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Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network

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Abstract. Migrations of large ungulates are globally threatened in environments affected by increasing human disturbance, rising large carnivore predation, deteriorating habitat quality, and changing climate. Animals migrating outside of protected areas can be exposed to greater human pressure, and this effect can be stronger when humans are perceived to be a predation risk, such as during hunting seasons. Using four consecutive years of satellite telemetry data (n = 138 migration events), we compared habitat selection, movement, and behavior of a large partially migratory herbivore while migrating through a heterogeneous landscape in spring and fall. We tested the hypothesis that fall hunting exacerbates the response of a large herbivore exposed to human disturbance while migrating through a road network. All elk (*Cervus elaphus*) selected greater forest cover, reduced movement rates, and avoided roads during fall-day than in any other season or time of day. Avoidance of roads was reduced during spring at night, for example, the time period of no hunting with fewest people on roads. Elk using stopovers in fall displayed different seasonal and diurnal behaviors between sexes in response to the disturbance. Females used steeper terrain during fall-day and males did not use this strategy in fall. Male avoidance of roads was much stronger than females during fall-day and males were less likely to cross a road during fall. Such responses are probably linked to higher hunting pressure on males vs. females. Finally, we found that elk spent more time feeding during spring migration compared to the fall migration and elk vigilance was >3 times higher in the fall hunting season. Our results provide insights into the effect of fear of humans on the ecology of both sexes of a migrating large herbivore when using stopovers. Such changes in behavior and stopover use might affect animal fitness by decreasing foraging, cause displacement from high-quality habitats, or affect the permeability of migration route stopovers.

Key words: *Cervus elaphus;* elk; hunting; migration; permeability; predation risk; radiotelemetry; resource selection functions; stopover; vehicle traffic; vigilance.

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INTRODUCTION

Migratory species can be important drivers of ecosystem processes (McNaughton 1994, Augustine and McNaughton 1998, Milner-Gulland et al. 2011), provide economic and social values to humans (Vors and Boyce 2009), and can serve as flagship species for conservation (Thirgood et al. 2004). There is growing concern over declines of large ungulate migration on several continents due to human developments and disturbance (Berger 2004, Ito et al. 2006, Bolger et al. 2008, Festa-Bianchet et al. 2011). To conserve migration, researchers have begun to investigate the effects of habitat loss, human disturbance (Hebblewhite et al. 2006, Voeten et al. 2010), and climate change (Walther et al. 2002, Monteith et al. 2011) on migratory behavior.

Several recent studies have investigated the disruption to migratory behavior (Bolger et al. 2008, Holdo et al. 2011, Lendrum et al. 2012) and the primary mechanisms of animal migration (Mysterud et al. 2001, Hebblewhite and Merrill 2007, Voeten et al. 2010, Milner-Gulland et al. 2011). These combined stressors can result in negative cumulative impacts to migrating animals by creating impermeable or semi-permeable movement barriers, reduced use of migration routes, or increased movement rates (Sawyer et al. 2013), which ultimately might result in population effects (Leblond et al. 2013, Middleton et al. 2013*a*). When animals migrate, they must balance access to essential resources with exposure to risk from predation and anthropogenic disturbances (Fryxell 1991). In areas of increasing human disturbance, it is a conservation challenge to provide suitable landscape conservation and management strategies for migratory populations (Bolger et al. 2008). One of these challenges is a shortage of research regarding key elements of herbivore behavioral responses to human disturbance (Alerstam 2006, Morales et al. 2010). Our research contributes insights into how human disturbance outside of protected areas can affect ungulate behavior during migration.

Some of the most widespread modifications of the natural landscape have been from the construction and maintenance of roads (Forman 2003, Beckmann et al. 2012). On the one hand, large herbivores in national parks often seem undisturbed by roads, habituated to traffic and people, and attracted by roadside vegetation and the protection from predators in areas near roads and human settlements (Rogala et al. 2011, Goldberg et al. 2014). Protected areas, however, are only a small fraction of wildlife habitat worldwide, and for ungulate populations outside parks, particularly those in regions facing hunting pressure, roads and high-traffic volumes have been shown to alter animal spatial behavior and distribution (Rowland et al. 2000, Frair et al. 2008, Bonnot et al. 2013). Hunting and other sources of human disturbance can cause large herbivores to respond to human-caused stimuli such as approaching vehicles as if these stimuli were predatory threats, causing animals to exhibit risk avoidance behaviors (Remis and Kpanou 2011, Ciuti et al. 2012*b*, Barnier et al. 2014). Hunting can be a significant contributor to the cumulative predation pressure on prey in multicarnivore ecosystems, indirectly affecting both prey and carnivore movement and behavior (Valeix et al. 2012, Schmidt and Kuijper 2015) and possibly compromising fitness (Hernández and Laundré 2005, Creel et al. 2007, Christianson and Creel 2010—but see White et al. 2011, Middleton et al. 2013*a*, *b*). Such human-driven risk effects on prey might be at least as significant as effects of large carnivores (Creel and Christianson 2008), including changes in habitat use (Hebblewhite et al. 2006, Lone et al. 2015), foraging behavior, group size, and physiology (Caro 2005). Many have studied indirect antipredator risks associated with human hunting, which occurs in numerous regions throughout the world (Proffitt et al. 2009, Ciuti et al. 2012*a*, *b*, Barnier et al. 2014, Lone et al. 2014). None, however, have investigated these risks during animal migration. Our study provides empirical data into how human disturbance affects the spatial and behavioral ecology of migrating ungulates.

We analyzed a unique dataset that combines habitat selection and movement rates of radio-tracked elk migrating through an intensively used road network, data on vehicle traffic on these roads, and elk behavioral observations to test the effect of human disturbance on elk behavior during migration. This partially migrating population of elk travels from winter to summer ranges in spring, when hunting is not permitted, and from summer to winter ranges in fall, when hunting is allowed (Ciuti et al. 2012*a*). We compared male and female elk movements, habitat selection, and their behavior during fall/spring seasons, and day/night time periods, with hunting or no hunting activity, representing numerous or few humans, respectively. Our study provided a unique opportunity to investigate the effect of human disturbance on elk behavior when humans compose a real threat compared to when they are not. We evaluated the hypothesis that hunting intensifies the response to human disturbance by this large herbivore while migrating through a road network in an unprotected area. We predicted that when elk migrate during fall hunting season, they would adopt more cautious behavior. We also predicted that behavioral responses to humans would be stronger during the day, when humans are actually present on roads, compared to night, when human presence in the area is significantly lower.

METHODS

Animal care and compliance

Our data collection complied with all relevant federal laws of Canada and provincial laws of Alberta. Procedures adopted in this study were reviewed and approved by the University of Alberta Animal Care and Use Committee—Biosciences (Animal care protocol no. 536-1003 AR University of Alberta, Edmonton, Canada), by all jurisdictions of the Alberta Government (Permit Numbers: BI-2008-19, RC-06SW-001, and 23181CN), and by Parks Canada (Permit Numbers: WL-2010-7292, WL-2010-5755).

Study site and elk population

Our study occurred during four consecutive years (2007–2010) within a montane ecosystem along the eastern slopes of the Rocky Mountains in southwest Alberta, Canada. This is a diverse landscape, ranging from flat agricultural grasslands in the east, to mixed conifer/deciduous forests and mountains in the west. Based on location of winter ranges, spatial distribution of migratory corridors, and summer range locations, elk sub-populations are commonly identified as "herds" by local managers (Paton 2012). Seven main herds are known and have been monitored in this region by our large-scale telemetry program (Ciuti et al. 2012*a*, Paton 2012). Here, we focused on the Castle-Carbondale herd, that is, a herd that we monitored intensively from 2007 to 2010 and for which we gathered detailed information about human use and vehicle traffic on roads (Ciuti et al. 2012*b*).

The annual home range of the Castle-Carbondale herd of southwest Alberta is an area under multiple jurisdictions administered by the provinces of Alberta and British Columbia. The winter range includes both private and provincial (i.e., public) land of Alberta, whereas migratory corridors and summer home ranges are on provincial lands in Alberta and to a lesser extent in British Columbia. Cattle ranching constituted the dominant land use on private land. Activities in the public land also included cattle grazing and natural gas extraction as well as recreational use including camping, all-terrain vehicle (ATV) use, hunting, fishing, and hiking (Ciuti et al. 2012*b*).

Elk in this region have experienced decades of disturbance by timber harvesting, natural gas extraction, cattle grazing, off-highway vehicle use, and hunting. However, during the last decade, there has been increasing human disturbance from recreational activities and resource extraction resulting in an increase in infrastructure, human activity, road density, and traffic volume on roads. Road densities in the Castle-Carbondale are at levels known to affect elk movements (0.55 km/km^2; Rowland et al. 2000, Frair et al. 2008). In the Castle-Carbondale, predation risk is from a variety of carnivores including grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Puma concolor*), wolves (*Canis lupus*), lynx (*Lynx canadensis*), and coyotes (*Canis latrans*). Cougars and wolves in this area are responsible of preying upon approximately 5% of the elk (figure estimated by collecting data on mortality causes in 182 radiocollared animals monitored by the montane elk research program in this area, http://montaneelk.com/), mostly during winter. Grizzly bears and black bears also pose a predation risk, especially to calves during spring (Griffin et al. 2011). For an overview on predator distribution and predator pressure on elk, see previous research conducted in the study area (Morehouse and Boyce 2011, Muhly 2011, Muhly et al. 2011). However, human hunting is the largest source of elk mortality in this region (Ciuti et al. 2012*a*, Paton 2012). Roughly 50% of males but <20% of females were shot in our long-term monitoring program, the former being more heavily targeted than the latter (Ciuti et al. 2012*a*). The 110-d male elk-hunting season (archery and rifle, early September until December) is controlled by hunting regulations, with few access restrictions to the public land where elk migratory corridors are located. Hunting of female elk occurs for 51 d with harvest managed by lottery for a limited number of permits.

Vehicle traffic data

We deployed 52 traffic counters (Diamond Traffic Products; Apollo, Oakridge, Oregon, USA) randomly distributed on trails and a variety of road types (i.e., paved roads, gravel roads, unimproved roads, truck trails, and ATV trails). Moreover, 21 trail cameras (Silent Image RM30; RECONYX, Creekside, Wisconsin, USA) were deployed at randomly selected locations on roads and trails. Trail cameras provided time-stamped photographs of motorized use that triggered the camera's infrared sensor. Using both traffic counter and trail-camera data, Northrup et al. (2012)

and Ciuti et al. (2012*b*) modeled traffic volume for the entire road network in our study site. We obtained estimates of traffic volumes for spring and fall migration, during the day and night. According to Ciuti et al. (2012*b*), nighttime was calculated on a monthly basis and was the time between the average sunset and average sunrise for each month. Likewise, daytime was the time between the average sunrise and average sunset. Based on trail-camera data, 95% of motorized traffic recorded within public lands, that is, where migratory corridors were located, was related to recreational activities (cars, trucks, Recreational Vehicles: 80%; ATVs such as quads and motorbikes: 15%), whereas only 5% was linked to industrial activities (ranching and natural gas extraction).

Elk captures and collection of GPS fixes

We used a helicopter and net-gun to capture 50 Castle-Carbondale elk during winter. Males ($n = 12$) were 1½-year-old at captures, whereas female ($n = 38$) aged 1–18-year-old (Ciuti et al. 2012*a*). Elk were blindfolded and hobbled to allow collaring and sampling with low impact to the elk. Female elk were equipped with 4400M GPS (Lotek, Newmark, Ontario, Canada) and GEN4-GPS (Telonics, Mesa, Arizona, USA) collars, whereas males were fitted with 4400 GPS/Argos collars (Lotek). GPS units were programmed to obtain location fixes every two hours. Female relocations were remotely downloaded in the field, whereas male data were received via email through the ARGOS system. All radiocollars were outfitted with a remote drop-off device programmed to disengage after 104 weeks. If the device failed, elk were recaptured by helicopter using a net-gun to retrieve the collars. All of the 50 radiocollars deployed to monitor the Castle-Carbondale elk were successfully retrieved.

Analysis of habitat selection by elk during migration

All data management and analyses were done using R (R Core Team 2015). During 2007–2010, we obtained 31,332 GPS fixes from the 50 migratory elk ($n = 12$ males and $n = 38$ females) traveling along migratory corridors (excluded summer and winter ranges) on public land. We eventually analyzed 138 migration events (73 spring and 65 fall, of which 111 were from females and 27 were from males). Spring-migration sample sizes were higher than fall migration because animal numbers were reduced by fall hunting. We used a Brownian bridge movement model (BBMM; Horne et al. 2007) to estimate individual elk utilization distribution for each seasonal migration. A sequence pathway of two-hour radiocollar GPS relocation data was collected between winter and summer home ranges during each spring and fall migration (Sawyer et al. 2009) to produce a BBMM graphic of stopovers for each elk.

Using the BBMMs, we were able to isolate stopover sites from steps taken to move from a stopover site to another. However, our data differed from, for example, mule deer migration and stopover use in Wyoming (Sawyer et al. 2009), which is characterized by stopover sites connected by long-distance movement paths. The Castle-Carbondale elk migration is a relatively slow process (20 d, on average), and the distance between elk stopovers was relatively short (<4 km distant from one location to the next one, on average) with 99% of relocations clustered in stopovers. During our study, the two-hour GPS telemetry relocation schedule was not able to capture a sufficient sample size for analyses of step-by-step movements connecting two consecutive stopover sites. Therefore, we primarily describe habitat selection within stopovers, that is, resting/feeding hotspots along the migratory corridors.

We estimated fine-scale resource selection functions (RSFs) for individual elk (Manly et al. 2002). We matched relocations (used) with random points within a 660 m radius buffer (matched-pair or conditional logistic regression approach; Duchesne et al. 2010). This allowed us to consider true available habitats for elk migrating along migratory corridors. Each observed location was paired with 10 random locations within the 660 m radius circle (a distance >90% of observed distances traveled between two-hour relocations). Based on the spatial location, elk used and random points were associated with a set of environmental predictors: canopy cover (*cc*, percentage), aspect (*aspect*, cos-transformed), terrain ruggedness (*r*, in meters sensu (Riley et al. 1999), distance to the closest road (*d*, in m), traffic on the closest road (tr, vehicle/h). We screened covariates for collinearity using the Pearson correlation coefficient, and for multicollinearity using the variance inflate factor ($|r_p| < 0.7$; VIF $\ll 3$).

We generated a set of a priori resource selection models established on biological assumptions (Table 1, two-first columns from left). Based on exploratory analyses and screening for non-linear relationships, we allowed for quadratic effects in canopy cover and ruggedness. For each individual, the resource selection model was fit using conditional logistic regression (binary response variable: 0 = available, 1 = used) using the survival package (Therneau and Grambsch 2000). Models were fit during spring (day, night) and fall (day, night). Using Akaike's information criterion (AIC), we selected the top-ranked model for each individual. Once we obtained parameter estimates for each individual conditional logistic regression, we averaged parameters for males and females separately to make inference on selection patterns at the population level (Fieberg et al. 2010). Some of the individual models did not include one or more parameter estimate, because excluded by model selection, and thus contributed with $\beta = 0$ to the mean. Following these procedures, we obtained averaged male and female beta (β) coefficients to estimate the final RSFs (Manly et al. 2002). In the parametric case, a RSF is an exponential function given samples of used and available resource units of the form

$$\mathrm{RSF} = w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 \cdots + \beta_n x_n)$$

which corresponds to the frequency of used resource units divided by the frequency of available resource units for any environmental covariate, x_i.

Analysis of movement and behavioral data of elk during migration

Step length (i.e., distance between two-hour telemetry relocations) is a proxy of elk mobility (Ciuti et al. 2012*a*). We derived step length using ARCMAP (ESRI, Redlands, California, USA) combined with GME (http://www.spatialecology.com/gme/) and R (R Core Team 2015), and we used these data to model movement rate during spring and fall migration. We modeled the variation in step lengths (log-transformed, in meters) by fitting a linear mixed model (lme4 package, Bates et al. 2015) with individual elk as random intercept. We fitted the following predictors as fixed effects and interactions terms: sex (males, females), season (spring, fall), time period (day, night), terrain ruggedness (including quadratic effect), canopy cover (including quadratic effect), distance to the closest road (log-transformed, including quadratic effect), traffic on the

Table 1. A priori model structures used to model male (M, n = 12) and female (F, n = 38) elk individual-level resource selection during spring (daytime, nighttime) and fall (daytime, nighttime) migrations.

		Spring day (%)		Spring night (%)		Fall-day (%)		Fall-night (%)	
Candidate model name	Candidate model structure	F	M	F	M	F	M	F	M
mainly environment	$\mathrm{cc} + \mathrm{cc}^2 + \mathrm{aspect}$	0	8	0	0	3	0	3	12
mainly antipredator	$r + r^2 + \mathrm{cc} + \mathrm{cc}^2$	38	33	35	33	16	12	27	13
humans only (1)	d	5	0	3	8	8	0	0	0
humans only (2)	$d + \mathrm{tr}$	0	0	0	0	0	0	3	0
environment and humans (1)	$\mathrm{cc} + \mathrm{cc}^2 + \mathrm{aspect} + d$	0	0	5	0	5	0	13	0
environment and humans (2)	$\mathrm{cc} + \mathrm{cc}^2 + \mathrm{aspect} + d + \mathrm{tr}$	0	8	0	0	3	0	5	12
antipredator and humans (1)	$r + r^2 + \mathrm{cc} + \mathrm{cc}^2 + d$	24	18	11	25	32	25	16	38
antipredator and humans (2)	$r + r^2 + \mathrm{cc} + \mathrm{cc}^2 + d + \mathrm{tr}$	17	25	21	17	19	25	23	25
environment, antipredator, and humans (1)	$r + r^2 + \mathrm{cc} + \mathrm{cc}^2 + \mathrm{aspect} + d$	11	8	17	17	11	38	5	0
environment, antipredator, and humans (2)	$r + r^2 + \mathrm{cc} + \mathrm{cc}^2 + \mathrm{aspect} + d + \mathrm{tr}$	5	0	8	0	3	0	5	0
"no humans" directly involved	***d* and/or tr not included in the model**	**38**	**41**	**35**	**33**	**19**	**12**	**30**	**25**
"humans" involved	***d* and/or tr included in the model**	**62**	**59**	**65**	**67**	**81**	**88**	**70**	**75**

Notes: Figures represent the percentages of a priori structures selected as top-ranked models (using the Akaike's Information Criterion) in elk individual modeling. Bold lines summarize the percentages of selected model structures that included or did not include road-related predictors, respectively. cc, canopy cover (%); cc^2, quadratic effect for canopy cover (%); aspect, aspect (cos-transformed); r, terrain ruggedness (m); r^2, quadratic effect for terrain ruggedness (m); d, distance from the closest road (m); tr, traffic on the closest road (vehicle/h).

closest road (log-transformed, including quadratic effect), the three-way interaction time period × season × sex, and related two-way interactions. All numerical predictors were scaled prior to fitting the model [$(x - \text{mean})/\text{standard deviation}$] to achieve model stability and convergence in the mixed modeling (which also applies to the mixed model described below).

The likelihood or road crossing was modeled by fitting a generalized linear mixed-effect model (binomial distribution of error; binary response variable: 1 = step walked by elk every two hours crossing a road, and 0 = step not crossing a road) with individual elk as random intercept. We fitted the following as fixed effects and interaction terms: sex (males, females), season (spring, fall), time period (day, night), terrain ruggedness (including quadratic effect), canopy cover (including quadratic effect), traffic on the closest road (log-transformed, including quadratic effect), the three-way interaction time period × season × sex, and related two-way interactions.

Elk behavioral observations were carried out during a more comprehensive field study carried out across herds in southwest Alberta (Ciuti et al. 2012*b*). During spring and fall migration, elk observations were carried out at dawn and dusk using binoculars (10 × 50) and spotting scopes (25–40 × 60) to observe elk within open areas of the Castle-Carbondale area. Observations were performed by the same two observers from roads without leaving the vehicle at a distance always >500 m. We recorded date, time, location, group size, and sex and age class composition for each group observed within the Castle-Carbondale herd. We collected data on female-dominated herds only (i.e., males <50%; Childress and Lung 2003). The position of each group was assessed with the combined use of a GPS (eTrex Legend; Garmin International, Olathe, Kansas, USA), a compass, and a rangefinder (Elite 1600 ARC; Bushnell, Overland Park, Kansas, USA). We divided elk into four age–sex classes (adult females with calf, adult females without calf, male and female yearling). Individual vigilance in randomly selected elk was estimated by a focal animal sampling rule and a continuous recording rule (Martin et al. 1993). To avoid observation of the same individual elk more than once, only one to four individuals were observed in each group. Each focal individual was observed for 15 min, until they were no longer visible, or they began to rest, whichever came first. Behavioral states (feeding, vigilance, traveling, grooming, and aggression) were recorded using a voice recorder (Ciuti et al. 2012*b*). We calculated vigilance rate (vigilance bouts/min), the proportion of time being vigilant (time vigilance/time active), the proportion of time traveling (time traveling/total time), and the proportion of time feeding (time feeding/total time active, i.e., foraging efficiency) for each individual. Data used in this study are a subsample from our previous research (Ciuti et al. 2012*b*) and represent 154 focal individuals (n = 59 adult females without calf, n = 40 adult females with calf, n = 25 yearling males, and n = 30 yearling females).

Our observations were designed to record vigilance behavior, that is, elk standing with the head at or above the shoulder level while looking for potential threats. Given the distance between observers and focal elk, we cannot exclude that part of the vigilance behavior might have been spent in chewing activities, enabling the elk to optimize the time budget by combining antipredator behavior with feeding-related activity. However, the vigilance bouts recorded for our sample population were always longer than a simple scanning event of the landscape, suggesting an actual loss of opportunities for feeding activities. Indeed, mean length of vigilance bouts was 89.4 s (standard error [SE] = 7.3 s), much longer than the time that would be needed (e.g., few seconds) by the animal to chew the grass and scan the landscape prior to taking a new food bite.

We tested for differences in the four behavioral metrics (vigilance rate; the proportion of time being vigilant, arcsin-square-root-transformed; the proportion of time traveling, arcsin-square-root-transformed; and the proportion of time feeding, arcsin-square-root-transformed) by fitting four linear models with season (spring, fall), herd size, and age–sex class (four levels) as predictors.

RESULTS

Elk migratory patterns

We analyzed 138 migration events (73 spring and 65 fall) in 50 elk (n = 12 males and n = 38 females, Table 2). Pooled data from all years resulted in a mean duration for migration of roughly 3 weeks in both spring and fall, although there was high individual variability (Table 2).

Table 2. Characteristics of the migratory behavior in 50 elk (38 females, 12 males) monitored with satellite telemetry from 2007 to 2010 in the Castle-Carbondale region, southwest Alberta.

Season	Migration length† (days)	Walked distance‡ (km)	Linear displacement§ (km)	Number of stopovers¶	Sojourn linear distance†† (km)
Fall	21.3 ± 2.0 (1–68)	60.1 ± 4.4 (11–163)	18.0 ± 0.7 (5–32)	7.2 ± 0.4 (1–17)	3.6 ± 0.4 (0.4–21.3)
Spring	19.7 ± 1.5 (2–65)	72.5 ± 4.7 (9–252)	20.0 ± 0.7 (6–34)	7.7 ± 0.4 (2–17)	3.4 ± 0.3 (0.7–13.3)

Notes: Mean ± standard error are shown along with range of variability within parentheses (minimum–maximum). Fall migrations started on average on 1st November (range: 23rd August–15th December) and ended on 19th November (4th September–1st January). Spring migrations started on average on 3rd May (19th March–17th June) and ended on 23rd May (2nd April–29th June).

† Defined as the time (in days) occurring between the first and the last satellite relocations recorded along the migration corridor, thus excluding relocations inside the winter and the summer ranges.

‡ Defined as the sum of the linear distances connecting consecutive satellite relocations recorded along the migratory corridor.

§ Defined as the linear distance between the first and the last relocations recorded along the migratory corridor.

¶ Identified by fitting Brownian bridge movement models on satellite relocations during migration.

†† Defined as the distance between two successive stopover sites.

High among-individual variability in migration duration was likely linked to high variability in the distance between individual winter and summer ranges (walked distance ranging from 9 to 252 km; linear displacement ranging from 5 to 34 km, Table 2). Likewise, the number of stopovers ranged from 1, for the shortest migration, to 17 for longer migrations. Distance between stopover sites was roughly 3.5 km on average both in spring and in fall (Table 2).

Habitat selection by elk during migration

We fitted individual conditional logistic regression models for spring (day, night) and fall (day, night) migrations, which we have reported in full as supplementary information (Appendix S1: R outputs S1–S4). Percentages of a priori model structures selected as top-ranked are presented (sensu AIC) in Table 1, showing a large among-individual variation in which model was supported. Antipredator-only models prevailed in spring, whereas models including human-related disturbance covariates (i.e., distance to and traffic on roads) prevailed in the fall (Table 1), with strikingly similar patterns between males and females (Table 1). The highest number of models including human disturbance predictors was selected during day period for the fall migration.

Parameter estimates for male and female elk were obtained by averaging individual modeling estimates (reported in Appendix S2: Table S1), which we used in RSFs (depicted in Figs. 1–5).

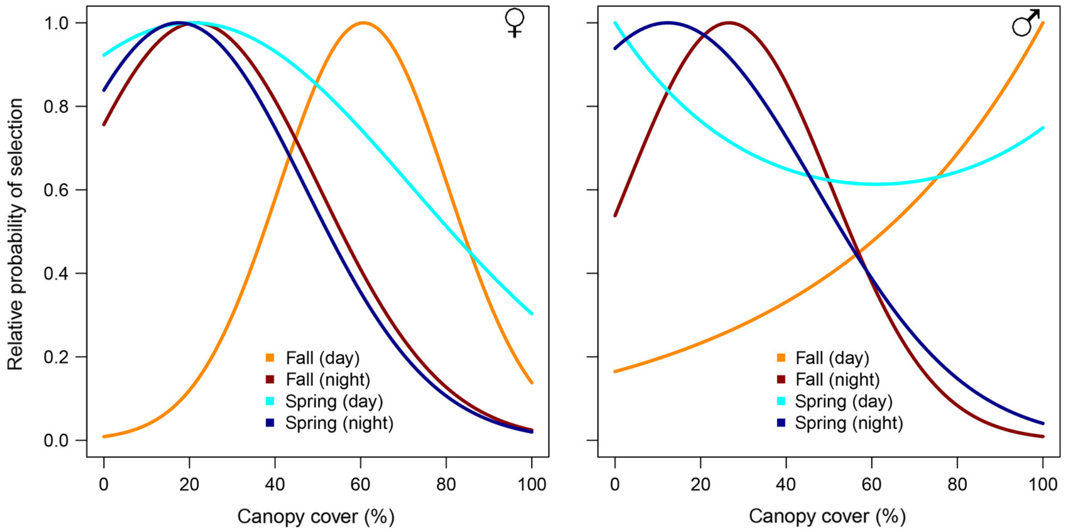

Fig. 1. Relative probability of selection for canopy cover (in percentage) by female and male elk during fall (daytime, nighttime) and spring (daytime, nighttime) migration, as predicted by resource selection functions.

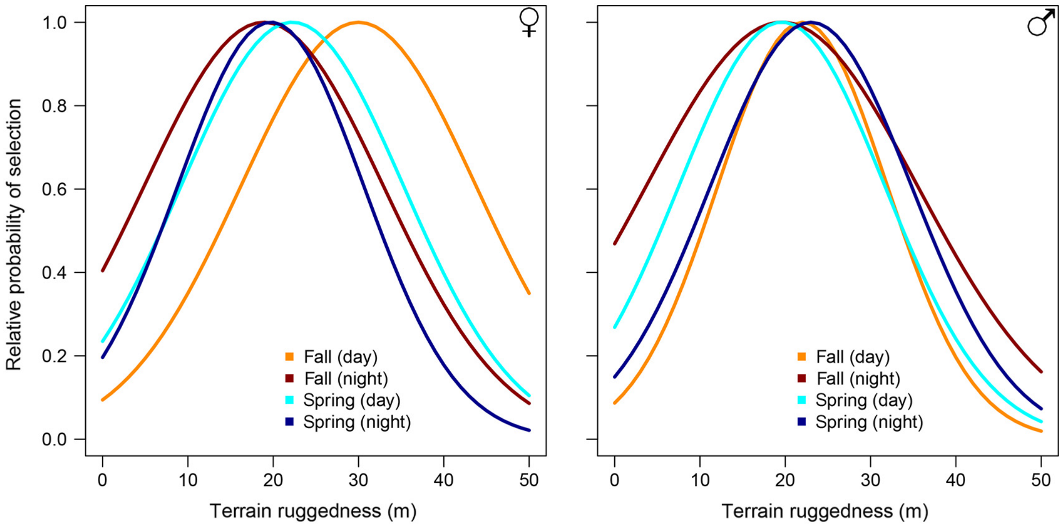

Fig. 2. Relative probability of selection for terrain ruggedness (in meters) by female and male elk during fall (daytime, nighttime) and spring (daytime, nighttime) migration, as predicted by resource selection functions.

Inter-individual variability in parameter estimates was reported in full as supplementary information (Appendix S3: Figs. S1–S7).

Both sexes selected for more forest cover (Fig. 1), females (but not males) selected for steeper terrain (Fig. 2), and both sexes (especially males) avoided roads (Fig. 3) to a greater extent during fall-day than any other season/time of the day. Both sexes avoided roads irrespective of traffic during spring and fall, during the day (with males showing the highest degree of avoidance during daytime in fall), and during the fall at night (females: Fig. 4; males: Fig. 5). However, avoidance of roads was reduced in spring at night by females (Fig. 4), when males actually showed the strongest selection for roads (Fig. 5). During spring nighttime, elk of both sexes were more likely to select for open areas (sensu Fig. 1) along primary roads with

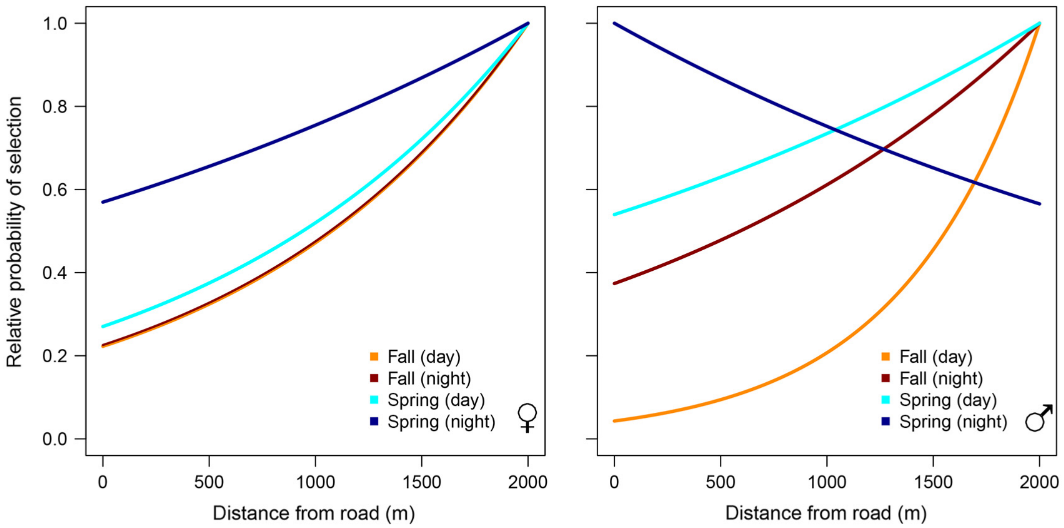

Fig. 3. Relative probability of selection for distance to roads (in meters) by female and male elk during fall (daytime, nighttime) and spring (daytime, nighttime) migration, as predicted by resource selection functions.

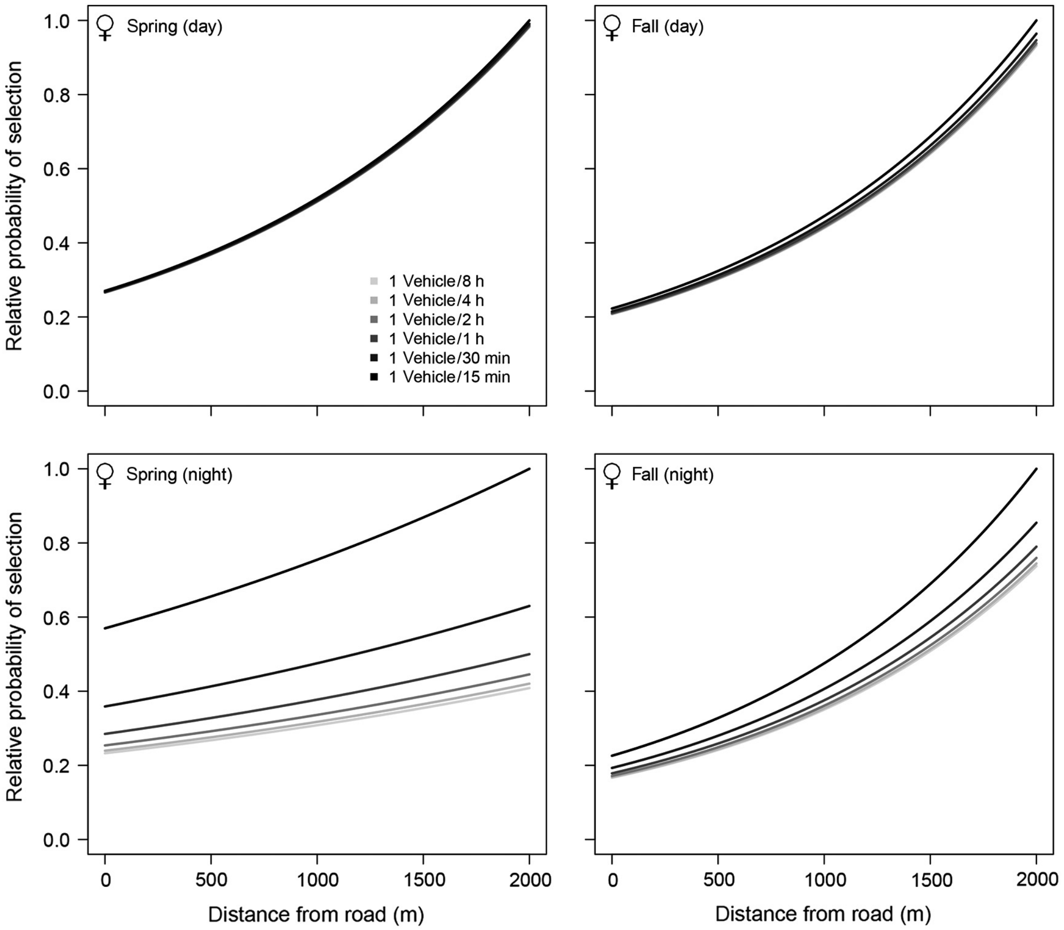

Fig. 4. Relative probability of selection for distance to roads (in meters) by female elk during spring (daytime, nighttime) and fall (daytime, nighttime) migration, as predicted by resource selection functions. Predictions were depicted for different vehicle traffic intensities on the closest road (six scenarios, ranging from 1 vehicle every 15 min to 1 vehicle every 8 h).

high-traffic (1 vehicle/15 min) rather than along secondary forest roads (1 vehicle/8 h, Figs. 4, 5 for females and males, respectively).

Elk movement rate and vigilance behavior during migration

During spring migration, we found that elk of both sexes had a significantly faster movement rate (m/2 h) during the day than during the night (Fig. 6; linear mixed-effect model, Appendix S2: Table S2). This was not true during fall migration, when elk significantly decreased their day movement rate to the level of that recorded at night (Fig. 6; linear mixed-effect model; Appendix S2: Table S2). Elk traveled longer distances in the daytime during the spring migration, whereas daily movement was more cautious during fall migration.

The likelihood of road crossing by male or female elk was significantly lower in the fall than in the spring (Fig. 7; generalized linear mixed-effect model; Appendix S2: Table S3), being the day-fall the period of the year when the lowest probability for an elk to cross a road was recorded. Road crossing was more likely in roads with lower traffic volumes (Fig. 8), with the greatest avoidance of roads depending on traffic recorded in the fall (Fig. 8).

We report results of elk direct behavioral observations (Fig. 9) carried out during daytime within open areas along the migratory corridors

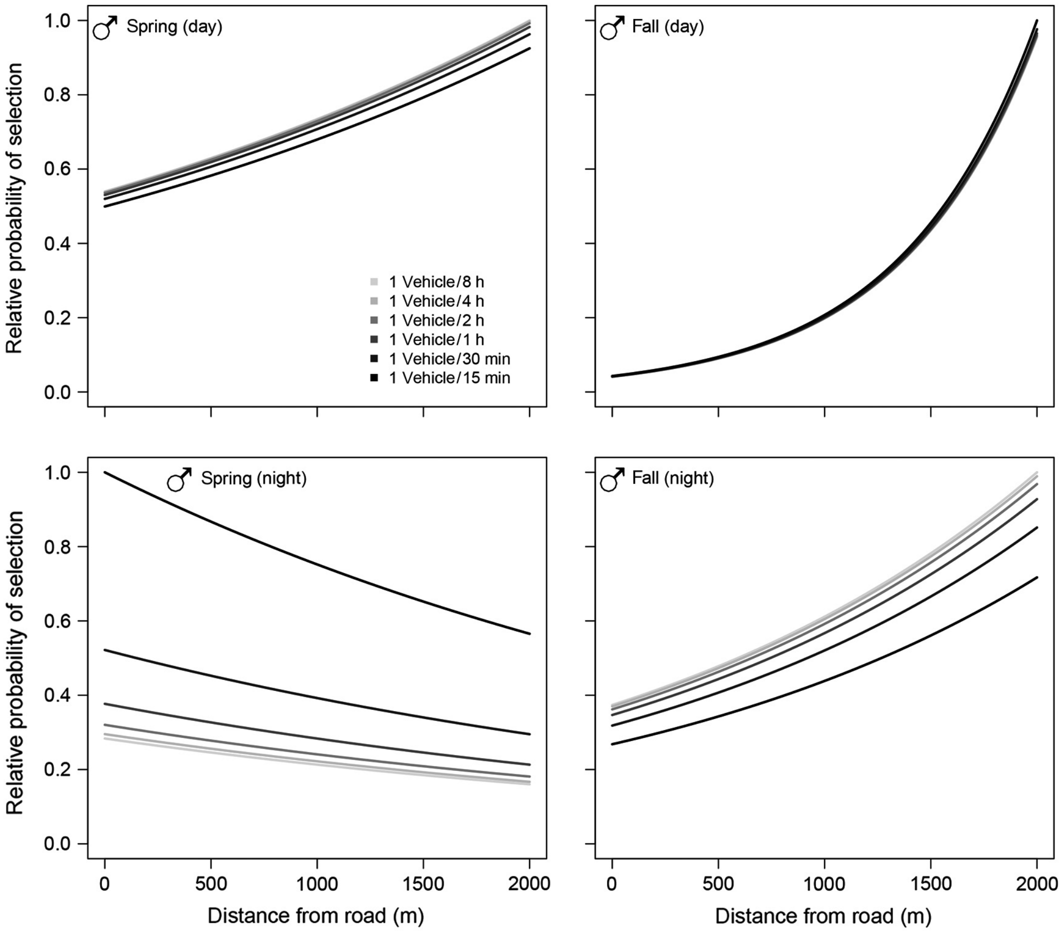

Fig. 5. Relative probability of selection for distance to roads (in meters) by male elk during spring (daytime, nighttime) and fall (daytime, nighttime) migration, as predicted by resource selection functions. Predictions were depicted for different vehicle traffic intensities on the closest road (six scenarios, ranging from 1 vehicle every 15 min to 1 vehicle every 8 h).

(observations on 154 randomly selected individuals). We found that animals spent more time feeding during spring migration than in the fall migration (Fig 8a; linear model, effect of season: $\beta = 0.199$, SE = 0.068, $t = 13.409$, $P < 0.001$, with fall being the reference level), whereas elk were more vigilant in fall compared to spring (Fig. 9b, effect of season: $\beta = -0.125$, SE = 0.046, $t = -2.689$, $P = 0.008$). When located in an open area, elk spent more time traveling during the fall migration compared to spring migration (Fig. 9c, effect of season: $\beta = -0.177$, SE = 0.054, $t = -3.248$, $P = 0.001$), with the end result that elk were less likely to persist within open areas when hunting was allowed. We found that vigilance rate was >3 times higher in the fall compared to spring (Fig. 9d, effect of season, $\beta = -0.590$, SE = 0.097, $t = -6.026$, $P < 0.001$). All linear models included herd size as a confounding factor ($P < 0.05$), as well as age–sex classes ($P > 0.05$).

DISCUSSION

Throughout spring and fall, humans use the landscape, but when fall hunting is associated with human presence, disruption of elk behavior during migration increases. Few studies have presented such a detailed analysis and quantification of the behavioral modifications occurring

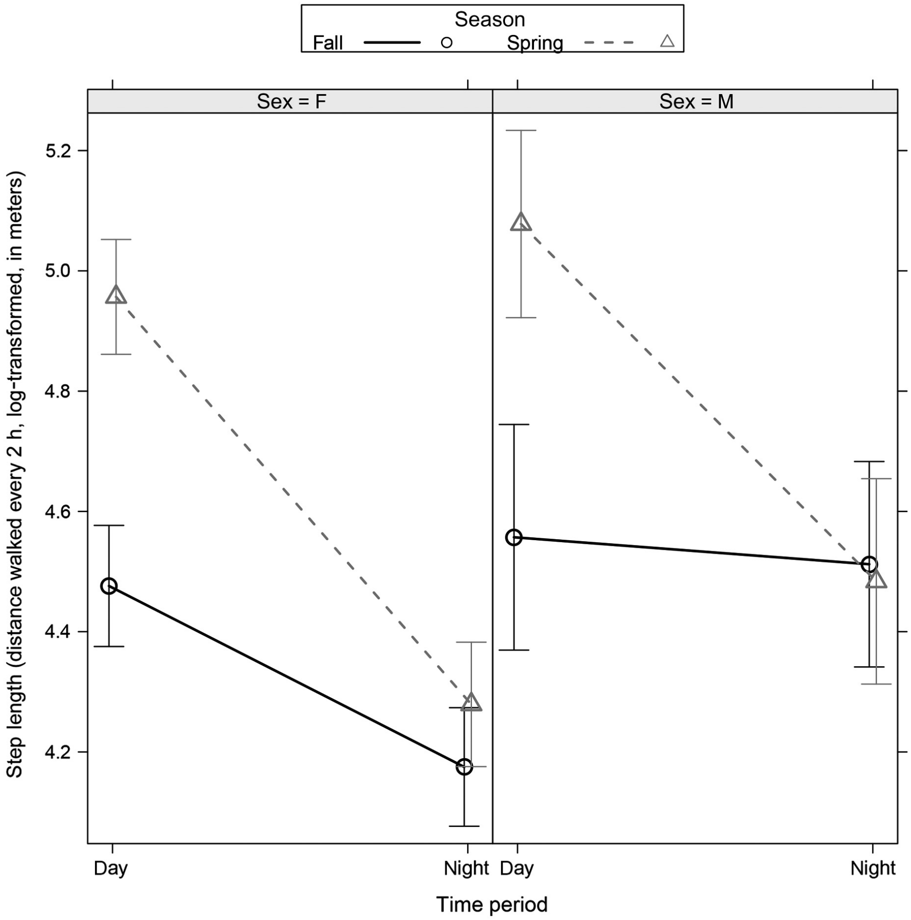

Fig. 6. Step lengths (distance walked every two hours, in meters, log-transformed) predicted by the linear mixed-effect model for female and male elk during fall (daytime, nighttime) and spring (daytime, nighttime) migration. Error bars are marginal 95% confidence intervals.

in a large herbivore during its migration. Our results identify the mechanisms and the related elk behavioral response by which fall hunting (compared to spring) affects ungulates using migration stopovers, that is, (1) increased selection for safer habitats; (2) reduced selection for areas close to roads depending on their vehicle traffic, reduced likelihood of road crossing, and landscape permeability; (3) overall decreased daily movement rates; (4) decreased time within open areas to avoid predation risk, decreased time foraging, and increased vigilance. Results of this study are important for the conservation of mammals that undertake partial migration in jurisdictions where hunting occurs. Conserving suitable landscapes for migratory ungulate populations in areas of increasing human disturbance is a challenging conservation issue in North America (Bolger et al. 2008). Understanding mechanisms affecting migration is critical for avoiding human disturbances from blocking or reducing permeability of migration routes (Sawyer et al. 2012, Benz et al. 2016). The lack of stopover permeability (e.g., reduced likelihood of crossing the road network) could reduce the benefits of migration, and influence the ability of species to modify range due to climate change (Minor and Urban 2008). Low permeability might affect the degree to which migratory individuals would be required to or able to alter their traditional migratory paths and effect the rate of migration to seasonal ranges (Lendrum et al.

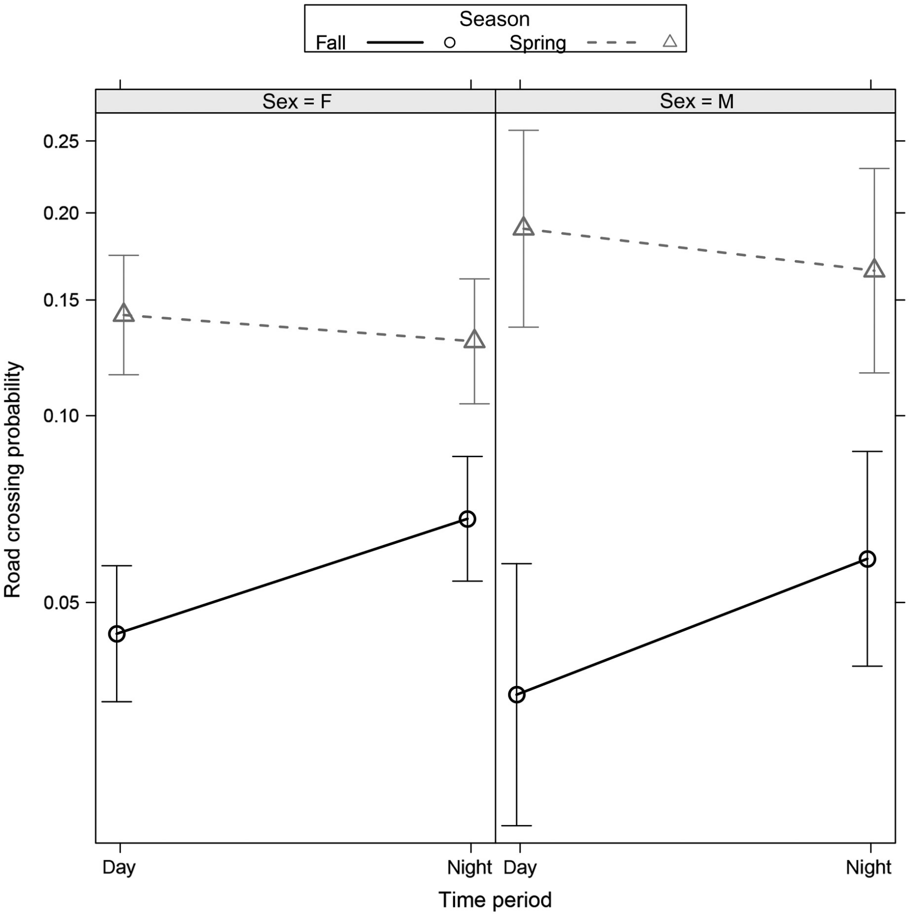

Fig. 7. Likelihood of road crossing predicted by the generalized linear mixed-effect model for female and male elk during fall (daytime, nighttime) and spring (daytime, nighttime) migration. Error bars are marginal 95% confidence intervals.

2012). Disruption of stopovers during migration has potential to be an important management and conservation risk for migratory species outside parks and protected areas.

Resource selection function results of elk migration indicate, during fall-day, all elk selected forested areas to find cover from human hunters (Edge and Marcum 1991, Ciuti et al. 2012*a*). Migrating elk using stopovers also avoided roads in all seasons, but increased their response to roads and traffic volume during fall hunting season. The only time that elk were located near to high-traffic roads was at night during the spring, when humans were not perceived as a threat because hunting was not allowed. Most interestingly, there were differences in responses to human hunters between sexes. Females used steeper terrain during fall-day and males did not use this strategy in hunting season. Male avoidance of roads was much stronger than females during fall-day, a possible reaction to the higher hunting pressure on males vs. females. These shifts in elk distribution from disturbance to areas away from roads can reduce access to high-value habitats near roads (Edge and Marcum 1991, Rowland et al. 2000). However, both sexes appeared to compensate for displacement by moving closer to roads at night, possibly accessing higher-quality forage sites, a choice they made more often in spring. Spring elk movement was diurnal, with greater movement during the day than during the night, whereas fall migration switched to more cautious movements, moving similarly during the

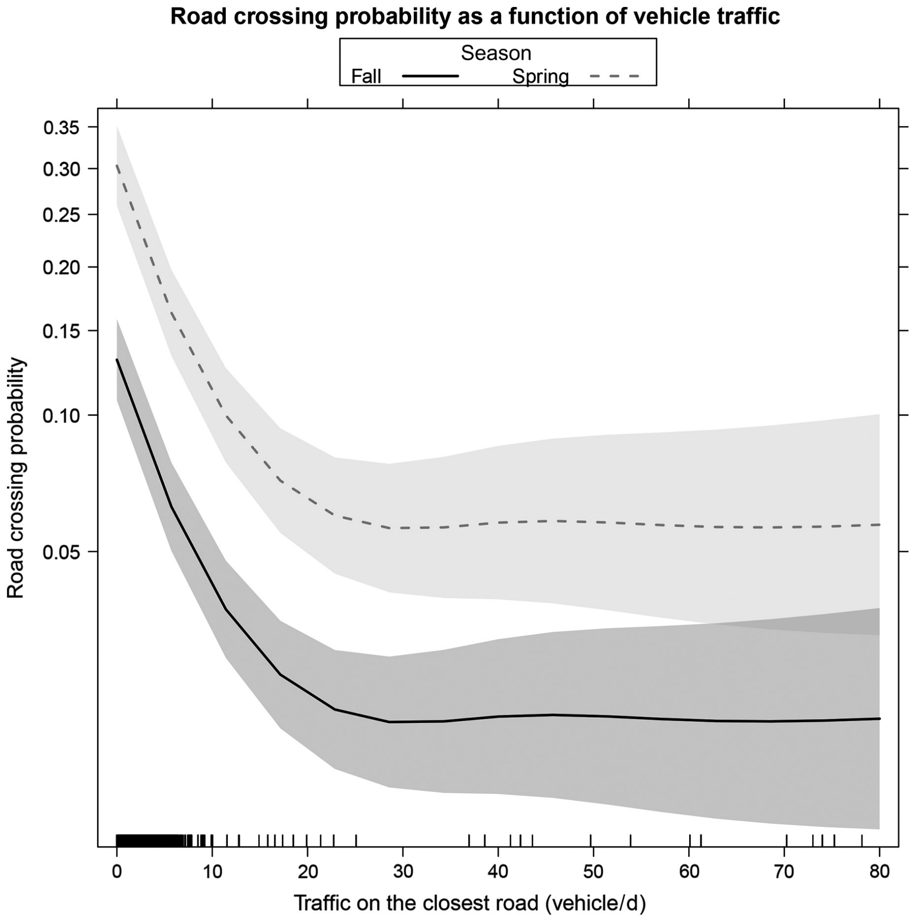

Fig. 8. Road crossing probability as a function of vehicle traffic, as predicted by the generalized linear mixed-effect model fitted to explain the likelihood of road crossing (binary response: 1 = road crossed, 0 = road not crossed) along steps walked every two hours by male and female elk during spring and fall migration. Shaded areas are marginal 95% confidence intervals.

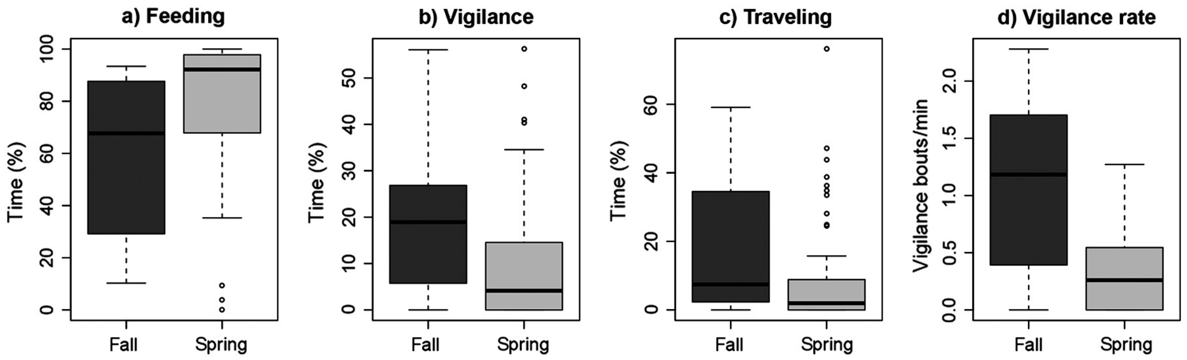

Fig. 9. Proportion of time spent in feeding (time feeding/total time active, i.e., foraging efficiency), vigilance (time being vigilant/time active), traveling (time traveling/total time), and vigilance rate (the number of vigilance bouts/min) in 154 focal individuals observed along spring and fall migratory corridors.

night and day. In highly disturbed areas, migratory animals may increase their travel rate along preferred paths, moving through the area quickly in spring (Lendrum et al. 2012) or be more cautious in their movements in fall (Ciuti et al. 2012*a*).

For spring migration, stopover habitat selection was mainly driven by non-hunting-related environmental conditions, which represented foraging and resting activities of migrating elk, plus their response to potential risk from natural predators. Similar to hunted elk in other jurisdictions of North America (Brodie et al. 2013), predation by natural predators in this study is greater in winter and spring, with the majority of elk mortality related to hunting harvest in fall (Ciuti et al. 2012*a*, *b*).

Understanding herbivore behavior due to hunting pressure is important for management because these responses may outweigh the effect of direct predation (Janis and Clark 2002, Creel and Christianson 2008, Périquet et al. 2010). In response to disturbance, our observation data showed that elk increased vigilance and traveled quickly within open areas during fall hunting season. A quicker traveling rate within open areas could also reduce time spent in the open, thus reducing detectability to lessen hunter mortality risk (Mysterud 1999, Sih and McCarthy 2002, Hochman and Kotler 2007, Ciuti et al. 2012*a*) and create a potential loss of feeding opportunities due to shorter persistence within meadows (Mysterud 1999, Creel et al. 2005, Hernández and Laundré 2005, Hochman and Kotler 2007). Elk adjusted behavioral strategies during migration, when risk due to hunting created a landscape of fear greater than "natural" predation risk (Proffitt et al. 2009, Ciuti et al. 2012*b*, Bonnot et al. 2013, Norum et al. 2015). There was a reduction in feeding activity during fall migration possibly affecting the ability of elk to further increase body condition for winter (Cook 2011, Middleton et al. 2013*a*, *b*)—particularly if foraging efficiency and intake does not offset the energetic demands of moving (Bender et al. 2008, Seidel and Boyce 2016) caused by a lower-quality diet (Barnier et al. 2014).

Comparable to reduced habitat quality or increased predation, the disturbance effects of semi-permeable barriers on migration route function could potentially reduce the benefits of migration (Sawyer et al. 2013). A loss or major decline of this partially migratory population from migratory to the resident segment of the herd would result in a change in elk distribution (Hebblewhite et al. 2005, 2006). A change in elk distribution could impact vegetation dynamics by overgrazing on the population's winter range and undergrazing on other ranges, resulting in changes to plant productivity and biodiversity. Predators using elk as prey might in turn change their distribution to overlap with the changed elk distribution (Nelson et al. 2012). If a permanent year-round shift of elk and predators to current elk winter range occurred, it could result in increased negative human/wildlife interactions (both carnivores and ungulates) in agriculture or ranch lands located on or nearby the existing winter range (Morehouse and Boyce 2011).

Vehicle traffic and human disturbance have much higher effects on elk because of the increased fear of humans due to hunting. To reduce these effects to stopover permeability, access management (i.e., gating roads) can be highly effective at reducing traffic volume and minimizing disturbance effects on wildlife, particularly elk and grizzly bears (Northrup et al. 2012). Restricted access regulations and gating of roads within 500–1000 m to important stopover sites during migration could be used to manage traffic activity. Restricting new roads outside of the preferred buffer distance would be beneficial to elk and other species by controlling road densities (Frair et al. 2008, Boulanger and Stenhouse 2014). Alternatively, human hunting could be a tool for displacing ungulates from high human–wildlife conflict areas by spatially and temporally changing hunting opportunities in hunting units (Proffitt et al. 2009, Apollonio et al. 2010).

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DGP, SC, and MSB contributed materials/analysis tools and prepared data for analyses. SC analyzed the data. All authors edited and approved the first draft written by DGP and SC.

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Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1841/full