Disparity in conspecific interaction and vigilance behaviour in a partially-migratory elk herd *(Cervus canadensis)* on a sympatric winter range

by

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Abstract

Sociality incurs costs and benefits for group-living animals that may influence small-scale behavioural trade-offs such as vigilance and foraging. I examined interaction, vigilance, and foraging behaviours among elk in the partially migratory Ya Ha Tinda elk herd (*Cervus canadensis*) in Alberta, which exhibits a western migration to montane summer ranges in Banff National Park, while resident elk remain on the sympatric winter range year-round. In recent years, a third eastern migratory tactic has emerged, moving to industrial forest lands east of Ya Ha Tinda during the summer. Previous studies have shown that despite high spatial overlap, western migrants showed different vigilance patterns in areas of human and predation risk than resident elk, which was attributed to differential exposure to predators and humans during the summer. However, the influence of social interactions on foraging and vigilance behaviours among the three migrant tactics is not well known, and it is unknown how eastern elk respond to human and predation risk on the winter range. I examined social interactions at the home range, foraging patch, and individual levels using GPS telemetry data to compare home range overlap and sequential patch use among collared female elk on the winter sympatric range and used direct observations of interaction behaviours in focal elk to assess differences in interaction rates and aggression among individuals. I used behavioural observations to examine the influence of conspecific interactions, predation risk, and human activity on vigilance behaviour during foraging, and the cost of those interactions in terms of time to resume feeding. I determined the influence of environmental factors and where the focal individual was located relative to other elk on the amount of time spent vigilant directly after a conspecific interaction compared to routine vigilance (no interaction), and assessed whether vigilance levels differed among migratory tactics. I found all migrant tactics had a high degree of home range overlap that increased as winter progressed, and migrant elk were more likely to enter foraging patches following resident elk. While interaction rate and duration were similarly low among all tactics, eastern migrants were more aggressive than both western migrant and resident elk. However, interactions made up < 2% of total observation time and disruption times from foraging following interactions were similar among all tactics. Similarly, vigilance bouts were not longer or more frequent following interactions compared to routine vigilance. Instead, vigilance in elk was more strongly related to environmental variables. My study uniquely addresses the influence of conspecific interactions as a differential cost among migrant tactics on a sympatric winter range, and contributes to our understanding of the influence of small-scale behavioural trade-offs on the maintenance of migratory tactics in a partially-migratory population.

Preface

This thesis is an original work by Madeline R. M. Trottier. 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.

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CHAPTER 1 – CONSPECIFIC INTERACTIONS AND THE INFLUENCE OF MIGRATORY TACTIC IN A PARTIALLY-MIGRATORY ELK POPULATION

Living in groups provides anti-predator benefits for ungulates (Fryxell, 1995; Geist, 1974; Krause & Ruxton, 2002) as well as improves an individual's ability to locate and access forage through the transmission of information and cues from conspecifics through social information (Van De Waal, Borgeaud, & Whiten, 2013; Rosenthal et al., 2015; Jesmer et al., 2018; Bonnell, Henzi, & Barrett, 2019). Group living can benefit individuals by reducing chances of predation by increasing predator detection (Jarman, 1974; Krause & Ruxton, 2002), diluting predation risk (Bertram, 1978; Fryxell, 1995; Caro, 2005) and reducing vigilance costs during encounter-limited foraging (Berger, 1978; Robinson & Merrill, 2013). However, group living can also increase the risk of intraspecific competition through exploitation or interference (Molvar & Bowyer, 1994; Focardi & Pecchioli, 2005; Smith & Cain, 2008; Marino, 2010). Both exploitative competition and aggressive interactions are costly to individuals, with the former affecting access to preferred resources (Appleby, 1980) and the latter disrupting foraging by requiring vigilance for conspecific attacks (Clutton-Brock & Huchard, 2013) and posing a risk of physical injury. For example, Alaskan moose (*Alces alces*) reduced foraging time as group size increased in conjunction with aggressive conspecific interactions (Molvar & Bowyer, 1994); in horses, similar interruptions in foraging resulted in lower body condition (Giles et al., 2020). Therefore, social relationships are an important component of the complex trade-off between resource access, predation risk, and environmental constraints governing activity and behaviour patterns of group-living ungulates.

Migration is a behavioural tactic employed by numerous species as a means of increasing lifetime reproductive fitness across in a heterogenous landscapes (Fryxell & Sinclair, 1988). By moving onto seasonal ranges, migrants can obtain forage and water resources (Merkle et al., 2016); Aikens et al., 2017; Middleton et al., 2018), reduce exposure to predation and parasites (Mysterud, 2013), and reduce competition on shared ranges (Gillis et al., 2008; Mysterud et al., 2011). In partially migratory species, migration is expressed by a subset of the population, while another subset remains as residents. For ungulates in montane systems, partial migration typically consists of migrants dispersing to allopatric summer ranges and returning to a sympatric range in the winter because they have reduced forage availability or winter conditions are mild. As such, groups of individual ungulates may be socially isolated and exposed to different conditions during the summer (Chapman et al., 2011). Segregation in summer likely reduces competition and the extent of that segregation may be density dependent. For example, in red deer (*Cervus elaphus*) migration distances have been shown to increase with density, which suggests avoidance of competitive interactions on the summer range (Mysterud et al., 2011). When migrant individuals return to sympatric ranges in winter, relatedness and familiarity among individuals may influence group formation, space-use overlap and conspecific interactions (Rossiter, Jones, Ransome, & Barratt, 2002; Tóth et al., 2009; Djaković et al., 2012). Bushbuck females (*Tragelaphus scriptus*) had higher home range overlap among related animals than non-related animals, which along with lower among-kin aggressive interactions, suggests there may be an advantage of forming coalitions with known conspecifics (Wronski & Apio, 2006). Although higher spatial overlap among individuals would be expected to increase conspecific interactions, association in space is not always equivalent to a corresponding increase in rates of conspecific interactions. For example, variation in association strength between reticulated giraffe (*Giraffa camelopardalis reticulata*) dyads did not correspond with home range overlap; similarly, joint space-use in white-tailed deer corresponded nonlinearly with contact rates among individuals with only an initial increase (Schauber et al, 2007). This suggests that when extrinsic and intrinsic factors encourage high overlap among individuals at the home range level, more complex social systems emerge at finer scales and group members adopt behavioural rules to enable them to function as a social unit (Hemelrijk, 2000; Rands et al., 2006).

The Ya Ha Tinda elk herd is an example of a partially migratory population that has undergone shifts in migration over the last 20 years in conjunction with a decline in population size since the late 1990s, attributed to an increase in wolf numbers in the area (Hebblewhite et al., 2006). Historically, 90% of the population migrated west onto high-elevation summer ranges in Banff National Park while a smaller proportion remained as residents on the sympatric winter range. Now, western migrants have declined to approximately 18% of the population despite higher quality summer forage resulting in higher pregnancy and calf weights (Hebblewhite et al., 2006; Hebblewhite et al., 2018; Berg et al., 2021). In addition, a third migrant tactic of elk migrating eastward during the summer has emerged in the past decade, which is exposed to earlier forage green-up and higher calf survival (Berg et al., 2021; Martin, Hebblewhite, & Merrill, 2021). Despite the differences on each summer range, each migratory tactic experienced similar growth rates (Mark Hebblewhite & Merrill, 2011). It was hypothesized that differences in foraging behavior of resident elk contributed to offsetting lower forage quality in summer through differences in winter habitat selection and movement but this has not been supported (Merrill et al., 2020). Instead, as the winter elk population has declined, cohesion among individuals on the winter range has increased (Merrill et al., 2020), which may suggest that small-scale behavioural differences in conspecific interactions result in a foraging advantage over migrant elk (Robinson & Merrill, 2013).

Social behaviour may govern foraging advantages on the sympatric winter range when the elk are most aggregated. At the same time, previous studies have shown that differences in vigilance behaviour may also put resident elk at an advantage during the winter by reducing the foraging cost of vigilance through multitasking (Robinson & Merrill, 2013). Currently, it is unknown how conspecific interactions may influence vigilance behaviour and whether differences in aggression by one migratory tactic may impose a greater cost on foraging by vigilance for conspecifics compared to for predation. In addition, Robinson and Merrill (2013) found resident elk were less vigilant of human activity than western migrants, but eastern migrants were not studied. With the recent emergence of eastern migrants as a third migratory group, it is unknown how summer exposure to high human recreation on their summer range potentially may influence their vigilance behavior and how they may interact with individuals in the other migratory tactics on the sympatric winter range.

In this thesis, I contrasted conspecific interactions and vigilance behaviours among resident, eastern migrant, and western migrant elk on the Ya Ha Tinda winter range to determine whether these behaviours produce differential foraging costs. I hypothesized there would be differences among tactics because differential exposure to forage quality and predation risk on allopatric summer ranges (Hebblewhite & Merrill, 2011; Berg et al., 2021). In Chapter 2, I focus on interactions among migrant and resident elk on the winter range at three scales of analysis, i.e., home range, foraging patch, and feeding site, and discuss how patterns in conspecific interactions at each level may reflect differential foraging advantages among migrant tactics. I used locations from GPS-collared female elk to examine home-range overlap and sequences of patch use on the winter range, and direct observations of interaction behaviours of focal elk to assess differences in interaction rates and aggression among individuals. In Chapter 3, I used behavioural observations to examine the influence of conspecific interactions, predation risk, and human activity on vigilance behaviour during foraging, and the cost of those interactions in terms of time to resume feeding. I determined the influence of environmental factors and where the focal individual was located relative to other elk on the amount of time spent vigilant directly after a conspecific interaction compared to routine (no conspecific interaction), and assessed whether vigilance levels differed among migratory tactics. My thesis uniquely addresses the influence of conspecific interactions as a differential cost among migrant tactics on a sympatric winter range, and contributes to our understanding of the influence of small-scale behavioural trade-offs on the maintenance of migratory tactics in a partially-migratory population.

STUDY AREA

The Ya Ha Tinda is a 40-km^2 grassland located in west-central Alberta, Canada, along the eastern slopes of the Rocky Mountains adjacent to Banff National Park that is the winter range of the partially migratory Ya Ha Tinda elk herd. The area encompasses a Parks Canada horse ranch that is surrounded by crown lands where natural resources are managed by the Alberta provincial government. Two provincially managed public campgrounds (Bighorn and Eagle Creek) located to the east of Ya Ha Tinda have recreational use from spring to fall, primarily consisting of equestrian users.

The area has an east-west elevational gradient of 1,350m in the east to 2,800m in the west, and consists of a large montane rough fescue (*Festuca campestris*) grassland interspersed with willow-bog birch (*Salix sp. – Betula glandulosa*) shrubland, aspen (*Populus tremuloides*) stands, and conifer stands consisting of primarily lodgepole pine (*Pinus contorta*) forests at low elevation and Engelmann spruce and white spruce (*Picea engelmannii* and *P. glauca*) at higher elevations (Hebblewhite et al. 2006). Warm westerly winds (i.e., chinooks) occur frequently in the winter, resulting in an average snowpack generally < 25cm on the central grasslands (Morgantini, 1995). During this study, temperatures in winter (1 November – 31 March) averaged -7°C, ranging from -33°C to 9°C (Scalp Creek Station, Government of Alberta 2021), and snow depths were an average of 4.4cm, ranging from 0 to 14.1 cm (Sundre A Station, Government of Alberta 2021).

Winter elk numbers on the Ya Ha Tinda have shown fluctuations over the past 50 years, having increased from a population of ~350 in the late 1970s to a maximum of ~2,200 elk in 1992 (Morgantini, 1995). More recently, the population has declined by about 70% to current estimates of 411 ± 54 from 2014 – 2016 (Berg et al., 2021), concurrent with recolonization and increase of wolves in the area. Simultaneously, there has been a decrease from about 70 to 30% of the population migrating off the Ya Ha Tinda in summer (Martin, Hebblewhite, & Merrill, 2021), with a substantive re-emergence of elk migrating eastward from the Ya Ha Tinda instead of westward into Banff National Park (Berg et al., 2021). Historically, 95% of elk migrated ~50km west into high elevation ranges in Banff National Park, with a small proportion remaining residents year-round and rarely migrating ~40km eastward onto low-elevation public lands with high recreation and industrial use (Morgantini & Hudson, 1988; Hebblewhite et al., 2006). Over the course of two decades, ratios of residents to western migrants to eastern migrants have shifted from 15:14:1 during the early years of the study (2002 – 2006) to 10:1:5 during later years (2013 – 2016; Berg, 2019). During the summer, western migrants have access to 10% higher forage quality compared to resident elk, resulting in higher pregnancy rates and fall calf weights (Hebblewhite et al., 2008). Similarly, eastern migrants are exposed to a higher percentage of cut and burned areas (Berg et al., 2021) with earlier green-up (Killeen et al., 2016) and potentially higher quality forage, although pregnancy and calf weights do not differ between eastern migrants and residents (Berg et al., 2021). Concurrently, resident elk experience highest neonatal mortality rates from bear predation (Berg et al., 2022), the highest exposure to wolf predation risk (MacAulay et al., 2022; Flowers, 2019), and higher human disturbance compared to eastern and western migrants (Berg et al., 2021; MacAulay et al., 2022). However, resident elk also display habituation to human activity, and are able to exploit such areas of predation refuge in order to reduce wolf predation risk from ~70 to ~15% higher risk than western migrants (Hebblewhite & Merrill, 2007, 2009).

A limited-quota, antlered elk hunt is permitted from late August through November, though hunting is prohibited within fenced pastures of the Ya Ha Tinda ranch and within a 365-m sanctuary zone bordering the main road. No recreational hunting of female elk is allowed within the WMU, though First Nations hunting is permitted year-round. Other ungulates in the area include white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*) and domestic horses (*Equus caballus*). Major predators on the landscape include cougars (*Felis concolor*), coyotes (*Canis latrans*), grizzly (*Ursus arctos horribilis*) and black bears (*Ursus americanus*), with wolves (*Canis lupus*) being the main predator on elk year-round (Hebblewhite et al., 2018).

CHAPTER 2 – PERILS OF GROUP LIVING: SOCIAL INTERACTIONS AT MULTIPLE SCALES IN A PARTIALLY-MIGRATORY ELK POPULATION

1. Introduction

Individuals make trade-offs to live in groups (Fryxell, 1995; Geist, 1974; Krause & Ruxton, 2002). Individuals in a group can reduce their chances of predation by increasing the probability of detecting predators (Jarman, 1974; Krause & Ruxton, 2002), reducing per-capita mortality risk by dilution (Fryxell, 1995; Caro, 2005; Wrona & Dixon, 2015) and reducing vigilance costs during encounter-limited foraging (Berger, 2007; Robinson & Merrill, 2013). Group living may also facilitate access to food based on social knowledge of forage abundance and quality (Valone, 1989; Beauchamp & Giraldeau, 1997; Dall et al., 2005). At the same time, group members may incur foraging costs due to competition from forage depletion and interference from conspecifics or direct injury from aggressive individuals (Appleby, 1980; Molvar & Bowyer, 1994; Smith & Cain, 2008; Marino, 2010; Côté, 2000; Ceacero et al., 2012). As such, the social relationships among group members are a key component influencing the trade-offs group members make between resource access and predation risk (Bowyer et al., 2020).

In large herbivores, conspecific interactions related to group living can manifest themselves at multiple spatial scales (Senft et al., 1987), and interactions at one scale may influence behaviors at subsequent scales (Rettie & Messier, 2000; (Johnson et al., 2002a, 2002b; Bowyer & Kie, 2006). At the home-range scale, individuals or groups of individuals may spatially segregate from others to reduce competition, defend resources, or avoid physical injuries (Horne, Garton, Krone, & Lewis, 2007; Vanpé et al., 2009; Wittemyer, Getz, Vollrath, & Douglas-Hamilton, 2007). In contrast, overlap of ranges may provide competitive benefits among groups or information sharing opportunities during foraging (Rossiter, Jones, Ransome, & Barratt, 2002; Tóth et al., 2009; Djaković et al., 2012) that may outweigh the costs of competition when population densities are low (Matthysen, 2005). A common example of this is female philopatry in many ungulate species (e.g., white-tailed deer [*Odocoileus virginianus*], Porter et al., 1991); Soay sheep [*Ovis aries*], Coltman, Pilkington, & Pemberton, 2003; bushbuck [*Tragelaphus sylvaticus*], Apio et al., 2010). Indeed, philopatry has been linked to lower mortality risk in black-tailed deer with higher home range overlap (Bose et al., 2017).

At the scale of the patch, patterns of interactions during foraging center on movement decisions related to entering and occupying a patch. Social foragers may experience scramble competition, where individuals exploit food patches before others can feed. In this instance, occupying a patch first is an advantage because individuals gain priority access to resources (Barrette & Vandal, 1986). During coordinated group movements, the position an animal occupies (e.g., leader or follower) has been correlated with dominance ranking in some species, with higher ranking animals tending to initiate movements (Conradt & Roper, 2003; Dumont et al., 2005; Šárová, Špinka, & Panamá, 2007; Šárová et al., 2010). This may give dominant leaders an additional advantage of making movement decisions that best fulfill their own physiological requirements (Fischhoff et al., 2007; Sueur et al., 2013; Patin, Fortin, Sueur, & Chamaillé-Jammes, 2019). At the same time, following individuals can either avoid aggressive, conspecific attacks or gain information about resources (Hemelrijk, 2000; Clark & Mangel, 1984; Beauchamp & Giraldeau, 1996).

In social foraging groups, the transmission of social information is dependent on the interactions individuals have with conspecifics mediated by social relationships among individuals (Camacho-Alpízar & Guillette, 2023). Because social information does not spread among group members at random, factors influencing social position subsequently influence the amount and flow of information among groups (Krause et al., 2015; Camacho-Alpízar & Guillette, 2023). Advantages such as information on resource patch location or quality may be available to group members that have more access to social information. Individual behavioural traits such as dominance may influence this – for example, in black-capped chickadees (*Poecile atricapillus*) dominant individuals received information from conspecifics at a higher rate than subordinate individuals (Jones et al., 2017). In an information-sharing group, the ability to exploit the findings of conspecifics may also be most advantageous to dominant group members when resources are easily monopolized (Garber, Bicca-Marques, & de Azevedo-Lopes, 2009) and dominant animals can further exploit resource discoveries of conspecifics. In experimental feeding trials in house sparrows, dominant birds tended to exploit the food discoveries of subordinates through aggressive encounters once food was located (Barta & Giraldeau, 1998; Liker & Barta, 2002). Thus, the social position an individual holds may infer an advantage through both resource access and competitive ability.

At the scale of a feeding site, individuals most closely interact with conspecifics of a foraging group, which may involve direct interactions reflecting differences in dominance interactions (Sterck, Watts, & Van Schaik, 1997). In contest competition, dominant individuals interfere with subordinate conspecifics through direct agonistic interactions thus allowing priority access to resources. Subordinate group members may incur foraging costs by increasing vigilance for dominant conspecifics (see Chapter 3) or due to the direct displacement of them from a feeding site (Appleby, 1980; Molvar & Bowyer, 1994; Smith & Cain, 2008; Marino, 2010; Côté, 2000; Ceacero et al., 2012). As such, studying the multi-scale, social interactions among individuals living in a group is key to understanding trade-offs that group members make between resource access and predation risk (Bowyer et al., 2020).

Partial migration occurs when some members of a population migrate and others do not, and is thought to be maintained through conditional fitness by balancing the trade-offs of the costs and benefits of migration. We studied behavioral interactions between migrant and resident elk in a partially migratory Ya Ha Tinda elk (*Cervus elaphus*) population at multiple scales when on their sympatric winter range adjacent to Banff National Park in Alberta. In the past fifty years, the population size has expressed fluctuations, rising to a high of approximately 2200 elk in the 1990s prior to declining to 400 – 500 animals over the last two decades (Berg et al., 2021), largely attributed to the recolonization of wolves in the area (Hebblewhite et al., 2006). Concurrently, there has been a shift in the proportions of migratory and resident elk; in the late 1990s, 95% of the herd migrated west onto high-elevation summer ranges in Banff National Park, which has declined to approximately 18% at the time of this study. Additionally, a third migrant tactic has increased in the past 20 years, with elk moving to low-elevation, multiple-use land east of the Ya Ha Tinda (Hebblewhite et al., 2006; Hebblewhite et al., 2018; Berg et al., 2021). Previous studies have shown that elk migrating to summer ranges in Banff National Park had higher pregnancy rates and fall calf weights that were linked to higher forage quality, implicating they return to the winter range in better condition than resident elk (Hebblewhite, Merrill, & McDermid, 2008; Hebblewhite & Merrill, 2011). Because growth rates of the migratory tactics were similar (Hebblewhite et al., 2018; Martin, Hebblewhite, & Merrill, 2021), it was hypothesized that resident elk compensated for lower summer nutrition by exhibiting winter habitat selection and movements that reflected exposure to higher forage resources than migrant, but this hypothesis was not supported; instead as the wintering elk population declined elk aggregation among individuals within migratory tactics increased (Merrill et al., 2020), suggesting that conspecific interactions may determine foraging advantages.

In this chapter, we focus on how interactions between migrant and resident elk at the home range, patch, and feeding-sites scales may reflect foraging advantages among elk across the three migratory tactics. We hypothesized that behaviors of resident elk would reflect dominance over migrant elk in winter because as year-round residents, they were more familiar with the range and less familiar migrant conspecifics. As a result, we predicted weekly home range overlap of resident would be greater than between migrants and residents. We also expected residents to occupy foraging patches before migrants more frequently than at random compared to migrants, affording a foraging advantage. In contrast, migrants would follow residents into patches gaining information from familiarity of residents with resources on the winter range. At the feeding site, we expected residents would displace migrants with aggressive interactions more often than migrants would displace residents. Additionally, resource concentration can influence interaction rates (Côté, 2000). Therefore, after controlling for elk age and number of elk in close proximity, we expected that interaction rates to increase at sites with lower biomass and as winter progressed because resources become depleted.

2. Methods

2.1 Elk capture, collaring, and monitoring

Adult female elk were immobilized, fit with unique ear-tags in both ears, and collared with GPS collars (Vectronic Aerospace, Berlin, Germany; models Vectronic Survey or Vectronic VertexLite, and Lotek Wireless, Newmarket, Ontario, Canada; model Lotek LifecyclePro) in winter between 2009 and 2020 by free-range darting from horseback (see Berg 2021 for elk capture details). Elk were aged via cementum annuli of a vestigial canine extracted at capture (Keiss, 1969). Collars collected GPS locations at 2-hour, 6-hour, and 13-hour fix rates, but telemetry data used were rarified to include only 2-hour fix rates and included only locations situated on the Ya Ha Tinda ranch lands between 1 November – 31 March. We omitted potentially erroneous GPS fixes (< 1%, including DOP > 10 or unreasonably long steps). All capture, handling, and observations of elk was in accordance with protocols approved by the Canadian Council on Animal Care Guidelines and approved by the University of Alberta Biosciences Animal Care and Use Committee (AUP#00000624).

2.2 Elk migration tactic

Individual elk were classified as resident (R), eastern (E) or western (W) migrants using the net-squared displacement method (NSD; Bunnefeld et al., 2011) in the R package 'migrateR' (Spitz et al., 2017) and post-hoc visual inspection using spring and summer locations from 6-hour or 13-hour fixes (Eggeman et al., 2016). Migrants generally moved > 15 km from the Ya Ha Tinda winter range for > 30 days (Eggeman et al., 2016). Migratory elk were classified by post-hoc visual inspection of summer ranges as being western migrants if they summered in or adjacent to Banff National Park west/south of the Ya Ha Tinda winter range or as being eastern migrants if they summered east of the Ya Ha Tinda winter range on multiple-use lands. Six of the 78 individuals (8%) in the study switched tactics during the summer between winters (western to resident n = 3; eastern to resident n = 2; resident to eastern n =1).

2.3 Home range analysis and overlap

To assess whether elk in different migratory tactics spatially avoided each other at the home-range scale, and whether the degree of spatial overlap changed over the winter, we compared weekly overlap in home ranges among elk following different migratory tactics. We determined weekly 95% home ranges of 78 elk using utilization distributions (UDs) on 30 – 168 2-hour elk GPS locations/week collected during the winters (1 November – 31 March) of 2015 – 2018 (Appendix A). We derived home ranges based on a fixed kernel analysis (Worton, 1989) with the reference bandwidth as the smoothing parameter using the R package 'adehabitatHR' (v 1.8.20; Calenge, 2007; 2015). In a study using elk telemetry data, Kie (2013) found that the reference bandwidth produced a more accurate estimate of a known home range with large sample sizes compared to least-squares cross-validation or *ad hoc* bandwidths; in this study, visual inspection of the outputs of this method adequately represented elk winter space use. We determined overlap between home ranges of two elk using a Volume of Intersection index (VI, Seidel, 1992), which accounts for intensity of use in overlapping areas of the home range and ranges from 0 (no overlap) to 1 (complete overlap).

We calculated pair-wise VI between for 165 individual elk-winters (Appendix A) and took the mean of pairs for each of 9 combinations of migratory tactics (e.g., resident-resident, RR; eastern-eastern, EE; and western-western, WW) and resident-migrant pair type (resident-eastern, RE; resident-western, RW) during each week. To determine differences in VI among migratory pair type and whether this changed over time, we modelled VI as a function of pair type (RR, RE, RW, EE, WW), week of the winter, and their interaction using a beta regression model. We used Akaike's Information Criterion corrected for small sample size (AICc) to select the best-fit model. We included elk pair ID as a random effect to account for pairs with multiple occurrences, and used resident-resident pair type as the reference category.

2.4 Sequential use of patch locations

We assessed patterns in the sequential use of locations on the Ya Ha Tinda by elk following different migratory tactics to determine whether elk avoided interactions while foraging through spatiotemporal segregation by sequentially occupying areas. We determined sequential use of areas on the winter range by elk from 1 November to 31 March of 2015 – 2018. We defined an event as the instance of use (GPS locations) of a cell by an elk and a "use sequence" as the occupancy of a cell by an individual elk (subsequent elk) within a 4-hr period after the same cell was occupied initially by a different elk (lead elk). To derive a use sequence, we delineated 2289 unique 100-m^2 cells across the winter range delineated as the extent around all GPS points used during the winter period by focal elk (Figure 1). We used 2-hour diurnal (0600 – 1900 h) GPS locations from 78 GPS-collared elk (45 resident, 18 eastern, and 15 western elk) to define sequences because they were most active and assumed foraging during this time (Merrill et al., 2020). We classified use sequences as one of that same 9 migratory combinations used in the VI analysis above, where order of the migratory tactic indicates the lead elk and subsequent elk occupying a cell.

We tested for differences in the probability of different types of use sequences observed from random expectation and other use sequence types following the approach of Martinig et al. (2020), which was developed to test whether predators followed prey or prey followed predators through movement passages more than expected at random as documented on remote cameras. We first determined the expected probability (p_e) that a type of use sequence occurred (e.g., for RM, a migrant occupies a cell given it was occupied by a resident within 4 hr) based on the number of events of each type of migratory elk in the sequences as:

$$p_e(y|x) = \frac{x}{n} \cdot \frac{y}{n}$$

where n is the total number of events (i.e., GPS locations) of elk included in the observed use sequences, x and y are the number of events of each migratory type in a type of use sequence of interest (e.g., RM, x = number of events of residents; y = number of events of migrants).

Once p_e is calculated for a specific type of use sequence (e.g. RM), we used p_e to derive the expected number of observations (k_e) of that sequence type in the observed dataset as:

$$k_e = (m) \cdot p_e$$

where m is the total number of use sequences of any type in the observed data. We conducted a two-tailed binomial test to determine whether the observed probability (p_o) of a use sequence occurring differed significantly from the expected probability (p_e) using the *binom.test* function in the base R package ‘stats’ (v 3.6.3; R Core Team 2022). The binomial test uses the following equation for $p_o > 0$ and $0 > p_e > 1$:

$$p_o = \binom{n}{k_o} p_e^{ko} (1 - p_e)^{n-ko}$$

We calculated the 95 percent confidence intervals around $\boldsymbol{p_o}$ and inferred a significant difference between the observed p_o and the expected number of use sequence p_e and concluded they differed if they did not fall within confidence intervals of p_o.

2.5 Feeding-site interactions

We assessed whether individual elk following different migratory tactics interacted at different rates or displayed different types of interactions during foraging at a feeding site scale, as well as factors influencing interactions among elk. We observed 45 unique focal animals with 18 of the 45 individuals sampled in both years for a total of 64 elk-winters. Elk were observed 5 – 8 times (mean ± SE = 7 ± 0.13) per winter between 14 January to 4 April 2019 (n = 30 focal elk) and 23 January 2020 – 3 April 2020 (n = 34). For each observation, focal animals were drawn randomly without replacement from a sample of collared elk prior to being located via telemetry to reduce observer bias. There was a minimum of 48 hours between observations on the same individual. Elk were observed from a distance of 80 – 1500m using a 60x magnification spotting scope (Vortex Optics, Barneveld, WI) between 0700 to 1900, with observations occurring mostly between 0700-1000 (50.7%) and 1600-1900 (31.5%) when elk actively forage (Merrill et al. 2020).

Focal elk were continuously monitored until the animal moved out of sight, bedded down, began ruminating while standing, or became vigilant to the observer. Changes in interactions were recorded into a handheld voice recorder (Olympus VN-541PC) and later time-stamped using the program JWatcher^{TM} (Blumstein, Daniel, & Evans, 2006). We defined an interaction with the focal animal as a conspecific approaching within 2 m. An interaction event began upon the cessation of a previous behaviour (e.g., foraging, vigilance) and ended with the resumption of the previous behaviour or onset of another (Fortin, Boyce, & Merrill, 2004b). We classified interactions based on the response of the focal animal as one of three responses. An aggressive response occurred when the focal animal approached a conspecific and the interaction result in either a physical contact (bite, kick, head swing) or a threat (ears pinned, head back, teeth bared, movement in the direction of the conspecific; Thouless & Guinness, 1986) and the conspecific was displaced by at least one elk length (2 m). A submissive response occurred when the focal animal was physically displaced at least one elk length by an aggressive conspecific either through contact or a threat (Fournier & Festa-Bianchet, 1995; Veiberg et al., 2004). A neutral response occurred when an individual was physically contacted by a conspecific without displacement, without returning an aggressive response, or displayed affiliative behaviour such as allogrooming. The identity and migrant tactic of focal animals was known whereas the identity and tactic of interacting conspecifics was not unless the conspecific was also a collared individual.

At the initiation of an observation, we recorded the position of the focal animal in the herd (centre or periphery) and elk density around focal animals. We followed Liley & Creel (2008) and designated an animal in the centre if an attacking predator would encounter at least one other elk before the focal elk, and peripheral if an attacking predator would encounter the focal before a centrally located conspecific. Density was measured as the number of elk in 1 elk length (~ 2-m), 5 elk lengths (~10-m), and 10 elk lengths (~20-m) in concentric circles around the focal animals. At the end of an observation period, the UTM coordinates of the midpoint of the foraging path of the focal animal were determined using a compass (Garmin eTrex, Garmin, Olathe KS) and a rangefinder (m; Leupold RX-2800 TBR/W, Leupold & Stevens Inc., Beaverton OR), and plotting the location in the field using satellite imagery (Google Earth Engine, 2019). Within 2 – 5 days of an observation and prior to new snowfall, we sampled the amount of forage biomass (g/m^2) from 1 – 2 0.25-m^2 quadrats from ungrazed areas within 5 m of the estimated foraging path midpoint. We clipped graminoids (including grasses) and forbs in the quadrat to 2cm from the ground, dried at 50°C for 48hrs, and weighed to the nearest 0.1g. If snow covered vegetation at the sampling point, we first measured snow depth at the centre of the quadrat, then removed all snow from the sampling area before clipping vegetation. Shrubs were excluded from biomass estimates as previous fecal analysis of winter elk diets indicated that elk primarily foraged on grasses and graminoids during the winter (Hebblewhite, 2006), and elk were observed eating shrubs in 0.01% of observations.

We assessed whether the rate of interactions (number/minute) differed among migratory tactics and factors influencing the rate of interactions. We first tested whether mean interaction rate among all three tactics, regardless of interaction type, differed between years using a negative binomial mixed-effects model of the number of interactions and included an offset of the natural of observation time (minutes). We included a random effect of ID to account for multiple observations on the same animal, and included year as a factor if a difference was found. We then modelled the rate of all interactions as a function of elk age, migratory tactic, local elk density (number of elk in 2-m, 10-m, and 20-m radius concentric circles around the focal animal), position in the herd (periphery or centre), forage biomass along the foraging path, and Julian day. We tested for correlation among variables prior to modelling and did not use variables correlated at $r = |0.5|$ in the same model. Elk-specific factors included age (years) determined through tooth cementum annuli (Keiss, 1969). To determine whether age influenced differences in interaction rates, we tested for age differences between migrant tactics using an ANOVA. Group-specific factors included local density (number of elk in 2-m, 10-m, and 20-m radius concentric circles around the focal) and position in the herd (periphery or centre; described in Methods). Because density measurements at each radius are inherently non-independent and interaction rates had a qualitatively similar relationship to density at each radius (2-m, 10-m, 20-m; Appendix C), we evaluated each measure of density using AIC_c model selection and selected the density whose univariate model had the lowest AIC_c (Appendix C). Environmental factors included forage biomass (estimated g/m^2 from samples at observation locations) and day of winter from 1 January. All analyses were performed using R Statistical Software (R Core Team 2022).

We modeled counts of interactions using a negative binomial, mixed-effects model with length of the observation period (minutes) as an offset, and elk ID as a random effect to account for multiple observations on the same individual. We used the *glmmTMB* function from the R package 'glmmTMB' (v1.4.1717; Brooks et al., 2017). We used an AIC_c model selection framework to examine support for variables influencing interaction rates, where models within ΔAIC_c of 2 were considered equally supported. Eastern migrants and the central position within a group were set as reference classes. Next, we assessed whether the focal elk was more likely be aggressive (1) or submissive (0) during an interaction given the Julian day, migratory status, age, number of elk around the focal animal, position in the group, and forage biomass at the site. We used the *glmer* function from the R package 'lme4' (v1.1.31; Bates et al., 2015) to perform this analysis using a mixed-effects logistic regression model with a logit link, including elk ID as a random effect to account for multiple observations across years. Prior to analyses, we tested for correlation among variables and did not use variables correlated at $r = |0.5|$ in the same model.

3. Results

3.1 Home range overlap

We analyzed home range overlap based on 175 elk-winters (105 residents, 37 eastern migrants, 33 western migrants). We found no difference in mean VI values of elk pairs among years ($P = 0.39$, df = 3, Kruskal-Wallis $\chi^2 = 3$) and thus pooled VI values across winters for analysis. Mean weekly home range overlap among all migratory types across the winter was generally high (0.83 ± 0.12, $\bar{x} \pm$ SD). Twenty-four of the 59,122 (0.04%) elk pairs analyzed had a VI of zero. There was little model uncertainty in the top model indicating VI increased over time and differed among migratory tactic pairs (Table 2.1). All pair types increased overlap as the winter progressed, and VI values among all migratory tactics became more similar during late winter. Eastern elk had the highest overlap with other eastern elk compared to resident-resident pairs, with western-western pairs showing lowest overlap (Table 2.2).

3.2 Sequential use of patch locations

We observed a total of 171,370 events for 78 elk across the winter, of which 64% were residents, 22% were eastern migrants, and 14% were western migrants. From these events, we observed from 1446 – 38 507 sequences per pair type with resident-resident sequences making up the majority (40%) of sequences and western-western sequences making up the smallest proportion (1%).

Eastern and western migrants used areas previously occupied by residents more than expected at random, whereas other residents used areas previously occupied by residents less than expected (Table 2.3). Residents but not western migrants used areas less after eastern migrants, whereas eastern migrants used areas sequentially after other eastern migrants more than expected. Only eastern migrants used areas previously occupied by western migrants more than expected.

3.3 Feeding-site interactions

We observed 135 interactions in 2019 and 122 in 2020 for a total of 257 interactions among all migratory tactics during 76.8 hours of observation. We omitted 9 interactions between an adult female and her calf during 2019 from the analysis. Of the 248 responses recorded, 125 were from residents, 73 from eastern migrants, and 50 from western migrants. Rates of interactions did not differ between years (- 4.9 ± 3.3; $\beta \pm$ SE); thus, data from both years were pooled in further analyses.

Mean rates of any type of interaction for resident, eastern, and western migrants were 0.065 ± 0.04, 0.068 ± 0.08, and 0.043 ± 0.05 ($\bar{x}$ ± SD) per minute (Figure 2.3a), respectively, with more aggressive interactions by eastern migrants and more neutral interactions by resident elk (Figure 2.3b, $\chi^2 = 9.43$, df = 4, $P = 0.05$). Elk density within one elk-length best explained number of interactions with a focal animal better than other densities (Appendix C) and was the only density variable included in further analyses. No other variables were highly correlated. However, eastern migrants were younger in age (7.25 ± 3.5 years) than both residents (10.55 ± 4.4 years) and western migrants (10.33 ± 3.7 years, $P < 0.05$, df = 2, F = 26.23).

There was high model uncertainty (7 models within $\Delta 2$ AIC$_c$) in predicting rates of interactions between the focal animal and other elk but number of animals nearby and low biomass at site were consistently in the top models (Table 2.4, Appendix D), with rate of interactions increasing with increasing elk density and lower forage biomass. There was only moderate support for rate of interactions differing between migratory tactics once elk density and biomass were accounted for (Table 2.5). Resident and western migrants both exhibited lower interaction rates compared to eastern migrants, with most uncertainty in resident and eastern migrant differences as the CI of the β parameter for resident elk overlapped zero (Table 2.5).

There also was model uncertainty in predicting whether a focal animal would respond aggressively or submissively in an interaction, with the top models consistently including the day of winter, elk age, and density of elk nearby (Table 2.4). Elk were more aggressive as the winter season progressed, were younger, and when density was lower. There was evidence that both resident and particularly western elk were less aggressive than eastern elk (Table 2.6).

4. Discussion

We studied the social interactions among elk following different migratory tactics on their sympatric winter range at 3 spatial scales and found differences in behaviour at the patch and feeding-site scale but not at the home-range scale. Home range overlap was generally high among all migrant tactics when on their sympatric winter range indicating elk did not spatially segregate to any large extent. Within migratory tactics, we expected to see the highest overlap among resident elk because they consistently remained in the same large group year-round, but instead overlap was highest among individual eastern migrants. This contrasts with previous studies of group cohesion on the Ya Ha Tinda winter range, where both resident and migrant elk associated most strongly with other residents (Robinson, Hebblewhite, & Merrill, 2010; Merrill et al., 2020). Prior studies on the Ya Ha Tinda have contrasted only overlap and cohesion between residents and western migrant elk, thus the addition of eastern migrants as a new component of the herd is a novel addition. In contrast, overlap was least between western migrants, which may reflect that western migrant elk summer in small, isolated groups (Hebblewhite & Pletscher, 2002).

Despite these patterns, overlap among all tactics increased in late winter, which we attribute to grassland forage being depleted and forcing elk to aggregate in areas with the highest remaining biomass. Elk in winter show strong selection for high forage biomass areas (Merrill et al., 2020), and forage depletion over the winter can be as high as 94% on the Ya Ha Tinda (McInenly, 2003). Aggregation in response to forage depletion has been observed in moose (van Beest, Mysterud, Loe, & Milner, 2010), where selection for high forage biomass increased as available high-quality forage declined (and see Edenius, 1991; Shipley, Blomquist, & Danell, 2011), and similarly white-tailed deer altered forage selection in response to depletion (Kohlmann & Risenhoover, 1994). Alternatively, higher aggregation by elk may be in response to high wolf predation risk. For example, Merrill et al. (2020) reported that as the Ya Ha Tinda elk population size declined, aggregation of elk increased in winter, which they attributed to being an anti-predator behavior because wolf predation is the highest source of mortality in adult female elk in our study area (Hebblewhite et al., 2018).

Because there was little evidence of spatial segregation at the broad scale, we expected to find differences in elk following different migratory tactics at the scale of the patch and feeding-site. We expected that because resident elk were more familiar with foraging opportunities, they would show first occupancy of patches and be dominant over migrant elk, giving them a foraging advantage on the winter range. At the patch scale, this hypothesis was supported because resident elk occupied patches first with both eastern and western migrants subsequently using patches after resident elk more than expected, whereas residents used areas previously occupied by residents less than expected. These behaviors suggest migrant elk may exploit residents' knowledge of foraging opportunities across the range (sensu Merkle, Fortin, & Morales, 2014) and capitalize on social information available from residents. While resident animals may be at an advantage by accessing forage areas first, migrants may also be at an advantage if they followed resident elk because they lack the knowledge of resource distribution on the winter range. At the same time, a further advantage for migrant elk in following residents may have been that that resident elk were most familiar with the spatial distribution of predation risk. Robinson and Merrill (2013) showed that resident elk on the Ya Ha Tinda expressed more vigilance in risky areas on the winter range (i.e., near timber edge and far from humans) compared to western migrants, which may reflect a greater familiarity with patterns of wolf use in the area. Indeed, the strategy of migrants in exploiting the residents' information about the trade-offs in foraging and predation risk may contribute to why we see little spatial segregation at the scale of the home range.

At the feeding-site scale, we also expected residents to be dominant and to be more aggressive compared to migrants over high-value resources in order to compensate for lower quality summer forage. However, resident elk did not display more aggression as would be expected when biomass was low. Additionally, Merrill et al. (2020) found little difference between resident and migrant density-dependent habitat selection on the winter range, suggesting foraging decisions made by resident elk are not compensatory for summer forage quality. A limitation in our observations was that not all elk were marked such that we could recognize both interacting individuals (only focal identity was known). This limited us in being able to determine dominance hierarchies among females on the winter range and to fully assess behavioral responses of elk in different migratory tactics to each other. Nonetheless, residents comprised the majority of the wintering herd with about twice the number of residents as in either of the other migratory tactic (Berg et al., 2021). As a result, it is likely that most resident interactions were with other residents. Resident elk engaged in relatively more neutral interactions overall (Figure 2.3), which includes affiliative behaviours such as allogrooming that may serve to reinforce social bonds (Sato, Tarumizu, & Hatae, 1993; Val-Laillet et al., 2009) that exist with other familiar residents. Weckerly (1999) found that female Roosevelt elk displayed a high degree of social bonding within groups, which consequently contributed to group stability. Because resident elk retain large, cohesive groups in summer (Hebblewhite et al., 2006; Eggeman et al., 2016), it is likely there is a fairly well-established social hierarchy compared to migrant elk.

Instead, we found eastern migrant elk were the most aggressive, while western elk interacted less and were more likely to be submissive than the other two tactics. Eastern elk generally were younger than resident and western elk on average, which we would not have expected — other studies have shown an inverse relationship between age and aggression with younger animals tending to be more submissive (Rutberg, 1986). In female red deer, younger animals learn to be subordinate to older females early on, because dominance is influenced by experience (Thouless & Guinness, 1986). This ranking is often retained even when both animals reach similar body size and fighting ability (Franklin, Mossman, & Dole, 1975; Rutberg, 1986). However, Thouless and Guinness (1986) also reported that young female red deer were more likely to engage with and win against older females if both animals were unfamiliar with one another and a previous dominance relationship had not been established (Lazo, 1994; Weckerly, 1999). We found eastern migrants had high home range overlap with both western and resident elk, which may increase the chance that eastern elk encountered unknown older females against which they are able to win bouts.

Despite these differences, overall rates of interaction were relatively infrequent, took place quickly (Chapter 3), and rarely resulted in physical contact, which is similar to other studies of wild group-living ungulates (Rutberg, 1986; Sih, Bell, & Johnson, 2004; Le Pendu et al., 1995, 2000). Nevertheless, interactions increased under certain conditions. As might be expected, we found elk interacted more frequently with conspecifics when in an environment where the local density of elk was high, which is consistent with other ungulate studies. For example, Vander Wal et al. (2012) found that even when not resource-limited, elk increased encounter rates with increasing group densities. At high neighbour density, a random search rate during foraging would be expected to result in encountering more conspecifics (Mobæk et al., 2012). Although we did not address movement rates and patterns specifically in response to conspecifics in our study, elk on the Ya Ha Tinda have been shown to increase step length and decrease residence time in foraging patches with overall increasing population density (Merrill et al., 2020), but whether this translates into an actual increase in interactions would depend on conspecific vigilance and navigation in response to other individuals. Additionally, although interaction frequency was not strongly correlated with position in the herd, interactions decreased on the periphery (Appendix D) as might be expected if central animals experience higher neighbour density.

At the same time, because conspecific interaction frequency increased with low biomass, the importance of resource defense as forage biomass declines may result in increased aggression, especially under high local conspecific density. Contrary to our expectation, lower forage biomass did not increase the probability that an elk interacted aggressively as expected if resource defense was highly important (Weckerly, 1999). This may reflect that in tight aggregations, the risk of aggression may outweigh the benefits of competition for resources as the cost of engaging in agonistic encounters with numerous potential competitors becomes too high. Vander Wal et al. (2012) found that female elk interacted less aggressively when highly aggregated compared to moderately aggregated. More individuals in close proximity also may also reduce an individual's ability to identify opponents (Kendrick et al., 1995). Côté (2000) noted that at crowded bait sites, mountain goats were more likely to respond submissively when approached by an unidentified aggressor from behind, regardless of dominance ranking. Interactions among female elk on the Ya Ha Tinda may instead primarily reflect the maintenance of social relationships within the herd rather than direct resource competition (Pendu et al., 2000; Weckerly & Ricca, 2013).

Frequent conspecific interactions can diminish search and foraging time and present a foraging cost. When discrete foraging patches have higher value and are defendable (Vickery et al., 1991), such as during late winter when forage is depleted or snow is present (Robinson & Merrill, 2012), aggressive elk may gain an advantage over submissive conspecifics and gain access to limited forage resources. However, because both forage quality and distribution are relatively homogenous across the Ya Ha Tinda grassland, the benefit of exploiting others' forage patches may be less than the cost of engaging in aggressive take-overs. Furthermore, the time elk spent in any interaction was relatively short (~ 5 second/interaction) and time spent interacting with conspecifics comprised < 1.5% of time observed during active foraging (Chapter 3), indicating conspecific interactions may impose little direct limitation on foraging time in the open grasslands of the Ya Ha Tinda. Instead, the foraging costs may be related more to elk investing time into pre-emptive vigilance or post-interaction vigilance for conspecific attacks (Chapter 3), with a corresponding decrease in cropping rate especially during encounter-limited foraging (Thouless, 1990; but see Kurpiers & Weckerly, 2022).

Our study shows that elk use multiple-scale strategies to in how they interact on their sympatric winter to cope with foraging under high risk. Elk on the Ya Ha Tinda were not spatially segregated at the home range scale, likely due in part to the anti-predator benefits of grouping and distribution of forage. Instead, small-scale patterns of interactions were evident at the patch and individual level on the winter range. Although resident elk may be at an advantage from better knowledge of risk and forage areas on the winter range (Robinson & Merrill, 2013), migrant elk may offset this by following residents into areas of higher forage. Furthermore, aggressive eastern elk may not only exploit resident knowledge, but capitalize on conspecific foraging discoveries by competing for resources (Beauchamp & Giraldeau, 1996). Behavioural differences may influence density-dependent fitness balancing between strategies; lower proportions of aggressive eastern elk may benefit from exploiting less dominant elk that occur at higher proportions, which may instead benefit from stronger social ties on the winter range (Bouissou et al., 1976; Cameron, Setsaas, & Linklater, 2009). Although interactions occurred at low frequency and took up little overall foraging time, the potential for interactions to influence other behaviours (i.e., vigilance, foraging efficiency) should not discount social interactions as an important consideration in future studies of small-scale behavioural trade-offs between migratory tactics on a shared range.

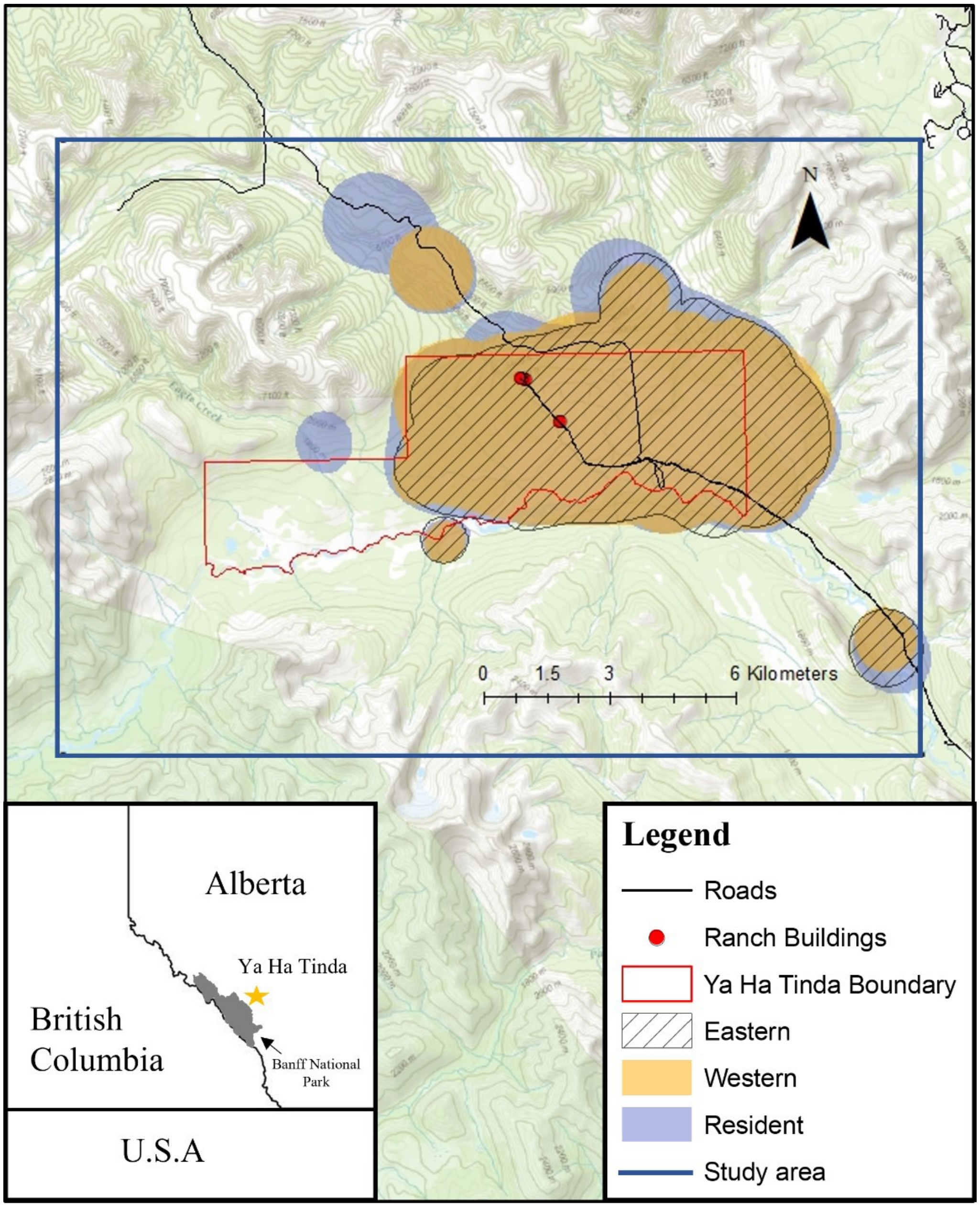


Figure 2.1. Study area of the Ya Ha Tinda winter range in the foothills of the Rocky Mountains in Alberta, Canada during winters 2015 – 2018. Includes average elk 95 % utilization distributions of GPS-collared resident (blue), eastern (grey hatch), and western (yellow) elk. The extent of the winter study area, determined by the extent of all GPS locations recorded during 1 November – 31 March, is shown by the dark blue rectangle. Roads are shown as dark grey lines, the boundary of the YHT property is shown in red, and ranch buildings are indicated by red circles.

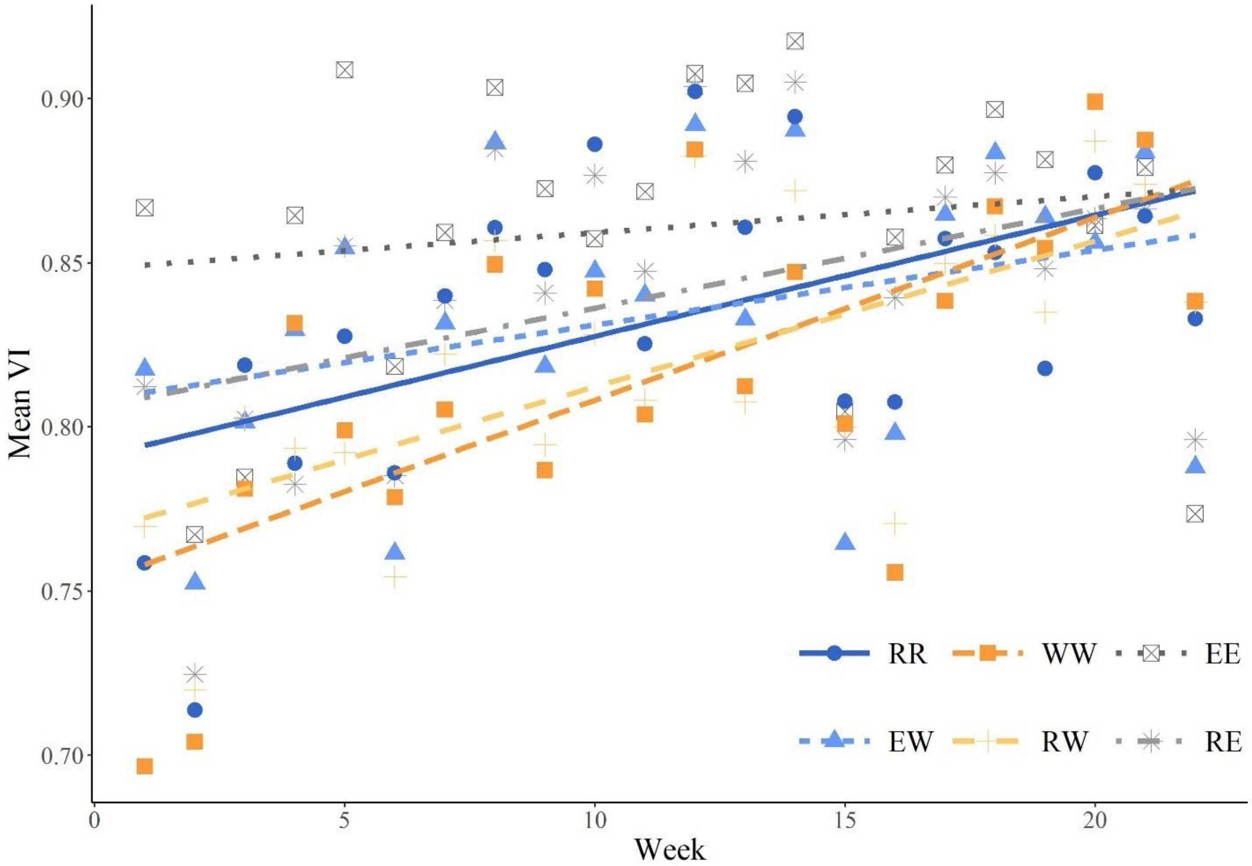


Figure 2.2 Average weekly Volume of Intersection (VI) values between all migratory pair types (resident-resident, resident-eastern, resident-western, eastern-eastern, western-western, and eastern-western) across the 2015 – 2018 winter period (n weeks = 22) on the Ya Ha Tinda ranch, adjacent to Banff National Park, Alberta Canada. Lines represent a linear model fit.

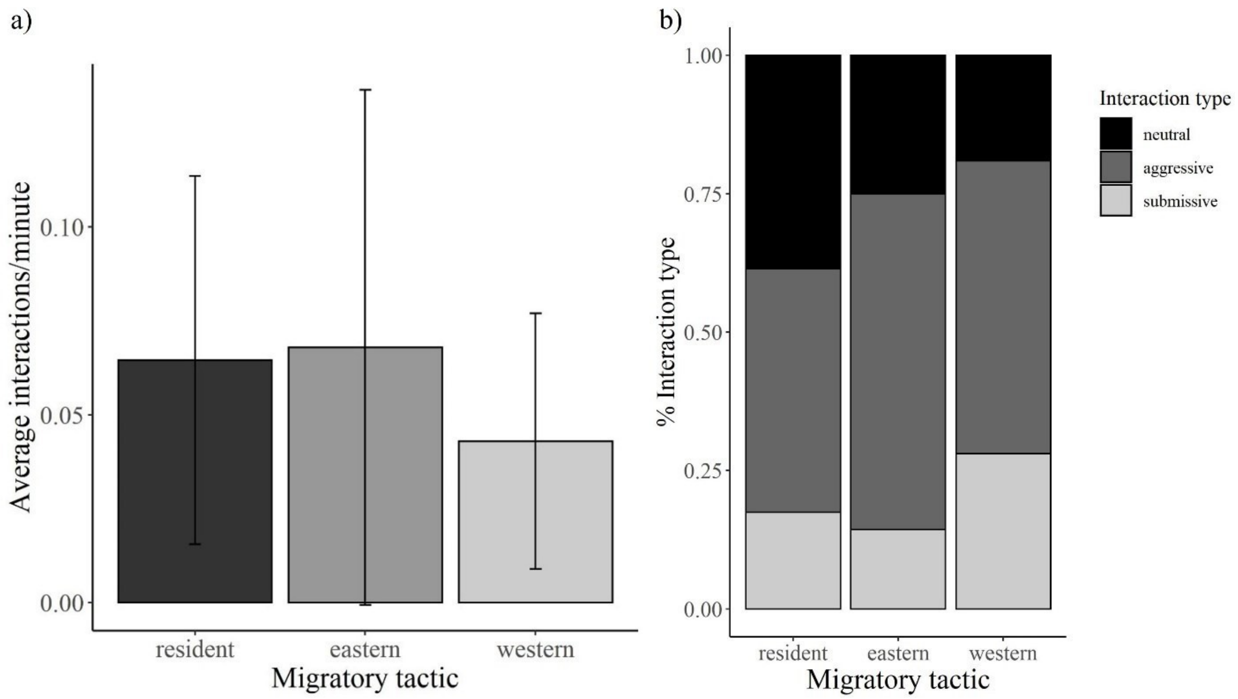


Figure 2.3. Mean interaction rate (interactions/minute; panel a) and proportion of total interactions classified as neutral, aggressive, or submissive (panel b) during behavioural observations for resident, eastern, and western elk during winters 2019 – 2020 on the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada. Error bars indicate ± 1 SE.

Table 2.1. Summary of model selection results for Volume of Intersection values between home ranges of resident, eastern, and western elk based on 95% kernel utilization distributions across 22 weeks during the winters (1 November – 31 March) of 2015 – 2018 on the Ya Ha Tinda ranch, adjacent to Banff National Park, Alberta Canada. Covariates include pair type, week of winter, and their interaction. The reference category for pair type was set to resident-resident.

Model structure	k	AIC_c	Δ AIC_c	AIC_c Wt.
Pair type + week + pair type x week	14	-103849	0.00	1.00
Pair type + week	9	-103676	173.0	0.00
Week	4	-102949	900.0	0.00
Pair type	8	-101730	2119.0	0.00
Null	3	-100842	3007.0	0.00

Table 2.2. Beta coefficients (*β*) with standard error (SE), upper and lower 95% confidence intervals (CI) for the top model parameters based on AIC_c model selection for a beta regression model predicting volume of intersection values between elk pair utilization distributions. VI values were calculated from GPS-collar data collected during the winters (1 November – 31 March) of 2015 – 2018 on the Ya Ha Tinda ranch, adjacent to Banff National Park, Alberta Canada. Resident-resident was used as the reference pair type.

		95% CI	
Variable	*β* ± *SE*	Lower	Upper
Intercept	1.19 ± 0.01	1.17	1.21
Pair type – resident-eastern	0.28 ± 0.02	0.24	0.32
Pair type – resident-western	- 0.27 ± 0.02	-0.31	-0.23
Pair type – eastern-eastern	0.62 ± 0.04	0.54	0.69
Pair type – western-western	- 0.48 ± 0.05	-0.58	-0.38
Pair type – eastern-western	0.20 ± 0.04	0.12	0.28
Week	0.02 ± 0.001	0.02	0.02
Week x resident-eastern	- 0.004 ± 0.001	-0.01	-0.002
Week x resident-western	0.007 ± 0.001	0.01	0.01
Week x eastern-eastern	- 0.02 ± 0.002	-0.02	-0.01
Week x western-western	0.02 ± 0.003	0.02	0.01

Table 2.3. Sequences of use for resident (n = 45), eastern migrant (n = 18) and western migrant (n = 15) elk on the Ya Ha Tinda between 1 November – 31 March, 2015 – 2018. Number of observed sequences (n = 96 302) were calculated from diurnal GPS collar fixes, with the number of sequences per pair type indicated by k_o. Number of expected sequences (k_e) are based on the binomial distribution of observed (p_o) and expected (p_e) probabilities. Included are 95% CIs and *P* value calculated for the difference in observed (p_o) and expected probabilities (p_e). Significance is inferred if the observed probability and corresponding 95% CIs do not overlap with associated expected probability, p_e.

Pair type*	No. observed sequences (k_o)	No. expected sequences (k_e)	Observed probability (p_o)	Observed 95% CI (p_o)	Expected probability (p_e)	*P* value
RE	15084	14652	0.157	(0.154, 0.159)	0.152	< 0.005
RW	7919	7570	0.082	(0.081, 0.084)	0.079	< 0.005
RR	38507	39287	0.400	(0.397, 0.403)	0.408	< 0.005
ER	14396	14652	0.149	(0.147, 0.152)	0.152	0.022
EW	2867	2823	0.030	(0.029, 0.031)	0.029	0.401
EE	5677	5464	0.059	(0.057, 0.060)	0.057	0.003
WR	7452	7570	0.077	(0.076, 0.079)	0.079	0.159
WE	2954	2823	0.031	(0.030, 0.032)	0.029	0.013
WW	1446	1459	0.015	(0.014, 0.016)	0.015	0.752

*Pair type R = resident, W = western migrant; E = eastern migrant, where first letter indicates migratory tactic entering area first, second letter indicates migratory tactic subsequently entering

Table 2.4. Model selection results for two candidate model sets including number of interactions between focal elk and conspecifics and type of interactions (aggressive or submissive) during foraging observations based on AIC_c model selection. Covariates included in the models include migrant, focal elk age, Julian day of winter, biomass, position, and density of conspecifics. Models were considered competitive if within Δ2 AIC_c**.** Observations were recorded during January - April 2019 – 2020 from GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta Canada. Full model selection results in Appendix D.

Number of interactions	k	AIC_c	Δ AIC_c	AIC_c Wt.
Density - biomass	5	789.6	0.00	0.21
Density – biomass + migrant tactic	7	790.2	0.61	0.12
Density - biomass + position	6	790.6	0.95	0.13
Density - biomass - day	6	790.6	0.99	0.13
Density - biomass - age	6	790.6	1.01	0.13
Density – biomass + migrant tactic – day	8	791.3	1.63	0.10
Density – biomass + migrant tactic + position	8	791.5	1.82	0.09
Density – biomass + migrant tactic – age	8	791.8	2.15	0.07
Null	3	807.0	17.32	0.00
Type of interaction (aggressive/submissive)				
Day - density - age - migrant tactic	7	181.8	0.00	0.26
Day - density - age	5	182.3	0.53	0.20
Day - density- age - biomass - migrant tactic	8	182.9	1.10	0.15
Day - density - age - biomass	6	183.2	1.43	0.13
- Density - age - migrant tactic - biomass	7	184.6	2.86	0.06
Null	2	192.4	10.64	0.00

Table 2.5. Beta coefficients (*β*) with standard error (SE) and upper and lower 95% confidence intervals (CI) for parameters of the top 5 models based on AIC_c model selection for a negative binomial mixed-effects model of the number of interactions observed among resident, eastern, and western migrant elk. Covariates included density, biomass, focal age, and Julian day of winter (from January 1). Central position and eastern migrant were set as reference categories for position and migrant tactic. Observations were recorded during January – April, 2019 – 2020 from GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta Canada. Full results from top model estimates can be found in Appendix D.

		95% CI	
Variable	*β* ± *SE*	Lower	Upper
Density	0.32 ± 0.07	0.19	0.47
Biomass	- 0.002 ± 0.001	- 0.004	0.0001
Resident	- 0.13 ± 0.23	- 0.59	0.32
Western	- 0.49 ± 0.27	- 1.02	- 0.04
Intercept	- 2.89 ± 0.26	- 3.40	- 2.38

Table 2.6. Beta coefficients (β) with standard error (SE) and upper and lower 95% confidence intervals (CI) for parameters of the top 4 models based on AIC_c for a logistic mixed-effects model of interaction types observed among resident, eastern migrant, and western migrant elk. A random effect of individual elk was included in all models. Density, biomass, focal age, and day of winter were included in candidate models. Eastern migrants were set as the reference migrant tactic. Full results from top model estimates can be found in Appendix D.

		95% CI	
Variable	$\beta \pm SE$	Lower	Upper
Age	- 0.15 ± 0.06	- 0.27	- 0.04
Day	0.03 ± 0.01	0.003	0.05
Density	- 0.43 ± 0.15	- 0.71	- 0.14
Resident	- 0.15 ± 0.62	- 1.37	1.06
Western	- 1.28 ± 0.65	- 2.56	0.00
Intercept	1.94 ± 0.94	0.10	3.78

CHAPTER 3 – INFLUENCE OF CONSPECIFIC INTERACTIONS ON VIGILANCE BEHAVIOUR AMONG MIGRANT TACTICS IN A PARTIALLY-MIGRATORY ELK POPULATION

1. Introduction

Vigilance behaviour increases the likelihood of detecting stimuli in the environment and thus is an important strategy to evade predation and avoid harmful interactions with conspecifics (FitzGibbon, 1989; Boland, 2003; Watson, Aebischer, & Cresswell, 2007). Variation in vigilance as an anti-predator tactic can be influenced by habitat conditions such as openness and distance to cover, group size and position in a group, and the predator community (Mcnamara & Houston, 1986; Caro, 2005; Halofsky & Ripple, 2008; Liley & Creel, 2008; Pays et al., 2012). For example, mule deer were more vigilant in forested habitat where visibility was lower compared to open areas and on the edge of a forest where predation risk from cougars was highest (Hernandez, Laundre, & Gurung, 2005). Conspecific monitoring for others' responses to predation risk also can be advantageous (Dehn, 1990; Ellard & Byers, 2005), and collective predator detection may decrease per capita vigilance and increase time for other behaviors (Pulliam, 1973; Powell, 1974; Kenward, 1978; Elgar, 1989). Indeed, in many group-living species, there exists a negative relationship between individual vigilance and group size (Elgar 1989; Dannock, Blomberg, & Goldizen, 2013; Ortiz et al., 2019; Han et al., 2020; but see Jones, 1998; Rose & Fedigan, 1995; Treves et al., 2001) such that improved detection of predators through group vigilance has long been considered a major influence of group formation (Hamilton, 1971; Alexander, 1974).

Vigilance also is used for directly monitoring conspecifics to gain social information related to food location (Bertram, 1980; Smith et al., 2004; Coolen, Giraldeau, & Lavoie, 2001) and to avoid injury from aggressive encounters (Waite, 1987; Weckerly, Ricca, & Meyer, 2001). In fact, as group size increases, vigilance has been shown to shift primarily from anti-predator to predominantly conspecific monitoring, although this can vary across circumstances (Treves, 1998; Favreau, Goldizen, & Pays, 2010). For instance, conspecific vigilance may increase with more group members in close proximity (Hirsch, 2002; Kutsukake, 2006; Gaynor & Cords, 2012) because the threat of agonistic contest competition increases (Knight & Knight, 1986). Blumstein et al. (2001) reported vigilance time in quokka (*Setonix brachyrus*) increased in response to the number of neighbours within 10-m compared to 50-m distance. Similarly, time spent vigilant and the length of vigilance bouts in giraffes (*Giraffa camelopardalis*) increased when neighbours were present within 10 m (Cameron & Du Toit, 2005). At the same time, vigilance may decrease as individuals in a group engage in scramble competition for fewer resources (Beauchamp & Giraldeau, 1996; Blumstein et al., 2001; Rieucau & Giraldeau, 2009). In this case, the dominance status of neighbours may influence vigilance behaviour (Gaynor & Cords, 2012), as subordinate animals may be prone to more frequent or intense attacks and consequently direct more visual attention to dominant or unfamiliar animals when nearby either before or after an interaction (McNelis & Boatright-Horowitz, 1998; Cameron & Du Toit, 2005; Pannozzo et al., 2007; MacIntosh & Sicotte, 2009).

At the same time, vigilance by individuals can interfere with behaviours such as searching, cropping forage, and grooming (Mooring & Hart, 1995; Normandeau et al., 2022), imposing a potential cost. A number of studies have shown that as time devoted to vigilance increased, foraging efficiency declined (Peterson & Weckerly, 2018 but see van Deventer & Shrader, 2021). For example, forage ingestion rate in impala (*Aepyceros melampus*) decreased as vigilance increased (Smith & Cain, 2008b); similarly, elk cropping rate decreased as vigilance rate increased (Kurpiers & Weckerly, 2022). However, recent work also has shown that vigilance may not impose a foraging cost in ungulates if individuals are faced with handling-limited rather than encounter-limited foraging (Spalinger & Hobbs, 1992), because they can process food (chew) during “spare time” while being vigilant (Fortin et al., 2004; Fortin et al., 2004b; Robinson & Merrill, 2013). By synchronizing vigilance with ‘spare time’, ungulates can effectively reduce the foraging cost of vigilance from predators, provided vigilance does not exceed available spare time (Fortin et al., 2004). At the same time, conspecific interactions may reduce time for vigilance when encounter limited or spare time when handling limited if animals do not continue to process forage while interacting with conspecifics (Beauchamp, 2001; Beauchamp, 2003). Additionally, if a conspecific interaction is disruptive, it may take an individual more time when displaced by an interaction to find the next bite, which may lower foraging efficiency and intakes rates. While previous studies have addressed impacts of conspecific vigilance on foraging (Fortin et al., 2004; Robinson et al., 2013), few studies have addressed the direct impacts of conspecific interactions on vigilance behaviour to assess these behavioural trade-offs.

In this Chapter, we compare the influence of social interactions and environmental variables on the vigilance behaviour of elk (*Cervus canadensis*) in a partially migratory population on their sympatric range in winter to compare behavioral responses of individuals following different migratory tactics. The Ya Ha Tinda elk population winters on an open-fescue (*Festuca campestris*) grassland adjacent to Banff National Park. In summer, elk follow three migratory tactics where the majority (64%) of elk are resident remaining on the winter range year-round, and the rest are migratory with about equal numbers of elk currently migrating to high-elevations summer ranges in Banff National Park and to low-elevation, summer ranges on private and provincial multiple-use lands east of the Ya Ha Tinda winter range (Berg et al., 2021). We expected that elk within the three migratory tactics would behave differently in their vigilance response to predators and conspecifics because of their different experiences on summer ranges. Generally, elk that migrate into Banff National Park (western migrants) are in small, isolated groups that are exposed to high quality forage, high predation risk from bears and low human disturbance, whereas elk migrating onto private and provincial lands (eastern migrants) are exposed to earlier green-up, high cougar predation risk, and to more human recreational activities (Berg et al., 2021; MacAulay et al., 2022). In contrast, resident elk are exposed to high wolf predation risk and human activity (Hebblewhite, Merrill, & McDermid, 2008; Hebblewhite & Merrill, 2009; Berg et al., 2021). At the same time, residents display habituation to human activity that leads to two behavioral changes. First, they more readily exploit predation refuges that exist near ranch buildings than migrants, reducing exposure to wolf predation risk. For example, exposure to wolf predation risk in summer dropped from ~70 to ~15% higher risk than what western migrants experienced because of higher use of areas near human activity that wolves avoid (Hebblewhite & Merrill, 2007, 2009; Robinson, Hebblewhite, & Merrill, 2010). Also, residents show differences in vigilance behaviours from western migrant elk, in that they show better synchronization of vigilance with spare time during foraging (Robinson & Merrill, 2013). However, because numbers of eastern migrant elk have only recently increased, it is not known whether they are habituated to human activity due to higher recreational traffic on their summer range and have patterns of use and vigilance more similar to resident or western migrants.

We predicted that elk overall would increase vigilance (head up) time during foraging observations when local elk density was high, elk were near timber, and where forage biomass was high (handling-limited foraging) as elk would have more spare time in which to be vigilant (Robinson et al., 2013). We hypothesized that resident elk would express less vigilance than eastern or western migrants near areas of human activity because they are more habituated to humans than migrants, but would display similar levels of vigilance to migrants near timber due to high wolf predation risk. We also predicted that submissive individuals would spend more time vigilant than aggressive individuals to avoid potential aggressive contacts, and that submissive individuals would exhibit a greater residual effect from an interaction by taking longer to return to feeding than an aggressive elk after an interaction, which could incur a foraging cost. Finally, because eastern elk were more aggressive than other migratory tactics (Chapter 2), we predicted that conspecific interactions would impose the least time spent disturbed from foraging in eastern migrants compared to resident or western migrant elk.

2. Methods

2.1 Behavioural observations

We observed elk behaviours during foraging bouts on 45 unique focal elk, with 18 of the 45 (40%) individuals sampled in both study years (n = 64 elk-winters). Elk were observed 5 – 8 times (7 ± 0.13, mean ± SE =) per winter between 14 January to 4 April 2019 (n = 30 focal elk) and 23 January 2020 – 3 April 2020 (n = 34). Focal animals were randomly selected for observation prior to being located, and were not resampled within 48 hours of the previous observation. The majority of these day-time observations occurred between 0700 – 1000 (51 %) and 1600 – 1900 (32 %) when elk were most actively foraging (Merrill et al., 2020). Observations were performed at a distance of 80 – 1500 m using a 60x magnification spotting scope (Vortex Optics, Barneveld, WI). Focal animals were continuously monitored until the elk moved out of sight, bedded down, began ruminating while standing for >2 minutes, or became vigilant to the observer. During an observation period, the start time of each of 5 foraging behaviours were recorded using a handheld voice recorder (Olympus VN-541PC) and later time-stamped using the program JWatcher^{TM} (Blumstein et al., 2006). We defined searching/foraging as head down below the shoulder while cropping forage while stationary or slowly moving. We also noted the number of bites of forage taken (jerking motion of the head while foraging) when visible. Other behaviors we recorded were grooming, which was considered self-grooming (with teeth or hind foot; Normandeau, 2022). Pawing was recorded when elk used their front legs to move away snow prior to cropping.

A vigilance bout began when an elk raised its head above the shoulder and was stationary or moving slowly while looking around, and ended when the head was lowered. We distinguished between two types of vigilance. Vigilance after a conspecific interaction (see below) occurred immediately after an interaction and continued until the focal began another behaviour or dropped its head below shoulder and began to search for forage. Routine vigilance included time with head up looking around that was not immediately preceded by a conspecific interaction. Total vigilance was considered as all vigilance recorded during an observation, including both routine and interaction vigilance. We further distinguished in how we sampled vigilance. Routine and post-interaction vigilance could occur during the same observation period. In such an observation, we expected routine vigilance could reflect the residual influences of an interaction on vigilance. As a result, we classified vigilance that occurred in an observation period when there were no conspecific interactions as uninterrupted vigilance to compare uninterrupted to routine vigilance to see if they differed.

An interaction was defined as a focal animal coming into contact with or directing movement towards a conspecific, and began when the previous behaviour (e.g., foraging/searching) ceased and ended with the resumption of another behaviour (e.g., vigilance, foraging; Fortin et al., 2004). Interactions were classified based on the response of the focal animal. An aggressive interaction occurred when the focal animal threatened (e.g., ear pinning, teeth baring, movement in the direction of the conspecific) or made contact (e.g., biting, kicking, head swing) with a conspecific (Thouless & Guinness, 1986), resulting in the conspecific being displaced by at least 2 m. A submissive interaction was recorded when the focal elk was physically displaced by at least 2 m by an aggressive conspecific, either through direct contact or by threat (Fournier & Festa-Bianchet, 1995; Veiberg et al., 2004). A neutral interaction occurred when a focal animal and conspecific came in contact without displacement or an aggressive response by either elk, or displayed allogrooming, an affiliative behaviour. During interactions, the identity and migrant tactic of focal animals was known, while the identity of conspecifics was not known. Finally, we considered the entire duration from the initiation of an interaction until the focal animal began cropping forage again as the total disruption time from an interaction.

At the outset of each observation period, we recorded the position (central or peripheral) of the focal elk in the herd as well as local density of conspecifics around the focal elk (number of elk within 2-m, 10-m, or 20-m concentric circles). The location of focal animals in the herd was determined following Liley & Creel (2008), where an animal was considered central if an attacking predator would encounter one or more elk before the focal animal, and peripheral if an attacking predator would encounter the focal before any centrally located conspecific. At the end of each observation, we estimated the UTM coordinates of the midpoint of the foraging path of the focal animal was using a compass (Garmin eTrex, Garmin, Olathe KS) and a rangefinder (m; Leupold RX-2800 TBR/W, Leupold & Stevens Inc., Beaverton OR), and plotted the location in the field using satellite imagery (Google Earth Engine, 2019). We determined the straight-line distance from the midpoint of each focal animal's foraging path during an observation to the closest forest edge (timber) and to the closest Ya Ha Tinda ranch building using GIS (ArcMap ERDAS, Norcross, GA) to represent wolf predation risk and human activity, respectively. We used these metrics as Robinson et al. (2010) showed that elk displayed higher vigilance for wolf predation near timber, and human activity was highest near ranch buildings during daylight hours (pers. obs.).

We also estimated forage biomass at the midpoint of the foraging path by sampling the amount of graminoids and forbs (g/m^2) from ungrazed areas adjacent to the estimated midpoint of each focal animal's foraging path, within 2 – 5 days of an observation and prior to new snowfall. If snow was present in the quadrat, we first measured snow depth from the centre of the quadrant before removing all snow from the sampling area prior to clipping vegetation. We clipped standing biomass to 2 cm from the ground, dried samples at 50°C for 48hrs, then weighed dried samples to the nearest 0.1g. Shrubs were excluded from biomass estimates as elk were observed eating shrubs in 0.01% of observations, and previous fecal analysis of winter elk diets at the Ya Ha Tinda indicate that graminoids are the primary forage source in the winter (Hebblewhite, 2006).

2.2 Statistical analysis

We first tested for differences between years in mean time (seconds) spent foraging, interacting, being vigilant, grooming, and pawing during an observation as a function of year using a negative binomial mixed-effects model. We included an offset of observation time (minutes) to account for length of observation period and elk ID to account for multiple observations on the same individual. We included year as a random effect in subsequent analyses of conspecific interactions and vigilance only if we found differences in behaviours between years.

We tested whether the mean time (in seconds) elk spent in different behaviors (foraging/searching, interaction, vigilance, pawing, and grooming) differed among migratory tactics during an observation using negative binomial mixed-effects models including an offset of observation time (minutes) and a random effect of elk ID. We then tested whether mean duration (seconds) of interaction bouts (i.e., single event) differed among interaction types (aggressive, submissive, neutral), migratory tactic, and their statistical interaction using a generalized linear mixed-effects model (GLMM) with elk ID as a random effect using *glmmTMB* (glmmTMB package in R; v1.4.1717; Brooks et al., 2017).

Next, we tested whether mean duration (seconds) of vigilance bouts differed by the type of interaction it followed (aggressive, submissive, neutral, routine), migratory tactic, and their interaction using a generalized linear mixed-effects model (GLMM) with elk ID as a random effect using *glmmTMB* (glmmTMB package in R; v1.4.1717; Brooks et al., 2017). We also tested for differences in the frequency of behavioral bouts within an observation period using a negative binomial mixed-effects model of vigilance type, migrant tactic, and their interaction also with an offset of observation time and a random effect of elk ID. Finally, we tested for differences in mean time spent vigilant during an observation after conspecific interactions (aggressive, submissive, neutral) and in routine vigilance (no interaction) by migrant tactic and their interaction using a negative binomial mixed-effects model of seconds vigilant, with an offset of the of observation time and elk ID as a random effect.

In addition, we assessed whether relative aggressiveness observed in individual elk during observations influenced their total vigilance in two steps. First, we determined the proportion of aggressive interactions initiated by each focal animal out of the total number of interactions (aggressive and submissive), and used this to order individual elk ID along a gradient of the proportion of aggressive interactions we observed them in (Appendix H). We considered elk with > 0.75 as aggressive individuals. Based on this classification, we determined whether total vigilance per observation (seconds) differed among high- and low-ranked individuals using a Kruskal-Wallis rank-sum test of mean vigilance and rank.

We assessed the factors influencing time spent in routine, interaction, and total vigilance (routine + interaction) in three separate models, using a negative binomial, mixed-effects model and a model selection based on Akaike's Information Criterion corrected for small sample size (AIC_c). We included an offset of observation time and elk ID as a random effect. Covariates in the model included local elk density (number of elk in 2-m, 10-m, and 20-m radius concentric circles around the focal animal), position in the herd (1, periphery; 0, centre), day of winter (from January 1), forage biomass along the foraging path (g/m^2), distance to ranch buildings (m), and distance to the closest timber edge (m). In all candidate model sets, we then added migratory tactic (resident as reference) alone and interacting with other variables to test whether inclusion of migrant tactic improved the top model. We tested for correlation among variables prior to modelling and did not use variables correlated at $r \geq |0.5|$ in the same model. Models within AIC_c < 2 of the top model were considered equally supported. All analyses were performed using R statistical software (R Core Team, 2022).

2.3 Foraging cost

We tested whether disruption time differed among migrant tactics using a negative binomial mixed-effects model with an offset of observation time and included a random effect of elk ID. Finally, we then compared the slopes of the relationships between foraging time and time spent in interaction, routine, and total vigilance time using negative binomial mixed-effects models with an offset of observation time and random effect of elk ID. We assessed the differences in the slopes of these models slopes by using the overlap of the 95% confidence limits. All analyses were performed using R statistical software (R Core Team, 2022).

3. Results

We observed a total of 180 foraging bouts in 2019 and 268 in 2020 for a total of 448 observations during 76.8 hours of observation. Behavioural observations lasted from 2 to 15 minutes and averaged 10.3 ± 4.2 minutes ($\bar{x}$ ± SD). We omitted one observation (0.2%) in which routine vigilance consisted of > 99% of the observation (Appendix G-1) and one observation in which interaction time was > 80% of the observation (consisting of 9 interactions between an adult female and her calf) as behavioural outliers (Appendix G-2). The remaining 446 observation periods consisted of 205 observations from residents, 123 observations from eastern migrants, and 119 observations of western migrants. We analyzed 248 interactions between focal elk and conspecifics, of which 125 were from resident elk, 73 from eastern migrants, and 50 from western migrants. Because biomass estimates were not possible for 37 (8%) of the observation periods, this reduced the sample size for relating environmental factors to vigilance to only 409 observation periods. Only vigilance was higher (48%; -77.2 ± 1.3, β ± SE) in 2019 than 2020 (Appendix F), thus year was added as a random effect in vigilance modelling analyses.

3.1 Elk behaviours

Across migratory tactics, foraging comprised the majority of the observation period on a focal elk averaging over 83.7 ± 0.17% (mean ± SD; range 4 –100%), with vigilance averaging 8.9 ± 10.7% and other behaviors including interaction time averaging < 1.5 ± 0.06% (Figure 3.2). There were no differences in the mean time (seconds/minute) spent foraging, interacting, vigilant, or spent in other foraging behaviours among migrant tactics (Table 3.1).

Conspecific interactions occurred in 29% of observation periods. The mean duration (seconds) of each interaction type did not differ (Figure 3.3; Table 3.2) with interaction bouts being short, averaging 5.2 ± 4.9 (seconds; $\bar{x}$ ± SD) for aggressive, 5.5 ± 5.1 for submissive and 5.6 ± 6.8 for neutral interactions, with no difference between migratory tactics (Table 3.2) or interaction type x migratory tactic interaction (Table 3.2; Figure 3.3). Elk became vigilant after 33% (n = 82) of recorded interactions of which 53% of interactions were aggressive, 15% were submissive, and 32% were neutral. In contrast, routine vigilance was observed in 92% of the observation periods. There was no difference in the mean duration of vigilance bouts after different types of conspecific interactions (Table 3.2; Figure 3.4a), while western migrants showed longer vigilance bouts than other migrant tactics following aggressive interactions (Table 3.2; Figure 3.4a).

However, routine vigilance bouts were more frequent than interaction vigilance bouts (Table 3.3; Figure 3.5b) and as result time spent in routine vigilance was greater (14.21 ± 0.21% observation; Table 3.3, Figure 3.5) than vigilance after interactions (0.4 ± 0.17% observation; Table 3.3, Figure 3.5). Vigilance duration, frequency and time spent vigilant during an observation period did not differ among any vigilance type, whereas the frequency of routine vigilance in western migrants was lower than other migrants (Table 3.3; Figure 3.4b).

We calculated the proportion of times a focal elk was aggressive for 24 elk observed interacting ≥ 3 times during foraging observations, which was 53% of focal animals. Of these, 11 elk (46%) were aggressive more than 75% the time (Appendix H). There was no difference in the mean vigilance observed between aggressive and submissive elk (Kruskal-Wallis H = 1.61, df = 1, p = 0.20).

3.2 Environmental influences on vigilance

Environmental covariates were not collinear except for number of elk within distances of the focal elk ($r > 0.50$). Because 1 elk-length best explained vigilance in a preliminary analysis (Appendix I), we used this metric in further analyses over 5- and 10-elk distances to reflect elk density. We report results of models where we included observations with no vigilance (n = 37, 8%) because there were no differences in model results where observations with no vigilance were omitted.

There was considerable model uncertainty in assessing time elk spent in two of the three vigilance types modelled (Table 3.4). The most competitive models indicated that routine vigilance (n = 377) decreased over the winter, increased when close to timber edge, when on the periphery of a group, and with higher elk density and near buildings; however, the confidence limits of the β coefficients for density, buildings, and periphery overlapped zero (Table 3.5). In contrast, the most competitive models for time spent in interaction vigilance (n = 58) indicated that interaction vigilance only increased near timber. The top model of total vigilance (n = 446) also showed high model uncertainty; the most competitive model indicated that total vigilance decreased over the time and increased in proximity to timber and with higher density, although beta estimates of density overlapped zero (Table 3.5). In all three model sets, the addition of migrant tactic to the top model did not improve model fit and thus there were no differences in total, routine, or interaction vigilance among tactics (Appendix J).

3.3 Foraging costs

Disruptions in foraging after a conspecific interaction were recorded during 26% of the observation periods (n = 118). There were no differences among migrant tactics in mean time to return to feeding after a conspecific interaction (eastern -0.03 ± 0.42; western -0.41 ± 0.43; β ± SE, Figure 3.6). Foraging time declined for every second of increased vigilance time following an interaction (-0.07 ± 0.007; β ± SE), compared to increasing routine vigilance (-0.03 ± 0.004) and increasing total vigilance (-0.03 ± 0.0004).

4. Discussion

Elk following different migratory tactics are exposed to different foraging opportunities, predation risk, and human disturbances on allopatric summer ranges that appear to influence how density-dependent fitness balancing occurs in the partially migratory Ya Ha Tinda elk population (Hebblewhite et al., 2018; Berg et al., 2021; Smolko et al., in prep.). Previous studies at Ya Ha Tinda have shown that when on their sympatric winter range, two of the migratory tactics (residents and western migrants) differed in their vigilance responses to predation risk and humans and in their abilities to synchronize vigilance with food handling (Robinson & Merrill, 2013); a more recent behavioral study indicated that elk following the emerging eastern migratory tactic were more aggressive and displaced other elk from feeding sites (Chapter 2). In this study, we addressed whether differential interactions among elk in the three migratory tactics influenced vigilance behaviours including post-interaction return to foraging. We expected that aggressive eastern elk would spend less time vigilant following interactions than submissive individuals, as submissive animals would be more vigilant for further aggressive attacks, and thus incur longer disruptions during foraging. Contrary to our predictions, we found duration and proportion of time individual elk spent interacting were similar among migratory tactics, and that the corresponding post-interaction vigilance also did not differ, suggesting that despite differences in aggressive behaviors among migrant tactics (Chapter 2), these did not translate into differential reductions in foraging time. The similarity among migratory tactics may not be expected for two reasons.

First, interactions among all migrant tactics were short (< 8 seconds/interaction) and all interactions made up only ~2% of the total time spent when elk were actively foraging, suggesting these do not constitute a large cost to foraging. The short duration of interactions in elk on the Ya Ha Tinda is consistent with interaction patterns in other studies of female elk (Weckerly, 1999), caribou (Weckerly & Ricca, 2014), bison (Rutberg, 1986), and mouflon (Le Pendu et al., 1995, 2000). Because interactions among elk on the Ya Ha Tinda were mostly agonistic (i.e., aggressive or submissive) rather than neutral (Chapter 2), the small amount of time spent in these behaviors likely reduced the potential risk of injury and facilitated foraging in the large aggregations on the winter range, especially as the population has declined and aggregation increased (Merrill et al., 2020). Duration of neutral/affiliative behaviours did not differ from other interactions, as might be expected if neutral interactions were an important component of establishing and maintaining affiliative bonds among elk, as has been reported in cattle (*Bos taurus*; Sato et al., 1993; Val-Laillet et al., 2009) and horses (Cameron et al., 2009). However, allogrooming, which comprised majority of the time spent in neutral interaction disrupting foraging other than vigilance, was reported to occur primarily during resting periods in these elk (Normandeau et al., 2022), or may occur at night as reported for cattle (Val-Laillet et al., 2009), thus our observations recorded during active foraging periods may under-represent the importance of neutral interactions in elk.

Second, we predicted that elk would respond to conspecific interactions by increasing vigilance for conspecifics following interactions, particularly following submissive interactions as submissive animals might be more vigilant for further aggression. As a result, we expected eastern elk to spend less time in post-interaction vigilance. However, we found little evidence of vigilance duration following an interaction differing among type of interaction or migratory tactic, despite longer average interaction vigilance bout lengths. The lack of differences may result from a low sample size of post-interaction vigilance, because interaction vigilance was observed in only 29% of our behavioral observations. In contrast, routine vigilance bouts interrupted foraging much more frequently, occurring in 93% of observations; despite shorter average bout length, time spent in routine vigilance was consequently 48 times that of time spent vigilant after a conspecific interaction (Appendix F). Favreau et al. (2010) found a similar pattern in grey kangaroos (*Macropus giganteus*), with a lower proportion of total vigilance time devoted to conspecific monitoring. We suggest that the comparatively lower amount of time devoted to vigilance after an interaction compared to routine vigilance indicates that the foraging cost of routine vigilance, which may be related more to predation risk (Robinson & Merrill, 2013), likely posed a greater cost to foraging than interacting with conspecifics even in large aggregation of elk. If true, the relatively high routine vigilance may support why elk at the Ya Ha Tinda may be willing to forage in large groups under higher predation risk; that is, the cost of interference competition does not outweigh the advantages of the anti-predator benefits of grouping such as greater predator detection and dilution in predation risk (Jarman, 1974; Fryxell, 1995; Krause & Ruxton, 2002; Caro, 2005).

Complicating the above interpretation is that distinguishing between antipredator and conspecific vigilance is difficult to discern in wild ungulate populations. This is further compounded by the possibility of synchronous scanning for both predators and competitors (Ebensperger et al., 2006; Beauchamp, 2009). Moreover, antipredator and conspecific vigilance may be seemingly contradictory in response to the same stimuli. Favreau et al. (2010) showed that increasing group size of grey kangaroos resulted in a decrease in the proportion of vigilance time spent scanning the environment but an increase in the proportion of vigilance directed at neighbours, with the result being no net effect of group size on vigilance overall. Similarly, other social factors may influence vigilance that are unrelated to what we might consider important predictors of behaviour. For example, vigilance in bighorn sheep is contagious among neighbours in response to the cessation of chewing, but not to other variables of vigilance bouts (such as head-up initiation or gaze direction) of neighbours (McDougall & Ruckstuhl, 2018). Furthermore, vigilance behaviours may overlap with other activities. While we have defined vigilance in elk as time spent with the head above the shoulders looking around, it is possible that elk are also capable of remaining vigilant for conspecifics while foraging with the head down, which may provide a means of reduced conspecific vigilance foraging costs while still obtaining information about neighbours (Fernández-Juricic, Smith, & Kacelnik, 2005).

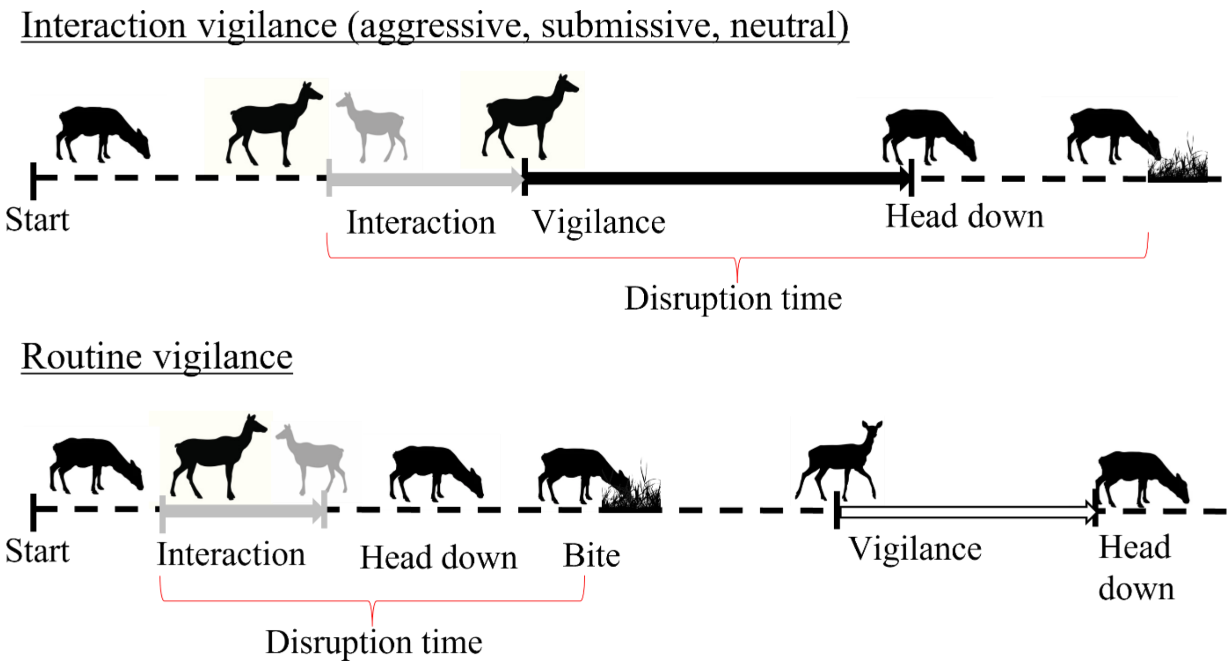
Although vigilance directed at conspecifics may have comprised a small proportion of the time that disrupted foraging, our modeling makes it clear that density of neighboring animals increased the time spent vigilant overall and likely reflects competitive interactions. We also expected that individual aggressiveness/submissiveness ranking of elk would result in an increase in vigilance in submissive animals, but we found no evidence for this, and thus did not find the expected decrease in time spent vigilant after an interaction by the more aggressive eastern migrants. This result may, in part, be compromised by knowing the migratory identity only of the focal and not the conspecific with which the focal animal interacted. Because not all elk were marked, we were unable to determine a true hierarchical dominance rank of elk in the herd instead of a relative measure of aggressiveness. Villagrán et al. (2020) observed that the frequency of aggressive interactions was positively related to increased dominance rank in female pampas deer (*Ozotoceros bezoarticus*), and it has been shown elk tend to increase vigilance in the presence of dominant counterparts (Weckerly, 2001). However, lacking a hierarchical measure of dominance among focals, relating vigilance to a win-loss ratio of aggressive and submissive interactions may not accurately reflect vigilance responses of submissive animals to higher ranked conspecifics.

It is clear from this study and previous studies by Robinson and Merrill (2013) that vigilance by elk is additionally contingent on environmental conditions. Because routine vigilance decreased as winter progressed, this may reflect temporal changes in available forage and condition as biomass on the winter range is depleted. Liley and Creel (2008) observed a similar trend in elk on the winter range in Yellowstone National Park, where as elk declined in nutritional condition, vigilance was constrained as more active time was allocated to foraging. Distance to timber edge also influenced the expression of vigilance during foraging, which previously has been associated with higher wolf (Robinson et al., 2010). This result is consistent with observations of elk in Yellowstone National Park. Halofsky and Ripple (2008) also showed elk vigilance increased when closer to conifer edge, where elk vulnerability from wolf predation was highest (Bergman et al., 2006). This was attributed to a greater familiarity of patterns of wolf use and risk at the Ya Ha Tinda, which was primarily around the perimeter of the grasslands in the surrounding timber (Robinson et al., 2010), especially during the day (Hebblewhite &

Merrill, 2008). No concomitant data on wolf use of the area was available to confirm use along timber edges during our study period. However, because elk learn and respond to risky areas (Liley & Creel, 2008; Weterings et al., 2022), not just to the presence of predators directly (Lung & Childress, 2007) it is likely that elk still perceive timber edge as a risky area and react with vigilance accordingly. While vigilance is often inversely related to group size, attributed to a reduction of individual predation risk in a group (Childress & Lung, 2003), during our study elk were primarily observed in a single large herd of females (ca. 370) which remained constant over the winter, thus group size effects on vigilance were likely minimal (Laundré, Hernández, & Altendorf, 2001; Wolff & Van Horn, 2003; Halofsky & Ripple 2008). Nevertheless, grouping and location may jointly influence vigilance. For example, position in the group was a main determinant of vigilance in this study and elsewhere (Lipetz & Bekoff, 1982; Lung & Childress, 2007; Robinson & Merrill, 2013), where elk on the periphery showed more vigilance than central conspecifics, consistent with the assumption of higher edge predation risk (Stankowich, 2003).

We found proximity to human infrastructure influenced total vigilance in elk, but the effect was not greater for migrant than resident elk (i.e., no Building x Migratory tactic interaction; Appendix 10.2) as reported by Robinson and Merrill (2013). They attributed the difference in total vigilance between migratory tactics to habituation of resident elk to humans during the summer. We suggest two possible reasons for not finding a difference in this study. First, reduced population size during this study (~350 elk) compared to the period of study of Robinson and Merrill (2013: ~ 700 elk) resulted in higher cohesion among elk (Merrill et al., 2020) and migrant elk more closely mimicked space use patterns of resident elk. Alternatively, elk were attracted to periodic supplemental feeding sites of horses in pastures near ranch buildings, which can influence long-term elk behavior (Burcham, Edge, & Marcum, 1999). In fact, feeding during this study may have human-conditioned a larger proportion of the elk wintering on the Ya Ha Tinda than during the previous study when no feeding occurred (Robinson et al., 2010). Two decades earlier during the decline of the migrant to resident ratio, elk had open access to hay that was fed to horses during late winter, which was one hypothesis for the observed change in migrant tactic proportions. However, what role feeding at that time had on elk shifting to be resident elk and its population dynamics remains unclear (Hebblewhite et al., 2006).

In conclusion, we found no major differences in how conspecifics within different migratory tactics responded in terms of vigilance in response to other elk or based on their location in space, indicating no group gained a substantive foraging advantage. Vigilance that was likely directed at conspecifics, both before and after a conspecific interaction, composed a small percent of the active time during diurnal foraging of elk relative to routine vigilance when no interactions occurred, and migrant tactics did not differ in the amount of disruption time from taking bites of forage after interactions. However, foraging rate declined faster in response to interaction vigilance compared to total or routine vigilance, which may reflect other mechanisms, such as differences in cropping rate or overall feeding time, that could potentially reflect feeding advantages that we did not measure. For example, Thouless (1990) showed a decrease in red deer bite rate when subordinate animals foraged near dominant animals, and impala increased steps per minute during foraging with increasing neighbour proximity (Smith & Cain, 2008b). Further, if differences exist in the ability of resident elk to synchronize routine vigilance with spare time (time spent chewing) as reported by Robinson and Merrill (2013), resident elk may still have a foraging advantage on winter range when foraging is handling limited. Nonetheless, our results indicate that for species like elk that are gregarious, interference competition during group foraging may not outweigh the advantages of aggregating under the high predation risk that exists at the Ya Ha Tinda (Hebblewhite et al., 2018; Robinson et al., 2010), especially in open habitats like grasslands where forage resources are relatively abundant for elk. At the same time, the trade-offs between vigilance for conspecifics and predation may shift in a density-dependent manner. For example, total vigilance increased with the density of neighbors. At high population densities, this may contribute to fission-fusion group dynamics to alleviate conspecific costs and partially explain why elk aggregated as the number of elk declined, as reported by Merrill et al. (2020).



Interaction vigilance (aggressive, submissive, neutral)

Routine vigilance

Figure 3.1. Examples of interaction vigilance (top panel, vigilance immediately preceded by an aggressive, submissive, or neutral interaction) and routine vigilance (bottom panel, no interaction immediately preceding vigilance). Dotted lines represent foraging behaviour, light grey lines indicate a conspecific interaction occurring, black lines represent an interaction vigilance bout, and white lines represent a routine vigilance bout. Red bars indicate disruption time during foraging, initiated at the start of a conspecific interaction and ending with the first bite following. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada.

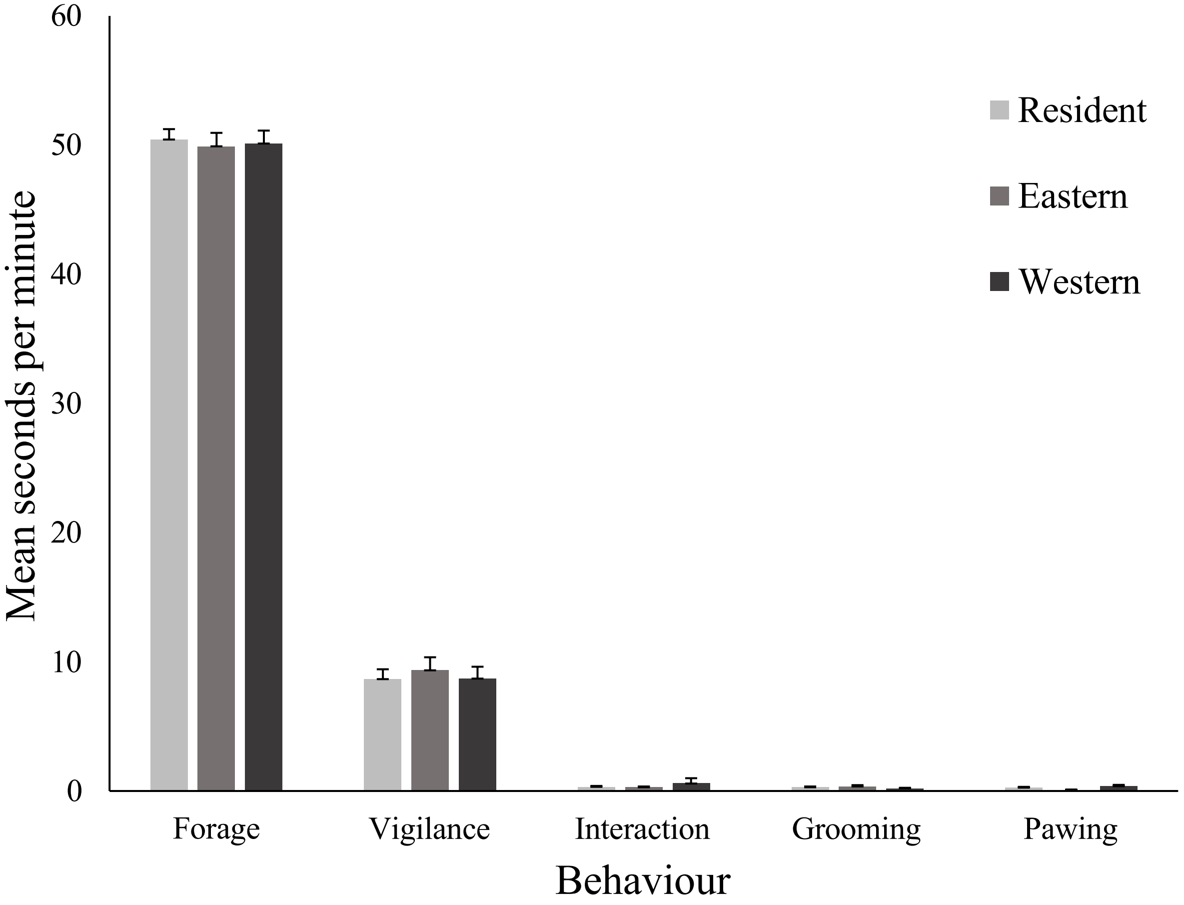


Figure 3.2. Mean seconds per minute of observation of behaviours (seconds/minute) observed during foraging bouts by eastern, resident and western migrant elk on the Ya Ha Tinda winter range in Alberta, Canada. Included are foraging time, total vigilance time, time spent interacting, grooming, and pawing. Observations were recorded during diurnal (0700 – 1900) foraging bouts. Error bars report +1 SE. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada.

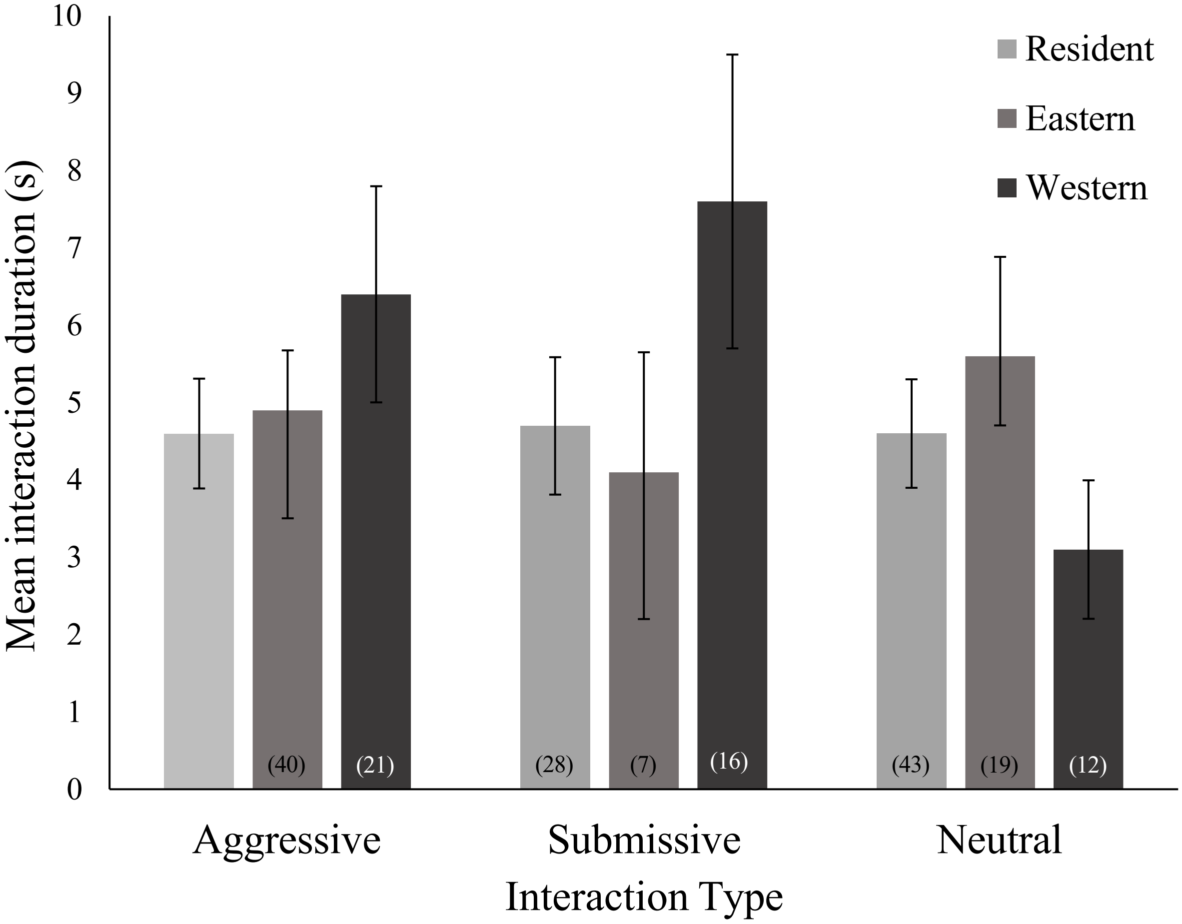


Figure 3.3. Mean duration (seconds) of aggressive, submissive, and neutral interaction bouts among resident, eastern, and western migrant elk on the Ya Ha Tinda winter range, Alberta, Canada. Observations were recorded during diurnal (0700 – 1900) foraging bouts. Error bars indicate ± 1 SE and sample size of each interaction type are indicated in parenthesis. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada.

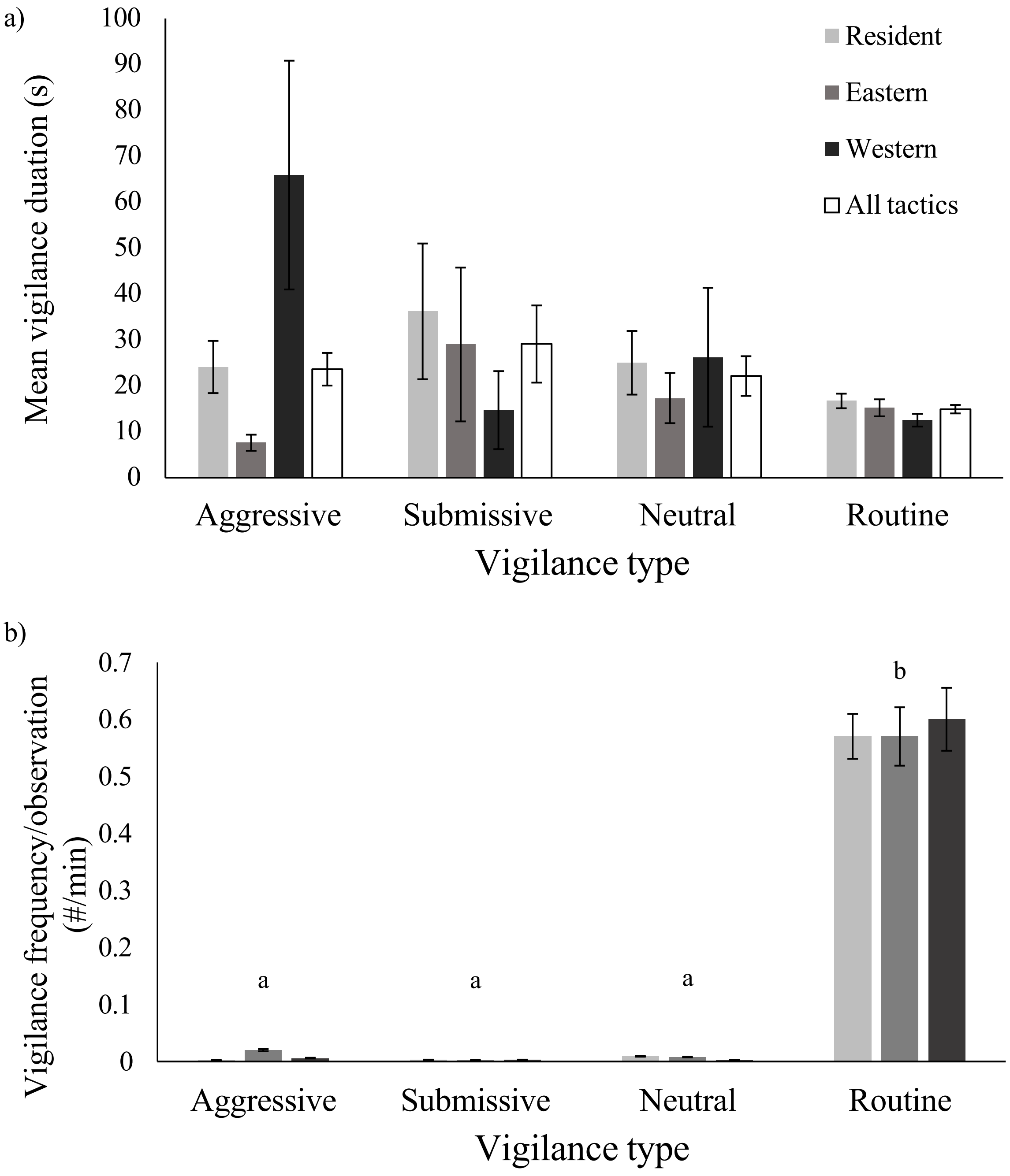


Figure 3.4. Mean duration vigilance bouts (a; seconds) and mean frequency of vigilance bouts (b; number of bouts/minutes observation) occurring after aggressive, submissive, and neutral interactions as well as vigilance bouts not preceded by an interaction in elk. Observations were recorded during diurnal (0700 – 1900) foraging bouts on resident, eastern, and western migrant elk. Error bars indicate ± 1 SE and superscripts indicate any significant differences in vigilance frequency among vigilance types. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada.

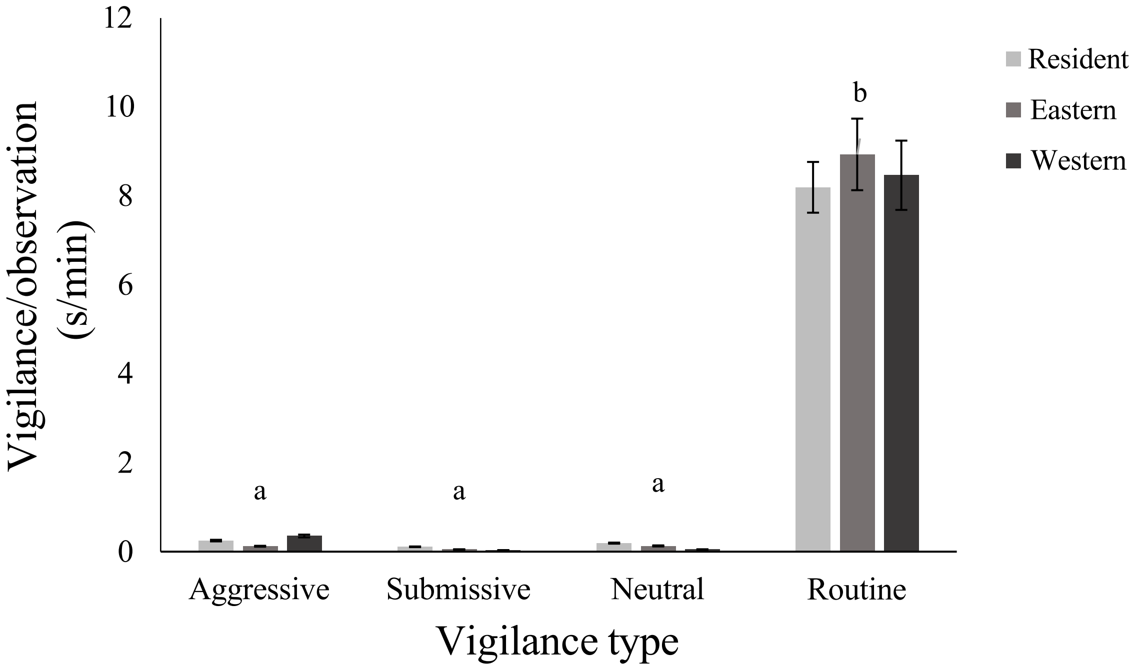


Figure 3.5. Mean seconds per minute spent vigilant during observations (seconds/minute). Vigilance types include interaction vigilance following submissive interactions, aggressive interactions, neutral interactions, and routine vigilance (not preceded by an interaction) in all observations. Error bars indicate ± 1 SE and superscripts indicate significant differences in seconds of vigilance per minute of observation among vigilance types. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada.

Table 3.1 Beta coefficients and upper and lower 95% confidence intervals (CI) for model parameters testing differences among resident (reference), eastern, and western migrant elk in time spent foraging, vigilant, interacting with conspecifics, and engaging in other foraging activities (i.e., pawing snow, grooming). Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada.

			95% CI	
Behaviour	Variable	*β* ± *SE*	Lower	Upper
Foraging	Eastern	- 0.02 ± 0.04	- 0.10	0.06
	Western	- 0.003 ± 0.04	- 0.08	0.08
	Intercept	3.91 ± 0.02	3.87	3.95
Vigilance	Eastern	0.04 ± 0.16	- 0.27	0.35
	Western	0.02 ± 0.16	- 0.29	0.33
	Intercept	2.14 ± 0.09	1.96	2.32
Interactions	Eastern	- 0.02 ± 0.45	- 0.90	0.86
	Western	0.08 ± 0.48	- 0.86	1.02
	Intercept	1.21 ± 0.27	0.68	1.74
Other	Eastern	- 1.22 ± 0.44	- 0.69	1.03
	Western	0.17 ± 0.45	- 1.22	0.54
	Intercept	- 0.34 ± 0.27	- 1.75	- 0.69

Table 3.2. Beta coefficients (*β*) with standard error (SE) and 95% confidence intervals for separate generalized linear mixed-effects models of interaction bout duration (seconds) and vigilance bout duration (seconds). The interaction duration model included resident, eastern, and western migrants, interaction types (aggressive, submissive, neutral), and their statistical interaction, while vigilance duration was compared among migrant tactics, vigilance types (routine, aggressive, submissive, neutral), and their statistical interaction. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada.

Interaction duration	*β ± SE*	Lower CI	Upper CI
Eastern migrant	- 0.93 ± 3.10	- 7.02	5.15
Western migrant	1.23 ± 3.68	- 5.99	8.44
Submissive	- 0.29 ± 3.49	- 7.14	6.55
Neutral	3.09 ± 2.77	- 2.35	8.52
Eastern submissive	- 1.09 ± 5.61	- 12.09	9.89
Western submissive	3.85 ± 5.96	- 7.85	15.55
Eastern neutral	- 1.16 ± 4.62	- 10.22	7.90
Western neutral	- 5.18 ± 6.16	- 17.27	6.90
Intercept	7.24 ± 2.06	3.21	11.27
Vigilance bout duration			
Eastern migrant	- 1.92 ± 5.34	- 12.39	8.55
Western migrant	- 5.21 ± 5.02	- 15.05	4.62
Aggressive	4.42 ± 8.45	- 12.14	20.98
Submissive	18.61 ± 14.59	- 10.00	47.22
Neutral	2.32 ± 8.82	- 14.97	19.62
Eastern aggressive	- 12.53 ± 12.37	- 36.78	11.71
Western aggressive	49.01 ± 16.11	17.44	80.58
Eastern submissive	- 5.41 ± 25.21	- 54.82	44.00
Western submissive	- 16.29 ± 25.14	- 65.59	32.99
Eastern neutral	- 0.73 ± 14.73	- 29.61	28.14
Western neutral	11.39 ± 21.82	- 31.38	54.17
Intercept	17.66 ± 3.27	11.26	24.06

Table 3.3. Beta coefficients (β) with standard error (SE) and 95% confidence intervals for separate negative binomial mixed-effects models of vigilance bout frequency (number) and vigilance time (seconds) among migrant tactics, vigilance types (routine [reference], aggressive, submissive, neutral), and their interaction. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch in Alberta, Canada.

Vigilance bout frequency	β ± *SE*	Lower CI	Upper CI
Eastern migrant	0.08 ± 0.12	- 0.15	0.33
Western migrant	0.11 ± 0.12	- 0.13	0.35
Aggressive	- 4.11 ± 0.23	- 4.57	- 3.66
Submissive	- 5.32 ± 0.41	- 6.13	- 4.51
Neutral	- 4.23 ± 0.24	- 4.71	- 3.75
Eastern aggressive	0.53 ± 0.33	- 0.12	1.20
Western aggressive	- 0.52 ± 0.45	- 1.41	0.37
Eastern submissive	- 0.11 ± 0.71	- 1.51	1.29
Western submissive	- 0.16 ± 0.72	- 1.57	1.24
Eastern neutral	0.10 ± 0.39	- 0.67	0.88
Western neutral	- 1.26 ± 0.63	- 2.50	- 0.02
Intercept	- 0.64 ± 0.22	- 1.08	- 0.20
Vigilance seconds per minute			
Eastern migrant	0.98 ± 0.62	- 0.22	2.19
Western migrant	0.42 ± 0.63	- 0.80	1.64
Aggressive	- 7.95 ± 0.51	- 8.95	- 6.95
Submissive	- 8.08 ± 0.51	- 9.08	- 7.09
Neutral	- 8 .01 ± 0.50	- 9.00	- 7.01
Eastern aggressive	- 0.86 ± 0.83	- 2.49	0.76
Western aggressive	- 0.16 ± 0.84	- 1.81	1.49
Eastern submissive	- 0.80 ± 0.84	- 2.43	0.82
Western submissive	- 0.35 ± 0.84	- 2.01	1.29
Eastern neutral	- 0.80 ± 0.83	- 2.43	0.83
Western neutral	- 0.41 ± 0.84	- 2.07	1.23
Intercept	8.23 ± 0.65	6.97	9.50

Table 3.4. Summary of model selection results for negative binomial mixed-effects models relating total vigilance (s), routine vigilance (s), and interaction vigilance (s) during foraging observations based on AIC_c model selection. Models were considered competitive if within Δ2 AIC_c. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada. Full model selection results in Appendix J.

Routine vigilance (s)	k	AIC_c	Δ AIC_c	AIC_c Wt.
– Timber + density – buildings – day + periphery	9	4443.6	0.00	0.279
– Timber + density – buildings – day	8	4444.1	0.57	0.210
– Timber + density – day + periphery	8	4444.3	0.74	0.192
– Timber + density – day	7	4444.9	1.31	0.145
– Timber – day	6	4445.1	1.58	0.126
– Timber + density – day – migrant tactic	9	4448.2	4.63	0.028
Null	4	4456.1	12.58	0.001
Interaction vigilance (s)				
– Timber	5	427.3	0.00	0.40
– Timber – buildings	6	429.7	2.36	0.12
Null	4	431.7	4.37	0.05
Total vigilance (s)				
– Timber + density – day	7	4738.5	0.00	0.273
– Timber – day	6	4739.2	0.67	0.195
– Timber + density – day + periphery	8	4739.4	0.91	0.173
– Timber + density – building – day	8	4739.5	0.94	0.170
– Timber + density – building – day + position	9	4740.3	1.79	0.111
– Timber + density – day – migrant tactic	9	4741.4	2.90	0.006
Null	4	4750.3	11.7	0.001

Table 3.5. Beta coefficients (β) with standard error (SE) and upper and lower 95% confidence intervals (CI) for parameters of the top models based on $\mathrm{AIC_c}$ model selection for a negative binomial mixed-effects model of routine vigilance observed in elk. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada. Full results from top model estimates can be found in Appendix J.

Routine vigilance (s)		95% CI	
Variable	$\beta \pm SE$	Lower	Upper
Timber	- 0.12 ± 0.05	- 0.23	- 0.03
Day	- 0.006 ± 0.002	- 0.01	- 0.002
Density	0.08 ± 0.05	- 0.02	0.18
Periphery	0.17 ± 0.11	- 0.05	0.39
Buildings	- 0.08 ± 0.05	- 0.18	0.02
Intercept	2.54 ± 0.22	2.11	3.01
Interaction vigilance (s)			
Timber	- 0.38 ± 0.13	- 0.63	- 0.13
Intercept	- 0.34 ± 0.30	- 0.97	0.29
Total vigilance (s)			
Timber	- 0.17 ± 0.06	- 0.29	- 0.05
Day	- 0.006 ± 0.002	- 0.01	- 0.002
Density	0.11 ± 0.06	- 0.01	0.23
Intercept	2.56 ± 0.28	2.01	3.11

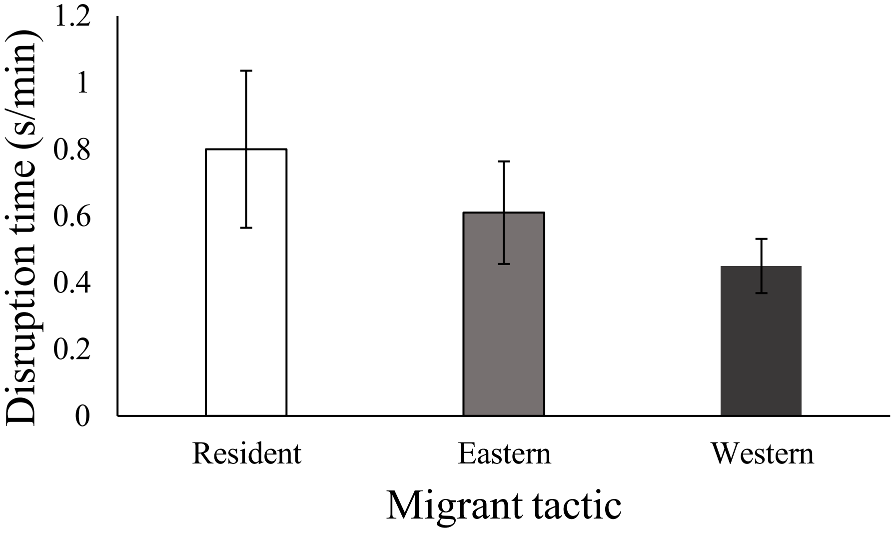


Figure 3.6. Mean disruption time (time from interaction to return to first bite; s/min observation) of individual elk following resident, eastern, and western migratory tactics. Error bars indicate ± 1 SE. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta Canada.

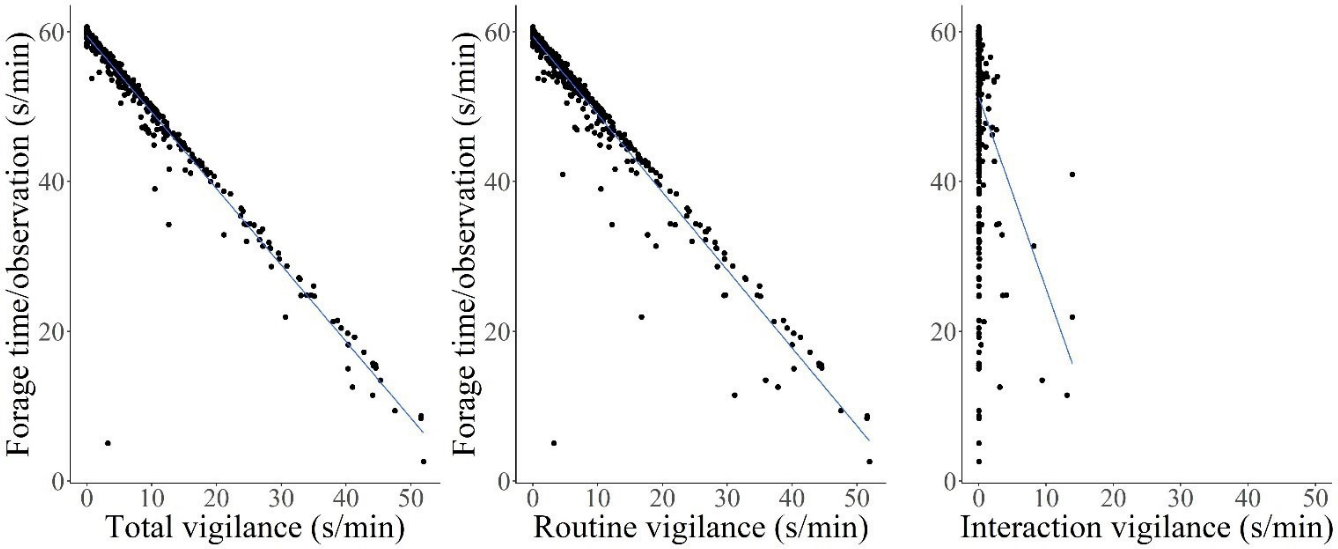


Figure 3.7. Foraging time (seconds/minute observation) in response to seconds per minute of observation of routine, interaction, and total vigilance (seconds/minute observation). Blue lines represent linear model fits of the data. Observations were recorded during January – April 2019 – 2020 on GPS-collared elk at the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta Canada.

CHAPTER 4 – INFLUENCE OF CONSPECIFIC INTERACTIONS ON THE WINTER RANGE ON PARTIAL MIGRATION

Partial migration, where a proportion of individuals in a population migrate while others remain as residents (Dingle & Drake, 2007), is becoming more recognized as a common phenomenon in ungulate populations (Berg et al., 2019). It is reported to be maintained as a population-level stable state where fitness balancing between tactics is mediated by counteracting density-dependent survival and reproduction of migrants and residents (Lundberg, 1987; Kaitala et al., 1993; Cressman & Křivan, 2006). Alternatively, an individual's propensity to migrate may be influenced by density-dependent trade-offs between costs and benefits that influence the individual's state, which may include their behavior among conspecifics in the population (Swingland, 1983; Lundberg, 1987; Chapman et al., 2011). Two conditions proposed to influence an individual's ability to decide to migrate include condition-dependent physiological requirements or competitive exclusion (Swingland & Lessels, 1978; Adriaensen & Dhondt, 1990; Chapman et al., 2011). In this thesis, we addressed how conspecific interactions differ among ungulates following different migrant tactics on a sympatric range in a partially migratory population, which could provide insight on how partial migration is maintained.

Previous studies on the Ya Ha Tinda elk population suggested that migrant elk have a nutritional advantage during the summer over resident elk, yet residents and migrants exhibited equal overall fitness (Hebblewhite & Merrill, 2009; Martin, Hebblewhite, & Merrill, 2021). Robinson et al. (2010) hypothesized that differential foraging behavior on sympatric winter ranges might offset the influence of summer advantages of western migrants, but density-dependent responses in movements and habitat selection at small and large scale were similar among migratory tactics (Merrill et al., 2020), with strong selection for forage biomass that was traded off only at high predation risk. Instead, overall aggregation of the remaining elk increased as the population declined, which was attributed to high wolf predation (Merrill et al., 2020). However, increased aggregation can intensify scramble or contest competition, especially over time as forage is depleted (Molvar & Bowyer, 1994; Kausrud et al., 2006). As result, we hypothesized that the frequency and duration of conspecific interactions could directly influence foraging costs through foraging disruptions, or indirectly by increasing vigilance for conspecific interactions. In turn, this could also indirectly reduce foraging efficiency by increasing time spent searching for the next bite following an interaction, such that foraging costs for each migrant tactic would depend on their overall dominance behaviour. We hypothesized that residents would be dominant because they remained on the winter range year-round, similar to resident European robins, which excluded migrants from ideal breeding territories as migrants arrived on the summer range from wintering grounds (Adriaensen & Dhondt, 1990). At the same time, individuals may benefit from group gregariousness because of social learning (Van De Waal, Borgeaud, & Whiten, 2013; Rosenthal et al., 2015; Jesmer et al., 2018). Because year-long residence likely made resident elk more familiar with navigating trade-offs in foraging under the high predation risk in this system (Hebblewhite et al., 2018), we also hypothesized migrants would exploit information from residents and follow residents to feeding patches, which could be one reason Merrill et al. (2020) found little difference in habitat selection.

Overall, we found only limited evidence for differential foraging costs to elk following different migratory tactics that might explain how foraging in winter might offset the nutritional advantages of migration. At the home-range and patch scale it seems advantageous for migrants to aggregate and follow resident elk to exploit forage resources while under high predation risk (Merrill et al., 2020). At the same time, at the scale of the feeding site, eastern migrants were more aggressive, displacing elk following other migratory tactics. While eastern migrants may have increased access to forage, costs in terms of decreased search or foraging time did not differ between migratory tactics and seemed minimal. As a result, it is unlikely that conspecific interaction time was great enough to offset foraging advantages afforded to elk that migrated. In contrast, vigilance for predators, which comprised 48 times the time allocated to conspecific interaction, has been shown to impose a foraging cost especially in encounter-limited foraging, and that resident elk have an advantage because they are more efficient in synchronizing spare related to chewing time with vigilance (Robinson et al., 2012; Robinson & Merrill, 2013).

A second way that conspecific interactions on the sympatric range may influence the maintenance of partial migration, but not studied here, is in the propensity of an individual to migrate. Elk on the Ya Ha Tinda have been documented to be flexible in their migratory tactic and switch migrant tactics at a rate of 15% per year (Eggeman et al., 2016). Conditional migration requires a mechanism, with physiological requirements and competitive exclusion being two suggested mechanisms (Swingland & Lessells, 1979; Chapman et al., 2011). Above we argue conspecific interactions during foraging did not appear to greatly alter the foraging advantages of any migratory tactic, indicating differential forage quality on summer range likely drives elk condition and perhaps reproduction, although differential bear predation on calves during calving complicates this interpretation (Berg et al., 2022). Martin et al. (2021) found that the switching rates over an 18-year period at the Ya Ha Tinda tended toward the tactic of higher fitness, suggesting the proportion of migrant and residents in the population was related not only by the density-dependent vital rates (Kaitala et al., 1993; Lundberg, 1987) but also by an individual's attempt to maximize fitness by switching to the migratory tactic with the highest fitness.

Elk can assess the fitness of their own migratory tactic in terms of their reproductive success, which has been shown in studies where survival rates of young are associated with range fidelity (Welch, Rodgers, & McKinley, 2000; Tremblay et al., 2007; Bose et al., 2017), but how elk on the Ya Ha Tinda assess fitness of other migratory tactics is unknown. We speculate on two possible mechanisms related to conspecific interactions on the winter range. First, we suggest that elk may learn the reproductive success of individuals within migratory tactics based on association with other individuals and their offspring during the winter (Boulinier & Danchin, 1997; Brown et al., 2000). Second, success of other tactics may be transmitted through associations on the winter range, mediated by the outcomes of social interactions. Martin et al. (2021) reported that western migrants expressed a higher propensity to switch to the resident tactic compared to eastern migrants. At low densities, relaxed aggression from resident elk may facilitate exploitation of resident knowledge of resources in western migrants, which showed higher overlap with residents on the winter range than with other western migrants. Despite higher forage quality on western summer ranges, by following residents into areas of human habituation western migrants may learn of foraging advantages associated with human activity, which may condition western migrants to remain on the winter range year-round. While the observations of elk exploiting supplemental horse feeding in the pasture are novel to this study period, Hebblewhite et al. (2006) noted hay as an attractant that may have influenced western switching during the early 2000s. Eastern elk also aggregated with other migrant tactics and followed resident elk into foraging areas more frequently, but displayed higher aggression during foraging. This may provide a competitive advantage on the winter range through exploitation of other tactics, but may also encourage the maintenance of migratory behaviour in eastern elk in order to alleviate costs from competition during the summer, reflected in the lower propensity of eastern elk switching to residency. As more studies suggest that migration is a polymorphic behaviour in ungulates determined through costs and benefits of trade-offs among migrant tactics (Gaudry et al., 2015; Martin, Hebblewhite, & Merrill, 2021), the inclusion of small-scale behavioural differences among tactics should continue to be taken into account as a driver of migratory decisions.

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Appendix A – Summary of GPS location data and volume of intersection pairs calculated among migrant and resident elk

Table A-1. Samples sizes (n of individual elk) per week during the winter period (Nov 1 – Mar 31) with > 30 fixes used to calculate volume of intersection indices between pairs. Total number of individual elk per week is shown, including total number of elk per week for each winter (2015 – 2018). Total number of elk-winters per week for all winters is also included. A total of 78 individual elk were included totalling 175 elk-winters across all winters.

Week	n (elk ID) 2015-2018	n (elk ID) 2015	n (elk ID) 2016	n (elk ID) 2017	n (elk ID) 2018	n (elk-winters) 2015-2018
1	55	17	11	38	27	93
2	55	17	11	38	24	90
3	57	21	8	41	26	96
4	56	21	6	41	25	93
5	54	19	6	41	26	92
6	45	7	5	41	24	77
7	46	8	5	41	25	79
8	46	8	4	40	25	77
9	46	7	4	40	24	75
10	45	7	4	41	24	76
11	46	8	4	41	24	77
12	45	8	4	39	23	74
13	45	8	4	40	24	76
14	44	8	3	17	11	39
15	47	11	4	39	21	75
16	47	13	27	40	20	100
17	46	13	35	40	17	105
18	49	18	42	40	17	117
19	53	20	42	40	17	119
20	52	20	42	39	0 (38 total)*	101
21	52	18	42	39	0 (37 total)*	99
22	48	18	42	39	0 (37 total)*	99

*total number of elk during week with <30 relocations

Table A-2. Sample sizes of VI values calculated for each elk pair type at a weekly scale (n weeks = 22) across all winter periods (Nov 1 – Mar 31; 2015–2018), as well as sample sizes for each elk pair type in individual winters.

Pairtype	n pairs: all winter	n pairs 2015	n pairs 2016	n pairs 2017	n pairs 2018
RR	23020	1044	3684	13408	4884
RE	18368	708	3464	11840	2356
RW	9768	1540	2008	4432	1788
EE	3364	154	732	2280	198
WW	1086	500	216	264	106
EW	3516	356	870	1880	410
Total	59122	4302	10974	34104	9742

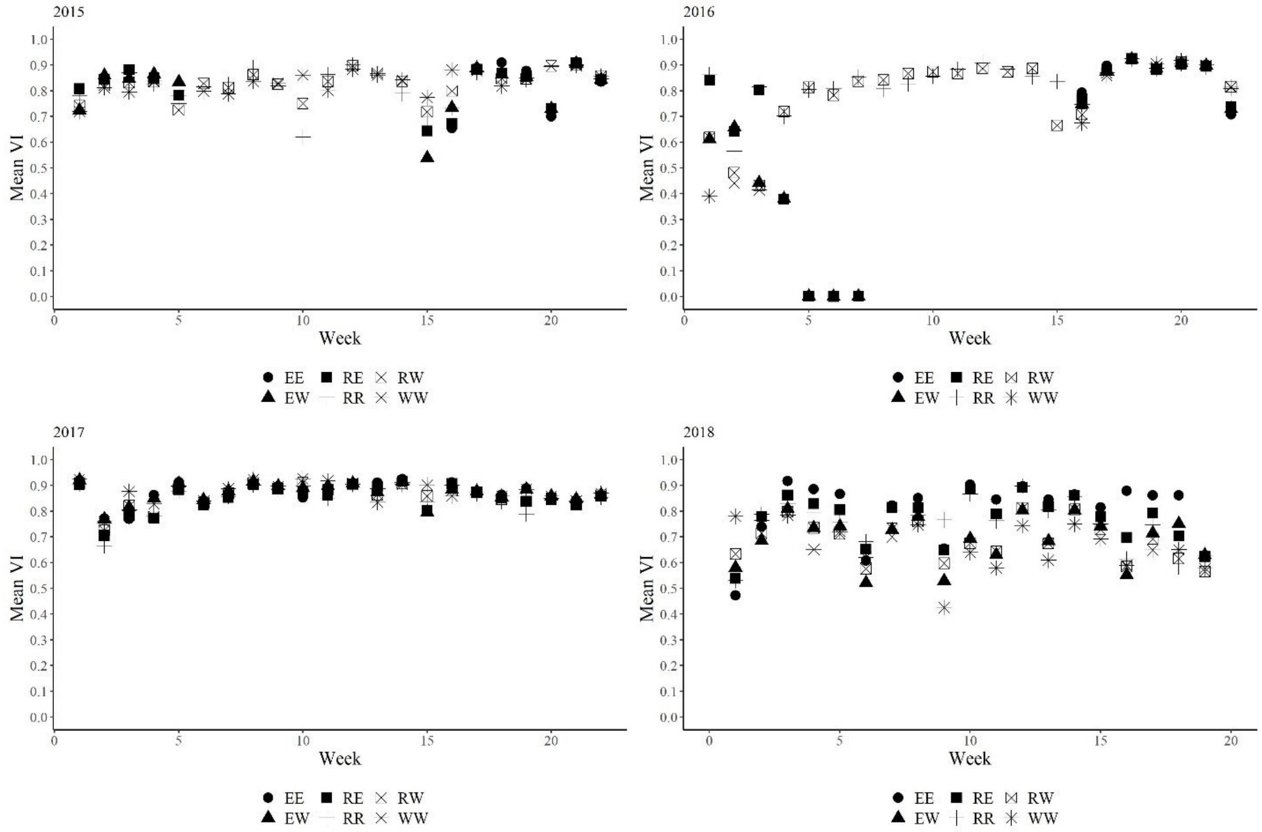


Figure A-3. Average VI calculated for all elk pair types (resident-resident, resident-eastern, resident-western, eastern-eastern, western-western, eastern-western) per week across winters 2015 – 2018 (n weeks = 22). Data were collected from GPS-collared elk on the winter range at the Ya Ha Tinda ranch, adjacent to Banff National Park in Alberta, Canada.

Appendix B – Sample sizes of focal elk observed during behavioural observations

Table B-1. Number of resident, eastern, and western migrants observed during behavioural observations as well as total number of interactions, number of neutral interactions, and number of aggressive/submissive interactions observed.

Migrant Tactic	Elk	Obs.	Interactions	Neutral	Aggro/Sub
Resident	23	205	125	46	79
Eastern	11	124	73	18	55
Western	11	120	50	12	38
Total	45	449	248	76	172

Appendix C – Interaction rate related to local elk density

Table C-1. Summary of model selection results based on AIC_c for number of interactions between focal elk and conspecifics at 2-m, 10-m, and 20-m radius concentric circles.

Model	k	AIC_c	ΔAIC_c	AIC_c Wt.
Density – 2m	3	871.2	0.00	0.93
Density – 10m	3	876.4	5.21	0.07
Density – 20m	3	883.2	12.06	0.00

Appendix D – Relating interaction rate and aggressiveness among resident and migrant elk to environmental factors on the Ya Ha Tinda winter range

Table D-1. Model selection using AIC_c for number of interactions between focal elk and conspecifics. Covariates included age, day of winter, biomass, position, and density of conspecifics Competitive models (within Δ AIC_c of 2) are shown above the horizontal line.

Model	k	AIC_c	Δ AIC_c	AIC_c Wt.
Density	4	789.2	0.00	0.15
Density - biomass	5	789.6	0.44	0.12
Density - position	5	790.1	0.91	0.09
Density - age	5	790.3	1.11	0.08
Density - position - biomass	6	790.6	1.38	0.07
Density - biomass - day	6	790.6	1.43	0.07
Density - biomass - age	6	790.6	1.44	0.07
Density - day	5	790.7	1.52	0.07
Density - position - age	6	791.2	1.97	0.06
Density - biomass - day - age	7	791.7	2.47	0.04
Density - biomass - day - position	7	791.7	2.52	0.04
- Age - biomass - day - position	7	791.7	2.52	0.04
Density - position - day	6	791.7	2.53	0.04
Density - age - day	6	791.9	2.67	0.04
Global	10	794.1	4.90	0.01
- Position	4	806.0	16.77	0.00
- Biomass - position	5	806.3	17.10	0.00
Null	3	807.0	17.76	0.00
- Biomass	4	807.2	18.00	0.00
- Age - position	5	807.3	18.06	0.00
- Biomass - age - position	6	807.6	18.39	0.00
- Day	4	808.2	19.01	0.00
- Age	4	808.3	19.08	0.00
- Age - biomass	5	808.5	19.31	0.00
- Day - biomass	5	808.5	19.31	0.00
- Biomass - age - day	6	809.1	19.90	0.00
- Age - day	5	809.5	20.35	0.00
- Day - position	5	809.5	20.35	0.00

Table D-2. Beta coefficients (β) with standard error (SE) and upper and lower 95% confidence intervals (CI) for parameters of the top 5 models of the number of interactions observed among resident, eastern migrant, and western migrant elk. Covariates include density, biomass, focal age, and day of winter.

Variable	$\beta \pm SE$	95% CI	
		Lower	Upper
Density	0.32 ± 0.07	0.18	0.46
Biomass	- 0.002 ± 0.001	- 0.004	0.000
Intercept	- 3.07 ± 0.22	- 3.50	- 2.64
Density	0.32 ± 0.07	0.19	0.47
Biomass	- 0.002 ± 0.001	- 0.004	0.000
Resident	- 0.13 ± 0.23	- 0.59	0.32
Western	- 0.49 ± 0.27	- 1.02	0.04
Intercept	- 2.89 ± 0.26	- 3.40	- 2.38
Density	0.31 ± 0.07	0.17	0.45
Biomass	- 0.002 ± 0.001	- 0.005	0.001
Periphery	- 0.22 ± 0.21	- 0.64	0.19
Intercept	- 2.97 ± 0.24	- 3.44	- 2.50
Density	0.32 ± 0.07	0.18	0.46
Biomass	- 0.002 ± 0.001	- 0.005	0.001
Day	- 0.005 ± 0.005	- 0.014	0.004
Intercept	- 2.75 ± 0.37	- 3.48	- 2.02
Density	0.32 ± 0.07	0.18	0.46
Biomass	- 0.002 ± 0.001	- 0.005	0.001
Age	- 0.02 ± 0.02	- 0.07	0.02
Intercept	- 2.83 ± 0.30	- 3.42	- 2.24

Table D-3. Summary of model selection results based on AIC_c for interaction type (aggressive or submissive) between focal elk and conspecifics. Covariates included age, day of winter, biomass, position, and density of conspecifics. Competitive models (within Δ AIC_c of 2 are shown above the horizontal line.

Model Structure	k	AIC_c	Δ AIC_c	AIC_c Wt.
density + age + day	5	182.3	0.00	0.34
density + biomass + age + day	6	183.2	0.89	0.22
density + biomass + age	5	184.8	2.51	0.01
density + age	4	184.9	2.61	0.09
density + day	4	186.5	4.16	0.04
density + position + age	5	186.5	4.19	0.04
density + position + day	5	186.9	4.59	0.03
density + biomass + day	5	187.3	5.03	0.03
density + biomass + day + position	6	188.0	5.71	0.02
age + day	4	188.9	6.57	0.01
density	3	188.9	6.59	0.01
density + biomass	4	188.9	6.65	0.01
biomass + age + day	5	190.6	8.27	0.01
density + position	4	190.6	8.27	0.01
density + position + biomass	5	190.7	8.41	0.01
age	3	190.7	8.42	0.01
day	3	190.8	8.51	0.01
age + biomass	4	191.9	9.56	0.00
age + biomass + day + position	6	192.0	9.66	0.00
day + position	4	192.1	9.84	0.00
day + biomass	4	192.4	10.13	0.00
age + position	4	192.7	10.40	0.00
biomass	3	193.5	11.22	0.00
biomass + age + position	5	193.9	11.60	0.00
position	3	194.4	12.08	0.00
biomass + position	4	195.6	13.25	0.00
null	3	807.0	624.66	0.00

Table D-4. Beta coefficients (*β*) with standard error (SE) and upper and lower 95% confidence intervals (CI) for parameters of the top 4 models interaction types observed among resident, eastern migrant, and western migrant elk. Covariates include density, biomass, age, and day of winter.

		95% CI	
Variable	*β* ± *SE*	Lower	Upper
Density	- 0.43 ± 0.15	- 0.71	- 0.14
Resident	- 0.15 ± 0.62	- 1.37	1.06
Western	- 1.28 ± 0.65	- 2.56	0.00
Age	- 0.15 ± 0.06	- 0.27	- 0.04
Day	0.03 ± 0.01	0.003	0.05
Intercept	1.94 ± 0.94	0.10	3.78
Density	-0.42 ± 0.15	-0.71	-0.13
Age	-0.15 ± 0.06	-0.27	-0.03
Day	0.03 ± 0.01	-0.01	0.05
Intercept	1.55 ± 0.94	-0.29	3.39
Density	-0.46 ± 0.15	-0.75	0.17
Age	-0.15 ± 0.06	-0.27	-0.03
Biomass	-0.004 ± 0.004	-0.01	0.00
Day	0.02 ± 0.01	0.00	0.04
Resident	-0.18 ± 0.63	-1.41	1.05
Western	-1.29 ± 0.66	-2.58	0.00
Intercept	2.53 ± 1.13	0.32	4.74
Density	-0.45 ± 0.15	-0.74	-0.16
Age	-0.16 ± 0.06	-0.28	-0.04
Biomass	-0.004 ± 0.003	-0.01	0.00
Day	0.02 ± 0.01	0.00	0.04
Intercept	2.23 ± 1.15	-0.02	4.48

Appendix E – Study area and locations of focal elk behavioural observations across winters of 2019 – 2020

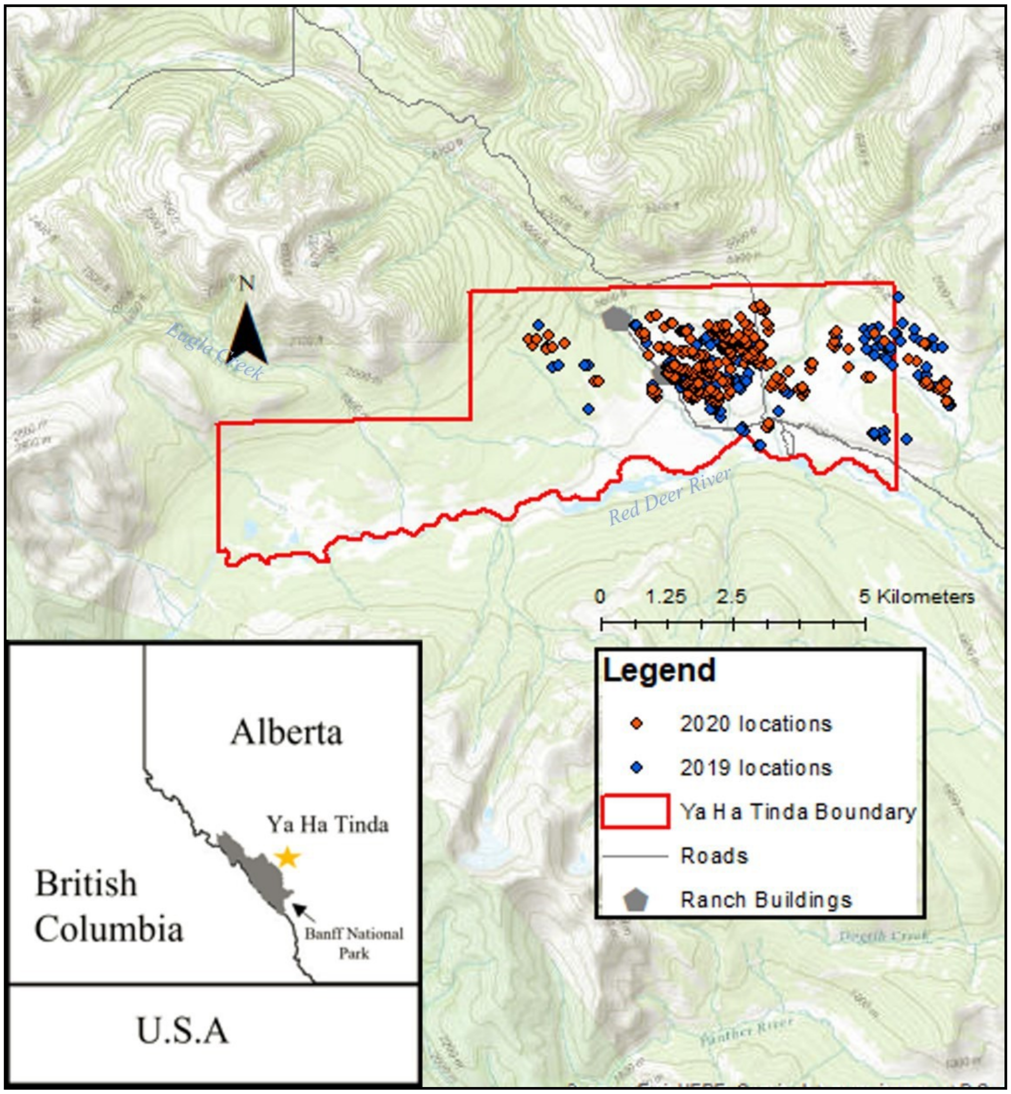


Figure E-1. Location of the Ya Ha Tinda winter range located in the eastern foothills of the Rocky Mountains in Alberta, Canada. Included are locations of elk observed during foraging bouts during the winters (January – April) of 2019 (blue circles) and 2020 (orange circles). Roads are show in dark grey lines, the Ya Ha Tinda ranch property is shown in red, and ranch buildings are indicated by grey pentagons.

Appendix F – Mean proportion of observation time spent in foraging behaviours between 2019 – 2020

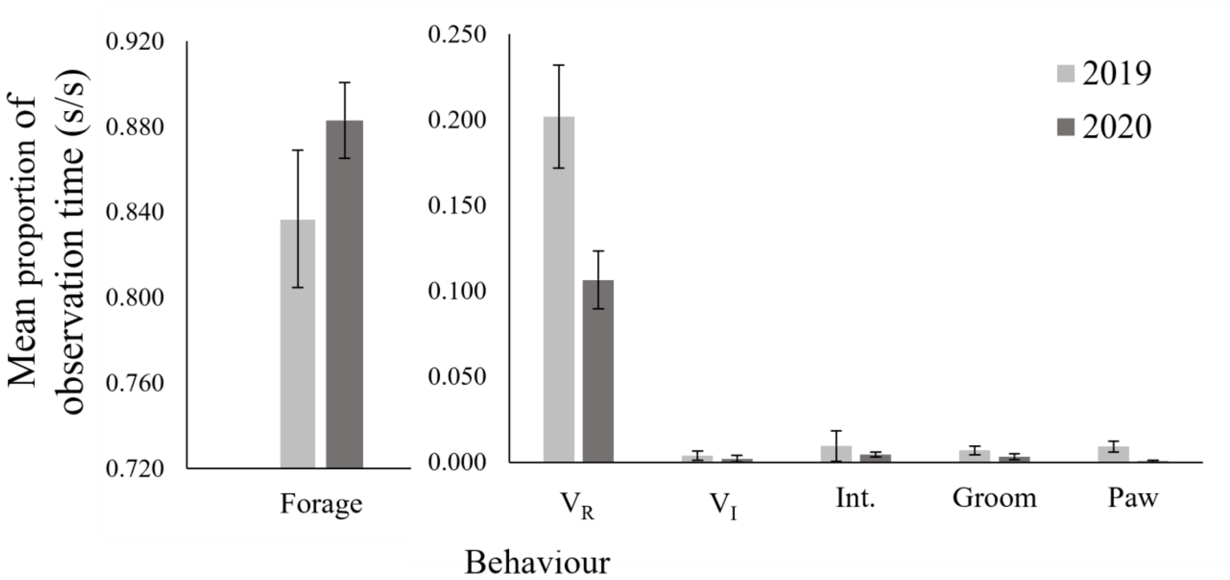


Figure F-1. Mean proportion of time (s/s) engaged in six behaviours (forage; routine vigilance [V_R]; interaction vigilance [V_I]; interactions [Int.]; grooming; and pawing) during behavioural observations. Confidence limits for each year are reported.

Appendix G – Behavioural outliers of vigilance and interaction time during foraging observations

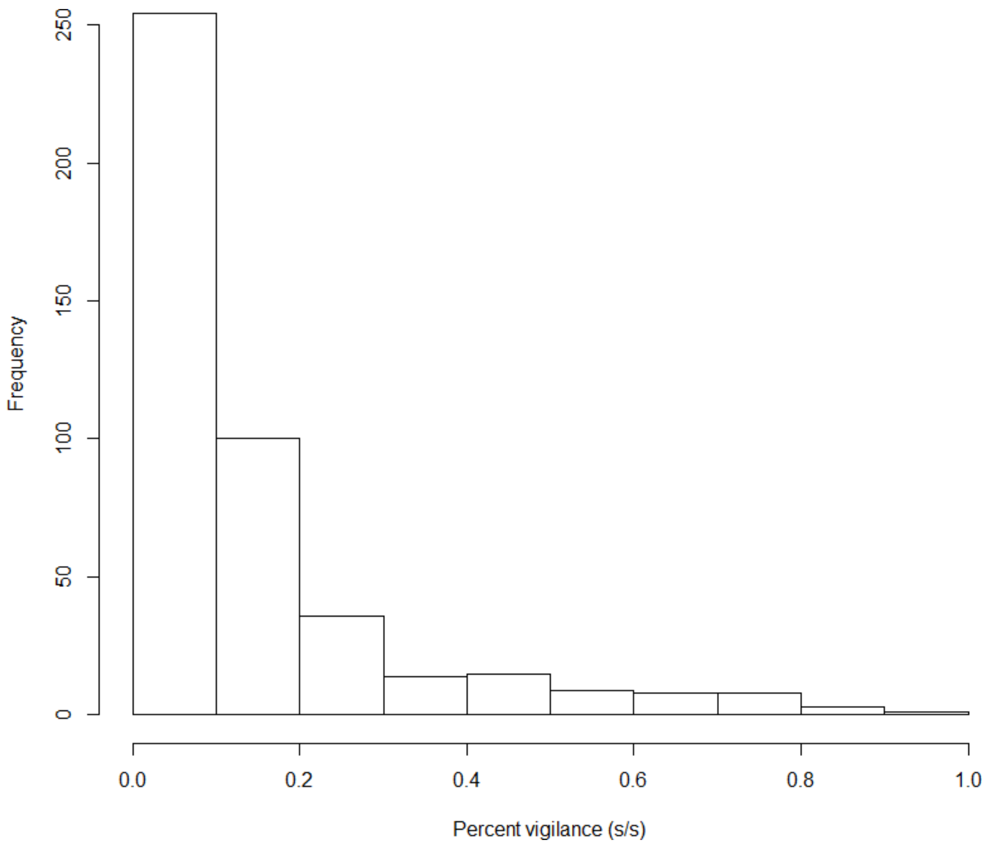
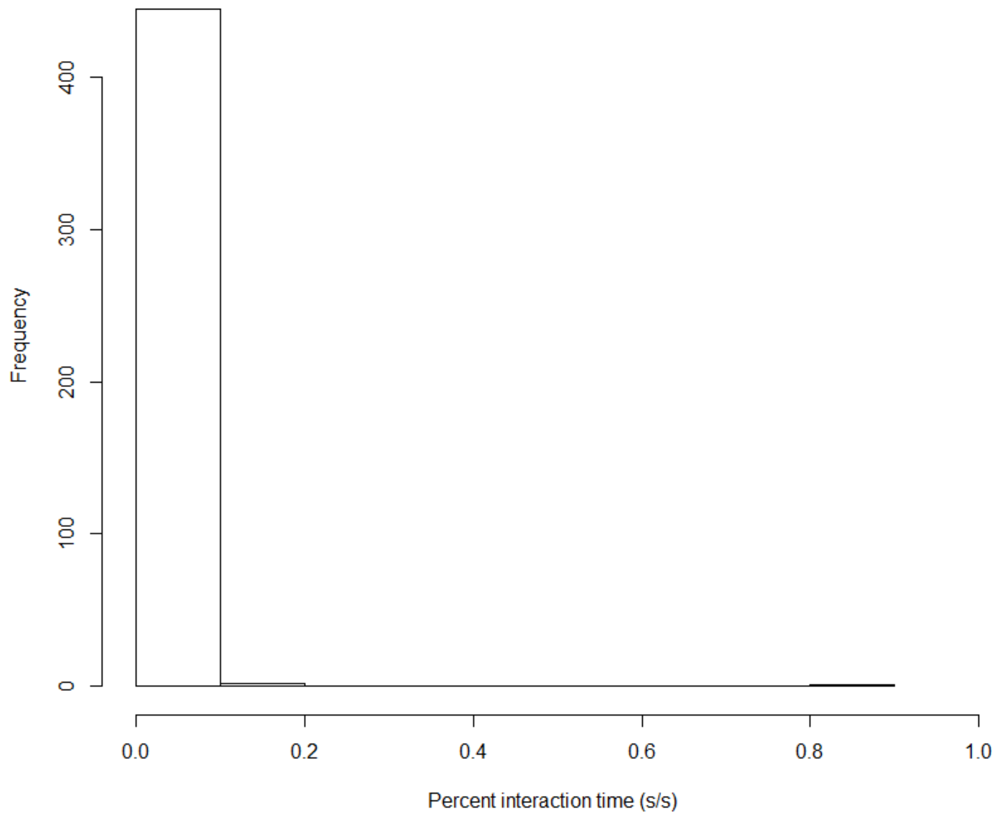


Figure G-1. Histogram of percentage of observation duration spent interacting during foraging observations. One observation with a percent of time spent interacting > 80% between a female elk and her calf was removed from the analysis as an outlier of interaction behaviour.



Appendix G-2. Histogram of percentage of observation duration spent vigilant during foraging observations. One observation with a percent vigilant > 97% was removed from the analysis as an outlier of vigilance behaviour.

Appendix H – Range of relative aggression rank among focal elk based on aggressive and submissive interactions

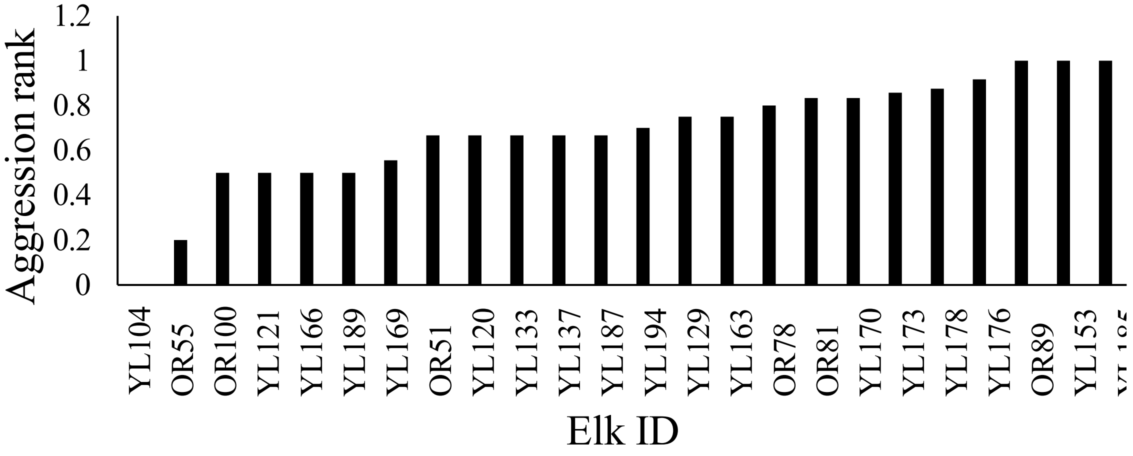


Figure H-1. Range of relative aggression rank among focal elk observed interacting on the winter range at the Ya Ha Tinda ranch. Rank ranges from 0 – 1, with values closer to 1 denoting more aggression.

Appendix I – Vigilance response to local elk density

Table I-1. Model selection results of routine vigilance in response to local density around the focal within 1 elk-length (~2m radius), 5 elk-lengths (~10m radius), and 10 elk-lengths (~20m radius).

Routine vigilance (s)	k	AIC_c	Δ AIC_c	AIC_c Wt.
2 -m	4	646.2	0.00	0.52
10 -m	4	646.6	0.39	0.43
20 -m	4	650.8	4.55	0.05

Appendix J – Relating total, routine, and interaction vigilance to environmental factors on the winter range

Table J-1. Full model selection results for models relating total vigilance (s/min) during foraging observations based on AIC_c model selection. Covariates in the candidate models included position, conspecific density, biomass estimates (g/m^2), distance to timber edge (m), distance to buildings (m), and migrant tactic.

Total vigilance (s)	k	AIC_c	Δ AIC_c	AIC_c Wt.
– Timber + density – day	7	4387.4	0.00	0.22
– Timber – day	6	4387.5	0.06	0.21
– Timber + density – day – buildings	8	4388.1	0.66	0.16
– Timber + density – day + position	8	4388.5	1.12	0.12
– Timber + density – day – buildings + position	9	4389.1	1.73	0.09
– Timber + density – day + migrant tactic	9	4390.5	3.09	0.05
– Timber + density – day – buildings + migrant tactic	12	4391.5	4.06	0.03
– Timber + density – day + position + migrant tactic	10	4391.6	4.18	0.03
– Timber + density	6	4392.3	4.93	0.02
– Timber + density – day – buildings + position + mig	13	4392.7	5.30	0.02
– Timber – timber^2	5	4392.8	5.38	0.02
Density – day	6	4393.8	6.35	0.01
– Day	6	4393.8	6.36	0.01
Density – day – buildings	5	4394.7	7.26	0.01
– Day – buildings	7	4394.7	7.29	0.01
Density – day – buildings + position	6	4395.3	7.89	0.00
Density	8	4395.9	8.46	0.00
Density – buildings	5	4396.2	8.76	0.00
Null	6	4396.9	9.47	0.00
– Buildings	4	4397.3	9.90	0.00
Position	5	4397.6	10.21	0.00
Biomass	5	4398.9	11.47	0.00
– Buildings – buildings^2	5	4399.2	11.79	0.00
Migrant tactic	6	4399.6	12.15	0.00

Table J-2. Beta coefficients (*β*) with standard error (SE) and upper and lower 95% confidence intervals (CI) for parameters of the top 5 models of total vigilance (seconds) observed among resident, eastern migrant, and western migrant elk. Covariates in the candidate models included position, conspecific density, biomass estimates (g/m^2), distance to timber edge (m), distance to buildings (m), and migrant tactic.

Variable	*β* ± *SE*	95% CI	
		Lower	Upper
Timber	- 0.17 ± 0.06	0.29	- 0.05
Density	0 .09 ± 0.06	- 0.03	0.21
Day	- 0.007 ± 0.002	- 0.01	- 0.003
Intercept	2.54 ± 0.26	2.03	3.05
Timber	- 0.17 ± 0.06	- 0.29	- 0.05
Day	- 0.007 ± 0.002	- 0.01	- 0.002
Intercept	2.56 ± 0.28	2.01	3.11
Timber	- 0.17 ± 0.06	- 0.29	- 0.05
Density	0.11 ± 0.06	- 0.01	0.23
Day	- 0.007 ± 0.002	- 0.01	- 0.002
Periphery	0.13 ± 0.12	- 0.11	0.37
Intercept	2. 48 ± 0.27	1.95	3.01
Timber	- 0.17 ± 0.06	- 0.29	- 0.05
Density	0.09 ± 0.06	- 0.03	0.21
Day	- 0.007 ± 0.002	- 0.01	- 0.002
Buildings	- 0.06 ± 0.06	- 0.18	0.06
Intercept	2.53 ± 0.17	2.20	2.86
Timber	- 0.17 ± 0.06	- 0.29	- 0.05
Density	0.11 ± 0.06	- 0.01	0.23
Day	- 0.007 ± 0.002	- 0.01	- 0.002
Building	- 0.07 ± 0.06	- 0.19	0.05
Periphery	0.13 ± 0.12	- 0.11	0.37
Intercept	2.46 ± 0.27	1.93	2.99

Table J-3. Summary of full model selection results models relating routine vigilance (s/min) during foraging observations based on AIC_c model selection. Vigilance models include an offset of the natural log of duration of observation (min), and all models include a random effect of individual elk ID and year. Models within Δ2 AIC_c are indicated by the solid black line.

Routine vigilance (s)	k	AIC_c	Δ AIC_c	AIC_c Wt.
– Timber + density – day – buildings + position	9	4127.1	0.00	0.25
– Timber + density – day – buildings	8	4127.6	0.51	0.19
– Timber + density – day + position	8	4128.5	1.45	0.12
– Timber – day	6	4128.7	1.65	0.11
– Timber + density – day	7	4129	1.92	0.09
Density – day – buildings + position	8	4130.7	3.65	0.04
– Day – buildings	6	4131.1	4.00	0.03
Density – day – buildings	7	4131.3	4.22	0.03
– Timber + density – day – buildings + position + mig	13	4131.4	4.35	0.03
– Timber + density – day – buildings + migrant tactic	12	4131.8	4.75	0.02
Density – day	6	4132.3	5.25	0.02
– Timber + density – day + position + migrant tactic	10	4132.3	5.25	0.02
– Day	5	4132.6	5.54	0.02
– Timber + density – day + migrant tactic	9	4132.8	5.71	0.01
– Timber + density	6	4135.5	8.48	0.00
Density – buildings	6	4135.6	8.51	0.00
– Buildings	5	4135.6	8.55	0.00
– Timber	5	4135.8	8.74	0.00
– Timber – $timber^2$	6	4136.4	9.34	0.00
Density	5	4136.8	9.72	0.00
– Buildings – $buildings^2$	6	4137.4	10.33	0.00
Null	4	4137.5	10.42	0.00
Position	5	4137.6	10.54	0.00
Migrant tactic	6	4141.4	14.34	0.00

Table J-4. Beta coefficients (*β*) with standard error (SE) and upper and lower 95% confidence intervals (CI) for parameters of the top 5 models of routine vigilance (seconds) observed among resident, eastern migrant, and western migrant elk. Covariates in the candidate models included position, conspecific density, biomass estimates (g/m^2), distance to timber edge (m), distance to buildings (m), and migrant tactic.

		95% CI	
Variable	*β* ± *SE*	Lower	Upper
Timber	- 0.12 ± 0.05	- 0.22	- 0.02
Density	0.08 ± 0.05	- 0.02	0.18
Day	- 0.006 ± 0.002	- 0.01	- 0.002
Buildings	- 0.08 ± 0.05	- 0.18	0.02
Periphery	0.17 ± 0.11	- 0.05	0.39
Intercept	2.49 ± 0.15	2.20	2.86
Timber	- 0.12 ± 0.05	- 0.22	- 0.02
Density	0.07 ± 0.05	- 0.03	0.17
Day	- 0.006 ± 0.002	- 0.01	- 0.002
Buildings	- 0.08 ± 0.05	- 0.18	0.02
Intercept	2.53 ± 0.002	2.53	2.53
Timber	- 0.12 ± 0.05	- 0.22	- 0.02
Density	0.09 ± 0.05	- 0.02	0.19
Day	- 0.006 ± 0.002	- 0.01	- 0.002
Periphery	0.20 ± 0.11	- 0.02	0.42
Intercept	2. 47 ± 0.22	2.04	2.90
Timber	- 0.12 ± 0.05	- 0.22	- 0.02
Density	0.07 ± 0.05	- 0.03	0.17
Day	- 0.006 ± 0.002	- 0.01	- 0.002
Intercept	2.54 ± 0.22	2.11	2.97
Timber	- 0.13 ± 0.05	- 0.23	- 0.03
Day	- 0.006 ± 0.002	- 0.01	- 0.002
Intercept	2.56 ± 0.23	2.11	3.01

Appendix J-5. Summary of full model selection results for negative binomial mixed-effects models relating interaction vigilance (s/min) during foraging observations based on AIC_c model selection. Covariates in the candidate models included position (peripheral [reference] or central), conspecific density, biomass estimates (g/m^2), straight-line distance to the nearest forest (timber) edge (m), distance to the nearest Ya Ha Tinda ranch building (m), and migrant tactic (resident, eastern, or western). Vigilance models include an offset of the natural log of duration of observation (min), and all models include a random effect of individual elk ID and year. Models were considered competitive if $\Delta AIC_c < 2.0$, indicated by the solid black line. Observations were recorded from GPS-collared elk on the Ya Ha Tinda ranch adjacent to Banff National Park, Alberta, Canada during January - April 2019 – 2020.

Interaction vigilance (s)	k	AIC_c	ΔAIC_c	AIC_c Wt.
- Timber	5	427.3	0.00	0.40
– Timber – buildings	6	429.7	2.36	0.12
– Timber + density	6	429.7	2.40	0.12
– Timber + density + position	7	430.8	3.44	0.07
– Timber + density + biomass	7	431.2	3.85	0.06
Null	4	431.7	4.37	0.05
– Timber + density – buildings	7	432	4.65	0.04
Biomass	5	432.9	5.54	0.03
– Timber – buildings + migrant tactic	8	433.4	6.1	0.02
– Timber + density + migrant tactic	8	433.5	6.17	0.02
– Day	5	433.8	6.49	0.02
Density	5	433.8	6.51	0.02
Position	5	433.9	6.53	0.02
– Buildings	5	434.1	6.77	0.01
Migrant tactic	6	435.1	7.78	0.01
– Timber + migrant tactic	9	435.9	8.56	0.01
Density – buildings	6	436.3	8.93	0.01