Linking partial migration to endo- and ectoparasite infection of collared and uncollared elk (*Cervus canadensis*)

by

Jacalyn L. Normandeau

A thesis submitted in partial fulfilment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences

University of Alberta

Abstract

Ungulate ecology studies can focus on forage-predation interactions, but parasites also can have significant impacts on body condition, fecundity, and survival in ungulates. The effects of migration on parasite exposure are not well understood, but exposure may differ on allopatric summer ranges. I studied parasites in a partially migratory elk (*Cervus canadensis*) population that winters at the Ya Ha Tinda bordering Banff National Park in Alberta. Close to 50% of the elk remain on the Ya Ha Tinda year-round with equal numbers of elk migrating westward into the high elevations of Banff National Park and eastward to low-elevation industrial forests. I sampled fecal pellets of unmarked elk from May to August 2017 and 2018 to compare diversity and abundance of parasite groups in elk following each of the three migratory tactics. I also sampled pellets of radiocollared elk from March to April 2018 and 2019 to relate prevalence and intensity of liver flukes (*Fascioloides magna*) to previous summer's use of wetlands, elevation, forage biomass, and areas of elk concentration. Parasite eggs were isolated from pellets and identified via morphology microscopically. In winter, I compared hair loss due to grooming for winter tick (*Dermacentor albipictus*) and grooming behaviours among the migratory tactics. I assessed behaviours of 66 focal individuals on the winter range in 2019 and used close-up images taken from horseback to quantify hair loss. I focused on liver flukes because they are capable of causing mortality in elk at high intensity of infection and on winter ticks because they can promote weight loss and mortality. For endoparasites, I assessed predictions contrasting parasite levels among migratory tactics with hypotheses indicating that migration (1) allowed elk to escape parasite exposure, (2) exposed migrants to novel parasites or habitats of secondary hosts on allopatric ranges, and (3) potentially facilitated recovery on the allopatric range. For ticks, I assessed whether hair loss was related to grooming and whether grooming for ticks was

costly by reducing foraging, rumination, and vigilance. I also assessed whether radiocollars alleviated tick irritation and therefore reduced grooming or whether they promoted hair loss. I found migrant elk had more diverse and higher parasite abundance than resident elk. Prevalence and intensity of liver flukes were highest in eastern migrants, which was consistent with earlier migration to a warmer, low-elevation summer range with a greater extent of secondary host habitat (i.e., the wetland). An increase in grooming in winter was associated with a decrease in foraging time and an increase in time spent resting, but grooming comprised only 1.1% (~ 2 minutes during a 12hr period) of the elk activity budget during the daylight hours. Radio-collars had an additive effect on neck hair loss and I found no evidence of collars reducing tick infestation. Higher infections of internal parasites in eastern migrants of the Ya Ha Tinda elk population could reduce the relative fitness benefits that have promoted the emergence of this migratory tactic. My study is among the first to assess fine-scale habitat use of individual elk relating to liver fluke infection and to quantify grooming for ticks in elk across all activities, adding to our understanding of how parasites may directly and indirectly contribute to a shifting pattern in migration.

Preface

This thesis is an original work by Jacalyn Normandeau. Field methods were in accordance with the Canadian Council on Animal Care Guidelines and approved by the University of Alberta Biosciences Animal Care and Use Committee (Protocol # AUP00000624).

To date, no manuscripts have been submitted for publication.

Dedication

"Jacky, not all elk poops are created equal."

- Maegan McCoy, May 2017

"My quads and calves are sore from uphills and my knees are sore from downhills and my ankles are sore from rocks/slopes and my toes are sore from my boots and also I found two blisters on my feet. All totally worth it though!"

- Monica Winkel, July 2018

Acknowledgements

This project would not have been possible without funding and in-kind support from National Science and Engineering Research Council, Parks Canada, Safari Club International – Northern Alberta Chapter, National Science Foundation, Rocky Mountain Elk Foundation, Alberta Conservation Association, Friends of the Eastern Slopes Association, University of Alberta, University of Montana, and University of Calgary.

I am so grateful to Dr. Evelyn Merrill for giving me this tremendous opportunity. Thank you for your dedication to and belief in your students, your constant challenges to grow as biologist, and for the great food at lab potluck dinners. You are truly inspirational and it was a privilege to be your student. I thank Dr. Susan Kutz for her patience in welcoming a lost graduate student hoping to study parasites with her invaluable expertise. I thank Dr. Colleen Cassady St. Clair for thinking out-of-the-box about my work and providing inspiration for my second data chapter. Additional thanks to Dr. Kim Mathot for acting as my external examiner.

Data collection for this project was contingent on support from Parks Canada and the Ya Ha Tinda ranch staff. I thank Rick Smith and Jean Smith for making the ranch a home away from home and for allowing payment for truck rescue (and the many ways they helped me daily) with chocolate chip cookies and music on their deck. I thank Tom McKenzie for enlightening conversations about nature, learning, hockey, and horsemanship but most of all for believing in the merit of research and the use of horses therein. He took his personal time to teach me to ride from scratch and I owe a significant portion of the data I collected to his efforts. I also thank Rob Jennings, James Spidell, and Tyler Ritchie for taking their time to further my riding skills. I thank Parks Canada staff Jesse Whittington, Blair Fyten, and Karsten Heuer for providing logistical support for backcountry trips throughout the project.

I thank my technicians Maegan McCoy and Monica Winkel and my volunteer Giuditta Migiani for accompanying me on all my crazy field plans to collect elk poop. I hope they enjoyed their time in the mountains as much as I enjoyed their friendship. I thank Colleen Sutheimer, Mateen Hessami, and Trevor Weeks for the many adventures at the Ya Ha during fieldwork. Thank you to the Merrill, Boyce, and Boutin labs, especially Kara MacAulay, Mitch Flowers, Phil Walker, Maria Dobbin, Kelly Mulligan, Maddie Trottier, and Kim Wilke-Budinski for providing constant advice, commiseration, and friendship. I thank Hans Martin for help in all aspects of my project and Jodi Berg for hiring a random kid to catch elk calves, as I would not be here without that chance she took. I also thank my friends Célie Intering and Eilidh Smith for helping me become confident on horseback and for collecting poop with me, just for fun. I thank Old Tom and the folks in his tent for welcoming us researchers into their fold and providing us with valuable knowledge on the trails and the daily comings and goings of our neighbours the elk, deer, bears, wolves, and cougars. I thank Colin Letain and Angie Schneider for teaching me everything I know about parasite identification, Mariana Nagy-Reis, Peter Smolko, and Stephanie Peacock for providing modelling advice, and Drs. Margo Pybus and Bill Samuel for inspiration and advice.

This whole thing is really the fault of my Mom, Dad, and grandparents for handing down a love of adventure and for teaching me outdoorsmanship at a young age, which I realize now is a great privilege. They always encouraged me to pursue my dreams. I thank my brother Lukas for sharing my love of the outdoors and for the support through all the risks we take. I dedicate this thesis to my Oma; I can just picture her face if she could see the place I am now. Lastly, I would like to thank Mistaya, Palliser, Buck, Blue, and Skipper for carrying me around the beautiful Ya Ha Tinda on my journeys to understand.

Table of Contents

List of Tables

List of Figures

CHAPTER 1 — PERSPECTIVES ON MIGRATION AND COLLARING IN RELATION TO PARASITE INFECTION

In ungulates, parasites affect host body condition (Hughes et al., 2009; Irvine et al., 2006; Licina, 2014) reproduction (Albon et al., 2002; Mulvey et al., 1994; Mulvey and Aho, 1993) and longevity (Pybus et al., 2015; Schmitz and Nudds, 1994), but the interaction between migration and parasite infection in collared and uncollared ungulates is not well understood (Mysterud et al., 2016; Pruvot et al., 2016). Parasites in ungulates include ectoparasites (ticks and biting lice) and endoparasites (gastrointestinal worms, lungworms, and liver flukes) that can be transmitted environmentally (i.e., lungworm transmitted through fecal deposition of larvae and ingestion of those larvae from nearby forage) and through secondary hosts (i.e., giant liver fluke egg development into larvae inside snail hosts and subsequent ingestion of those larvae from aquatic vegetation). Appendix A provides a review of elk parasites in Alberta and their lifecycles. Because ungulates congregate in winter, winter ranges can become highly contaminated with parasites due to increased fecal deposition containing larvae and eggs (Lankester and Peterson, 1996). However, despite the potential for high contamination, density-dependent transmission is low in winter (Churcher et al., 2005) because most endoparasites and their secondary hosts remain dormant during harsh conditions (Carlsson et al., 2012; Lankester and Peterson, 1996). Instead, parasites are more likely to infect hosts during more favourable environmental conditions in spring and summer (Bergstrom, 1975; Pruvot et al., 2016) when migratory and resident tactics of partially migratory populations occupy different ranges.

Two major parasites of ungulates in North America are giant liver fluke (*Fascioloides magna*) and winter tick (*Dermacentor albipictus*; Figure 1.1). Giant liver fluke is a trematode with an indirect lifecycle, capable of causing mortality in ungulates if infection is high enough

(Pybus et al., 2015). Liver fluke is transmitted through an aquatic Lymnaeid snail secondary host (Pybus, 2001). Eggs excreted in feces take 35 days on average to develop into larvae that locate a snail, taking 40-60 days to develop before leaving the snail host to encyst on nearby aquatic vegetation where they are consumed by an ungulate host (Pybus, 2001; Swales, 1935). Larval development is based on environmental conditions and temperatures lower than 20°C retard development (Olsen, 1944). Infection occurs during snow-free periods when aquatic vegetation is available to grazing herbivores, but peak infection occurs in spring and late summer to early fall (Pybus, 2001; Pybus et al., 2015). Liver fluke infection is cumulative throughout an individuals' life but is mainly related to exposure >6 months prior as the prepatent period (i.e., time between ingestion of fluke larvae and egg excretion in pellets) is 6-7 months including migration to the liver, maturation to adulthood, and mating.

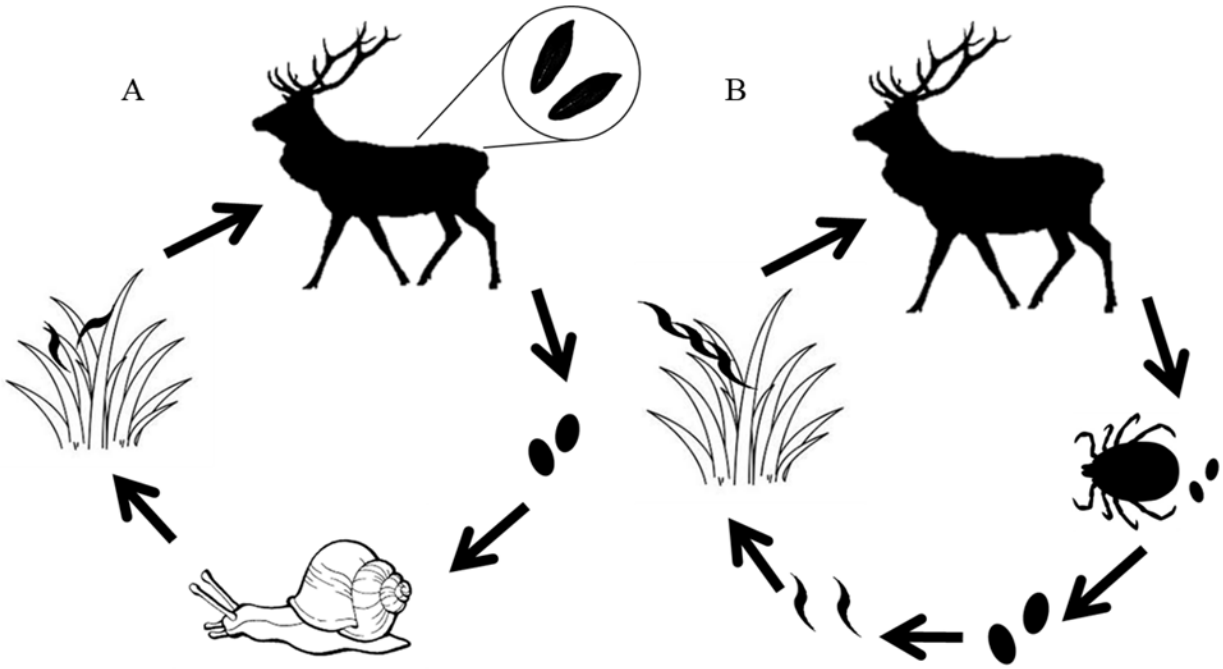

Figure 1.1. (A) Giant liver fluke (*Fascioloides magna*) indirect lifecycle involving an aquatic snail secondary host and (B) winter tick (*Dermacentor albipictus*) direct lifecycle involving a single definitive host.

In contrast, winter tick is a large, one-host tick that completes its entire lifecycle of blood-feeding, moulting, and mating on a single host within one year with infection resetting annually (Allan, 2001). Gravid female ticks that are on hosts in winter drop off the host in spring, lay eggs that hatch into larvae in the environment during the summer, and from early September to November larvae ascend vegetation in search of a host (Drew and Samuel, 1985). Drew and Samuel (1987) found that temperature-dependent larval development was slower in aspen habitats with dense canopy cover that reduces temperature compared to open bogs and grassland. Once on a host, larvae feed on blood during October and November and molt to the nymph stage before dormancy during December and January. In late January and early February, nymphs feed on blood before molting into adults who mate before engorged adult females drop off in March and April (Samuel, 2004). Irritation due to biting ticks occurs from late January to March as nymphs take a blood meal with peak irritation due to blood meals taken by adult females in late March – April (Samuel, 2004). This irritation results in grooming that can result in extensive hair loss with compromised thermoregulation (Scholander et al., 1950) and interferance with other activities such as feeding and vigilance (Mooring and Hart, 1995; Mooring and Samuel, 1999). Through increased time spent grooming and blood lost to ticks, infestation is known to reduce body condition, increase weight loss, promote anemia, and cause mortality in ungulates (Glines and Samuel, 1989; Samuel, 2004; Welch et al., 1991).

Migration from ranges where ungulates winter in higher concentrations is proposed as a disease reduction mechanism by escape from infected winter ranges, “culling” through death of highly infected individuals during strenuous migration, or recovery from infection on summer ranges (Folstad et al., 1991; Mysterud et al., 2016; Pruvot et al., 2016; Shaw and Binning, 2016). However, migration may facilitate infection through exposure to novel habitats (Teitelbaum et

al., 2018), infection “hot spots” through host concentration on stopover areas (Altizer et al., 2011), and environmental tracking of suitable parasite transmission habitats (Teitelbaum et al., 2018). Additionally, migration may disperse parasites to new locations, sometimes over long distances (Bauer and Hoye, 2014), and may facilitate super-spreading of infection (Fritzsche McKay and Hoye, 2016). Hypotheses regarding the migration-parasite infection relationship can be tested via multiple endoparasite species, however ectoparasites can play an important role in host fitness and may also be influenced by migration.

Ectoparasites are well documented to elicit hair loss from grooming (McLaughlin and Addison, 1986; Mooring and Samuel, 1999, 1998). For example, ungulates experimentally infested with winter tick can experience extensive premature loss of winter hair through grooming (Welch et al., 1991). Grooming may be energetically costly (Mooring, 1995; Mooring and Samuel, 1999) or predispose individuals to higher predation risk (Mooring and Hart, 1995) if grooming interferes with forage, ruminating, or vigilance (Crowell-Davis et al., 1985; Mooring and Hart, 1995; Mooring and Samuel, 1999). However, no studies address the impact that collars may contribute to ectoparasite infestation and hair loss. Radio telemetry of very high frequency (VHF) collars and Global Positioning System (GPS) collars that collect location data are both common means of monitoring wildlife (Cooke et al., 2004). Very few studies have assessed the effect of collars on behaviour, condition, and survival (Brooks et al., 2008; Cid et al., 2013; Horback et al., 2012; Moll et al., 2009) but some studies show that collars can cause lesions, abrasions, and hair loss under some circumstances (Hopkins and Milton, 2016; Krausman et al., 2004). Radiocollars could potentially impact ectoparasite infection by either facilitating tick attachment at hair loss around a collar or removing ticks on the neck, reducing infestation. Furthermore, differential ectoparasite infestation could result from exposure on migrant summer

ranges (Mysterud et al., 2016) which can have implications for tick infestation and hair loss in partially migratory populations the following winter.

In this thesis, I explore the relationship between parasitism and migration and assess whether collars help or hinder ectoparasite infection in elk. We address these topics by comparing infestation levels and behaviour of elk that winter at the Ya Ha Tinda located on the eastern edge of Banff National Park. Migration of the partially migratory elk population has been studied for the past ~50 years using VHF and GPS collars to monitor elk movements (Morgantini and Hudson, 1988). The elk population has declined from a high of ~2200 individuals in the 1990s to a current estimate of ~400-500 individuals (Berg et al., 2016; Martin et al., 2019). During the decline, there was a shift in the proportion of individuals migrating predominately westward into BNP (western migrants), to an increase in elk remaining on winter range at the Ya Ha Tinda year-round (residents) and in elk that migrate eastward (eastern migrants) onto low-elevation industrial lands along the Red Deer river (Eggeman et al., 2016).

In the first chapter of this thesis, I address specific hypotheses about the effects of migration on parasitism by quantifying endoparasite egg excretion at the population level through unmarked individuals on summer ranges and at the individual level through collared focal animals in a partially migratory elk population at the Ya Ha Tinda. Using both population sampling and modelling of individual elk liver fluke egg counts in pellet samples, I compared infection (parasite diversity and giant liver fluke prevalence and intensity) among migration tactics to assess support for 5 hypotheses for how parasite infestation may be linked to migration in this system. In the second chapter, I assess the potential costs of ectoparasite infestation on foraging and rumination in different migration tactics of the Ya Ha Tinda elk population. I used behavioural observations from focal individuals in winter to determine if increased grooming

comes at a cost to foraging, rumination, or vigilance in each of the migratory tactics. I expect that if differences in grooming time between migration tactics occur, elk would mitigate the cost of extra grooming by synchronizing grooming with less costly activities (i.e., resting). I assigned hair loss scores for the withers and neck areas using pictures of elk photographed from horseback (10-50m) to represent ectoparasite infestation to link either ectoparasites or collars to neck hair loss scores. I also assessed the effect of radiocollars on withers hair loss and neck grooming time to determine if collars affect tick infestation.

STUDY AREA

The Ya Ha Tinda (YHT) is a 40km^2 rough fescue (*Festuca campestris*) grassland adjacent to Banff National Park (BNP) along the eastern slopes of the Rocky Mountains in central Alberta, approximately 60km north of the town of Banff and 60km west of Sundre. The Ya Ha Tinda is the winter range of a partially migratory elk population that has been studied since the early 1970s (Drs. Morgantini, Merrill, and Hebblewhite) that migrates up to 60km west to the Lake Louise/Hector Lake area in Banff National Park, 50km south towards the town of Banff in the national park, and 40km east onto low-elevation industrial crown land along the Red Deer River (Figure 1.2).

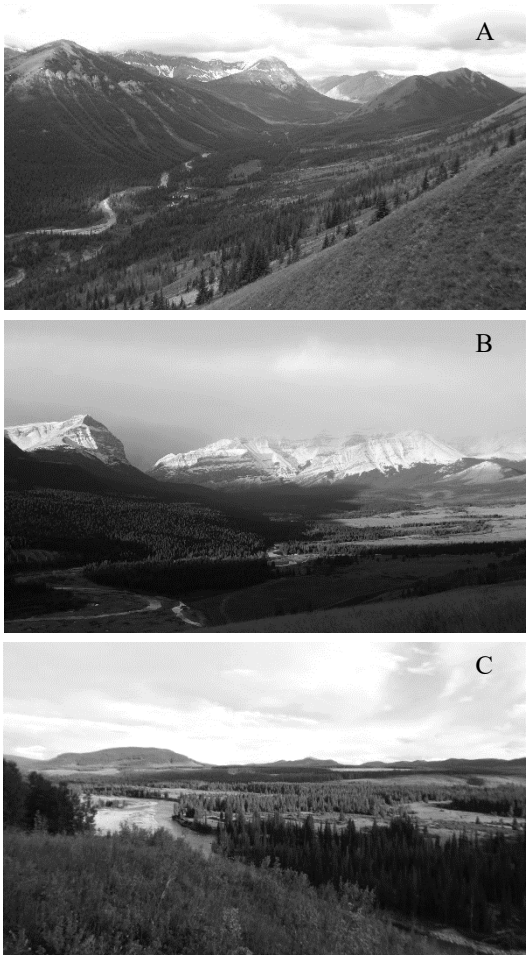

Figure 1.2. The study area including high-elevation Banff National Park (A), the Ya Ha Tinda (B), and low-elevation eastern lands along the Red Deer River (C).

According to tracked elk, in the early portion of the long-term study (2002-2004) an average of 74% of collared elk migrated but in the later portion (2016-2018) only 37% on average migrated with only 30% migrating in 2018 (Martin et al. 2019). The ratio of western migrants to residents to eastern migrants averaged 14:15:1 during the early period of 2002 – 2006, whereas during the late period (2013 – 2016), the ratio averaged 1:10:5 (Berg, 2019), showing a significant decrease in western migrants and an increase in the eastern migration tactic from ~4% in the early period to ~30%-35% in the later

period (Killeen et al., 2016; Martin et al., 2019). The median dates of migration of eastern migrants are between 2-3 weeks earlier than western migrants, which could be due to earlier green-up at the low elevations in the east (Killeen et al., 2016). We assumed elk did not switch migration status between years, although ~15% of elk could switch in any one year (Eggeman et al., 2016).

Hebblewhite et al. (2008) reported that, compared to resident elk, western migrants were exposed to 10% higher forage quality on the summer range, which was associated with higher pregnancy and fall calf weights. Berg (2019) then reported that pregnancy rates and neonatal calf weights did not differ between residents and eastern migrants. At the same time, calf mortality of resident elk was 80% higher than calves of elk that migrated eastward (Berg 2019). Robinson et al. (2010) showed that resident elk had higher wolf predation risk at night on the winter range through fine-scale movements and use of human refuge. Flowers (2019) used remote cameras to find preliminary evidence that elk may mitigate predator exposure risk pre-emptively. Elk in winter had a 68% longer return time at sites when wolves occurred between elk visits with the greatest effect within the first 15 days and in summer any predator visit delayed elk return time at any site (Flowers, 2019). Using locations of predator scats, Spilker (2019) showed that predator selection at the Ya Ha Tinda varies across space and that canids and ursids selected for low-use, non-motorized linear features, while cougars selected for areas of low conifer cover and high proportion of edge habitat. Based on elk presence in these scats, predation risk from wolves and coyotes was greatest around the Ya Ha Tinda, cougar risk was greater east of Ya Ha Tinda, and bear risk was more patchy, corresponding mainly to high herbaceous biomass (MacAulay, 2019).

The Ya Ha Tinda experiences high equestrian use throughout the summer in two campgrounds and year-round use of the Ya Ha Tinda Parks Canada Horse Ranch. The eastern areas along the Red Deer River have a greater industrial footprint from logging and oil and gas as well as high recreational camping and off-highway vehicle use. The Banff National Park backcountry is used by hikers, horseback riders, and Parks Canada staff but has been headquarters for the Banff Bison Reintroduction project and has seen high helicopter use between Banff townsite, Windy Warden cabin along the Panther River, and the Ya Ha Tinda. The Hector Lake area in Banff National Park has high vehicle use of the Icefield Parkway (Highway 93) but little non-motorized use off the road.

The area has a strong east-west elevation gradient ranging from 1,350m on the eastern edge to 3,300m in the western portion. The vegetation can be classified into 3 ecoregions: montane, subalpine, and alpine. The montane ecoregion is dominated by lodgepole pine (*Pinus contortus*) interspersed with Engelmann spruce (*Picea engelmannii*), shrubland areas comprised of willow (*Salix spp.*) and bog birch (*Betula glandulosa*), aspen (*Populus tremuloides*) parkland, and grasslands. Subalpine and alpine ecoregions occur mainly in Banff National Park and were composed of Engelmann spruce, subalpine fir (*Abies lasiocarpa*), and lodgepole pine forest interspersed with willow-shrub riparian communities, subalpine grasslands, and avalanche terrain. The alpine region is composed of shrub-forb meadows, rock, scree, snow, and ice (Hebblewhite et al., 2006). Calculated from pooled home ranges of GPS-collared elk from each migration tactic from 1 May – 31 October, the resident summer range is approximately 720km^2, while the eastern range is 660km^2, and the western range is 2530km^2. Within those ranges, eastern elk have the highest stream density (1.8km of streams/km^2), followed by resident elk (1.5km of streams/km^2), and western elk (0.9km of streams/km^2). Linear feature (trails, roads,

and cutlines) densities were highest on the eastern range (4.19 km/km^2), followed by the resident range (2.11 km/km^2), and lowest on the western range (0.93 km/km^2). Wetlands made up 0.5% of area within the resident range and 2.5% and 1.2% of eastern and western ranges, respectively. Grasslands made up 5.5% of area within the resident home range and 5.1% and 2.2% of the eastern and western ranges, respectively.

The minimum air temperature in the study area in 2017-2018 was -36.9 ºC and the maximum was 33.8 ºC (Government of Alberta). Mean daily temperatures during the summer (May to October 2017 and 2018) were mild across the range of the elk population with 5.9 ºC at Bow Summit near Hector Lake (Bow Summit Station, Government of Alberta, 2019), 7.3 ºC at the Ya Ha Tinda (Scalp Creek Station, Government of Alberta 2019), and 10.7 ºC in the east (Coal Camp Creek Station, Government of Alberta 2019), similar to the 10-year average (2008-2018) at each station of 5.8 ºC, 6.9 ºC, and 10.1 ºC, respectively. From January to April, while the elk occupied their winter range, the mean daily temperature was -7.1ºC (ranging from -34.4 ºC to 20.6ºC), colder than the 10-year average of -5.6 ºC (Scalp Creek Station, Government of Alberta 2019). Average precipitation across 1 May – 31 Oct in 2017-2018 was 2.20-mm/day near Hector Lake, 2.15mm-day at the Ya Ha Tinda, and 1.65-mm/day to the east of Ya Ha Tinda.

Ungulates in the study area include white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and feral horses (*Equus caballus*). Domestic horses are present at the Ya Ha Tinda Parks Canada horse ranch year-round and domestic cattle are found on provincial grazing leases east of the Ya Ha Tinda from ~ June to September. Plains bison (*Bison bison bison*) were reintroduced into Banff National Park ~30km south-west of Ya Ha Tinda in 2017 in an enclosed area and were released into a larger reintroduction zone within the park in July 2018.

Bison were treated with de-worming drugs that reduced parasite burden prior to release and a baseline parasite survey carried out by Parks Canada showed negligible risk of bison introducing novel parasites to the study area (Normandeau, 2019). Appendix A gives a detailed review of elk parasites and Appendix B reviews parasite overlap between ungulates in Alberta. Major predators of elk in the study area include wolves (*Canis lupus*), grizzly (*Ursus arctos*) and black bears (*U. americana*), and cougars (*Puma concolor*) along with coyote (*Canis latrans*), lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*) also present in the area.

The Ya Ha Tinda ranch itself is federally managed, but wildlife management in the area surrounding falls within provincial jurisdiction. Hunting is prohibited within Banff National Park boundaries, in the Ya Ha Tinda fenced pastures, and along the Ya Ha Tinda wildlife sanctuary, a 365m buffer on either side of Ya Ha Tinda Ranch road from the Red Deer River Provincial Recreation Area to the Ya Ha Tinda ranch. Antlered elk hunting is allowed at the Ya Ha Tinda via a draw-system and in Wildlife Management Units 316, 318, 416, 417, 418, and antlerless special licenses are permitted only in WMU 318.

CHAPTER 2 — LIVING WITH LIVER FLUKE: DOES MIGRATION MATTER?

1. Introduction

Studies of ungulate populations focus on forage and predation interactions, but parasites can be as important in reducing individual fitness (Albon et al., 2002; Hughes et al., 2009; Tompkins and Begon, 1999). Parasites affect host body condition (Davidson et al., 2015; Irvine et al., 2006), fecundity (Akinyi et al., 2019; Albon et al., 2002; Hicks et al., 2019), and survival (Pybus et al., 2015; Schmitz and Nudds, 1994). In partially migratory populations where some individuals migrate and others are sedentary (Chapman et al., 2011), parasites could alter the relative fitness of migratory tactics, but the interaction between migration and parasite infection is not well understood (Mysterud et al., 2016; Pruvot et al., 2016; Risely et al., 2017). Migration can result in exposure to different environmental conditions that could affect parasite exposure and transmission. For instance, Mysterud et al. (2016) found red deer (*Cervus elaphus*) that migrated longer distances to summer at higher elevations had lower tick infestation. Folstad et al. (1991) found migrating caribou (*Rangifer tarandus tarandus*) in Norway had significantly lower warble fly larvae (*Hypoderma tarandi*) abundance than those that did not migrate.

Several hypotheses have been proposed for how differences in parasite infections in migrant and resident individuals may arise. Migrants may reduce parasite infection by escaping contaminated ranges before a peak infectious period when conditions for parasite transmission improve (Fritzsche McKay and Hoye, 2016; Loehle, 1995; Mysterud et al., 2016; Pruvot et al., 2016), or by recovering from infection on allopatric ranges due to separation from infectious habitats or by improving condition because they access higher quality forage resources (Coop and Kyriazakis, 1999; Shaw and Binning, 2016). If high parasite infection contributes to death when individuals are subject to the costs of migration (Risely et al., 2017; Shaw and Binning,

2016), migrants may seem to have low parasite infection because heavily infected individuals are "culled". Conversely, migrants may have higher parasite infections because they are exposed to novel parasites or more secondary hosts on allopatric ranges, along migration corridors, in stop over areas (Altizer et al., 2011; Bauer and Hoye, 2014; Koprivnikar and Leung, 2015; Leung and Koprivnikar, 2016; Vanderwaal et al., 2015), or because they track forage green up, which is associated with higher temperatures that promote favourable parasite transmission conditions (i.e. environmental tracking; Altizer et al., 2006; Teitelbaum et al., 2018). Finally, individuals following a migratory tactic may be disproportionately exposed to parasites through contact rates or increased fecal deposition of infective stages if they are more concentrated due to a predation refuge or patchy distribution of habitat (Fritzsche McKay and Hoye, 2016; Hegemann et al., 2019; Lankester and Peterson, 1996).

In this paper, we compared the parasite infection levels of elk (*Cervus canadensis*) in a partially migratory population to address a subset of these hypotheses (Table 2.1). The elk population winters on the Ya Ha Tinda (YHT) bordering Banff National Park (BNP) in Alberta (Figure 2.1) and has declined since the early 2000s from over 1200 to about 400-500 elk. During the decline, there was a shift in the proportion of individuals migrating predominately westward into Banff National Park (western migrants), to an increase in elk remaining on winter range (residents). Today, about equal numbers of elk migrate eastward (eastern migrants) onto low-elevation industrial lands along the Red Deer river as into Banff National Park (Eggeman et al., 2016). Because eastern migrants migrate to low-elevation ranges 2-3 weeks earlier than western migrants (Killeen et al. 2016), we predicted they would have either the lowest parasite infection because they escaped high parasites on the winter range in spring (Table 2.1: H_1) or the highest parasite infection if exposed to favourable parasite conditions earlier and possibly longer (H_2).

Alternatively, we predicted that if conditions on summer range rather than timing of migration contributed to parasite infection, differences in parasite infection would be consistent with habitat diversity or the extent of suitable habitat of secondary hosts on allopatric ranges (H_3). Because Hebblewhite et al. (2008) reported that western migrants were exposed to as much as 10% higher forage quality on the summer range and had higher pregnancy and fall calf weights than residents, we expected lower parasite infection in western migrants if nutrition promotes recovery from infestation (Coop and Kyriazakis, 1999; Shaw and Binning, 2016). However, Berg (2019) reported similar pregnancy rates but 80% higher calf mortality of resident elk than eastern migrants, which may allow them to recover because of lower demands of lactation (Cook et al., 2004). Therefore, if summer body condition influences parasite infection, we expected eastern migrants would have the highest parasite infestation, and western migrants would have lower infestation than resident elk (H_4). Finally, we hypothesized that if elk use of predation refuges concentrate elk on summer ranges (Berger, 2007; Gibeau et al., 2002; Musiani et al., 2010; Shannon et al., 2014), resident and eastern migrants would have higher infection levels than western migrants (H_5) because human use (e.g., equestrian use, camping, and off-highway vehicle activity) that predators avoid is more common on the Ya Ha Tinda and crown-land east of the Ya Ha Tinda (Hebblewhite et al., 2006).

We focused on differences in parasites among migratory tactics at the population and individual-elk level. At the population level, we compared parasite diversity and infection levels of fecal samples from unmarked elk on allopatric summer ranges. At the individual-animal level we collected feces from individual GPS-collared elk in late winter and related liver fluke (*Fascioloides magna*) prevalence and intensity to exposure of habitat characteristics during the previous summer when difference in exposure is expected to be most pronounced. We focused

the individual-elk analysis on giant liver fluke because it can cause mortality in elk (Pybus et al., 2015). Liver flukes are an environmentally transmitted trematode where the adults infect the liver of an ungulate host, releasing eggs into the feces that hatch and invade aquatic snail secondary hosts, multiply, and develop into an infective stage that encysts on aquatic vegetation to be consumed by another ungulate host (Pybus et al., 2015). Liver fluke transmission occurs only during the snow-free summer period and peaks in spring and fall due to availability of infective stages from snail secondary hosts (Pybus, 2001). Our study is one of the few that relates parasites of individual, free-ranging cervids to their use of the environment and contributes to a growing understanding of the relationship between parasitism and migration (Kołodziej-Sobocińska, 2019; Satterfield et al., 2018).

2. Materials and methods

2.1 Pellet Collection

We collected elk pellets from adult female elk for analysis of *F. magna* eggs using two sampling designs. At the population level, we used collared elk to locate elk groups with the goal of collecting ~30 fresh pellet samples/migratory tactic/time interval. Collections for each migratory tactic were made in spring (11 – 31 May 2017, 4 – 27 May 2018) on winter range and in summer (2 July – 24 August 2017, 30 June – 23 August 2018) on allopatric summer ranges (Appendix D). Using collared female elk avoided resampling the same group, improving the independence of samples. Pellets were sampled after elk groups had moved away. We collected pellets of different size, shape, and colour at least 5 m apart (Vanderwaal et al., 2015), and in proportion to ≤ 20% of the number of elk in the group to ensure pellets came from different animals. We collected only fresh pellets (< 1 day old), which were identified as being wet on the outside with a mucous coating present and green and wet on the inside (Brambilla et al., 2013).

We avoided sampling male elk by collecting samples from groups composed mainly (> 70%) of adult female elk only and did not include pellets of elk calves to control for sex and age differences in parasite infection.

At the individual elk level, we collected 3 pellet samples from each of 39 GPS-collared elk (24 residents, 6 western migrants, 9 eastern migrants) on the winter range from 25 March to 21 April 2018 and 16 elk (11 residents, 3 western, 2 eastern) from 8 April to 18 April 2019 with 15 elk sampled in both years and a total of 55 elk-years. We sampled liver fluke eggs at this time and related them to habitat use in the previous summer (1 May – 31 October 2017 and 2018) because *F. magna* egg excretion in pellets occurs ≥ 6 months after exposure (Foreyt, 1996; Pybus et al., 2015). Fresh pellets were collected by watching focal elk from horseback 10 to 50m away, noting the location visually or with a small flagging-taped rock, and waiting until the elk had moved from the immediate area to collect the sample. We derived migration status of collared elk from sequential locations of 2-hour or 6-hour fixes using a net-squared displacement approach (Bunnefeld et al., 2011) and visual inspection with migrants classified as moving > 15 km from their winter range for > 30 days (Killeen et al. 2016). We tested for an effect of fix rate on individual use of landcover types or performance of the final model with test data from the same individual rarified from a 2-hour fix rate to a 6-hour fix rate (Appendix E). All elk monitoring and pellet sampling were consistent with Canadian Council on Animal Care Guidelines and approved by the University of Alberta Biosciences Animal Care and Use Committee (Protocol # AUP00000624).

2.2 Egg Extraction from Pellets

Pellet material (~ 2g) was analysed fresh within 1-7 storage days in an air-tight plastic bag in a cool place to prevent development of eggs and larvae before analysis. *F. magna* eggs

were isolated from pellets using the FlukeFinder® method of differential sieving and sedimentation (2 ± 0.2g of pellets) and examined under a dissecting scope (Edwards 2013). We isolated all other parasite eggs via differences in specific gravity using the Wisconsin Double-Centrifugation technique (4 ± 0.2g of pellets) to float eggs onto slide covers that were examined under a microscope as described by Edwards (2013). Eggs and larvae were classified via morphology only, where only genus or larger groupings could be identified except for *F. magna*. In both cases the sample unit is the pellet group, where random subsamples of 2g and 4g were chosen from a pile of pellets for each respective parasite analysis. For individual elk liver fluke analysis, we collected three randomly selected subsamples of 2g from each pellet group for a sum of 6g total/pellet group. We present liver fluke prevalence, abundance and intensity at the population and individual level at 2g to allow direct comparison but present fluke egg presence and intensity in 6g of pellet sample to increase detection probability and variation in egg counts for the individual models.

2.3 Statistical Analyses

At the level of the population, we used a Kruskal-Wallis rank sum test with a post-hoc Dunn's multiple comparisons test to compare diversity between migration tactics using species, genus, or taxonomic groups as possible (α=0.05; vegan and dunn.test, Dinno, 2017; Okansanen et al., 2019). We tested whether fluke egg presence or counts in pellet samples related to migration tactic (resident is reference category) and year collected (2017 as reference) using logistic regression or a zero-truncated negative binomial regression (glm and vglm from the R packages stats and VGAM, respectively; R Core Team, 2019; Yee, 2010).

At the level of the individual elk, to ensure that age, presence of a calf mid-summer, and body condition the previous winter did not influence differences in fluke egg abundance, we

tested for age differences between collared elk from each migration tactic using an ANOVA, the number of elk with observation of calf at heel using a Chi-squared test, and for differences in body condition the previous winter using a non-parametric Kruskal-Wallis rank sum test. We tested for differences in median group size of residents (n = 174), eastern migrants (n = 99), and western migrants (n = 10) using counts from group classification data on the allopatric summer ranges in 2017 and 2018 with a Kruskal-Wallis rank sum test. We used a logistic mixed-effects model to test for presence of liver fluke eggs in pellet samples (glmer from the R package `lme4`; Bates et al., 2015). We used a negative binomial, mixed-effects model to compared liver fluke eggs among migratory tactics when counts were greater than zero (i.e., zero truncated) with individual elk as a random effect (glmmTMB from the R package glmmTMB, Brooks et al., 2017). We assessed other model structures truncating the count data based on values other than 0 (i.e., values <10) but these models did not differ from the null (ΔAICc < 2, Appendix F).

We modelled winter liver fluke egg presence and counts in individual GPS-collared elk using the covariates of year (2017 reference), elk age (years) based on incisor cementum annuli (Keiss, 1969), and 4 environmental variables. Values of environmental variables (30 x 30m cell) were weighted by use of the respective GPS-collared elk within 3 different seasonal ranges: spring (1 May – 30 June), summer (1 May – 31 October) and fall (1 September – 31 October) but we report the results only for the summer (1 May – 31 October) covariate extraction time period because these models best fit the data (Appendix G). Weights represented the elk's exposure to the cell and were based on its relocations and determined using a dynamic Brownian Bridge approach (Kranstauber et al., 2012) by season (R packages move, raster, and rgdal, Bivand et al., 2019; Hijmans, 2019; Kranstauber et al., 2019). We scaled covariates to a mean of 0 and

standard deviation of 1 prior to modeling and variables with Pearson correlations > |0.5| correlation were not used in the same model.

Environmental covariates included elevation (m), wetland extent, herbaceous forage biomass (g/m^2), and a metric of overall intensity of use derived from a resource utilization function (RUF) of all GPS-collared elk monitored between 2013-2016. We took elevation from a digital 30m elevation model (DEM). Wetlands within an individual elk's home range were determined by digitizing wetland polygons in flat treeless areas with a 250m buffer of water features on aerial imagery taken 29 September 2015 (Appendix H). We used peak growing season (1 August) herbaceous forage biomass determined by Hebblewhite et al. (2008). Briefly, they estimated peak biomass for a cell from sampling plant standing biomass at > 983 sites across the summer extent of the Ya Ha Tinda elk population from 2002-2004 and developed a model to predict biomass as a function of year, elevation, aspect and distance to continental divide from a general linear model (Hebblewhite, 2006). Cover type was updated to 2016 for burns and timber harvest (Smolko, 2014). We used the prediction based on 2004 (330 mm of precipitation) because it most closely matched precipitation in 2017 (300 mm) and 2018 (310 mm). RUF was derived from data on 66 adult female elk monitored across the study area from 2013-2016 and model inputs included herbaceous forage biomass, burned areas, edge habitat, and wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) resource selection functions (for details see MacAulay, 2019).

Finally, because calf at heel from cow-calf resight and elk body condition scores (Cook et al., 2010) at capture in late February/early March were available for some individuals (n = 50 and 24 elk-years for calf and body condition, respectively), we used these data to assess whether the above variables improved best-fit model of liver fluke presence and intensity from the full

data set using only the subset of data. Calf at heel was determined by sight-resight in summer (Hebblewhite and Merrill, 2011) whereas body condition scores reflected body condition in the previous winter (Berg 2019, unpublished data).

3. Results

3.1 Population-level results

Parasite richness in 4g samples of pellets of western migrants and eastern migrants in summer was higher than residents (0.81 and 0.71, respectively vs. 0.45; $p < 0.001$, df = 2, Kruskal-Wallis $\chi^2 = 32.4$; Table 2.2) but did not differ from each other ($p = 0.12$). Western migrants in summer also had higher evenness ($p = 0.01$, df = 2, Kruskal-Wallis $\chi^2 = 18.2$) and consistently higher mean abundance (number of eggs per 4g across all samples) in parasite groups than eastern migrants and residents (0.31, 0.15, and 0.079 in western migrants, eastern migrants, and residents, respectively ;Table 2.2). The exceptions were the giant liver fluke, which had higher abundance in eastern migrants ($p < 0.001$, df = 2, Kruskal-Wallis $\chi^2 = 42.00$), and *Eimeria* spp., which was higher in residents ($p = 0.01$, df = 2, Kruskal-Wallis $\chi^2 = 6.54$, Table 2.2).

We found no difference in either prevalence (proportion of all samples; $p = 0.47$, df = 1, $\chi^2 = 0.53$) or intensity (number of eggs per 2g in samples only with eggs present; $p = 0.28$, df = 1, Kruskal-Wallis $\chi^2 = 1.19$) in early (May) and late summer (July/August) in either year and so we pooled samples across these two periods for further analyses. Across migratory tactics, liver fluke egg sample prevalence and intensity of infection were lower in 2017 than 2018 (prevalence 0.35 vs. 0.45; intensity of infection 7.2 eggs/2g vs. 14.0 eggs/2g; Table 2.3). Eastern migrants had higher liver fluke prevalence in summer than residents in both years, but prevalence was higher than western migrants only in 2017; western migrants had higher prevalence than residents only in 2018 (Figure 2.2a, Tables 2.3-2.4: migration tactic x year interactions). In

contrast, intensity of infection of eastern migrants was higher than western migrants and residents in both years (Figure 2.2b, Table 2.3-2.4: no migration tactic x year interaction).

3.2 Individual elk

We found no difference in age ($p = 0.78$, $df = 2$, $F = 0.26$) or body condition scores ($p = 0.89$, $df = 2$, Kruskal-Wallis $\chi^2 = 0.24$) among residents (9.4 ± 4.2, $n = 24$; 3.57 ± 0.96; $n = 15$), eastern (8.4 ± 4.4, $n = 9$; 3.54 ± 0.92; $n = 6$), or western migrants (9.7 ± 2.2, $n = 7$, 3.58 ± 0.42; $n = 3$). Western migrants had a lower number of calves at heel detections (50%) than residents (100%, $p < 0.001$, $df = 1$, $\chi^2 = 13.82$) but not lower than eastern migrants (92%, $p = 0.11$, $df = 1$, $\chi^2 = 2.50$; n=50). We found no direct correlations between abundance of liver fluke eggs in 2g feces and elk age ($r = -0.04$, $p = 0.61$) or body condition score ($r = -0.06$, $p = 0.60$) and abundance of liver fluke eggs in elk with calves at heel did not differ from those without calves at heel ($p = 0.10$, $df = 1$, Kruskal-Wallis $\chi^2 = 2.65$). Resident elk had the largest group sizes on the summer range across 2017 and 2018 (39.9 ± 42.5; $\bar{x} \pm SD$) compared to eastern (9.5 ± 11.7, $p < 0.001$, $df = 2$, Kruskal-Wallis $\chi^2 = 51.73$) and western migrants (4.7 ± 4.6, $p < 0.001$).

We found no correlation between sampling date during the winter and liver fluke egg abundance in either 2018 ($r = -0.12$, $p = 0.19$) or 2019 ($r = -0.14$, $p = 0.36$). Liver fluke prevalence in 2g of feces was higher in both eastern migrants and residents in 2018 than 2017 (Figure 2.2c) whereas intensity in 2g of feces was similar across years (Figure 2.2d). In contrast, western migrants had similar egg prevalence across years but higher intensity in 2018. Eastern migrants had higher prevalence than residents ($p = 0.055$, $df = 1$, $\chi^2 = 3.67$) but did not differ from western migrants ($p = 0.35$, $df = 1$, $\chi^2 = 0.87$; Table 2.2) whereas eastern migrants had consistently higher intensity than residents ($p < 0.001$, $df = 2$, Kruskal-Wallis $\chi^2 = 19.98$) and western migrants ($p = 0.009$; Table 2.2).

3.3 Environmental influences on giant liver fluke in individual elk

Overall, liver fluke eggs were not detected in 9.4% and 10.4% of pellet groups when we combined 2g to 6g pellet samples from individual elk sampled in 2017 and 2018, respectively. There was no significant difference between prevalence in 6g of feces between eastern migrants (0.58) and residents (0.38; $p = 0.20$, $df = 1$, $\chi^2 = 1.66$) or eastern migrants and western migrants (0.58; $p = 0.27$, $df = 1$, $\chi^2 = 1.24$). Intensity per 6g of liver fluke eggs was consistently higher in eastern elk (60.4 ± 62.1; $\bar{x} \pm SD$) than residents (20.8 ± 16.9, $p = 0.009$, $df = 2$, Kruskal-Wallis $\chi^2 = 5.85$) and western migrant elk (31.1 ± 37.1, $p = 0.048$).

Herbaceous forage biomass and RUF were correlated ($r = 0.90$) because RUF was a function of herbaceous forage biomass (Appendix I) and therefore they were not entered into the same model. Across models, presence was higher in 2018, increased with wetland extent and elk age, decreased with increasing herbaceous forage biomass or RUF with a negative interaction between wetland and forage biomass or RUF (Table 2.5). There was less support for including RUF than herbaceous forage biomass. Because only the coefficients of wetland extent and herbaceous forage biomass did not overlap zero, we concluded the parsimonious model including these two variables was most plausible in explaining liver fluke prevalence in elk (Table 2.6). Using a subset of data from collared individuals, previous winter's body condition score and mid-summer calf at heel did not improve the model top model (i.e., wetland and forage, Appendix J).

There also were several equally supported models predicting liver fluke egg intensity (Table 2.5) with liver fluke egg intensity being higher in 2018 and increasing with wetland, decreasing elevation, RUF, and age, with a negative interaction between elevation and wetland (Table 2.5). However, only the confidence limits of elevation did not overlap zero (Table 2.6).

There were no interactions among year and other factors, but responses did differ by migration tactic (Figure 2.3). Neither calf at heel in mid-summer nor previous winter's body condition improved the top model (i.e., elevation) using the subset of data (Appendix J).

4. Discussion

All distinct parasite groups we detected in this study had been previously reported in elk in Alberta, Banff National Park, or the Ya Ha Tinda except for *Capillaria* sp., which we detected for the first time in western migrant Ya Ha Tinda elk (Edwards, 2013; Flook and Stenton, 1969; T. M. Stock and Barrett, 1983). We found little support for the migratory escape hypothesis because migrants had higher diversity of parasites and higher infestations of liver flukes. In contrast, Pruvot et al. (2016) reported that liver fluke prevalence across 10 elk populations in Alberta decreased with an increasing proportion of the population being migratory. Contrary to our sampling of parasite diversity in unmarked individuals within a single partially migratory elk population, Pruvot et al. (2016) assessed the prevalence of one parasite across populations defined as migratory or non-migratory. Shaw et al. (2018) showed that across 19 studies, parasite diversity was more likely to be higher in individuals that migrate, whereas prevalence, intensity, and abundance of a single parasite was more variable and could be higher in residents, i.e. supporting migratory escape. This trend was consistent across a variety of host taxa (i.e., invertebrates, fish, birds, and mammals). In this study we also found high prevalence and intensity of a single parasite (giant liver fluke) in migrant elk, showing no support for migratory escape in this population across three metrics of parasite infection.

Instead, our results support higher parasite richness and intensity of some parasites in migratory elk consistent with the hypothesis that migration exposes elk to a broader spatio-temporal range of environments and infective stages (Koprivnikar and Leung, 2015; Leung and

Koprivnikar, 2016; Teitelbaum et al., 2018). Higher diversity of parasites in western migrants may be related to their overlap with elk in Banff National Park during summer. For example, we found *Capillaria* sp., a nematode with a direct lifecycle and a 2-month prepatent period during summer, in western migrants only that has not been detected previously in residents or eastern migrant elk (Edwards, 2013). In contrast, we found higher liver fluke intensity in eastern migrants than western migrants even though liver fluke were present in both western migrants and residents. Flook and Stenton (1969) argued that liver fluke infection was rare in the Bow Valley of Banff National Park before elk migrating from Kootenay National Park brought liver fluke eastward around 1960. Specifically, they reported < 1% of the of 339 samples of male and female elk collected between 1960 and 1965 in the Red Deer and Cascade drainages in Banff National Park were infected with liver fluke. From 1984-1991, Pybus et al. (2015) documented 61% prevalence of liver flukes in the Bow Valley elk in Banff National Park and recorded 7 elk dying as a direct result of liver fluke infection. They suggested that large montane marshes facilitated liver fluke establishment in the eastern portion of Banff National Park where migratory movements of the Bow Valley elk population were common (Woods, 1991). Summer ranges of the migratory Banff elk may have overlapped those of the western migrant elk from Ya Ha Tinda in the late 1970s, when > 95% of the Ya Ha Tinda population migrated into Banff National Park (Morgantini and Hudson, 1988). In 2010, Pruvot et al. (2016) reported prevalence levels of 27±10% in pellets from unmarked elk on the Ya Ha Tinda winter range between March and May. During the same period, we found overall prevalence of liver flukes in Ya Ha Tinda elk between 36-41% during the winters of 2017 and 2018, suggesting an increasing trend in liver flukes across this region that may be related to migratory behaviour.

Western migrants that follow green-up into montane areas gain access to higher forage quality (Aikens et al., 2017; Merkle et al., 2016), which Hebblewhite et al. (2008) reported could be 10% greater for western migrant than resident elk in the Ya Ha Tinda population. From pellet samples collected on allopatric summer ranges in 2017, we also showed fecal nitrogen was higher in western migrant elk compared to residents and eastern migrants in summer (Appendix K). Despite the potential for nutrition faciliating recovery, we found that western migrant elk had higher parasite richness than resident elk. The potential increase in immunocompetence gained from higher forage quality (Coop and Kyriazakis, 1999; Navarro-Gonzalez et al., 2010) in western migrants does not appear to outweigh transmission from infective stages on the western summer range, but may influence the impact on body condition. Although our sample was limited, we did not find that mid-winter body fat levels influenced parasite intensity. Instead, we found both collared and uncollared elk that migrated eastward had the highest intensity levels of liver flukes. Migrating 2-3 weeks earlier may have exposed eastern migrants to high-transmission habitats during the spring when parasites leave dormancy due to warmer temperatures (Bergstrom, 1975; Loehle, 1995). The summer range of eastern migrants is 200-600m lower in elevation and 3.3 - 4.9ºC higher in daily temperature on average in April-May and 1.3 - 3.6ºC from May to October, respectively (Government of Alberta, 2019). Because temperature is inversely correlated with elevation at these sites ($r = -0.94$, $p = 0.002$; Appendix L), the early warm temperature could promote favourable liver fluke development and transmission conditions through increased larval production in snails and survival of cysts on vegetation (Olsen, 1944). Earlier migration of eastern migrants may allow for longer exposure to these favourable conditions, leading to increased infection.

Furthermore, summer ranges of elk that migrated eastward from Ya Ha Tinda contained more wetlands that may have increased exposure to secondary hosts contributing to the highest liver fluke intensity we found (Appendix C). Pruvot et al. (2016) found a positive relationship between liver fluke prevalence at the population level and the average amount of lakes and small ponds (i.e., snail secondary host habitat necessary for transmission) within the population home range. Similarly, Pybus et al. (2015) found that higher proportion of wet habitats in an individual elk home range related to higher intensity of liver fluke infection. Results of this study support these findings. In fact, liver fluke intensity may be highest when there is a combination of definitive host concentration and duration of favorable environmental conditions that promote the greatest increase in liver fluke in elk. Definitive host concentration can contribute to infection through increased deposition of eggs in feces (Lankester and Peterson, 1996), which hatch to larvae, invade snail hosts, and progress to infective stages, creating a "hotspot" of exposure. However, we found little support that aggregation of eastern migrant elk per se increased liver fluke transmission. In fact, resident elk had the largest group sizes on the summer range in 2017 and 2018 compared to eastern and western migrants on the smallest summer range (Appendix C). Vanderwaal et al. (2015) also reported that liver fluke infection was not associated with white-tailed deer (*Odocoileus virginianus*) density per se. Density-dependent parasite transmission may not depend on elk density alone but in combination with whether predation refuges coincide with secondary host habitats.

Declines in migratory behaviour of ungulates with increasing resident populations is becoming a regional phenomenon (Barker et al., 2019; Phillips and Szkorupa, 2011) and the implications for parasite and disease dynamics are only recently becoming of interest (Altizer et al., 2011; Bauer and Hoye, 2014). For the Ya Ha Tinda elk, migration did not allow elk to escape

parasites and over time may have facilitated transmission among populations over broader areas as we hypothesize for liver flukes in western migrants. We have not observed an inflation of parasite infection through concentration of definitive hosts on winter range year-round, as was observed in the Bow Valley elk population (Pybus et al., 2015). This likely reflects that for some parasites, such as liver flukes, the Ya Ha Tinda range may not be highly suitable habitat. We would expect increased parasite infection in residents if conditions were suitable given the increase in resident elk over the last decades. In contrast, high prevalence and intensity of liver fluke in eastern migrant elk indicates that the emergence of new migratory patterns to areas that include suitable range for parasites could increase the parasite prevalence and intensity over short periods. For example, assuming similar representation of samples, liver fluke prevalence in the Ya Ha Tinda population may have increased by 50% in 8 years (Pruvot et al., 2016). Land use and climate changes could modify host-parasite interactions (Barker et al., 2019; Jore et al., 2011; Kutz et al., 2013, 2009) indirectly by altering the distribution of habitat suitability for both secondary and definitive hosts, especially if trends are increasing (Pybus et al., 2015). At the same time, effects of parasites on ungulates may depend on the concomitant changes in forage and predators that also are linked to land use and climate change (MacAulay, 2019; Smolko, 2014; Spilker, 2019).

Table 2.1. Hypotheses predicting the effects of migration on parasite infection in populations and individuals and the potential tactic-level effect on migration within the Ya Ha Tinda elk population.

			Predictions for parasite infection of migratory tactics		
Hypothesis	Description of hypothesis	Conditions on allopatric ranges	West	Resident	East
H1: Migratory Escape	Early migration reduces exposure to concentrations of infective stages on contaminated winter range.	Eastern migrants leave the winter range 2-3 weeks earlier on average than western migrants (Killeen et al., 2016)	Medium	High	Low
H2: Environmental Tracking	Early environmental tracking of favourable temperatures increases duration of exposure	The eastern summer range is at lower elevation on average than the resident and western summer ranges (1560m, 1740m, and 1880m; Appendix C)	Low	Medium	High
H3: Habitat Diversity	Exposure to greater diversity of habitats and more secondary host habitat increases infection and diversity	Eastern and western migrants are exposed to more diverse habitats and have more wetland habitat on their summer range than resident elk (Appendix C)	High	Low	High
H4: Migratory Recovery	Exposure to high quality forage on the summer range promotes recovery and lower infection	Western migrants are exposed to higher forage quality on summer range (Hebblewhite et al., 2008) but eastern migrants follow green-up in spring	Low	High	Low
H5: Concentration	Higher concentration of environmental infective stages increases parasite exposure	Resident and eastern elk may be more concentrated on smaller summer ranges (Appendix C)	Low	High	High

Table 2.2. Prevalence with confidence intervals and mean (± SD) abundance and intensity of infection of parasite groups in 4g of elk feces collected from unmarked elk groups (population-level) on their summer ranges from 11 May through 24 August in 2017 and 2018 and of liver flukes eggs in 2g of feces collected from individually marked elk from 25 March to 21 April 2018 and 8 April to 18 April 2019.

	Eastern	Resident	Western	Overall
Population-level	n=96	n = 183	n = 51	n =330
Parasite Richness	0.71 ± 0.60	0.45 ± 0.62	0.81 ± 0.65	0.58 ± 0.63
Pielou's Evenness	0.15 ± 0.33	0.079 ± 0.24	0.31 ± 0.43	0.12 ± 0.30
Abundance				
Capillaria sp.	0	0	0.15 ± 0.80	0.02 ± 0.32
Dictyocaulus sp.	0.16 ± 0.69	0.20 ± 2.13	0.07 ± 0.30	0.17 ± 1.61
Eimeria sp.	0.07 ± 0.59	1.91 ± 12.93	0	1.05 ± 9.53
Moniezia sp.	0.12 ± 1.13	0	0.68 ± 3.85	0.14 ± 1.64
Nematodirines	0	0.02 ± 0.25	0.05 ± 0.28	0.06 ± 1.15
Protostrongylidae	0	0.02 ± 0.15	0.05 ± 0.46	0.02 ± 0.21
Trichuris sp.	0.05 ± 0.42	0.12 ± 1.15	0.10 ± 0.05	0.04 ± 0.33
Trichostrongyle-type egg	0.14 ± 1.13	0.14 ± 1.56	0.44 ± 1.43	0.17 ± 1.17
Strongyloides sp.	0.09 ± 0.63	0.02 ± 0.16	0.38 ± 1.44	0.16 ± 1.33
Fascioloides magna				
Prevalence	0.65 (0.54,0.74)	0.29 (0.23,0.36)	0.39 (0.26,0.54)	0.41 (0.36,0.46)
Abundance	23.86 ± 6.90	4.93 ± 2.32	3.07 ± 1.09	10.62 ± 3.44
Intensity	40.76 ± 70.34	18.55 ± 55.42	8.20 ± 6.84	27.21 ± 60.65
Individual elk -level	n = 11	n = 35	n = 9	n = 55
Fascioloides magna				
Prevalence	0.51 (0.41, 0.62)	0.34 (0.29,0.40)	0.38 (0.28,0.50)	0.38 (0.34,0.43)
Abundance	11.75 ± 19.60	2.64 ± 4.38	6.04 ± 10.67	5.12 ± 10.88
Intensity of infection	20.24 ± 20.59	6.98 ± 5.58	10.55 ± 12.22	11.36 ± 13.79

Table 2.3. Summary of model selection results analysed from 2g of feces at the population level based on AICc for F. magna egg presence by migration tactic and year.

Model Structure	k	AICc	Δ AICc	AICc Wt.
Presence				
Migration tactic + year + migration tactic x year	5	417.4	0.00	0.60
Migration tactic	3	419.4	2.05	0.21
Migration tactic + year	4	419.7	2.30	0.19
Year	2	447.2	29.77	0.00
Null	1	448.5	31.12	0.00
Intensity				
Migration tactic + year	4	1028.3	0.00	0.60
Migration tactic	3	1029.7	1.43	0.30
Migration tactic + year + migration tactic x year	5	1032.2	3.91	0.09
Year	2	1035.65	7.34	0.02
Null	1	1313.8	285.5	0.00

Table 2.4. Beta coefficients (β) and standard error (SE), upper and lower 95% confidence intervals (CI) for the top model parameters based on AICc for models predicting F. magna egg presence and intensity in 2g of feces at the population level. Resident was used as a reference.

	Presence			Intensity		
		95% CI			95% CI	
Variable	$\beta \pm SE$	Lower	Upper	$\beta \pm SE$	Lower	Upper
Intercept	-1.15 ± 0.27	-1.71	-0.64	0.99 ± 0.93	-0.82	2.81
Migration tactic eastern	2.11 ± 0.50	1.18	3.14	0.98 ± 0.41	0.17	1.78
Migration tactic western	-0.12 ± 0.57	-1.34	0.95	-1.00 ± 0.54	-2.06	1.78
Year 2018	0.42 ± 0.34	-0.24	1.10	0.80 ± 0.40	0.03	1.57
Eastern x year	-0.92 ± 0.59	-2.12	0.21	--	--	--
Western x year	1.01 ± 0.71	-0.37	2.47	--	--	--

Table 2.5. Summary of model selection results based on AICc for liver fluke egg presence and counts in 6g of individual elk feces in 2017 and 2018. All models include a random effect of elk ID and threshold of zero (2017 was used as the reference year and elk resource utilization function is RUF).

Model Structure	k	AICc	Δ AICc	AICc Wt.
Presence (logistic)				
Wetland – forage	4	190.0	0.00	0.21
Wetland – forage + year	5	190.8	0.89	0.14
Wetland – forage – wetland x forage	5	191.6	1.63	0.09
Wetland – forage – age	5	191.6	1.63	0.09
Wetland – RUF	4	191.6	1.94	0.08
Wetland – forage + year – year x forage	6	191.9	2.18	0.07
Wetland – forage + year – year x wetland	6	192.1	2.65	0.06
Wetland – forage – wetland x forage + year	6	192.6	2.68	0.06
Wetland – forage – age + year	6	192.6	2.76	0.05
Null	2	198.4	8.44	0.003
Intensity (zero-truncated negative binomial)				
– Elevation	3	643.9	0.00	0.10
– Elevation – RUF	4	644.1	0.20	0.09
– Elevation + wetland – elevation x wetland	5	644.7	0.77	0.07
– Elevation + year	4	644.9	0.97	0.06
– Elevation – RUF + year	5	645.4	1.44	0.05
– Elevation + wetland	4	645.9	1.95	0.04
– Elevation – age	4	645.9	2.00	0.04
– Elevation + wetland – elevation x wetland + year	6	646.0	2.09	0.04
– Elevation + RUF – elevation x RUF	5	646.1	2.19	0.03
– Elevation – forage + year	5	646.2	2.27	0.03
– RUF + wetland + RUF x wetland	5	646.4	2.47	0.03
Null	2	646.7	2.78	0.03

Table 2.6. Beta coefficients (β) with standard error (SE), upper and lower 95% confidence intervals (CI) for the top model parameters based on AICc for a logistic and zero-truncated negative binomial model predicting liver fluke egg counts in 6g of individual elk feces in 2017 and 2018. The elk resource utilization function is RUF.

			95% CI	
Model	Variable	$\beta \pm SE$	Lower	Upper
Presence (logistic)				
Model 1	Intercept	-0.18 ± 0.36	-0.94	0.56
	Wetland	1.54 ± 0.60	0.55	2.93
	Forage	-1.46 ± 0.58	-2.83	-0.47
Model 2	Intercept	-0.31 ± 0.38	-1.13	0.45
	Wetland	1.59 ± 0.61	0.58	3.02
	Forage	-1.49 ± 0.59	-2.91	-0.49
	Year 2018	0.57 ± 0.52	-0.44	1.63
Model 3	Intercept	-0.02 ± 0.42	-0.89	0.88
	Wetland	1.41 ± 0.64	0.22	2.84
	Forage	-1.44 ± 0.61	-2.83	-0.37
	Wetland x forage	-0.26 ± 0.38	-1.08	0.47
Intensity (zero-truncated negative binomial)				
Model 1	Intercept	2.83 ± 0.28	2.28	3.39
	Elevation	-0.46 ± 0.21	-0.88	-0.04
Model 2	Intercept	2.86 ± 0.27	2.34	3.38
	Elevation	-0.48 ± 0.20	-0.87	-0.10
	RUF	-0.32 ± 0.23	-0.77	0.14
Model 3	Intercept	2.86 ± 0.26	2.35	3.38
	Elevation	-0.67 ± 0.26	-1.19	-0.15
	Wetland	-0.13 ± 0.24	-0.60	0.34
	Elevation x Wetland	-0.29 ± 0.18	-0.65	0.07

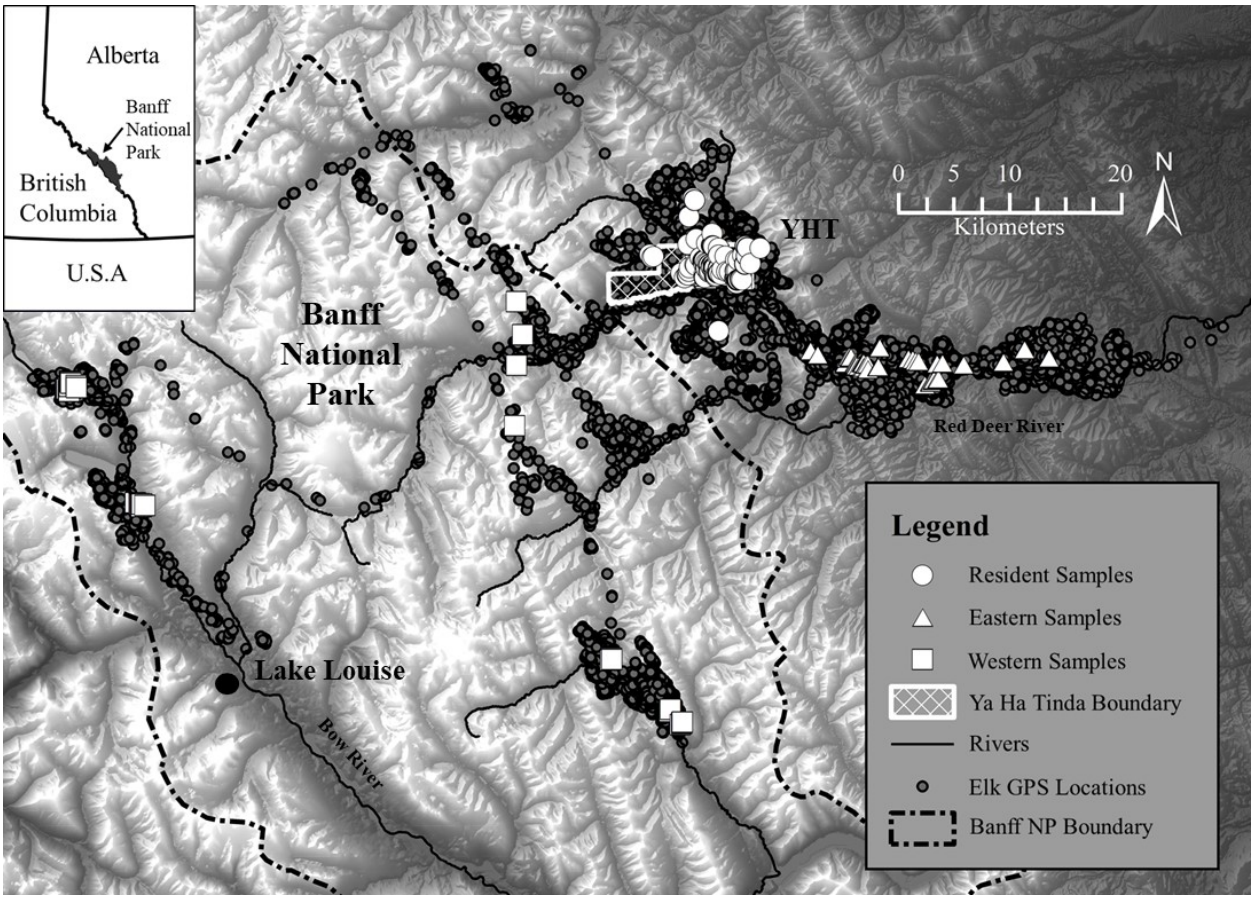

Figure 2.1. The Ya Ha Tinda (YHT) in relation to Banff National Park in western Canada and locations of elk fecal samples collected in 2017-2018 by migration tactic.

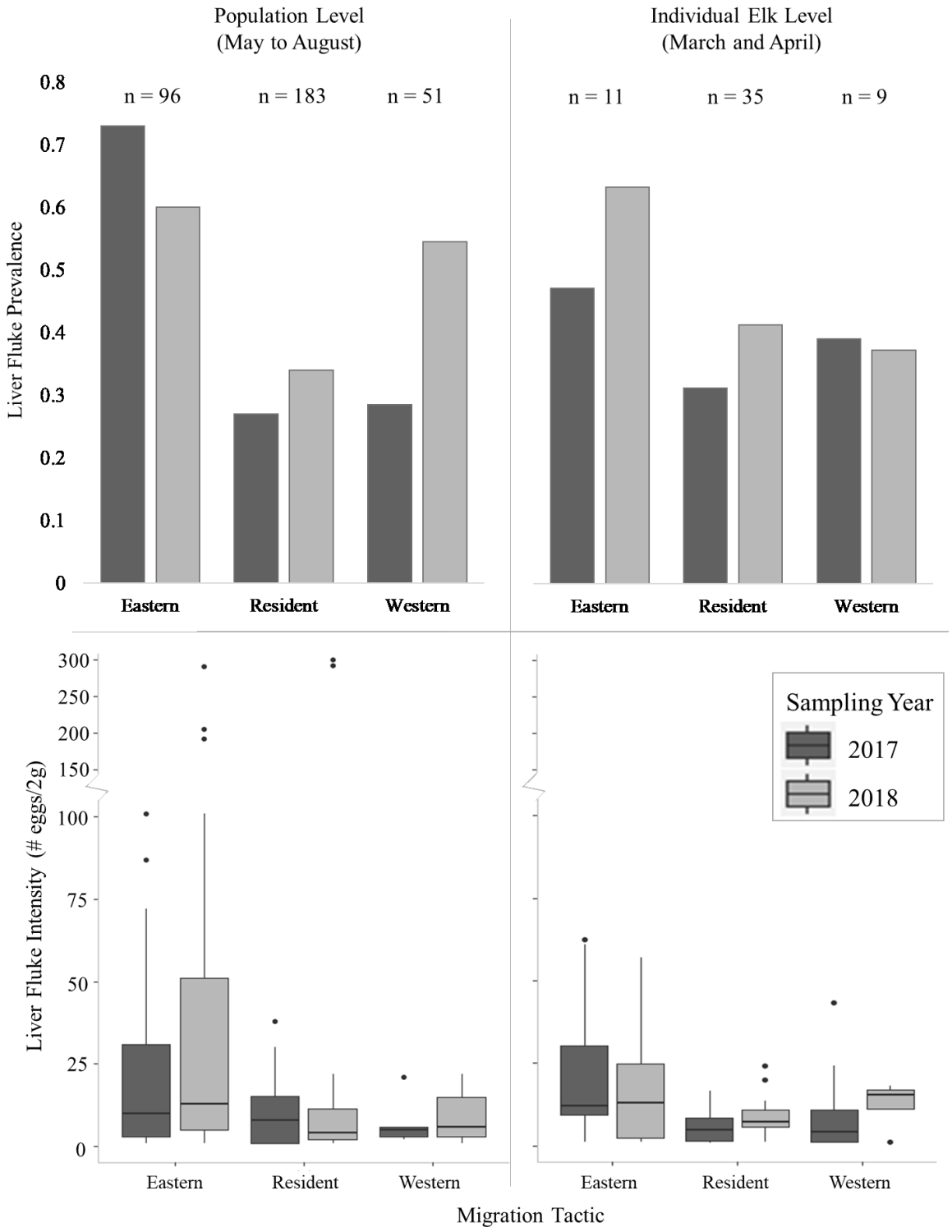

Figure 2.2. Liver fluke prevalence (top: infected animals/all animals sampled for 2g samples) and liver fluke intensity (bottom; number of eggs/2g of pellets) detected in each elk migrant tactic at the population (left) and individual level (right) separated by sampling year (2017 in dark grey, 2018 in light grey).

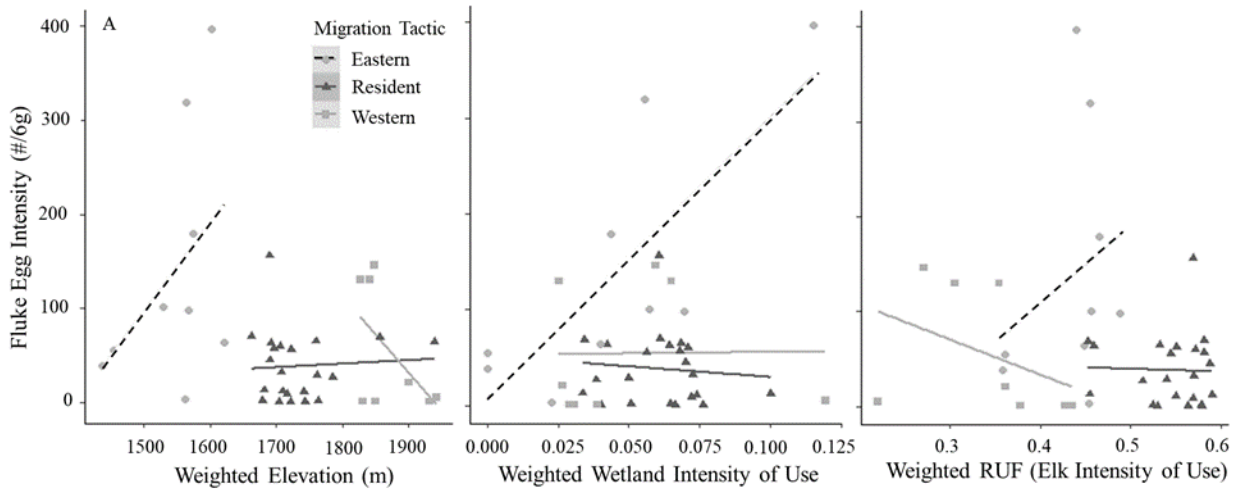

Figure 2.3. Plots of (A) weighted elevation, (B) weighted wetland intensity of use, and (C) weighted RUF by liver fluke egg intensity in 6g of individual elk pellets showing differing trends by migration tactic.

CHAPTER 3 — WHAT MAKES ELK TICK: HAIR LOSS AND WINTER TICK IN COLLARED AND UNCOLLARED ELK

1. Introduction

Ectoparasite infestation can reduce body condition and cause mortality in ungulates but grooming to remove ectoparasites may have negative effects on ungulate hosts (Glines and Samuel, 1989; Samuel, 2004; Welch et al., 1991). First, excessive loss of hair may compromise thermoregulation and increase energy expenditure in ungulates in colder climates (McLaughlin and Addison, 1986; Mooring and Samuel, 1999, 1998; Scholander et al., 1950). For example, McLaughlin and Addison (1986) found depleted visceral fat stores in moose with high hair loss, suggesting increased energy expenditure to compensate for heat loss from denuded skin. However, costs are dependent on air temperature (Welch et al., 1990) and the extent of hair loss (Samuel, 1991). Second, grooming behaviour may interfere with search time, biting rates, handling (i.e., chewing), and rumination time because these behaviours are mutually exclusive. Mooring and Samuel (1999) reported oral grooming was negatively correlated with time spent feeding in moose based on activity scans and Mooring (1995) reported that feeding time declined with time spent grooming in male impala (*Aepyceros melampus*). Third, time spent grooming may also interfere with vigilance (Crowell-Davis et al., 1985; Mooring and Hart, 1995; Mooring and Samuel, 1999), which could predispose individuals to higher predation risk (Mooring and Hart, 1995). Mooring and Hart (1995) reported that grooming impala responded by looking on average 8 seconds later than nearby individuals when subject to a simulated predator. Demands for grooming may be particularly costly in terms of vigilance when there is no spare time (sensu Fortin et al., 2004; Robinson and Merrill, 2013) such as when foraging is encounter-limited under low forage availability.

Grooming for ectoparasites can also elicit hair loss in ungulates. For example, moose with high tick (*Dermacentor albipictus*) infestations are known to lose 44% to 72% of their torso hair (McLaughlin and Addison, 1986; Welch et al., 1991). Hair loss due to ticks is related to the extent of grooming (Mooring and Samuel, 1999, 1998) rather than tick biting per se. Further, the extent of hair loss is not always associated with a count of adult ticks in a specific body region, rather it best relates to overall tick infestation (Steinberg 2008; Bergeron and Pekins 2014, McLaughlin and Addison 1986, Glines and Samuel 1984). This is because the grooming response is mediated by two mechanisms: 1) stimulus-driven grooming, which occurs in response to biting ticks being present (Hart et al., 1992; Mooring, 1995), and 2) grooming bouts at periods of high infection controlled by the central nervous system for removing ticks before attachment (Hart et al., 1992; Mooring and Samuel, 1998; Spruijt et al., 1992). As a result, hair loss can be used as an indicator of overall tick infestation (Glines and Samuel, 1989; McLaughlin and Addison, 1986; Samuel, 2007). Hair loss due to grooming for ticks can be distinguished from seasonal shedding because it typically takes the form of a "notch" or more severe "collar" at the base of the neck in elk (Figure 3.1), which in moose produces a "ghost" colour where broken hair shafts give groomed hair a distinctive white appearance (Mooring and Samuel, 1999, 1998; Welch et al., 1991).

Radiocollars are a second source of hair loss in ungulates. Global Positioning System (GPS) and very-high frequency (VHF) collars are used commonly in large ungulate studies to track survival, habitat use, migration, and calf recruitment (Brook, 2010; Hebblewhite et al., 2008; Sawyer and Kauffman, 2011). While technological limitations of telemetry collars are well studied (Frair et al., 2010; Hebblewhite and Haydon, 2010; Ironside et al., 2017; Tomkiewicz et al., 2010), there are only a limited number of studies addressing the impacts of collars on the

behaviour, condition, and survival of collared animals (Brooks et al., 2008; Hopkins and Milton, 2016; Moll et al., 2009; Rasiulis et al., 2014). Direct effects of collars include hair loss and neck lesions. For example, Krausman et al. (2004) found shape of GPS collars influenced hair loss and neck lesions in mule deer (*Odocoileus hemionus*), whereas Hopkins and Milton (2016) report hair loss, abrasions, and tissue damage on the neck of 69% of GPS-collared mantled howler monkeys (*Alouatta palliata*), even when using a relatively advanced collar design. Radiocollars could potentially impact ectoparasite infestation by either facilitating tick attachment around a collar or by removing ticks on the neck, reducing infestation.

In this study we addressed the hypothesis that tick infestation and associated grooming plays an important role in mediating time spent foraging, ruminating, and vigilant, and that time spent in these behaviours may differ among elk migratory tactics due to differences in tick infestations and associated grooming. However, because telemetry collars may reduce tick infestation and confound our conclusions, we assessed whether ticks, hair loss, and grooming time were influenced by collar presence and type. First, we predicted that increased hair loss on the withers area (Figure 3.2) is related to increased tick infestation measured at the time of capture (Table 3.1: H_1) and that ticks on captured elk and hair loss on withers do not differ between collared and uncollared elk (H_2). Second, controlling for tick infestation on the withers, we predicted collared elk groomed less but have higher neck hair loss than uncollared elk (H_3) implicating that collars, not tick infestation, increased neck hair loss. Third, we assessed whether grooming influenced time allocated to foraging, rumination, or vigilance (H_4) and whether there were differences in total time spent grooming, calculated using individual activity budgets, among collared elk following different migratory tactics (H_5). If there are differences in tick infestations of red deer (*Cervus elaphus*) between migrant and resident tactics as suggested by

Mysterud et al. (2016), grooming for ectoparasites may contribute to fitness differences between migration strategies in partially migratory populations.

We addressed these hypotheses by observing collared and uncollared elk (*Cervus canadensis*) wintering on the Ya Ha Tinda, a remnant mountain fescue (*Festuca campestris*) grassland adjacent to Banff National Park (BNP) in Alberta. The Ya Ha Tinda elk population is a partially migratory elk population that declined from about 1200 elk in the early 2000s to a current 400-500 wintering elk. The majority of the population previously migrated westward into Banff National Park, but since the mid-2000s, there has been as been a build-up of resident elk remaining on the winter range and a shift in the number of elk migrating eastward onto low-elevation industrial lands along the Red Deer River (Eggeman et al., 2016). Elk were collared in winter as part of a long-term study on changing migratory behaviours. We used close-up pictures of focal elk to quantify hair loss and directly observed grooming, foraging, rumination, and vigilance behaviours of collared and uncollared individuals from January – March 2019 to assess our hypotheses.

We focused on hair loss and winter ticks because infestation is known to reduce body condition, increase weight loss, promote anaemia, and cause mortality in ungulates (Glines and Samuel, 1989; Samuel, 2004; Welch et al., 1991). Ticks are an environmentally transmitted single-host ectoparasite where adult females drop off the ungulate host in spring (April and May) to lay eggs, larvae attach to another host in fall (mid-September to mid-October), and mature into adults following 3 blood meals on the definitive host (Mooring and Samuel, 1999). Nymphs cause some irritation as they take blood meals from late January to March but peak irritation occurs from blood meals of adult females in late March – April (Samuel, 2004). Hair loss from ticks follows the annual cycle with hair loss regrowing in summer after the peak hair loss in late

March and April (Samuel, 2004). To date, no study has examined the cost of grooming for winter ticks on foraging, rumination, and vigilance behaviour in individual ungulates or how collars may alter this cost.

2. Methods

2.1 Elk capture and collaring, tick counts at capture, and migration status

Female elk in this study were free-range darted from horseback in winter between 2009 and 2019 to immobilize, ear-tag in both ears, and collar individuals with either VHF or GPS collars (see Berg 2019 for details on elk capture). All capture, handling, and subsequent observations of elk followed approved protocols consistent with Canadian Council on Animal Care Guidelines and approved by the University of Alberta Biosciences Animal Care and Use Committee (Protocol # AUP00000624). During the study we observed a total of 66 previously captured focal adult female elk. All collared elk in the study had carried a collar for at least one year prior to observations and all uncollared elk had been without a collar for at least one year. In addition, we counted ticks on 20 immobilized females (12 new individuals) that were captured from 5-9 March 2019 following Sine et al. (2009). We counted ticks by parting the hair with a pencil along a 30-cm transect on the withers. We recorded life stage for every tick encountered as either nymph, engorged nymph, or adult (Appendix M). If a collar was present before capture (n = 8), we noted any damage to neck skin and tissue from the collar.

All elk in the study were aged via incisor cementum annuli using a tooth sample collected at capture (Keiss, 1969). Migration status of collared elk was derived from sequential telemetry locations of 6 or 13hr fixes using a net-squared displacement approach (Bunnefeld et al., 2011) and visual inspection with migrants classified as moving > 15 km from their winter range for > 30 days (Killeen et al., 2016). We classified ear tagged-only individuals using previous year's

GPS-locations or direct observations of animals on ranges during the preceding summer. We assumed elk did not switch migration status between years, although ~15% of elk could switch in any one year (Eggeman et al., 2016).

2.2 Focal Elk Hair Loss

Hair loss was determined for 20 elk immobilized from 5-9 March 2019 and for the 66 focal elk from 17-18 April 2019. We sampled hair loss on the neck and withers 4 times in the middle of each month from January to April to ensure that April hair loss was representative of an individual's cumulative hair loss over the winter (Appendix N). We assigned hair loss scores to focal individuals based on side-profile images taken with a high-zoom Nikon Coolpix P510 digital camera from horseback so the animals could be approached as close as 10 to 50m. We obtained images from both sides of the elk when possible and the larger hair loss score was taken in cases where hair loss pattern was asymmetrical on either the withers or neck. The neck area was defined as the area a collar could slide up and down the neck if present, and the withers defined by the area adjacent to and directly posterior of the neck until the midway point down the back between the highest point on the shoulders and the beginning of the white-haired rump area (Figure 3.2). Loss of hair was defined as hair that was <50% of the height of surrounding hair shafts at the skin level where the hair follicle emerges. We recorded the number of grid cells (5cm x 5cm) with >50% hair loss in the withers and neck areas for each focal individual and the number of cells with hair loss was used to assign a hair loss score from 1-16 cells. Images were resized and rotated according to a consistent template to standardize elk body size in pictures across all individuals for the neck and withers hair loss scoring grids (Appendix N).

2.3 Behavioural Observations

Behavioural observations were taken 9 times on 66 elk (Table 3.2) between 15 January – 22 April 2019 during the period from 0700 to 1900 through a spotting scope from a distance of 275 – 1100m to avoid disturbing the focal animal. We selected collared elk randomly prior to locating the elk via telemetry to reduce observer bias and we sampled elk from each migration tactic equally across daylight hours (Appendix O). Uncollared individual (ear-tagged only) elk were selected haphazardly each time they were sampled. Observations lasted for up to 15 minutes or until the focal individual moved out of sight. Once an observation started on a focal animal, start and stop times of each of 6 behaviours were continuously recorded into a voice recorder (Olympus VN-541PC) and later coded using the program JWatcher^{TM} to quantify durations. Foraging was defined as head below shoulders searching for forage, vigilance as when the elk was standing or slowly walking with head above shoulders looking around, resting when bedded but not engaged in rumination, and rumination while bedded with the elk visibly chewing based on the motion of the lower jaw interspersed with regurgitation and swallowing. Rumination while standing accounted for < 0.1% of total rumination and was not included in the analysis. Grooming was defined as either oral grooming (licking or biting coat with teeth, restricted to the hindquarters; Mooring and Samuel, 1998), scratch grooming (scratching the head/neck [hereafter "neck"] or withers area with hind hoof; Mooring and Samuel, 1998) or combined grooming, which included both oral and scratch grooming. For each observation of scratch grooming we recorded whether the focal elk grooming manipulated a collar in any way if present. We also recorded the behaviour immediately preceding grooming to calculate whether the duration of grooming differed depending on which activity preceded it. Conspecific interaction was defined as an interruption of any activity to interact with another individual.

2.4 Statistical Analysis

We tested whether withers hair loss score at capture was related to total number of ticks on withers (abundance) of elk at capture (H_1, n = 20) using Spearman rank correlation (cor.test function from the package stats; R Core Team, 2019). We determined whether counts of ticks on the withers differed between previously collared (n = 8) and uncollared elk (n = 12, H_{2A}) using a Kruskal-Wallis rank sum test ($\alpha = 0.05$). We also determined whether wither hair loss on GPS-collared (n = 38), VHF-collared (n = 10), and uncollared (n= 18) focal animals differed using a Kruskal-Wallis rank sum test and a Dunn's post hoc test (H_{2B}; packages stats and dunn.test; Dinno, 2017).

We used ordinal regression and model selection based on (Akaike Information Criteria for small sample sizes; AICc) to assess whether neck hair loss scores in April were related to wither hair loss in April, elk age, and collar type (none, VHF, GPS) or their interactions (H_{3A}). To assess the assumption of proportional odds of the ordinal regression we used likelihood ratio tests using the nominal_test and clm functions in the ordinal package in program R (Christensen, 2019). We used a general linear model (GLM) to determine whether mean time spent neck grooming per individual (9 observations/individual) in winter on focal elk was related to April withers hair loss, elk age, collar type or their interactions (H_{3B}; glm from the R packages stats; R Core Team, 2019).

We used separate, generalized linear mixed models (GLMM) with elk ID as a random effect to determine whether time (s) spent in each activity of foraging, ruminating, resting, or vigilant decreased with time spent grooming during observations (H_4), controlling for age, and observation length with an offset (lmer from the R package lme4; Bates et al., 2015). Because the model for each behaviour included the same animals and had the same input variables, we

compared differences in slope magnitude (beta coefficients) between grooming and the alternative activity using the overlap of the 95% confidence limits. Prior to model selection analyses, we tested for collinearity in input variables and did not use correlated variables ($r < |0.55|$) in the same model. We tested for a difference in the duration of time spent grooming during each activity using a Kruskal-Wallis rank sum test and a Dunn's post hoc test.

To compare migratory tactics, we first assessed differences in withers hair loss score using a two-way ANOVA of migration status, collar type, and their interactions (anova function from stats; R Core Team, 2019). We then used a GLMM with a random effect of elk ID to test for differences in time spent in combined grooming among the different migration tactics (resident as reference), accounting for wither hair loss score, collar type, age, and their interactions (H_5). We tested for differences in mean proportion of time spent in each activity and mean duration of grooming separately among migration tactics using Kruskal-Wallis rank sum tests.

Finally, we compared estimated total time spent grooming per 15 min (900s) among migration tactics where total time spent grooming for a standardized 15-min observation period for each individual was estimated following equation (Eq. 1).

(Eq. 1) $$\frac{total\ grooming\ (s)}{activity\ (900\ s)} = \frac{grooming\ (s)}{activity\ (s)} \times \frac{activity\ (s)}{observation\ length\ (s)} \times 900\ (s)$$

We tested for differences in estimated total grooming (in contrast to combined grooming we observed) for each activity by migration tactic using Kruskal-Wallis rank sum tests ($\alpha = 0.1$) to assess whether fitness trade-offs related to grooming differ across migration tactics. All analyses were conducted using R statistical software (R Core Team, 2019).

3. Results

The number of adult ticks on the withers of 20 adult female elk in early March averaged 3.7 ± 4.9 ($\bar{x}$ ± SD)/per 30cm transect while engorged nymphs averaged 1.5 ± 3.0 and un-engorged nymphs averaged 8.8 ± 9.9 for a total of 14.0 ± 15.6 ticks/per 30cm. Approximately 64% of total ticks on the withers across animals were nymphs, and approximately 23% of the nymphs were engorged. No engorged adults were detected on the withers transects. The number of adults and nymphs on the withers of elk were correlated ($r = 0.61$, $p = 0.005$). Neither number of adults ($r = -0.02$, $p = 0.93$), nymphs ($r = -0.23$, $p = 0.33$), nor total number of ticks ($r = -0.20$, $p = 0.41$) on the withers were related to withers hair loss score. In addition, there was no difference between tick abundance on previously collared or uncollared elk ($p = 0.88$, $df = 1$, Kruskal-Wallis $\chi^2 = 0.023$). Focal individuals ranged in age from 3 to 20 years old and included 74% residents, 14% eastern migrants, and 12% western migrants. GPS-collared individuals averaged younger than VHF-collared individuals ($p = 0.004$, $df = 2$, Kruskal-Wallis $\chi^2 = 7.14$) and uncollared elk ($p = 0.15$). Eastern migrant individuals were younger on average than residents ($p = 0.014$, $df = 2$, Kruskal-Wallis = 5.11) and western migrants ($p = 0.036$; Table 3.2).

Withers hair loss score did not differ between uncollared elk and either GPS- or VHF-collared elk ($p = 0.27$, $df = 1$, Kruskal-Wallis $\chi^2 = 1.19$; Table 3.2). Hair loss on withers of uncollared elk (ear-tagged only) was not correlated with hair loss on the neck, with uncollared elk having almost no neck hair loss (Table 3.2). Collars had an additive effect on neck hair loss score when we accounted for hair loss on the withers, but the magnitude of this effect did not change with increasing hair loss on the withers (i.e., no collar x withers hair loss interaction). GPS collars had about 50% greater effect on neck hair loss score than VHF collars (Table 3.3). There was some support for neck hair loss increasing with age, but the confidence limits of the

coefficient for age overlapped zero. Despite hair loss, we found no evidence of lesions or skin damage on the neck due to collars on elk that had a collar for at least one year prior to capture (n = 8).

Behavioural observation periods ranged from 3 to 15 min and averaged 12.8 ± 3.6 min ($\bar{x}$ ± SD) with 67% of observations 15 minutes in length. Approximately 42% of observation periods contained any type of grooming behaviour but grooming averaged only 1.1 ± 2.4% of any observation period. Thirty-five percent of combined (oral and scratching) grooming occurred in the neck area, with the rest distributed along the hindquarters. Of the times a collared animal groomed its neck, only 5% involved the foot rotating a collar. The best supported model of time spent grooming on the neck was a positive relationship to age alone (Table 3.3) because confidence intervals of the beta coefficient between hair loss on withers and neck grooming overlapped zero (Table 3.4). We found no support for an association between time spent grooming the neck and the presence of a collar or collar type (Table 3.3).

Combined grooming occurred primarily during resting (40%) or while vigilant (36%). Only 14% and 10% of combined grooming occurred during foraging and rumination, respectively, whereas these activities comprised 43.9 ± 40.4% ($\bar{x}$ ± SD) and 22.6 ± 36.1%, respectively, of the elk activity budget during daylight hours (0700-1900, Appendix O). Grooming did not interrupt conspecific interactions except for allogrooming (grooming another elk), which accounted for < 0.01% of combined grooming and was mainly done by a single ear-tagged elk. Approximately 40% of all scratch grooming with the foot on the neck occurred during foraging and ~30% of scratch grooming occurred during resting (Appendix P). Oral grooming with teeth on the hindquarters occurred primarily during resting and vigilance with ~40% of oral grooming during each.

An increase in combined grooming was associated with a decrease in foraging time and an increase in resting time, and the confidence intervals of model beta coefficients for these variables did not overlap zero (Table 3.5). Time spent in combined grooming had a greater effect ($\beta = -3.27 \pm 0.73$; $\beta \pm SE$) on time spent foraging compared to resting ($\beta = 2.13 \pm 0.62$). Grooming had no effect on vigilance or rumination was because the confidence intervals overlapped zero (Table 3.5). Additionally, the duration of grooming bouts during foraging was shorter than during resting, vigilance, and rumination ($p < 0.001$ for each, df = 3, Kruskal-Wallis $\chi^2 = 31.17$), but did not differ among resting, vigilance, and rumination ($p = 0.13$; Figure 3.3).

Withers hair loss score differed between migration tactics ($p = 0.030$, df = 2, Kruskal-Wallis $\chi 2 = 6.49$). Eastern migrants had higher withers hair loss score (6.8 ± 4.7) than residents (3.6 ± 3.6, $\bar{x} \pm SD$; $p = 0.008$, df = 2, $F = 6.03$) and western migrants (2.4 ± 2.9, $p = 0.014$) but residents and western migrants did not differ ($p = 0.71$). Collar type had no effect on withers hair loss among migratory tactics (i.e., no interaction; $p = 0.66$, df = 2, $F = 0.41$). In contrast, we found no difference in time spent in combined grooming between migration tactics (Figure 3.4, Appendix Q). The proportion of time elk spent in each activity type did not differ among animals following different migratory tactics (foraging: $p = 0.41$, df = 2, Kruskal-Wallis $\chi^2 = 1.77$; resting: $p = 0.36$, df = 2, Kruskal-Wallis $\chi^2 = 2.06$; vigilance: $p = 0.93$, df = 2, Kruskal-Wallis $\chi^2 = 0.15$; rumination: $p = 0.75$, df = 2, Kruskal-Wallis $\chi^2 = 0.58$; Figure 3.4).

Eastern migrants showed higher estimated total time (s/15 min) spent grooming during resting than residents ($p = 0.060$, df = 2, Kruskal-Wallis $\chi^2 = 3.55$) and western migrants ($p = 0.037$), whereas during rumination and vigilance they groomed less than residents ($p_{rumination} = 0.093$, df = 2, Kruskal-Wallis $\chi^2 = 2.18$; $p_{vigilance} = 0.025$, df = 2, Kruskal-Wallis $\chi^2 = 3.95$) and western migrants ($p_{rumination} = 0.093$, $p_{vigilance} = 0.075$; Figure 3.5). Total estimated grooming

during foraging did not differ among migration tactics ($p = 0.47$, $df = 2$, Kruskal-Wallis $\chi^2 = 1.50$).

4. Discussion

We found a higher mean tick density on the withers of elk at the Ya Ha Tinda in 2019 ($0.47 \pm 0.52/cm^2$, $\bar{x} \pm SD$, $n = 20$, Appendix M) compared to elk in Elk Island National Park ($0.057 \pm 0.014/cm^2$, $n = 16$) and Jasper National Park ($0.174 \pm 0.062/cm^2$, $n = 6$) between 1990-1996 and on the National Elk Refuge in Wyoming in 1987 ($0.22 \pm 0.20/cm^2$, $n = 9$; Samuel et al., 1991; Samuel and Mooring, 1998). However, we counted ticks in a transect on the withers only, where we expected to find highest tick densities, whereas Mooring and Samuel (1998) and Samuel et al. (1991) made counts in areas across the whole-body of dead elk instead of transects on live elk. Nonetheless, Samuel et al. (1991) found highest densities of ticks ($> 0.65/cm^2$) on the withers, where we sampled.

Despite a lack of correlation between number of ticks on a 30cm transect along the withers of 20 elk, we submit withers hair loss score is likely indicative of tick infestation of an individual. We may have detected a potential correlation if counts were conducted at peak irritation from adult tick engorgement in mid-to-late April when peak withers hair loss would be expected. McLaughlin and Addison (1986) recommended flying aerial surveys for moose hair loss in late March/April when hair loss correlated more directly to tick infestation. We sampled in early March, when 64% of ticks were nymphs, similar to other findings indicating 57% of ticks were nymphs in early March and April (Mooring and Samuel, 1998). Further, there may be a lag time in hair loss with hair loss related to tick counts up to one month prior (Glines and Samuel, 1984; McLaughlin and Addison, 1986). Therefore, we used only a measure of withers hair loss score in late April, which is close to peak hair loss from grooming for ticks, to be

indicative of tick infestation (Bergeron and Pekins, 2014; Samuel, 2007; Steinberg, 2008). We also found mean grooming over time increased with withers hair loss score, indicating high tick infestation causing irritation following the stimulus grooming hypothesis (Mooring and Samuel, 1999, 1998).

We hypothesized that telemetry collars could potentially influence tick infestation on the necks of elk, which in turn could evoke differential responses in time spent grooming. We conclude that higher hair loss on the neck of collared elk compared to uncollared elk is due to rubbing of collars, because previously collared elk did not have higher tick counts on the withers during captures than previously uncollared elk, and GPS- and VHF-collared elk show no difference from uncollared elk in withers hair loss (i.e., our proxy for lower tick infestation). Despite the increased neck hair loss with collars, we found no lesions or tissue/skin damage on necks of collared elk. We predicted that elk would use their hind foot to rotate the collar to alleviate irritation due to tick infestation (W. M. Samuel, *pers. comm*.), but if they do, the effect is likely minor, as it comprises only 5% of grooming observations on the neck (compared to 95% direct hoof scratching) in collared elk. We could not directly assess whether collars themselves rubbed ticks off on the neck and whether this would influence grooming because we could not count ticks. However, we found some evidence for an association between elk age and both neck hair loss and grooming on the neck. The body size principle predicts that smaller (i.e., younger) individuals need to groom more for ectoparasites because they have a larger surface-area to body size ratio and thus more potential for cost due to ticks (Hart et al., 1992; Mooring and Samuel, 1998). However, these studies only compared calves to adults, not age within adult females.

We found evidence that when time was spent grooming during foraging it reduced foraging time, whereas when elk groomed during resting, resting time was extended. Because

eastern migrants had greater loss of hair on the withers, we assumed they had higher tick infestation, potentially due to higher larval survival on the warmer eastern summer range in spring when engorged female ticks drop off hosts (3.3 - 4.9º C higher in daily temperature on average in April-May; Drew and Samuel, 1987). As a result, we expected to see eastern migrants exhibit higher combined grooming time and lower foraging time, which we did not find. Two explanations for this exist. First, if tick infestation was high, eastern migrants may have groomed pre-emptively in the fall prior to peak tick irritation in winter. For example, Mooring and Samuel (1998) suggested it would be more effective for elk to groom at larval attachment to remove larvae and avoid the energetic and thermoregulatory costs of grooming for nymphs and adult ticks in late winter or early spring when they are most energetically stressed. However, this hypothesis was not supported because withers hair loss score was similar among elk from each migratory tactic in January and increased across winter (Appendix N).

Instead, eastern elk spend relatively more time grooming during resting than residents and western migrants. It is unknown if elk can groom more thoroughly while resting as opposed to other activities but increased grooming while resting is consistent with the expectations that elk will minimize costs of grooming by synchronizing grooming with an the activity least likely to impinge on searching for and processing forage, i.e., resting (Hart, 1995). Mooring (1995) also reported reduced feeding with increased grooming in male impala, which they attributed to seasonal variation in forage availability reducing constraints on grooming (i.e., grooming increased in the rainy season with the availability of abundant green forage). Because our study was performed over a short time period (i.e., January to April instead of over a full year), seasonal changes in forage availability are not likely confounding our results as green-up had not yet occurred on the winter range by late April. Impala that stay in large groups also decreased

vigilance that may then be available for grooming (Mooring and Hart, 1995). In this study, adult female elk were in a group of >300 on the winter range, however differences in cohesion among migration tactics within the large group could add an effect of group size on grooming rate at the Ya Ha Tinda (Robinson et al., 2010). Despite no clear trend between increased grooming during vigilance and time spent vigilant across all migration tactics, we found some evidence that eastern migrants with higher tick infestation do have to trade-off grooming during foraging with grooming during other activities. When eastern migrants increased grooming during vigilance, vigilance time decreased ($\beta = -0.68 \pm 0.70$; $\beta \pm SE$) whereas increased grooming during vigilance did not decrease vigilance time in resident ($\beta = 0.087 \pm 0.37$) and western migrant elk ($\beta = 0.075 \pm 0.37$). Therefore, increased grooming can have consequences for vigilance trade-offs with foraging and antipredator strategies (Mooring and Hart, 1995) in elk with high tick infestation. For example, while estimated total grooming during 15 minutes of activity may be negligible (i.e., ~ 3 seconds/15 minutes of vigilance), grooming could constitute as much as 5 minutes during vigilance, 1 minute during rumination, 2 minutes during foraging, and 6 minutes during resting over a 24-hour period of each activity. Therefore, the cumulative time sent grooming over a 24-hour period could influence activity trade-offs between acquisition of forage and predator defence.

Pathogenicity of winter tick is hypothesized to decrease with time spent in North America by host species because ticks have lower pathogenicity in white-tailed deer (millions of years in North America) than they have than in elk (11,000 – 70,000 years in North America) and moose (10,000 – 24,000 years in North America; Samuel 2004). Moose are more likely to experience adverse effects of winter tick than elk (Mooring and Samuel, 1998; Samuel et al., 1991), and consequently, most studies focus on the effect of winter tick in moose with few

studies addressing grooming behaviours for winter tick in elk. In this study, we found evidence that elk at the Ya Ha Tinda, with relatively high winter tick infestations and showing high withers hair loss, are able to adjust their grooming behaviours to minimize the loss of foraging time by synchronizing grooming with less costly activities, such as resting. However, synchronizing grooming with less costly activities may increase per capita predation risk, due to reduced vigilance with high tick infestation as demands for grooming increase. Because elk form larger groups than moose and deer, elk may off-set the risk associated with effective grooming strategies and reduced pathogenicity compared to moose (Samuel, 2004; Welch et al., 1991). Even so, grooming takes up only a small portion (~1%) of the overall activity budget of an elk, at least during the daytime. The importance of these behaviour adjustments may be contingent on other forage-predation trade-offs that limit their behavioural flexibility.

Table 3.1. Hypotheses predicting the effects of migration on parasite infection in populations and individuals and the potential tactic-level effect on migration of the Ya Ha Tinda elk population.

Hypothesis	Predictions	Focal Area
H_1: Hair loss on withers is indicative of tick infestation.	At capture, counts of ticks on withers increases with increasing hair loss.	Withers
H_2: Collared elk are not subject to higher tick infestation or hair loss overall than uncollared elk.	Elk with collars do not have higher ticks on withers at capture (H_{2A}) or higher hair loss on withers (H_{2B}) in winter than uncollared elk.	Withers
H_3: Collars reduce the tick irritation on the neck leading to lower neck grooming.	Neck hair loss increases (H_{3A}) and neck grooming decreases (H_{3B}) in collared elk compared to uncollared for the same level of hair loss on withers.	Neck
H_4: Grooming for ectoparasites limits time spent foraging, ruminating, or vigilant.	As overall grooming increases, time spent foraging, ruminating, and vigilant decreases.	Full Body
H_5: Tick infestation and time spent grooming differ between migratory tactics.	Hair loss on withers (H_{5A}) and time spent grooming differ (H_{5B}) among migratory tactics controlling for collar presence.	Withers, Full Body

Table 3.2. Sample sizes and mean ages (years ± SD) for hair loss scores and grooming observations of 66 focal elk by collar type and migration tactic.

	Eastern		Resident		Western		Overall	
Collar Type	No.	Age	No.	Age	No.	Age	No.	Age
GPS	5	7.4 ± 4.3	27	10.0 ± 4.4	6	11.3 ± 3.0	38	9.8 ± 4.3
VHF	0	NA	8	14.5 ± 3.4	2	12.5 ± 0.7	10	14.1 ± 3.1
Ear tags only	4	7.8 ± 6.9	14	12.2 ± 4.3	0	NA	18	11.1 ± 5.1
Overall	9	7.6 ± 5.2	49	11.3 ± 4.5	8	11.6 ± 2.6	66	10.8 ± 4.55
Average Withers Hair Loss Score								
GPS		6.8 ± 6.1		4.7 ± 3.4		3.2 ± 2.9		4.8 ± 3.8
VHF		NA		2.8 ± 4.3		0.0 ± 0.0		2.2 ± 4.0
Ear tags only		6.5 ± 4.2		2.2 ± 3.0		NA		3.2 ± 3.7
Overall		6.8 ± 4.7		3.6 ± 3.6		2.4 ± 2.9		3.9 ± 3.8
Average Neck Hair Loss Score								
GPS		7.2 ± 7.5		6.6 ± 5.4		8.3 ± 6.3		8.9 ± 4.4
VHF		NA		6.9 ± 5.3		2.5 ± 3.5		4.0 ± 5.7
Ear tags only		4.8 ± 4.9		3.4 ± 5.0		NA		0.2 ± 0.8
Overall		5.2 ± 5.8		6.1 ± 5.6		4.8 ± 5.1		5.8 ± 5.6

Table 3.3. Summary of model selection results based on AICc for neck hair loss and average time spent grooming the neck over 9 observations per individual related to withers hair loss score and collar type (GPS, VHF, or uncollared). Number of parameters in the model is denoted by k.

Model	k	AICc	Δ AICc	AICc Wt.
Neck Hair Loss				
Collar + withers hair loss score	5	244.5	0.00	0.59
Collar + withers hair loss score + age	6	245.6	1.10	0.34
Collar + withers hair loss + collar x withers hair loss	8	249.5	4.99	0.05
Collar + withers hair loss + collar x withers hair loss + age	7	251.2	6.66	0.02
Collar + age	4	255.4	10.90	0.003
Null	1	292.9	48.44	0.00
Neck Grooming Time				
Age	2	188.7	0.00	0.46
Age + withers hair loss score	4	190.7	2.02	0.17
Null	1	190.7	2.08	0.17
Age + collar	4	192.0	3.31	0.09
Withers hair loss score	3	192.9	4.28	0.05
Age + withers hair loss score + collar	6	194.3	5.62	0.03
Age + collar + age x collar	5	196.7	8.05	0.008
Age + collar + withers hair loss score + collar x hair loss	7	198.4	9.74	0.004

Table 3.4. Beta coefficients (β) and upper and lower 95% confidence intervals (CI) for the top model parameters based on AICc for models predicting neck hair loss score and average time spent grooming the neck area for focal individuals. Uncollared was used as the reference for collar type.

	Neck Hair Loss			Neck Grooming Time		
		95% CI			95% CI	
Variable	$\beta \pm SE$	Lower	Upper	$\beta \pm SE$	Lower	Upper
Intercept	0.00 ± 1.21	-2.37	2.37	1.13 ± 0.19	0.76	1.51
GPS collar	5.21 ± 1.02	3.43	7.50	--	--	--
VHF collar	3.47 ± 1.18	1.27	6.02	--	--	--
Withers hair loss	0.27 ± 0.08	0.12	0.43	--	--	--
Age	--	--	--	0.06 ± 0.03	0.003	0.11

Table 3.5. Beta coefficients (*β)* and upper and lower 95% confidence intervals (CI) for the parameters of models testing the effect of time spent grooming on time spent foraging, vigilant, ruminating, or resting with a fixed effect of age, a random effect of individual, and an offset to control for observation length.

Activity	Variable	$\beta \pm SE$	95% CI	
			Lower	Upper
Foraging	Intercept	-635.38 ± 229.50	-1082.87	-183.73
	Combined grooming	-3.25 ± 0.72	-4.66	-1.84
	Age	-1.39 ± 3.22	-7.68	4.90
Resting	Intercept	-1058.78 ± 196.41	-1443.04	-674.51
	Combined grooming	2.10 ± 0.62	0.89	3.31
	Age	-0.57 ± 2.53	-5.52	4.38
Rumination	Intercept	-1414.0 ± 219.30	-1844.95	-986.13
	Combined grooming	0.096 ± 0.69	-1.25	1.45
	Age	2.60 ± 3.15	-3.57	8.76
Vigilance	Intercept	281.37 ± 97.89	90.09	472.98
	Combined grooming	0.044 ± 0.31	-0.56	0.64
	Age	-0.99 ± 1.32	-3.56	1.58

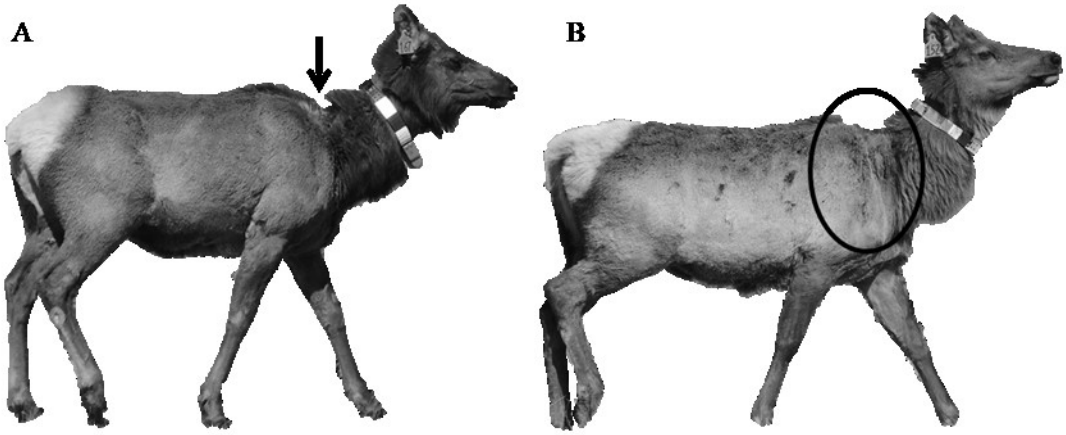

Figure 3.1. Characteristic “notch” (A) and “collar” (B) hair loss patterns on elk caused by grooming for winter tick (*Dermacentor albipictus*).

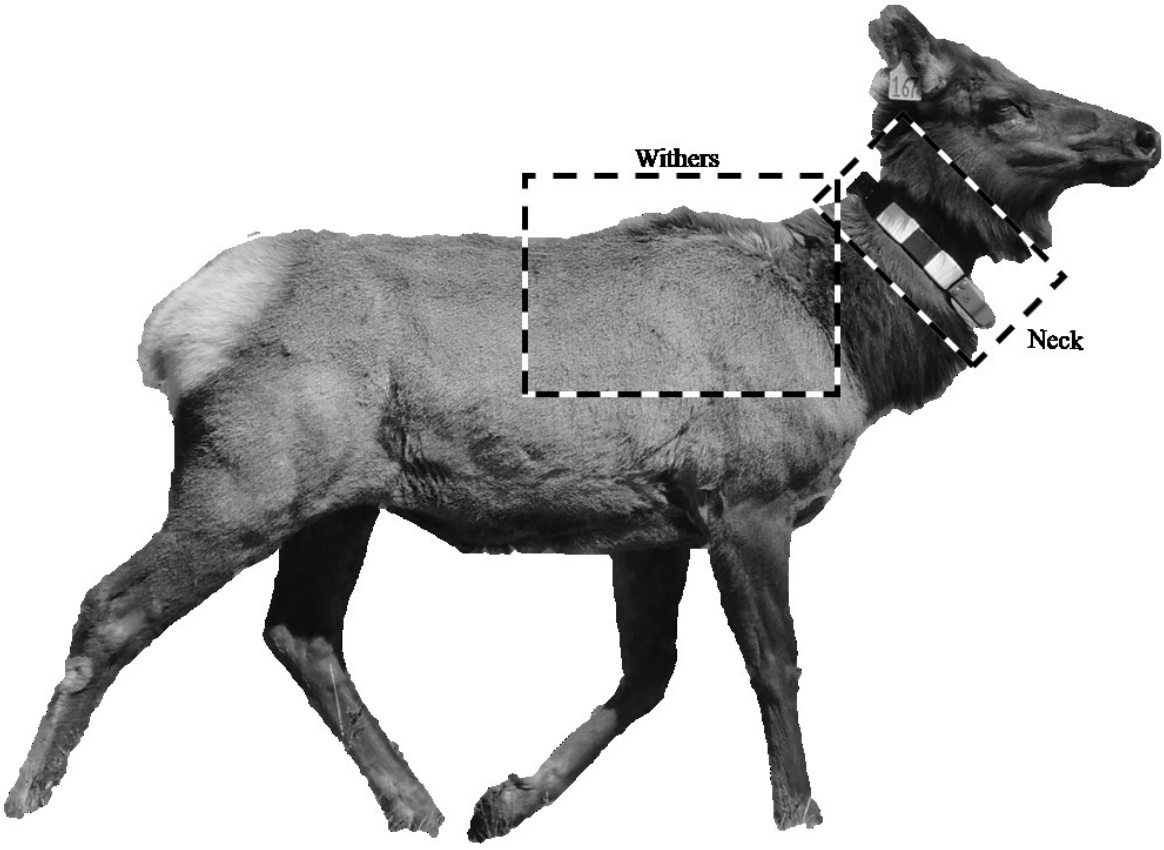

Figure 3.2. Delineations of withers and neck areas for hair loss scores.

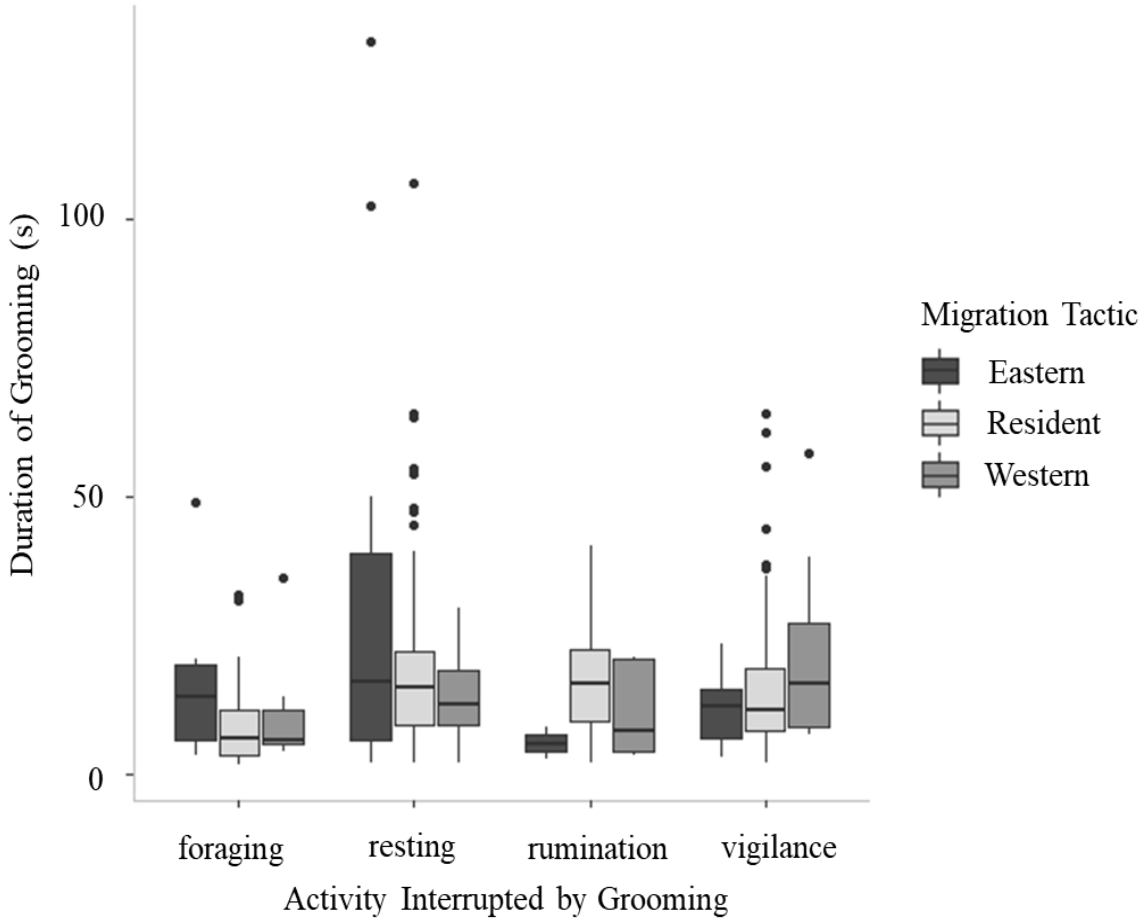

Figure 3.3. The duration of combined grooming that occurred during each of the four most common activities separated by migration tactic (conspecific interactions were not included as no grooming interrupted that activity). There were no significant differences between proportions of each activity across migration tactics, however elk overall spent less time grooming during foraging.

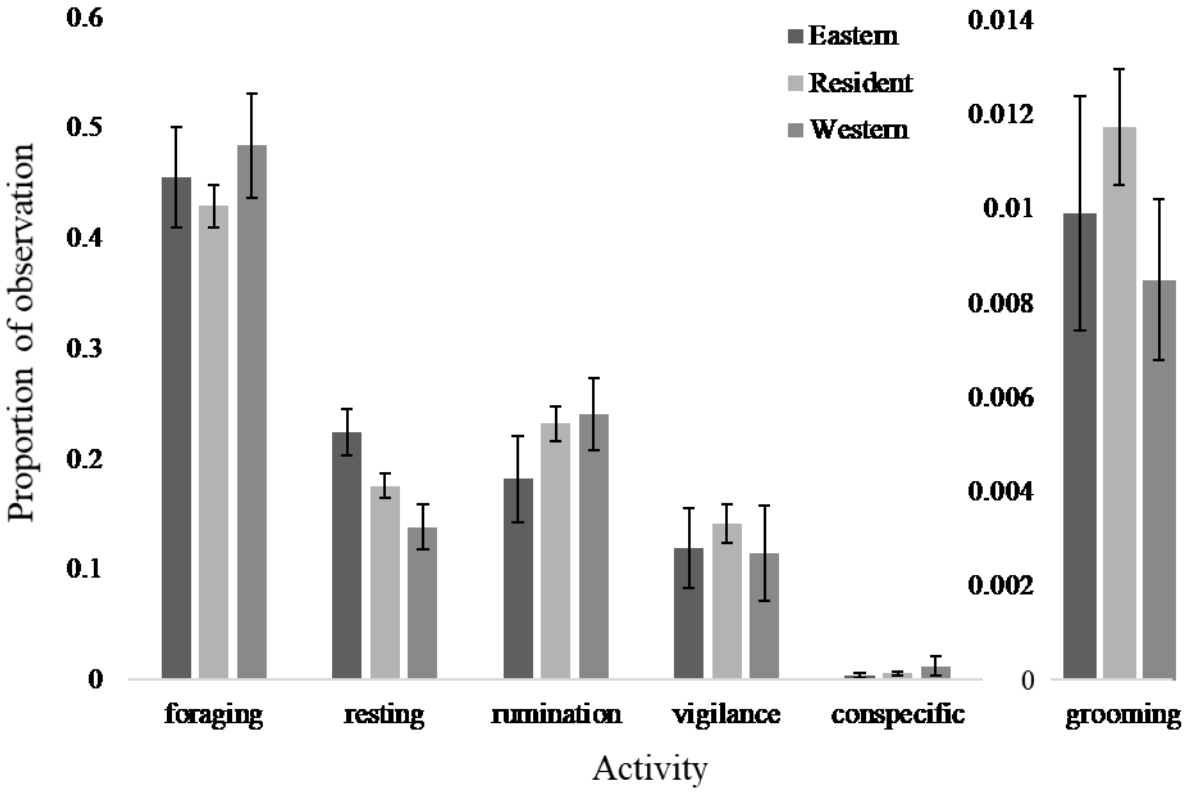

Figure 3.4. The mean proportion of time spent doing each of 6 activities by migration tactic. Error bars report 1 standard error. There were no differences in any proportion of time spent in an activity between migratory tactics within an activity.

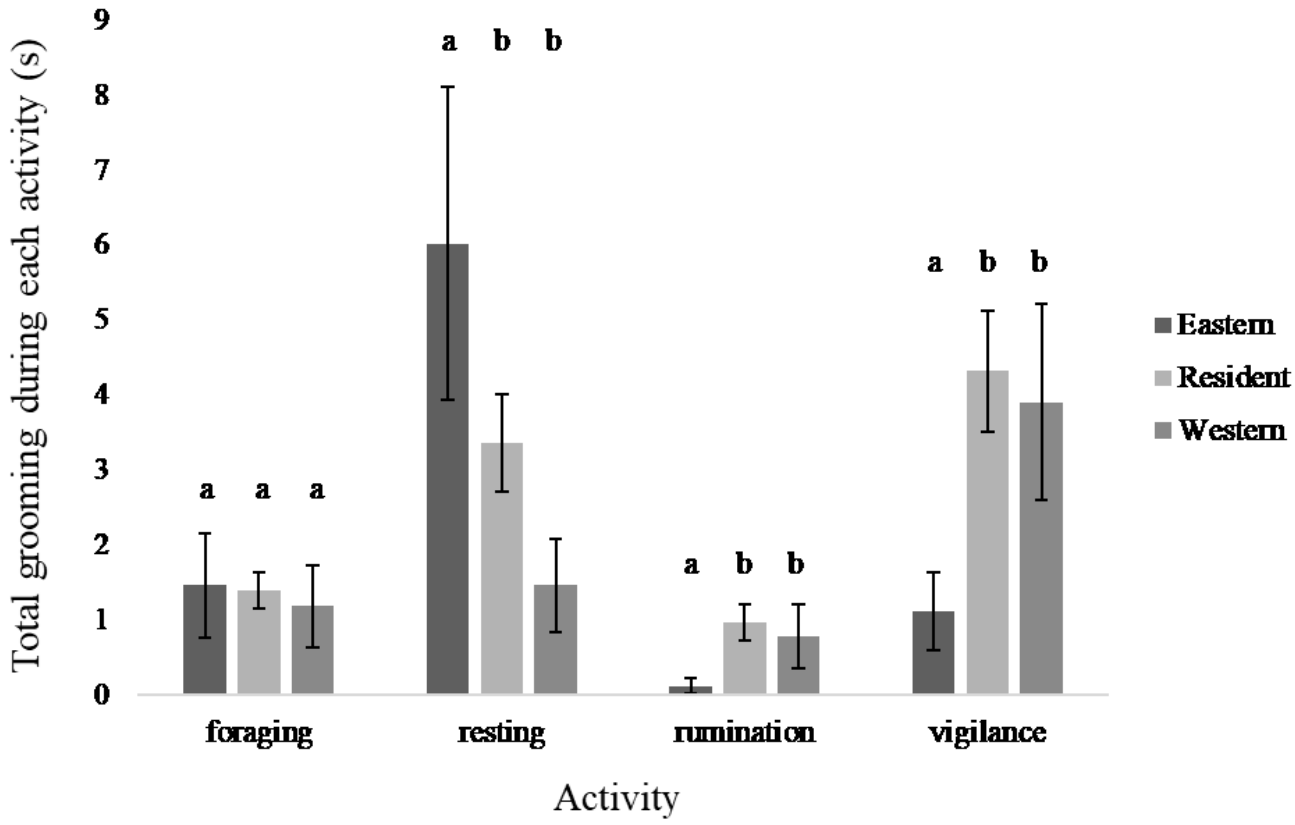

Figure 3.5. The total duration of grooming standardized to 15 minutes during each activity calculated as in Eq. 1. Error bars report 1 standard error. Significance (α=0.10) is designated with letters where a different letter indicates significant difference between migration tactics within an activity.

CHAPTER 4 — CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The elk population of the Ya Ha Tinda is an ideal study system to assess the role of partial migration in disease infection, because the long-term elk study provides background information on survival (Hebblewhite and Merrill, 2011), forage quality (Hebblewhite et al., 2008), predation (MacAulay, 2019; Robinson et al., 2010; Spilker, 2019), calf recruitment (Berg, 2019), and migration history (Eggeman et al., 2016; Hebblewhite et al., 2006; Killeen et al., 2016). In this thesis, I took the first steps in quantifying differences in parasite infection across migration tactics in the partially migratory elk population at the Ya Ha Tinda. I sought to expand on the previous studies by assessing differences in parasitism between shifting migration tactics. I used evidence for infestations of endo- and ecto-parasites and behaviours of elk at the Ya Ha Tinda to test hypotheses about the relationship between migration tactic and parasitism.

I did not find support for the hypothesis that elk escape parasites by migration as proposed by Loehle (1995). Instead, I found evidence for diversity and intensity of some parasites, such as liver flukes, being highest in migrants, which is most consistent with exposure to novel environments (Teitelbaum et al., 2018). In particular, high infestations in eastern migrants may result from earlier migration and use of wetland areas that increase their exposure to secondary hosts (i.e., snails) in both time and space. It is possible that western migrants overlapping with elk from the Bow Valley population on summer range played a role in the initial introduction of parasites into Banff National Park. Liver flukes were documented in western migrants of the Ya Ha Tinda elk population in 1962 by Flook and Stenton (1969) and in 2010 by Pruvot et al. (2016), but it may not have been until the recent increase in elk migrating eastward, to areas with higher secondary host habitat, that infestation levels increased to the high levels we report. It appears that warmer temperatures at low elevation have aggravated the levels

of liver flukes in addition to exposure to wetland secondary host habitat; elk use of areas with high forage, including wetlands, at low elevation, was associated with individuals with high intensity of liver flukes. In contrast the high forage quality western migrants were exposed to during the summer may have helped keep parasite infection in check across the diversity of species they were exposed to.

At the same time, eastern migrants also had higher tick infestations on winter range, as evident by higher hair loss, which I submit relates to overall tick infestation, despite the lack of correlation between the withers hair loss and ticks in the 20 elk captured in this study. Elk did not appear to trade-off foraging and rumination to groom; instead, grooming occurred most often when elk were resting and being vigilant. Trade-offs between vigilance and grooming may have subjected migrant elk to a disadvantage in terms of avoiding predators, because migrants spend more time vigilant in response to both natural predators and humans that they are not habituated to (Robinson and Merrill, 2013).

Although parasitism can directly affect survival, more common parasites cause subclinical effects that are hard to detect (Gunn and Irvine, 2016; Kortet et al., 2010). Similar to a "landscape of fear" (Laundré et al., 2010), recent studies also have suggested there may be a "landscape of disgust" where individuals alter their distribution and activities to mitigate disease infection (Buck et al., 2018; Weinstein et al., 2018). When compounded with other costs, subclinical effects may influence the relative fitness of individuals in partially migratory populations. Sublethal effects can impact body condition (Sánchez et al., 2018), reproduction (Hicks et al., 2019), and energy-budgets (Butler et al., 2018), depending on the specific parasite species (Budischak et al., 2016) with individual immunity altering susceptibility and tolerance of infection (Burgan et al., 2019). Western migrants have access to higher forage quality on the

summer range (Hebblewhite et al., 2008), which has the potential to increase immunocompetence (Coop and Kyriazakis, 1999), compared to lower forage quality in resident elk and higher calf survival in eastern migrant elk which can lead to increased costs of lactation (Berg, 2019). Given these differences, subclinical effects of parasites could impact the fitness of migration tactics differently across seasons and years.

Management Recommendations

Elk are an important game species across North America, but also locally at the Ya Ha Tinda for wildlife viewing and for hunting via a highly competitive draw system. The Ya Ha Tinda elk population has experienced both a population decline since the 2000s and a decline in migration over the past few decades, which is a common theme in Rocky Mountain elk populations (i.e., Phillips and Szkorupa, 2011). Shifts in these migratory patterns over the years have been studied with state-of the-art telemetry, but the impact of collars on individuals has not been evaluated as is true for most telemetry studies. Although neck hair loss did not correspond to irritation or lesions under the collar, and seasonal recovery of hair loss was evident, adverse effects to thermoregulation from neck hair loss in elk during winter may be a consideration because we found neck hair loss was greater than was expected due to ectoparasites alone. I recommend further studies to assess individual's collar fit using notes during collar attachment (i.e., number of fingers under the collar, etc.) and my approach to measuring hair loss to evaluate collar design and fit to rule out human-induced hair loss from collars.

Higher parasite prevalence and intensity in an increasing proportion of the population (i.e., eastern migrant female elk) could contribute to increasing population-level parasite infections or their spread to other populations east of Ya Ha Tinda depending on range overlap.

My study documented the distribution of parasites only in female elk, but bull elk collaring was initiated 2 years ago as part of the the Ya Ha Tinda long-term elk study (Martin et al., 2019). In 63 adult bulls whose feces I sampled at capture in January of 2018 and 2019, I found liver fluke egg prevalence (44% and 70%) and intensity (17 ± 23 eggs/2g and 44 ± 45 eggs/2g) were similar to eastern migrant female elk. High parasite levels in males are consistent with studies supporting higher parasite infection due to testosterone-mediated difference in immunity and variation in habitat use (Zuk and McKean, 1996). However, preliminary information on movements of collared bulls also indicate they may be exposed to liver fluke infection through use of wetland habitats east of the Ya Ha Tinda or in Banff National Park. Alternatively, bull elk may be more susceptible to parasites in the fall, compared to females, because of reduced body condition due to the rut (Bobek et al., 1990; Mitchell et al., 1976). Both Flook and Stenton (1969) and Pybus et al. (2015) reported similar prevalence in male and female elk at the Ya Ha Tinda and Banff National Park in the 1960s and 1980s, respectively. Pybus et al. (2015) found an average prevalence of 62% in male elk in the Bow Valley of Banff National Park between 1984 and 1991 which is similar to what we report across years in our study. I recommend the continued monitoring of parasite infection prevalence and intensity in bull elk along with other aspects of their ecology to obtain a complete picture when predicting hunting quotas and making management decisions.

Lastly, Parks Canada has conducted a baseline survey of parasite eggs in a herd of 36 plains bison (*Bison bison bison*) that were reintroduced into Banff National Park (2017 – present), concluding it is very unlikely that the reintroduced bison brought novel parasites to the Park (Normandeau, 2019). They collected and analysed bison feces prior to and immediately after their release in 2017, and during the summer of 2018. They also collected pellet samples

from other ungulates in the north eastern portion of Banff National Park, including the Ya Ha Tinda elk, to determine parasites present in feces and potential parasite groups for cross-transmission. I also recommend continued monitoring of bison parasites and their distribution across areas of the Park as the population expands, because they have the potential to influence intra and inter-specific parasite transmission in the ungulate community.

REFERENCES

Aikens, E.O., Kauffman, M.J., Merkle, J.A., Dwinnell, S.P.H., Fralick, G.L., Monteith, K.L., 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecol. Lett. 20, 741–750. https://doi.org/10.1111/ele.12772

Akinyi, M.Y., Jansen, D., Habig, B., Gesquiere, L.R., Alberts, S.C., Archie, E.A., 2019. Costs and drivers of helminth parasite infection in wild female baboons. J. Anim. Ecol. 1029–1043. https://doi.org/10.1111/1365-2656.12994

Albon, S.D., Stien, A., Irvine, R.J., Langvatn, R., Ropstad, E., Halvorsen, O., 2002. The role of parasites in the dynamics of a reindeer population. Proc. R. Soc. Biol. 269, 1625–1632. https://doi.org/10.1098/rspb.2002.2064

Allan, S.A., 2001. Ticks (Class Arachnida: Order Acarina), in: Parasitic Diseases of Wild Mammals, Second Edition. pp. 72–106.

Altizer, S., Bartel, R., Han, B.A., 2011. Animal migration and infectious disease risk. Science 331, 296–302. https://doi.org/10.1126/science.1194694

Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M., Rohani, P., 2006. Seasonality and the dynamics of infectious diseases. Ecol. Lett. 9, 467–484. https://doi.org/10.1111/j.1461-0248.2005.00879.x

Anderson, C.R., 2000. Nematode parasites of vertebrates: their development and transmission, 2nd ed. CABI Publishing, New York. https://doi.org/10.1017/CBO9781107415324.004

Barker, K.J., Mitchell, M.S., Proffitt, K.M., DeVoe, J.D., 2019. Land management alters traditional nutritional benefits of migration for elk. J. Wildl. Manage. 83, 167–174. https://doi.org/10.1002/jwmg.21564

Basir, M.., 1950. The morphology and development of the sheep nematode, *Strongyloides papillosus* (Wedl, 1856). Can. J. Res. 28, 173–196.

Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Bauer, S., Hoye, B.J., 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science (80). 344. https://doi.org/10.1126/science.1242552

Becklund, W.W., Senger, C.M., 1967. Parasites of *Ovis canadensis canadensis* in Montana, with a checklist of the internal and external parasites of the Rocky Mountain bighorn sheep in North America. J. Parasitol. 157–165.

Berg, J.E., 2019. Shifts in strategy: Calving and calf survival in a partially migratory elk population. University of Alberta.

Berg, J.E., Spilker, E., Killeen, J., Hebblewhite, M., Merrill, E.H., 2016. Ya Ha Tinda elk and predator studies: 2015-2016 update. Department of Biological Sciences, University of Alberta, Edmonton.

Berger, J., 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biol. Lett. 3, 620–623. https://doi.org/10.1098/rsbl.2007.0415

Bergeron, D.H., Pekins, P.J., 2014. Evaluating the usefulness of three indices for assessing winter tick abundance in northern New Hampshire. Alces 50, 1–15.

Bergstrom, R.C., 1975. Prevalence of *Dictyocaulus viviparus* infection in Rocky Mountain elk in Teton County, Wyoming. J. Wildl. Dis. 11, 40–44.

Bergstrom, R.C., Kass, T., 1982. Nematodes and nematodirosis, in: Diseases of Wildlife in Wyoming. pp. 199–201.

Bivand, R., Keitt, T., Rowlingson, B., 2019. rgdal: bindings for the "Geospatial" data abstraction library. R package version 1.4-4.

Bobek, B., Perzanowski, K., Weiner, J., 1990. Energy expenditure for reproduction in male red deer. J. Mammal. 71, 230–232.

Brambilla, A., von Hardenberg, A., Kristo, O., Bassano, B., Bogliani, G., 2013. Don't spit in the soup: Faecal avoidance in foraging wild Alpine ibex, *Capra ibex*. Anim. Behav. 86, 153–158. https://doi.org/10.1016/j.anbehav.2013.05.006

Brook, R.K., 2010. Habitat selection by parturient elk (*Cervus elaphus*) in agricultural and forested landscapes. Can. J. Zool. 88, 968–976. https://doi.org/10.1139/Z10-061

Brooks, C., Bonyongo, C., Harris, S., 2008. Effects of global positioning system collar weight on zebra behavior and location error. J. Wildl. Manage. 72, 527–534. https://doi.org/10.2193/2007-061

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.

Buck, J.C., Weinstein, S.B., Young, H.S., 2018. Ecological and evolutionary consequences of parasite avoidance. Trends Ecol. Evol. 33, 619–632. https://doi.org/10.1016/j.tree.2018.05.001

Budischak, S.A., Jolles, A.E., Vanessa, O., 2016. Differential host responses to parasitism shape divergent fitness costs of infection. Anim. Physiol. Ecol. 0–2. https://doi.org/10.1111/ijlh.12426

Bunnefeld, N., Börger, L., Van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J., Ericsson, G., 2011. A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. J. Anim. Ecol. 80, 466–476. https://doi.org/10.1111/j.1365-2656.2010.01776.x

Burgan, S.C., Gervasi, S.S., Johnson, L.R., Martin, L.B., 2019. How individual variation in host tolerance affects competence to transmit parasites. Physiol. Biochem. Zool. 92, 49–57. https://doi.org/10.1086/701169

Butler, A., Daunt, F., Newell, M., Hicks, O., Ito, M., Sato, K., Burthe, S.J., Green, J.A., 2018. The energetic cost of parasitism in a wild population. Proc. R. Soc. B Biol. Sci. 285, 20180489. https://doi.org/10.1098/rspb.2018.0489

Carlsson, A.M., Justin Irvine, R., Wilson, K., Piertney, S.B., Halvorsen, O., Coulson, S.J., Stien, A., Albon, S.D., 2012. Disease transmission in an extreme environment: Nematode parasites infect reindeer during the Arctic winter. Int. J. Parasitol. 42, 789–795. https://doi.org/10.1016/j.ijpara.2012.05.007

Chapman, B.B., Brönmark, C., Nilsson, J.Å., Hansson, L.A., 2011. The ecology and evolution of partial migration. Oikos 120, 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x

Christensen, R.H.B., 2019. ordinal - regression models for ordinal data. R package version 2019.4-25.

Churcher, T.S., Ferguson, N.., Basanez, M.G., 2005. Density dependence and overdispersion in the transmission of helminth parasites. Parasitology 131, 121–132. https://doi.org/10.1017/S0031182005007341

Cid, B., Costa, R.D.C., Balthazar, D.D.A., Augusto, A.M., Pires, A.S., Fernandez, F.A.S., 2013. Preventing injuries caused by radiotelemetry collars in reintroduced red-rumped agoutis, *Dasyprocta leporina* (Rodentia : Dasyproctidae), in Atlantic Forest, southeastern Brazil. Zoologia 30, 115–118.

Cook, R.C., Cook, J.G., Mech, L.D., 2004. Nutritional condition of Northern Yellowstone elk. J. Mammal. 85, 714–722.

Cook, R.C., Cook, J.G., Stephenson, T.R., Myers, W.L., Mccorquodale, S.M., Vales, D.J., Irwin, L.L., Hall, P.B., Spencer, R.D., Murphie, S.L., Schoenecker, K.A., Miller, P.J., 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. J. Wildl. Manage. 74, 880–896. https://doi.org/10.2193/2009-031

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: A mechanistic approach to ecology. Trends Ecol. Evol. 19, 334–343. https://doi.org/10.1016/j.tree.2004.04.003

Coop, R.L., Kyriazakis, I., 1999. Nutrition – parasite interaction. Vet. Parasitol. 84, 187–204.

Crowell-Davis, S.L., Houpt, K.A., Carnevale, J., 1985. Feeding and drinking behavior of mares and foals with free access to pasture and water. J. Anim. Sci. 60, 883–889. https://doi.org/10.2527/jas1985.604883x

Davidson, R.K., Ličina, T., Gorini, L., Milner, J.M., 2015. Endoparasites in a Norwegian moose (*Alces alces*) population - Faunal diversity, abundance and body condition. Int. J. Parasitol. Parasites Wildl. 4, 29–36. https://doi.org/10.1016/j.ijppaw.2014.12.005

DeBruyn, N.P. De, 2010. Gastrointestinal nematodes of western Canadian cervids: Molecular diagnostics, baselines and management considerations. University of Calgary.

Dies, K.H., Coupland, R.W., 2001. Prevalence of gastrointestinal helminths in domestic bison herds in northwestern Alberta. Can. Vet. J. 42, 295–296.

Dikmans, G., 1931. Two new species of nematode worms of the genus *Ostertagia* from the Virginia deer, with a note on *Ostertagia lyrata*. Proc. United States Natl. Museum.

Dinno, A., 2017. dunn.test: Dunn's test of multiple comparisons using rank sums. R package version 1.3.5.

Drew, M.L., Samuel, W.M., 1987. Reproduction of the winter tick, *Dermacentor albipictus*, under field conditions in Alberta, Canada. Can. J. Zool. Can. Zool. 65, 2583–2588. https://doi.org/10.1139/z87-391

Drew, M.L., Samuel, W.M., 1985. Factors affecting transmission of larval winter ticks, *Dermacentor albipictus*, to moose, *Alces alces* L., in Alberta, Canada. J. Wildl. Dis. 21, 274–282.

Dunkel, A.M., Rognlie, M.C., Johnson, G.R., Knapp, S.E., 1996. Distribution of potential intermediate hosts for *Fasciola hepatica* and *Fascioloides magna* in Montana, USA. Vet. Parasitol. 62, 63–70. https://doi.org/10.1016/0304-4017(95)00859-4

Durden, L.A., 2001. Lice (Phthiraptera), in: Parasitic Diseases of Wild Mammals, Second Edition. pp. 3–17.

Durette-Desset, M.C., Samuel, W.M., 1992. Nematodirinae (Nematoda: Trichostrongyloidea) chez l'Oreamnos americanus en Alberta, Canada, description du Nematodirus becklundi sp. nov. Can. J. Zool. 70, 212–219.

Durette-Desset, M.C., Samuel, W.M., 1989. Nematodirinae (Nematoda: Trichostrongyloidea) d'Antilocapra et d'Ovis en Alberta, Canada. Ann. Parasitol. Hum. comparée 64, 469–477.

Duszynski, D.W., Upton, S.J., 2001. Enteric Protozoans: Cyclospora, *Eimeria*, Isospora, and *Cryptosporidium* spp. Parasit. Dis. Wild Mammals, Second Ed. 416–459. https://doi.org/10.1002/9780470377000.ch16c

Edwards, B.C., 2013. Home ranges, resource selection, and parasite diversity of urban versus rural elk (*Cervus elaphus*). Univ. Calgary.

Eggeman, S.L., Hebblewhite, M., Bohm, H., Whittington, J., Merrill, E.H., 2016. Behavioural flexibility in migratory behaviour in a long-lived large herbivore. J. Anim. Ecol. 85, 785–797. https://doi.org/10.1111/1365-2656.12495

Erhardova-Kotrla, B., 1971. Occurrence of *Fascioloides magna* (Bassi, 1875) in Czechoslovakia. Food Agric. Organ. United Nations.

Flook, D., Stenton, J.E., 1969. Incidence and abundance of certain parasites in wapiti in the national parks of the Canadian Rockies. Can. J. Zool. 47, 795–803.

Flowers, M.J., 2019. The Waiting Game: Elk avoid predator encounters at fine spatial scales. University of Alberta.

Folstad, I., Nilssen, A.C., Halvorsen, O., Andersen, J., 1991. Parasite avoidance: the cause of post-calving migrations in Rangifer? Can. J. Zool. 69, 2423–2429. https://doi.org/10.7557/2.10.3.862

Foreyt, J., 1996. Mule Deer (*Odocoileus Hemionus*) and elk (Cervus elaphus) as experimental definitive hosts for Fascioloides magna. October 32.

Fortin, D., Boyce, M.S., Merrill, E.H., 2004. Multi-tasking by mammalian herbivores: overlapping processes during foraging. Ecology 85, 2312–2322.

Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J., Pedrotti, L., 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philos. Trans. R. Soc. B Biol. Sci. 365, 2187–2200. https://doi.org/10.1098/rstb.2010.0084

Fritzsche McKay, A., Hoye, B.J., 2016. Are migratory animals superspreaders of infection? Integr. Comp. Biol. 56, 260–267. https://doi.org/10.1093/icb/icw054

Gibeau, M.L., Clevenger, A.P., Herrero, S., Wierzchowski, J., 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. Biol. Conserv. 103, 227–236.

Glines, M. V., Samuel, W.M., 1989. Effect of Dermacentor albipictus (Acari: Ixodidae) on blood composition, weight gain and hair coat of moose, *Alces alces.* Exp. Appl. Acarol. 6, 197–213. https://doi.org/10.1007/BF01193980

Glines, M. V., Samuel, W.M., 1984. Development of the winter tick, *Dermacentor albipictus*, and its effect on the hair coat of moose, *Alces alces*, of central Alberta, Canada. Acarology 1208–1214.

Graesser, F.E., 1957. Lungworm disease of cattle in Alberta. Can. J. Comp. Med. 21, 355–358.

Gunn, A., Irvine, R.J., 2016. Subclinical parasitism and ruminant foraging strategies-a review. Wildl. Soc. Bull. 31, 117–126.

Hart, B.L., 1995. Differential grooming rate and tick ioad of territorial male and female impala, *Aepyeeres metampas* 6, 94–101.

Hart, B.L., Hart, L.A., Mooring, M.S., Olubayo, R., 1992. Biological basis of grooming behaviour in antelope: the body-size, vigilance and habitat principles. Anim. Behav. 44, 615–631. https://doi.org/10.1016/S0003-3472(05)80290-8

Hebblewhite, M., 2006. Linking predation risk and forage to ungulate population dynamics. Univ. Alberta.

Hebblewhite, M., Haydon, D.T., 2010. Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. Philos. Trans. R. Soc. B Biol. Sci. 365, 2303–2312. https://doi.org/10.1098/rstb.2010.0087

Hebblewhite, M., Merrill, E., McDermid, G., 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecol. Monogr. 78, 141–166. https://doi.org/10.1890/06-1708.1

Hebblewhite, M., Merrill, E.H., 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. Oikos 120, 1860–1870. https://doi.org/10.1111/j.1600-0706.2011.19436.x

Hebblewhite, M., Merrill, E.H., Morgantini, L.E., White, C. a., Allen, J.R., Bruns, E., Thurston, L., Hurd, T.E., 2006. Is the migratory behavior of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildl. Soc. Bull. 34, 1280–1294. https://doi.org/10.2193/0091-7648(2006)34[1280:ITMBOM]2.0.CO;2

Hegemann, A., Fudickar, A.M., Nilsson, J., 2019. A physiological perspective on the ecology and evolution of partial migration. J. Ornithol. https://doi.org/10.1093/femsre/fux056/4644831

Hicks, O., Green, J.A., Daunt, F., Cunningham, E., Newell, M., Butler, A., Burthe, S.J., 2019. Sub-lethal effects of natural parasitism operate through maternal not paternal reproductive success in a wild population. Ecology e02772. https://doi.org/10.1002/ecy.2772

Hijmans, R.J., 2019. raster: Geographic data analysis and modeling. R package version 2.9-23.

Hoberg, E.P., Kocan, A.A., Rickard, L.G., 2001. Gastrointestinal strongyles in wild ruminants, in: Parasitic Diseases of Wild Mammals, Second Edition. pp. 193–227.

Hopkins, M.E., Milton, K., 2016. Adverse effects of ball-chain radio-collars on female mantled howlers (*Alouatta palliata*) in Panama. Int. J. Primatol. 37, 213–224. https://doi.org/10.1007/s10764-016-9896-y

Horback, K.M., Miller, L.J., Andrews, J., Kuczaj, S.A., Anderson, M., 2012. The effects of GPS collars on African elephant (*Loxodonta africana*) behavior at the San Diego Zoo Safari Park. Appl. Anim. Behav. Sci. 142, 76–81. https://doi.org/10.1016/j.applanim.2012.09.010

Hughes, J., Albon, S.D., Irvine, R.J., Woodin, S., 2009. Is there a cost of parasites to caribou? Parasitology 136, 253–65. https://doi.org/10.1017/S0031182008005246

Ironside, K.E., Mattson, D.J., Arundel, T.R., Hansen, J.R., 2017. Is GPS telemetry location error screening beneficial? Wildlife Biol. 2017, 1–7. https://doi.org/10.2981/wlb.00229

Irvine, R.J., Corbishley, H., Pilkington, J.G., Albon, S.D., 2006. Low-level parasitic worm burdens may reduce body condition in free-ranging red deer (*Cervus elaphus*). Parasitology 133, 465–475. https://doi.org/10.1017/S0031182006000606

Isenstein, R.S., 1963. The life history of *Cooperia oncophora* (Railliet, 1898), a nematode parasite of cattle. J. Parasitol. 49, 235–240.

Jore, S., Viljugrein, H., Hofshagen, M., Brun-Hansen, H., Kristoffersen, A.B., Nygård, K., Brun, E., Ottesen, P., Sævik, B.K., Ytrehus, B., 2011. Multi-source analysis reveals latitudinal and altitudinal shifts in range of *Ixodes ricinus* at its northern distribution limit. Parasites and Vectors 4, 1–11.

Kates, K.C., Turner, J.S., 1955. Observations of the life cycle of *Nematodirus spathiger*, a nematode parasitic in the intestine of sheep and other ruminants. Am. J. Vet. Res. 16, 105–115.

Keiss, R.E., 1969. Comparison of eruption-wear patterns and cementum annuli as age criteria in elk. J. Wildl. Manage. 33, 175–180.

Killeen, J., Merrill, E.H., H, B., S, E., J, B., Hebblewhite, M., 2016. Migration patterns of the Ya Ha Tinda elk herd, 2002-2014. Department of Biological Sciences, University of Alberta, Edmonton.

Kołodziej-Sobocińska, M., 2019. Factors affecting the spread of parasites in populations of wild European terrestrial mammals. Mammal Res. https://doi.org/10.1007/s13364-019-00423-8

Koprivnikar, J., Leung, T.L.F., 2015. Flying with diverse passengers: Greater richness of parasitic nematodes in migratory birds. Oikos 124, 399–405. https://doi.org/10.1111/oik.01799

Kortet, R., Hedrick, A. V., Vainikka, A., 2010. Parasitism, predation and the evolution of animal personalities. Ecol. Lett. 13, 1449–1458. https://doi.org/10.1111/j.1461-0248.2010.01536.x

Kranstauber, B., Kays, R., Lapoint, S.D., Wikelski, M., Safi, K., 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. J. Anim. Ecol. 81, 738–746. https://doi.org/10.1111/j.1365-2656.2012.01955.x

Kranstauber, B., Smolla, M., Scharf, A.K., 2019. move: visualizing and analyzing animal track data. R package version 3.2.0.

Krausman, P.R., Bleich, V.C., Cain, J.W., Stephenson, T.R., Deyoung, D.W., Mcgrath, P.W., Swift, P.K., Pierce, B.M., Jansen, B.D., 2004. Neck lesions in ungulates from collars incorporating satellite technology. Wildl. Soc. Bull. 32, 987–991.

Kutz, S.J., Checkley, S., Verocai, G.G., Dumond, M., Hoberg, E.P., Peacock, R., Wu, J.P., Orsel, K., Seegers, K., Warren, A.L., Abrams, A., 2013. Invasion, establishment, and range expansion of two parasitic nematodes in the canadian arctic. Glob. Chang. Biol. 19, 3254–3262. https://doi.org/10.1111/gcb.12315

Kutz, S.J., Ducrocq, J., Verocai, G.G., Hoar, B.M., Colwell, D.D., Beckmen, K.B., Polley, L., Elkin, B.T., Hoberg, E.P., 2012. Parasites in ungulates of arctic North America and Greenland. A view of contemporary diversity, ecology, and impact in a world under change, Advances in Parasitology. 79, 99-252

Kutz, S.J., Jenkins, E.J., Veitch, A.M., Ducrocq, J., Polley, L., Elkin, B., Lair, S., 2009. The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host-parasite interactions. Vet. Parasitol. 163, 217–228. https://doi.org/10.1016/j.vetpar.2009.06.008

Lankester, M.W., Peterson, W.J., 1996. The possible importance of wintering yards in the transmission of *Parelaphostrongylus tenuis* to white-tailed deer and moose. J. Wildl. Dis. 32, 31–38. https://doi.org/10.7589/0090-3558-32.1.31

Laundré, J.W., Hernandez, L., Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. Open Ecol. J. 3, 1–7. https://doi.org/10.2174/1874213001003030001

Leung, T.L.F., Koprivnikar, J., 2016. Nematode parasite diversity in birds: the role of host ecology, life history and migration. J. Anim. Ecol. 85, 1471–1480. https://doi.org/10.1111/1365-2656.12581

Levine, N.D., 1980. Nematode parasites of domestic animals and man, 2nd ed. Burgess Publishing Co., Minneapolis.

Lichtenfels, J.R., Pilitt, P.A., Hoberg, E.P., 1994. New morphological characters for identifying individual specimens of *Haemonchus* spp.(Nematoda: Trichostrongyloidea) and a key to species in ruminants of North America. J. Parasitol. 107–119.

Licina, T., 2014. Gastrointestinal parasites in moose (*Alces alces*) - which ones and what consequences? Hedmark Univ. Coll.

Loehle, C., 1995. Social barriers to pathogen transmission in wild animal populations. Ecology 76, 326–335.

MacAulay, K.M., 2019. Spatial mortality risk for elk (*Cervus elaphus*) in a multi-predator community on the Rocky Mountain East Slopes, Alberta. University of Alberta.

Martin, H., Hebblewhite, M., Normandeau, J., Hessami, M., Flowers, M., Trottier, M., Merrill, E.H., 2019. Ya Ha Tinda elk and predator study: Annual report 2018-2019. Wildlife Biology Program, University of Montana, Missoula; Deprtment of Biological Sciences, University of Alberta, Edmonton.

McLaughlin, R.F., Addison, E.M., 1986. Tick (*Dermacentor albipictus*)-induced winter hair-loss in captive moose (Alces alces). J. Wildl. Dis. 22, 502–510. https://doi.org/10.7589/0090-3558-22.4.502

McTaggart - Cowan, I., 1951. Nematode parasites of vertebrates: their development and transmission.

Mehlhorn, H., 2015. Encyclopedia of Parasitology. Springer Science & Business Media. https://doi.org/10.1007/978-3-662-43978-4

Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D., Oates, B.A., Sawyer, H., Scurlock, B.M., Kauffman, M.J., 2016. Large herbivores surf waves of green-up in spring. Proc. R. Soc. B 283, 20160456. https://doi.org/10.1098/rspb.2016.0456

Mitchell, B., McCowan, D., Nicholson, I.A., 1976. Annual cycles of body weight and condition in Scottish Red deer, *Cervus elaphus*. J. Zool. 180, 107–127. https://doi.org/10.1111/j.1469-7998.1976.tb04667.x

Moll, R.J., Millspaugh, J.J., Beringer, J., Sartwell, J., Woods, R.J., Vercauteren, K.C., 2009. Physiological stress response of captive white-tailed deer to video collars. J. Wildl. Manage. 73, 609–614. https://doi.org/10.2193/2008-266

Monnig, H.O., 1947. Veterinary Helminthology and Entomology: the diseases of domesticated animals caused by helminth and arthropod parasites. Baltimore.

Mooring, M.S., 1995. The effect of tick challenge on grooming rate by impala. Anim. Behav. 50, 377–392. https://doi.org/10.1006/anbe.1995.0253

Mooring, M.S., Hart, B.L., 1995. Costs of allogrooming in impala: Distraction from vigilance. Anim. Behav. 49, 1414–1416. https://doi.org/10.1006/anbe.1995.0175

Mooring, M.S., Samuel, W.M., 1999. Premature loss of winter hair in free-ranging moose (*Alces alces*) infested with winter ticks (*Dermacentor albipictus*) is correlated with grooming rate. Can. J. Zool. 77, 148–156. https://doi.org/10.1139/cjz-77-1-148

Mooring, M.S., Samuel, W.M., 1998. Tick-removal grooming by elk (*Cervus elaphus*): testing the principles of the programmed-grooming hypothesis. Can. J. Zool. 76, 740–750. https://doi.org/10.1139/z97-247

Morgantini, L.E., Hudson, R.J., 1988. Migratory patterns of the wapiti, *Cervus elaphus*, in Banff National Park, Alberta. Can. F. Nat. 102, 12–19.

Mulvey, M., Aho, J.M., 1993. Parasitism and mate competition: Liver flukes in white-tailed deer. Oikos 87, 185–190.

Mulvey, M., Aho, J.M., Rhodes, O.E., 1994. Parasitism and White-Tailed Deer: Timing and Components of Female Reproduction. Oikos 70, 177–182.

Musiani, M., Morshed Anwar, S., McDermid, G.J., Hebblewhite, M., Marceau, D.J., 2010. How humans shape wolf behavior in Banff and Kootenay National Parks, Canada. Ecol. Modell. 221, 2374–2387. https://doi.org/10.1016/j.ecolmodel.2010.06.019

Mysterud, A., Qviller, L., Meisingset, E.L., Viljugrein, H., 2016. Parasite load and seasonal migration in red deer. Oecologia 180, 401–407. https://doi.org/10.1007/s00442-015-3465-5

Narsapur, V.S., Prokopic, J., 1979. The influence of temperature on the development of *Moniezia expansa* (Rudolphi, 1810) in oribatid mites. Folia Parasitol. (Praha). 26, 239–243.

Navarro-Gonzalez, N., Verheyden, H., Hoste, H., Cargnelutti, B., Lourtet, B., Merlet, J., Daufresne, T., Lavín, S., Hewison, A.J.M., Morand, S., Serrano, E., 2010. Diet quality and immunocompetence influence parasite load of roe deer in a fragmented landscape. Eur. J. Wildl. Res. 57, 639–645. https://doi.org/10.1007/s10344-010-0474-x

Normandeau, J., 2019. Ungulate fecal parasite baseline survey prior to bison reintroduction in Banff National Park. Park Canada Banff Bison Reintroduction Project.

O'Connor, L.J., Walkden-Brown, S.W., Kahn, L.P., 2006. Ecology of the free-living stages of major trichostrongylid parasites of sheep. Vet. Parasitol. 142, 1–15. https://doi.org/10.1016/j.vetpar.2006.08.035

Okansanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: community ecology package. R package version 2.5-5.

Olsen, O.W., 1944. Bionomics of Lymnaeid snail *Stagnicola bulimoides techella*, the intermediate host of the liver fluke in southern Texas. J. Agric. Res. 69, 387–403.

Phillips, B., Szkorupa, T., 2011. East Kootenay elk monitoring project. Fish and Wildlife Branch, Province of British Columbia, Cranbrook.

Pruvot, M., Lejeune, M., Kutz, S., Hutchins, W., Musiani, M., Massolo, A., Orsel, K., 2016. Better alone or in ill company? The effect of migration and inter-species comingling on *Fascioloides magna* infection in elk. PLoS One 11, 1–16. https://doi.org/10.1371/journal.pone.0159319

Pybus, M.J., 2001. Liver Flukes, in: Parasitic Diseases of Wild Mammals, Second Edition. pp. 121–149.

Pybus, M.J., 1990. Survey of hepatic and pulmonary helminths of wild cervids in Alberta, Canada. J. Wildl. Dis. 26, 453–459.

Pybus, M.J., Butterworth, E.W., Woods, J.G., 2015. An expanding population of the giant liver fluke (*Fascioloides magna*) in elk (*Cervus canadensis*) and other ungulates in Canada. J. Wildl. Dis. 51, 431–445. https://doi.org/10.7589/2014-09-235

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasiulis, A.L., Festa-Bianchet, M., Couturier, S., Côté, S.D., 2014. The effect of radio-collar weight on survival of migratory caribou. J. Wildl. Manage. 78, 953–956. https://doi.org/10.1002/jwmg.722

Risely, A., Klaassen, M., Hoye, B.J., 2017. Migratory animals feel the cost of getting sick: A meta-analysis across species. J. Anim. Ecol. 301–314. https://doi.org/10.1111/1365-2656.12766

Robinson, B.G., Hebblewhite, M., Merrill, E.H., 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? Oecologia 164, 265–275. https://doi.org/10.1007/s00442-010-1620-6

Robinson, B.G., Merrill, E.H., 2013. Foraging-vigilance trade-offs in a partially migratory population: Comparing migrants and residents on a sympatric range. Anim. Behav. 85, 849–856. https://doi.org/10.1016/j.anbehav.2013.02.004

Samson, J., Holmes, J.C., Jorgenson, J.T., Wishart, W.D., 1987. Experimental infections of free-ranging Rocky Mountain bighorn sheep with lungworms (*Protostrongylus* spp.; Nematoda: Protostrongylidae). J. Wildl. Dis. 23, 396–403. https://doi.org/10.7589/0090-3558-23.3.396

Samuel, C.E., Farris, D.A., 1977. Mechanism of interferon action Kinetics of interferon action in mouse L929 cells: Translation inhibition, protein phosphorylation, and messenger RNA methylation and degradation. Virology 83, 56–71.

Samuel, W.M., 2007. Factors affecting epizootics of winter ticks and mortality of moose. Alces 43, 39–48.

Samuel, W.M., 2004. White as a ghost: Winter ticks and moose. The Federation of Alberta Naturalists, Edmonton.

Samuel, W.M., 1991. Grooming by moose (*Alces alces*) infested with the winter tick, Dermacentor albipictus (Acari): a mechanism for premature loss of winter hair. Can. J. Zool. 69, 1255–1260.

Samuel, W.M., Mooring, M.S., 1998. Tick defense strategies in bison: The role of grooming and hair coat. Behaviour 135, 693–718.

Samuel, W.M., Welch, D.A., Smith, B.L., 1991. Ectoparasites from elk (*Cervus elaphus nelsoni*) from Wyoming. J. Wildl. Dis. 27, 446–451.

Sánchez, C.A., Becker, D.J., Teitelbaum, C.S., Barriga, P., Brown, L.M., Majewska, A.A., Hall, R.J., Altizer, S., 2018. On the relationship between body condition and parasite infection in wildlife: a review and meta-analysis. Ecol. Lett. https://doi.org/10.1111/ELE.13160

Satterfield, D.A., Marra, P.P., Sillett, T.S., Altizer, S., 2018. Responses of migratory species and their pathogens to supplemental feeding. Philos. Trans. R. Soc. B Biol. Sci. 373. https://doi.org/10.1098/rstb.2017.0094

Sawyer, H., Kauffman, M.J., 2011. Stopover ecology of a migratory ungulate. J. Anim. Ecol. 80, 1078–1087. https://doi.org/10.1111/j.1365-2656.2011.01845.x

Schmitz, O.J.., Nudds, T.D.., 1994. Parasite-mediated competition in deer and moose: how strong is the effect of meningeal worm on moose? Ecol. Appl. 4, 91–103.

Scholander, P.F., Walters, V., Hock, R., Irving, L., 1950. Body insulation of some arctic and tropical mammals and birds. Biol. Bull. 99, 225–236.

Shannon, G., Cordes, L.S., Hardy, A.R., Angeloni, L.M., Crooks, K.R., 2014. Behavioral responses associated with a human-mediated predator shelter. PLoS One 9. https://doi.org/10.1371/journal.pone.0094630

Shaw, A.K., Binning, S.A., 2016. Migratory recovery from infection as a selective pressure for the evolution of migration. Am. Nat. 187, 491–501. https://doi.org/10.1086/685386

Shaw, A.K., Sherman, J., Barker, F.K., Zuk, M., Shaw, A.K., 2018. Metrics matter: the effect of parasite richness , intensity and prevalence on the evolution of host migration. Proc. R. Soc. B 285, 20182147.

Sine, M., Morris, K., Knupp, D., 2009. Assessment of a line transect field method to determine winter tick abundance on moose. Alces 45, 2–3.

Smolko, P., 2014. Ekologia parcialne migrujcich populacii jelena lesneho (*Cervus elpahus*). Technicka Univerzita Vo Zvolene.

Spilker, E., 2019. Spatial predation risk and interactions within a predator community on the Rocky Mountains East Slopes, Alberta. University of Alberta.

Spruijt, B.M., van Hooff, J.A., Gispen, W.H., 1992. Ethology and neurobiology of grooming behavior. Physiol. Rev. 72, 825–852. https://doi.org/10.1152/physrev.1992.72.3.825

Steinberg, B., 2008. Algonquin Park moose hair-loss survey report 2008. Algonquin Provincial Park, Ontario.

Stock, T. M., Barrett, M.W., 1983. Helminth parasites of the gastrointestinal tracts and lungs of moose (Alces alces) and wapiti (*Cervus elaphus*) from Cypress Hills, Alberta, Canada. Proc. Helminthol. Soc. Wash. 50, 246–251.

Swales, W.E., 1935. The life cycle of *Fascioloides magna* (bassi, 1875), the large liver fluke of ruminants, in Canada: With observations on the bionomics of the larval stages and the intermediate hosts, pathology of Fascioloidiasis magna, and control measures. Can. J. Res. 12, 177–215.

Teitelbaum, C.S., Huang, S., Hall, R.J., Altizer, S., 2018. Migratory behavior predicts greater parasite diversity in ungulates. Proc. R. Soc. B Biol. Sci. 285, 20180089. https://doi.org/10.1098/rspb.2018.0089

Thapar, G.S., Singh, K.S., 1954. Studies on the life-history of *Trichuris ovis* (Abligaard, 1795). Proc. Indian Acad. Sci. - Sect. B 40, 69–88.

Tomkiewicz, S.M., Fuller, M.R., Kie, J.G., Bates, K.K., 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philos. Trans. R. Soc. B Biol. Sci. 365, 2163–2176. https://doi.org/10.1098/rstb.2010.0090

Tompkins, D.M., Begon, M., 1999. Parasites can regulate wildlife populations. Parasitol. Today 15, 311–313.

Uhazy, L.S., Holmes, J.C., 1971. Helminths of the Rocky Mountain bighorn sheep in western Canada. Can. J. Zool. 49, 507–512.

Vanderwaal, K.L., Windels, S.K., Olson, B.T., Vannatta, J.T., Moen, R., 2015. Landscape influence on spatial patterns of meningeal worm and liver fluke infection in white-tailed deer. Parasitology 142, 706–718. https://doi.org/10.1017/S0031182014001802

Vannatta, J.T., 2016. The giant liver fluke: A review, intermediate host habitat, and infection in a white-tailed deer population in Minnesota. Univ. Minnesota.

Walker, M.L., Becklund, W.W., 1970. Checklist of the internal and external parasities of deer, *Odocoileus hemionus* and *O. virginianus*, in the United States and Canada. Beltsville.

Weinstein, B.S.B., Buck, J.C., Young, H.S., 2018. A landscape of disgust. Science (80-.). 359, 1213–1215.

Welch, D.A., Samuel, W.M., Hudson, R.J., 1990. Bioenergetic consequences of alopecia induced by *Dermacentor albipictus* (Acari: Ixodidae) on moose. J. Med. Entomol. 27, 656–660. https://doi.org/10.1093/jmedent/27.4.656

Welch, D.A., Samuel, W.M., Wilke, C.J., 1991. Suitability of moose, elk, mule deer, and white-tailed deer as hosts for winter ticks (*Dermacentor albipictus*). Can. J. Zool. 69, 2300–2305.

Woods, J.G., 1991. Ecology of a partially migratory elk population. University of British Columbia.

Yee, T.W., 2010. The VGAM package for categorical data analysis. J. Stat. Softw. 32, 1–34.

Zuk, M., McKean, K.A., 1996. Sex differences in parasite infections: Patterns and processes. Int. J. Parasitol. 26, 1009–1024. https://doi.org/10.1016/S0020-7519(96)00086-0

Appendix A – Review of Elk Parasites in Alberta

Elk in Alberta can be infected by two main groups of parasites: ectoparasites and endoparasites (Table A-1). The major ectoparasites in elk are winter ticks (*Dermacentor albipictus*) and biting lice (*Damalinia concavifrons*), which cannot be sampled in feces. Both winter tick and biting lice have a wide geographic distribution, with high abundance in mountain areas including Banff National Park (Flook and Stenton, 1969). Ticks and lice can have a one to three host life cycle. *D. concavifrons* is the only parasite of elk transmitted by direct contact, transferring from one individual to another when elk are in close proximity. Mating occurs on the host with subsequent deposition of eggs by the female and an average generation time of 45 days (Durden, 2001). In contrast, *D. albipictus* is a large, one-host tick that is transmitted through the environment and completes its entire lifecycle of blood-feeding, molting, and mating on a single host (Allan, 2001). Gravid females drop off the host in April and oviposition on the ground begins in June, followed by larval development over the summer (Drew and Samuel, 1985). In September and October larvae ascend vegetation to attach to a new host (Drew and Samuel, 1985). Both *D. albipictus* and *D. concavifrons* can have adverse effects on the host at high infection levels by creating itching that leads to excessive grooming, especially in moose (Allan, 2001). Microclimate affects the infective tick larvae survival with a temperature-dependent larval development with a shorter incubation period in grassland compared to densely canopied aspen forests (Drew and Samuel, 1987).

Endoparasites of elk have a wide geographic distribution across North America and include nematodes (gastrointestinal worms or lungworms), cestodes (tapeworms), protozoa (single-celled parasites), and trematodes (liver flukes). All endoparasites of elk in Alberta are detectable in feces except for *Echinococcus granulosus*. Studies of clinical effects of

endoparasites on elk are very limited (Hoberg et al., 2001), however, *Fascioloides magna* has been shown to cause mortality in BNP elk (Pybus et al., 2015). Development of parasites with environmental life stages is highly contingent on optimal temperature conditions that differ for

Table A-1. Parasites of elk in Alberta, listed by location and collected by autopsy of dead elk or through collection of fecal samples. BNP is Banff National Park, KNP is Kootenay National Park, and WLNP is Waterton Lakes National Park. Parasite denotes the species or genus, collection shows where the elk came from, sampling methods are either autopsy or flotation of eggs from pellet samples, the organ is the area of the host infected by the parasites, and detected in feces shows whether eggs or larvae of the parasite can be detected in pellet samples.

Parasite	Collection Location in Alberta	Sampling Method	Organ in Elk	Detected In Feces?	Literature Source
		Ectoparasites			
Dermacentor albipictus	Ya Ha Tinda, BNP, KNP	Autopsy	Skin	No	Flook and Stenton, 1969
Damalinia concavifrons	BNP, KNP	Autopsy	Skin	No	Flook and Stenton, 1969
		Endoparasites			
Capillaria sp.	BNP	Fecal	Intestines	Yes	Edwards, 2013
Cooperia oncophora	Cypress Hills	Autopsy	Intestines	Yes	Stock and Barrett, 1983
Dictyocaulus viviparous	Ya Ha Tinda, BNP	Autopsy	Lungs	Yes	Flook and Stenton, 1969
Echinococcus granulosus	Ya Ha Tinda, BNP, JNP	Autopsy	Intestines	No	Bill Samuel
Eimeria sp.	Ya Ha Tinda	Autopsy	Intestines	Yes	Bill Samuel
Fascioloides magna	Ya Ha Tinda, WLNP, BNP, KNP	Autopsy, Fecal	Liver	Yes	Flook and Stenton, 1969; Pruvot et al., 2016; Edwards, 2013
Moniezia benedeni	Ya Ha Tinda	Autopsy	Intestines	Yes	Flook and Stenton, 1969; Bill Samuel
Nematodirella alcidis	Cypress Hills	Autopsy	Intestines	Yes	Stock and Barrett, 1983
Nematodirus helvetianus	Cypress Hills	Autopsy	Intestines	Yes	Stock and Barrett, 1983
Ostertagia sp.	Cypress Hills	Autopsy	Stomach	Yes	Stock and Barrett, 1983
Spiculopteragia boehmi	BNP	Fecal	Intestines	Yes	DeBruyn, 2010
Thysanosoma actinoides	BNP, KNP	Autopsy	Intestines	Yes	Flook and Stenton, 1969
Trichostrongylus axei	Ya Ha Tinda	Autopsy	Intestines	Yes	Bill Samuel
Trichuris sp.	Ya Ha Tinda, BNP	Autopsy, Fecal	Intestines	Yes	Bill Samuel; Edwards, 2013
Trichuris ovis	BNP	Autopsy	Intestines	Yes	Flook and Stenton, 1969

each parasite but remain around an average of 20°C and typically include enough moisture to avoid desiccation (Duszynski and Upton, 2001; Hoberg et al., 2001; Pybus, 2001). Only *F. magna* and Protostrongylidae require aquatic environments to complete their life cycle through secondary hosts (Hoberg et al., 2001; Pybus, 2001).

Nematodes (Gastrointestinal): Gastrointestinal nematodes have short development periods but are capable of arrested development or resistance to the cold. Research shows that gastrointestinal nematodes do not transmit below 8°C and are infective from mid-April through mid-October (Johnstone, 2000). *Trichuris sp.* is a member of the order Enoplida and has an infective first larval stage (L1), which develops inside the egg once feces are deposited into the environment where it is consumed along with vegetation (Kutz et al., 2012). Larvae are formed in around 20-35 days (Thapar and Singh, 1954). *Capillaria* sp., also of the order Enoplida, are found in the small intestine of ruminants. They have an incubation period of 1-2 weeks, a prepatent period of 2 months, and patency of up to 1 year (Mehlhorn, 2015). In the order Strongylida, *Ostertagia sp.* are stomach worms with the potential for arrested development and are among the most pathogenic strongyles in North America (Hoberg et al., 2001). Adults release eggs into host feces that develop in the environment into larvae with an infective third stage (L3) that when consumed has a 2-3 week prepatent period inside the host before signs of infection are displayed (Hoberg et al., 2001). Nematodirines are a family of strongyles that are thread-necked strongyles with an infective L3 that develop in the environment after fecal excretion for 3-4 weeks with a minimum prepatent period of 2-3 weeks in some species (Kates and Turner, 1955). The genus *Trichostrongylus* is characterized by an infective L3 developing in 7-9 days with a prepatent period of 15-23 days that can extend up to 15 months for *T. axei* (Hoberg et al., 2001; Levine, 1980). Similarly, *Cooperia sp.* are transmitted through the environment and *C.*

oncophora take around five days to develop from eggs to larvae with a 17-22 day prepatent period (Isenstein, 1963). *Spiculopteragia boehmi*, has a short infective cycle of 2-3 weeks (O'Connor et al., 2006)O and is an introduced parasite in the Banff elk population and was detected in 12% of Banff elk fecal samples (DeBruyn, 2010). Lastly, *Strongyloides sp.* have an infective L3 female larvae that are excreted in host feces as eggs and develop on the pasture or assume a free-living stage that mate to produce more infective L3 females (Basir, 1950). Prepatent period is 7-9 days and larvae can enter through ingestion during foraging or skin penetration (Basir, 1950). Short prepatent periods of gastrointestinal nematodes from days to around a month mean that infection is likely occur during the current season.

Nematodes (Lungworms): Lung-dwelling nematodes of elk including Protostrongylidae and *Dictyocaulus sp.* have similar early lifecycles: adult worms in the lungs produce first stage larvae (L1) that move up from the lungs, are swallowed into the digestive tract, and are excreted in feces (Kutz et al., 2012). However, Protostrongylidae require a gastropod intermediate host to complete their lifecycle to the infective L3 stage (Anderson, 2000) while *Dictyocaulus sp.* develop to L3 in the environment (Kutz et al., 2012). *Dictyocaulus sp.* seasonal infectivity shows negligible transmission in winter (Flook and Stenton, 1969) with larvae rarely surviving on winter pasture in cold climates (Monnig, 1947).

Cestodes (Tapeworms): Elk are the secondary hosts to *Echinococcus granulosus*, *Moniezia sp.* and *Thysanosoma sp.*, of which the definitive hosts are canids, mainly wolves (*Canis lupus*), for *E. granulosus* and oribatid mites for *Moniezia sp.* and *Thysanosoma sp.* (Kutz et al., 2012). However, *E. granulosus* cannot be detected in elk feces because cysts form in elk tissue that is ingested by the canid definitive host, trophically transmitting the parasite (Kutz et al., 2012). In contrast, *Moniezia sp.* and *Thysanosoma sp.* are transmitted by a mite secondary host requiring

between 27-97 days to develop in the mite, depending on environmental conditions (Narsapur and Prokopic, 1979). Both *Moniezia sp.* and *Thysanosoma sp.* eggs are excreted in elk feces and can be detected in our study.

Protozoa: *Eimeria spp.* are single-celled gastrointestinal parasites that complete a life cycle involving asexual and sexual stages to form oocysts passed in the feces of elk. The oocysts then form spores in the environment before being ingested by the host (Duszynski and Upton, 2001). These spores are dependent on environmental conditions such as oxygen, temperature, moisture, and exposure to UV radiation (Duszynski and Upton, 2001) but certain species of *Eimeria* may be freeze-tolerant (Kutz et al., 2012). This lifecycle requires only 5-8 days to complete at an optimal temperature of 20-23°C but spores can be viable from 49 days to 86 weeks in the environment (Duszynski and Upton, 2001).

Trematodes (Liver Flukes): *F. magna* is transmitted through a gastropod secondary host (Pybus, 2001). Eggs excreted in elk feces take 35 days to develop into larvae to locate a snail host of the family Lymnaeidae (Swales, 1935). The larvae then take about 40-60 days to develop before leaving the snail host to encyst on nearby aquatic vegetation, where they are consumed by an ungulate host (Pybus, 2001). Larval development is based on environmental conditions and temperatures lower than 20°C retard development (Pybus, 2001). These infective larvae remain viable for long periods on vegetation with peak infection occurring in spring and late summer to earlyfall (Pybus, 2001). The prepatent period, once *F. magna* has been ingested by the host including migration to the liver and maturation to adulthood for egg excretion, can last from 3-7 months after infection (Erhardova-Kotrla, 1971). Thus, *F. magna* infection is cumulative throughout an individuals' life but is mainly related to exposure in the previous 6 months.

In conclusion, no winter transmission is likely to occur (Churcher et al., 2005) because parasite development to infective life stages is condition dependent. Even if environmental stages are resistant to harsh conditions and survive excretion onto winter pasture, cold temperatures arrest development until environmental conditions become more favourable in spring. Thus, the winter range may become contaminated with parasite stages in arrested development and elk that leave the winter range in the spring before more favourable conditions occur may "escape" a peak infectious period (Pruvot et al., 2016). High host concentration and subsequent concentration of environmental stages can increase transmission of environmentally transmitted parasites. In addition, summer range differences including temperature can influence transmission by affecting environmental stage development and secondary host habitat required to transmit Protostrongylidae and *F. magna*. We will be focusing on endoparasites in feces because they can be detected non-invasively in feces of GPS-collared female elk.

Appendix B – Comparison of Parasite Species Found in Alberta Ungulates

Table B-1. Gastrointestinal and pulmonary nematodes and liver trematodes of ungulates in Alberta, listed by parasite species and ungulate species in which they have been detected.

Parasite	Ungulate Species	Literature Source
Capillaria sp.	bison, elk	15,19
Cooperia oncophora	bison, elk, mule deer	1,11,20
Dictyocaulus hadweni	bison	3
Dictyocaulus viviparous	deer, elk, moose	5,14
Fascioloides magna	deer, elk, moose	5,19
Haemonchus contortus	bison, mule deer	1,6,20
Haemonchus placei	white-tailed deer	20
Marshallagia marshalli	bighorn sheep, mountain goat, both deer	2,4,20
Moniezia benedeni	elk	5
Moniezia sp.	bison	16
Nematodirella alcidis	elk, moose	11
Nematodirella antilocaprae	bighorn sheep	13
Nematodirella longissimespiculata	mule deer	6
Nematodirus odocoilei	mountain goat, mule deer	6,18,20
Nematodirus oiratianus interruptus	bighorn sheep, mountain goat	4,9
Nematodirus andersoni	bighorn sheep	12
Nematodirus becklundi	mountain goat	14
Nematodirus davtiani	bighorn sheep, mountain goat	4,8
Nematodirus filicollis	bighorn sheep, mountain goat, mule deer	2,4,6
Nematodirus helvetianus	bison, elk, mountain goat, mule deer	10,11,18,20
Nematodirus maculosus	bighorn sheep, mountain goat	7,8
Ostertagia bisonis	mule deer and white-tailed deer	20
Oesophagostomum radiatum, sp.	bison	1
Ostertagia sp.	bison, elk, moose, mountain goat, both deer	1,2,11,20
Protostrongylus spp.	bighorn sheep	12
Spiculopteragia boehmi	elk, mule deer, white-tailed deer	20
Teladorsagia circumcinctal	bighorn sheep, mountain goat, mule deer	2,4,6
Trichostrongylus axei	bison, elk	1,17
Trichostrongylus colubriformis	white-tailed deer	20
Trichostrongylus longispicularis	moose	11
Trichostrongylus sp.	mule deer	6
Trichuris ovis	elk	5
Trichuris sp.	bison, elk	5,16,19

1. Dikmans (1939); 2. McTaggart-Cowan (1951); 3. Graesser (1957); 4. Becklund and Senger (1967); 5. Flook and Stenton (1969); 6. Walker and Becklund (1970); 7. Uhazy and Holmes (1971); 8. Samuel et al. (1977); 9. Lichtenfels and Pilitt (1983a); 10. Bergstrom and Kass (1982); 11. Stock and Barrett (1983); 12. Samson et al. (1987) 13. Durette-Desset and Samuel (1989); 14. Pybus (1990); 15. Durette-Desset and Samuel (1992); 16. Dies and Coupland (2001); 17. Bill Samuel un pub; 18. Unpublished records, US National Parasite Collection; 19. Edwards (2013); 20. DeBruyn (2010)

Table B-2. Sample prevalence (in percent; infected individuals/all individuals sampled) of each parasite species detected in the study area from May through August 2017 separated by host species with number of fecal samples collected recorded below.

Parasite Species	Bighorn Sheep	Deer	Cattle	Feral Horse
Nematodirines	83	5	0	40
Marshallagia sp.	83	0	0	0
Dorsal Spine Larvae	3	20	0	0
Protostrongylidae	83	0	0	0
Eimeria sp.	81	0	20	0
Trichuris sp.	22	5	0	0
Dictyocaulus sp.	0	5	0	0
Trichostrongyle-type egg	42	10	27	100
Strongyloides sp.	0	10	53	0
F. magna	0	5	7	0
Sample Size	36	20	30	20

Appendix C – Features on the Summer Range of Each Migration Tactic

Table C-1. Proportion of wetland extent, average herbaceous forage biomass, average elk resource utilization function (RUF), and average elevation within the summer range (1 May – 31 October) of each migration tactic. "Range" is the average within a composite home range of each migration tactic whereas "Use" is the average value within the composite home range weighted by relative utilization based on GPS locations for elk of each migration tactic from 2017 and 2018 with equal number of locations for each animal. Linear feature density and total extent of each summer range were calculated within a composite home range of each migration tactic only.

Landscape Features	Migration tactic					
	Eastern		Resident		Western	
	Range	Use	Range	Use	Range	Use
Proportion of wetland extent	0.025	0.012	0.005	0.004	0.012	0.008
Avg. RUF (0 to 1)	0.41	0.45	0.37	0.56	0.23	0.35
Avg. Herbaceous forage biomass (g/m^2)	46.1	54.5	39.8	84.6	37.5	51.8
Avg. Elevation (m)	1618	1560	2030	1737	2242	1878
Linear Feature Density (km/km^2)	4.19		2.11		0.93	
Extent of summer range (km^2)	660		720		2530	

Appendix D – Sample Sizes of Population-Level Sampling by Year and Season

Table D-1. Number of samples collected for each migration tactic per season by year for unmarked elk.

Migration Tactic	2017		2018		Total
	Spring	Summer	Spring	Summer	
Western	5	18	9	19	51
Resident	18	57	32	76	183
Eastern	8	21	25	42	96
Total	31	96	66	137	330

Appendix E – Comparing 2-hr and 6-hr Fix Rates for Modelling

The GPS data for this study period of May through October in 2017 and 2018 can be classified into three separate fix rates: 2-hour, 6-hour, and 13-hour fixes. The 2017 GPS data for most individuals (n=34) has 2-hour fix rates except for 5 Vectronic iridium collars with 6-hour fix rates for a total of 39 individuals in 2017. Two individuals from 2017 did not have enough data to include in the analysis with <100 fixes for the time period and less than two full months of data. The 2018 GPS data comprised of two fix rates, 6-hours for Vectronic collars and 13-hour for Lotek Globalstar collars and resulted in less individuals due to malfunctioning collars that did not collect fixes at routine intervals for a total of 16 individuals from 2018. We created Brownian Bridge utilization distributions for each GPS-collared elk using relocations and used relative use metrics of a cell (30 x 30m) to weight exposure to covariates including elevation and wetland extent. To test whether fix rate is affecting the model results we did a two-step process: 1) we tested whether fix rate affected the percentage of GPS points that fell within the extent of wetlands and 2) we rarified 2017 2-hour fix rates to 6-hours and re-ran the same models to check that results were the same with covariates extracted from Brownian Bridge models made from the original and rarified location data.

Fix Rate and Wetland Percentage

I tested whether a difference in fix rate (2-hour, 6-hour, or 13-hour) affected the percentage of an individuals GPS points that fell within a wetland raster pixel (coded 1 for presence of a wetland and 0 for absence of wetland) to determine if fix rate affected the representation of a covariate for our model. I randomly chose 10 elk from 2017 that had 2-hour fix rates and rarified those rates to 6-hour and 13-hour rates with 700 and 350 GPS points

respectively by removing all points except those that fell at 1:00, 7:00, 13:00 and 19:00 for 6-hour fixes and 1:00 and 13:00 for 13-hour fixes. I calculated the percentage of points that fell within a wetland for each individual at each fix rate (Table E-1) and used a paired t-test to determine if there was a significant difference between percent wetland at each fix rate.

Table E-1. Percent wetland as the number of GPS points falling inside and outside a wetland raster for 10 elk at 2-hour, 6-hour, and 13-hour fix rates to test whether fix rate affects percent wetland for individual elk in 2017

Elk ID	Percent wetland (%)		
	2-hour fix	6-hour fix	13-hour fix
YL163	5.82	6.52	9.00
OR100	6.28	7.09	6.16
OR60	2.93	3.59	3.85
YL112	5.74	6.51	6.21
YL158	5.97	3.00	6.51
YL166	3.88	4.05	4.47
YL168	1.98	1.96	2.25
YL124	7.03	6.20	8.00
YL137	7.23	6.80	5.83
YL161	6.05	5.87	6.03

Percent wetland did not differ significantly between 2-hour and 6-hour fixes ($t = 0.37$, $df = 9$, $P = 0.36$) but did differ significantly at an alpha value of 0.1 between 2-hour fixes and 13-hour fixes ($t = -1.47$, $df = 9$, $P = 0.087$). I chose to use only those individuals with 6-hour fixes to create Brownian Bridge utilization distributions for a second year of data (n=40 individuals in total with 15 individuals repeated in both years).

Rarified Fix Rate in Models

The covariates wetland, elevation, and RUF extracted from 2-hour fix rate location data and 6-hour fix rate location data had >0.98 correlation. We ran 6 models with two covariates each with the 2-hour covariates and the 6-hour covariates and ran a paired t-test on the beta

coefficients to determine if there was any difference between model results by fix rate. We found that there was no significant difference between the beta coefficients of the same models ran using each fix rate ($t = 1.43$, $df = 23$, $p = 0.17$).

Appendix F – Models With <10 Eggs as Cut-off Instead of Zero

Table F-1. Summary of model selection results based on AICc for F. magna egg presence and counts in individual elk samples in 2017. All models include a random effect of elk ID. The threshold for egg detection was at least 10 eggs. The elk resource utilization function is RUF.

Model Structure	k	AICc	Δ AICc	AICc Wt.
Presence (logistic)				
Null	2	131.7	0.0	0.17
Wetland	3	132.3	0.58	0.13
Wetland – elevation + wetland x elevation	5	132.7	1.04	0.10
Wetland – RUF + wetland x RUF	5	133.1	1.43	0.08
– Elevation	3	133.3	1.64	0.07
– Age	3	133.6	1.91	0.07
⋮	⋮	⋮	⋮	⋮
– Elevation – RUF – elevation x RUF	5	137.0	5.35	0.012
Intensity (zero-truncated negative binomial)				
– Elevation – RUF	4	334.3	0.0	0.37
– Elevation – RUF + wetland – age	6	335.4	1.06	0.22
– Elevation – RUF + elevation x RUF	5	336.2	1.85	0.15
– RUF	3	337.5	3.22	0.07
– RUF + wetland	4	338.6	4.31	0.04
– RUF – age	4	338.7	4.37	0.04
– RUF + wetland – age	5	339.9	5.58	0.02
– Elevation	3	340.0	5.69	0.02
Wetland – RUF + wetland x RUF	5	340.6	6.25	0.02
Null	2	340.9	6.61	0.01

Appendix G – Exploring Spatial and Temporal Scales of Covariate Extraction

To determine what difference, if any, exists between individual elk utilization distributions (UD) at spatial and temporal scales, I found the volume of intersection (VI) between UDs for four scales: spring (1st May – 30 June), fall (1st Sept – 31st October), the full transmission season (1st of May – 31st of October), and on the allopatric range for migrants created by inspecting individual GPS data to determine the dates of departure from and arrival back on the winter range. We randomly selected 10 migrant and 10 resident elk for a total of 20 individuals to obtain the VI between each scale within individual (Table G1).

The VI between the full season and fall and spring was on average 0.66 and 0.61 respectively. However, migrants and residents differed significantly in their VI in both spring ($t = -2.25$, $df = 10$, $p = 0.048$) and fall ($t = 1.69$, $df = 10$, $p = 0.065$). The VI between the full season and allopatric summer ranges was on average 0.43 which also suggests that utilization differs depending on the spatial scale chosen and whether or not winter range use in early spring and late fall is included. Migrants have a different VI on average across spatial and temporal scales during the *F. magna* infection season compared to resident elk which may affect the extraction of covariate values weighted by Brownian Bridge Utilization distributions. Therefore, we tested covariates from each spatial scale in our models with AICc model selection and selected the most ecologically relevant top models due to a lack of prior knowledge about which scale is most correct. We extracted covariates at the 4 spatial scales for 2017 elk data and ran logistic and zero-truncated negative binomial models for each scale. We found that only top models made with GPS locations from 1 May through 31 October had performed better than the null, suggesting that the most effective spatial scale encompasses the allopatric summer ranges as well as spring and fall habitat use.

Table G-1. Volume of Intersection (VI) between utilization distributions of 20 individual elk for 4 scales: fall (1st Sept – 31st October), spring (1st May – 30 June), full transmission season (1st of May – 31st of October; full), and on allopatric summer ranges for migrants only (adjusted for individual dates of arrival on and departure from the summer range; allo).

elk ID	migration tactic	VI_full to fall	VI_full to spring	VI_spring to fall	VI_full to allo	VI_allo to fall	VI_allo to spring	AVERAGE
OR54	resident	0.736	0.581	0.459	NA	NA	NA	0.592
OR97	resident	0.693	0.585	0.425	NA	NA	NA	0.567
OR100	resident	0.724	0.521	0.356	NA	NA	NA	0.534
YL133	resident	0.736	0.512	0.400	NA	NA	NA	0.549
YL156	resident	0.746	0.636	0.523	NA	NA	NA	0.635
YL161	resident	0.736	0.506	0.359	NA	NA	NA	0.533
YL162	resident	0.727	0.570	0.467	NA	NA	NA	0.588
YL163	resident	0.718	0.555	0.413	NA	NA	NA	0.562
YL174	resident	0.726	0.497	0.378	NA	NA	NA	0.534
YL179	resident	0.629	0.581	0.335	NA	NA	NA	0.515
YL154	eastern	0.741	0.700	0.548	0.762	0.566	0.656	0.662
YL155	eastern	0.299	0.675	0.194	0.422	0.003	0.403	0.333
YL158	eastern	0.709	0.743	0.812	0.463	0.292	0.311	0.555
YL166	eastern	0.615	0.593	0.701	0.366	0.346	0.574	0.533
YL170	eastern	NA	0.804	NA	0.866	NA	0.800	0.823
YL173	western	0.463	0.735	0.397	0.352	0.055	0.442	0.407
OR55	western	0.822	0.256	0.176	0.170	0.169	0.016	0.268
OR60	western	0.350	0.661	0.335	0.371	0.000	0.467	0.364
OR78	western	0.810	0.759	0.634	0.252	0.269	0.169	0.482
YL168	western	0.650	0.798	0.751	0.315	0.152	0.215	0.480
AVERAGE		0.665	0.613	0.456	0.434	0.206	0.405	0.526

* NA represents no data for summer allopatric ranges for resident elk that do not leave the winter range or a lack of data after Sept 30th for YL170 and thus no fall utilization distribution.

Appendix H – Wetland Layer Workflow

Lymnaeid snail habitat includes marshes, ephemeral wetlands, vernal pools, and muddy banks of slow-moving streams where aquatic vegetation grows (Dunkel et al., 1996; Vannatta, 2016). Vanderwaal et al. (2015) found that cover types with higher *F. magna* risk to deer included marshes and wet meadows. Fast-moving streams with steep elevation gradients and rocky riparian areas adjacent to the Red Deer River were not included in the wetland layer.

The wetland layer was created using a coloured aerial image from Google Earth Pro taken on 29 September 2015. A hydrology layer for the area was added on top of the aerial imagery (Figure H-1A). A wetland was classified based on presence of the hydrology layer in a treeless area with little to no relief. A shape was drawn by hand around the wetland area (Figure H-1B) and a 250m buffer was added (Figure H-1C) to account for both drawing error and the 2 or 6-hour fix-rate of GPS locations. This would ensure that if an elk was near a wetland area we would capture use of that area. Though some species of lymnaeid snails are not found in ponds, ponds were also included in the wetland layer because a small proportion of wetlands in the study area were identified as ponds (~ 4% of wetlands on or near the Ya Ha Tinda, 0% of wetlands east along the Red Deer river, and ~ 1% of wetlands in Banff National Park). Due to the large size of the study area, ground-truthing was only completed on a small portion of identified wetland areas but was done in each of the three summer ranges in areas of high elk use.

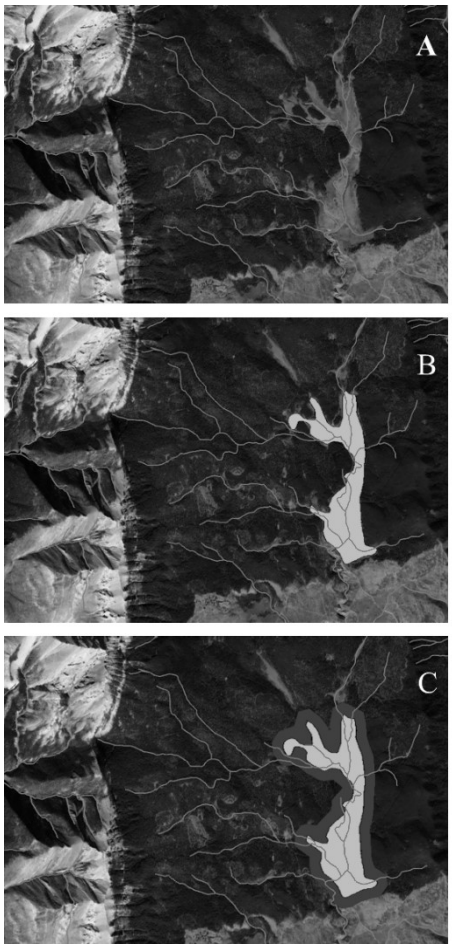

Figure H-1. The process of digitizing an aerial photograph from the hydrology layer (A) to a wetland (B) with a 250-m buffer (C).

Appendix I – Correlations Between Continuous Variables in Liver Fluke Analysis

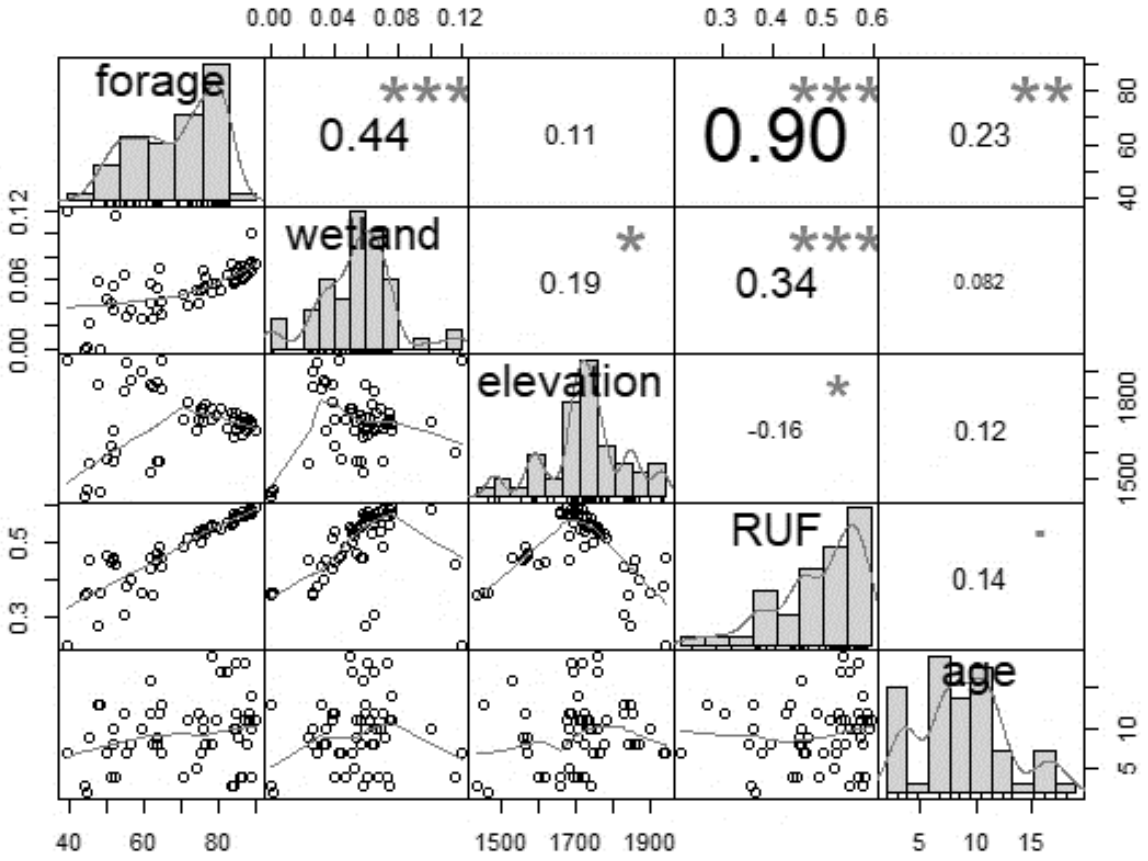

Figure I-1. Correlations between continuous covariates in analysis of individual elk liver fluke egg counts showing low to moderate correlation between predictor variables in 2017 and 2018 combined except for herbaceous forage biomass and RUF which have a correlation of 0.90.

Appendix J – Adding Calf at Heel and Body Condition to Top Models

Table J-1. Summary of model selection results based on AICc for liver fluke egg presence and intensity in individual elk samples in 2017 and 2018 adding calf at heel to the top model using a subset of individuals for which the data is available. All models include a random effect of elk ID and a detection threshold of zero (2017 was used as the reference year and elk resource utilization function is RUF).

Model Structure	k	AICc	Δ AICc	AICc Wt.
Presence (logistic)				
Wetland – forage + year	5	174.8	0.00	0.64
Wetland – forage + year + calf	6	176.1	1.28	0.34
1 + year	3	181.3	6.51	0.03
Intensity (zero-truncated negative binomial)				
– Elevation + year	4	559.1	0.00	0.64
– Elevation + year + calf	5	560.9	1.86	0.25
1 + year	3	562.7	3.61	0.11

Table J-2. Summary of model selection results based on AICc for liver fluke egg presence and intensity in individual elk samples in 2017 and 2018 adding body condition the previous winter to the top model using a subset of individuals for which the data is available. All models include a random effect of elk ID and a detection threshold of zero (2017 was used as the reference year and elk resource utilization function is RUF).

Model Structure	k	AICc	Δ AICc	AICc Wt.
Presence (logistic)				
Wetland – forage + year + body condition	6	90.6	0.00	0.44
Wetland – forage + year	5	91.1	0.51	0.34
1 + year	3	92.0	1.44	0.22
Intensity (zero-truncated negative binomial)				
1 + year	3	306.9	0.00	0.57
– Elevation + year	4	307.9	1.10	0.32
– Elevation + year + body condition	5	309.9	3.01	0.12

Appendix K – Forage Quality Measured in 2017

We compared fecal nitrogen in pellets of elk following the different migratory tactics to reflect forage quality (Blanchard et al. 2016). Pellets for fecal nitrogen were collected from 1 May – 15 October 2017 where 2g of pellets were randomly collected from pellet groups of unmarked elk from each migration tactic (19 residents, 19 eastern migrants, and 19 western migrants), oven dried at < 50°C, ground to a homogenized sample, and total nitrogen was measured using an Elemental Analyzer (Blanchard et al. 2016). We tested whether fecal nitrogen values were normally distributed using a Shapiro-Wilk normality test (`shapiro.test`) and for differences in mean fecal nitrogen between seasons and migration tactics using Analysis of Variance (`aov` functions from the R package `stats`, R Core Team 2019). Percent fecal total nitrogen was significantly different between seasons ($p < 0.001$, $df = 2$, $F = 29.43$; $\bar{x}\pm$SD), averaging higher in summer (3.09 ± 0.37) than either spring (2.36 ± 0.37) or fall (2.36 ± 0.28). During the summer but not spring, western migrants had higher fecal total nitrogen than both residents ($p = 0.025$, $df = 2$, $F = 6.08$) and eastern migrants ($p = 0.010$).

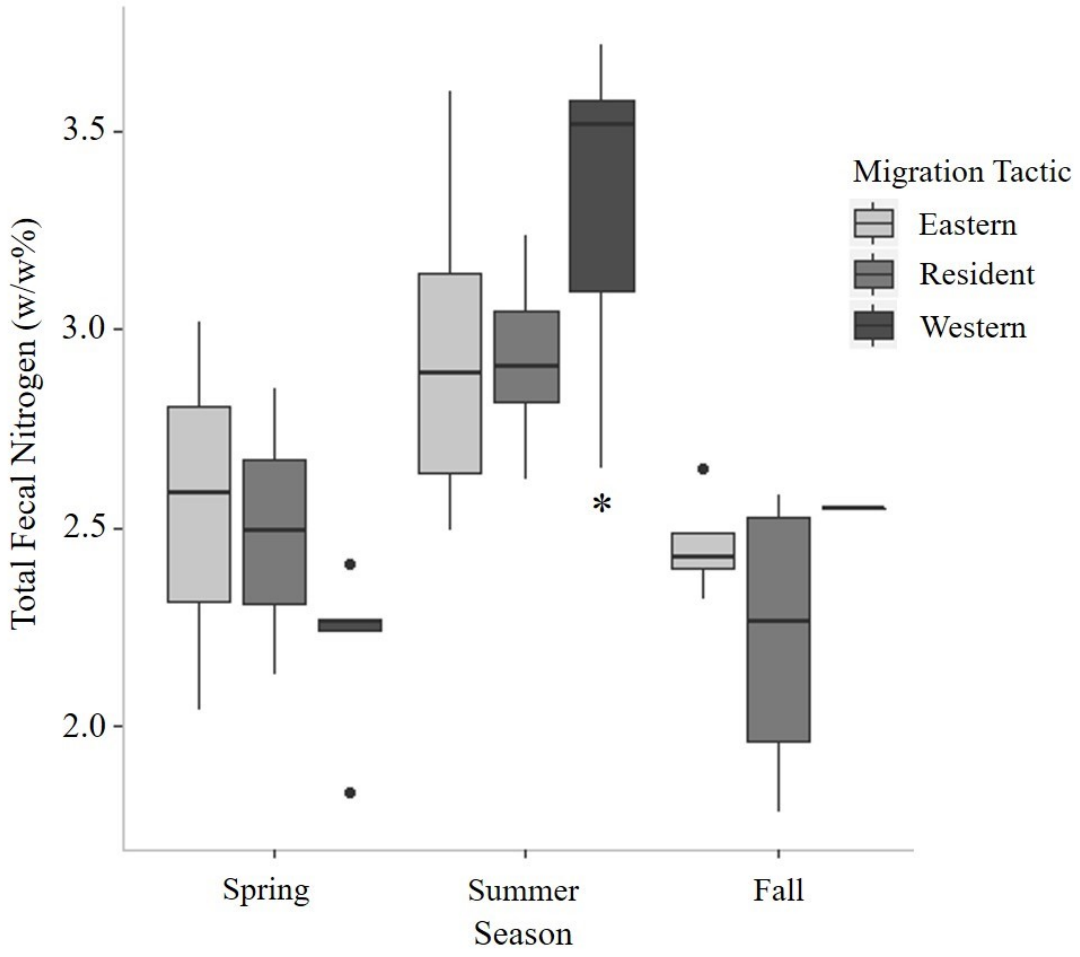

Figure K-1. Fecal nitrogen measured from spatially and temporally pooled samples for western migrants (n = 19), residents (n = 15), and eastern migrants (n = 19) in spring (1 May to 31 May), summer (1 July to 15 August), and fall (15 Sept to 15 Oct) of 2017.

Appendix L – Correlation Between Elevation, Temperature, and Forage

Elevation can be used as a proxy for temperature and snail habitat suitability where higher temperatures promote *F. magna* infection through faster development of larvae and increased exposure to snail hosts once snow melts and habitat because suitable for transmission. We calculated average temperatures in 2017 and 2018 as a full year average across both years, summer (1 May through 31 October) temperatures in both years, and summer temperatures for each year separately from seven weather stations in an east-west and elevation gradient across our study area (Figure L-1).

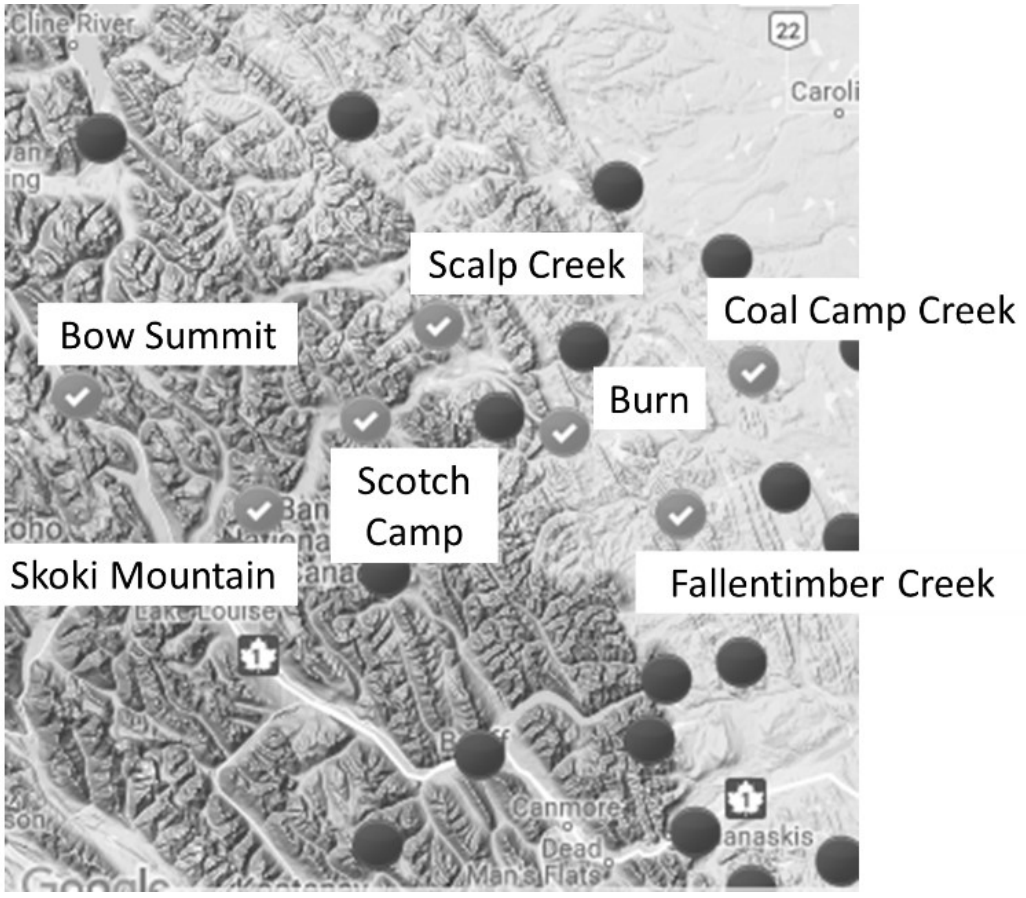

Figure L-1. Locations of weather stations across the study area with those used in the analysis as purple check marks.

Average temperatures are higher at lower elevations than higher elevations ($r = -0.94$, $p = 0.002$), making elevation a proxy for temperature in our study area (Table L-1, Figure L-2). Snow depth was not available at these locations but would be a good indicator of snail habitat suitability as well. All weather data was obtained from Agriculture and Forestry Alberta (https://agriculture.alberta.ca/acis/alberta-weather-data-viewer.jsp).

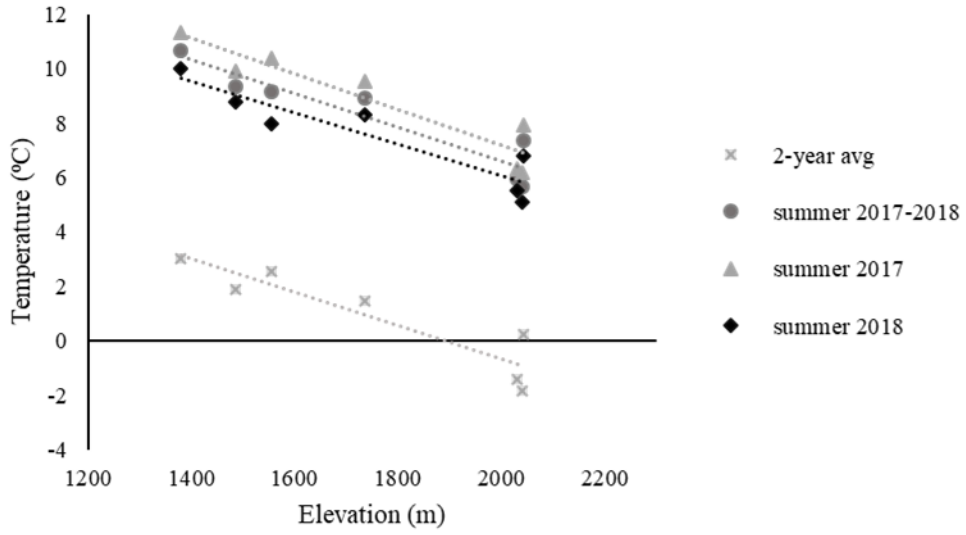

Figure L-2. Average temperatures across the study area in 2017 and 2018 showing a decline in temperature along an increasing elevation gradient.

Table L-1. Two-year (2017 to 2018) and summer (1 May through 31 October) average temperatures (temp) across the study area ordered from low to high elevation from the foothills east of Banff National Park through to Lake Louise. All temperatures are presented as degrees Celsius.

Weather Station	Elevation (m)	2-year average temp	Summer temp 2017-2018	Summer temp 2017	Summer temp 2018
Coal Camp Creek	1380	3.03	10.66	11.31	10.02
Burn	1486	1.89	9.37	9.94	8.80
Fallentimber Creek	1555	2.54	9.17	10.39	7.96
Scotch Camp	1737	1.49	8.92	9.53	8.31
Bow Summit	2031	-1.40	5.94	6.35	5.52
Skoki Mountain	2040	-1.85	5.65	6.18	5.11
Scalp Creek	2042	0.25	7.36	7.93	6.78

We determined the correlation between herbaceous forage biomass and elevation at the landscape level using values extracted at 1000 random points within the study area. Elevation was weakly negatively correlated to herbaceous biomass ($r = -0.11$, $p < 0.001$) where lower elevations have higher herbaceous forage biomass (Figure L-3).

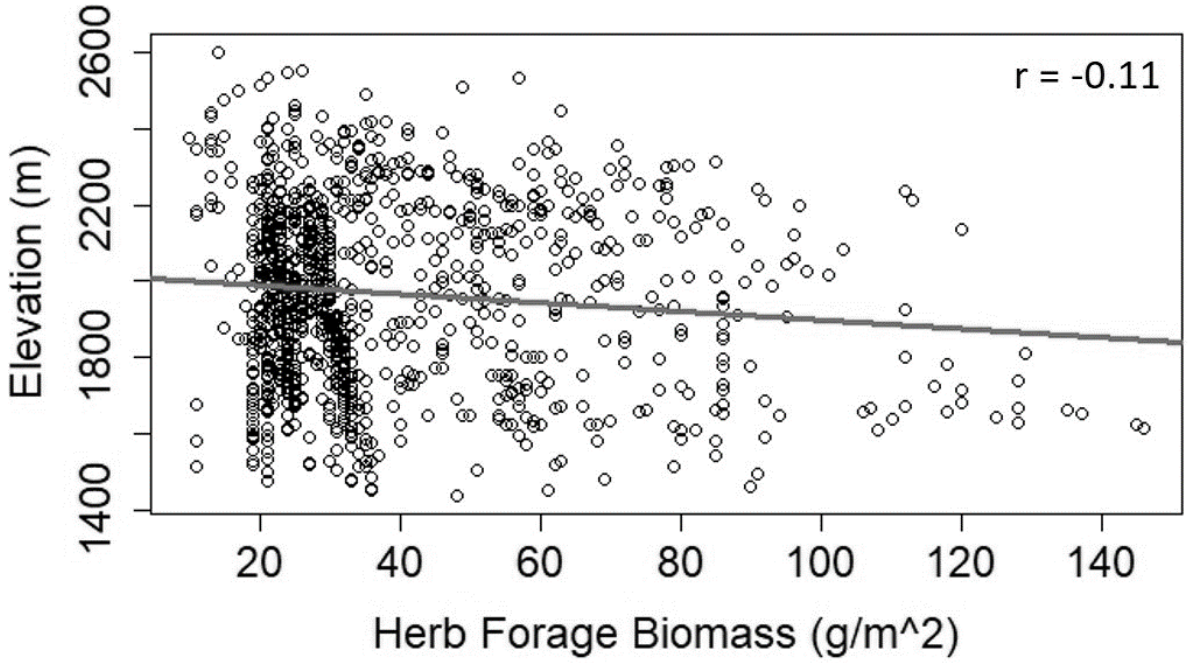

Figure L-3. Correlation between forage and elevation values extracted at 1000 random locations within the study area ($r = -0.11$, $p < 0.001$).

Appendix M – Tick Counts on Withers from Captured Elk by Life Stage

Table M-1. Number of ticks in each life stage counted on the withers (30cm line transect) during captures of focal female elk from March 5 - 9 2019. Individuals were either previously collared (n = 12) or uncollared (n = 8) and a GPS-collar was put on each individual.

Elk ID	Collar type	Total ticks on withers	Adults	Nymphs not engorged	Engorged nymphs
YL177	collar	13	0	0	13
YL182	collar	3	3	0	0
YL178	collar	1	1	0	0
OR24	collar	2	1	0	1
YL170	collar	32	3	2	27
YL167	collar	22	6	6	10
YL190	uncollared	12	3	2	7
YL185	collar	4	2	0	2
YL187	uncollared	3	0	0	3
YL188	uncollared	3	0	0	3
YL189	uncollared	17	1	0	16
YL191/X	uncollared	60	15	10	35
YL192	uncollared	4	1	0	3
YL193	uncollared	24	2	2	20
YL194	uncollared	0	0	0	0
YL195	uncollared	33	10	8	15
YL196	uncollared	2	0	0	2
YL197	uncollared	13	10	0	3
YL198	uncollared	1	0	0	1
YL153	collar	30	15	0	15

We found a mean tick density of $0.47 \pm 0.52/cm^2$ ($\bar{x} \pm SD$) across all 20 elk along the 30cm withers transect by averaging the tick densities in the 30cm transect for each individual.

Appendix N – Progression of Hair Loss and Hair Loss Scoring

We collected a hair loss score for the neck and withers at 4 time periods near the middle of each month: January 15-16, February 19 and 21, March 14, and April 16-18. Loss of hair was defined as hair that was <50% of the height of surrounding hair shafts at the skin level where the hair follicle emerges. The number of grid cells with >50% hair loss was recorded in the withers and neck area for each focal individual, and a hair loss score from 1-16 was assigned according to the number of cells with hair loss. Withers and neck hair loss scores for each individual progressed throughout the sampling season (January – April) and scores were consistent within an individual (Normandeau, personal observation; i.e., an elk with high hair loss in April progressed in hair loss from January onwards in an approximately linear trend).

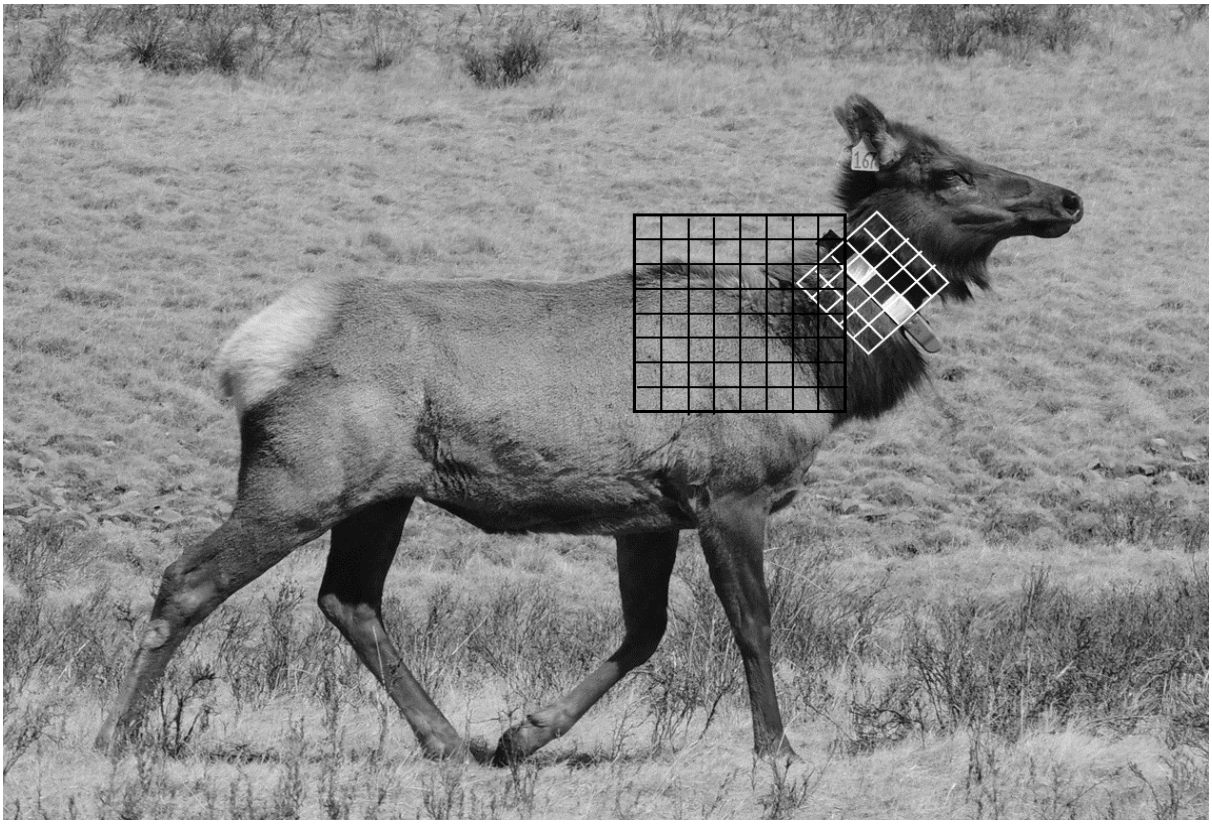

Figure N-1. Hair loss scoring grids for the neck (in white) and the withers (in black). Squares are approximately 5cm x 5cm.

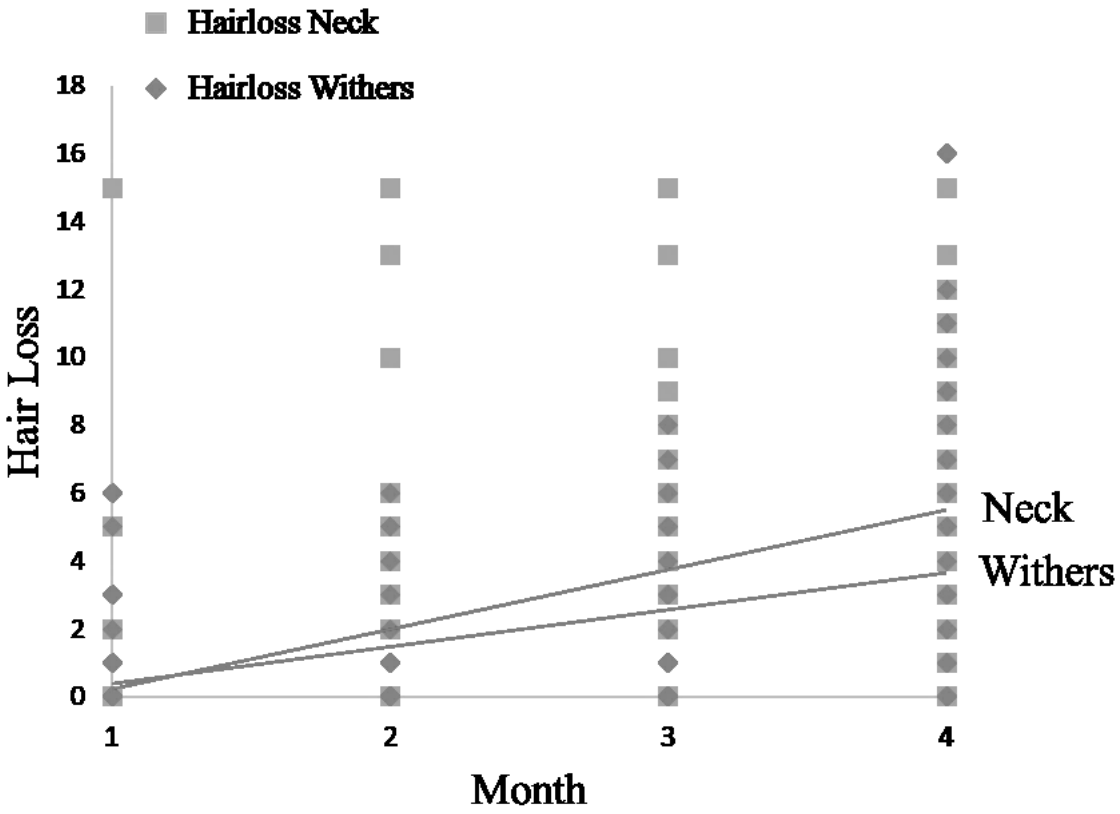

Figure N-2. Progression of withers and neck hair loss scores from January (month = 1) to April (month = 4) using 4 hair loss scores from pictures of the same individuals (n = 66) in the middle of each month.

Withers hair loss score did not differ between eastern migrants (0.80 ± 1.93) and residents (0.77 ± 1.62; $p = 0.36$, $df = 2$, Kruskal-Wallis $\chi^2 = 2.71$) or western migrants (0.00 ± 0.00; $p = 0.14$) during the first hair loss score collected in from 15-17 January 2019.

Appendix O – Elk Daily Activity Budget Separated by Migration Tactic

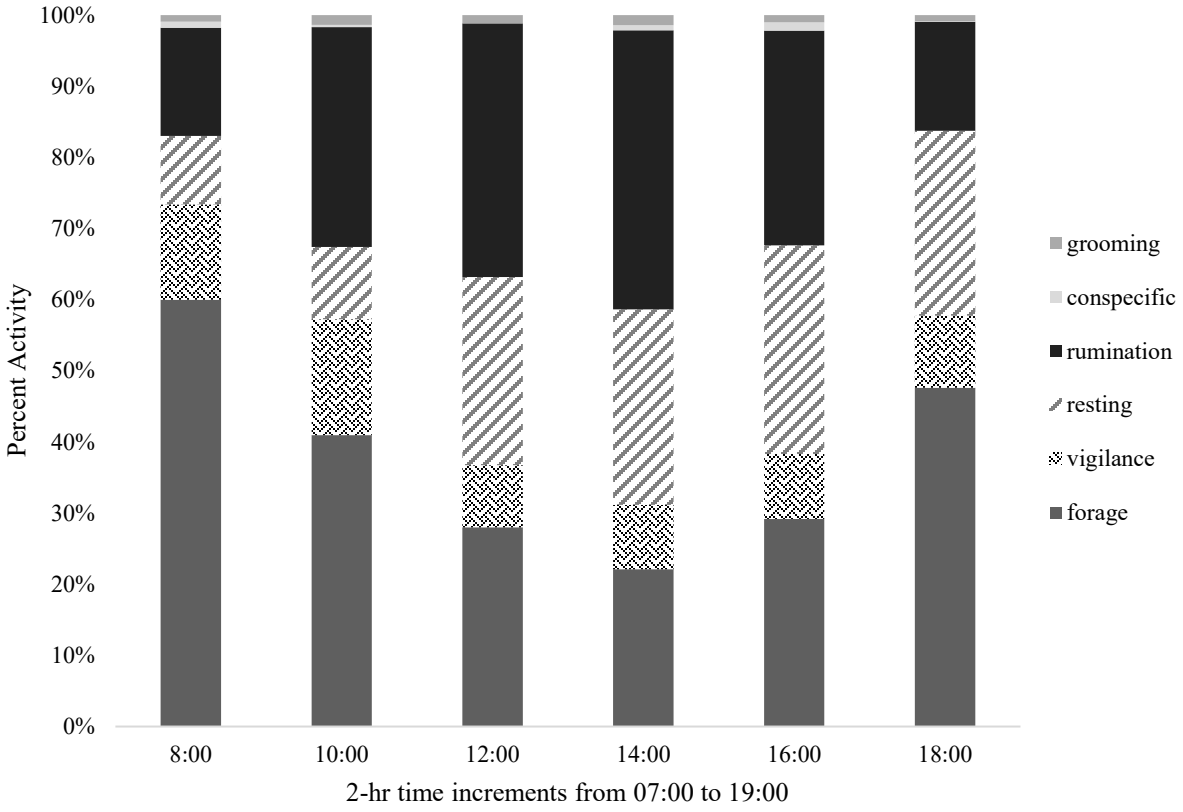

Figure O-1. Average elk activity budget during winter daylight hours (07:00 to 19:00) using the average across all focal individuals observed during each 2-hr time period (i.e., 08:00 represents all observations between 07:00 and 09:00).

Table O-1. The percentage of start times during the day separated into three periods did not differ among migration tactics during morning ($p = 0.93$, $df = 2$, $\chi2 = 0.15$) or midday ($p = 0.33$, $df = 2$, $\chi2 = 2.23$) but did differ during the evening period ($p < 0.001$, $df = 2$, $\chi^2 = 99.53$) which only comprised of 26% of observations.

	% of total observations	Eastern	Resident	Western
morning (7:00 – 10:00)	42	44	41	42
midday (10:00 – 15:00)	32	28	33	26
evening (15:00 – 19:00)	26	29	25	32

Appendix P – Allocations of Oral and Scratch Grooming by Activity

Table P-1. Percentage of oral grooming on the hindquarters, scratch grooming on the head, neck, and withers, and combined oral and scratch grooming that occurred during each activity.

	Oral grooming (%)	Scratch grooming (%)	Combined grooming (%)
Foraging	8	38	14
Resting	38	30	40
Vigilance	39	16	36
Rumination	9	10	10
Conspecific interaction	0	0	0

Appendix Q – Combined Grooming Time by Migration Tactic

Table Q-1. Summary of model selection results based on AICc for total time spent grooming by migration tactic while controlling for collar type, age, and observation length. All confidence intervals overlapped zero in the top model.

Model Structure	k	AICc	Δ AICc	AICc Wt.
Null	3	4976.4	0.00	0.71
Migration tactic + age	5	4977.0	0.56	0.18
Migration tactic + collar	5	4979.2	2.75	0.06
Migration tactic	4	4980.0	3.54	0.04
Migration tactic + collar + migration tactic x collar	6	4981.6	5.15	0.02
Migration tactic + collar + age	5	4985.6	8.55	0.00
Migration tactic + age + migration tactic x age	6	4986.9	9.80	0.00