The Journal of Wildlife Management 1–14; 2021; DOI: 10.1002/jwmg.22099

Research Article

Mothers' Movements: Shifts in Calving Area Selection by Partially Migratory Elk

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ABSTRACT Loss of migratory behavior or shifts in migratory ranges are growing concerns to wildlife managers. How ungulates prioritize safety from predators at the expense of high-quality foraging opportunities during calving may be key to understanding these shifts and long-term reproductive success. We compared trade-offs in selection for forage and predation risk by elk (*Cervus canadensis*) following 3 migratory tactics (western and eastern migration and resident) during 2 time periods in a declining (by almost 70% from 2002–2016), partially migratory elk population adjacent to Banff National Park in Alberta, Canada. We hypothesized that regardless of migratory tactic, maternal elk would show stronger trade-offs between high-quality foraging associated with higher predation risk and forage resources of lower-quality yet lower risk on calving ranges than on ranges used during summer because of vulnerability of their offspring. Additionally, we hypothesized these trade-offs would occur at high (2002–2006) and low (2013–2016) elk population sizes. We used a machine-learning algorithm to predict dates of parturition based on global positioning system (GPS) movements of elk equipped with vaginal implants ($n = 60$) and predictions were within 1.43 ± 0.85 (SE) days of the known date. We applied the model to an additional 58 GPS-collared elk without vaginal implants. Based on changes in localized movements, we defined calving areas as the 26 days post-parturition and compared habitat characteristics of calving areas to 10 similar-sized areas centered on random locations during summer for the same individual in a latent selection framework. Across the 2 time periods, parturition occurred from 8 May–11 July with median parturition dates differing among migratory tactics and residents shifting towards an earlier parturition date in the later period. All elk, regardless of migratory tactic and time period, selected calving areas with greater forage resources than were available on areas used during summer, with no evidence for greater selection of areas that reduced predation risk at the expense of higher-quality foraging. Calving season selection for areas with abundant forage exposed western migrants to high risk of bear (*Ursus* spp.) predation, residents to high risk of wolf (*Canis lupus*) predation, and eastern migrants to low risk of bear and wolf predation. Patterns in exposure to predation risk during calving between migratory tactics were consistent with the recent decline in western migrants and increase in eastern migrants, implying that conditions on calving areas contributed to observed changes in the number of elk following these tactics. © 2021 The Wildlife Society.

KEY WORDS calving, elk, habitat selection, partial migration, predation, random forest, risk.

Migration in large herbivores is advantageous in seasonal environments when it affords prolonged access to high-quality forage and reduces predator exposure (Fryxell and Sinclair 1988, Bolger et al. 2008, Mysterud et al. 2011), but in recent decades, there have been declines in migratory behavior and migratory wildlife populations across the globe (Bolger et al. 2008, Wilcove and Wikelski 2008, Harris et al. 2009). Where migration is lost, animals and their movements commonly become limited to a single seasonal range or are restricted by changes in land use (Serneels and Lambin 2001), artificial feeding (Jones et al. 2014, Barker et al. 2018), or resource availability (Post and Forchhammer 2008, Middleton et al. 2013*a*) related to habitat loss and fragmentation, which may be exacerbated by climate change (Holdo et al. 2011, Tucker et al. 2018).

Received: 25 June 2020; Accepted: 11 May 2021

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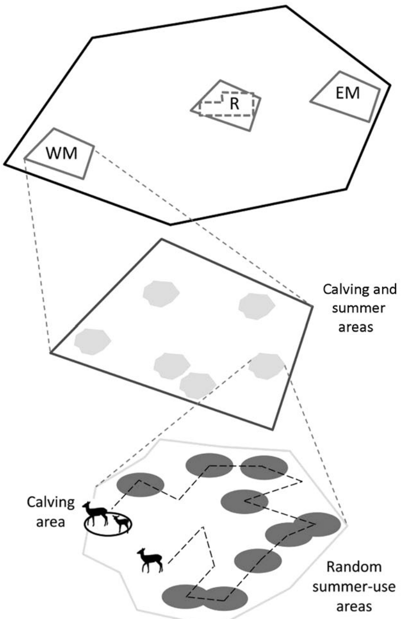
In the case of partial migration, a mix of residents and migrants within a population can be maintained over the long term if fitness is equal, or if individuals switch between migratory tactics (Eggeman et al. 2016, Berg et al. 2019). Environmental changes may alter the relative fitness and benefits to individuals following a particular migratory tactic or can promote new migratory patterns. For example, resident elk (*Cervus canadensis*) in the Clarks Fork population in Wyoming, USA proportionally increased over 21 years because of severe drought and predator recovery on migrant ranges (Middleton et al. 2013*a*). Similarly, the proportion of long-distance migrants in the Jackson population of elk decreased while short-distance migrants increased over 35 years, likely because of changes in calf recruitment rather than switching between migratory tactics (Cole et al. 2015). The bighorn sheep (*Ovis canadensis*) population in the Teton Mountains of Wyoming was partially migratory before human development encroached on low-elevation winter ranges but has been able to persist as high-elevation residents (Courtemanch et al. 2017). Shifts in migratory behavior could result from animals following 1 migratory tactic dying out over time, individuals switching among tactics, or in the case of novel migration, animals finding alternative resources that improve reproductive fitness (Mysterud et al. 2011, Morrison and Bolger 2012, Berg et al. 2019). Few researchers have succeeded in directly linking underlying mechanisms to migratory shifts because long-term monitoring is required yet also difficult. An understanding of the behavioral changes that occur during these shifts could help prevent future losses in migratory behavior.

Environmental conditions of areas used to rear offspring may play a key role in explaining shifts in migratory behavior of large herbivores. The large lifetime fitness costs that result from loss of offspring and the long-term cohort effects of early life development (Albon et al. 1987, Hamel et al. 2009, Pigeon et al. 2017) suggest intense selection of behaviors during parturition (Bowyer et al. 1999, Bongi et al. 2008, Simard et al. 2014). Survival of neonates depends on the need to meet necessary nutritional requirements while mitigating the risk of predation (Bowyer et al. 1999). Lactation is the most energetically demanding stage of reproduction for the mother, and herbivores alter feeding behavior and activity budgets to meet nutritional demands (Clutton-Brock et al. 1982, Hamel and Côté 2008, Oftedal 2018). At the same time, neonates are particularly vulnerable to predation because of their small size and limited mobility.

Maternal selection at the scale of the offspring-rearing area to balance the threat to young, while meeting nutritional demands (Roff 1992, Stearns 1992, Bowyer et al. 1999), may be key to explaining changing patterns in partially migratory populations where spatial patterns in resources and predation risk exist. This may be particularly important for species following the postpartum hider strategy. Compared to a follower strategy where precocial neonates move with their mothers shortly after birth, a hider neonate conceals itself and remains relatively motionless, with the mother returning to feed and care for it until it is mobile (Lent 1974). A hider tactic is hypothesized to avoid aggressive interactions with conspecifics, improve pair bonding, and decrease detection by predators at a time when the neonate's ability to escape is poor (Fitzgibbon 1990, Ebensperger 1998, Dwyer and Lawrence 2005). In areas under heavy predation, especially where there are multiple predator species or predators with efficient search tactics, maternal females may not be able to simply choose the area with the highest forage quality and let hiding minimize the risk. Limited mobility also compromises the female's ability to exploit a broader range of forage conditions, and makes the isolated mother and neonate predictable in space to predators for a short time, without the associated group-benefits against predation (Lima and Bednekoff 1999, Ciuti et al. 2009, Panzacchi et al. 2010). As a result, selection of areas that meet the requirements of the mother and neonate would be expected to be more stringent during calving than later in summer (Parker et al. 2009) because neonate mortality has a major influence on annual variation in the population growth of many ungulates (Gaillard et al. 1998, Van Moorter et al. 2009).

The Ya Ha Tinda elk population is a partially migratory population that winters adjacent to Banff National Park in Alberta, Canada (Hebblewhite 2006) and that has declined by 70% since the early 2000s, exhibiting concomitant changes in proportions of the population following different migratory tactics (Hebblewhite et al. 2006, Eggeman et al. 2016). In 2001–2004, the ratio of western migrants to elk remaining on the Ya Ha Tinda year-round was 3:1 (Hebblewhite et al. 2006), but over time a new eastern migratory tactic to low-elevation (~1,400 m) multi-use forest emerged, and the ratio of western migrants to residents to eastern migrants at the time of this study in 2016 was roughly 1:10:5. Elk were subject to a suite of predators that varied spatially across the area. Wolves (*Canis lupus*) returned to Banff National Park in the mid-1980s (Morgantini 1995), and they were the leading cause of known mortality for adult female elk (Hebblewhite et al. 2018). Grizzly bear (*Ursus arctos*) populations were relatively stable in Banff National Park over the last decade but had lower densities outside the park on adjacent provincial lands (Whittington and Sawaya 2015, Whittington et al. 2018). Grizzly bears were the leading cause of known mortality for neonatal elk calves (Berg 2019).

We focused on the critical calving period to assess the role that trade-offs in selecting for forage and predation risk may play in changing patterns in migration using data from the Ya Ha Tinda elk population. We compared the selection patterns of migratory and resident elk during calving in 2002–2006 (early) and 2013–2016 (late). Hebblewhite and Merrill (2009) reported differential trade-offs by elk following different migratory tactics in summer. We therefore hypothesized that female elk would show even greater trade-offs in selection for areas to minimize predation risk at the expense of high-quality forage on calving ranges than on areas used in summer because of calf vulnerability (i.e., a negative forage quality or quantity × predator interaction; Fig. 1).



Hypothesis: maternal elk trade off high-quality foraging resources associated with high predation risk for low forage quality, but lower predation risk, more on calving grounds than on areas used in summer, due to calf vulnerability.

Predictions:

Maternal elk migrating westward (WM) to high elevations in Banff National Park will show the strongest trade-off of high-quality foraging for lower forage quality and lower bear predation risk during calving because of higher bear densities. Trade-offs will be stronger over time because bear densities increased while WM proportionally decreased.

Maternal resident elk (R) will show the strongest trade-off of high-quality foraging for lower forage quality and lower wolf predation risk because risk from wolves is highest on the winter range. Selection to avoid wolves will be constant over time because wolf predation is density-independent.

Maternal elk migrating eastward (EM) to low-elevation, multiple-use lands will show no or the least trade-off of high-quality foraging for lower predation risk because predators are managed and human activity is high.

Figure 1. Framework for testing for forage-predation risk trade-offs made during calving in the partially migratory Ya Ha Tinda elk population, Alberta, Canada, during 2002–2006 and 2013–2016, with predictions made for elk following different migratory tactics. Black oval represents the calving area, and gray ovals represent 10 same-sized areas along the GPS track of the same individual in summer.

Because bears are the major predator on elk calves, we predicted elk would show the strongest trade-off (i.e., the most negative interaction) in selecting areas for forage that was lower quality but avoiding risk from bears compared to wolves. We predicted this would be particularly true for elk migrating into Banff National Park because bear densities are highest in the park, and bear predation on adult elk migrating into the park is higher than on elk following other migratory tactics (Hebblewhite et al. 2018). In contrast, we predicted elk migrating eastward to calve on low-elevation, multiple-use forests would show the least trade-off (i.e., no or the least negative interaction) in selecting areas of forage quality or quantity while avoiding risk from bears or wolves because predators are not as abundant, likely because of high human activity and wolf trapping (Whittington and Sawaya 2015, Whittington et al. 2018, Spilker 2019).

Hebblewhite et al. (2018) reported evidence for density-dependent bear, but not wolf, predation on elk in this population. Therefore, we expected the most consistent selection strategies between the 2 time periods where wolf predation risk was highest. Where bear predation risk was highest, we expected elk would increase their relative trade-off of quality foraging opportunities for lower-quality areas that avoided the increased *per capita* risk of bear predation (Fig. 1). If changes in trade-offs for foraging resources and predation risk during calving were consistent with observed demographic trends in the respective migratory tactics, this would support the notion that elk behavior during calving may be key to understanding how shifts in migration occur.

STUDY AREA

The study took place from 2002–2016 and the 7,000-km^2 study area straddled the boundary between Banff National Park (BNP) and adjacent provincial lands located in west-central Alberta, Canada (51°38′N, −115°30′W). Parks Canada administered the Ya Ha Tinda ranch (44 km^2) central to the study area that elk used as winter range, though Alberta's provincial government managed the natural resources. The winter range consisted of a large montane rough fescue (*Festuca campestris*) grassland (20 km^2) interspersed with bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticosa*), and willow (*Salix* spp.), and was surrounded by forest (Holland and Coen 1982). The mountainous terrain of BNP decreased in ruggedness and elevation (1,400–3,500 m) from west to east across the study area. Predator occurrence also declined, but anthropogenic activity (industrial and recreational) increased from west to east. The study area was subject to wild and prescribed fires (~7,000 ha, 15% of study area) and to an increase in forest cutting with >3,000 ha cut since 2000, primarily at low elevations (P. Smolko, University of Alberta, unpublished data).

Climate was cold continental with long, snowy winters (Oct–Apr, $\bar{x} = -4.1$°C) and a short summer (May–Sep, 9°C). Low precipitation and westerly winds (i.e., chinooks) kept the eastern part of the study area mostly snow-free in winter (Holland and Coen 1982), with an average of 157 cm of snowfall. Precipitation averaged 31.9 cm, though could be <10 cm in summer during drought years (Environment Canada 2018).

The highest minimum count of elk that wintered at Ya Ha Tinda (primarily adult female and immature elk) was approximately 2,200 individuals in 1992 (Morgantini 1995), and declined by 70% from 1,398 elk counted in 2002 to 450 elk in 2016 (Fig. 2). From 1977 to 1987, the majority (~90%) of the population migrated west from the Ya Ha

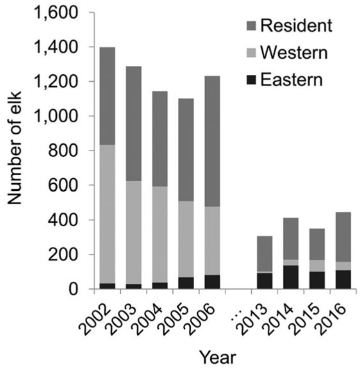


Figure 2. Population and the estimated number of elk following each migratory tactic based on winter counts and movements of collared elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002–2006 and 2013–2016.

Tinda winter range to summer at higher elevations in BNP (Morgantini and Hudson 1988). The ratio of western migrants to residents to eastern migrants shifted from an average of 14:15:1 during the early period of 2002–2006 to 1:10:5 in the late period of 2013–2016 (Fig. 2).

Wolves recolonized the study area by the mid-1980s after extirpation by the 1950s (Morgantini 1995), and numbers likely remained stable into the early 2000s (Hebblewhite 2006). Grizzly bear numbers ranged from 5.25 bears/1,000 km^2 outside BNP (Alberta Environment and Parks 2016) to 12.4–15.1 bears/1,000 km^2 inside the park (Whittington and Sawaya 2015, Whittington et al. 2018) and kept black bears (*U. americanus*) at moderately low densities (Alberta Environmental Protection 1993). On provincial lands east of the park, wolves maintained a presence but were liberally hunted and trapped, whereas grizzly bears were subject to limited hunting until they received protection in 2006. Other main predators of elk in the system included coyotes (*C. latrans*) and cougars (*Puma concolor*; Morgantini 1995), which increased in the last several decades (Knopff et al. 2014). Ungulates other than elk included white-tailed (*Odocoileus virginianus*) and mule deer (*O. hemionus*), moose (*Alces alces*), bighorn sheep, and mountain goats (*Oreamnos americanus*), though mountain goats were mostly in BNP (Stelfox 1993, Morgantini 1995). Plains bison (*Bison bison*) were extirpated by the 1870s but were recently reintroduced in 2018 (Soper 1941, Parks Canada 2017).

METHODS

Elk Capture, Monitoring, and Migration

Aerial surveys conducted by Alberta Fish and Wildlife (2002–2010) or Parks Canada (2011–2016) and repeated verifications of elk numbers from the ground confirm that >90% of the Ya Ha Tinda elk population, and all collared elk, wintered at Ya Ha Tinda (Hebblewhite 2006, Hebblewhite et al. 2006, Eggeman et al. 2016). We captured and fit adult female elk with global positioning system (GPS) radio-collars (Lotek Wireless, Newmarket, Ontario, Canada; models 2200, 3300, 4400, or 7000) during winter from 15 January to 31 March, 2002–2016. We did not use data from elk radio-collared during 2007–2012 because the number of collared migrant elk was limited owing to a focus on aversive conditioning of resident elk during this time (Spaedtke 2009). We used corral traps baited with hay, helicopter net gunning, or ground darting from horseback to capture and collar elk. We determined pregnancy through rectal palpation at capture or from elk blood serum (Huang et al. 2000, Duquette et al. 2012). The study was approved by the University of Alberta Animal Care protocols (353112, 611812, 611912, 611/11/11, 611/11/13, 00000624) and University of Montana Institutional Animal Care and Use Committee (MH-004-16).

We fit pregnant elk captured in 2013–2016 with small vaginal implant transmitters (VITs; model M3960, Advanced Telemetry Systems, Isanti, MN, USA) to allow birth sites to be precisely located. We used very high frequency telemetry to monitor maternal elk and their VITs 2–5 times daily mid-May to mid-July; when a VIT expelled, a ground crew located the birth site and recorded the GPS coordinates. We determined time of birth to the nearest half hour through a code emitted by a precise event transmitter (PET) on the VIT.

We used a combination of net squared displacement (Bunnefeld et al. 2011, Spitz et al. 2017) and spatial rules to classify GPS-collared elk as migrants or residents in a particular year (Eggeman et al. 2016). We classified elk as resident only if they remained within 15 km of the Ya Ha Tinda winter range during calving and summer, and we classified elk as migrants if they calved and summered a minimum of 30 days on ranges >15 km from the winter range. Western migrants were those elk that migrated westward from winter range to summer at higher elevations within or along the front ranges of BNP. Eastern migrants were those elk that migrated to lower elevations east of the Ya Ha Tinda winter range.

Modeling Parturition Date

We used known parturition events from 60 elk and the associated 2-hour movement data collected from GPS-collars deployed from 1 May to 15 July, 2013–2016, to build a model for predicting the date of parturition using a random forest algorithm in program R (version 3.4.3; R Core Team 2017, Hayes 2019). An advantage of the random forest method is that it can grow an ensemble of many classification trees, each developed from predictor variables, improving predictive accuracy over an individual model (Hastie et al. 2009, Severson et al. 2017). Random forest models are also robust to sparsity; their convergence does not depend on the overall number of variables but rather the number of highly predictive variables (Biau 2012). We therefore included 180 variables in the random forest as possible covariates: 5 descriptive statistics ($\bar{x}$, median, SD, max., and sum) for each of 6 movement statistics (step lengths, relative turning angles, absolute turning angles, Euclidean displacement, and parallel and orthogonal variances) over 6 moving-time windows (4, 24, 48, 96, 192, and 216 hr). We calculated parallel and orthogonal variance by constructing dynamic bivariate

Gaussian bridges using the R package move (Kranstauber and Smolla 2016). Dynamic bivariate Gaussian bridges relax assumptions of the standard Brownian bridge movement models by separating variance in movement into forward and right-angle components, which captures changes in animal behavior (Kranstauber et al. 2014).

Our approach followed Evans and Cushman (2009) and Murphy et al. (2010) by first identifying the most informative candidate variables among the movement statistics calculated for the 60 parturition events (rf.modelSel function in the rfUtilities R package; Evans and Murphy 2016, Evans et al. 2011). We then produced the final predictive algorithm from 1,000 bootstrapped random forest models constructed from the covariates retained during the first stage of covariate selection. In each bootstrap iteration, we randomly selected and withheld 20% of the data ($n = 12$ elk-years; i.e., out-of-bag sample) to assess model robustness. We constructed a random forest model with the remaining 80% ($n = 48$ elk-years) to predict a parturition date for the withheld 20%. After the 1,000 iterations, we obtained a distribution of predicted parturition dates for each parturition event, and we used the median of this distribution to predict the final date of parturition.

We applied the final random forest model to GPS data from 58 elk with unknown parturition dates; we did not know elk pregnancy for 7 of these elk, but we assumed these elk were pregnant based on $87 \pm 0.02\%$ (SE) pregnancy rates in 2002–2006 and 2013–2016. Eleven elk from 2002–2006 had 6-hour (instead of 2-hr) fix rates in either early May or July. We removed GPS data from the first week of May for 4 of these elk, the first 2 weeks of May for 7 elk, and during ≥ 1 24-hour period in July for 5 elk to prevent gaps in the data from creating spurious movement statistics (Method S1, Tables S1–2, available online in Supporting Information).

Habitat Selection and Use of Calving Areas

We defined movement-based calving areas identified by a threshold in the length of time after birth that movements remained localized. We used 73 known and 58 predicted dates of calving ($n = 131$; Table 1). We used the GPS locations of the elk to derive daily 95% utilization kernels using the plug-in method for the smoothing factor in the ks R package (Duong et al. 2018). We plotted the average size (km^2) of the daily 95% utilization kernels against the number of days since calving to identify a temporal breakpoint between the expanding size of the area used by female elk-calf pairs as calves gained mobility and the asymptote of area used by female elk-calf pairs daily throughout summer. We identified the breakpoint and corresponding threshold number of days using a piecewise or broken stick regression model (Johnson et al. 2002) in the segmented R package (Muggeo 2017). Calving areas were the 95% utilization kernels of the GPS locations obtained before the temporal breakpoint.

We assessed selection by elk for calving areas by comparing characteristics of areas used by individual elk during calving to areas they used later in summer (second-order selection *sensu* Johnson 1980) using a matched-case design within the same year (Fig. 1). We matched an elk's calving area with 10 available circular areas of the same size and centered on randomly selected GPS locations from the post-calving period (i.e., after the threshold number of days for calving up to 31 Aug). With this design, we assumed similar landscape features to be available during the calving period on the calving and summer-use areas, so we interpreted model coefficients as the relative difference in selection between habitat features available in calving areas and those in the randomly selected summer-use areas (Latham et al. 2011). We derived beta coefficients for the exponential model (Fortin et al. 2005, Avgar et al. 2016) using conditional logistic regression with a random effect for individual elk using the coxme R package (Therneau 2018).

Table 1. Number of collared elk used in comparing selection of calving and summer areas between 3 migratory tactics and 2 time periods (early: 2002–2006 and late: 2013–2016) in the Ya Ha Tinda elk population, Alberta, Canada, 2002–2016.

Year	Western migrants	Residents	Eastern migrants
2002		1	
2003	5	1	
2004	7	5	
2005	1	5	
2006	4	6	
…			
2013	2	12	3
2014	3	13	7
2015	4	11	4
2016	6	19	12
Total	32	73	26

To avoid collinearity (correlation $|r| \geq 0.60$), correlated variables not used in the same models included forage biomass and normalized difference vegetation index (NDVI) because we adjusted forage biomass for phenological changes based on NDVI, and forage biomass and the extent of burn or herbaceous-shrub land cover (because non-forested areas also had the highest forage biomass; Hebblewhite et al. 2008, Robinson et al. 2012). We compared final models including covariates and their interactions using Akaike's Information Criterion adjusted for small sample size (AIC$_c$) and model weights. We then examined whether characteristics of calving areas in the best models differed among calving areas for the western and eastern migrants and residents and between the early and late time periods using Kruskal-Wallis with Dunn's (1961) Bonferroni adjustment for multiple comparisons.

Environmental Covariates

We measured covariates at 30×30-m resolution and averaged values within a calving area. Prior to analysis, we centered and standardized covariates using the mean and standard deviation across years and elk.

Forage greenness and forage biomass.—We measured forage greenness using NDVI from 250-m resolution moderate resolution imaging spectroradiometer, which we interpreted as a metric of herbaceous forage quality central to elk diet in open-canopy areas in summer (Hebblewhite 2006: Tables A2.5a and A2.11, Borowik et al. 2013). We used the NDVI values closest to the parturition date of individual elk and averaged the values across open land cover within the calving area.

Similarly, we used total (herbaceous + shrub) forage biomass (g/m^2) at time of calving, averaged across open-canopy areas within the calving area (additional details in Method S2, available online in Supporting Information). We estimated forage biomass spatially with the dynamic forage model of Hebblewhite et al. (2008) that used field-sampled annual peak (~1 Aug) forage biomass in 2002–2004 to estimate herbaceous and shrub biomass at a 30-m^2 resolution as a function of year, land-cover type, elevation (m), aspect (°), and distance to the continental divide (km). For 2005–2016, we used the peak biomass estimate from 2002–2004 with the most similar precipitation (Alberta Climate Information Service 2018) because 2002 had average (180 mm), 2003 had low (167 mm), and 2004 had high (319 mm) precipitation, and the effect of precipitation on biomass (herbaceous + shrub) depended on year. We also adjusted for annual changes in forage availability within burned or timber-harvested areas (data obtained from BNP's fire database and Sundre Forest Products, Sundre, AB) using previously derived forage growth models (P. Smolko, unpublished data) in the study area for burns and by Visscher and Merrill (2009) for stands aged 1–20 years in an area immediately north of the Ya Ha Tinda. We assumed biomass reached pre-disturbance levels after 15 years post-harvest or post-fire. To account for seasonal plant growth, we adjusted the peak forage biomass available to a particular animal using the ratio of the mean NDVI_i from the nearest 16-day period at the time of animal location to the maximum mean ($\mathrm{NDVI}_{\max}$) observed during the growing season of the same year (Hebblewhite et al. 2008). We did not limit forage abundance to specific vegetative species because of the diversity of elk diets (Hebblewhite 2006).

Land cover types.—We used a land-cover map derived from LANDSAT-TM (Franklin et al. 2001) to classify 16 vegetative land-cover categories (Hebblewhite 2006). We updated the land-cover map each year of our study with new burns and forest cuts, and we reclassified old burns and cuts (>15 yr) to moderate-cover conifer forest. We combined herbaceous, shrub, alpine herbaceous, and alpine shrub land cover into 1 category (herb-shrub), and burned forest, grassland, and shrub <15 year into another category (burn). We expressed the extent of these land-cover types, the amount of regenerating forest <15 year (cut), and the amount of edge (edge, defined by the linear border between open and closed-canopied cover types, buffered by 50 m to each side), as the percentage of each calving area.

Predation risk.—We modeled predation risk to elk by wolves (wolf) based on the work of Hebblewhite and Merrill (2007) and by grizzly bears (bear) based on the work of Nielsen (2005; Method S3, available online in Supporting Information). We estimated wolf predation risk by multiplying the population-level resource selection function (RSF) from collared wolves in 2002–2004 and the spatial density of wolves adjusted by kill rate/pack/day (Thurber et al. 1994) to derive annual probability density functions (PDFs). We extended the wolf RSF estimates to 2005–2016 by incorporating annual changes in land cover and distance to edge. We calculated spatial density for each pack as the product of wolf distribution (kernel density estimation) and kill rate (Y). We estimated kill rates based on Thurber et al. (1994) from annual estimates of pack size (X): $Y = 0.385 \times (1.000 - 0.726^X)$. Where annual estimates of a pack size were missing in a certain year ($n = 18$ pack size-years), we used the mean size of all wolf packs in 2002–2016 (i.e., 6.4 ± 1.4). We summed PDF values in areas where wolf packs overlapped. For areas outside pack boundaries (<5%) that elk used, we assumed PDFs were the mean of those from the nearest wolf boundary. We multiplied the final PDFs by the wolf RSFs to create population-level predation risk models for 2002–2016.

We estimated grizzly bear predation risk to elk based on an RSF derived from location data of 11 GPS-collared bears from 1999–2006 during the hypophagia (1 May–15 Jun) and early hyperphagia (16 Jun–31 Jul) stages (Nielsen 2005). We estimated the RSF values based on forest canopy, land-cover type, terrain features, and human use. We predicted bear RSF values for 2013–2016 based on updated land-cover layers (G. B. Stenhouse, personal communication). We based spatial density of grizzly bears on density estimates inside BNP from 2006–2008 and 2012–2014 and on provincial lands outside the park from 2005 that indicated grizzly bears in the park were about 2.62 times higher than outside the park. We used a linear decline to smooth the density estimates along the park border with a moving window the same size as a female grizzly's average home range ($520\,\mathrm{km}^2 \approx 12.9$-km radius; Stevens 2002) and centered on the park border. We then multiplied the annual RSFs by the PDF.

Finally, we tested for correlation between the telemetry-based RSFs and RSFs created from wolf and bear scat locations (Spilker 2019), and also compared the predation risk values at 740 locations of wolf scat and 373 locations of grizzly bear scat with wolf and bear predation risk measured at 1,000 randomly generated locations.

RESULTS

Parturition Dates

The random forest model predicted 31 of the 60 dates used for modeling birth date to the exact day, and 22 of the remaining 29 dates within 1 day of the actual date of calving. The mean number of days between the calving dates predicted by the random forest model and the observed day of calving was −1.43 ± 0.85 (SE) days ($n = 60$; Fig. 3). Step length over long time windows (e.g., 192, 216) and parallel variance over shorter time windows (e.g., 24, 48) had the greatest influence on the accuracy in predicting parturition date based on importance values (Tables S3–4, available online in Supporting Information).

All dates of parturition (including the 73 known and 58 predicted dates) occurred between 8 May and 11 July

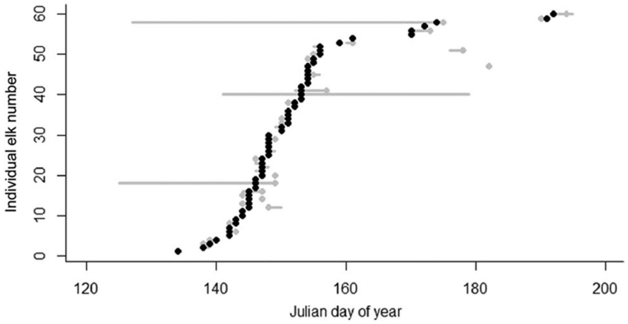


Figure 3. Known (black) versus predicted (grey) parturition dates ($n = 60$) of elk in the Ya Ha Tinda population, Alberta, Canada, 2013–2016. Predicted dates resulted from a random forest model that included variables related to movement: step length, turning angles, Euclidean displacement, and time of day. Grey bars denote the middle 2 quartiles of predicted dates. Results have been ordered along the *x*-axis by known parturition date for ease of interpretation.

(Fig. 4). The median parturition date for eastern migrants (27 May, $n = 26$) was earlier than the median parturition date of western migrants during the early (6 Jun, $n = 17$, Kolmogorov-Smirnov D [K-S D] = 0.44, $P = 0.04$) and late periods (4 Jun, $n = 15$, K-S $D = 0.44$, $P = 0.05$), and residents in the early (5 Jun, $n = 18$, K-S $D = 0.54$, $P = 0.004$) but not the late period (30 May, $n = 55$, K-S $D = 0.16$, $P = 0.78$). We did not detect a difference between the median parturition dates of the early and late periods for western migrants (K-S $D = 0.24$, $P = 0.75$), but parturition was earlier for residents in the late period compared to the early period (K-S $D = 0.42$, $P = 0.02$).

Calving Area Delineation and Size

We identified a 26-day (±2.03 SE) period after parturition during which movements increased more dramatically before reaching an asymptote (piecewise regression $R^2 = 0.91$, $n = 73$; Fig. 5). We used this threshold to delineate 26-day calving areas that averaged 8.24 ± 4.67 km² for known parturition dates and 14.18 ± 10.98 km² for predicted dates ($\bar{x} = 10.87 \pm 8.59$ km², range = 0.42–46.53 km² for all elk; Fig. S8, available online in Supporting Information); we did not detect a difference between the distributions of calving area sizes for known and predicted parturition dates (K-S $D = 0.5$, $P = 0.39$). We also did not detect a difference in the size of calving areas between resident elk in the early (14.68 ± 7.27 km²) and late (10.80 ± 6.95 km²) periods (Dunn's Bonferroni $P = 0.40$), or in the size of calving areas of western migrants between the early (14.95 ± 14.87 km²) and late (9.20 ± 9.57 km², $P = 1.00$) periods. Eastern migrants had smaller calving areas (6.66 ± 2.93 km²) than residents (10.80 ± 6.95 km², $P = 0.04$) but not western migrants (9.20 ± 9.57 km², $P = 1.00$).

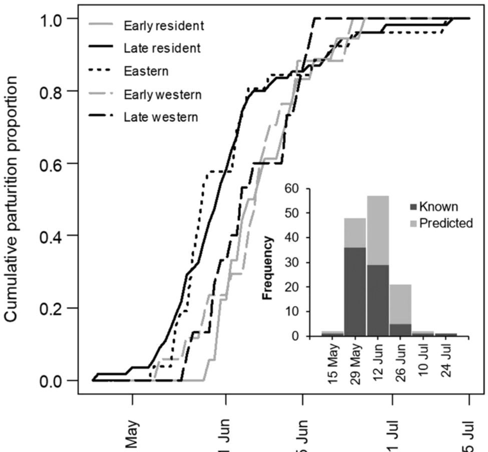


Figure 4. Cumulative frequency of known ($n = 73$) and predicted ($n = 58$) parturition dates for elk following 3 migratory tactics and 2 time periods (early: 2002–2006 and late: 2013–2016) in the Ya Ha Tinda elk population, Alberta, Canada. Inset shows the distribution of the known and predicted dates of parturition.

Habitat Use on Calving Areas

The amount of herbaceous and shrub land cover in calving areas differed between migratory tactics (Kruskal-Wallis $\chi^2_4 = 41.71$, $P < 0.001$; Fig. 6; Table S9, available online in Supporting Information). Calving areas of resident elk included greater extents of herbaceous-shrub land cover in both the early (Dunn's Bonferroni $P = 0.004$) and late ($P < 0.001$) periods than those of western migrants, whereas the calving areas of eastern migrants had the lowest extents ($P < 0.05$; Fig. 6). Instead, calving areas of eastern migrants had the highest proportions of forest cuts and, as a result, edge habitat ($P < 0.05$; Fig. 6). Calving areas of residents also had higher extents of burned areas during the late period compared to the early period ($P = 0.002$; Fig. 6). Because forage biomass is highest in open areas, differences in forage biomass used by the different migratory tactics (K-W $\chi^2_4 = 21.59$, $P < 0.001$) were consistent with their differences in herbaceous-shrub land cover (Fig. 6). We did not detect a difference between NDVI values in calving areas of western migrants and residents in either time period (early: $P = 1.00$, late: $P = 1.00$; Fig. 6), nor did we detect a difference between NDVI values in calving areas of eastern migrants and residents ($P = 1.00$) or western migrants ($P = 1.00$) in the late period (Fig. 6). When comparing the early period to the late period, NDVI was higher during the early period for the residents only ($P = 0.002$; Fig. 6).

Predation risk in calving areas differed between migratory tactics for wolves (K-W $\chi^2_4 = 81.36$, $P < 0.001$) and grizzly bears (K-W $\chi^2_4 = 80.29$, $P < 0.001$; Fig. 6). Wolf risk was higher in calving areas of resident elk than in calving areas of western or eastern migrants in both time periods ($P < 0.05$; Fig. 6). Predation risk from grizzly bears was highest in the calving areas of western migrants during both time periods, followed by calving areas used by residents in both periods, and lowest in calving areas of eastern migrants ($P < 0.05$; Fig. 6).

Habitat Selection During Calving Compared to Summer

Interactions between forage-related variables (NDVI and biomass) and predation risk of bears or wolves did not improve the model fit in any migratory tactic or time period (Table S8, available online in Supporting Information), indicating elk did not trade off quality or

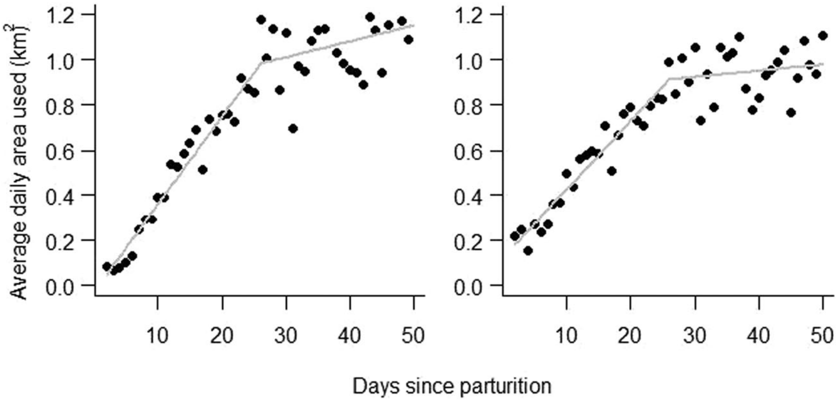


Figure 5. Average area (km^2) used every 24 hours since day of parturition by maternal elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002–2006 and 2013–2016. Left panel is the daily area used by elk since known ($n = 73$) dates of parturition, and right panel is the area used since both known and predicted ($n = 131$) dates of parturition. Both panels show a breakpoint at 26.0 ± 2.03 (SE) days. Lines represent a fitted segmented or piecewise regression model ($R^2 = 0.91$ and 0.88).

quantity of forage under predation risk. Instead, elk selected for larger extents of foraging resources on their calving areas than what was available on summer-use areas across all migratory tactics and in both time periods (Table 2). Western migrants in the early study period selected for calving areas with high extents of herbaceous-shrub land cover, particularly where NDVI values were high (i.e., positive herb-shrub × NDVI interaction). Western migrants in the late period showed similar selection for areas with high extents of herbaceous-shrub land cover and high NDVI values where burned land cover also occurred, depending on the extent of the burn (i.e., negative NDVI × burn interaction). Selection for foraging and calving areas by western migrants during the early time period was associated with high predation risk by bears, whereas western migrants avoided high predation risk by wolves during the late period.

Table 2. Top models with standardized coefficients indicating the latent selection differences between calving areas and areas used during summer by migrant and resident elk in the Ya Ha Tinda population, 2002–2006 and 2013–2016, Alberta, Canada. Predation variables included wolf (wolf) and grizzly bear (bear) resource selection function values, and habitat characteristics included forage greenness measured by normalized vegetation difference index (NDVI), forage biomass available (g/m^2; forage), and amount (%) of herbaceous or shrub land cover (herb-shrub), edge (edge) or burned habitat (burn), or cut forest (cut) within calving areas.

Time	Migratory tactic	Parameter	β	SE
2002–2006	Western	Bear	2.48	0.79
		NDVI	1.68	0.55
		Herb-shrub	2.87	0.93
		NDVI × herb-shrub	1.88	0.72
	Resident	Wolf	21.22	8.59
		NDVI	4.60	1.71
		Burn	33.33	14.16
		Wolf × burn	27.96	12.38
2013–2016	Western	Wolf	−2.10	0.78
		NDVI	1.76	0.74
		Herb-shrub	3.56	1.21
		Burn	3.03	1.07
		NDVI × burn	−0.92	0.45
	Resident	Wolf	0.41	0.41
		NDVI	2.08	0.42
		Herb-shrub	1.85	0.45
		Edge	−0.92	0.46
		Cut	9.25	4.66
		Wolf × herb-shrub	−0.71	0.27
	Eastern	Wolf	−3.58	1.52
		NDVI	1.92	0.80
		Herb-shrub	3.64	0.85
		Burn	1.06	0.46
		Cut	1.43	0.35
		Burn × cut	0.84	0.31

Resident elk during both time periods also consistently selected for calving areas with high mean NDVI values, and resident elk during the late period selected for high extents of forest cuts but against areas with edge (Table 2). Early residents selected for areas with high extents of burned land cover, particularly where predation risk by wolves was also high (i.e., positive wolf × burn interaction), and later residents selected for high extents of herbaceous-shrub cover, depending on predation risk by wolves (i.e., negative wolf × herb-shrub interaction).

Elk that migrated east of the Ya Ha Tinda winter range also selected calving areas with high percentages of herbaceous-shrub land cover and high NDVI values (Table 2). They additionally selected for burned and cut forest areas, particularly where these co-occurred in greater extents (i.e., positive burn × cut forest interaction). Eastern migrants showed stronger selection against areas of high wolf risk for calving than what occurred on areas used in summer.

DISCUSSION

Contrary to our hypothesis, we found little evidence that, at the scale of the calving range, elk traded off their use of high-quality forage resources for lower quality and safety from predation more on areas used during calving than on summer-use areas, despite the presumed vulnerability of newly born elk calves (Testa 2002). Researchers have reported that elk and other ungulates trade off quality forage associated with high predation risk to avoid risk from predators at the scale of the calf-rearing area (Barbknecht et al. 2011, Pitman et al. 2014, Lehman et al. 2018) and the birth site (Bergerud et al. 1984, Festa-Bianchet 1988,

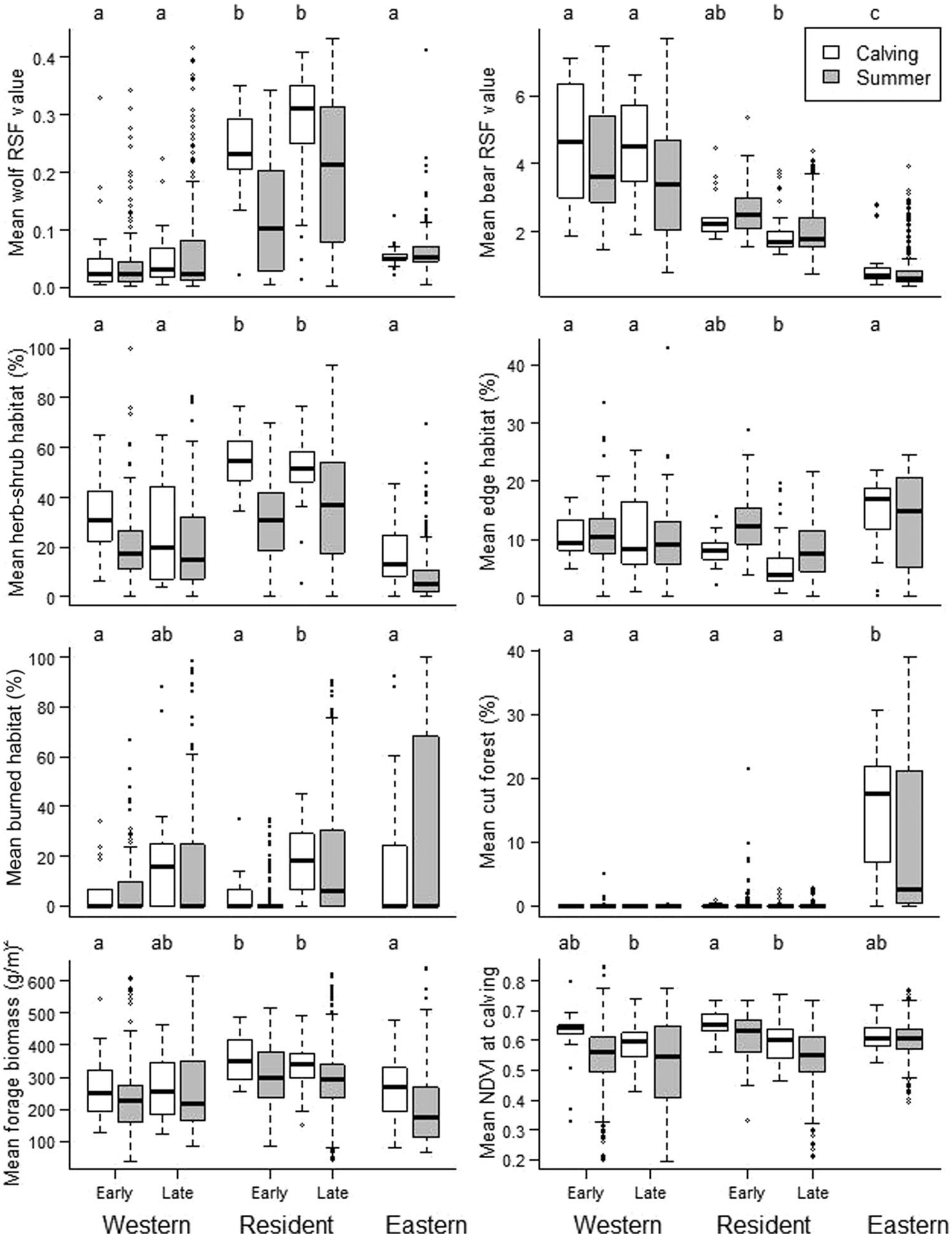


Figure 6. Comparison of predation risk and habitat characteristics in 26-day calving areas ($n = 131$) and summer areas of elk with 3 different migratory tactics and during 2 time periods (early: 2002–2006 and late: 2013–2016) in the Ya Ha Tinda elk population, Alberta, Canada. Predation risk included wolf and grizzly bear resource selection function (RSF) values, and habitat characteristics included forage greenness measured by normalized vegetation difference index (NDVI), forage biomass available (g/m^2; forage), and amount (%) of herbaceous or shrub (herb-shrub) land cover, edge or burned habitat, or cut forest. Small letters within each panel refer to differences of use during calving between migratory tactics and time periods.

Bowyer et al. 1999, Barten et al. 2001). In particular, we expected to see a negative interaction between forage and grizzly bear risk for the western migrants because of higher bear densities within BNP. But predation risk for western migrants was additive only, indicating that where elk responded to predation risk during calving, it was not at a greater expense of foraging areas when compared to summer. Maternal elk in our study, regardless of migratory tactic or time period, consistently selected for calving ranges with relatively large extents of actively growing vegetation. For example, elk consistently selected for areas with high NDVI values, reflecting productive, shrubby, herbaceous areas. Where these areas were not as readily available and predators were not as abundant (i.e., east of the Ya Ha Tinda), elk also did not trade quality forage for lower quality and safety from predation. Instead, they avoided areas of high risk by wolves, while also selecting for other open, productive land-cover types, including burns and forest cuts (Daubenmire 1968, Singer and Harter 1996).

Elk selection for foraging areas during the calving period exposed western migrants in particular to high grizzly bear risk because like elk, bears selected for shrubby, herbaceous areas during May and early June (Nielsen 2005). Ungulate migration is predicted to maximize access to forage, but predation may alter the benefits of a particular movement tactic (Berg et al. 2019). In the case of elk at Ya Ha Tinda, westward migration to high-elevation summer ranges exposed elk to higher forage quality, leading to higher pregnancy rates and calf mass in winter (Hebblewhite and Merrill 2011). Yet such westward migration also exposed their calves to the highest risk of grizzly bear predation because at the large scale, there were about 2 times the number of bears in BNP. These large-scale effects may have been further intensified at the fine scale by overlapping habitat selection between bears and elk. Because of the remoteness of the park, we did not have data on whether that exposure resulted in more calves killed by bears compared to other areas. High juvenile mortality from bears is consistent with our study's decline in western elk and mark-resight data on calves in summer and fall that indicated western migrants have lower calf survival compared to residents (Hebblewhite et al. 2018). As further support, adult collared elk that migrate into the park have higher mortality due to bears (Hebblewhite et al. 2018). This pattern is broadly consistent with elk migrations from the surrounding area into Yellowstone National Park in the United States, where high-elevation migrants are also exposed to higher grizzly bear-caused neonate mortality (Barber-Meyer et al. 2008, Middleton et al. 2013*b*). The pattern of habitat selection in western migrants did not change across time, despite a drop in the elk population size and a relative increase in bears in this area. This further supports the notion that selection for valuable forage areas is key during calving even in the face of high predation risk. Thus, differences in large carnivore densities across national park boundaries may set up ecologically significant gradients in predation risk that affect management of migratory elk populations across western North America.

In contrast to western migrants, resident elk were exposed to lower grizzly bear predation risk but to the highest predation risk by wolves. Nevertheless, we still did not find that resident elk traded off high-quality foraging under high risk during calving, or even that they avoided risky areas as much as on they do in summer (Hebblewhite and Merrill 2009; P. Smolko, unpublished data). The Ya Ha Tinda consists of a large, grassland complex surrounded by forests. Robinson and Merrill (2013) reported that vigilance of elk at Ya Ha Tinda increased with proximity to forest edge, indicating that elk perceive such areas as risky. During calving, resident elk dispersed across the area to isolate themselves, but in the later period, showed selection against forest edges where wolves or cougars are known to stalk prey (Holmes and Laundre 2006, Rearden et al. 2011). Resident elk may be able to a large degree avoid wolf and cougar predation on their calves by using or avoiding specific areas, such as burns or forest edges, within the larger landscape, in contrast to predation from bears that may be harder to avoid because of bears' systematic search strategy (Gunther and Renkin 1990, Zager and Beecham 2006, Mazur and Seher 2008, Rayl et al. 2015). Wolf and cougar predation on resident elk calves was low compared to bear predation (Berg 2019), which was consistent with other studies of elk calf mortality (Barber-Meyer et al. 2008, Griffin et al. 2011).

Although eastern migrants avoided areas of high wolf risk, they were no exception and did not trade off quality foraging areas for lower quality and lower predation risk more on areas used during calving than on those used in summer. Low overall predation risk from wolves in the east resulted from wolves being subject to legal trapping and hunting for up to 10 months each year, and some illegal harvest the rest of the year (Theuerkauf et al. 2003, Hebblewhite 2006). A lower number of bears was also likely because of high human activity, or that bears were less keyed into the east because elk increased their calving there only recently. Nevertheless, Berg (2019) reported that mortality by bears on elk calves of eastern migrants was higher than mortality by wolves during calving, even though predation rates on eastern migrant calves were low overall compared to residents and western migrants. Further, with relatively low extents of herbaceous vegetation and shrublands, eastern migrant elk additionally selected for burns and forest cuts, which Spilker (2019) reported wolves did not select. Studies in Yellowstone also indicated that downfall and regenerating vegetation in burns and cuts may provide cover for hiding calves and downed logs might make travel more difficult for wolves compared to elk (Mao et al. 2005, Forester et al. 2007, Mech et al. 2015).

Consistent selection across migratory tactics and over time for key foraging areas at the scale of the calving area suggests elk prioritized high nutritional requirements over evading predation postpartum. Elk remained generally near the parturition site for an average of 26 days, making the availability of directly adjacent forage key to meeting the nutritional demands of raising a calf as opposed to ungulates that use a following strategy. Further, elk inherently avoid risk of encountering predators to some degree because they isolate themselves to calve (Vore and Schmidt 2001). For example, isolation by some ungulates during parturition has evolved to avoid predators that key into large groups of prey (Vore and Schmidt 2001, Hudson et al. 2002), whereas others select for cover to conceal their young (Bongi et al. 2008, Ciuti et al. 2009, Van Moorter et al. 2009) or for open areas with high visibility that allows predator detection (Poole et al. 2007, Pinard et al. 2012, Blank et al. 2015). Isolation, where calves can also select small-scale cover to hide, may be a particularly effective strategy against predators with a coursing hunting style, such as wolves. Pitman et al. (2014) reported concealing vegetative cover influenced selection of young calves (i.e., <2 weeks of age). As calves become more mobile, elk are able to switch anti-predator tactics and return to social groups that provide greater predator detection and dilution of predation risk (Hebblewhite and Pletscher 2002).

The lack of evidence that elk trade off quality foraging areas associated with high risk for areas of lower quality to avoid predation more on areas used during calf-rearing than on areas used in summer implicates the potential selective advantages for maintaining access to high-quality forage to promote rapid calf growth (Forchhammer et al. 2001, Pettorelli et al. 2002, Feder et al. 2008). Daily food intake during lactation influences milk production and composition (Chan-McLeod et al. 1994, Landete-Castillejos et al. 2003, Oftedal 2018). Where nutritional resources are inadequate to meet these requirements, maternal body stores can be depleted such that offspring growth is depressed (Landete-Castillejos et al. 2003, Oftedal 2018), and the ability of adults to recoup body condition for subsequent reproduction limited (Clutton-Brock et al. 1989; Testa 2004*a*, *b*). The early growth of juvenile ungulates has been linked to calf body condition at the onset of winter and overwinter survival (Cook et al. 2004). Differences in early growth can also produce long-term demographic effects and have implications for variation in many life-history traits such as age and body size at maturity and lifetime reproductive success (Albon et al. 1987, Kruuk et al. 1999, Sæther et al. 2003).

Previously, our data indicated that the Ya Ha Tinda population was top-down regulated with wolves being the major source of mortality for adults, bear predation being key to neonates, and cougars playing a minor role (Hebblewhite et al. 2018, Berg 2019). Elk selection for forage resources on calving areas compared to summer areas at the expense of exposing calves to predation risk during the calving period is consistent with this hypothesis, but the spatial gradient in predation risk also may influence calf survival of elk following migratory tactics differentially. If grizzly bear predation of adult elk is dependent on elk density as suggested by Hebblewhite et al. (2018), we also might expect predation on calves of elk that migrate into BNP to decline over time. But density-dependent mortality of elk calves may not follow the same trajectory as adults because the strong selection for foraging areas makes calves more predictable. Wide-ranging grizzly bears (Craighead 1974), in particular, are highly effective in their search tactics for juvenile ungulates in spring (Gunther and Renkin 1990, Zager and Beecham 2006, Mazur and Seher 2008, Rayl et al. 2015). As a result, predation on calves may have contributed to a long-term decline in elk following the western migratory tactic that is not yet evident in elk following the other tactics. In contrast, wolf predation appears to be density-independent and to impose less of a constraint on early calf recruitment than bears but has the greatest effect year-round on adult female mortality (Hebblewhite et al. 2018). The strong landscape gradients in predation risk (especially that of grizzly bears) in our system may be reflective of predation gradients that are emerging across boundaries between other national parks, protected landscapes, and open public or private lands across western North America. The pattern we observed of greater exposure to high predation risk by bears in high-elevation, protected areas, especially if interfaced with lower-elevation private lands where agricultural subsidies and predator harvests keep elk from migrating (Wilmers and Levi 2013, Barker et al. 2018), may set up shifts in population dynamics that reduce the benefits of migrations and challenge elk managers across the West.

MANAGEMENT IMPLICATIONS

Conserving ungulate populations in places where carnivore populations are increasing is an ongoing management challenge, particularly when multiple jurisdictions have different management objectives. Our study indicated that growing carnivore populations may have a major influence on shifting migratory tactics in ungulates over time because of predation during calving, potentially exacerbating overall population declines or declines in the proportion of animals that migrate to higher-risk areas. Carnivore management, though extremely controversial, might provide the best opportunity for managing declining ungulate populations in areas of high predation risk. When regulation of carnivores is not an option, such as in protected areas, or where it is difficult to achieve effectively, increased efforts to protect ungulates, their migratory pathways, and seasonal ranges may be needed to help conserve partially migratory populations. On the other hand, results of our study also showed that growing carnivore populations may promote new, emerging ungulate migration patterns. A better understanding of what is influencing these changes will facilitate protection of these new migrations and could allow persistence of partially migratory ungulates in the face of environmental change.

ACKNOWLEDGMENTS

We thank R. W. and J. E. Smith, D. L. Gummer, and B. Hunt for project support, and J. Whittington and B. M. Fyten for coordinating wolf and elk capture and monitoring efforts. We thank M. M. Hayes for helpful discussion and support in predicting parturition, and K. L. Monteith, C. C. St. Clair, A. E. Derocher, and 2 anonymous reviewers for providing comments and discussion on earlier drafts of the manuscript. G. B. Stenhouse contributed grizzly bear resource selection functions. Financial and in-kind support came from Alberta Environment and Parks; Parks Canada; Natural Sciences and Engineering Research Council Discovery Grant to E. H. Merrill; Alberta Conservation Association; Minister's Special License—Hunting for Tomorrow and Alberta Fish & Game Association; Rocky Mountain Elk Foundation; Safari Club International Foundation; Safari Club—Northern Alberta Chapter; CICan; Science Horizons; TD Friends of the Environment; Alberta Sport, Parks, Recreation & Wildlife Foundation; Friends of the Eastern Slopes Association; Sundre Forest Products; fRI Research; National Aeronautics and Space Administration (USA, NNX11A047G to M. Hebblewhite); National Science Foundation (USA) Long-term Research in Environmental Biology grant (LTREB) to M. Hebblewhite and E. H. Merrill (1556248); and the Nestor and Sue Cebuliak, Bill Samuel, and William Wishart Graduate Awards.

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Associate Editor: Scott McCorquodale.

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