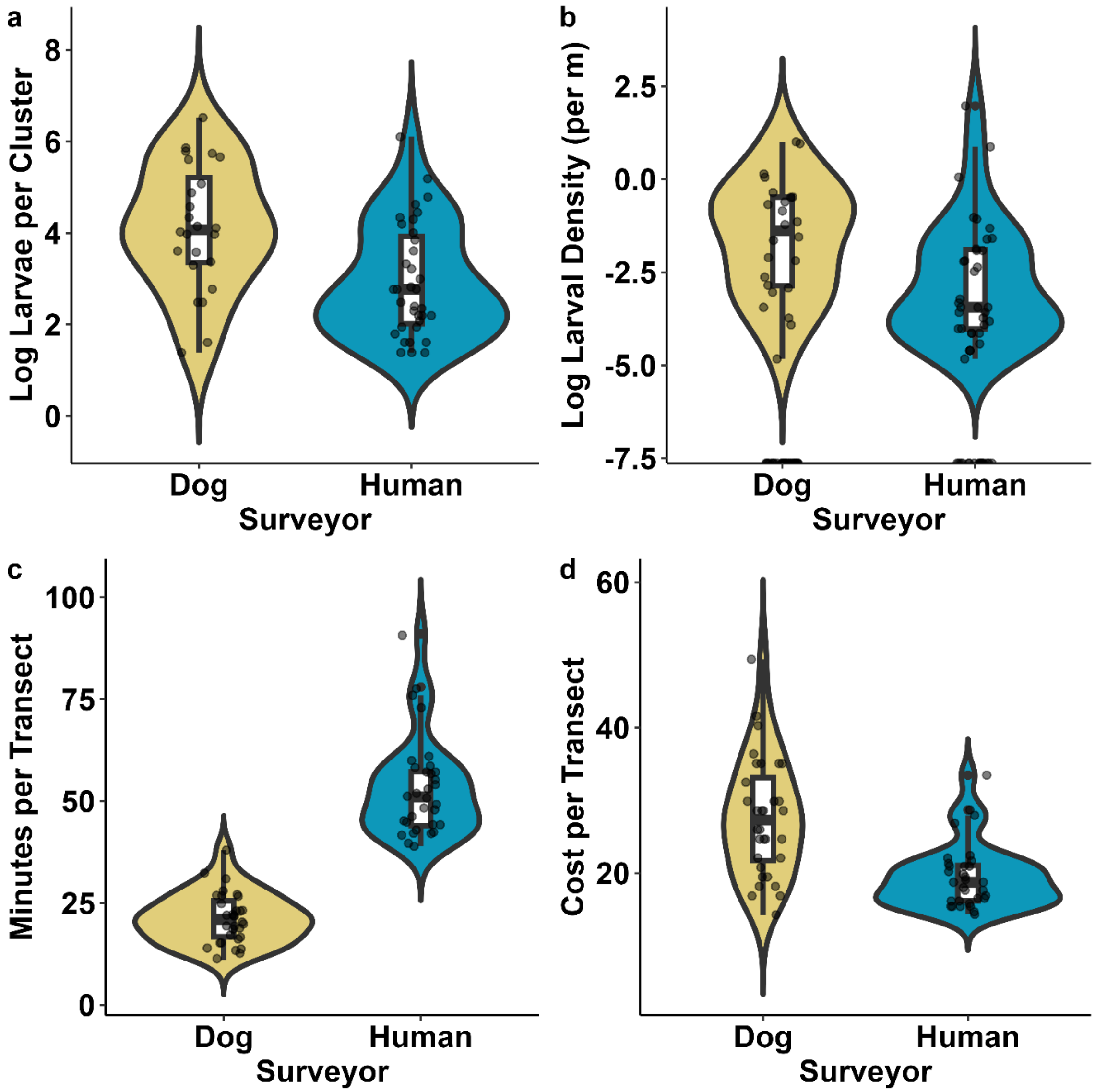

Figure 3: a) Violin and boxplots visualizing the number of *Dermacentor albipictus* larvae detected per cluster identified in surveillance plots and transects, on a logarithmic scale, surveyed by human-only team using traditional tick drag method and a team assisted by a scent detection dog with handler. b) Larval density detected via human-only tick drags versus dog-assisted teams on a logarithmic scale. c) Visualizations of minutes spent to survey 32 individual 250 m transects by both human-only and scent detection dog-assisted teams. d) Visualizations of dollars spent to survey 32 individual 250 m transects based on $22.08/hour rate for a single human surveyor and $73.75/hour for scent detection dog-assisted team plus $22.08/hour rate to survey Trained Final Response (TFR) locations.

Ticks were detected on 31 of 50 total (62%) TFRs and CoBs called by a scent detection dog and their handler across both transect and surveillance surveys. A total of 23 out of 28 (82%) TFRs were positive for ticks with an average cluster size of 123 larvae per detection (95% CI=61-184) while 8 out of 22 (41%) CoBs were positive for ticks and on average yielded 24 larvae per detection (95% CI=0-57). In total, 13 out of 25 (52%) of all TFRs and CoBs were positive for ticks on the first day of field surveys while 18 of 25 (80%) were positive on the second day.

On average, both the scent detection dog team and traditional tick drag methods found a larval cluster every 5 meters. The scent detection dog and handler also identified four tick clusters off-transect while on-route to survey sites. Distance from transect or search route line to identified tick cluster for the scent detection dog team was on average 109cm for TFRs (95% CI=56-161) and 93 cm for CoBs (95% CI=4-183).

The average time to complete a 250m transect for the scent detection dog, handler, and tick drag technician was 24 minutes (95% CI=21-27) costing \$27 per transect (95% CI=\$24-\$30) when accounting for salary alone compared to 53 minutes (95% CI=49-58) and \$20 per transect (95% CI=\$18-\$21) for the traditional tick drag method using a single tick drag technician (Figures 3c & 3d). The average time to complete a 500 x 500 m surveillance plot for the dog-assisted team was 122 minutes (95% CI=107-137) and cost \$123 per plot (95% CI=\$115-\$131) compared to 144 minutes (95% CI=93-194) and \$53 per plot (95% CI=\$34-\$72) for the traditional drag method. The combined efforts of dog handler, dog, and tick drag technician took 16 hours or two working days to survey thirty-two 250 m transects and cost a total of \$1,275.32 (\$39.84 per transect), including salary, per diem, and lodging compared to 29 hours or four working days and \$840.32 (\$26.25 per transect) for a tick drag technician on their own (Table 2). The dog-assisted team required 7 hours or 1 day to survey three 500 x 500 m surveillance plots costing \$711.41 (\$237.14 per plot) while the traditional tick drag method took 8 hours or 1 day and cost \$226.64 (\$75.55 per plot).

Overall survey speed for the scent detection team across both survey types was 11 meters per minute (95% CI=10-13) and 5 meters per minutes (95% CI=4-6) for the human-only tick drag method.

Discussion

These field trials represent the first documented attempt to train and deploy scent detection dogs to search for a hard tick species in the field. Winter tick larval cluster sizes detected by a scent detection dog tended to be larger than those detected via human-only dragging, implying that scent strength may relate to cluster size (Figure 3a). Finding larger clusters of ticks may be desirable for risk-assessment purposes in tick-borne disease systems where infestation burdens are relevant for pathology as is the case for the *D. albipictus*-moose and cattle fever tick systems. Though the number of tick-positive transects and number of detection events overall did not differ remarkably between dog-assisted and human surveys (Table 1), dog-assisted surveys were roughly two times faster, which may prove critical for surveillance projects spanning large areas (Figure 3d). A scent detection dog team costs roughly three times as much as a human-only surveyor on an hourly basis and required site revisits to sample TFRs and CoBs, limiting the cost-effectiveness of dog surveys compared to the traditional tick drag method for the 32 transects and 3 surveillance plots examined in this study (Figure 3c). Field training and teaching appropriate search patterns required 8 days and \$4,246 in direct costs for the scent detection dog team, which was more than ten times the training costs for a human surveyor at $376.64 in direct costs and one training day. We expect field training time and costs for the scent detection dog team to decrease in subsequent years of tick sampling since dogs have shown the ability to recognize target scents for long periods of time [23, 24, 25, 26]. Interestingly, we found no overlap (within 5 m) in detection events between a scent detection dog-assisted survey team and the traditional tick drag method, implying that both methods have imperfect detection probabilities and highlighting the need for repeated sampling design, additional exploration of alternative survey methods, and accounting for detection probabilities in the analysis of tick abundance data.

While larvae were not recovered in 38% of overall alerts (both full TFRs and CoBs) made by the scent detection dog team, it is possible that questing larvae were present but not found via the imperfect drag method. Additionally, false positive rates changed over time potentially as both dog and handler learned the context of target scent cues and as Frost was able to be rewarded immediately for performing a TFR on visible tick clusters. Except for a few high infestation cases of thousands of larvae on the tips of vegetation, larval *D. albipictus* clusters are difficult to immediately identify and, thus, difficult to quickly reward Frost for positive identification. Even so, a handful (n=8) TFRs or CoBs were able to be immediately identified as positive for tick larvae without dragging, which may have reinforced field training and led to decreasing false positive rates over time. We believe that it is likely that Frost's detection performance would have continued to improve with additional time and financial resources for training.

Determining tick species distribution and abundance at larger scales is vital to accurately assessing current and future disease risk. A major hindrance to widespread active surveillance for ticks has been logistic constraints, unlike other vectors like mosquitos which can be caught with traps near urban centers, only a handful of tick vectors are effectively trapped with dry ice traps and host-trapping grids are not easy to monitor by groups such as pest management councils (Holcomb et al. 2023, Lippi et al. 2021, Wisely and Glass 2019). Here we explore a potential efficient tick surveillance method using scent detection dogs, a growing resource for conservation and other groups around the United States. Future research could investigate the ability of dogs to differentiate between species of ticks, which seems plausible given their ability to discriminate between the sign of closely related species like grizzly (*Ursus arctos*) and black bear (*Ursus americanus*) scat (Wasser et al. 2004). Such an ability would be especially useful if dogs were to be used to search ports-of-entry, international livestock shows, or other potential introduction avenues for high-risk tick species. Tick systems like the cattle fever tick (*Rhipicephalus microplus*) system on the United States-Mexico border may benefit from increased survey speeds and the ability to detect ticks on hosts at potential invasion hot spots (Showler, Pérez de León and Saelao 2021). The invasion and spread of the long-horned tick (*Haemaphysalis longicornis*) across the eastern U.S. is another example of a system where widespread surveillance for questing ticks and attachment to livestock hosts may benefit from faster methods (Thompson et al. 2022, Trout Fryxell et al. 2021).

Conclusions

Scent detection dogs may benefit widespread, well-funded tick surveillance projects, but the traditional tick drag method is still likely to be the most cost-efficient tick surveillance approach for ecological association or abundance surveys. The lack of agreement between tick status using both methods implies important limitations in detection probability and accuracy for the widely-used tick drag method and raises the need to account for detection biases and estimating false negative rates if tick drag data are used to extrapolate distribution or abundance across out-of-study areas (Dantas-Torres et al. 2013, Kjellander et al. 2021, Newman et al. 2019). Overall, we found that dog-assisted crews do not remarkably outperform human-conducted tick drag surveys but are faster and may be useful in niche survey situations, such as surveys for tick species with potential for high aggregations, detecting invasive species, sampling unconventional surfaces like animals or shipping containers, and surveying over large areas.

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Availability of Data and Materials

All data and associated metadata are available from Koser et al. (2024): https://www.sciencebase.gov/catalog/item/66f1cd96d34e0606a9dc8599.

Authors' Contributions

TK led project design, survey design, data analysis, and manuscript preparation. AH planned and conducted field surveys, assisted with data collection, and reviewed early manuscript drafts. AC and BW provided logistical support including property permissions and reviewed late-stage manuscript drafts. PC advised TK on project design and reviewed analyses and manuscript at all stages.

Ethics Approval and Consent to Participate:

Not applicable

Consent for Publication:

AH gives consent for publication of Figures 2 and 3.

Competing Interests:

The authors of this paper declare no conflicts of interest.

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CHAPTER FOUR

ENVIRONMENTAL ASSOCIATIONS WITH WINTER TICK (*DERMACENTOR ALBIPICTUS*) OCCUPANCY, ABUNDANCE, SURVIVAL, AND REPRODUCTION IN JACKSON HOLE, WYOMING

Contribution of Authors and Co-Authors

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Abstract

Environmental factors like temperature and moisture availability are known to limit key processes in tick life cycles but scaling findings from small-scale field or laboratory studies to landscape-level patterns in tick occupancy and abundance has proven difficult. Local adaptation in tick populations to regional climate conditions could partially explain difficulties in expanding findings in broadly distributed tick species. The winter tick (*Dermacentor albipictus*) is a widespread one-host tick species with a range spanning from the Yukon territory in northern Canada as far south as the Mexican state of Chiapas. Winter ticks infest a wide range of wildlife host species in North America but are notorious for infesting moose (*Alces alces*) at rates high enough to cause negative health impacts including anemia, early spring hair loss (alopecia), and even death. We hypothesized that although previous research on winter ticks has shown high sensitivities to snow presence in spring, desiccating conditions in summer would be a stronger driver of winter tick population dynamics in western, mountainous systems where populations may be locally adapted to high snow volumes in spring. We used hierarchical N-mixture models to examine relationships between snow water equivalent, minimum spring temperatures, maximum summer temperatures, and vapor pressure deficits with winter tick occupancy and abundance in Jackson Hole, Wyoming from 2020-2022. We found winter tick occupancy to increase with warmer summer temperatures and decrease with drier summer conditions. Spring conditions had little affect on occupancy rates and neither suite of environmental variables fit the abundance data well. Fitting models to tick data, which is typically highly over dispersed, remains challenging even when accounting for imperfect detection biases with hierarchical N-mixture models. Future studies on tick-climate relationships should consider imperfect detection,

the potential for local adaptation, and explore new methods for handling highly heterogeneous tick data.

Introduction

Investigating distributional, abundance, and behavioral shifts in parasitic species like hard ticks (Acari: Ixodidae) under anthropogenic climate change is increasingly important for agencies managing human and animal health (Altizer et al. 2013; Cohen et al. 2020; Polley, Hoberg and Kutz 2010). Ticks spend large proportions of their life cycle off-host where they are exposed to environmental conditions which affect key developmental processes like egg laying and host seeking (Dantas-Torres 2015; Gilbert 2021; Ogden et al. 2021; Ostfeld and Brunner 2015). While numerous studies have explored the impacts of climate variables on tick populations, extrapolating findings to estimate tick-borne disease risk across space or time remains challenging due to the complex interplay between climate, tick biology, and host ecology across wide geographic ranges (Brunner et al. 2023; Sumilo et al. 2007). Local adaptation to environmental conditions like temperature and moisture availability may be partially responsible for variations in responses to climate perturbations across a species range (Estrada-Peña 2008; Estrada-Pena and Venzal 2007).

Many tick species of concern for human and animal health like the brown dog tick (*Rhipicephalus sanguineus*), eastern blacklegged tick (*Ixodes scapularis*), and winter tick (*Dermacentor albipictus*) are distributed across much of the U.S. and can be found in a wide variety of habitats with different vegetation structures, soil types, host communities, and seasonal weather patterns (Chenery et al. 2023; Eisen 2022; Sonenshine 2018). Research on broadly-distributed tick species like *Ixodes ricinus* in Europe have found adaptation to local conditions which may impact expected shifts in temperature or humidity-dependent abundance and distribution under climate change (Estrada-Peña 2008). Research interest in the abiotic factors affecting the winter tick, a major pest of moose (*Alces alces*) in North America, has been focused on the Northeast and Midwest areas of the U.S. and the Canadian provinces of Ontario and Alberta, but relatively little is known about the winter tick and its ecology in the western U.S where humidity, snowfall patterns, and seasonal temperature profiles differ from most previously studied regions (Addison et al. 2016; Addison, Johnson and Fyvie 1979; Debow et al. 2021; DeCesare et al. 2024; Garner and Wilton 1993; Jones et al. 2019; Samuel 2007). In this study we explored patterns in winter tick reproduction, occupancy, abundance, and relationships with abiotic factors in Jackson Hole, Wyoming and compared our findings to previous research. Winter tick infestations on moose and other ungulates of Jackson Hole, situated in the southern portion of the Greater Yellowstone Ecosystem (GYE) in northwest Wyoming, have been noted as far back as the late 19th century (Brimeyer and Thomas 2004; Houston 1967). Moose are relatively recent inhabitants of the GYE, believed to have arrived in the early-to-mid 19th century alongside settlers potentially due to the increased availability of forage from timber cut blocks (Brimeyer and Thomas 2004; DeCesare et al. 2019). Moose in this region belong to the Shiras subspecies (*Alces alces shirasi*) which is smaller than other moose subspecies and occupies some of the southernmost territories for moose in the Northern Hemisphere. Moose at the southern extent of their range have faced several emerging population threats including climatic extremes exceeding physiological thresholds, habitat loss, and parasites (Becker, Kauffman and Anderson 2010; DelGiudice et al. 2011; Lenarz et al. 2010; Nadeau et al. 2017; Wattles and DeStefano 2011; Weiskopf, Ledee and Thompson 2019).

Historically, reports of high winter tick infestations on Shiras moose have been sparse, limited to infrequent epizootic reports made by state game and fish agencies and incidental reports from trappers and hunters (Brimeyer and Thomas 2004; Houston 1967). Recent interest in declining hunter opportunities and depressed population trends for Shiras moose herd units in the core of their range have raised concern over the potential impacts of parasites like winter ticks, prompting several agencies including Montana Fish Wildlife & Parks, Idaho Department of Fish and Game, Utah Division of Wildlife Resources, and Wyoming Game and Fish Department to establish or update moose monitoring and research projects (DeCesare et al. 2024; Nadeau et al. 2017). DeCesare et al. (2024) collected winter tick infestation data from Shiras moose monitoring projects and found climate signals across temporal and spatial scales indicating an overall greater infestation risk in warmer regions and years which largely agreed with previous studies on winter tick-moose-climate interactions. Moose are known to modify their behavior during warmer time periods and to become physiologically stressed under warmer conditions which may impact their grooming ability and energy budgets available to address high winter tick infestations, potentially confounding climate relationships to the winter tick-moose system when using infestation data alone (Dussault et al. 2004; Melin et al. 2014; Thompson et al. 2020). To further investigate the findings outlined in DeCesare et al. (2024), we explored relationships between winter tick occupancy and abundance and a similar suite of abiotic factors using both repeated field surveys and a reproduction monitoring study.

Methods

Larval Winter Tick Field Collections

Field collections for questing larval winter ticks in Jackson Hole took place during the fall seasons of 2020-2022 (Figure 1). Three sites remained consistent across all three sampling years while two sites changed between years to capture different environmental gradients of interest. Consistently sampled sites include Wilson, Pacific Creek, and Buffalo Valley. Sites in the National Elk Refuge, Gros Ventre, Teton Village, and Phillips Ridge areas were added in 2021 and 2022 and were chosen to capture variation along elevational gradients and host presence (elk-dominated, moose-dominated, and used by both species). Sites in Grand Teton National Park were sampled in 2020 but left out in 2021 and 2022 due to ease of access, visibility, and safety concerns. Total estimated snowfall in Jackson Hole was ~ 451” for the winter of 2019-2020, ~ 437” for 2020-2021, and ~ 304” for 2021-2022. Average snowfall from 2012-2022 was ~ 462” (Center 2024).

Transect locations at the Wilson site were located along the banks of the Snake River at some of the lowest elevation points in Jackson Hole (~1,880m). Wilson is a residential community with wide variations in vegetation communities, but sites sampled in this project primarily included an overstory dominated by *Populus angustifolia* (narrow-leaf cottonwood) and an understory consisting of mixed grasses and forbs as well as young *Salex spp.* (willows). Pacific Creek and its affiliated sampling locations are situated just north of Grand Teton National Park within Bridger-Teton National Forest along Pacific Creek Road. At ~2,120m, Pacific Creek contains lodgepole pine stands, cottonwood galleries, willow communities along riparian zones, and mixed sagebrush (*Artemsia* spp.) meadows. Finally, Buffalo Valley is just due east of Pacific Creek at ~2,110m with similar vegetation communities but drier, more open conditions than Pacific Creek. The National Elk Refuge (NER) is a 98-km^2 refuge established in 1912 to protect and manage the winter range for the Jackson elk herd. Sitting at roughly 1,900 m, the refuge itself consists mostly of native grassland and irrigated hay meadows with an extensive floodplain from Flat Creek. Transect locations in the NER site cohort also included 12 locations further upriver along the Gros Ventre River up to an elevation of ~2,100m. Phillips Ridge is part of the larger Teton Range and sits northeast of Teton Pass/WY22. Transect locations on the ridge ranged from 2,200m to 2,440m in elevation and primarily included lodgepole pine (*Pinus contorta*) forest and scattered *Salex spp.* and other shrub stands. Teton Village includes maintained ski and winter recreation areas nestled within the Jackson District of Bridger-Teton National Forest. Transects at these sites included residential and lodgepole pine forest habitats ranging from 2,150 m to 2,350 m in elevation.

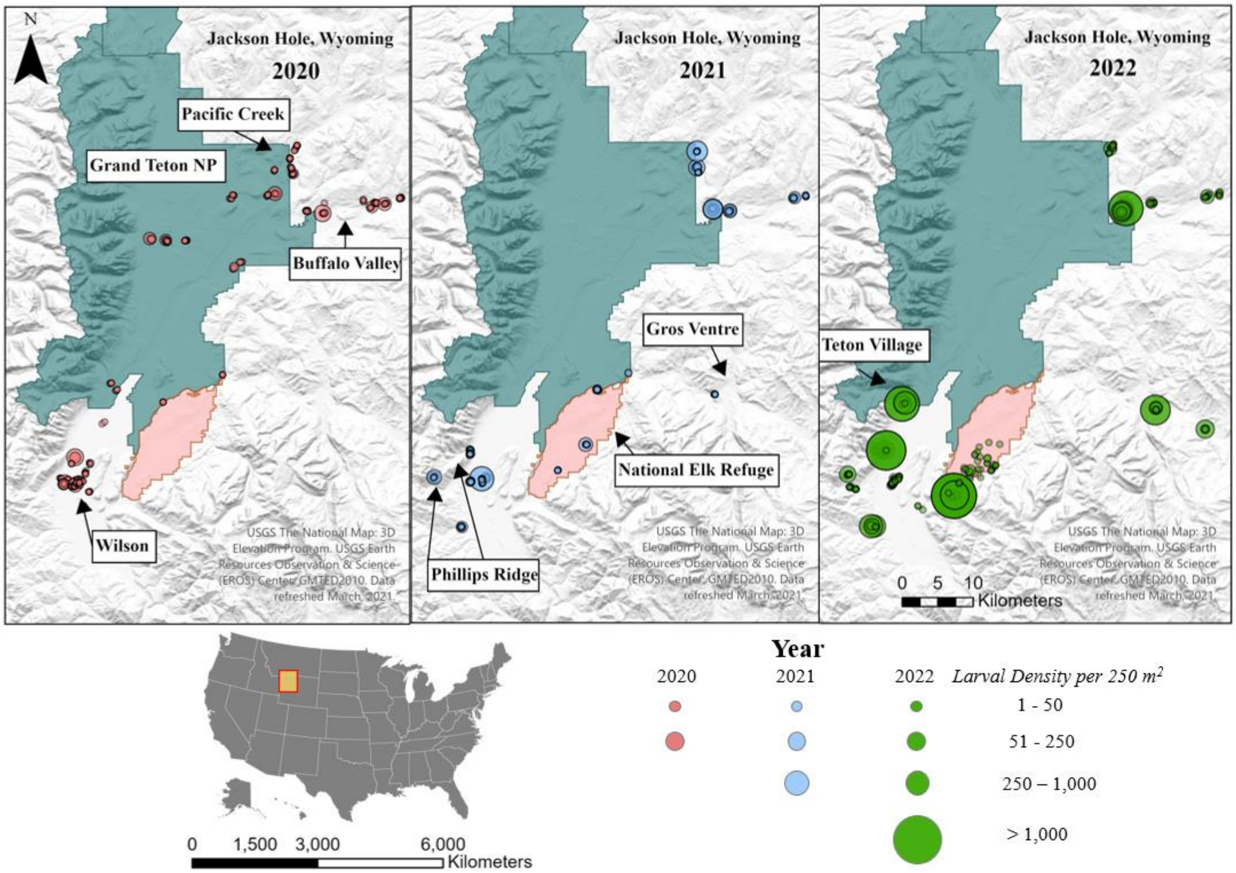

Figure 1: Maps of Jackson Hole, Wyoming with locations for 250 m transects surveying for questing larval winter ticks (*Dermacentor albipictus*) from 2020-2023. Bubble size relates to the number of larval ticks recovered from all repeated visits at a given transect within the year.

At each site we selected 2-4 250m transect locations within 500m of a focal point. We searched for transect routes that followed game paths and marked a 250m path using a GPS device and flagging tape. We dispersed transect locations haphazardly between the available major communities (willow, cottonwood, conifer, sagebrush, grassland). Transects at each site were sampled for questing winter tick larvae 2-4 times from mid-September to early November. Sampling frequency depended on weather and road conditions, sampling did not occur on days with heavy rainfall, snowfall, or when roads were too wet or snow-covered to be safely traversed. Transects were sampled using a traditional tick drag protocol whereby a technician drags a $1m^2$ flannel cloth across available vegetation at marked transect locations, using a GPS device to check location relative to prescribed path if needed (Salomon, Hamer and Swei 2020). Technicians would check for attached larvae on the drag cloth roughly every 10 paces. If larvae were detected, the technician would extract attached larvae using a lint roller and preserve 10 larvae in 75% ethanol for identification using a dichotomous key (Brinton, Beck and Allred 1965). The technician would then use a either a physical or Survey123© form to record likely vegetation type, height, and take a representative photo of vegetation along the path before detection. Larvae on lint roller sheets would be placed in plastic bags and given a detection event label and counted later in the day or sampling week. Dominant vegetation class (willow, cottonwood, conifer, sagebrush, grassland), weather conditions (sunny, partly cloudy, stormy), and host sign (moose/elk/mule deer/other, pellets/remains/prints/live animals, low/medium/high density) were recorded at the beginning of each transect as well as microclimate conditions (temperature, relative humidity, wind speed) at .75m above the ground using a Kestrel mini weather station (Kestrel 3000 Pocket Weather Station; Nielsen-Kellerman, Chester, PA, USA).

Abiotic factors and hypothesized impacts on winter tick occupancy and abundance

Previous research has identified moisture availability, temperatures below biological thresholds in spring and above thresholds in summer, and snow cover in spring and fall as limiting conditions for winter tick survival, abundance, and host attachment rates (Addison et al. 2016; Ball 2017; Drew and Samuel 1986; Drew and Samuel 1985; Healy et al. 2020; Holmes et al. 2018; Hoy et al. 2021; Pouchet et al. 2024; Samuel 2007; Wright 1969; Yoder et al. 2015; Zarnke et al. 1990). Empirical studies from Alberta and Ontario have been largely corroborated by findings in the Northeast, finding that winter tick epizootics correlate with mild winter conditions in the spring season. Winter-like conditions in the Rocky Mountain West may extend far past the typical end of the winter tick drop-off season in mid or late May, thus we hypothesize that winter ticks in this region of North America may have adapted to be more resilient to conditions like deep snowpack and cool temperatures in spring. Summers in the western U.S. can also be much drier than in other parts of the country, exposing eggs and newly hatched larvae to potentially desiccating conditions which is the largest source of mortality for winter ticks after oviposition (Yoder et al. 2015). We considered two models, one using a suite of predictors based on previous research mainly targeting conditions in spring, and another targeting conditions in summer, and assessed their respective abilities to describe observed variation in winter tick occupancy and abundance across Jackson Hole, WY. The model based on previous research included average minimum daily surface temperature from March to May and cumulative snow water equivalent from March to May. Our hypothesized ‘Western/summer’ model included average maximum daily surface temperature from June to August, mean daily vapor pressure deficit from June to August, and elevation of sampling site. We obtained temperature, snow water equivalent, and relative humidity data using *Daymet* version 4 in the statistical software program *R* at a 1 x 1 km resolution at each transect location and across all three sampling years (Thornton et al. 2022).

Alongside these environmental variables we also included landscape variables known to impact microclimate conditions (Addison et al. 2016; Ball 2017). We included dominant vegetation type as determined from tick drag surveys (willow, cottonwood, conifer, sagebrush, grassland) and elevation. Because winter tick activity seasons typically resemble a bell curve with a predictable peak in abundance and detection probability, we also included Julian date of sampling as a factor affecting detection probability (Chenery et al. 2020; Drew and Samuel 1985). Finally, detection probability for many tick species is influenced by day-of-sampling environmental conditions like temperature, precipitation, wind speed, and relative humidity (Dobson 2013; Glass et al. 2019; Sirén et al. 2024). We included temperature from a Kestrel mini weather station on the sampling date to account for variations in detection probabilities.

Reproduction Monitoring Microclimate Stations

Between March and May 2021 and 2022 we collected fed adult female *D. albipictus* ticks from moose bedding sites in Jackson Hole, WY. Up to five ticks were taken from a bedding site and weighed then deployed at reproduction monitoring stations. Monitoring stations used in 2021 were located in Wilson and Buffalo Valley to compare survival and reproduction rates in a low elevation, residential, riparian system to a higher elevation, rural, mixed conifer forest-willow system. Monitoring stations in 2022 included the Wilson and Buffalo Valley sites as well as an additional site on Phillips Ridge at a much higher elevation with deeper snowpack in spring. Monitoring stations in 2021 were 2.5m x 2.5m wire mesh cages with five tick ‘arenas’ inside for containing fed adult female ticks. Stations were fitted with HOBO U23 Pro v2 Temperature/Relative Humidity Data Loggers with probes situated within available leaf litter. Loggers recorded temperature and humidity values every hour from deployment to larval retrieval in late September. Stations in 2022 were 1.5m tall, 50cm diameter circular wire mesh cages with plastic netting around the bottom 1m of the cage to prevent ticks from moving beyond the enclosure. One tick was deployed per station in 2022 with one temperature and relative humidity logger deployed per every five cages. Stations were visually checked weekly for questing larvae in the fall starting in early September. Cages were removed in late November and vegetation above 20 cm was cut and frozen at -20 C° for two days after which larvae were presumed to be dead and were poured onto a flat surface and counted. Sixty fed adult female winter ticks were deployed at monitoring sites in 2021 and in 2022.

Statistical Analysis

We analyzed occupancy and abundance using a hierarchical modeling framework accounting for imperfect detection in the package *unmarked*. For both occupancy and abundance data we fit a detection process model with visit-specific covariates (Julian date, temperature) and population covariates, which for spring/drop-off season models included spring snow water equivalent and minimum daily average temperatures while summer/larval quiescence models included elevation, cumulative vapor pressure deficit, and average daily maximum temperature. Variables were scaled to set mean to 0 and standard deviation for 1 as mentioned above. We tested for the existence of interaction and polynomial terms by comparing AIC_c and Goodness-of-Fit values. We also estimated Percent of Area Occupied (POA) using the *unmarked* package.

We only considered factors with Pearson's correlation coefficients <0.5 to avoid multicollinearity. We tested for zero inflation and overdispersion using the package *DHARMa*. We analyzed relationships between average relative humidity and temperature during the off-host season and survival and larval abundance in microclimate stations using generalized linear models (GLMs) with binomial and lognormal distributions respectively using the package *glmmTMB*. Adjusted predicted values, marginal means, and graphics were generated using the packages *ggplot2* and *ggeffects*. Goodness-of-fit and Nagelkerke's adjusted R^2 estimates for comparing models were generated using the package *AICcmodavg*.

Results

We collected totals of 6,395 larval winter ticks in 2020, 9,951 in 2021, and 20,092 in 2022. Ticks were found on ~ 22% of transects in 2020, ~ 33% in 2021, and ~ 20% in 2022. Larval density per 250 m^2 transect ranged from 83.05 in 2020, 100.51 in 2021, and 324.06 in 2022. Questing occurred starting early September and larvae were recovered from sites until snow inhibited surveys in late November. Temperatures at which larvae were recovered ranged from 40.1 C° to -12.3 C°.

Occurrence

All estimates are presented respective to scaled increases or decreases in given response variables. We found that larval winter tick occurrence increased with increasing average daily maximum temperatures in summer (Estimate = 0.347, SE = 0.245, $z = 1.42$, $p = 0.016$, Figure 2c, Table S1) and decreased with increasing cumulative vapor pressure deficits (Estimate = -0.284, SE = 0.185, $z = -1.53$, $p = 0.013$, Figure 2d, Table S1). Changes in average daily minimum temperature and snow water equivalent over spring produced <0.05 differences in occurrence (Figure 2a, Figure 2b, Table S1). The summer/larval quiescence season model ($\hat{c}$ = 3.01, AIC = 997, χ^2 = 362.30) displayed lower overdispersion and explained more variation versus a null model than the spring/drop-off season model ($\hat{c}$ = 11.32, AIC = 1007, χ^2 = 569.12). Probability of occupancy was estimated to be 0.623 or 62.3% across all sites and years.

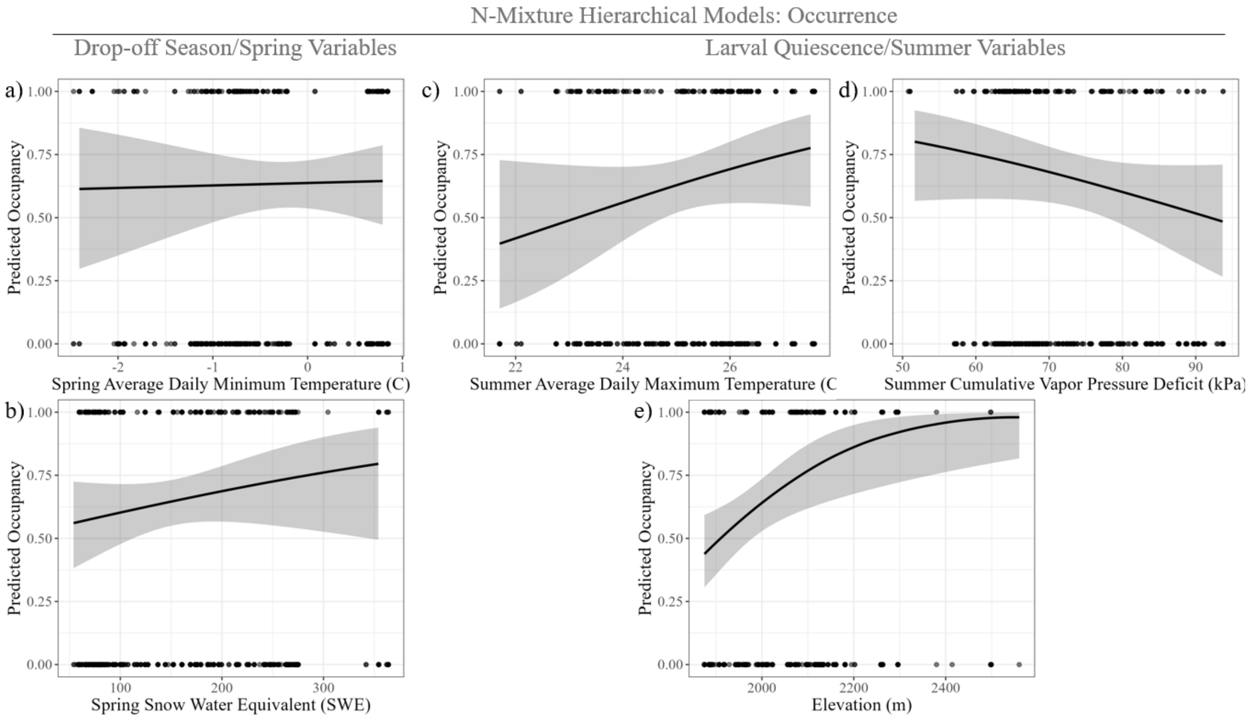

Figure 2: Lines represent predicted occupancy values from N-mixture hierarchical models for values of given predictor variables. Shaded regions represent 95% confidence intervals. Drop-off season and larval quiescence season variables were tested using separate models.

Abundance

Selected variables did not produce strong responses in larval winter tick abundance (Estimates < 0.5, $p > 0.10$, Figure 3, Table S1). Neither the spring drop-off model nor the summer larval quiescence model fit the abundance data well ($\hat{c} > 20$, AIC > 5000, $\chi^2 > 1000$).

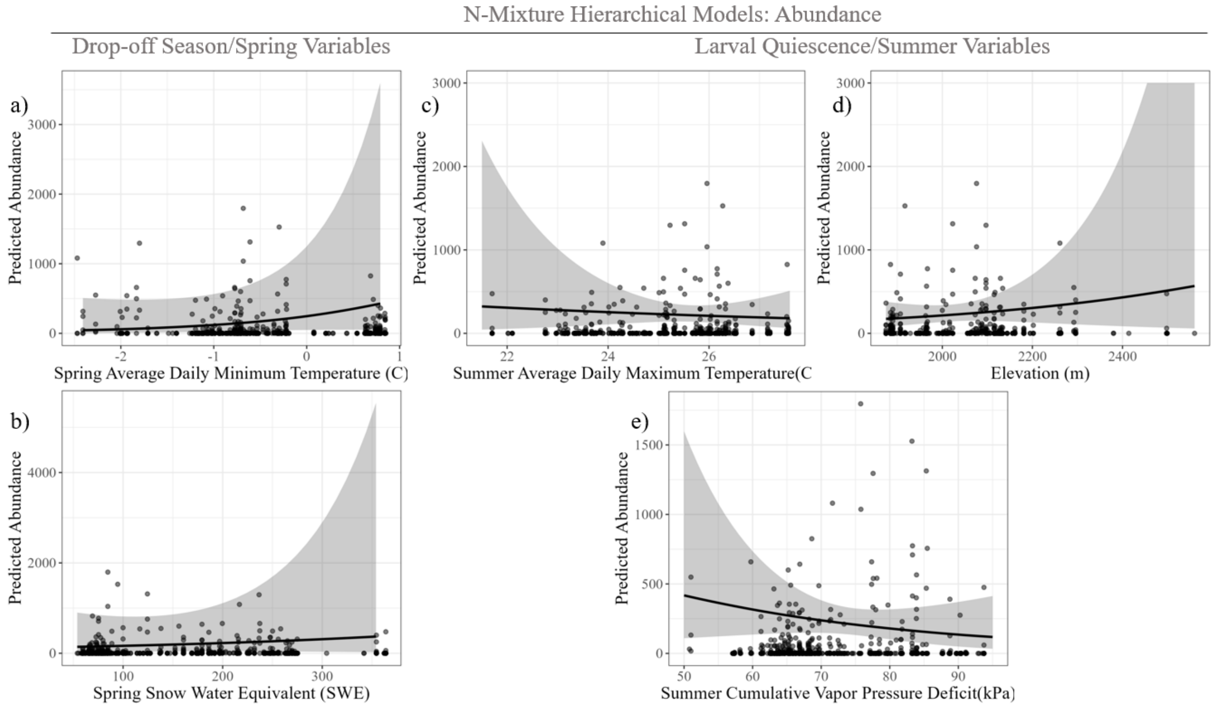

Figure 3: Lines represent predicted abundance values from N-mixture hierarchical models for values of given predictor variables. Shaded regions represent 95% confidence intervals. Drop-off season and larval quiescence season variables were tested using separate models.

Reproduction Monitoring Surveys

Overall survival of fed adult female winter ticks and quiescent larvae increased with increasing average temperatures over the off-host season (Estimate: 0.11, 95% CI: 0.45: 0.18, $z < 0.001$, Figure 4). The number of questing larvae produced by fed adult winter ticks placed in microclimate and reproduction monitoring stations fit with a second order polynomial term with the average temperature in Celsius across the entire off-host season ($\chi^2 = 20.44$, $p < 0.001$, Figure 4). Female ticks deployed at sites in Wilson in 2022 were on 35.5cm of snow which melted by April 5th and produced on average 855 larvae (SD: ±121) while ticks deployed at Buffalo Valley were on 121cm of snow which melted by May 16th and produced 655 larvae (SD: ±110) on average and ticks deployed at Phillips Ridge persisted on 147cm of snow which melted by June

16th and produced on average 578 larvae (SD: ±199). There were no clear relationships between larvae production, fed adult female tick and quiescent larvae survival, and relative humidity at microclimate monitoring stations.

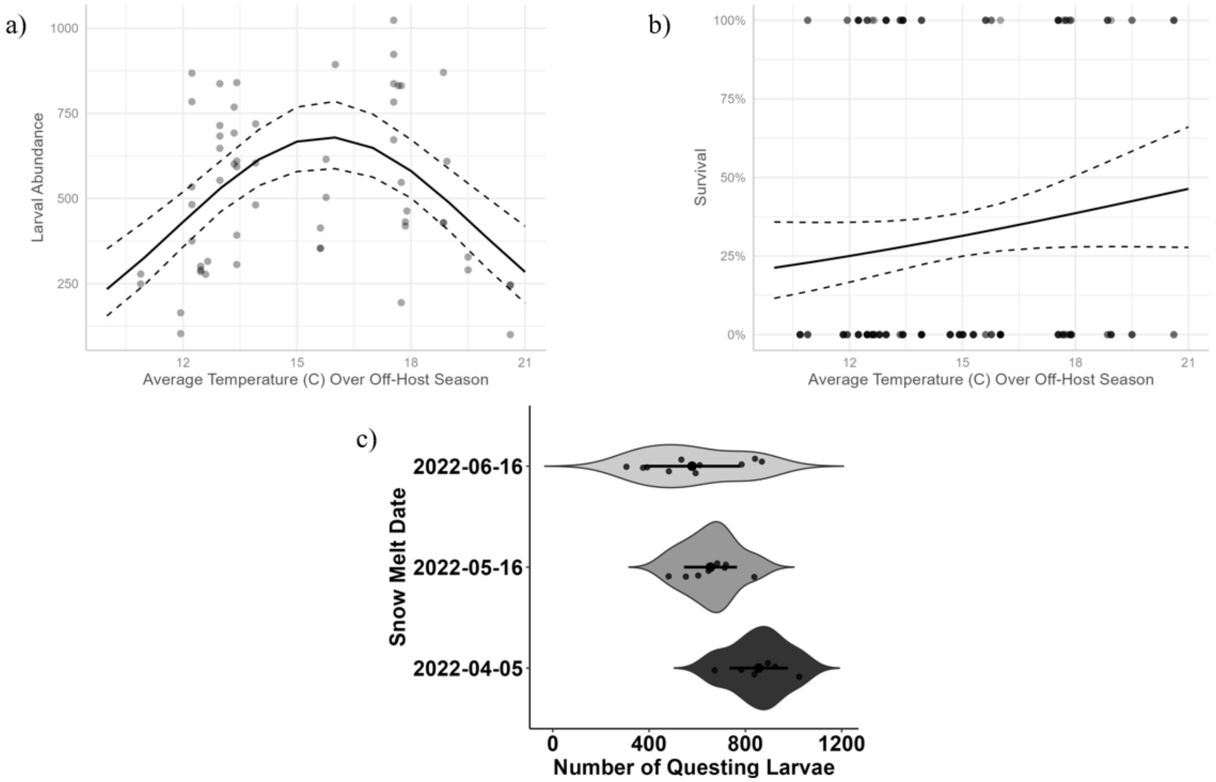

Figure 4: a) Number of questing larvae produced by fed adult female ticks in microclimate monitoring stations against average temperature (Celsius) over the off-host season at a station measured via HOBO RH & Temperature Data Loggers ©. Line represents second order polynomial term for predicted values of larval abundance over temperature and dashed lines represent 95% confidence intervals. b) Survival rates of fed adult female ticks and quiescent larvae to produce questing larvae in microclimate monitoring stations against average temperature (Celsius) over the off-host season at a station. Line represents predicted occurrence values against temperature and dashed lines represent 95% confidence intervals. c) Violin plots displaying point spread of larvae produced by fed adult female ticks in 2022 placed in three different sites (Wilson, Buffalo Valley, Phillips Ridge). Point ranges represent means and + 1 standard deviation.

Discussion

Our hypothesis that warmer, drier conditions in summer would lead to lower winter tick abundance and occupancy rates was not supported. The only strong relationship among the suite of climate variables we examined was a positive relationship between occupancy and summer maximum temperatures and a negative relationship with vapor pressure deficit (Figure 2). We did recover predicted relationships between winter tick off-host survival and reproduction with temperature and snow melt timing in our microclimate studies (Figure 3). We consistently recovered larvae in late October through late November at temperatures between 0 C° and -12.3 C° (Figure S1, S2) which are often considered inhibitory to larval winter tick activity (Holmes et al. 2018). Future winter tick-moose research in western systems should investigate the potential that some winter tick larvae populations could be locally adapted to colder temperatures and snow presence. Projects employing fall drag surveys for winter ticks or estimating variables associated with the fall questing season may wish to consider activity seasons lasting well into the winter months.

We used environmental covariates derived from an extrapolated, remotely-sensed dataset which likely misrepresents the environmental conditions experienced by winter ticks on the ground (Boehnke et al. 2017). Microclimate conditions, which are controlled by small-scale factors like vegetation structure and soil type, likely vary dramatically within the 1 km spatial scale of the raster dataset used here and may explain why relationships were not recovered. Future studies would benefit from assessing microclimate conditions at survey sites using remote data loggers to analyze long-term relationships between variations in temperature and humidity and tick survival and production, as has been done with other tick vectors like *Ixodes scapularis* (Dumas et al. 2022).

Climate change is likely to shift snow accumulation further into the spring season from March to April in the southern Greater Yellowstone Ecosystem with temperatures expected to increase by 7% in the next 50 years (Hostetler et al. 2021). More snow and rain falling in the middle of winter tick drop-off season versus the beginning could limit winter tick populations under climate change, but such changes may be counteracted by warming conditions across the spring, summer, and fall seasons when winter ticks are off-host. Changes to habitats in the region like urbanization and conifer encroachment are likely to alter both habitat suitability for winter ticks and usage by cervid hosts like moose and elk. Future research on winter tick demographic responses under climate change should include fine-scale variables and host factors while also accounting for the limitations of survey methods.

Studies on tick abundance and occupancy patterns rarely account for imperfect detection rates even though temperature and activity seasons are well documented for many tick species (Dobson 2013; Salomon, Hamer and Swei 2020; Sirén et al. 2024). Hierarchical models like N-mixture models can allow for the specification of a detection probability submodel, providing information on probability of detection given presence, alongside a typical process submodel. Here we accounted for imperfect detection probabilities based on temperature at time of sampling and sampling date, meaning the interpretation of parameters is within the context of fluctuating detection chances across the winter tick questing season and range of temperature values impacting availability to be sampled (Kéry 2018; Madsen and Royle 2023). Our analyses could be improved by investigating polynomial terms and potential interactions in both the process and detection probability submodels.

Both the spring/drop-off and summer/larval quiescence abundance models poorly fit our data and did not outperform a null model. We believe this is largely due to overdispersion in the abundance data which was poorly explained by variation in selected predictors. Analyzing our data in a Bayesian framework, using random effects to account for within-site variation, could help with model specification and performance. Tick data remains difficult to examine with many tools common to examining relationships between environmental covariates and patterns in occupancy and abundance, thus novel methods from other systems should be explored such as integrated projection models and models using a Bayesian framework.

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CHAPTER FIVE

RELATING MOOSE MOVEMENT ECOLOGY TO WINTER TICK RISK IN THE SOUTHERN GREATER YELLOWSTONE ECOSYSTEM

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Abstract

Winter ticks (*Dermacentor albipictus*) are known to hyper aggregate on moose (*Alces alces*), leading to early spring hair loss, anemia, and even death. Dynamics in the winter tick-moose system are heavily dependent on climate factors like snow melt timing and temperatures in spring which drive epizootic patterns, but little attention has been given to the relationships between moose migratory behaviors and winter ticks. In this study we used GPS data from collared moose in Jackson Hole, Wyoming and a repeated early spring hair loss survey to quantify migratory behaviors and home range characteristics to analyze relationships with early spring hair loss categories: a characteristic sign of complications from winter tick infestations. We also investigated landscape characteristics with the spatial distribution of hair loss severity on moose during three successive years of opportunistic early spring hair loss surveys on moose. We found the degree of overlap between an individual moose's fall and spring home ranges to be a strong influencer on the probability of being in a higher hair loss category. We also found fall home ranges at higher elevations, with greater proportions of rural versus urban land cover, and lower host densities to correlate with lower hair loss categories. Moose migrating during the fall attachment season for winter ticks may have lower encounter rates with winter ticks, different grooming behaviors, or different energy budgets available to weather winter tick infestations, leading to reduced observations of complications from winter tick infestations in the following spring. Future research should incorporate host movement information during transmission seasons into the consideration of winter tick impacts on moose especially in the partially migratory populations of Shiras moose in the western U.S.

Introduction

Seasonal migrations can aid individual animal health and survival by increasing forage quality, reducing predation risk, and improving population connectivity and viability (Berg et al. 2019, Hebblewhite and Merrill 2007, Hebblewhite and Merrill 2009). Migrations can also impact disease dynamics by culling individuals with heavy pathogen loads (*i.e.*, migratory culling), releasing individuals from parasite-laden landscapes (*i.e.*, migratory escape), or separating heavily-burdened and low-burden populations (*i.e.*, migratory separation), among other scenarios (Altizer, Bartel and Han 2011, Hall, Altizer and Bartel 2014, Peacock et al. 2020). Whether an individual or population is deigned ‘migratory’ or ‘resident’ is often defined by overlap between summer and winter ranges, but migration in the context of parasite encounter rates may be more appropriately defined as overlap between transmission seasons which are specific to a given parasite’s phenology (Altizer, Bartel and Han 2011, Cagnacci et al. 2016). In this study we explore relationships between different classifications of migratory behavior in a partially migratory population of moose (*Alces alces*) and disease dynamics with an environmentally transmitted parasite: the winter tick (*Dermacentor albipictus*).

Migratory behaviors are a fixture of many ungulate species in the mountainous regions of the western United States including the Greater Yellowstone Ecosystem (Abraham et al. 2022, Middleton et al. 2020). Moose in the western U.S. belong to the Shiras subspecies (*Alces alces shirasi*) which is known to undergo seasonal migrations from low elevation habitats, typically abundant with browse forage species like *Salex* spp., in winter to higher elevation summer ranges in mountainous mixed-conifer forests (Becker, Kauffman and Anderson 2010, Burkholder 2012, Houston 1967, Kufeld and Bowden 1996). Many herd units in the core areas of Shiras moose range are suspected to be in decline or stable when forage availability suggests their populations should be increasing, yielding management concerns about population threats like predator pressure, habitat loss, and parasites like winter ticks (Nadeau et al. 2017). Winter tick impacts on Shiras moose are relatively understudied when compared to winter tick-moose systems in the northeastern U.S. or parts of Canada (Chenery et al. 2023). Some observations of early spring hair loss on Shiras moose, a characteristic sign of complications from high winter tick infestations, and an increasing awareness on how climate change affects parasite populations have prompted interest in western winter tick research (DeCesare et al. 2024, Ruprecht et al. 2020). Though studies are sparse, many Shiras moose populations are expected to be partially migratory with some individuals remaining residents year-round, some individuals varying migratory behaviors across years, and others undergoing predictable seasonal migrations. Unlike herding ungulate species like elk (*Cervus canadensis*) which aggregate and move across landscapes in large numbers, moose are mostly solitary outside the breeding season thus their migratory timings and corridors are highly variable from individual to individual (Becker 2008, Kufeld and Bowden 1996). Understanding how individual-level variations in migratory behaviors impact winter tick infestation rates and corresponding health conditions could help managing agencies and conservation groups address the consequences of declines in the prevalence of migratory behaviors (Cole et al. 2015, Kauffman et al. 2021, Middleton et al. 2020).

Winter ticks are a one-host tick species associated with some moose population declines within southern portions of their range in North America. Although winter ticks infest a wide range of ungulate and non-ungulate hosts, aggregations of >30,000 ticks per animal are reported primarily on moose (Chenery et al. 2023, Chenery et al. 2022). Such high infestation loads are known to cause excessive irritation on moose leading to early spring hair loss (*i.e.*, alopecia, also known as “ghost moose”) as well as anemia and even death, especially in calves (less than one year-old) (Addison, Fraser and McLaughlin 2019, Addison and McLaughlin 1988, Jones et al. 2019, McLaughlin and Addison 1986). Winter ticks attach to their hosts as larvae in the fall (mid-September until host attachment or winter conditions impede questing behavior) and remain on their host through successive life stages until adults feed, engorge, and drop off their host to lay eggs in spring (mid-April through May) (Samuel 2004, Samuel 2007). The process of hundreds to thousands of adult female winter ticks feeding is hypothesized to illicit a strong itching sensation in moose which will groom excessively to remove engorging ticks, damaging their winter coat during a time of nutrient restriction and highly variable winter-like conditions. Migrating specifically during the fall larval questing season could influence winter tick encounter rates if fall seasonal ranges avoid areas used by the same individual, or other moose or competent hosts like elk, in the preceding spring. Migrating moose in the fall could also influence winter tick exposure if fall home ranges include areas with conditions that hinder winter tick development and survival like high snow volumes in spring or desiccating conditions in the summer, common characteristics of high elevation forests in mountainous, western ecosystems (Ball 2017, Healy et al. 2020, Hoy et al. 2021, Pouchet et al. 2024, Samuel 2007).

Migratory behaviors can be difficult to measure across large proportions of moose populations, thus moose management and conservation stakeholders may also be interested in associations between disease outcomes and landscape variables which may be easier to assess for large numbers of animals or across wide geographic ranges. In the winter tick-moose system, large-scale disease outcome studies typically employ spring hair loss surveys whereby surveyors assess degrees of hair loss occurring before the annual winter coat molt (Chenery et al. 2022, Samuel 1989). Winter ticks are known to be negatively affected by late snow melt timing in the spring season, thus snow volumes during the previous spring season could influence winter tick infestation rates on moose at the same locale in the following spring if moose are assumed to use the same area year-round (Ball 2017, Healy et al. 2020, Holmes et al. 2018, Hoy et al. 2021, Pouchet et al. 2024, Samuel 2007). Additionally, host presence and density during the spring season could influence winter tick abundances at a given site in the following fall and relate to observed hair loss patterns in moose during the spring, again if moose are assumed to use the same area year-round (Ball 2017).

In this study we used data from global positioning system (GPS)-collared moose, tick counts, and hair loss surveys to investigate relationships between seasonal migratory classifications and fall home range characteristics with winter tick dynamics on moose. We also used landscape variables known or hypothesized to impact winter tick abundance to explore relationships between landscape characteristics and early spring hair loss severity on uncollared moose.

Methods

Study Area

Our study took place in the valley of Jackson Hole, Wyoming located in northwestern Wyoming, USA. Jackson Hole includes protected areas like the National Elk Refuge, Bridger-Teton National Forest, Grand Teton National Park, and the southern portions of Yellowstone National Park as well as mountain town communities like Wilson and Jackson. Elevations in the valley range from ~1,850 m in the Snake River flood plain to ~4,200 m in the Teton mountain range. Moose in the valley belong to either the Jackson or Sublette herd units and are commonly encountered in residential areas, sagebrush (*Artemsia* spp.) communities, willow-dominated (*Salex* spp.) riparian corridors, lodgepole (*Pinus contorta*) forests, and subalpine fur forests. Jackson Hole is considered to be part of the southern portion of the Greater Yellowstone Ecosystem (GYE) which is characterized as a relatively intact temperate North American ecosystem including large carnivores like grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) alongside migrating ungulate populations like bison (*Bison bison*), elk, mule deer (*Odocoileus hemionus*), and moose.

Telemetry Data and Hair Loss Surveys

Moose were collared in Wilson, Wyo January-February from 2021-2023 as part of road-crossing research conducted by Wyoming Game and Fish Department and Wyoming Department of Transportation. During captures, moose were fitted with GPS collars (Telonics GPS/Iridium, Mesa, AZ), given a health examination, and surveyed for winter tick load using the Sine, Morris and Knupp (2009) transect method. All capture protocols were approved by Montana State University Institutional Animal Care and Use Committee under Protocol 2020-97-128. Migratory behaviors for collared moose were analyzed by constructing 90% kernel density estimates (KDEs) for seasonal utility distributions with seasons defined as summer (June 15-August 15), spring (March 15-May 15), fall (September 15-November 15) and winter (December 15-February 15) using the *ks* package in the R statistical software (Silva et al. 2022, Team 2023). Percent overlap between spring and fall KDEs was defined as one metric for migratory behavior and compared to overlap between summer and winter KDEs.

We also summarized several fall home range characteristics using individual moose GPS collar data. We estimated elk and moose spring density per km^2 using 66 elk GPS datasets and 31 moose GPS datasets by overlapping 90% utilization polygons generated from individual KDEs then averaging density inside a moose's annual 90% fall KDE polygon. We also averaged elevation and National Land Cover Database (NLCD) classes within a moose's 90% fall KDE polygon. Land cover classes including deciduous forests, coniferous forests, mixed forests, shrubland, grassland, and wetland were categorized as "rural" while urban, agricultural, and cropland land cover classes were categorized as "urban".

Spring hair loss surveys for moose in Jackson Hole were carried out from 2021-2023 from ~ March 15th – May 15th (Figure 1). During surveys an individual surveyor would record the latest known locations for collared moose and plan to attempt four survey visits throughout the entire spring season. While searching for collared moose, a surveyor would opportunistically record hair loss category (1-5), location, age, sex, calf status, and take photographs of uncollared moose if encountered. Surveyors also recorded the major habitat type surrounding the moose during a sighting as either 'residential' or 'urban' for developed areas such as neighborhoods, developed trails in urban parks, or agricultural land as opposed to 'forest' or 'rural' for moose found on large, protected areas like within the boundaries of a National Forest or on the NER. Hair loss categories were defined as Category 1 (0-5% loss or damage), Category 2 (5-20% loss or damage), Category 3 (20-40% loss or damage), Category 4 (40-80% loss or damage), and Category 5 (>80% loss or damage, *i.e.* 'ghost moose') following Samuel (1989). We estimated previous spring host density (elk and moose) using the 66 elk and 31 moose GPS datasets mentioned above, which only calculated density for locations within 90% spring KDE polygons for collared animals and assumed a density of 1 animal per km^2 for animals sighted outside the polygon area.

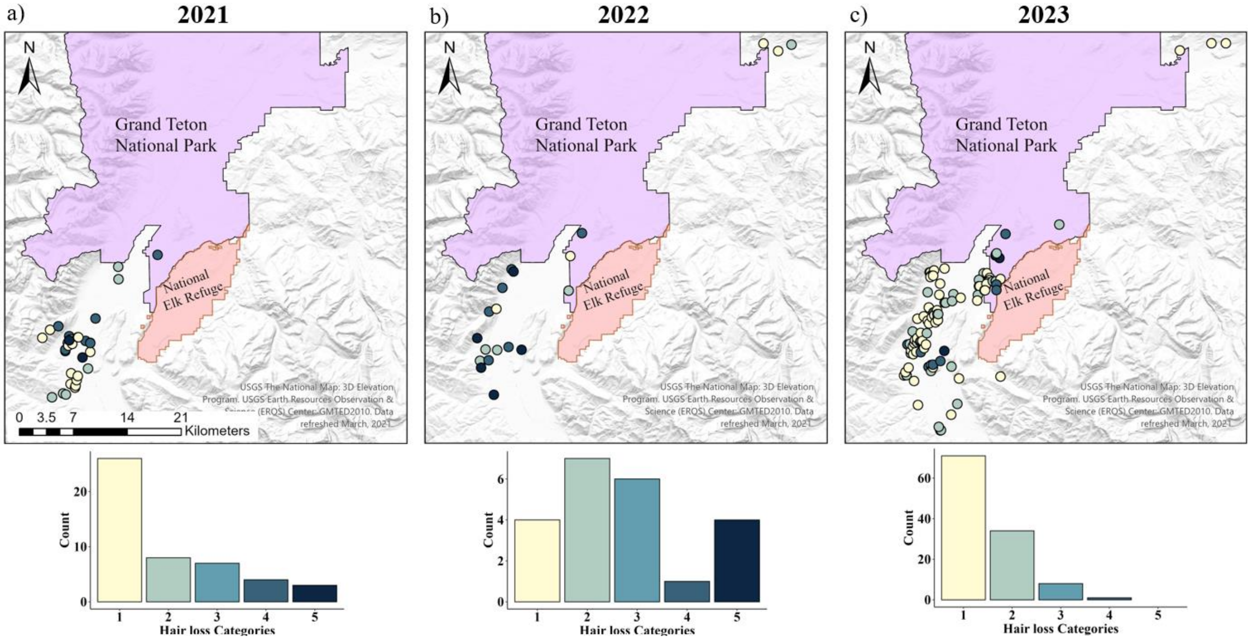

Figure 1: a-c) Maps of early spring hair loss survey locations from 2021-2023 with individual moose sightings represented by circles and colors denoting hair loss categories. Underneath each map is a frequency histogram representing the counts of sightings in a given hair loss category in the corresponding year.

Statistical Analysis

We used cumulative link models (CLMs) with logit links to explore relationships between tick load, migratory behavior, and hair loss categories on collared moose ($n = 17$) using the *ordinal* package in the statistical software: R (Christensen 2019, Team 2023). CLMs or proportional odds models are useful for analyzing relationships between covariates and ordinal response data when the differences between ordered categories is not necessarily known or inexact. The response variable was the highest hair loss category (1-5) recorded during the postcapture spring season with independent variables including *spring:fall seasonal home range overlap* (0-100% overlap), *summer:winter home range seasonal overlap* (0-100% overlap), *average elevation in fall home range* (m), *average estimated host density in fall home range* (individuals per 1 km^2), *percent 'rural' versus 'urban' habitats in fall home range* (0-100%), and *tick density at capture* (per cm^2). We used a separate CLM to examine relationships between migratory behavior and highest spring hair loss category for collared moose for all collaring years (n = 31 moose years) with identical predictors to the above CLM but without tick load since moose were not recaptured. We also used CLMs to explore relationships between all moose (both collared and unknown moose) surveyed for hair loss in spring from 2021-2023 (n = 184) and a suite of factors hypothesized to impact winter tick infestation rates on moose. Independent variables in this model included *estimated host density in fall home range* (individuals per 1 km^2), whether the moose was sighted in an 'urban' or 'rural' area, *elevation* (m), and *latitude*. Again, only the highest hair loss category among all spring revisits was used for collared moose. We scaled continuous variables to standardize means and standard deviations in all three CLMs. We also included data from all years in each CLM to aid model identification and convergence since multiple hair loss categories were poorly represented across years (<5% representation).

Results

We found probabilities of being in a higher hair loss category to increase with tick density at capture (Odds Ratio (OR) = 3.11, 95% CI: 1.02-15.90, $\beta = 1.14$, SE = 0.73, $p = 0.05$, Figure 2a) and decrease with higher proportions of fall home range designated as 'rural' versus 'urban'(OR = 0.09, 95% CI: 0.01-0.48, $\beta = -2.40$, SE = 1.02, $p = 0.02$, Figure 2b) for the CLM analyzing data from 17 moose with both tick load and telemetry information. We did not find significant impacts from summer:winter seasonal home range overlap, spring:fall seasonal home range overlap, host density in fall home range, or average elevation of fall home range on hair loss categories for this sample of moose (Figure 2c, Table S1).

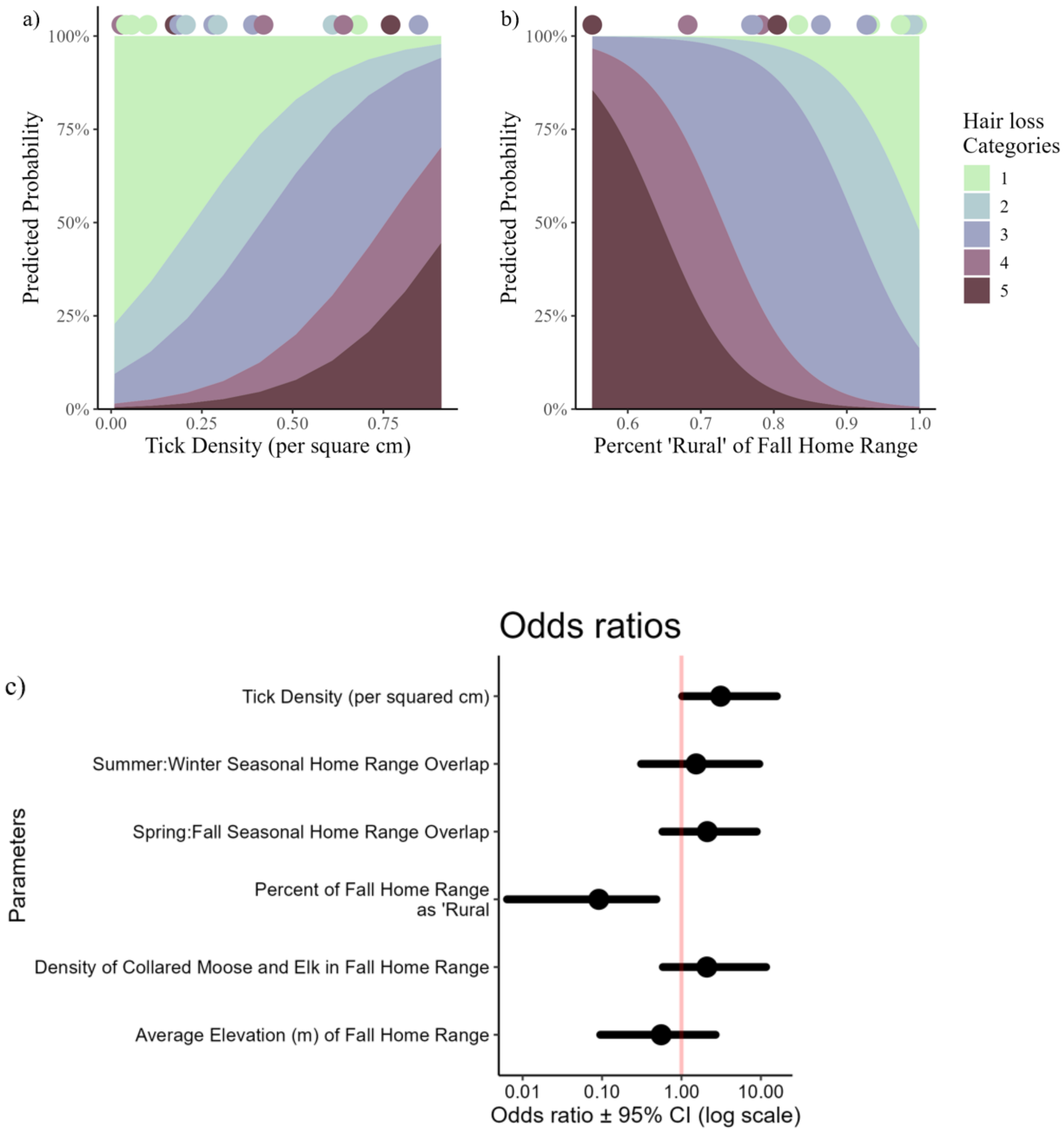

Figure 2: a-b) Stacked proportional probability surfaces representing cumulative predicted probabilities of a collared moose occurring in a hair loss category during the first year of capture (n=17) across values of variables *percent 'rural' versus 'urban' land cover classes in fall home range* (0-100%), and *tick density* (per cm^2)) tested using a cumulative link model. c) Odds ratios and 95% confidence intervals for parameters and their impacts on likelihood of being in a higher hair loss category.

When we investigated hair loss category relationships with migratory behaviors for collared moose across all collaring years (n = 31) we saw increasing probabilities of being in a higher hair loss category with greater overlap between spring:fall seasonal home ranges and decreasing probabilities with increasing average elevation of fall home range (Figure 3b, Figure 3c, Figure 3d). Odds of being in a higher hair loss category increased by 2.58 with increases in percent overlap of spring:fall seasonal home ranges (95% CI: 1.02-6.87, $\beta = 0.95$, SE = 0.47, $p = 0.04$, Figure 3b) as compared to no significant change in odds ratio of 2.04 (95% CI: 0.52-8.83, $\beta = 0.71$, SE = 0.71, $p = 0.32$, Figure 3a) with increases in summer:winter seasonal home range overlap. Odds ratios decreased significantly with increasing average elevation in fall home range (OR = 0.16, 95% CI = 0.04-0.53, $\beta = -1.86$, $p < 0.01$, Figure 3c). We detected no significant correlation between estimated density of collared elk and moose on fall home range (OR = 1.31, 95% CI = 0.53-3.65, $\beta = 0.27$, $p = 0.58$) nor percent of fall home range classified as ‘rural’ (OR = 0.51, 95% CI = 0.21-1.17, $\beta = -0.66$, $p = 0.12$) and odds of being in a higher hair loss category.

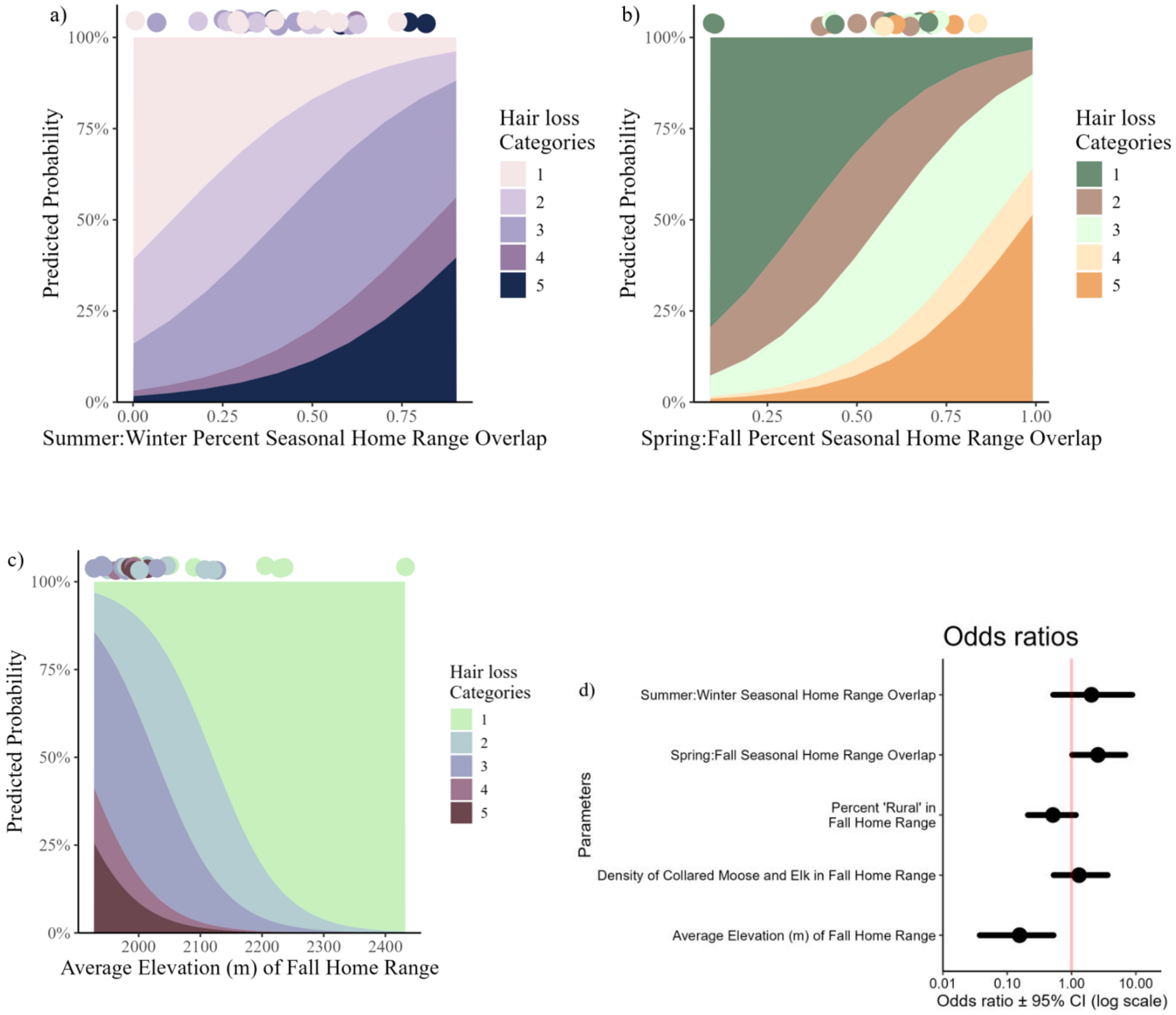

Figure 3: a-c) Stacked proportional probability surfaces representing cumulative predicted probabilities of collared moose occurring in given hair loss category across all collaring years (n=31) across values of variables (*spring:fall seasonal overlap* (0-100% overlap), *summer:winter seasonal overlap* (0-100% overlap), *average elevation in fall home range* (m) tested using a cumulative link model. d) Odds ratios and 95% confidence intervals for parameters and their impacts on likelihood of being in a higher hair loss category.

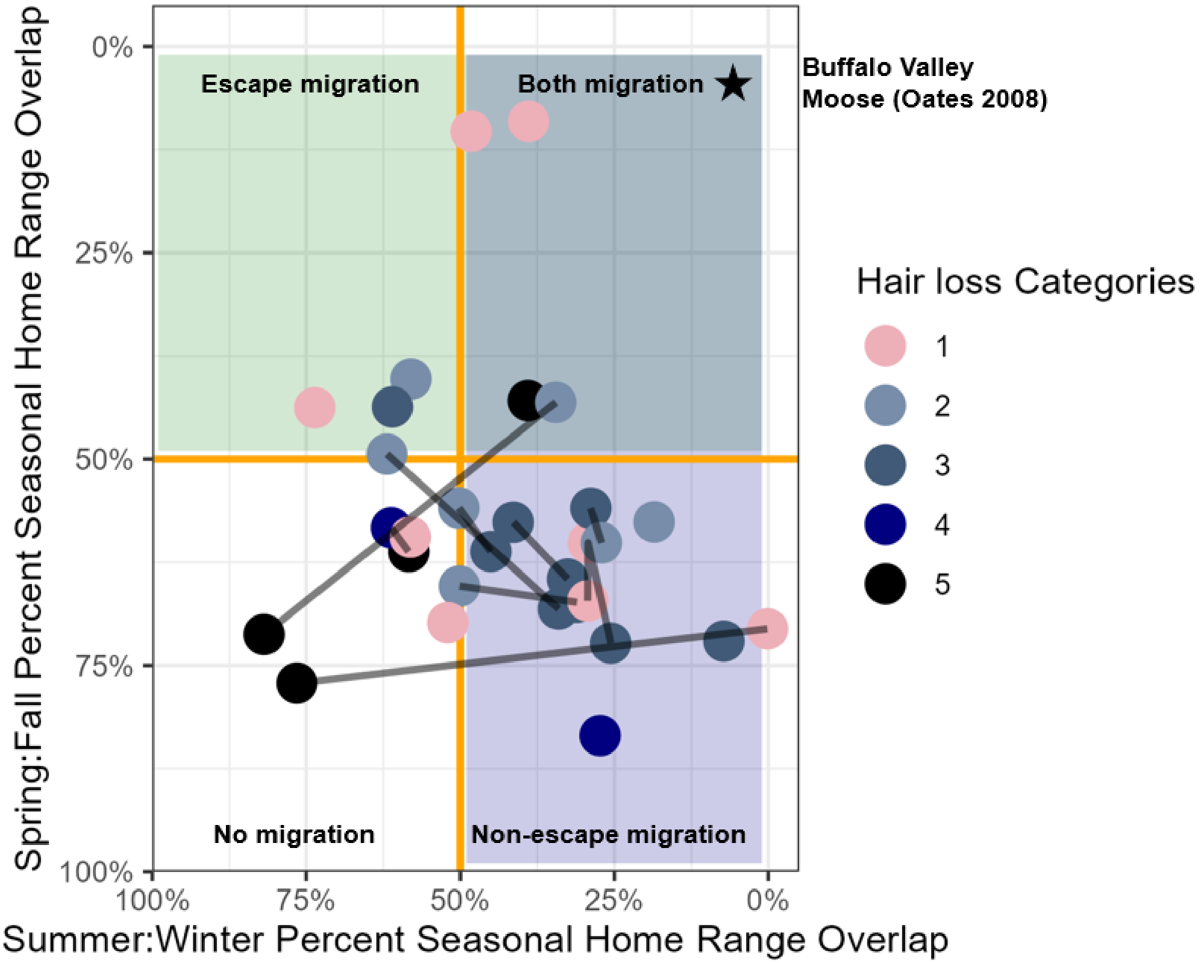

Figure 4: Correlation plot of spring:fall seasonal overlap versus summer:winter seasonal overlap for all moose years. "All adult female moose were considered migratory in 2005 (n = 16) and 2006 (n = 18). Only 2 moose had overlapping winter and summer ranges (1 in both years) and the greatest percent overlap observed for an individual moose within a year was 2.9%." (Oates 2008).

For all moose sighted during spring hair loss surveys, the odds of being in a higher hair loss category generally decreased with increasing latitude (Figure 5a). The odds of occurrence in a higher hair loss category decreased by 0.70 (95% CI: 0.47-1.00), β = -0.36, SE = 0.19, *p* = 0.05) with increasing latitude and did not change significantly with increasing elevation (OR =

0.91, 95% CI: 0.62-1.27, β = -0.10, SE = 0.18, *p* = 0.58). Odds of occurrence in higher hair loss categories were slightly lower when moose were sighted in an ‘urban’ versus ‘rural’ area (OR = 0.55, 95% CI: 0.30-1.00, β = -0.59, SE = 0.30, *p* = 0.05, Figure 5c). Probabilities of being in a higher hair loss category did not vary significantly with estimated host density at spring sighting location (OR = 1.26, 95% CI: 0.94-1.68, β = 0.23, SE = 0.15, *p* = 0.12, Figure 5b).

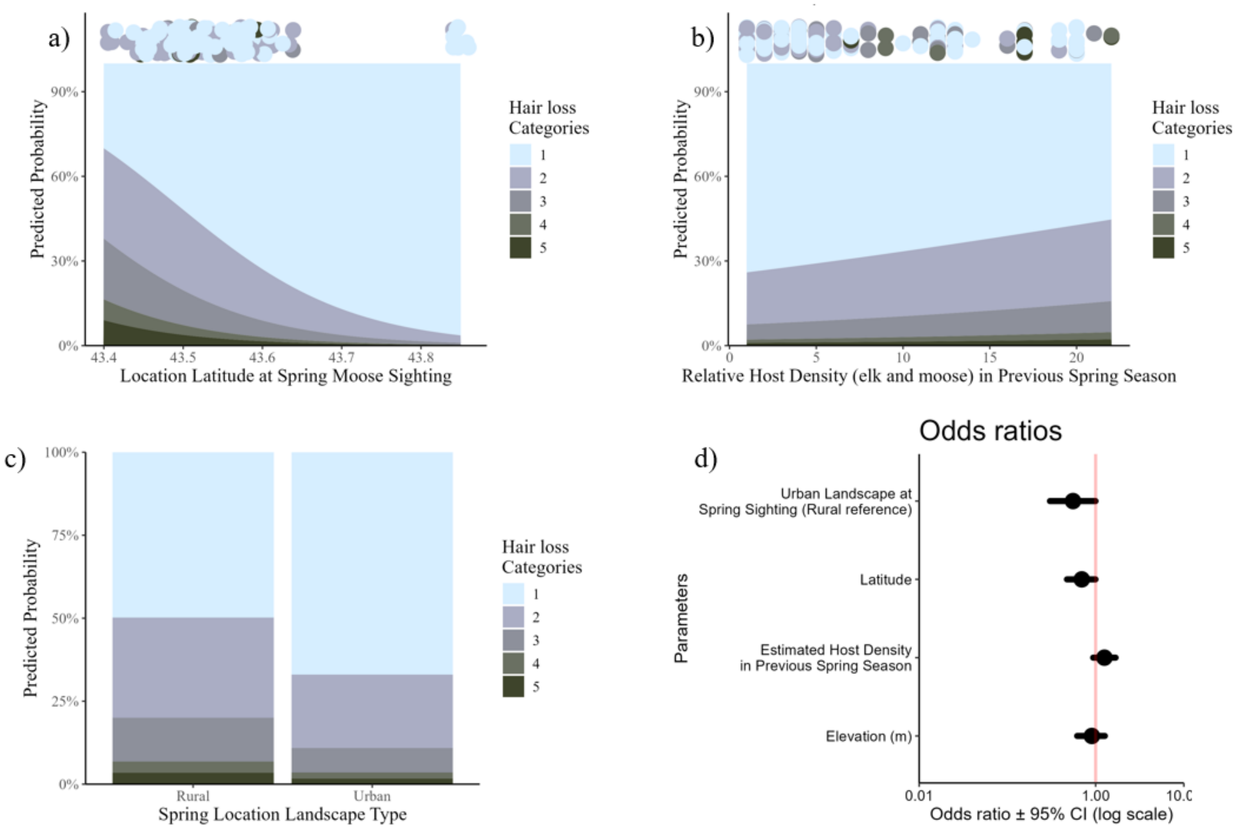

Figure 5: a-c) Stacked proportional probability surfaces representing cumulative predicted probabilities of moose occurring in a given hair loss category across values of variables: *average estimated host density* (individuals per 1 km^2), and *‘rural’ or ‘urban’ landcover type at spring sighting*) tested using a cumulative link model. d) Odds ratios and 95% confidence intervals for parameters and their impacts on likelihood of being in a higher hair loss category.

Discussion

We found percent overlap between spring and fall home ranges to have stronger impacts on probabilities of being in a higher hair loss category than percent overlap between summer and winter home ranges (Figure 3). Moose with fall ranges at higher elevations, with greater proportions of the range designated as 'rural' versus 'urban', and with lower estimated host densities in the preceding spring tended to be in lower hair loss categories (Figure 2, Figure 5). Elevation, land cover type, and spring host density impacts on hair loss categories were less pronounced when we analyzed opportunistic early spring hair loss survey data (Figure 4a-f). Partially migratory ungulate populations are common across the western U.S., especially in mountainous regions where dramatic seasonal shifts in environmental conditions and habitat variability across elevational gradients create dynamic landscapes (Berg et al. 2019, Kauffman et al. 2021, Middleton et al. 2020). Some individual Shiras moose are known to migrate from low elevation ranges in the winter to higher elevation ranges in summer, which could influence parasite exposure rates if parasite abundance or transmission seasons vary across ranges (Becker 2008, Burkholder 2012, Mysterud et al. 2016, Qviller et al. 2013). Many environmentally transmitted or vector-borne parasites, like *Paralaphostrongylus tenuis* (meningeal worm), *Elaeophora schneideri* (carotid arterial worm), and *Dermacentor albipictus,* are known or suspected to be limited by relatively colder temperatures, snow presence, and low relative humidity, conditions that could be expected to be more common at higher elevations versus low elevations (Ball 2017, DeCesare et al. 2023, Drew and Samuel 1986, Henningsen et al. 2012, Holmes et al. 2018, Lankester 2018, Samuel 2007). Although we did not find winter tick abundance to vary dramatically across elevational gradients in Jackson Hole during previous studies (unpublished data), hair loss severity on moose does appear to lessen if moose spend the fall at higher elevations. Variations in specific movement or foraging behaviors across seasonal ranges may affect winter tick encounter rates, it is also possible that grooming behaviors or nutritional conditions differ for individual moose across elevational gradients and migratory tendencies.

The relationships we examined in this study could also be considered in reverse: instead of migratory behaviors driving parasite exposure rates via variations in suitability of seasonal home ranges, it is possible that parasite load accumulated throughout the fall larval questing season could influence migratory tendencies in the following spring and summer seasons (Altizer, Bartel and Han 2011, Mysterud et al. 2016). Higher tick loads could reduce energy budgets available for migration thus reducing migratory behaviors. Greater tick infestations could also prompt avoidance activities in moose and lead to higher migratory behavior prevalences in the following spring and summer seasons after a winter tick epizootic (Samuel, Mooring and Aalangdong 2000). Investigating the specific directions of the relationships between migratory behaviors and winter tick load will likely take longer collaring intervals than available in our study but may be possible if collared moose were resighted every spring for several years.

The prevalence of migratory behaviors in ungulate populations is in decline across many mountainous ecosystems in the western U.S. as landscapes urbanize, supplemental forage becomes more accessible, and anthropogenic climate change reduces winter severity in some areas (Berg et al. 2019, Cole et al. 2015, Middleton et al. 2020). Changes in forage availability from, for example, landscaping for willow species in subdivisions across Jackson Hole, alongside warming spring temperatures could increase energetic budgets available for moose to withstand even heavy infestations with winter ticks (Hostetler et al. 2021). Future research on how warmer and more urban partially migratory ungulate populations interact with population health and disease risk will be needed to help managers address expectations around western ungulate species.

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CHAPTER SIX

CONCLUSION

Understanding how parasites and their hosts might respond to ecosystem changes is critical to conserving wildlife, maintaining healthy ecosystems, and limiting spillover risk to humans. In this dissertation we aimed to provide information on what factors will likely drive winter tick-moose dynamics in the western U.S. and influence Shiras moose populations in the future. I believe that this work will be of great benefit for both moose managers in the west and the greater wildlife disease ecology community. We used novel surveillance approaches and applied statistical methods to tick survey data in a new context, adding valuable insights to the greater vector-borne disease research community. We also used a series of competency surveys and host movement data to tackle the concept of host contributions to and interactions with the winter tick system. Together these works represent a meaningful step forward for the understanding of winter tick, moose, and climate interactions in the West as well as an important contribution to the study of wildlife disease ecology under environmental change.

In Chapter 2, we found that elk share similar host competency rates for winter ticks as moose. We examined infestation loads, winter tick abundances, and reproductive parameters between elk and moose and found them to be similar. We also found genetic differences between winter ticks from elk and moose in the same location to be less pronounced than differences between neighboring herds of the same species using a genome-wide association study, implying gene flow between winter ticks from the same location regardless of host species. These findings add another species, elk, to evidence that host movement and density patterns affect winter tick exposure and encounter rates for moose. Future research avenues include estimating competency for other ungulate hosts like mule deer, bison, and pronghorn which may play important roles linking elk and moose seasonal home ranges.

In Chapter 3, we demonstrated how one could train and deploy scent detection dogs on a survey for a hard ticks species and compared efficiency to the traditional human-only tick drag. The predominant survey type for detecting hard tick species in the field has hardly changed in the past 150 years yet the threat ticks and tick-borne diseases pose for wildlife, domesticated animal, and human health around the world has increased dramatically. Novel approaches are needed to scale tick surveillance studies across wider areas and into contexts where blanket drags are difficult or unfeasible. We successfully trained one scent detection dog to survey for winter tick larvae in the field and showed that detection rates were similar to a human-only tick drag. The scent detection dog team did take more time and resources to train, but we expect training costs to decrease with time since dogs have shown the ability to recognize target scent over long time periods. Scent detection dog-assisted surveys were roughly twice as fast as a traditional tick drag but cost nearly three times as much money per survey unit and required site revisits to drag for alerts. Although scent detection dogs are a feasible alternative to the traditional tick drag survey, their use will likely be limited to surveys over large areas and they could prove useful in niche scenarios like searching livestock at international competitions or surveying ports of entry for invasive ticks. Future research should determine the distinguishing ability of dogs to identify different tick species and whether or not they could be trained to search for ticks in shipping containers or on large animals like horses or cattle.

In Chapter 4, we investigated environmental drivers of winter tick abundance and occupancy patterns in Jackson Hole, Wyoming over three consecutive survey seasons from 2020-

2022. We aimed to account for imperfect detections based on sampling date and temperature using a hierarchical N-mixture modeling approach and correlate occupancy and abundance separately with hypothesized climatic factors. We found occupancy probabilities to increase with maximum summer average daily temperatures and decrease with increasing cumulative vapor pressure deficits in summer. We did not find associations with the other environmental variables examined and occupancy, nor did we find any associations with abundance, once again demonstrating that tick survey data can be especially difficult to analyze using current distribution modeling techniques. We did recover expected relationships between temperature and survival and abundance when analyzing impacts on reproducing winter ticks and their larvae production. There continues to be ample evidence that ticks are highly sensitive to temperature and moisture availability off-host, but scaling relationships to landscape expectations using remotely sensed and extrapolated climate data remains challenging. Decreasing costs for some microclimate data loggers could allow microclimate sampling across larger gradients of interest and create variables that better graph onto conditions experienced by ticks in the field.

Finally, in Chapter 5 we explored moose movement behaviors and landscape variable associations with winter tick load and degrees of early spring hair loss on moose in Jackson Hole. We used cumulative link models to explore how fall home range characteristics like percentage of seasonal home range overlap, average elevation, proportion of home range classified as ‘urban’ versus ‘rural’, and host density in the spring influence the probability of a collared moose being in a given hair loss category in the following spring. We found that moose with higher proportions of their home range classified as ‘urban’ and more overlap between their spring and fall home ranges were more likely to be in higher hair loss categories. We also found moose sighted in spring at higher latitude to be more likely to be in higher hair loss categories. The moose near Wilson, Wyoming are only partially migratory with significant overlap between their fall and spring home ranges. These moose spend large proportions of their fall in low elevation, urban areas with high densities of other hosts like elk which may all contribute to higher tick loads and more hair loss. Future projects should incorporate host movement behaviors and landscape variables like host density when accounting for individual risk factors in exposure to winter ticks. Additional research on individual moose responses to variations in tick load and hair loss year-on-year would also be helpful for determining if moose respond behaviorally to winter tick epizootics.

Continued research on winter tick, moose, and climate interactions will help managers and conservation groups address concerns around moose decline especially at the southern extent of moose range. Our work posits that non-moose movement and density alongside individual moose migratory tendencies should be included alongside known drivers of winter tick exposure on moose like snow fall patterns in spring and fall and desiccating conditions in summer. It is my hope that the legacy of this research will create a lasting knowledge base on the winter tick-moose system among wildlife and natural resource managers around Jackson Hole and grow interest in tick research around the northern Rocky Mountains.

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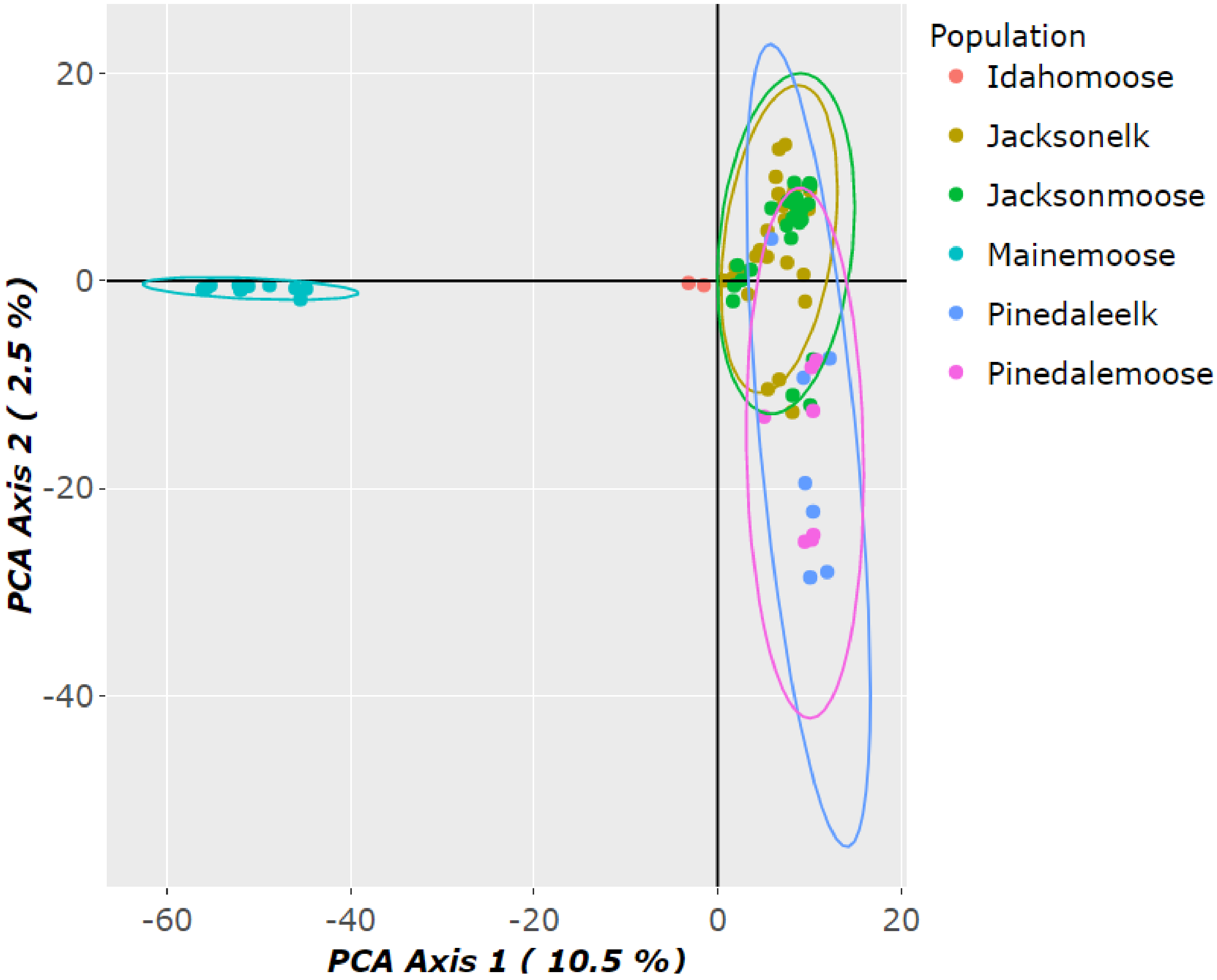
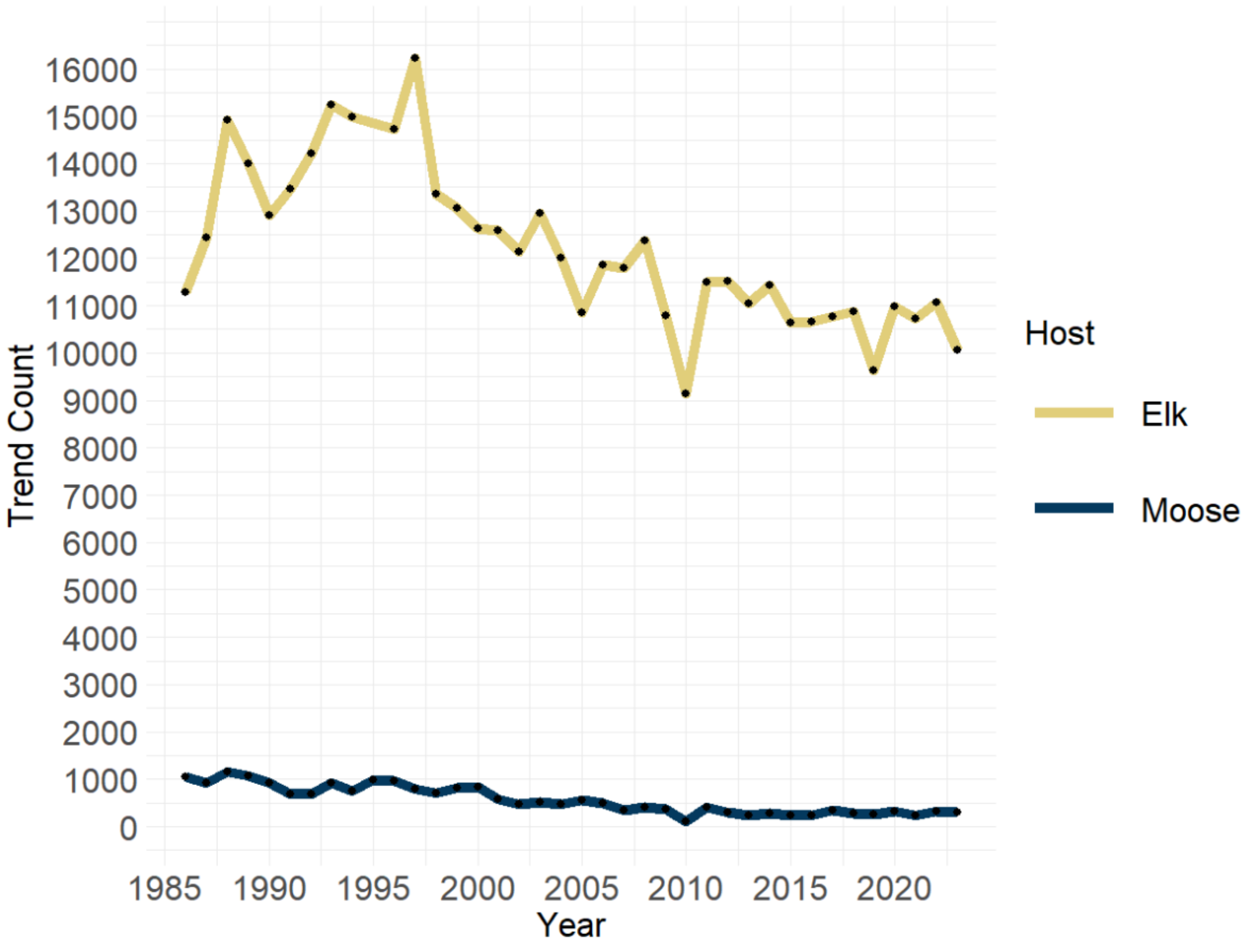
APPENDICES

APPENDIX A:

SUPPORTING INFORMATION FOR – CHAPTER TWO: WINTER TICK SHARING BETWEEN UNGULATES IN THE GREATER YELLOWSTONE ECOSYSTEM AND IMPLICATIONS FOR APPARENT COMPETITION



Appendix A Figure 1: Principal coordinates analysis (PCA) results using genomic SNPs (unfiltered) from winter tick (*Dermacentor albipictus*) extracted from elk (*Cervus canadensis*) and moose (*Alces alces*) in Jackson and Pinedale, WY as well as Maine and Idaho.



Appendix A Figure 2: Population trend counts for elk and moose in the Jackson herds from 1985 – 2020. Trend count data was provided by WGFD via annual the Jackson Office's Big Game Job Completion Reports.

Reproduction Model (Quasipoisson distribution)

Variable	*Estimate*	*Standard Error*	*t-value*	*p-value*
Host (ref:Moose)	0.310	0.255	1.217	0.227
Tick Weight	0.0009	0.0006	1.440	0.153
Canopy (ref:Open)	0.207	0.248	0.808	0.405
Elevation	-0.0001	0.0001	-0.027	0.786

On-host Transect Model (Negative binomial distribution w/ log link)

Variable	*Estimate*	*Standard Error*	*z-value*	*p-value*
Host (ref: Moose)	0.064	0.191	0.335	0.738
Host Status (Alive vs Dead)	-0.129	0.206	-0.624	0.532
Year	0.096	0.126	0.758	0.449

Tick Drag Model (Negative binomial distribution w/ log link)

Variable	*Estimate*	*Standard Error*	*z-value*	*p-value*
Host (ref: Moose)	-1.761	1.314	-1.340	0.180
Host (ref: Moose & Elk)	0.001	1.285	0.001	0.999

Appendix A Table 1: GLM and GLMM model outputs for three different models fit on winter tick reproduction survey data, on-host winter tick transect data, and tick drag survey data.

Winter Tick Reproduction Summary (Dataset 1)

Parameter	*Host species*	
	Moose (n=34)	*Elk (n=29)*
Tick survival (%)	25/50 (50%)	24/48 (50%)
Mean weight (mg)	716 (95%CI: 659-773)	687 (95%CI: 634-740)
Mean larvae produced	309 (95%CI: 214-405)	241 (95%CI: 158-323)
Activation Timing	September 26th	September 29th

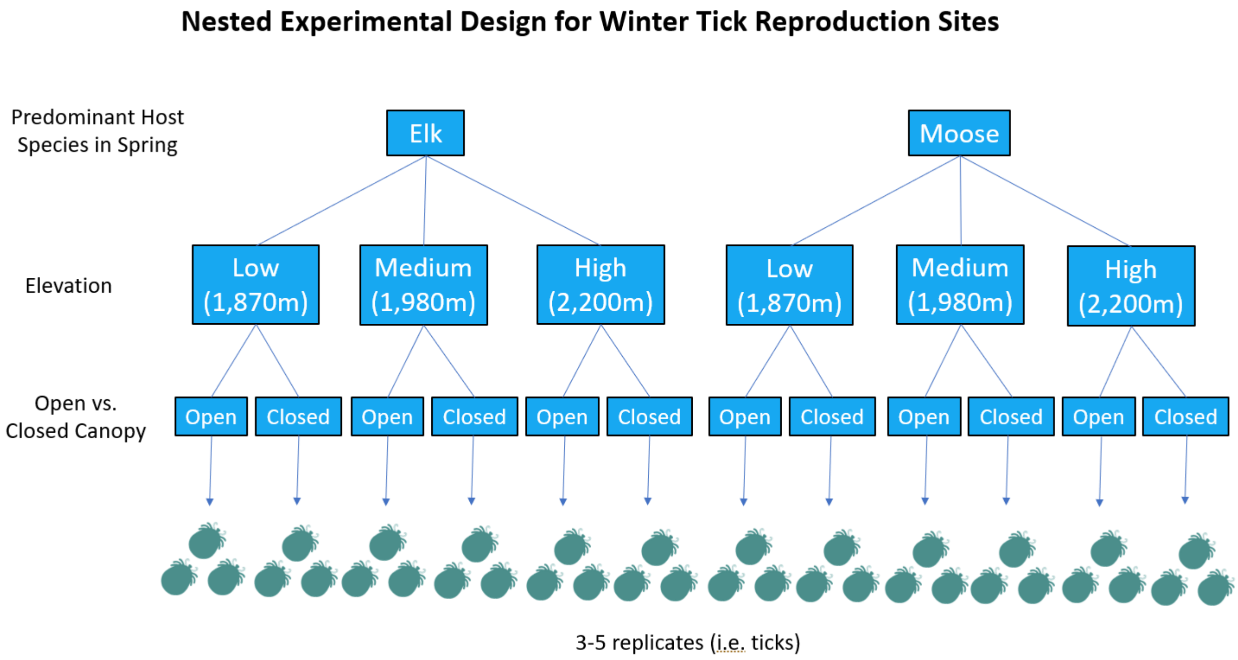
Winter Tick Infestation Loads On-Host Summary (Dataset 2)

Parameter	*Host species*	
	Moose (n=30)	*Elk (n=24)*
Mean tick load	66 (95%CI: 44-87)	66 (95%CI: 53-79)

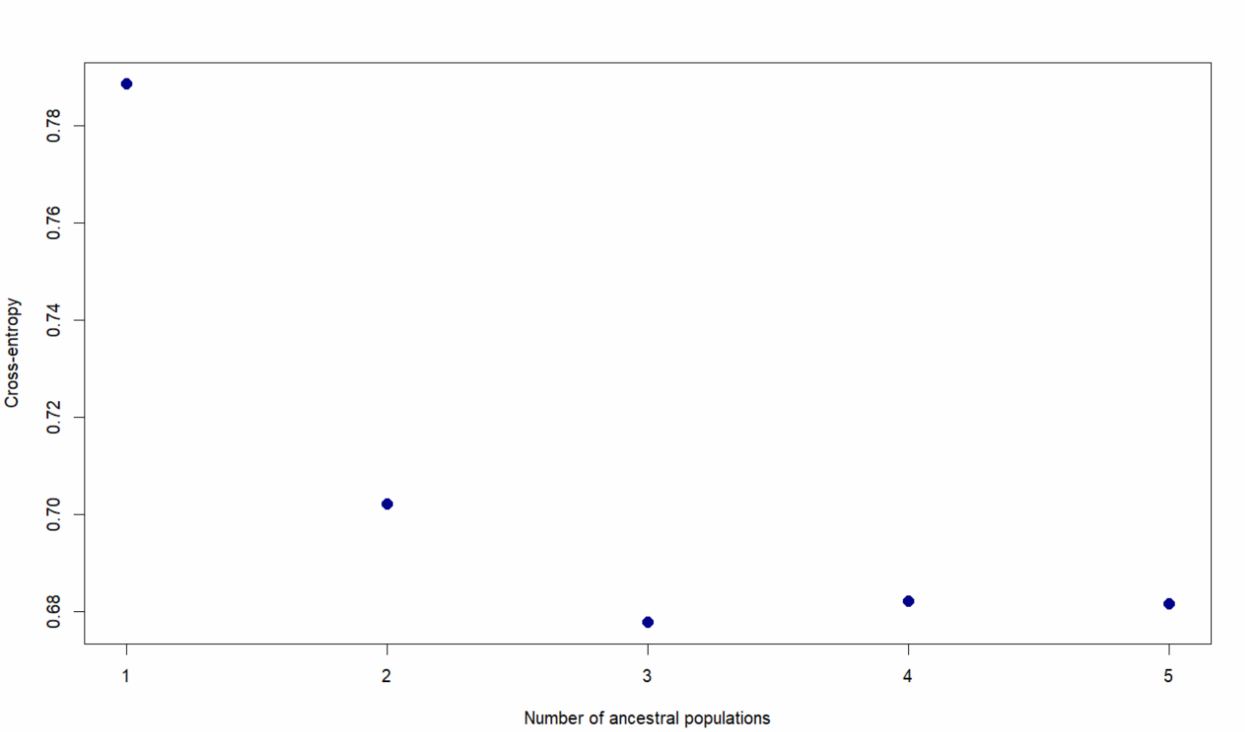
Winter Tick Questing Larvae Abundance on Tick Drags (Dataset 3)

Parameter	*Host species*		
	Moose	*Elk*	*Moose & Elk*
Positive Tick Drags(%)	22/132 (16.7%)	15/61 (24.6%)	26/122 (21.3%)
Mean Questing Larvae Abundance	50 (95%CI: 15-85)	101 (95%CI: 22-180)	320 (95%CI: 0-836)

Appendix A Table 2: Parameter values for three datasets comparing host competency between elk and moose for winter ticks.



Appendix A Figure 3: Sampling design for stratifying winter ticks fed on moose and elk across environmental variables known or suspected to impact reproduction rates and timing, including elevation, predominant host use, and open versus closed canopy structures.



Appendix A Figure 4: Cross entropy plot displaying decreasing entropy towards *K* = 2, *K* = 3 or greater groups.

Appendix A Section 1

Genome-wide SNPs study outgroup details:

Winter ticks from moose in Nez Perce-Clearwater National Forests, Idaho (n=5) were collected as part of ongoing moose research projects conducted by Idaho Fish and Game Department and the University of Idaho. Replete female winter ticks from moose mortalities in Maine (n=11) were collected in 2020 by LK (Lee Kantar) at the Maine Department of Inland Fisheries and Wildlife as part of an ongoing project to determine comparative physiological traits among winter tick populations. Ticks were sent to KO (Kennan Oyen) where they were kept in the lab and allowed to lay eggs and hatch into larvae. Following hatching samples of larvae were freshly frozen at -80C and stored until being transported to Bozeman, MT for use in this study.

APPENDIX B:

SUPPORTING INFORMATION FOR – CHAPTER FOUR: ENVIRONMENTAL ASSOCIATIONS WITH WINTER TICK (*DERMACENTOR ALBIPICTUS*) OCCUPANCY, ABUNDANCE, SURVIVAL, AND REPRODUCTION IN JACKSON HOLE, WYOMING

N-mixture model parameter estimates

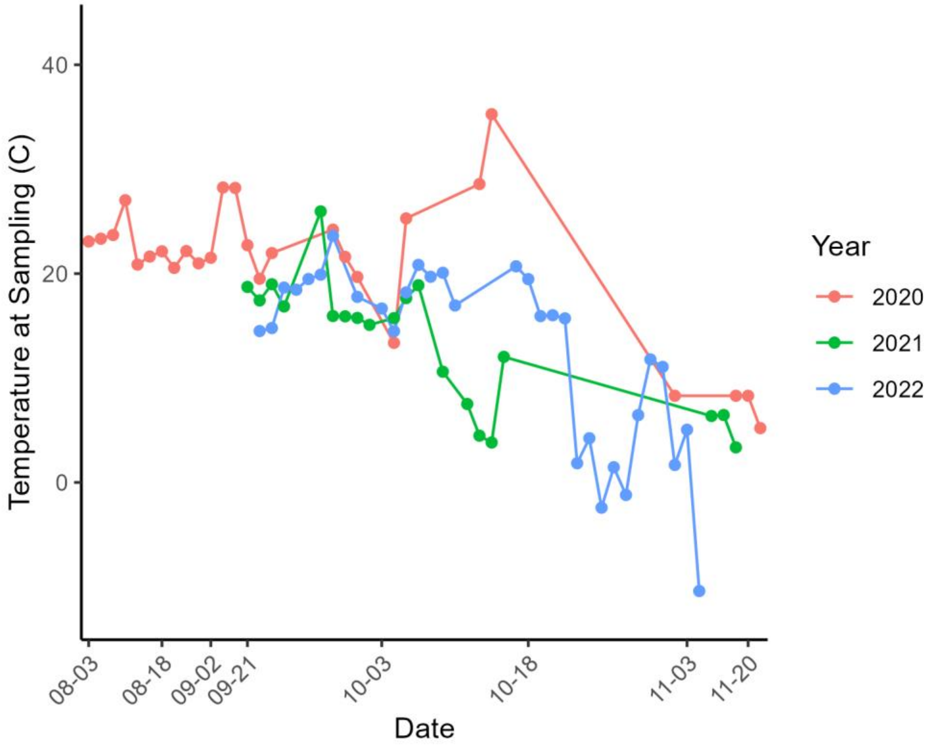
Type	**Model**	**Parameter**	**Estimate**	**SE**	***z* value**	***p* value**
Occupancy	Summer/larval quiescence	Intercept (λ)	0.663	0.244	2.72	0.007
		Average Daily Maximum Temperature (λ)	0.347	0.245	1.42	0.016
		Average Daily Vapor Pressure Deficit (λ)	-0.284	0.185	-1.53	0.013
		Elevation (λ)	0.798	0.281	2.84	0.004
		Intercept (ρ)	-3.249	1.372	-2.37	0.018
		Temperature (ρ)	-0.015	0.013	-1.15	0.251
		Date (ρ)	0.010	0.005	2.29	0.022
	Spring/drop-off	Intercept (λ)	0.547	0.208	2.633	0.008
		Average Daily Minimum Temperature (λ)	0.033	0.233	0.143	0.887
		Cumulative Snow Water Equivalent (λ)	0.029	0.257	1.133	0.257

		Intercept (ρ)	-2.949	1.395	-2.11	0.035
		Temperature (ρ)	-0.017	0.013	-1.32	0.188
		Date (ρ)	0.001	0.005	2.07	0.039
Abundance	Summer/larval quiescence	Intercept (λ)	5.395	0.224	24.096	<0.001
		Average Daily Maximum Temperature (λ)	-0.011	0.291	-0.398	0.691
		Average Daily Vapor Pressure Deficit (λ)	-0.023	0.228	-1.018	0.309
		Elevation (λ)	0.022	0.272	0.807	0.420
		Intercept (ρ)	0.233	0.036	6.4	<0.001
		Temperature (ρ)	-0.082	0.001	-70.1	<0.001
		Date (ρ)	-0.004	<0.001	-30.5	<0.001
	Spring/drop-off	Intercept (λ)	6.592	0.033	199.7	<0.001
		Average Daily Minimum Temperature (λ)	0.041	0.135	-3.24	0.642
		Cumulative Snow Water Equivalent (λ)	0.049	0.147	-3.70	0.813

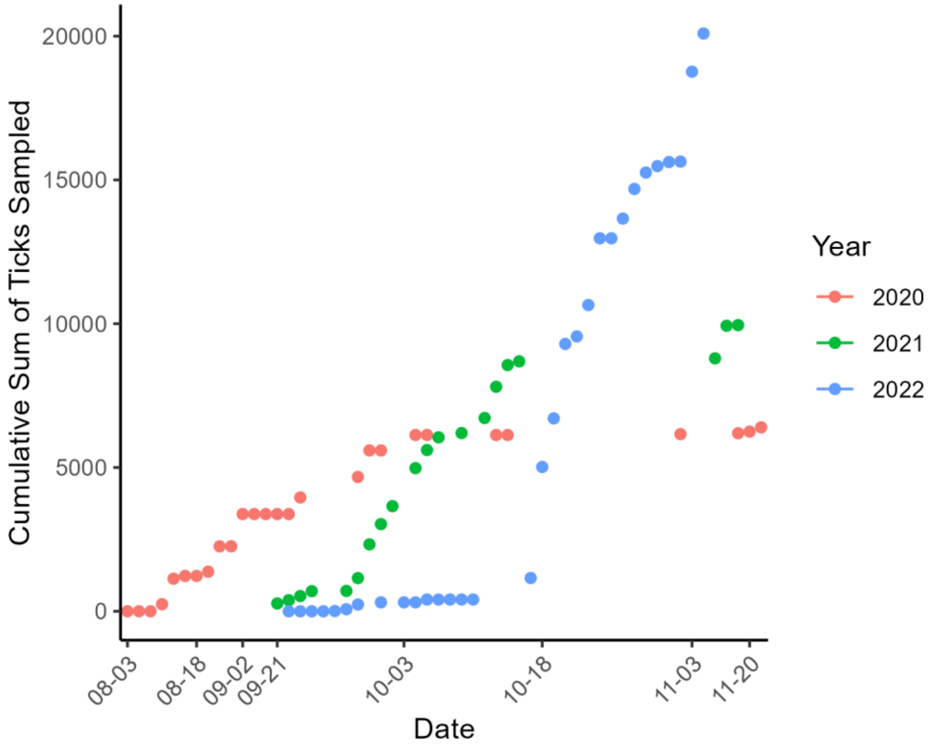
Intercept (ρ)	-2.805	0.036	-78.55	<0.001
Temperature (ρ)	0.006	0.001	4.76	<0.001
Date (ρ)	-0.001	<0.001	-7.12	<0.001

Appendix B Table 1: Model outputs from occupancy and abundance N-Mixture models with parameters for investigating differences in winter tick (*Dermacentor albipictus*) occupancy and abundance across climatic gradients.

Winter tick sampling season figures



Appendix B Figure 1: Average temperature (Celsius) during sampling day for three consecutive sampling years for winter tick (*Dermacentor albipictus*) measured with a Kestrel mini weather station.



Appendix B Figure 2: Cumulative sum of winter tick (*Dermacentor albipictus*) larvae across three successive sampling seasons from 2020-2023.