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ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range?

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Abstract Partially migratory populations, where one portion of a population conducts seasonal migrations (migrants) while the other remains on a single range (residents), are common in ungulates. Studies that assess trade-offs between migratory strategies typically compare the amount of predation risk and forage resources migrants and residents are exposed to only while on separate ranges and assume both groups intermix completely while on sympatric ranges. Here we provide one of the first tests of this assumption by comparing the amount of overlap between home ranges of GPS-collared migrant and resident elk and fine-scale exposure to wolf predation risk and forage biomass at telemetry locations on a sympatric winter range in west-central Alberta, Canada. Overlap between migrant and resident home ranges increased throughout the winter, and both groups were generally intermixed and exposed to equal forage biomass. During the day, both migrants and residents avoided predation risk by remaining in areas far from timber with high human activity, which wolves avoided. However, at night wolves moved onto the grasslands close to humans and away from timber. Resident elk were consistently closer to areas of human activity and further from timber than migrants, possibly because of a habituation to humans. As a result, resident elk were exposed to higher night-time predation risk than migrants. Our study does not support the assumption that migrant and resident elk are exposed to equal predation risk on their sympatric range when human presence alters predation risk dynamics and habituation to humans is unequal between migratory strategies.

Keywords Habituation · Home-range overlap · Partial migration · Ungulates · Wolf predation

Introduction

Long-distance migrations between allopatric ranges are common among ungulate 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). Partially migratory populations, where one portion of a population conducts seasonal migration (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 1987, 1988; Hebblewhite 2006). To understand the trade-offs made under each migratory strategy, studies typically compare the amount of predation risk and forage resources migrants and residents are exposed to while occupying separate ranges and assume they derive equal costs and benefits when together on their sympatric range (e.g., Kaitala et al. 1993; Ball et al. 2001; Hebblewhite and Merrill 2007; Hebblewhite et al. 2008).

In contrast, theoretical studies of partial migration in birds have long considered that residents are at an

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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 a higher survival, higher probability of breeding, and higher mating success than migrants because residents were able to exclude migrants from ideal breeding territories as the migrants returned from their wintering grounds. Similarly, Pérez-Tris and Tellería (2002) found considerable spatial segregation between resident and migrant blackcaps (*Sylvia atricapilla*) on their sympatric winter range because residents defended the most suitable breeding sites, while migrates concentrated in habitats with high food abundance. Ungulates are also known to segregate into stable, social groups (Clutton-Brock et al. 1982; Jenkins and Starkey 1982; Weckerly 1999) where dominant individuals exclude subordinates from productive foraging sites (Thouless 1990). Nevertheless, resident exclusion of migrants from either high-quality foraging sites or areas of low predation risk on sympatric ranges has not been studied in partially migratory ungulates. Ungulate habitat selection is often driven by a trade-off 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 (Loudon et al. 1983; Kjellander et al. 2004). Therefore, spatial segregation of migrant and resident animals on their sympatric range could result in different levels of fitness.

In the study reported here, we tested the assumption that migrant and resident individuals in a partially migratory elk (*Cervus elaphus*) population in the Canadian Rockies of west-central Alberta (Fig. 1) were exposed to equal forage and wolf (*Canis lupus*) predation risk while on their sympatric winter range (Hebblewhite and Merrill 2009). Migrants of this population move to high-elevation summer ranges in Banff National Park (BNP) while residents remain on the Ya Ha Tinda (YHT) winter range adjacent to BNP year-round (Fig. 1; Hebblewhite et al. 2006). Recent studies on the YHT elk population compared the consequences of migrating versus being sedentary and found that migrant elk are exposed to higher quality forage (Hebblewhite et al. 2008) and lower predation risk (Hebblewhite and Merrill 2007) than residents during the summer—yet the proportion of resident elk in this population has increased since the 1980s (Hebblewhite et al. 2006). To determine if migrant and resident elk were exposed to different forage resources and predation risk on the YHT winter range, we tested two hypotheses, each considering a different spatial scale. First, we tested the hypothesis that migrant and resident elk were spatially segregated on the winter range at the landscape-scale by examining the amount of overlap between the home ranges of each group. Second, even if migrant and resident elk were not spatially segregated at the landscape-scale, we hypothesized there were fine-scale differences in habitat use within home ranges that resulted in exposure to different forage resources and predation risk. We tested this hypothesis by

Fig. 1 Location of the Ya Ha Tinda (YHT, *dashed line*) on the eastern border of Banff National Park (BNP, *solid line*) in Alberta, Canada (*lower right corner*). Shown are daily GPS relocations of seven migrant (*black circles*) and four resident (*white circles*) elk during July and August, 2004, demonstrating the different summer ranges used by each migratory strategy. Both migrant and resident elk over-winter at the YHT
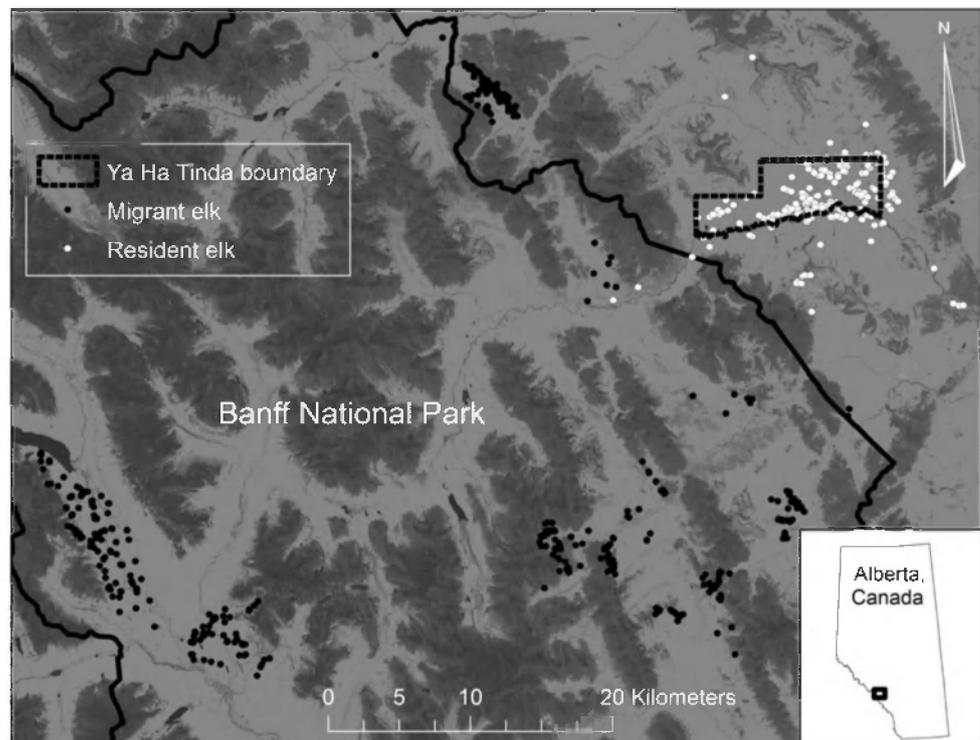
comparing relative predation risk and forage abundance at winter telemetry locations of migrant and resident elk, which was similar to the comparisons made on summer ranges (Hebblewhite and Merrill 2007; Hebblewhite et al. 2008). Because the migrant-to-resident ratio of this population has been decreasing (Hebblewhite et al. 2006), we expected resident elk would be exposed to lower predation risk and higher forage abundance than migrants at the YHT during winter.

Methods

Study site

The YHT is a 4000-ha winter range located on the eastern slopes of the Rocky Mountains adjacent to BNP in Alberta, Canada (Fig. 1). Parks Canada operates a horse ranch at the YHT and winters approximately 100 horses there each year. Two-thirds of the YHT is native rough fescue (*Festuca campestris*) grassland. The remaining third is predominantly lodgepole pine (*Pinus contorta*) forests merging into Engelmann spruce (*Picea engelmanii*) at higher elevations, but it is also interspersed with aspen (*Populus tremuloides*) forests and willow-bog birch (*Salix* spp.–*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 (*Alces alces*) are also present. The YHT elk population ranged from approximately 800 individuals in the early 1970s to >2000 in the early 1990s and consisted of approximately 850 individuals (580 migrants and 270 residents) during this study. Regardless of population size, the ratio of migrant to resident elk has steadily decreased from 12:1 to 2:1 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 the winter. Wolves are the most common predator of elk in this system; during the winter of 2003/2004 two packs consisting of six and 17 wolves, respectively, consistently hunted elk at the YHT (Hebblewhite and Merrill 2007).

Capture and monitoring of elk and wolves

Elk were captured annually from 2001 to 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 no. 353112; see Hebblewhite et al. 2006 for details). Twenty-six adult cows were equipped with GPS collars (models 2200 or 3300; LOTEK, Newmarket, ON) and unique plastic ear tags over this time period. We followed the approach of Hebblewhite et al. (2006) and used GPS collar data to define migrant elk as individuals that migrated between allopatric summer and winter home ranges defined by 95% minimum convex polygons, and residents as individuals whose summer and winter home-ranges overlapped. Based on this definition, the 26 elk equipped with GPS collars consisted of 18 migrants and eight residents. 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 the summer and helicopter net gunning and aerial darting during winter from 2002 to 2004 and equipped with GPS collars (model 3300sw; LOTEK) (see Hebblewhite and Merrill 2007 for details).

Home-range overlap

We described winter home ranges of elk 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). We estimated monthly UDs for each GPS-collared elk based on 2-h relocations collected during the winters (15 October to 15 April) of 2001–2005 using fixed kernel analysis (Worton 1989) with the plug-in method to determine the smoothing factor. The plug-in method is an objective, statistical technique that estimates a separate bandwidth for the x and y directions. In a simulation study, Gitzen et al. (2006) found that the plug-in method produced the most accurate estimate of a known UD when describing animal locations distributed like those seen for elk in this study ('partially clumped'). Smoothing factors and UDs were estimated using the KS package (Duong 2008) developed for the R statistical computing software (R Development Core Team 2008). Each UD represented a relative probability of use (sum to 1) and was directly comparable across elk. To measure home-range overlap between pairs of elk, we used the volume of the intersection index (VI), which estimates the volume of overlap between two UDs (VI ranges from 0 to 1, with 0 indicating no overlap and 1 indicating complete overlap) (Seidel 1992). The use of UDs and VI to estimate home-range overlap is more descriptive than traditional

Table 1 Mixed-effects models predicting the volume of intersection index (*VI*), and elk exposure to predation risk (*PR*) and vegetation biomass (*B*)

Dependent variable	Parameters and independent variables	n	n groups
VI	$-0.16MM + 0.13RR + 0.13nov + 0.12dec + 0.20feb + 0.28mar + 0.10apr + MM \times (0.06nov + 0.10dec + 0.03feb + 0.08mar + 0.15apr) + RR \times (0.12nov - 0.02feb - 0.09mar - 0.17apr + 0.74)$	335	167
PR	$-0.04M - 0.09mar - 0.05apr - 0.36t_d + M \times (0.04mar + 0.01apr + 0.02t_d) + 0.68$	9,014	20
B	$-0.41M - 15.93feb - 15.01mar - 3.90apr + M \times (-0.93feb + 2.90mar + 3.81apr) + 215.21$	1,391	25

Shown are the parameter estimates for each independent variable, total number of observations used for each model estimation (*n*), and the number of groups used to estimate random effects

All independent factors are represented with dummy variables: *MM* migrant-to-migrant pair type; *RR* resident-to-resident pair type; *nov, dec, feb, mar, apr* month dummy variables; *M* migration strategy variable (1 migrant, 0 resident); t_d time of day (1 day, 0 night)

measures (e.g., minimum convex polygon) because the intensity of use within overlapping portions of the home ranges is accounted for (Millspaugh et al. 2004; Fieberg and Kochanny 2005).

Using code we wrote in R, we calculated VI for all pairwise comparisons of elk UDs estimated from locations collected over the same time period. We then calculated the average VI (*VI*) between migrant elk UDs (pair type = *MM*), between resident elk UDs (pair type = *RR*), and between migrant and resident UDs (pair type = *MR*) for each winter month. If migrants and residents were spatially segregated during the winter, we 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*, we used a mixed-effects generalized linear model with *VI* as the dependent variable (arcsin transformed to meet assumptions of normality) and elk pair as the random effect (XTREG command in STATA ver. 10.0; StataCorp, College Station, TX). We 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 (Table 1).

Exposure to wolf predation risk

We estimated UDs for two wolf packs that hunted on the YHT winter range to provide spatially explicit measures of wolf predation risk. We 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 increases with pack size (Mech and Boitani 2003; Hebblewhite et al. 2004), we considered overall risk to be a function of both intensity of use (from UDs) and pack size, including both juvenile and adult wolves. We also considered an elk's chance of encountering a wolf (i.e., risk) to be higher in areas used by multiple packs so we added each

pack's UD (weighted by pack size) together to account for elevated risk in areas of territorial overlap. In contrast, Hebblewhite and Merrill (2007) modeled predation risk of this study area by combining a wolf resource selection function, 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 BNP) and over a coarser temporal scale (the entire summer) than were needed for this study.

We developed wolf UDs from 2-h GPS collar data collected only from February to April 2004 because this was the time period for which we had sufficient wolf locations to produce monthly UDs (>50; Seaman et al. 1999) and a large enough elk sample size to measure exposure during winter. We used data from only one wolf per pack because cohesion between radio-collared wolves within each pack during the winter was generally high, and the movement of one wolf likely represented movements of the entire pack (mean monthly *VI* between two wolves from the same pack = 0.79 ± 0.02). Separate day and night UDs for each month for each pack were developed to account for differences in diurnal and nocturnal habitat use by wolves (Theuerkauf et al. 2003b; Hebblewhite and Merrill 2007) and any seasonal variation (e.g., early vs. late winter). We 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). We estimated wolf UDs using the same method as that described for elk. We 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). We 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, we estimated predation risk of a 30×30 m pixel (PR_i) as:

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

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.

We first determined PR_I at elk GPS locations collected during the winter of 2003/2004 (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). By intersecting elk locations with our predation risk models, we were able to compare the average amount of risk that individual migrant and resident elk were exposed to. Differences in individual exposure to predation risk between migrants and residents should relate to different predation rates for each group. Therefore, with this analysis we were determining whether the migrant portion of this population was dying faster from predation than the resident portion, explaining the observed decline in the migrant to resident ratio (Hebblewhite et al. 2006). We compared migrant and resident exposure to predation risk using a mixed-effects generalized linear model with PR_I at elk locations as the dependent variable and individual elk as the random effect. We used dummy variables to represent elk migration strategy (M, 0 = resident, 1 = migrant), time of day (t_d, night = 0, day = 1), and month (as dummy variables) to determine if these variables influenced predation risk, and included interaction terms between each variable (Table 1).

In addition, we investigated the factors that an elk might associate with the spatiotemporal patterns in PR_I across the winter range. We 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 encompassing all elk locations collected from February to April 2004. We used t_d 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 edges (Hebblewhite and Merrill 2007). Five candidate generalized linear models comprised of different combinations of these variables along with interactions were compared (Table 2) using Akaike information criteria (AIC$_c$) to determine the most parsimonious model. Differences in the average value of each variable included in the top model at migrant and resident locations were tested using a two-way analysis of variance (ANOVA) ($M \times t_d$) to determine whether migrant and resident elk responded to these variables differently and whether their response changed during the night and day.

Exposure to forage

We compared exposure of migrant and resident elk only to herbaceous forage on open grasslands because 75% of migrant and resident telemetry locations occurred on grasslands during the winter, and 90% of winter elk diet at YHT consisted of graminoids (Hebblewhite 2006), which are found predominately on the grasslands. To estimate fine-scale spatial variation in herbaceous biomass across the grasslands, we used a LANDSAT Thematic Mapper image (30×30 m resolution) of the area taken on 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 we 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). We then used a model selection approach (AIC$_c$) 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 2009). Because no additional biomass is produced after senescence, these data represented initial winter forage abundance. Although the

Table 2 A priori candidate models estimating relative predation risk as a function of different combinations of time of day (t_d night or day), distance to human activity (d_r, in meters), and distance to timber (d_t, in meters) showing the corrected Akaike Information Criteria values (AIC$_c$), scaling criterion values (Δ_I), Akaike weights (W_I), and R^2 values for each

Model	AIC$_c$	Δ_I	W_I	R^2
$d_t + d_r + t_d + d_t \times t_d + d_r \times t_d + d_t \times d_r$	−4,528	0	>0.999	0.38
$d_t + d_r + t_d + d_t \times t_d + d_r \times t_d$	−4,498	30	<0.001	0.28
$d_t + d_r + t_d$	−3,012	1,516	<0.001	0.14
$d_r + d_t$	−2,982	1,546	<0.001	0.14
t_d	−1,699	2,829	<0.001	<0.01

biomass data and LANDSAT image were from different years, spatial variations in relative vegetation abundance are likely to be similar across years (McInenly 2003). The most parsimonious model to estimate September herbaceous biomass (B, g/m^2) was a function of $NDVI$ and the distance east (E, in meters) 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, $R^2 = 0.42$; Robinson 2009). Previous work also showed that herbaceous biomass at YHT increased along a west-to-east gradient on the grasslands (McInenly 2003).

To compare the exposure of migrant and resident elk to forage, we 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 foraging activity, we used the distance elk traveled between consecutive GPS locations collected at a 2-h fixed intervals 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 (Robinson 2009), which we defined as periods of active foraging. These periods occurred from 0800 to 1000 hours and from 1400 to 1600 hours in December, from 0800 to 1000 hours and from 1600 to 1800 hours in January and February, and from 0600 to 0800 hours and from 1800 to 2000 hours in March and April (Robinson 2009). We then tested for monthly differences in estimated standing biomass (B, g/m^2) at migrant and resident telemetry locations collected in the winter of 2003/2004 during the active time periods using a mixed-effects, generalized linear model with individual elk as the random effect, and M (0 = resident, 1 = migrant), month (as dummy variables), and $M \times$ month as the dependent variables (Table 1). To determine the mechanism driving any potential differences in exposure to forage between migrant and resident elk, we compared the average monthly NVDI and E values (see above) at migrant and resident telemetry locations taken during the active time periods using a two-way ANOVA with month and M as the factors.

Results

Home-range overlap

The amount of overlap between home ranges across all pairs of migrants and residents increased from October to March and then decreased in April (Fig. 2); home-range overlap was significantly higher in February and March than in October ($P < 0.003$), but similar to October in
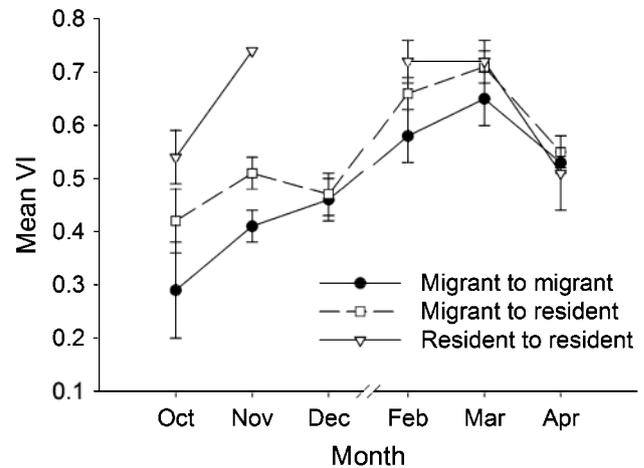

Fig. 2 Mean volume of intersection index (*VI*) representing average overlap between two migrant elk home ranges (*solid circle*), two resident elk home ranges (*open triangle*), and a migrant and a resident elk home range (*open square*) for each winter month from 2002 to 2005. *Error bars* represent $\pm$ 1 standard error (SE). No elk were equipped with GPS collars in January of any year, and only one resident elk was equipped with a collar during December

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), indicating both groups were not spatially segregated. Overlap between resident home ranges was higher than between migrant home ranges across all months ($P = 0.041$; Fig. 2). 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).

Exposure to wolf predation risk

Day and night spatial patterns of wolf movements were qualitatively different, resulting in spatiotemporal variations in predation risk (Fig. 3). 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. 3a). Conversely, night-time wolf habitat use was concentrated on the grasslands, resulting in relatively high predation risk in this habitat (Fig. 3b). The model that best described predation risk (Table 2) predicted that day-time risk was highest far from both areas of human activity and timber and safest close to human activity, but far from timber (Table 3). At night, predation risk increased with distance to timber, but it was unaffected by distance to human activity (Table 3).

Fig. 3 Example of the consistent spatial difference between day (**a**) and night (**b**) wolf predation risk on the Ya Ha Tinda grasslands (February 2004). This model assumes that predation risk is proportional to wolf intensity of use weighted by pack size
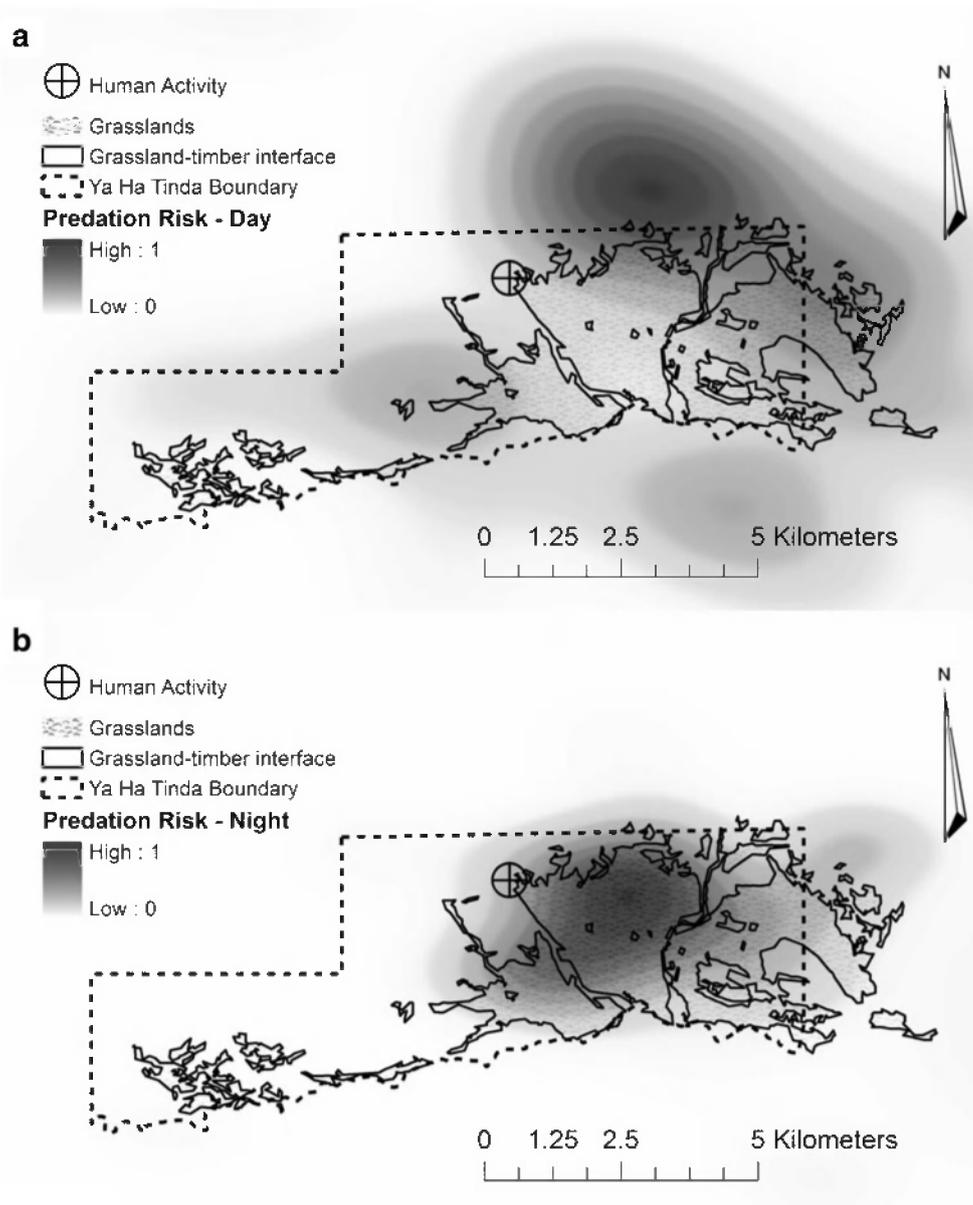
Spatiotemporal patterns in predation risk resulted in a significantly higher exposure of all elk to predation risk at night compared to the day ($P < 0.001$; Table 1, Fig. 4). Resident elk were exposed to higher risk than migrants across all months and times of day (M effect: $P = 0.013$; Table 1). Resident 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; $P = 0.019$; Table 1). 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 (t_d effect; Fig. 6). The relative decrease in distance to 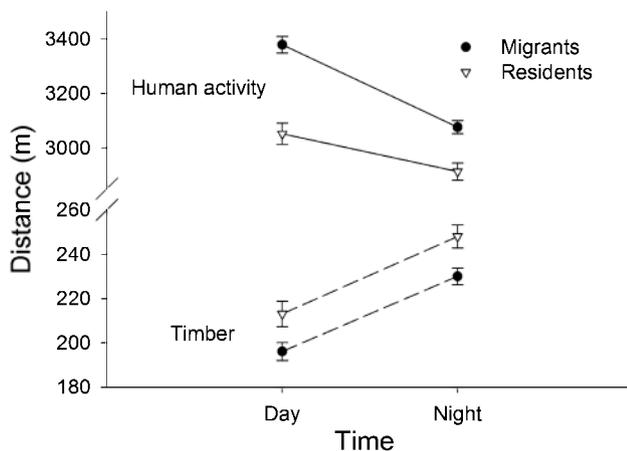timber from day to night was similar for both groups ($M \times t_d$: $F = 0.05$, $df = 1$, $P = 0.82$), but migrants experienced a larger relative decrease in distance to humans from day to night than residents ($M \times t_d$: $F = 6.58$, $df = 1$, $P = 0.01$) (Fig. 5). On average, residents still remained 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 (Fig. 5). Because night-time predation risk increased with distance to timber (Table 3), residents were exposed to higher night-time risk than migrants (Fig. 4).

Exposure to predation risk also varied across months, with a higher mean exposure in February than in March and April ($P < 0.001$; Table 1). Monthly fluctuations were
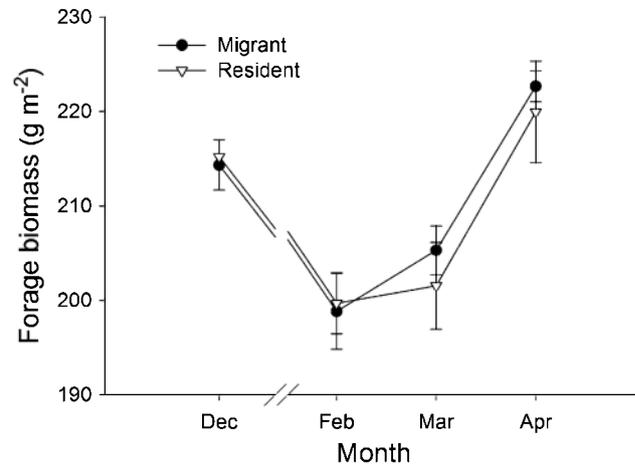
Table 3 Coefficients and standard errors of the variables in the top model (as determined from AIC analysis, Table 2) estimating relative predation risk at 1,500 random locations within areas used by elk on the Ya Ha Tinda winter range

Variable	Description	Coefficient	Standard error
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

All variables are statistically significant ($P < 0.05$)
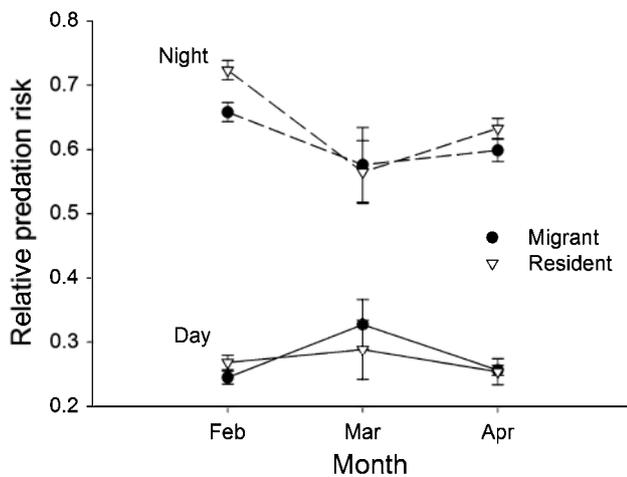
Fig. 4 Mean relative predation risk at migrant ($n = 13$) and resident elk ($n = 7$) telemetry locations collected during the winter of 2004, in relation to time of day and month. *Error bars* ±1 SE

Fig. 6 Mean monthly estimated standing herbaceous biomass at migrant ($n = 13$) and resident elk ($n = 7$) telemetry locations collected during the winter of 2003/2004. *Error bars* ±1 SE

Fig. 5 Mean day and night distances from migrant and resident elk telemetry locations to human activity and timber. *Error bars* ±1 SE

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 ($P < 0.001$; Table 1, Fig. 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 M and any month: $P > 0.331$; Fig. 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 center of the YHT (mean $E = 9,740$ m), then moved further west in February and March (mean $E = 8,538$ m and 9,194 m, respectively), and finally moved to the eastern portion of the YHT in April where biomass was highest (mean $E = 10,486$ 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).

Discussion

This study is among the first to test the common assumption that migrant and resident ungulates from a partially migratory population are exposed to similar conditions when on sympatric ranges (Fryxell et al. 1988; Albon and Langvatn 1992; Kaitala et al. 1993; Ball et al. 2001; Hebblewhite and Merrill 2009). Our findings do not support the hypothesis that elk were spatially segregated during the winter at the scale of the home range or that migrant elk were excluded from productive foraging habitat, but there were differences in exposure to predation risk. At the beginning of winter (October), home-range overlap was low both among and between migrant and resident elk, likely because the 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 with migrants—except in late winter (April). Migrant elk were more closely associated with residents than other migrants, indicating that residents likely formed a stable group, and migrants may have associated themselves with residents independent of each other. Both groups were exposed to equal herbaceous biomass, demonstrating that, unlike partially migratory bird populations (Andriaensen and Dhondt 1990), the resident elk did not exclude migrants from optimal habitats.

Resident elk were exposed to higher overall predation risk than migrants because of fine-scale differences in habitat use in relation to wolf avoidance of humans. Because wolves avoided human activity during the day by remaining far from human dwellings and close to adjacent timber, a predation refuge existed in the center of the grasslands. Resident elk used the predation refuge to a greater extent than migrants during the day and night because they had likely become habituated to humans during the summer when human recreational activity at YHT is high. Unlike residents, migrant elk encounter few humans in the backcountry of BNP where they remain during the summer (Hebblewhite and Merrill 2009) and may be less habituated to humans than residents, explaining why migrants were found further from human activity than residents on average. Higher use of the predation refuge during the day by resident elk than migrant elk did not result in differences in day-time exposure to predation risk because wolves were absent from the grasslands altogether. At night, both residents and migrants moved even closer to human activity and further from timber, but they were unable to avoid night-time exposure to risk because at night wolves moved onto the grasslands far from timbered areas. Residents remained significantly further from the timber than migrants at night, so resident elk experienced higher night-time exposure to predation risk than migrants.

The temporal variations in wolf response to humans observed in this and other studies (Theuerkauf et al. 2003a; Hebblewhite and Merrill 2008) highlights the importance of considering day and night predation risk separately when studying the effects of risk on prey behavior. Although human-caused predation refugia are common (e.g., Ripple and Beschta 2006; Beschta and Ripple 2007; Basille et al. 2009), the use of refugia by predators at night has received less attention (Beyer 2006), despite the fact that studies have reported diurnal variations in risk even in the absence of humans (Fischhoff et al. 2007; Valeix et al. 2009). In predation refugia that receive high human use, such as the town of Banff in BNP, where the human population is 10,000 (McKenzie 2001; Hebblewhite et al. 2005b), predator use of the refuge at night is unlikely. In systems with less human activity, such as the YHT, human-induced predation refugia may be curtailed at night when human activity is lowest. Recent studies of wolf predation risk in North America often neglect to model day and night predation risk separately (e.g., Kittle et al. 2008; Atwood et al. 2009), which will make temporal shifts in predation refugia undetectable. Temporal fluctuations in risk resulting from changing levels of human activity are particularly important when dealing with human-habituated prey. At YHT, although habituation to humans seems to be advantageous during the day, consistent use of the refuge at night may cause elk to be vulnerable because they become a predictable prey source for wolves (Lima and Dill 1990). Because wolves readily use the day-time refuge at night, there may be a 'cost' of resident habituation in the form of higher exposure to predation risk. It is not immediately clear why resident elk do not adjust their night-time distribution to avoid predation risk, but they may have adopted other antipredator behaviors, such as grouping or vigilance (Caro 2005).

Our measure of elk exposure to predation risk was based on wolf intensity of use at elk telemetry locations, which was chosen to reflect the risk of elk encountering wolves and may not equate to the risk of being killed by a wolf (Kauffman et al. 2007). For example, Hebblewhite et al. (2005a) 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 being encountered was lower than in forests. At night, when wolves are actively hunting, their use of habitat is likely driven by elk density (Theuerkauf et al. 2003b), so elk encounters with wolves may be unavoidable. Resident elk might reduce their risk of death by remaining on the grasslands close to humans and far from timber where wolf encounters are likely, but where their chances of actually being killed may be lower than in forested habitats where detection distance may be lower and forest

debris may impede escape (Kunkel and Pletscher 2000; Hebblewhite et al. 2005a). In addition, resident elk were more closely associated with each other than migrants were and may have further reduced risk of mortality by forming a cohesive group (Pulliam 1973; Hebblewhite and Pletscher 2002; Childress and Lung 2003; Caro 2005). A study directly comparing winter predation rates on migrants and residents is necessary to determine how different responses to predation risk affect overall fitness.

Over-winter depletion of forage, which can be as high as 94% at YHT (McInenly 2003), may alter the foraging costs to elk that remain in the predation refuge. If forage consumption is highest in the predation refuge, resident elk may incur foraging costs that we did not document because our forage measures did not account for over-winter utilization. Many studies demonstrate forage within predation refugia is more limited than without (e.g., Creel et al. 2005; Ripple and Beschta 2006; Beschta and Ripple 2007). Forage at YHT may have indeed been depleted within the predation refuge over the winter because the amount of overlap between elk home ranges decreased in April and all elk moved further east where herbaceous biomass was high. Although predation risk also increased in the eastern portion of the YHT because wolf home ranges were centered there, wolf use of forested habitats during the day allowed elk to access forage while maintaining relatively low exposure to predation risk even during late winter. If the proportion of residents within the YHT population continues to increase and resident elk remain within the human-caused predation refuge year-round, forage at the center of the grasslands will be depleted earlier in the winter. Early over-winter depletion of forage may force elk out of the predation refuge earlier than observed in this study, possibly creating the need to trade-off forage and predation risk.

In the absence of human-caused predation refugia, the benefits of migrating to obtain superior food resources or reduce predation risk (Fryxell et al. 1988; Albon and Langvatn 1992) likely outweigh the benefits of being sedentary. When non-migratory animals are able to avoid predation risk year-round by foraging within a predation refuge, migratory behavior may diminish and ultimately result in the loss of migratory behavior altogether (Berger 2004). Within partially migratory populations, residents may become more habituated to humans than migrants, allowing residents to exploit human-caused refugia more readily. 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.

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