

University of Alberta

FORAGING-PREDATOR AVOIDANCE TRADE-OFFS MADE BY
MIGRANT AND RESIDENT ELK (*CERVUS ELAPHUS*) ON THEIR
SYMPATRIC WINTER RANGE

by

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*To all prey and their predators for enduring the endless
struggle to outwit one another*

ABSTRACT

Migratory behaviour of the Ya Ha Tinda (YHT) elk population is diminishing while the number of residents remaining on the YHT winter range year-round is increasing. Previous research addressing the fitness consequences of each migratory strategy assumed there was no advantage to either segment when they shared the YHT winter range. In testing this assumption, I found no spatial segregation of migrant and resident home-ranges during winter. Both groups were exposed to similar forage resources and residents were exposed to higher night-time, but not day-time predation risk. Residents were better than migrants at reducing the foraging costs of vigilance and increased vigilance in areas of high wolf predation risk, but not near human activity because of habituation. Migrants were not habituated to humans and exhibited more constant vigilance regardless of spatial variations in risk. My results do not support the previous assumption. Instead, I found residents may be at an advantage on the winter range while forage is abundant and no snow is present.

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CHAPTER 1: INTRODUCTION

BACKGROUND

The widespread loss of migratory behaviour in ungulate populations around the world has received much attention because of their significant role in shaping ecosystem function (Sinclair and Caughley 1994, Smith and Robbins 1994, Sinclair 2003, Berger 2004). The causes of migration disruption are varied but often involve habitat fragmentation, human hunting (both legal and poaching), or a combination of both factors (Smith and Robbins 1994, Burcham et al. 1999, Mahoney and Schaefer 2002, Thirgood et al. 2004). Increased human activity and development in the backcountry has been blamed for the disruption of elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*) migrations in Yellowstone National Park, USA (Berger 2004). In Banff National Park (BNP), Canada, high human activity in conjunction with rebounding wolf populations has disrupted the migratory behaviour of elk populations (Woods 1991, McKenzie 2001, Hebblewhite and White et al. 2005).

More recently Hebblewhite et al. (2006) documented a decline in the migratory segment of one of the most significant elk populations in Alberta, Canada, the Ya Ha Tinda (YHT) herd. Historically, the majority of the population migrated from the YHT winter range, a rare montane rough fescue (*Festuca campestris*) grassland, 25 – 50 km west into the high elevations of BNP to summer (Morgantini and Hudson 1988). The population has always been partially migratory with a small number of residents remaining on the YHT all year, but the ratio of migrant to resident elk (M:R ratio) has declined from 12:1 to 3:1 over the past 30 years (Hebblewhite et al. 2006). This shift equates to a 390 % increase in the number of resident elk compared to only a 50 % increase in overall population size during the same time period. Increased numbers of resident elk foraging on this important winter range during summer may deplete forage available during winter when the elk have no other food source. The cause of the reduction in the proportion of migrating elk must be understood if

appropriate management strategies are to be applied to increase the proportion of migrants in this population.

Previous research on the YHT elk population addressed whether a change in summer predation risk associated with the recovery of wolves lead to a fitness advantage for resident elk over migrants reducing the M:R ratio (Hebblewhite 2006). During summer, migrant elk were exposed to higher quality forage on the BNP summer range than residents remaining on the YHT (Hebblewhite et al. 2008), resulting in higher pregnancy rates and body masses of migrant young of year. However, this demographic advantage was partially offset because migrants were exposed to higher predation risk during migration whereas residents were able to reduce predation risk by making fine-scale selection of areas with high human activity that were avoided by wolves and grizzly bears (a predation refuge; Hebblewhite and Merrill 2007). The trade-offs between forage and predator avoidance made by migrants and residents during summer resulted in higher estimated fitness for residents than for migrants that was consistent with the declining M:R ratio (Hebblewhite 2006).

Although the recent research at YHT provided insight into potential causes of the declining M:R ratio, it focused on differences between migratory strategies only during summer while both groups were occupying separate ranges. Similar to most studies of partially migratory ungulate populations (Fryxell et al. 1988, Albon and Langvatn 1992, Kaitala et al. 1993, Ball et al. 2001), Hebblewhite (2006) assumed migrant and resident elk were intermixed in a single herd and exposed to equal forage and predation risk while together on the sympatric range. However, this assumption has never been tested and ungulate populations are known to segregate into smaller, stable groups (Clutton-Brock et al. 1982, Jenkins and Starkey 1982, Lazo 1994, Weckerly 1999) and dominant individuals are known to exclude subordinates from foraging sites (Cassinello 2002). Exclusion of migrant elk by residents from optimal foraging sites or predation refugia on the winter range has not been investigated and may also contribute to the observed shift in the M:R ratio. Preliminary evidence indicates that migrant and resident elk of the YHT population are indeed spatially segregated on the winter range:

80% of elk harvested at the YHT by First Nations during winters from 2002 – 2004 were residents (N = 5), and if migrant and resident elk were intermixed during winter, the harvest should be unbiased (Hebblewhite 2006). If one population segment is exposed to higher predation risk than the other, even if they are not killed directly by predation, a demand for amplified antipredator behaviour such as vigilance (scanning for predators) could reduce forage intake (Illius and FitzGibbon 1994, Fortin et al. 2004b), thus putting that population segment at a disadvantage.

Alternatively, differential antipredator behaviour between migrants and residents could also be inherent and present even if both groups are intermixed on the winter range. For example, if migrants are more wary of wolves than residents because of higher migrant exposure to predation risk during migration (Hebblewhite and Merrill 2007), migrants may interrupt foraging to scan for predators (vigilance) more frequently than residents, even if winter exposure to predation risk is equal (Lima and Bednekoff 1999, Frair et al. 2007, Berger 2008). Although increased vigilance traditionally was assumed to directly reduce forage intake (Underwood 1982), more recent studies have shown that vigilance may be less costly to herbivores than traditionally assumed because animals are able to scan for predators while processing (i.e. chewing) their food (Illius and FitzGibbon 1994, Fortin et al. 2004a and 2004b). Despite this new model of ‘multi-tasking’, the foraging costs associated with potential differences in antipredator behaviour between migrant and resident elk and the effects these costs have on the M:R ratio should be investigated.

OBJECTIVES

The overall goal of this thesis was to determine if migrant and resident elk behaved differently on the YHT winter range and if these behavioural differences had the potential to put migrants at a disadvantage in terms of forage intake and exposure to wolf predation risk. Any disadvantage to migrants on the winter range may contribute to the declining M:R ratio observed in this herd and,

therefore, should be considered in any management strategy put forth to alleviate this problem.

In Chapter 2, I compared the distribution of migrant and resident elk on the YHT winter range at two spatial scales to determine if they were spatially segregated and exposed to different resources. First, I examined the degree of overlap between migrant and resident winter home-ranges to determine if they used similar areas of the winter range at the landscape-scale. I then examined relative wolf predation risk and forage abundance at migrant and resident telemetry locations to compare exposure to these factors at the home-range scale. In Chapter 3, I examined elk behaviour at the scale of the foraging site and compared the amount of time migrant and resident elk spent being vigilant while foraging and investigated the extent that vigilance compromised forage intake. I used these data to determine if migrant and resident elk had different abilities to detect and respond to the spatiotemporal variations in predation risk that are known to occur on the YHT winter range (Hebblewhite and Merrill 2008, Chapter 1). My study is among the first to determine if there are behavioural differences between migrant and resident ungulates in a partially migratory population when together on sympatric ranges, and whether these behavioural differences could contribute to one migratory strategy being advantageous over the other.

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CHAPTER 2: EXPOSURE OF MIGRANT AND RESIDENT ELK TO FORAGE AND PREDATION RISK ON THEIR SYMPATRIC RANGE

INTRODUCTION

Long-distance migration between allopatric ranges are common among animal populations and are thought to have evolved because migration maximizes access to high quality food resources and provides escape from predators (Fryxell et al. 1988, Albon and Langvatn 1992, Berger 2004, Hebblewhite and Merrill 2007, Hebblewhite et al. 2008). However, partially migratory populations, where one portion of a population conducts seasonal migrations (migrants) while the other remains on a single range (residents), are also common, and their coexistence has been attributed to density-dependent fitness balancing between the two strategies (see Swingland 1983 for a thorough review; Lundberg 1988, Hebblewhite 2006). To understand the trade-offs between migratory strategies in partially migratory populations of ungulates, studies generally emphasize the differences between costs and benefits incurred by migrants and residents while they are occupying separate ranges and assume they derive equal costs and benefits when animals are together on the same range. For example, field studies of partially migratory elk (*Cervus elaphus*) and moose (*Alces alces*) populations compared the quantity and quality of forage and the amount of predation risk migrants and residents were exposed to only when separated on different ranges (Albon and Langvatn 1992, Ball et al. 2001, Hebblewhite and Merrill 2007, Hebblewhite et al. 2008). Similarly, in models of partially migratory ungulate population dynamics, Fryxell et al. (1988) and Kaitala et al. (1993) both assumed equal forage consumption and mortality rates of migrants and residents when on their sympatric range.

It may be inappropriate to assume migrants and residents sustain equal costs and benefits on sympatric ranges because ungulate populations are known to segregate into stable, social groups (Clutton-Brock et al. 1982, Jenkins and Starkey 1982, Lazo 1994, Weckerly 1999) where dominant individuals exclude subordinates from productive foraging sites (Thouless 1990, Cassinello 2002). Theoretical studies of partial migration in birds have long considered that

residents are at an advantage on the sympatric range (von Haartman 1968, Taylor and Norris 2007), and empirical studies have confirmed this. For example, Andriaensen and Dhondt (1990) showed that residents of a partially migratory robin (*Erithacus rubecula*) population had higher survival, probability of breeding, and mating success than migrants because residents were able to exclude migrants from ideal breeding territories as they returned from their wintering grounds. Similarly, Pérez-Tris and Tellería (2002) found considerable spatial segregation between resident and returning migrant blackcaps (*Sylvia atricapilla*) on their sympatric winter range because residents defended the most suitable breeding sites, while migrants concentrated in habitats with high food abundance. Resident exclusion of migrants from either high quality foraging sites or areas of low predation risk on sympatric ranges has not been well studied in partially migratory ungulates. Ungulate habitat selection is often driven by a trade-offs between acquiring forage and avoiding predation (Fryxell et al. 1988, Houston et al. 1993, Hebblewhite and Merrill 2009) and exposure to these factors can determine life-time reproductive success (Kjellander et al. 2004, Loudon et al. 1983), so spatial segregation of migrant and resident animals on the sympatric range could have fitness consequences.

In this Chapter, I tested the assumption that migrant and resident individuals in a partially migratory elk population in the Canadian Rockies were exposed to equal forage and predation risk while on their sympatric winter range (Hebblewhite and Merrill 2009). Residents of this population remain on the Ya Ha Tinda (YHT) winter range adjacent to Banff National Park (BNP) year-round, while migrants move to high elevation summer ranges in BNP (Hebblewhite et al. 2006). On their summer range migrant elk are exposed to higher quality forage (Hebblewhite et al. 2008) and lower predation risk (Hebblewhite and Merrill 2007) than residents, but exposure to these factors on the YHT range during winter has not received direct attention.

To determine if migrant and resident elk were exposed to different forage resources and predation risk on the YHT winter range, I tested two hypotheses, each considering a different spatial scale. First, I tested the hypothesis that

migrant and resident elk were spatially segregated on the winter range at the landscape-scale by comparing the amount of home-range overlap between the two groups. Second, even if migrant and resident elk were not spatially segregated at the landscape-scale, I hypothesized there were fine-scale differences in habitat use within home-ranges that resulted in different exposure to forage resources and predation risk. I tested this hypothesis by comparing exposure of migrant and resident elk to predation risk and forage abundance at winter telemetry locations, which was similar to comparisons made between migrant and resident exposure on summer ranges (Hebblewhite and Merrill 2007, Hebblewhite et al. 2008). Because the resident portion of this herd has been increasing (Hebblewhite et al. 2006), I expected resident elk were exposed to lower predation risk and higher forage abundance than migrants.

METHODS

Study Site

The Ya Ha Tinda (YHT) is a 4000-ha winter range located on the eastern slopes of the Rocky Mountains adjacent to Banff National Park (BNP) in Alberta, Canada. Parks Canada operates a horse ranch at the YHT and winters ~ 100 horses there each year. Approximately two thirds of the YHT is native rough fescue (*Festuca campestris*) grassland making it one of Alberta's largest montane fescue grasslands (Hebblewhite and Merrill 2007). The remaining third is predominantly lodgepole pine (*Pinus contorta*) forests merging into Engelmann spruce (*Picea engelmannii*) at higher elevations, but is also interspersed with aspen (*Populus tremuloides*) forests and willow-bog birch (*Salix* sp.-*Betula glandulosa*) shrublands. Warm westerly winds (Chinooks) are common during the winter, which maintains a snow pack generally < 25 cm on the main grasslands (Morgantini 1995). Low snow depth, in combination with the high nutritional content of cured rough fescue (Pigden 1953), makes the YHT an ideal winter range for grazing ungulates and one of the two most important elk winter ranges in Alberta (Morgantini 1995). Elk are the dominant herbivore in the system, but mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), bighorn

sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and moose are also present. The YHT elk population ranged from ~ 800 individuals in the early 1970's to > 2000 in the early 1990's and consisted of ~ 800 individuals during this study; regardless of population size, the ratio of migrant to resident elk has steadily decreased from 12:1 to 3:1 over this time period (Hebblewhite et al. 2006). Grizzly bears (*Ursus arctos horribilis*) and black bears (*Ursus americanus*) are common in the summer, but wolves (*Canis lupus*), cougars (*Felis concolor*), and coyotes (*Canis latrans*) are the only active predators during winter. Wolves are the most common predator of elk in this system; during the winter of 2003/04 two packs ranging in size from 6-17 wolves consistently hunted the YHT elk herd (Hebblewhite and Merrill 2007).

Capture and monitoring of elk and wolves

Elk were captured annually from 2001-2005 using a corral trap baited with hay between January and March when migrants and residents were together on the YHT winter range (University of Alberta Animal Care Protocol # 353112; see Hebblewhite et al. 2006 for details). Twenty six adult cows were equipped with GPS collars (2200 or 3300, LOTEK, Newmarket, ON, Canada) and unique plastic ear tags over this time period. Because elk GPS collars were removed and redeployed generally in January of each year, no elk location data were available during this month. Wolves were captured using foot-hold traps in summer and helicopter netgunning and aerial darting during winter from 2002-2004 and equipped with GPS collars (3300sw, LOTEK) (University of Alberta Animal Care Protocol # 353112; see Hebblewhite and Merrill 2007 for details).

Determining elk migration strategy

I followed Hebblewhite et al. (2006) and used GPS collar data collected from 2001-2005 to define migrant elk as individuals that migrated between allopatric summer and winter 95% minimum convex polygon (MCP) home-ranges and residents as individuals whose summer and winter home-ranges overlapped.

Using this definition the 26 elk equipped with GPS collars from 2001-2005 consisted of 18 migrants and 8 residents.

Home-range overlap

I described elk home-ranges with utilization distributions (UDs), which define the home-range boundary ($x - y$ plane) and intensity of use (z -axis) throughout the home-range (Millspaugh et al. 2004). To measure home-range overlap between pairs of elk I used the Volume of Intersection index (VI), which estimates the volume of overlap between two UD's (VI ranges from 0 to 1, with 0 indicating no overlap and 1 indicating complete overlap) (Seidel 1992). Using UD's and VI to estimate home-range overlap is more descriptive than traditional measures (e.g. minimum convex polygon) because intensity of use within overlapping portions of the home-ranges is accounted for (Millspaugh et al. 2004, Fieberg and Kochanny 2005).

Using 2-hr locations collected from GPS collared elk during winters (15 October to 15 April) of 2001-2005 I estimated monthly UD's for each elk using fixed kernel analysis (Worton 1989) with the plug-in method to determine smoothing factor (Gitzen et al. 2006). Smoothing factors and UD's were estimated using the KS package (Duong 2008) developed for the R statistical computing software (R Development Core Team 2008). Using code written in R, I calculated VI for all pair-wise comparisons of elk UD's estimated from locations collected over the same time period and calculated the average VI between migrant elk UD's (pair type = *MM*), between resident elk UD's (pair type = *RR*), and between migrant and resident UD's (pair type = *MR*) for each winter month. If migrants and residents were spatially segregated during winter, I expected there to be more overlap between winter home-ranges of elk with the same migratory strategy (pair type *MM* and *RR*) than between elk with different strategies (pair type *MR*). To determine if pair type or month significantly affected VI, I used a mixed-effects generalized linear model with VI as the dependent variable (arcsin transformed) and elk pair as the random effect (XTREG command in STATA 10.0, StataCorp LB, College Station, TX). I used dummy variables for pair type

and month, using the *MR* pair type and October as the reference categories, and also included an interaction term between each pair type and month.

Exposure to wolf predation risk

To develop a spatially explicit wolf predation risk model, I estimated UD_s for each wolf pack that hunted on the YHT winter range and considered the risk of an elk being killed by wolves in a pixel (30 × 30 m) to be proportional to the intensity of use of that pixel by wolves. Because kill rate, and, therefore, predation risk, increases with pack size (Mech and Boitani 2006, Hebblewhite et al. 2004), I considered overall risk to be a function of intensity of use (from UD_s) and pack size. I also considered an elk's chance of encountering a wolf (i.e. risk) to be higher in areas used by multiple packs so I added each pack's UD (weighted by pack size, including pups) together to account for elevated risk in areas of territorial overlap. In contrast, Hebblewhite and Merrill (2007) modeled summer predation risk of this study area by combining a wolf resource selection function (RSF), a measure of wolf spatial density obtained with a kernel density estimator, and wolf pack size. Although they found this to be the best model when validated with elk kill sites, it was developed for a larger area (the YHT winter range and the front ranges of Banff National Park) and over a coarser temporal scale (the entire summer) than were needed for this study. During the current study, collars were deployed on the only two wolf packs that hunted elk on the YHT winter range, so by developing a UD for each pack, I described where wolves actually frequented during the time periods for which I estimated predation risk. Thus, I felt it was unnecessary to include a prediction of the relative probability of use by including an RSF in my model.

To develop wolf UD_s, I used 2-hr GPS collar data collected only from February to April 2004 because this was the only time period for which I had sufficient wolf locations to produce monthly UD_s (> 50) and a large enough elk sample size to measure exposure during winter. I used data from only one wolf per pack because cohesion between radio collared wolves within each pack during winter was generally high and movement of one wolf likely represented

movements of the entire pack (mean monthly VI between 2 wolves from the same pack = 0.79 ± 0.02). I developed separate day and night UD_s for each month for each pack to account for differences in diurnal and nocturnal habitat use by wolves (Theurekauf et al 2003, Hebblewhite and Merrill 2007) and any seasonal variation (e.g. early versus late winter). I classified wolf locations as day or night using sunrise and sunset times on the 15th of each month obtained from the National Research Council of Canada (<http://www.nrc-cnrc.gc.ca/eng/services/hia/sunrise-sunset.html>). I estimated all UD_s using the same method described in ‘*Home-range overlap*’. Each UD represented a relative probability of use (sum to 1) and were directly comparable across packs. I used a nonlinear model developed by Hebblewhite and Merrill (2007) with data from the same study area to predict daily kill rate (*KR*) for each pack as a function of pack size (*X*): $KR = 0.385 \times (1.00 - 0.726^X)$. Pack size was estimated using aerial sightings, snow tracking and den observations (Hebblewhite 2006). I then followed Hebblewhite and Merrill (2007) and weighted each UD by pack size by calculating KR_p for each pack, *p*, as the increase in kill rate relative to a pack size of two. Finally, I estimated predation risk of a 30 × 30 m pixel (PR_i) as:

$$PR_i = \sum_{p=1}^n (KR_p \times UD_{pi})$$

where UD_{pi} is the intensity of use of pack *p* at pixel *i*, and *n* is the total number of packs that used pixel *i*.

To compare exposure of migrant and resident elk to day- and night-time predation risk, I first determined PR_i at elk GPS locations collected during winter 2003/04 (subset of the data used to measure home-range overlap; 13 migrants, 7 residents) using the predation risk model that corresponded to the appropriate time of day and month that each GPS location was collected (e.g. February night). I then used a mixed-effects generalized linear model with PR_i at elk locations as the dependent variable and individual elk as the random effect. I used dummy variables to represent elk migration strategy (0 = resident, 1 = migrant), time of day (night = 0, day = 1), and month to determine if these variables influenced predation risk, and included interaction terms between each variable.

In addition, I investigated the factors that an elk might associate with the spatiotemporal patterns in PR_i across the winter range. I used a model selection approach to determine the best set of variables that predicted day and night values of PR_i at 1500 random locations within a minimum convex polygon derived from all elk locations collected from February to April 2004. I used time of day (t_d , day = 1 and night = 0) as the temporal variable and the distance to intact timber (d_t) and to the YHT Ranch buildings (d_r) as the spatial variables because previous work showed that wolves at the YHT avoid areas of high human activity and select for forest edge (Hebblewhite and Merrill 2007). I developed 5 candidate generalized linear models comprised of different combinations of these variables along with interactions (Table 2-1), and used Akaike information criteria (AIC_c) to determine the most parsimonious model. I then compared the average value of each variable included in the top model at migrant and resident locations using a two-way ANOVA (with migration strategy and time of day as factors) to determine whether migrant and resident elk responded to these variables differently, and whether their response changed during the night and day (i.e. migration strategy \times time of day interaction).

Exposure to forage

I compared migrant and resident elk exposure to forage only on open grasslands because 75% of all winter elk telemetry locations occurred on grasslands, and ~90 % of winter elk diet at YHT consisted of graminoids, which are found predominately on the grasslands (Hebblewhite 2006). To estimate fine-scale spatial variation in vegetation biomass across the grasslands, I used a LANDSAT Thematic Mapper image (30×30 m resolution) of the area taken 22 June 2003, which was the only summer image taken between 2001 and 2007 with sufficiently cloud-free skies to estimate forage abundance. From this image I calculated the Normalized Difference Vegetation Index ($NDVI$), which estimates forage abundance based on the difference between the red and near-infrared bands of light reflected at each pixel (Tucker 1979). I then used a model selection approach to determine the best set of variables, in addition to $NDVI$, to estimate

standing herbaceous biomass data collected from 47 plots during September 2005 after graminoids had stopped growing and senesced (Spaedtke unpublished data). Because no additional biomass is produced after senescence, these data represented initial winter forage abundance. The most parsimonious model to estimate September vegetation biomass (B g/m²) was a function of $NDVI$ and the distance east (E , m) from a datum point (UTM NAD 83, Zone 11: 0591224, 5731018) at the western boundary of the YHT: $B = 238.68NDVI + 0.013E - 17.11$ (Akaike weight = 0.76, $r^2 = 0.42$; Appendix 1). Previous work also showed that standing herbaceous biomass at YHT increased along a west to east gradient on the grasslands (McInenly 2003)

To compare exposure of migrant and resident elk to forage, I first determined the time periods that elk were actively foraging because elk benefit from exposure to forage only while actually consuming vegetation. As a measure of activity, I used the distance elk travelled between consecutive GPS locations collected at a 2-hr fix interval from December to April of 2001-2005, considering each month separately to account for changing sunrise and sunset times. For each month, there were two distinct peaks in activity roughly corresponding to dawn and dusk (Chapter 3: Fig 3-4), which I defined as periods of active foraging. These periods occurred from 0800-1000 and 1400-1600 in December; from 0800-1000 and 1600-1800 in January and February; and from 0600-0800 and 1800-2000 in March and April. I then tested for monthly differences in estimated standing biomass (B g/m²) at migrant and resident telemetry locations collected in winter 2003/04 during the active time periods using a mixed-effects, generalized linear model with individual elk as the random effect, and migration strategy (0 = resident, 1 = migrant), month, and a migration strategy \times month interaction as the dependent variables. To determine the mechanism driving any potential differences in exposure to forage between migrant and resident elk, I compared the average monthly $NDVI$ and E values at migrant and resident telemetry locations taken during the active time periods using a two-way ANOVA with month and migration strategy as the factors.

Correlation between forage and predation risk

If predation risk is highest where forage is most abundant, then elk must make a trade-off between acquiring forage and avoiding predation risk (Pulliam 1989, Hebblewhite and Merrill 2009). I calculated a Pearson's correlation coefficient to determine if there was a positive correlation between relative day and night predation risk and estimated vegetation biomass at 1500 random locations within a minimum convex polygon derived from all elk locations collected from February to April 2004.

RESULTS

Home-range overlap

Across all pairs of migrants and residents, the amount of overlap between home-ranges generally increased from October to March, and then decreased in April (Fig. 2-1); home-range overlap was significantly higher in February and March than in October ($P < 0.003$), but similar to October in November, December, and April ($P > 0.098$). Across all months, overlap between two migrant home-ranges (MM) and between two resident home-ranges (RR) was not different than that between migrant and resident home-ranges (MR) ($P = 0.105$ and $P = 0.322$, respectively). However, overlap between resident home-ranges was higher than between migrant home-ranges across all months ($P = 0.041$; Fig. 2-1). There was no interaction between any pair type and month ($P > 0.142$) indicating that monthly changes in overlap were similar for all pair types (Fig. 2-1).

Exposure to predation risk

Day and night spatial patterns of wolf movements were qualitatively different, resulting in spatiotemporal variations in predation risk (Fig. 2-2). During the day, wolf intensity of use was diffuse around the periphery of the grasslands within the surrounding timber, resulting in relatively low predation risk on the grasslands (Fig. 2-2a). Conversely, night-time wolf habitat use was concentrated on the grasslands, resulting in relatively high predation risk in this habitat (Fig. 2-2b). The model that best described predation risk (Table 2-1) predicted that day-time

predation risk was highest far from both human activity and timber, and safest close to human activity, but far from timber (Fig. 2-3a, Table 2-2). At night, predation risk increased with distance to timber but was unaffected by distance to human activity (Fig. 2-3b, Table 2-2).

Spatiotemporal patterns in predation risk resulted in significantly higher exposure of all elk to predation risk at night compared to the day ($P < 0.001$; Fig. 2-4). However, resident elk experienced a larger relative increase in exposure to risk from day to night than migrants (121 and 137% increase for migrants and residents, respectively; $P = 0.019$). Both groups moved closer to human activity ($F = 47.15$, $df = 1$, $P < 0.001$) and further from timber ($F = 54.65$, $df = 1$, $P < 0.001$) from day to night (time of day effect; Fig 2-5). The relative decrease in distance to timber from day to night was similar for both groups (migration strategy \times time of day interaction: $F = 0.05$, $df = 1$, $P = 0.82$), but migrants experienced a larger relative decrease in distance to humans from day to night than residents (migration strategy \times time of day interaction: $F = 6.58$, $df = 1$, $P = 0.01$) (Fig 2-5). However, residents still remained significantly closer to human activity ($F = 58.00$, $df = 1$, $P < 0.001$) and further from timber ($F = 14.25$, $df = 1$, $P < 0.001$) than migrants during both time periods (migration strategy effect; Fig. 2-5). Because night-time predation risk increased with distance to timber (Fig. 2-4), residents were exposed to higher night-time risk than migrants (Fig. 2-4).

Exposure to predation risk also varied across months with higher mean exposure in February than in March and April ($P < 0.001$). Monthly fluctuations were most pronounced at night and consistent for both migrant and resident elk, but residents experienced a larger decrease in exposure to risk from February to March than migrants (significant interaction term between migration strategy and March dummy variable: $P < 0.001$; Fig. 2-4).

Exposure to forage

Across all months standing herbaceous biomass at migrant and resident telemetry locations was similar ($P = 0.950$). Biomass at telemetry locations was higher in December and April than in February and March ($P < 0.022$) for both migrant and

resident elk (non-significant interaction terms between migration strategy and any month: $P > 0.331$; Fig. 2-6). Monthly changes in exposure to forage were largely driven by a distributional shift in use in the east-west direction; in December elk generally were located in the centre of the YHT (mean $E = 9740$ m), then moved further west in February and March (mean $E = 8538$ m and 9194 m, respectively), and finally moved to the eastern portion of the YHT in April where biomass was higher (mean $E = 10486$ m) ($P < 0.001$ for all pair-wise comparisons of E between months using the Bonferroni multiple comparison test). $NDVI$ values at active elk locations were significantly higher in December and February than in March and April ($P < 0.042$ using the Bonferroni multiple comparison test).

Correlation between forage and predation risk

A significant, positive correlation existed between predation risk and vegetation biomass at random, available locations during the day and night for all months (Table 2-3). Correlations were stronger during the day except in March, with the strongest correlation occurring during the day in April.

DISCUSSION

My hypothesis that migrant and resident elk were spatially segregated on the winter range was not supported, but migrants and residents did exhibit different spatial patterns in fine-scale habitat use, as alternatively predicted. At the beginning of winter (October), home-range overlap was low both among and between migrant and resident elk, likely because fall migration was not completed (Hebblewhite et al. 2006) and some migrants were still at the western edge of the YHT. As the season progressed home-range overlap increased between all elk, but residents consistently showed a stronger association with each other than migrants except in late winter (April). In fact, individual migrant elk were actually more closely associated with residents than other migrants, indicating that residents formed a stable group and individual migrants may have associated themselves with residents independently of each other. This may indicate residents form a cohesive group, possibly within the most suitable habitat on the

sympatric range (*sensu* Andriaensen and Dhondt 1990), while migrants try to gain access to these habitats by following residents (Thouless 1990, Weckerly 1999). However, migrants and residents were exposed to equal forage biomass, indicating resident elk were not excluding migrants from optimal forage resources.

In addition, resident elk were actually exposed to higher night-time predation risk than migrants because of fine-scale differences in habitat use between the two groups. During the day, both migrants and residents experienced low risk of predation while foraging on the grasslands relatively close to human activity and far from timber because wolves in this system avoided humans and selected forest edges, indicating the presence of a human-caused predation refuge (Fig. 2-2a and 2-3a; Hebblewhite and Merrill 2008). At night both migrants and residents moved even closer to human activity and further from timber (Fig. 2-5), but were unable to avoid night-time exposure to risk because at night wolves ignored humans and showed high intensity of use on the grasslands far from timber (Fig 2-2b and 2-3b; Hebblewhite and Merrill 2008). Night-time exposure of resident elk to predation risk was higher than migrant exposure because residents remained significantly further from timber than migrants (Fig. 2-5).

The diurnal difference in wolf response to humans observed in this and other studies (Theuerkauf, Jedrzejewski, Schmidt, and Gula 2003; Hebblewhite and Merrill 2008) highlights the importance of considering day and night predation risk separately when studying the effects of risk on prey behaviour. Studies of felid predation risk in African systems show diurnal variations in risk largely driven by the nocturnal behaviour of lions, which was reflected in prey behaviour (Fischhoff et al. 2007, Valeix et al. 2009). Recent studies of wolf predation risk in North America, however, often neglect to model day and night predation risk separately (e.g. Kittle et al. 2008, Atwood et al. 2009), which may lead to incorrect conclusions, especially if human activity plays a role in the system.

Because resident elk occupy the YHT during the summer when human activity is highest, they may have become more habituated to humans than

migrants explaining why residents utilized the human-caused predation refuge more intensely. Human-habituated elk in and around the town of Banff, AB, also benefited from wolf avoidance of humans (McKenzie 2001, Hebblewhite and White et al. 2005). However, human activity at the Banff town site is much higher than at YHT so wolves avoided Banff completely day and night. At YHT although habituation to humans seemed to be advantageous during the day, wolf tolerance of humans at night may have created a ‘cost’ of resident habituation in the form of higher exposure to predation risk.

However, my measure of elk exposure to predation risk was based on wolf intensity of use at elk telemetry locations, so I essentially modelled the risk of elk encountering wolves, which may not equate to the risk of being killed by a wolf. For example, Hebblewhite et al. (2005) found that in open grasslands the risk of an elk encountering a wolf was high, but the risk of being killed by a wolf after an encounter was actually lower than in forested habitats. At night when wolves are actively hunting, their use of habitat is likely driven by elk density (Theuerkauf, Jedrzejewski, Schmidt, and Okarma et al. 2003) so elk encounters with wolves may be unavoidable. Resident elk might have made the best of a bad situation by remaining on the grasslands close to humans and far from timber where wolf encounters are likely (and my measure of predation risk is therefore high), but chances of actually being killed may be lower than in forested habitats (Hebblewhite and Merrill et al. 2005). In addition, resident elk were more closely associated with other elk than migrants (Fig. 2-1), and may have further reduced the risk of mortality (even if the risk of wolf encounter was high) by forming a cohesive group (Pulliam 1973, Hebblewhite and Pletscher 2002, Childress and Lung 2003, Caro 2005). Although migrants experienced a lower risk of encountering wolves at night, they may have experienced a higher risk of death given an encounter because they remained closer to timber and formed a less cohesive group than residents. A study directly comparing winter predation rates on migrants and residents is necessary to determine how different responses to predation risk affect overall fitness.

Because predation risk and herbaceous biomass were positively correlated at available locations, indicating elk must make a trade-off between acquiring forage and avoiding predation (Houston et al. 1993, Hebblewhite 2006), one would assume higher resident exposure to predation risk would also result in higher exposure to forage. However, the positive correlation between risk and forage was strongest during the day when exposure of migrants and residents to predation risk was equal. During the day, elk spread out closer to timber, and particularly in April, toward the east where forage biomass was highest (McInenly 2003). Although predation risk also increased in these areas because wolf pack home-ranges were centred in the east (likely causing high day-time correlation between risk and forage), wolf avoidance of the grasslands during the day allowed both groups of elk to access forage while maintaining relatively low exposure to predation risk.

Over-winter depletion of forage, which can be as high as 94% at YHT (McInenly 2003), is another factor that may have affected trade-offs between forage and predator avoidance. If resident elk were remaining in large, highly associated groups far from timber and close to humans as a response to predation risk, forage in these areas may have been depleted faster than in areas frequented by the more spread out migrants. Creel et al. (2005) similarly found that predation risk altered elk habitat selection in the Greater Yellowstone Ecosystem, possibly affecting the spatial depletion of forage resources. In April, the amount of overlap between resident elk at YHT decreased and all elk moved further east, indicating forage may have indeed been depleted in the centre of the grasslands over the winter. If the proportion of residents in this population continues to increase (Hebblewhite et al. 2006), winter forage at the centre of the grasslands may be depleted to the point where the foraging costs of intensely using the human-caused predation refuge become a major disadvantage (also see Chapter 3). This may force residents to abandon this strategy and move further east where forage is more abundant and predation risk is elevated, especially during the day. This implies that a fitness balance between migrants and residents in this herd may be density dependant and that the proportion of residents will increase until

competition for forage on the winter range is too high. Density-dependent fitness balancing between migrants and residents has long been investigated theoretically (Lundberg 1987 and 1988, Kaitala et al. 1993, Taylor and Norris 2007), but empirical evidence for this phenomenon is limited (Hebblewhite 2006).

This study is among the first to directly test the common assumption that migrant and resident ungulates of a partially migratory population are intermixed into a single herd and exposed to similar environmental factors while together on their sympatric range (Fryxell et al. 1988, Albon and Langvatn 1992, Kaitala et al. 1993, Ball et al. 2001, Hebblewhite and Merrill 2007, Hebblewhite et al. 2008). Although my results show that when on the same range migrants and residents were not completely spatially segregated, I found that differences in fine-scale habitat use caused residents to experience a higher risk of encountering wolves at night than migrants. Both groups were able to exploit the predation refuge created at the YHT due to high human activity, which also allowed residents to reduce their exposure to predation risk during summer (Hebblewhite and Merrill 2007). The consequences of fine-scale differences in winter habitat use by migrant and resident elk on forage depletion and predator-caused mortality is unclear, but they may result in density-dependent fitness balancing between each strategy: as the proportion of resident elk in this herd increases, the benefits of being sedentary may diminish. Studies comparing the costs and benefits of different migration strategies in partially migratory populations should, therefore, take caution in assuming costs and benefits are equal when animals are together on the shared range. Ideally, such studies should directly compare predation and forage intake rates of migrants and residents on separate and sympatric ranges when contrasting the fitness consequences of each migratory strategy.

TABLE 2-1. *A priori* candidate models estimating relative predation risk (PR_i) as a function of different combinations of time of day (t_d = night or day), distance to human activity (d_r , m), and distance to timber (d_t , m) showing the corrected Akaike Information Criteria values (AIC_c), Δ_i 's, Akaike weights (W_i), and r^2 values for each.

Model	AIC_c	Δ_i	W_i	r^2
$d_t + d_r + t_d + d_t \times t_d + d_r \times t_d + d_t \times d_r$	-4528	0	>0.999	0.38
$d_t + d_r + t_d + d_t \times t_d + d_r \times t_d$	-4498	30	<0.001	0.28
$d_t + d_r + t_d$	-3012	1516	<0.001	0.14
$d_r + d_t$	-2982	1546	<0.001	0.14
t_d	-1699	2829	<0.001	<0.01

TABLE 2-2. Coefficients and standard errors (SE) of the variables in the top model (as determined from AIC analysis, Table 2-1) estimating relative predation risk at 1500 random locations within areas used by elk on the Ya Ha Tinda winter range. All variables are statistically significant ($P < 0.05$).

Variable	Description	Coefficient	SE
d_n	time of day (1 = day, 0 = night)	0.02380	0.00970
d_t	distance to timber	0.00086	0.00004
d_r	distance to humans	-0.00003	1.78×10^{-6}
$d_n \times d_t$	interaction term	-0.00105	0.00003
$d_n \times d_r$	interaction term	0.00002	2.39×10^{-6}
$d_r \times d_t$	interaction term	7.16×10^{-8}	1.27×10^{-8}
Constant	-	0.22203	0.00704

TABLE 2-3. Pearson's correlation coefficients (r) describing the relationship between estimated standing herbaceous biomass and monthly day and night predation risk at 1500 random locations within areas used by elk on the Ya Ha Tinda winter range. All correlations are highly significant ($P < 0.001$).

Month	Pearson's r	
	Day	Night
February	0.53	0.49
March	0.27	0.34
April	0.75	0.53

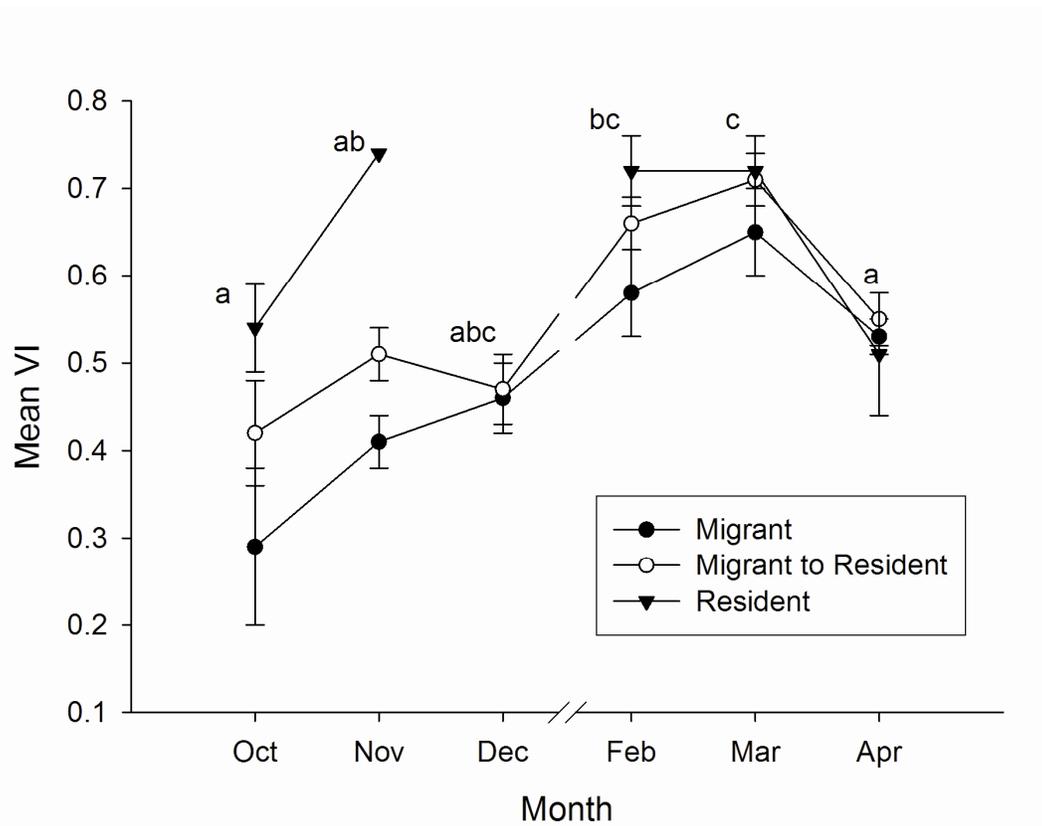


FIG. 2-1. Mean volume of intersection index (VI) representing average overlap between two migrant elk home ranges (solid circle), two resident elk home ranges (solid triangle), and a migrant and a resident elk home range (open circle) for each winter month from 2002-2005. Error bars represent ± 1 SE. Letters indicate the months for which VI averaged across pair types were not significantly different. Note: no elk were equipped with GPS collars in January of any year and only one resident elk was equipped with a collar during December.

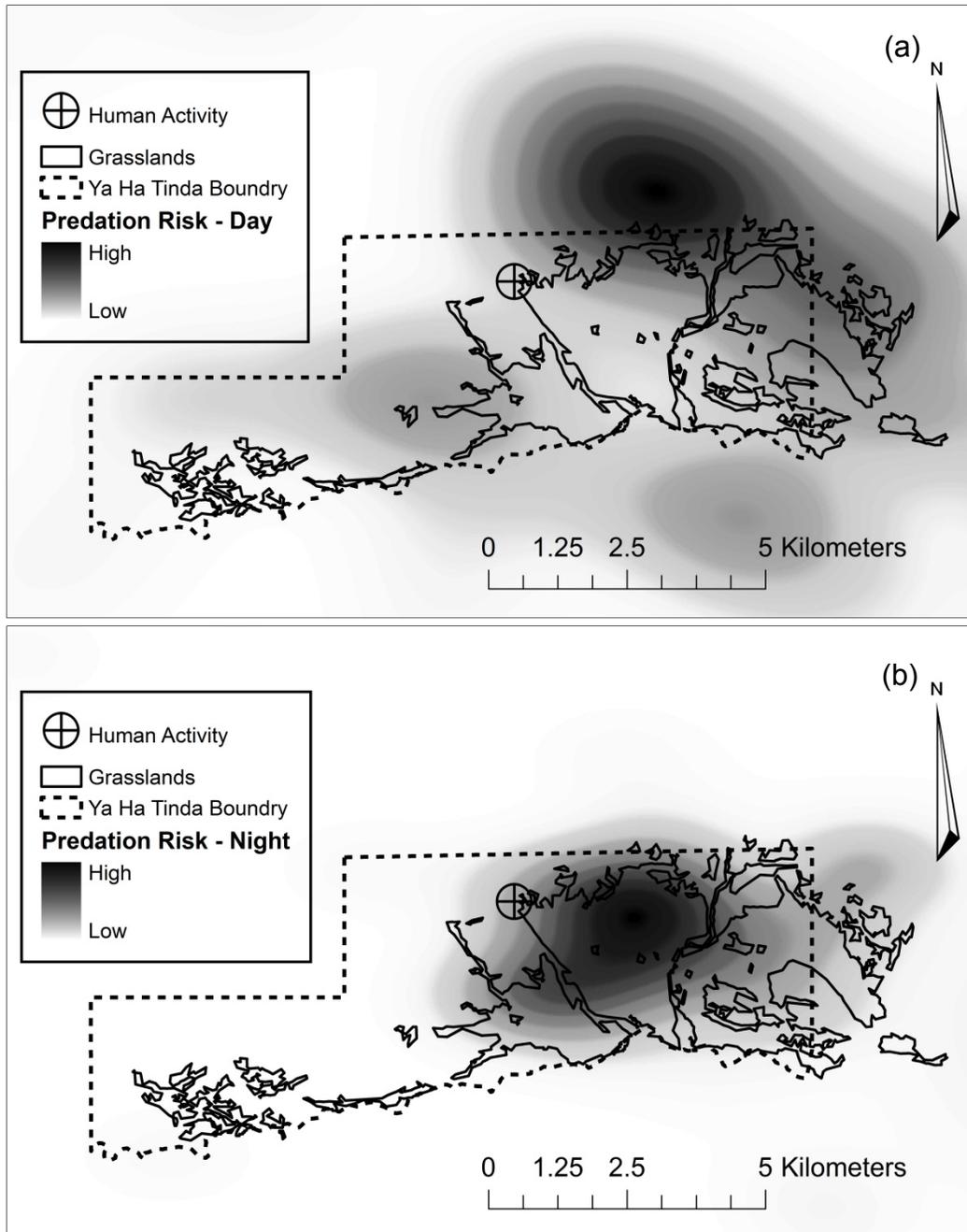


FIG. 2-2. Example of the consistent spatial difference between day (a) and night (b) relative wolf predation risk on the Ya Ha Tinda grasslands (February 2004). This model assumes predation risk is proportional to wolf intensity of use weighted by pack size (see text for details).

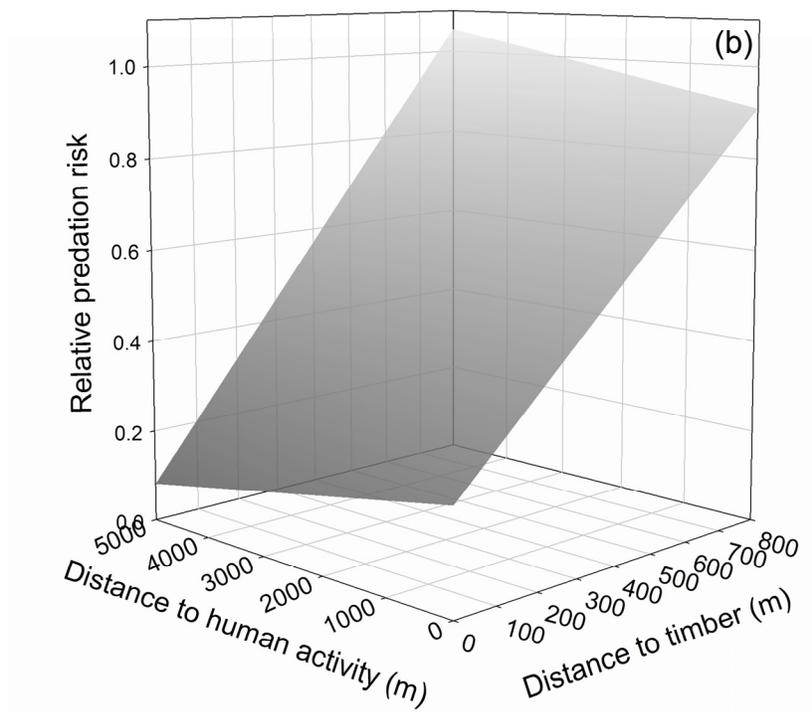
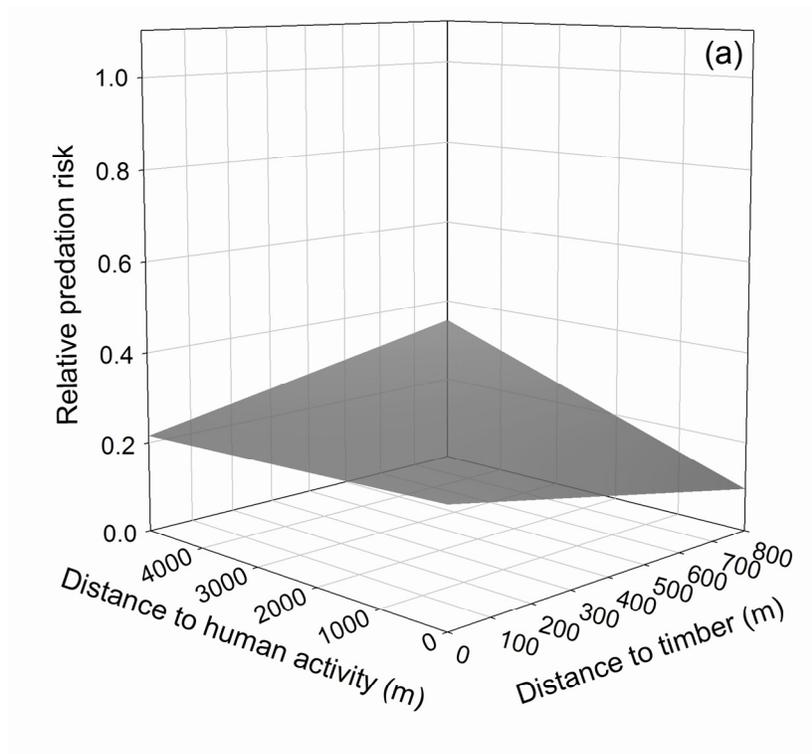


FIG. 2-3 Relative day (a) and night (b) predation risk in relation to distance from human activity and from intact timber as predicted by the model found to be most parsimonious using AIC_c analysis (Table 2-1).

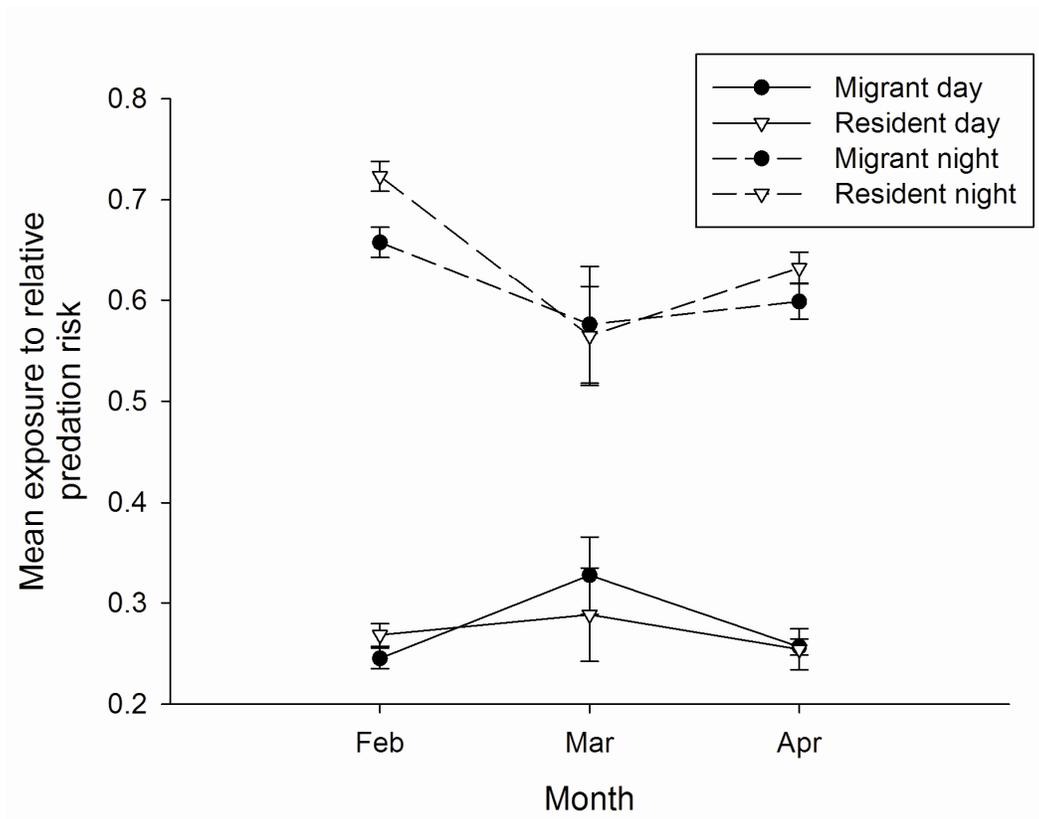


FIG. 2-4. Mean relative predation risk at migrant (n = 13) and resident elk (n = 7) telemetry locations (i.e. mean exposure to predation risk) collected during winter 2004, in relation to time of day and month. Error bars represent ± 1 SE.

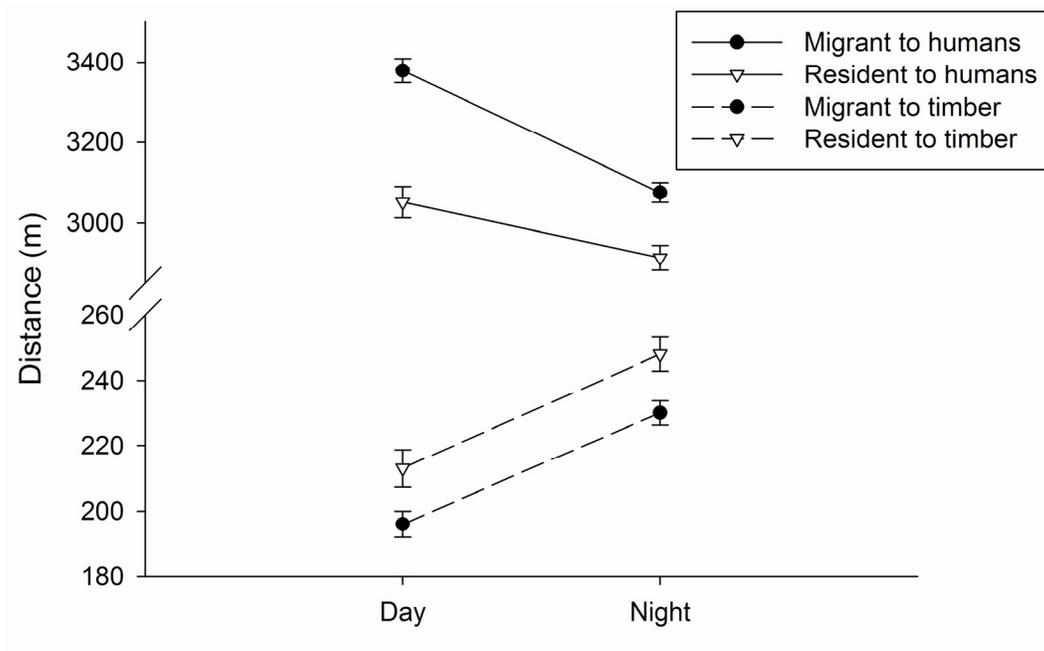


FIG. 2-5. Mean day and night distances from migrant and resident elk telemetry locations to human activity and timber. Error bars represent ± 1 SE.

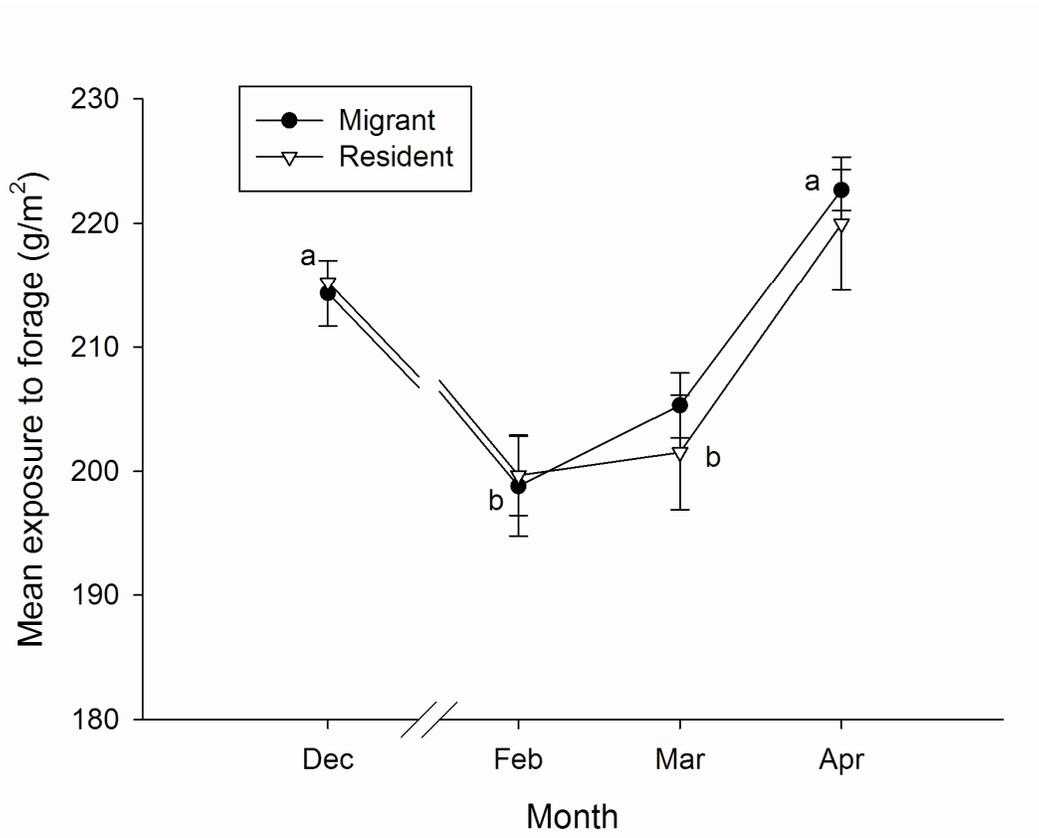


FIG. 2-6. Mean monthly estimated standing herbaceous biomass at migrant (n = 13) and resident elk (n = 7) telemetry locations (i.e. mean exposure to forage) collected during winter 2003/04. Error bars represent ± 1 SE. Letters indicate the months for which biomass averaged across migration strategies was not significantly different.

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CHAPTER 3: DOES EXPERIENCE INFLUENCE TRADE-OFFS BETWEEN FORAGING AND VIGILANCE IN A PARTIALLY MIGRATORY ELK POPULATION?

INTRODUCTION

A growing body of literature is demonstrating that the indirect costs of antipredator behaviours can be as influential to predator-prey dynamics as the direct lethal effect of predation (Schmitz et al. 1997, Lima 1998, Brown et al. 1999, Laundré et al. 2001, Preisser et al. 2005, Creel and Christianson 2008). Costly antipredator behaviour can include shifting habitat use to areas of lower predation risk that reduce access to abundant forage (Creel et al. 2005), increasing conspecific competition for food by foraging in larger groups (Grand and Dill 1999, Bednekoff and Lima 2004), and reducing forage intake by interrupting foraging bouts to scan for predators (Underwood 1982, Lima 1987, Bednekoff and Lima 1998). As a result, herbivores often adjust their behaviour adaptively to balance trade-offs between foraging and avoiding predation (Festa-Bianchet 1988, Houston et al. 1993, Hebblewhite and Merrill 2009).

Migration is a common behaviour in ungulates that potentially trades-off forage and predator avoidance because it allows ungulates to ‘escape’ predation by moving beyond the ranges of non-migratory predators (Bergerud et al. 1983, Fryxell et al. 1988), while also exposing them to different qualities and quantities of forage (Hebblewhite and Merrill 2008). Studies have compared the relative benefits of migrating versus being sedentary (a resident) by contrasting the trade-offs between exposure to predation and forage resources made by migrant and resident individuals in partially migratory populations when on different ranges (Fryxell et al. 1988, Albon and Langvatn 1992, Kaitala et al. 1993, Ball et al. 2001, Hebblewhite and Merrill 2007, Hebblewhite et al. 2008). However, whether differences in experiences gained while occupying separate ranges influences the way migrants and residents make foraging-predator avoidance trade-offs when they are reunited on their sympatric ranges has not been well addressed.

Antipredator responses to predation risk, particularly vigilance, have been shown to vary among individuals because of differences in past experience with predators (Berger et al. 2001, Berger 2008). Two general hypotheses have been proposed to explain how differences in past experience affect an animal's reaction to elevated predation risk. Traditionally, behavioural ecologists hypothesized that prey exposed to consistently high predation risk would be more vigilant than prey experiencing lower risk (Ferrari et al. 2009) simply because vigilant individuals are more likely to detect predators (Caro 2005). For example, moose (*Alces alces*) and elk (*Cervus elaphus*) with previous exposure to predators spent significantly more time vigilant when exposed to auditory and olfactory signals of predators than more inexperienced prey (Berger et al. 2001, Berger 2008). However, the traditional view does not address how herbivores might alter vigilance behaviour temporally to maximize forage intake under the constraints of predation (Lima 1987, Underwood 1982, Caro 2005).

The risk allocation hypothesis (RAH) accounts for the foraging costs of vigilance and proposes that the amount of vigilance expressed by prey is a product of the past temporal variations in predation risk it was exposed to (Lima and Bednekoff 1999). The RAH predicts animals exposed to infrequent bouts of high risk are more likely to accept the foraging costs of increased vigilance while risk is high because they can make up for lost foraging time by increasing their foraging activity (and decreasing vigilance) during lengthy bouts of low risk. In contrast, animals exposed to more consistent levels of high risk cannot afford the foraging costs of lengthy vigilance and are forced to forage (and not be vigilant) while risk is high to meet minimum nutritional requirements (Lima and Bednekoff 1999). Ferrari et al. (2009) recently contrasted these hypotheses referring to the RAH as a paradox because it predicts prey exposed to frequently high predation risk will in fact display less vigilance than prey exposed to high risk infrequently. In their literature review Ferrari et al. (2009) found mixed support for the RAH and attributed this to the fact that many studies did not meet some of the key assumptions of the hypothesis, specifically that prey have perfect knowledge of

the intensity and predictability of the risk regime, and forage requirements are a clear limiting factor for prey.

Another key assumption implicit in the RAH but not recognized by Ferrari et al. (2009) is that foraging and vigilance are mutually exclusive (i.e. vigilance has a foraging cost). Recent advances in our understanding of herbivore foraging behaviour show this assumption is not necessarily true for all herbivores (Illius and Fitzgibbon 1994, Cowlshaw et al. 2003, Fortin et al. 2004a, 2004b). For example, ungulates must stop harvesting bites while scanning for predators, but they can continue processing (i.e. chewing) vegetation in the mouth while being vigilant. For ungulates the foraging cost of vigilance, therefore, depends on whether forage intake is limited by the rate at which they encounter vegetation or the rate at which vegetation is handled (*sensu* Spalinger and Hobbs 1992). During encounter-limited foraging, any time spent vigilant would reduce the amount of time spent searching for vegetation, reducing encounter rate, and therefore forage intake rate (i.e. vigilance would have a foraging cost). During handling-limited foraging, however, herbivores are encountering bites of vegetation faster than they can process them, so they have 'spare time', which can be used to scan for predators without reducing forage intake (Illius and FitzGibbon 1994, Fortin et al. 2004a, 2004b). As long as ungulates are handling-limited and synchronize vigilance with spare time (referred to as multi-tasking; Fortin et al. 2004a) vigilance should not have a foraging cost. The ability of ungulates (and other herbivores) to multi-task may provide an additional explanation for the mixed support for the RAH in the literature (Ferrari et al. 2009). When ungulate forage intake is encounter-limited they will need to make trade-offs between foraging and vigilance and might behave according to the RAH. However, when ungulates are handling-limited they may be able to maintain higher vigilance levels than predicated by the RAH when predation risk is high because they can reduce the foraging costs of vigilance by multi-taking.

Although studies have demonstrated that previous experience affects how prey trade-off foraging costs and predator avoidance, none have considered the ability to maximize predator avoidance and forage intake simultaneously with the

use of spare time. In this chapter, I compared how elk with different migratory strategies within a partially migratory population, that experience different predation pressures when segregated in summer, responded to changes in predation risk when they were together on their sympatric range. The Ya Ha Tinda (YHT) elk population winters on a montane rough fescue (*Festuca campestris*) grassland (the YHT winter range) adjacent to Banff National Park (BNP). Approximately 60 % of the population currently migrates 25-50 km west into the high elevations of BNP to summer (migrants) while the rest remain on the YHT all year (residents). Wolves, and to a lesser extent grizzly bears, are the primary predators on elk in summer, whereas wolves are the primary predator at YHT in winter (Hebblewhite 2006). Hebblewhite and Merrill (2007) found that, once on their summer ranges, migrant elk were exposed to 15% lower wolf predation risk than residents who remained at YHT, but during the ~ 5 days of migration between summer and winter ranges migrants were exposed to a 170% increase in predation risk. In contrast, resident elk were exposed to more consistent levels of risk during summer because of higher wolf densities at the YHT relative to BNP (Hebblewhite and Merrill 2007).

I compared how migrant and resident elk responded to variation in predation risk while they were together on the YHT winter range when forage is likely to be most limiting and exposure to wolf predation risk is similar for migrants and residents (Chapter 2). While residents were exposed to consistently high wolf predation risk during summer, I hypothesized they learned to maintain high levels of vigilance during periods of high risk without compromising forage intake by synchronizing vigilance with spare time during handling-limited foraging. In contrast, I hypothesized that migrant elk learned they could afford the foraging costs of vigilance because they were exposed to high predation risk infrequently during summer, so they did not have to synchronize vigilance with spare time. If poor synchronization by migrants persists during winter when both population segments are exposed to similar wolf predation risk, migrants could be at a disadvantage, which may contribute to the declining migrant to resident ratio observed in this population (Hebblewhite et al. 2006). I predicted that during

winter resident elk synchronized vigilance bouts with spare time more frequently than migrants while handling-limited, causing vigilance to be more costly for migrants. To compensate for higher foraging costs of vigilance, I predicted migrant elk would either spend less time being vigilant than residents, particularly when foraging outside the human-caused predation refuge that exists at the YHT, where predation risk is highest (Chapter 2). Alternatively, I predicted migrants would compensate for higher foraging costs of vigilance by spending more time foraging throughout the day than residents.

To test my hypotheses I first compared the proportion of foraging time focal migrant and resident elk spent vigilant while controlling for factors that would influence immediate predation risk such as distance to human activity and to forest cover, group size and position of the focal animal within a group, and whether wolves were present at the time of observations (Childress and Lung 2003, Hebblewhite and Merrill 2007, Lung and Childress 2007, Winnie and Creel 2007, Liley and Creel 2008). Second, I evaluated whether vigilance levels were likely to reduce forage intake rates of each migratory segment. Following the approach of Fortin et al. (2004b), I first used the relationship between observed bite rate and encounter rate with vegetation to determine if intake rate was handling- or encounter-limited. If forage intake was encounter-limited, I assumed elk had no spare time available and all vigilance was costly. If forage intake was handling-limited, I estimated the amount of spare time available (*sensu* Fortin et al. 2004b) to migrants and residents to determine if one group had more potential to reduce the foraging costs of vigilance than the other. If spare time was available, I assessed whether one group was better at synchronizing vigilance with spare time to alleviate foraging costs. Finally, I compared total activity time of migrants and residents because even if elk had no spare time available or did not synchronize vigilance with spare time, they could compensate for reduced forage intake by increasing total daily foraging time.

METHODS

Study Site

The Ya Ha Tinda (YHT) is a 4000-ha winter range located on the eastern slopes of the Rocky Mountains adjacent to Banff National Park (BNP) in Alberta. Parks Canada administers the YHT as a working horse ranch and winters ~ 100 horses on the grasslands each year. Approximately two thirds of the YHT is natural rough fescue grassland making it one of Alberta's largest montane fescue grasslands (Hebblewhite and Merrill 2007). The remaining third is predominantly lodgepole pine (*Pinus contorta*) forests merging into Engelmann spruce (*Picea engelmannii*) at higher elevations, but is also interspersed with aspen forests (*Populus tremuloides*) and willow-bog birch (*Salix* sp.-*Betula glandulosa*) shrublands. Warm westerly winds (Chinooks) are common during the winter, which maintains a snow pack generally < 25 cm on the main grasslands (Morgantini 1995). A low snow pack, in combination with the high nutritional content of cured rough fescue (Pigden 1953), makes the YHT an ideal winter range for grazing ungulates; it is considered one of the two most important elk winter ranges in Alberta (Morgantini 1995). Elk are the dominant herbivore in the system, but mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and moose are also present. The YHT elk population ranged from ~ 800 individuals in the early 1970's to > 2000 in the early 1990's (Hebblewhite et al. 2006) and consisted of ~ 360 individuals during this study (pers. obs.). Grizzly bears (*Ursus arctos horribilis*) and black bears (*Ursus americanus*) are common in the summer, but wolves (*Canis lupus*), cougars (*Felis concolor*), and coyotes (*Canis latrans*) are the only active predators during winter. Wolves are the most common predator of elk; from 2002-2004 3 packs ranging in size from 6-17 wolves consistently hunted the YHT elk herd (Hebblewhite 2006). During this study only 2 packs containing at least 4 and 8 wolves were observed hunting elk (pers. obs.).

Capture and monitoring of elk and wolves

Elk were captured annually from 2001-2007 using a corral trap baited with hay between January and March when migrants and residents were together on the YHT winter range (University of Alberta Animal Care Protocol # 353112; see Hebblewhite et al. 2006 for details). Adult cows were equipped with GPS collars (2200 or 3300, LOTEK INC., Newmarket, ON) or VHF radiocollars (LMRT-4, LOTEK INC.) and unique, plastic ear tags. Each collar was outfitted with a unique combination of 3 coloured bands so individuals could be identified from a distance. During my 2007/08 winter field season there were 61 cow elk equipped with VHF radiocollars and no elk equipped with GPS collars. Additionally, VHF radiocollars (LMRT-3, LOTEK INC.) were deployed on 3 wolves from 2 packs (1 from the Ranch pack and 2 from the Red Deer pack) that were observed hunting elk at the YHT during this season. Wolves were captured using foot-hold traps in summer and helicopter netgunning and aerial darting during winter from 2002-2004 (University of Alberta Animal Care Protocol # 353112; see Hebblewhite and Merrill 2007 for details).

Determining elk migration strategy

Using radio telemetry I determined the percentage of days radio collared elk were present at the YHT during the summer period of 15 June to 31 August from 2004 to 2007. These dates are within the mean spring and fall migration dates of elk at YHT (4 June and 2 October, respectively; Hebblewhite et al. 2006). Elk were determined to be either present or absent from the YHT at least 3 days/week during this period (generally 4-7 days/week) by scanning for all radio-collared elk from a consistent location along the main road of the YHT using a roof-mounted omnidirectional antenna and marking elk as present if a signal was heard and absent if not (Spaedtke and Hebblewhite unpublished data). To maintain consistency with Chapter 1, I used the presence/absence data from 2004 to determine the percentage of observed summer days elk Hebblewhite et al. (2006) defined as migrants ($n = 3$) and residents ($n = 3$) were present at YHT. I found all migrants were present for $\leq 20\%$ of observed days and all residents for $\geq 65\%$ of

observed days. For the 61 elk equipped with VHF collars during this study I used presence/absence data from all years that each animal was collared and defined its migration strategy based on these criteria. Elk present for 21-64 % of summer days were excluded from this study because it was unclear whether they inconsistently migrated across years or were inconsistently detected on the YHT using the sampling protocol.

Field observations

Behavioural observations were made on 17 migrant and 19 resident radio-collared, cow elk from 10 January to 25 March 2008. Focal animals were observed systematically so that each animal was observed 1-7 times (mean \pm SE = 5 ± 1.6) during the winter with a minimum of 48 hours between subsequent observations on the same individual. Observations occurred throughout the day, but predominantly took place shortly after dawn and before dusk while elk were foraging. Once located via radio telemetry, elk were observed from 75-750 m away with a 60 \times magnification spotting scope (BAUSH & LOMB, Vaughan, ON). If elk became aware of the observer's presence at first approach, the observer waited until elk resumed normal foraging behaviour before initiating an observation. If an elk became vigilant toward the observer during an observation, the observation was terminated. An observation period lasted a maximum of 10 min or until the elk bedded or was out of sight. Observations < 2 min were not used in the analysis.

Elk behaviour was dictated into a digital voice recorder (VN-4100, OLYMPUS, Markham, ON) and later entered into JWatcherTM (Blumstein et al. 2006), a software package that time-stamps behaviours. I recorded every step (displacement of either front foot), pawing motion (movement of leg that resulted in displacement of snow), head lift above and drop below the shoulder, and the start and end of each conspecific interaction. I followed Fortin et al. (2004b) in defining a conspecific interaction as starting when an individual was disturbed by a conspecific and stopped feeding and lasted until feeding resumed, and a vigilance bout as starting when an elk raised its head above the shoulder and

lasted until another behaviour was initiated. I also noted every bite taken (jerking motion of the head while foraging) and every chewing motion (oscillation of the lower jaw) that occurred during vigilance when possible.

At the beginning of an observation I recorded whether the focal animal was at the centre or periphery of the group. A focal was considered central if an attacking predator approaching from any direction would encounter at least one elk within the group before encountering the focal animal and peripheral if the predator would encounter the focal animal before any central group member (Stankowich 2003, Liley and Creel 2008). I followed Creel and Winnie (2005) in defining a group as a number of elk with a relatively consistent distance between adjacent individuals moving in approximately the same direction at approximately the same rate. Using this definition, focal elk I observed were always within a large group of > 300 individuals. I therefore recorded elk density around the focal animal rather than group size by counting the number of elk within concentric circles with a radius of 1 (~ 2 m), 5 (~ 10 m) and 10 (~ 20 m) elk lengths around the focal animal. Before and after each observation I scanned for all radio-collared wolves using an H-haddock directional antennae. Because not all wolves in the area were collared, I also searched for any wolf sign including fresh scat, tracks, wolf kills and/or wolves themselves as I approached and left the elk. If wolf sign was observed on the day of the observation within 2 km of the elk or I detected wolves with radio telemetry, I recorded wolves as detected. If I did not detect wolves using these methods, it was impossible to determine if wolves were truly absent so I consider this a conservative estimate of wolf presence (Creel and Winnie 2005).

At the end of each observation, I estimated UTM coordinates of the midpoint of the focal animal's foraging path by measuring the distance (m; Laser Range Finder BUSHNELL, Richmond Hill, ON) and compass bearing to the midpoint of the animal's path relative to the observer's location (GPS unit GARMIN, Olathe, KS). Using a Geographic Information System (ArcMap 9.3, ERDAS, Norcross, GA) I determined the straight line distance from the midpoint of each animal's foraging path to the closest forest edge (timber) and to the YHT

Ranch buildings, which receives the highest level of human activity throughout the study site (pers. obs.). Within 2 days of each observation and prior to any new snow fall, I returned to the focal animal's location and estimated vegetation biomass (g/m^2) in 1-2 0.25 m^2 quadrats located in an ungrazed area adjacent ($< 5 \text{ m}$) to the midpoint of the focal animal's foraging path. To estimate biomass within a quadrat, graminoids and forbs were clipped to 2 cm from the ground, dried at 50° C for 48 hrs and weighed to the nearest 0.01 g. I excluded shrubs from biomass estimates because elk were never observed eating shrubs during this study and previous fecal analysis indicated elk diets were primarily graminoid based during winter at YHT (Hebblewhite 2006). If snow were present within a quadrat, I measured snow depth at the centre of the quadrat and scraped away all snow before clipping vegetation to 2 cm.

Statistical analyses of elk vigilance

I used a model selection approach and Akaike information Criteria (with sample size correction, AIC_c) to first compare 6 *a priori* hypotheses to determine what combination of variables best explained the proportion of time elk spent vigilant while foraging (T_v). I then tested whether adding migration status (M , 0 = resident, 1 = migrant), alone and interacting with each variable, to the top model explained additional variation in vigilance (i.e. produced a lower AIC_c value). To help develop *a priori* hypotheses I categorized variables as 'elk group', 'elk location', or 'external' variables and included different combinations of variable categories in each hypothesis (Table 3-1). I categorized the focal animal's position within the group (E_p , centre = 0, periphery = 1) and elk density around the focal animal (E_d elk/m^2) as 'elk group' variables, distance to human activity (d_r m) and distance to timber (d_t m) as 'elk location' variables, and wolf presence (w , 0 = not detected, 1 = detected) and snow depth (D cm) as 'external' variables. Using AIC_c analysis I determined models estimating the proportion of time elk spent vigilant performed best when the number of elk within 1 elk length ($\text{elk}/12.5 \text{ m}^2$) was used as a measure of elk density around the focal animal, so I used this measure in all subsequent models. I also developed a correlation matrix

that included all variables to avoid using highly correlated variables within a hypothesis (Appendix 2). To meet assumptions of normality, I arcsine transformed T_v prior to my analysis (Zar 1999). I used a random-effects maximum likelihood estimator (XTREG command in STATA 10.0, StataCorp LB, College Station, TX), which accounts for the dependence among repeated observations on the same individual (Wooldridge 2002), to fit a mixed-effects generalized linear model for each hypothesis.

Evidence for handling-limited foraging

Fortin et al. (2004b) and Bradbury et al. (1996) used the relationship between bite rate and vegetation biomass to determine if intake rate was encounter- or handling-limited. Increasing vegetation biomass should increase encounter rate with vegetation, so if intake rate is encounter-limited, bite rate should increase as vegetation biomass increases (Bradbury et al. 1996). However, increasing vegetation biomass also increases elk bite size (Wickstrom et al. 1984, Hudson and Watkins 1986), which increases the handling time of bites, so if intake rate is handling-limited, bite rate should decrease as vegetation biomass increases (Bradbury et al. 1996, Fortin et al. 2004b). However, during winter, biomass alone cannot be used as a surrogate for vegetation encounter rate because snow accumulation creates the need to paw in order to access the vegetation, increasing the amount of time required to encounter vegetation before a bite can be taken (Gaffney 1941, Sweeny and Sweeny 1984). As a result, elk may be handling-limited when foraging in a high biomass system under snow-free conditions, but become encounter-limited when snow accumulates. To account for the effects of snow, I estimated an elk's encounter rate with vegetation by considering both vegetation biomass and the time required to paw away snow when it was present. I considered elk to be encounter-limited if bite rate increased with estimated encounter rate, and handling-limited if bite rate remained constant or decreased with encounter rate (Bradbury et al. 1996, Fortin et al. 2004b).

To estimate an elk's encounter rate with vegetation, I first considered that encounter rate with vegetation in the absence of snow (λ g/min) can be expressed as:

$$\lambda = VWB \tag{1}$$

where V is the animal's foraging velocity in the absence of cropping (m/min), W is the animal's foraging path width (m), and B is the biomass of the vegetation within the foraging path (g/m^2) (Owen-Smith and Novellie 1982, Spalinger and Hobbs 1992, Illius and Fitzgibbon 1994, Bradbury et al. 1996, Fortin et al. 2002 and 2004b). In the past, studies treated V as a constant and used either the maximum velocity of a foraging animal in the absence of cropping (V_{max} , Spalinger and Hobbs 1992, Illius and Fitzgibbon 1994, Bradbury et al. 1996, Fortin et al. 2004a), V_{max} adjusted for the acceleration and deceleration of the animal (Shipley et al 1996, Fortin 2006), or $V_{max}/2$ (Fortin et al. 2004b) as estimates. Because variables such as topography, temperature, snow depth, elk density, and physical condition of the animal likely caused V to vary across observations, I followed Fortin et al. (2002) and calculated V individually for each observation by multiplying observed step rate (the number of steps taken with the head down divided by the amount of time elapsed while taking said steps) by the average step length measured throughout the study from tracks in the snow (0.638 ± 0.06 m, $N = 40$). I estimated foraging path width (W) as twice the distance from the centre of a foraging path (determined by tracks in the snow) to the furthest bite mark adjacent to that path (determined by craters in the snow: 1.10 ± 0.24 m, $N = 17$). Some authors measure plant density instead of biomass in the above equation (e.g. Illius and Fitzgibbon 1994, Fortin et al. 2004a), but I used biomass measured as described above because it was too difficult to estimate plant density in a graminoid-dominated system (Fortin et al. 2004b).

To determine encounter rate with vegetation when snow had accumulated on the ground (λ_s g/min), I incorporated the time required to paw away snow and uncover a bite of vegetation (P min/bite) and bite size (S g/bite):

(2)

$$\lambda_s = \frac{\lambda}{1 + \lambda \frac{P}{S}}$$

By substituting Eq. 1 into Eq. 2, encounter rate in the presence of snow can be expressed as:

(3)

$$\lambda_s = \frac{VWB}{1 + \frac{VWBP}{S}}$$

For 19 observations I calculated P (min/bite) by dividing the amount of time spent pawing before a series of bites by the number of bites taken after pawing. Using a model selection approach and AIC_c , I then found that P was best described as a function of snow depth (D cm) and vegetation biomass (B g/m²): $P = 0.00000215BD$ ($r^2 = 0.87$; Appendix 3). I used this model to estimate P for the remaining 50 observations where I measured snow depth in the vicinity of the foraging path (see above). Bite size (S g) was estimated as a function of B using an equation Hudson and Watkins (1986) developed from observations of elk grazing on senesced graminoids in a grassland system during the fall: $S = -1.29 + 0.27\ln(10B)$. The range of biomass seen at YHT (30-350 g/m²) fell within the range of biomass over which this equation was developed (~ 25 -350 g/m²).

To model the functional response of elk at YHT, I related λ_s calculated for each observation to observed bite rate. Bite rate (b_r , bites/min) was defined as the number of bites taken during an observation divided by the time spent with the head down (Bradbury et al. 1996). I used a model selection approach (AIC_c) to choose between 3 candidate models describing b_r as a function of λ_s : linear, quadratic, and asymptotic. I then examined the slope of the function described by the most parsimonious model and considered elk to be encounter-limited when the slope was > 0 and handling-limited when the slope was ≤ 0 (Bradbury et al. 1996, Fortin et al. 2004b).

Spare time and the foraging costs of vigilance

To determine the amount of vigilance that resulted in foraging costs to elk, I first estimated the proportion of each observation for which elk were handling-limited (see above) that was made up of spare time (Z). Fortin et al. (2004b) derived an equation to estimate Z :

$$Z = \frac{\frac{VWB}{R_{max}} - 1}{VWB \left(\frac{h}{S} + \frac{1}{R_{max}} \right)} - T_w \quad (4)$$

where R_{max} is the maximum chewing rate of vegetation (g/min), T_w is the proportion of foraging time spent interacting with conspecifics, h is the time required to crop a bite (min/bite), and V , W , B , and S are defined as above. I used Gross et al.'s (1993) estimates of R_{max} and h , which were 52.95 g/min and 0.012 min/bite, respectively. I used field observation as described above to estimate T_w . Finally, I modified Eq. 4 by substituting in Eq. 1 and replacing λ with λ_s from Eq. 3 to account for the time required to paw away snow (P):

$$Z = \frac{\left(\frac{VWB}{R_{max} + R_{max} \frac{PVWB}{S}} \right) - 1}{\left(\frac{VWB}{1 + \frac{PVWB}{S}} \right) \left(\frac{h}{S} + \frac{1}{R_{max}} \right)} - T_w \quad (5)$$

Equation 5 assumes elk consumed 100% of the vegetation biomass they encountered (Fortin et al. 2004b), but elk likely were selective and did not consider all vegetation eatable. To estimate the average percentage of encountered vegetation consumed by an elk during a foraging bout I first calculated the amount of vegetation encountered during each observation (B_λ g): $B_\lambda = dWB$, where d is the distance an elk traveled during an observation (m; the product of the number of steps taken and average step length). I then estimated

the amount of vegetation consumed during each observation (B_c g): $B_c = t_f b_r S$, where t_f is the total amount of time spent with the head down (min), and b_r (bites/min) and S (g/bite) are defined as above. I considered the percentage of encountered biomass consumed during one foraging bout to be B_c/B_λ . On average, elk consumed 5.6 ± 0.4 % ($N = 170$) of encountered vegetation. To determine how the selective foraging behaviour of elk affects spare time I first calculated Z using total vegetation biomass (B) in Eq 5, and then using 5.6% of B .

I considered Z to be the proportion of time elk could be vigilant without incurring foraging costs (Illius and Fitzgibbon 1994). I examined whether Z or the variables that affected Z (V , B , D , and T_w) differed between migrants and residents. For this comparison I developed mixed-effects generalized linear models using a random-effects maximum likelihood estimator (XTREG command in STATA 10.0, StataCorp LB, College Station, TX) with Z (arcsin transformed, Zar 1999), V , and T_w (arcsin transformed) as dependent variables, individual elk as the random effect, and migration status, biomass, and elk density as covariates within each model. I used the same modeling approach to determine if biomass (B), snow depth (D), and elk density (E_d) were significantly different at migrant and resident foraging locations. For those observations during which vigilance exceeded spare time (i.e. vigilance was costly) I compared the proportion of time spent vigilant (arcsin transformed) between migrant and resident elk using a mixed-effects generalized linear model.

Even if migrant and resident elk had spare time available, they needed to synchronize vigilance with spare time to eliminate foraging costs (Fortin et al. 2004b). For each observation I estimated the proportion of vigilance bouts that occurred during spare time. I considered a vigilance bout to have occurred during spare time if the elk (1) was chewing during the entire vigilance bout, and (2) took a bite directly after being vigilant without stepping. This indicated the elk likely arrived at the next bite before it was finished chewing the previous bite, resulting in spare time. To determine if either migrant or resident elk were better at synchronizing vigilance bouts with spare time, I tested for differences in the proportion of vigilance bouts that occurred during spare time (arcsine

transformed, Zar 1999) between migrants and residents using a mixed-effects generalized linear model (XTREG command in STATA 10.0, StataCorp LB, College Station, TX).

Elk foraging activity

To determine if either migrant or resident elk compensated for reduced intakes rates due to vigilance by spending more time foraging, I compared total time each group spent active over 24 hrs. As a measure of activity, I used the distance moved between consecutive GPS locations collected from 20 migrant and 7 resident elk at 2-hr fix intervals from January to March of 2002-2005 (Hebblewhite et al. 2006). I assumed the average distance between consecutive GPS locations increased when the animals were active and decreased when they were either ruminating or bedded for the evening. I compared the average distance that migrant and resident elk traveled over two hour periods throughout the day, analyzing each month separately to account for increasing photoperiod, using a paired t-test with distance traveled by migrants and residents paired by time of day.

RESULTS

Elk vigilance

The top model explaining variation in the proportion of time elk spent vigilant during observation bouts included elk group (position within the group and elk density), elk location (distance to human activity and to timber), and external (snow depth, wolf presence) variables (Table 3-1). Adding migration status with its interactions to the top null model reduced the AIC_c score by > 3, indicating migrant and resident elk reacted differently to variations in the variables within the top null model (Table 3-1). Resident elk spent more time vigilant when far from human activity and close to timber (Table 3-2; Fig. 3-1a), but migrants showed little change in vigilance levels regardless of their proximity to humans or timber (Fig. 3-1b). Resident elk decreased the proportion of time spent vigilant as

snow depth increased, but migrants increased vigilance as snow depth increased (Table 3-2).

Evidence for handling-limited foraging

The asymptotic model of bite rate as a function of vegetation encounter rate was most parsimonious (Table 3-3). Based on this model, bite rate initially increased with encounter rate indicating an encounter-limited functional response (Fig. 3-2). As encounter rate with vegetation increased the rate of increase in bite rate declined toward zero, indicating that intake rate became limited by vegetation handling time at high encounter rates (Fig. 3-2). The asymptote of the model (34.46 bites/min) represents an estimate of the maximum bite rate elk could attain under the constraints of handling time. However, due to the asymptotic nature of the model, bite rate only approaches 34.46 bites/min as λ_s goes to infinity. Thus, I assumed the value of λ_s that generated the lowest bite rate within the 95% confidence interval around the asymptote (32.82 bites/min) represented the threshold encounter rate (λ_s^*) where intake rate switched from being encounter-limited to handling-limited: 1656.70 g/min (Fig. 3-2). In subsequent analysis I considered elk to be handling-limited and benefit from spare time only when $\lambda_s \geq 1656.70$ g/min. Generally forage intake was encounter-limited only when elk had to paw through snow to encounter vegetation (Fig. 3-2). However, in some foraging bouts that occurred when snow was absent forage intake was still encounter-limited due to slow foraging velocity and/or low vegetation biomass.

Spare time and the foraging costs of vigilance

There was no difference in the amount of spare time (Z) available to migrants and residents regardless of the percentage of consumed biomass used to estimate Z ($P > 0.85$; Fig. 3-3). The lack of a difference in Z occurred despite the fact that migrant elk spent a higher proportion of time interacting with conspecifics (T_w) than residents ($\bar{T}_{w,migrants} \pm SE = 0.012 \pm 0.004$, $\bar{T}_{w,residents} \pm SE = 0.005 \pm 0.002$, $P = 0.01$) when foraging within similar elk densities. There was no difference between the snow depth ($P = 0.16$), vegetation biomass ($P = 0.31$), or elk density

($P = 0.73$) at migrant and resident foraging locations and both groups foraged at similar velocities ($P = 0.37$). The average amount of spare time available to both groups was greater than the average amount of time they spent vigilant for both estimates of Z (Fig. 3-3). However when considering each observation separately (including those for which no spare time was available due to encounter-limited foraging), elk vigilance actually exceeded spare time in 51-53% and 47-49% of migrant and resident foraging bouts, respectively. As a result both groups of elk experienced foraging costs due to vigilance in ~ half of all foraging bouts, regardless of spare time being available during some of these observations. The amount of time spent vigilant that exceeded spare time was similar for migrant and resident elk for both estimates of Z (10 and 14% of migrant and resident elk foraging bouts, respectively; $P > 0.12$ for both estimates of Z)

Although migrant and resident elk often had spare time available while foraging, both groups did not always synchronize vigilance with spare time. Within a foraging bout, the mean percentage of vigilance bouts that were synchronized with spare time was higher ($P = 0.03$) for resident elk ($70\% \pm 0.06$), than for migrants ($51\% \pm 0.07$).

Elk foraging activity

Migrant and resident elk exhibited similar diurnal patterns of activity with two clear peaks in activity that shifted somewhat over the winter (Fig 3-4). Elk were most active from 0800-1000 and 1600-1800 in January and February, and from 0600-0800 and 1800-2000 in March. Migrants and residents traveled similar distances between all 2-hr time intervals in January ($P = 0.66$) and February ($P = 0.15$), but migrants traveled farther (i.e. were more active) than residents in March ($P = 0.01$) (Fig. 3-4).

DISCUSSION

During handling-limited foraging, resident elk synchronized vigilance bouts with spare time (multi-tasking) more often than migrants, supporting my initial hypothesis. As predicted, residents were also more vigilant than migrants when

predation risk was high, which corresponded to areas far from human activity and close to timber because wolves in this system moved to the forest to avoid humans on the grasslands during the day (Chapter 2: Fig. 2-2 and 2-3; Hebblewhite and Merrill et al. 2005, Hebblewhite and Merrill 2007, Hebblewhite and Merrill 2008). Migrants, however, did not increase vigilance with wolf predation risk, which was expected because they were less efficient than residents at reducing the foraging costs of vigilance by multi-tasking. Migrants did not increase total daily foraging time relative to residents until the end of winter when grassland vegetation was likely depleted (McInenly 2003), supporting the prediction that migrants compensated for poor synchronization by lowering vigilance and not increasing foraging time.

In addition to poor synchronization of vigilance with spare time, migrants may not have increased vigilance with predation risk because they perceived predation risk differently than residents. Studies have shown ungulates naïve to wolves exhibited less vigilance when exposed to predation risk cues than experienced prey (Berger 1999 and 2008, Berger et al. 2001). Migrants are unlikely to be naïve to wolves *per se*, but may be less familiar than residents with habitat use patterns of wolves at YHT because migrants spend up to 5 months of the year on summer ranges in BNP where wolf predation risk differs from that at YHT (Hebblewhite and Merrill 2008).

Alternatively, migrants may have perceived predation risk differently because they were less habituated to humans than residents; migrant elk are unlikely to encounter humans on their summer ranges in the backcountry of BNP, whereas residents are consistently exposed to human activity at YHT during summer (pers. obs.). In Chapter 2 I found, on average, migrant elk were farther from human activity than residents, particularly during the day, supporting the theory that migrants are less habituated to humans. As a result migrant elk may have continuously perceived high predation risk in all areas of the YHT because of the opposing spatial patterns of humans and wolves in this system (Chapter 2). Only half of a migrant's vigilance bouts occurred during spare time, so vigilance often had a foraging cost. Therefore, migrants, may have been able to afford the

foraging costs of only moderate levels of vigilance in response to a continuously high perception of risk, as predicted by the risk allocation hypothesis (Lima and Bednekoff 1999). Migrant elk could be at a foraging disadvantage within the human-caused predation refuge because, unlike residents, they did not reduce vigilance levels when foraging close to human activity. By not increasing vigilance levels outside the predation refuge (possibly because of the foraging costs associated with consistent vigilance), migrants could experience higher predation rates than residents: evidence suggests vigilant individuals, along with their offspring, can flee from attacking predators faster (FitzGibbon 1990a, Packer and Abrams 1990, McNamara and Houston 1992, Lima 1994, Lima and Bednekoff 1999b) and are selected by predators less often than non-vigilant ones (FitzGibbon 1989, 1990b).

Because migrant and resident elk responded to spatial variation in human and wolf predation risk differently, the total foraging costs of vigilance incurred by each group depended on how much time they spent in different areas. I assessed the average amount of time elk spent vigilant by substituting the average day-time distance migrant and resident elk were from humans and timber (Chapter 2: Fig. 2-5) into the model predicting the proportion of a foraging bout elk spent vigilant (Table 3-2; holding other variables constant at the same values used in Fig. 3-1). From this, I estimated residents spent more than twice as much time vigilant than migrants when foraging in their average locations under snow free conditions (7% and 15% of migrant and resident foraging bouts, respectively). Although both groups had similar amounts of spare time available, residents were better than migrants at synchronizing vigilance with spare time. Therefore, as long as foraging was handling-limited, the overall foraging costs to each group may have been similar despite higher vigilance levels by residents. For example, when spare time was available 50% of migrant vigilance bouts occurred during spare time, which would reduced the amount of foraging time lost to vigilance to 3.5% of a foraging bout. Residents synchronized 70% of vigilance bouts with spare time so only 4.5% of an average resident foraging bout was lost to vigilance when spare time was available.

However, handling-limited foraging generally occurred only under snow-free conditions. At YHT snow depths as low as 3 cm caused elk to become encounter-limited eliminating spare time. Resident elk decreased the amount of time spent vigilant by 3% for every 5 cm increase in snow depth (holding all other variables constant: Table 3-2), possibly because they were not willing to accept the foraging costs of vigilance during encounter-limited foraging. If there are periods of heavy snow, particularly toward the end of winter when vegetation is depleted (McInenly 2003), high vigilance by residents when predation risk is high could be costly, potentially putting them at a nutritional disadvantage over migrants. The effects of snow limiting access to forage on herbivore functional response can have important influences on trophic dynamics. Wolf kill rates of ungulates increase with snow depth in many systems, which are generally attributed to limited mobility and congregation of ungulates in deep snow (Peterson and Allen 1974, Huggard 1993, Jedrzejewski et al 2002). My study shows that when snow is present (and no spare time is available) ungulates may be more vulnerable to predation also because they are forced to either accept the foraging costs of vigilance or reduce the amount of time spent vigilant (Lima and Bednekoff 1999).

This study also demonstrates the importance of considering the influence of snow on the functional response of herbivores. Previous theory assumed encounter-limited foraging occurs only when plants are inconspicuous or widely dispersed at a low biomass (Process 1 and 2 foraging; Spalinger and Hobbs 1992), which is generally not the case for ungulates grazing in gramanoid dominated systems. More recently Bradbury et al. (1996) found Thomson's gazelles grazing on shortgrass plains were handling-limited only during the wet season and became encounter-limited during the dry season when vegetation was less abundant. I observed a similar switch in the functional response of elk grazing at YHT except snow rather than vegetation abundance reduced encounter rate with vegetation, which has never been reported. Past modelling has emphasized only the influence of spatial vegetation abundance on encounter rate with bites (Spalinger and Hobbs 1992) yet forage access is an alternative mechanism that may influence encounter

rate. Here I provide a third condition for which herbivores experience encounter-limited foraging: bites of vegetation are continuous and spatially concentrated (as in Process 3 foraging; Spalinger and Hobbs 1992), but are not immediately accessible.

This study reveals the importance of understanding the functional response of ungulates when predicting how past experience influences trade-offs in foraging and vigilance. If ungulate forage intake is handling-limited, foraging and vigilance are not mutually exclusive so a direct trade-off may be unnecessary. However, ungulates with less experience with predators (both human and 'natural') may be less efficient at multi-tasking than prey exposed to higher past predation risk. Resident elk displayed low levels of vigilance when foraging within the human-caused predation refuge, possibly because of prior experience with humans (i.e. human habituation). When foraging outside the predation refuge, resident elk increased the amount of time spent vigilant and were likely able to reduce foraging costs by frequently multi-tasking. Migrant elk, however, seemed to be less habituated to humans and perceive risk to be high everywhere, but were inefficient at reducing the foraging costs of vigilance by multi-tasking. As a result, migrants may have been more pressured to trade-off vigilance for foraging than residents, explaining why they behaved according to the risk allocation hypothesis and expressed only moderate levels of vigilance (Lima and Bednekoff 1999). Studies examining the foraging costs of vigilance in ungulates not only need to consider the possibility that multi-tasking can eliminate foraging costs altogether, but also how past experience influences an individual's ability to multi-task. A lack of consideration for these factors may help to explain why Ferrari et al. (2009) found mixed support for hypotheses predicting how prey trade-off foraging and vigilance.

TABLE 3-1. *A priori* candidate models describing the proportion of time elk spent vigilant (T_v) as a function of different combinations of elk group (E_p and E_d), elk locations (d_i and d_r), and external variables (W and D) showing the corrected Akaike Information Criteria values (AIC_c), Δ_i 's, and Akaike weights (W_i) for each. See text for a description of variables.

Model	AIC_c	Δ_i	W_i
$E_p+E_d+d_i+d_r+W+D+M+M\times(E_p+E_d+d_i+d_r+W+D)$	-69.16	0	0.72
$E_p+E_d+d_i+d_r+W+D$	-65.73	3.43	0.13
d_r+d_i	-64.46	4.70	0.07
d_i+d_r+W+D	-63.86	5.30	0.05
E_p+E_d	-61.75	7.41	0.02
E_p+E_d+W+D	-61.60	7.56	0.02
$W+D$	-60.75	8.41	0.01

TABLE 3-2. Coefficients, standard errors (SE) and *P*-values of the variables in the top model (as determined from AIC analysis, Table 3-1) describing the proportion of time elk spent vigilant while foraging on the Ya Ha Tina winter range.

Variable	Description	Coefficient	SE	<i>P</i> -value
E_p	elk position (1 = periphery, 0 = centre)	0.01014	0.04144	0.81
E_d	elk density	0.02928	0.01241	0.02
d_t	distance to timber	-0.00021	0.00010	0.02
d_r	distance to humans	0.00009	0.00003	<0.01
D	snowdepth	-0.00632	0.00360	0.04
W	wolf presence (1 = detected, 0 = undetected)	-0.04407	0.04542	0.32
M	migration strategy (1 = migrants, 0 = residents)	-0.02941	0.12166	0.81
$M \times E_p$	interaction term	0.10041	0.05945	0.09
$M \times E_d$	interaction term	-0.01963	0.01856	0.29
$M \times d_t$	interaction term	0.00035	0.00014	0.01
$M \times d_r$	interaction term	-0.00008	0.00004	0.04
$M \times D$	interaction term	0.01620	0.00554	<0.01
$M \times W$	interaction term	-0.08915	0.07461	0.23
Constant	-	0.08946	0.08801	0.31

TABLE 3-3. Candidate models describing the relationship between bite rate (y) and encounter rate (λ_s) showing the r^2 , the corrected Akaike Information Criterion (AIC_c) value, Δ_i , and Akaike weight (W_i) for each.

Model	r^2	AIC_c	Δ_i	W_i
$y = b\lambda_s/(c+\lambda_s)$	0.944	1161.04	0.00	0.99
$y = a\lambda_s^2 + b\lambda_s + c$	0.251	1174.27	13.23	<0.01
$y = b\lambda_s + c$	0.162	1192.61	31.57	<0.01

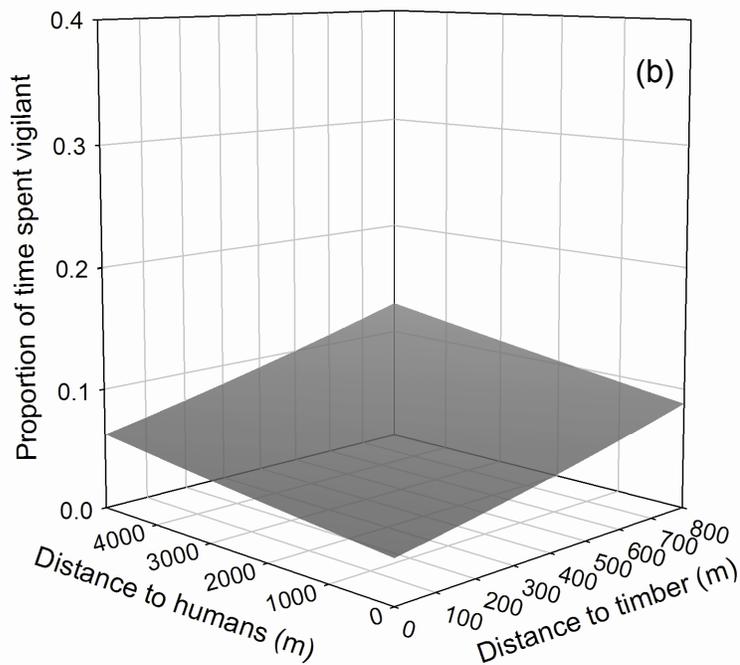
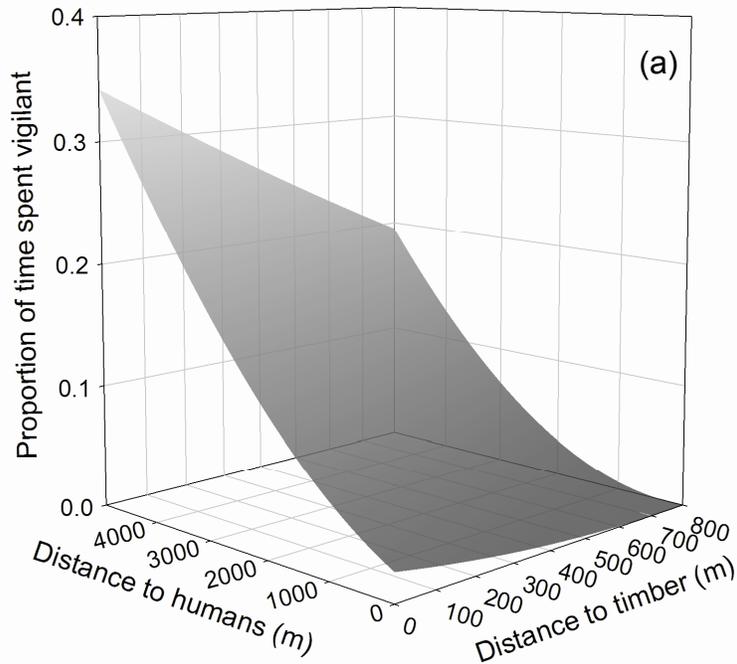


FIG. 3-1. Proportion of time resident (a) and migrant (b) elk spend vigilant (back-transformed) in relation to their distance to humans and to intact timber as predicted by the model found to be most parsimonious using AIC_c analysis (Table 3-1 and 3-2). Other covariates were held constant: $E_d = 1.8$ elk/12.5 m², $E_p = \text{centre (0)}$, $D = 0$ cm, $W = \text{undetected (0)}$. See text for a description of the variables.

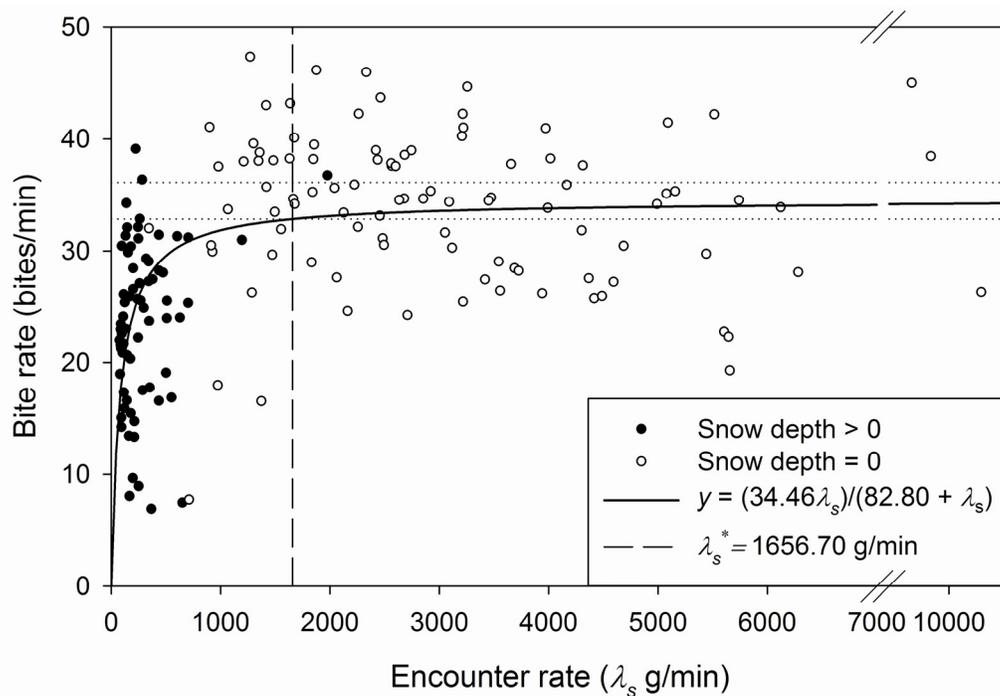


FIG. 3-2. Observed bite rate of elk as a function of their estimated encounter rate with vegetation (λ_s) when foraging in a snow depth > 0 (closed circles) and a snow depth = 0 (open circles). The solid line represents the asymptotic function found to be most parsimonious using AIC_c analysis (see Table 3-3). Dotted lines represent the 95% confidence intervals around the asymptote of the function. The dashed line represents the threshold encounter rate (λ_s^*) at which elk intake rate switches from being encounter-limited to handling-limited.

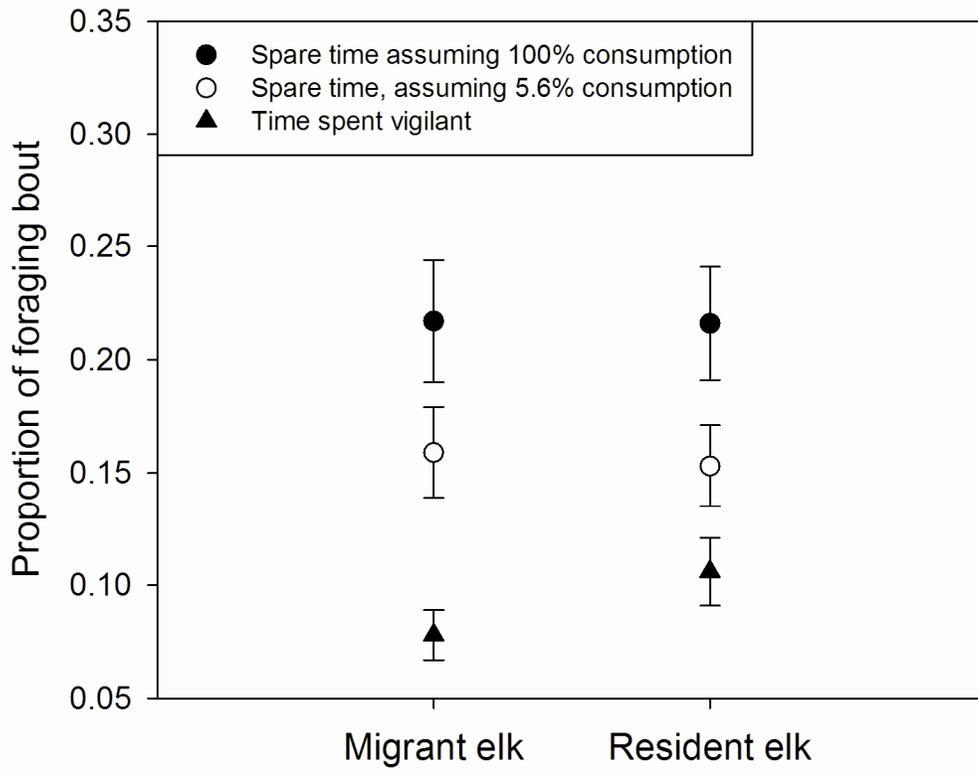


FIG. 3-3. Mean amount of spare time available to migrant and resident elk estimated using 100, and 5.6 % of total vegetation biomass (see text for details), and the mean amount of time migrant and resident elk spent vigilant while foraging during winter.

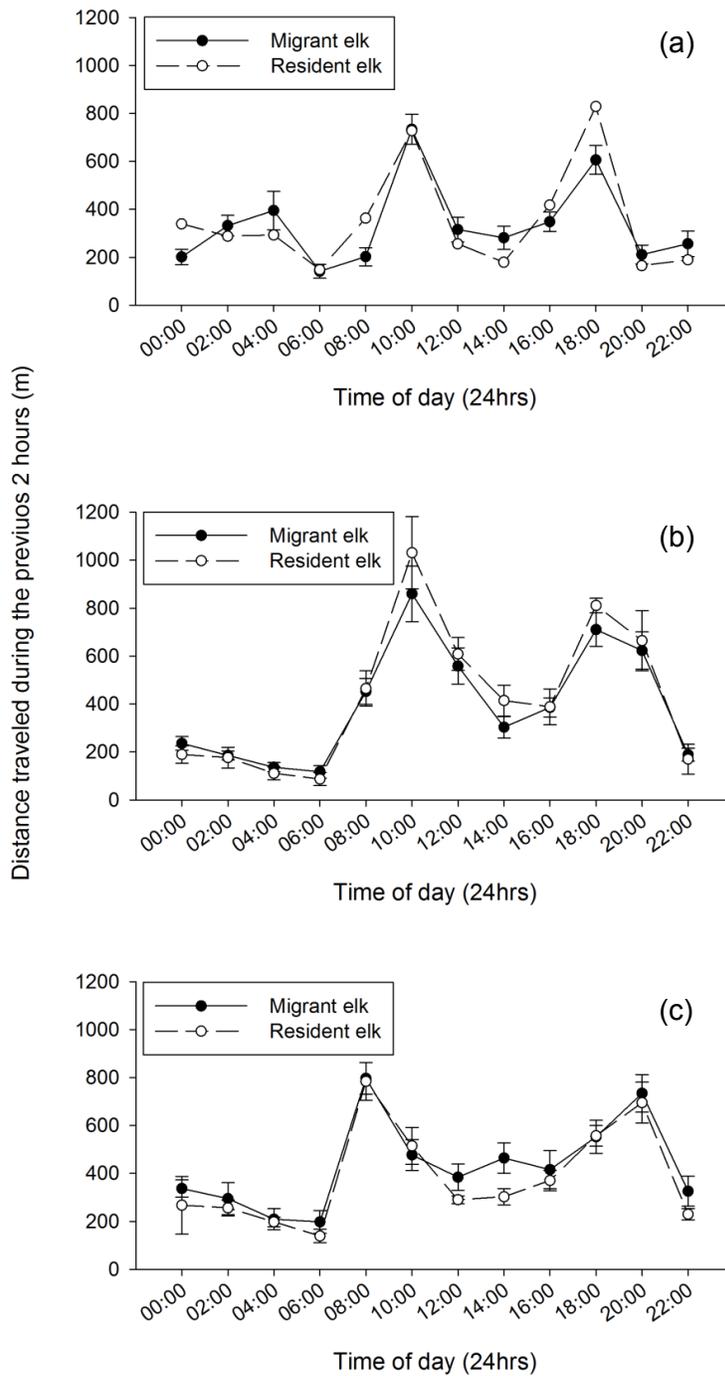


FIG. 3-4. Mean distance traveled by migrant and resident elk during 2 hour periods throughout the 24 hours of day in January (a), February (b), and March (c). Values are based on the distances between consecutive GPS locations obtained at 2 hour fix intervals from 2002-2005 averaged across all individuals and days for each month. Error bars represent ± 1 SE.

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CHAPTER 4: SYNTHESIS

SUMMARY

Previous studies examining the disruption of ungulate migration blame either direct causes, such as loss of migratory corridors (Berger 2004) and over-harvesting (Toweill and Thomas 2002) or indirect causes that change the costs and benefits of migration (Hebblewhite et al. 2006). For example, human settlement in the Bow Valley of BNP created a predation refuge, which made it more beneficial for elk (*Cervus elaphus*) to remain near these settlements year-round rather than conduct their historic migration (McKenzie 2001, Hebblewhite and White et al. 2005). Hebblewhite and Merrill (2007) similarly found that resident elk of the YHT population exploited a human-caused predation refuge from wolves (*Canis lupus*) during summer, which likely contributed to the increasing proportion of residents observed in that population (Hebblewhite 2006). My results showed that resident elk benefit from inhabiting the YHT winter range year-round because they become habituated to humans and more efficient at trading off foraging opportunities and predator avoidance than migrants.

In Chapter 2 I found migrant and resident elk of the Ya Ha Tinda (YHT) were not spatially segregated on their sympatric winter range, supporting the previous assumption that both groups intermix into a single herd during winter. However, at the scale of the foraging site each segment displayed different responses to spatial variables (distance to human activity and timber) that may have resulted in different risks of predation by wolves. Both migrant and resident elk exploited a predation refuge created by day-time wolf avoidance of humans, and were exposed to equal predation risk during the day. At night, however, when humans were less active, wolves move into the grasslands and used areas of that were far from timber. Because resident elk foraged closer to the ranch and farther from timber than migrants, they were exposed to higher night-time predation risk than migrants. However, it is unclear whether residents actually experienced higher predation rates because I did not account for antipredator behaviours, such as grouping and vigilance, which might decrease the chances of

an elk being killed by a wolf after an encounter (Hebblewhite and Merrill et al. 2005, Caro 2005).

Although both groups were exposure to similar day-time predation risk and forage, in Chapter 3 I found that migrants and residents displayed different vigilance responses to changes in predation risk. Resident vigilance levels varied positively with wolf predation risk at the YHT, whereas migrants maintained consistent vigilance levels regardless of spatial variations in risk. Because migrants were less habituated to humans than residents they did not reduce vigilance levels within the human-caused predation refuge as observed in residents. Both groups had similar amounts of spare time available to reduce the foraging costs of vigilance, but migrants were less efficient than residents at synchronizing vigilance with spare time. As a result, migrants may not have been able to afford the foraging costs of increased vigilance when predation risk was high (*sensu* Lima and Bednekoff 1999). As a result, residents may be at an advantage in terms of forage intake and predator avoidance. However, the resident advantage exists only during handling-limited foraging when spare time is available to reduce the foraging costs of vigilance. Elk were handling-limited during most of the winter, but snow accumulation, in conjunction with winter vegetation depletion, caused elk intake rate to become encounter-limited, eliminating spare time and the resident advantage. A continual increase in the resident portion of this herd would increase summer grazing pressure on the YHT grasslands, potentially reducing availability of forage during winter and exacerbating the reduction of spare time.

I demonstrated differences in the way migrant and resident elk trade-off foraging and predator avoidance on their sympatric range, but future work is needed to determine the fitness consequences of these behavioural differences. For example, it is important to directly compare predator-caused mortality of migrant and resident elk on the winter range. I found residents were exposed to higher night-time wolf predation risk than migrants (Chapter 2), but residents also seemed better than migrants at corresponding vigilance with wolf predation risk (Chapter 3). Understanding how behavioural differences translate into actual

mortality rates would provide more insight into the demographic consequences of my results. Similarly, an investigation of the effects of over-winter vegetation depletion on elk distribution and functional response would help determine how changes in elk density and the migrant to resident ratio would influence exposure to forage and predation risk. If a larger number of elk grazing on the YHT during summer speeds up winter vegetation depletion, both migrant and resident elk may be forced to graze outside the human-caused predation refuge during winter. In addition, forage intake may become encounter-limited, which would eliminate spare time and potentially alter the way both migrants and residents respond to predation risk.

MANAGEMENT IMPLICATIONS

Hebblewhite et al. (2006) reported that the migratory behaviour of the YHT elk population has been declining over the past 30 years with increasing numbers of resident elk remaining on the Ya Ha Tinda winter range year-round. There are several negative ecological consequences that could arise from this decline in migratory behaviour (Berger 2004). First, increased numbers of resident elk foraging on the YHT winter range during summer may deplete forage available for winter when other food resources are limited. Second, decreased numbers of elk migrating to summer ranges in Banff National Park could deplete food resources for top carnivores, such as wolves and grizzly bears (*Ursus horribilis*), residing in BNP. If the management objectives are to maintain the migratory segment of the YHT elk population and reduce the number of resident elk, then potential causes of the increase in the migrant to resident ratio need to be identified so appropriate management strategies can be applied. Hebblewhite (2006) found that by exploiting the human-caused predation refuge during summer at YHT, residents had a higher chance of survival than migrants, which experienced high predation rates while migrating to summer ranges in BNP. I found when both groups were at YHT during winter, residents were able to take advantage of the predation refuge more than migrants, because residents were more habituated to humans. Based on my results and those of Hebblewhite's

(2006), it seems any management strategy that (1) removes the human-caused predation refuge on the grasslands, (2) reduces elk access to the predation refuge, (3) reduces resident habituation to humans, or (4) directly reduces the number of residents will help to increase the proportion of migrants in the YHT elk population.

To remove the human-caused predation refuge would involve removing the YHT ranching operation and restricting public access to the YHT grasslands. This may be the most direct management option, but the YHT Ranch contains cultural and historical significance and its removal would likely invoke a negative response from members of the public. Similarly, recreation opportunities at the YHT are extensive (e.g. horseback riding, hunting, camping, and hiking) and restricting access to the area would be unpopular with the public. Therefore, removing the predation refuge is not a feasible option.

Instead, elk access to the predation refuge could be controlled by erecting an elk-proof fence around the refuge with multiple large gates. An elk-proof fence with gates has been proposed previously, and it was suggested that it replace the existing 7.5 km of outer, central pasture fences, which are elk permeable (Parks Canada 2005). The fence would encompass the section of the grasslands immediately southeast of the YHT Ranch buildings and include ~ 20% of the grassland habitat at the YHT. The proposed fence also encompasses the area of the grasslands avoided by wolves during the day (i.e. the predation refuge; Chapter 2). Keeping the gates closed during summer would protect the forage within the predation refuge from resident grazing, potentially increasing winter carrying capacity of the YHT winter range. In addition, keeping the gates closed during summer would potentially increase resident mortality by forcing resident elk into adjacent areas with high wolf predation risk. This would directly decrease the proportion of residents in the population

Keeping the gates closed during winter, however, would exclude elk from important forage resources and likely reduce the carrying capacity of the winter range. On average, 24% of elk telemetry locations occurred within the proposed fenced area during the winter from 2002-2005 (unp. data). Because the amount of

winter forage available outside the YHT grasslands is limited, excluding both migrant and resident elk from the predation refuge during winter may lead to nutritional deficiencies for the entire population. Elk exclusion during winter would likely increase predation rates in general, but behavioural differences between migrants and residents (Chapter 3) may result in different predation rates for each group, at least during the initial few years of constructing the fence. Residents were more vigilant than migrants when away from the predation refuge, indicating they may experience lower predation rates than migrants if excluded from the predation refuge during winter. However, because residents previously had access to the refuge year-round, they may rely on consistent access to it to successfully avoid predation. Migrants must successfully avoid predation in BNP during summer where no refuge exists, so they may be better than residents at avoiding predation during winter if the refuge is inaccessible. Because of the important winter forage resources within the predation refuge and the uncertainty surrounding the effects of excluding the entire population from the predation refuge during winter on the relative predation rates of migrant and resident elk, I suggest leaving the gates open during winter if an elk-proof fence is built around the predation refuge.

The aversive conditioning project currently being conducted at the YHT (Spaedtke 2009), where resident elk are herded off the grasslands during summer by riders on horseback, also reduces resident access to the predation refuge. As with fencing, this would protect the grasslands from summer grazing (Spaedtke 2009) and likely increase predation rates on residents. Although aversive conditioning on horseback is stressful to elk to some degree, it may actually increase resident habituation to humans. Increased habituation of residents might cause them to spend even more time in the predation refuge during winter, increasing their forage and predator avoidance advantage over migrants (Chapter 3).

Another management strategy is to directly reduce the number of residents through hunting or culling. This could be done in three ways. First, a limited cow harvest could be implemented in early fall before migrants return from their fall

migration (prior to Oct 1; Hebblewhite et al. 2006). Second, if a limited cow harvest was opened during winter, I would expect the human-habituated resident elk to be more vulnerable and experience higher mortality rates than migrants, at least during the initial years of the hunt. This strategy would be more risky than the first because migrants and residents are intermixed on the winter range, so some migrant mortality is also likely. However, first nation harvests from winter 2002-2004 were resident-biased, providing further evidence that residents are more vulnerable to human hunting than migrants (Hebblewhite 2006). Third, a formal cull of resident elk could be implemented, where residents are shot at YHT during summer. This strategy has been implemented to reduce the number of habituated elk within the town site of Banff, and has proven to be effective (Cliff White, pers. comm.).

Previously, it was assumed all things were equal for migrant and resident elk when they were together on the YHT winter range. The results from my thesis show managers that migrant and resident elk behave differently in response to humans and predators even while intermixed in a single herd, indicating management strategies applied to this population during winter can have different effects on each group. Managers can use the recommendations provided above to take advantage of these behavioural differences to reduce the number of residents in this population, if that is the management goal.

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APPENDICES

APPENDIX 1: MODELLING THE SPATIAL ABUNDANCE OF GRASSLAND VEGETATION BIOMASS AT THE YA HA TINDA

Model	AIC _c	Δ_i	W_i	r^2
<i>NDVI + E</i>	505.15	0	0.77	0.42
<i>NDVI + E + slope</i>	507.53	2.39	0.23	0.40
<i>NDVI</i>	522.071	16.92	< 0.01	0.13
<i>NDVI + slope</i>	524.369	19.22	< 0.01	0.11

E = distance (m) east from a datum point at the western edge of the Ya Ha Tinda Range (UTM NAD 83, Zone 11: 0591224, 5731018)

NDVI = the normalized difference vegetation index

slope = deviation from horizontal in degrees

APPENDIX 2: CORRELATIONS BETWEEN VARIABLES WITHIN THE MODELS
 PREDICTING THE PROPORTION OF TIME ELK SPEND VIGILANT

	M	E_p	E_d	d_r	d_t	W	D
Migration status (M)	1.00	-0.01	0.06	-0.11	0.06	-0.10	-0.11
Elk position (E_p)		1.00	-0.07	0.09	-0.20	0.07	0.15
Elk density (E_d)			1.00	-0.19	-0.03	-0.07	-0.09
Distance to humans (d_r)				1.00	-0.18	0.21	0.47
Distance to timber (d_t)					1.00	-0.18	-0.24
Wolf presence (W)						1.00	0.20
Snow depth (D)							1.00

APPENDIX 3: MODELLING THE TIME REQUIRED FOR AN ELK TO PAW AWAY SNOW
AND UNCOVER A BITE OF VEGETATION

Model	AIC _c	Δ_i	W_i	r^2
$D \times B$	-201.719	0	0.57	0.87
$D + D \times B$	-199.786	1.93	0.22	0.87
$B + D \times B$	-199.674	2.04	0.21	0.87
D	-192.219	9.50	< 0.01	0.79
$D + B$	-190.687	11.03	< 0.01	0.79

D = snow depth (cm)

B = vegetation biomass (g/m²)