Elk migration patterns and human activity influence wolf habitat use in the Greater Yellowstone Ecosystem

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Identifying the ecological dynamics underlying human-wildlife conflicts is important for the management and conservation of wildlife populations. In landscapes still occupied by large carnivores, many ungulate prey species migrate seasonally, yet little empirical research has explored the relationship between carnivore distribution and ungulate migration strategy. In this study, we evaluate the influence of elk distribution and other landscape features on wolf habitat use in an area of chronic wolf-livestock conflict in the Greater Yellowstone Ecosystem, USA. Using three years of fine-scale wolf (n = 14) and elk (n = 81) movement data, we compared the seasonal habitat use of wolves in an area dominated by migratory elk with that of wolves in an adjacent area dominated by resident elk. Most migratory elk vacate the associated winter wolf territories each summer via a 40-60 km migration, whereas resident elk remain accessible to wolves year-round. We used a generalized linear model to compare the relative probability of wolf use as a function of GIS-based habitat covariates in the migratory and resident elk areas. Although wolves in both areas used elk-rich habitat all year, elk density in summer had a weaker influence on the habitat use of wolves in the migratory elk area than the resident elk area. Wolves employed a number of alternative strategies to cope with the departure of migratory elk. Wolves in the two areas also differed in their disposition toward roads. In winter, wolves in the migratory elk area used habitat close to roads, while wolves in the resident elk area avoided roads. In summer, wolves in the migratory elk area were indifferent to roads, while wolves in resident elk areas strongly avoided roads, presumably due to the location of dens and summering elk combined with different traffic levels. Study results can help wildlife managers anticipate the movements and establishment of wolf packs as they expand into areas with migratory or resident prey populations, varying levels of human activity, and front-country rangelands with potential for conflicts with livestock.

Key words: large carnivore conservation; elk; wolves; Greater Yellowstone Ecosystem; partial migration; habitat use; ungulate migration; livestock conflict.

INTRODUCTION

Large carnivores present persistent management and conservation challenges because they can kill domestic livestock, compete with humans for ungulate prey (Reynolds and Tapper 1996), and range widely across landscapes that are increasingly human-dominated (Woodroffe and Ginsberg 1998). The density of large carnivore species is often determined by the density and distribution of their prey (Carbone and Gittleman 2002) and understanding this relationship can help wildlife managers to predict and mitigate human-carnivore conflicts.

In many systems, migratory behavior results in the seasonal redistribution of large ungulates at vast geographic scales. Well known, long-distance migrants such as African wildebeest (*Connochaetes taurinus*) and barren-ground caribou (*Rangifer tarandus*) can migrate over 1,000 km, and species such as elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), and bison (*Bison bison*) move 20-200 km (Berger 2004, Sawyer et al. 2005). Such migratory movements are primarily driven by the seasonal availability of high-quality forage but may also reduce the exposure of prey to denning predators (Fryxell and Sinclair 1988) and thus, reduce the numeric response of predators to their migratory prey (Fryxell et al. 1988). Ungulate migrations differ in length, and the degree to which carnivores follow migrating prey is highly variable. Some carnivores do not move seasonally with their preferred prey due to the need to attend young at a fixed den location (Fryxell and Sinclair 1988). In contrast, some spotted hyaenas in the Serengeti (*Crocuta crocuta;* Hofer and East 1993) and cougars (*Puma concolor*) in the Sierra Nevada Mountains (Pierce et al. 1999) follow seasonal prey movements by making ‘commuting’ trips or sometimes fully migrating with their prey. Little empirical research has explored the relationship between seasonal carnivore distribution and ungulate migration strategies in the context of carnivore-human conflict.

Migration is likely to play an important role in seasonal wolf habitat selection patterns because wolf distribution has been widely linked to the distribution (Messier 1984, Ballard et al. 1997), abundance (Massolo and Meriggi 1998, Potvin et al. 2005) and diversity (Ciucci et al. 2003) of prey, including prey that migrate. For example, Ballard et al. (1997) characterized 11% of study wolves in northwest Alaska as migratory, because they followed migratory caribou (*Rangifer tarandus*) herds. Depending on the extent to which they follow migratory prey, wolf territories have been considered static from season to season (Messier 1984, Ballard et al. 1997), partially migratory (Ballard et al. 1997), or fully migratory (Walton et al. 2001). In the Greater Yellowstone Ecosystem (GYE), gray wolves prey primarily on migratory elk and establish their territories on elk winter range (Smith et al. 2004). Outside the core protected area of Yellowstone National Park (YNP), however, the low-elevation valleys where many ungulates winter are typically dominated by private lands and livestock grazing. Conflict between wolves and livestock can be locally chronic in these areas (Bangs et al. 2005), and the resulting wolf mortality can be the primary cause of death of these wolf populations (Smith et al. 2010). The coincidence of summer livestock grazing and the departure of migratory elk (i.e., the ‘replacement’ of native with domestic prey) has been hypothesized as a key driver of wolf-livestock conflict in the GYE (Garrott et al. 2005), but this notion has not been empirically evaluated. Variability in the abundance of native prey has also been linked to wolf depredation patterns in European systems (e.g., Sidorovich et al. 2003).

In recent years, declining ratios of migratory to resident elk have been documented in partially migratory populations of both the GYE (Middleton et al., in press) and Banff National

Park in Canada (Hebblewhite et al. 2005, Hebblewhite et al. 2006). In these ecosystems, resident elk subpopulations are often associated with front-country habitats, which are outlying areas characterized by lower elevation and a greater proportion of private land close to human development. The declining proportion of migrants in these populations has been partly attributed to higher rates of predation inside parks, where large carnivores are protected or recovering, than outside parks, where carnivore populations are often lethally managed. The growing abundance of resident elk, which remain year-round on low elevation front-country habitats (Hebblewhite et al. 2006; Middleton et al. in press.), may serve as an attractant to bring wolves into closer year-round contact with domestic livestock and exacerbate rates of conflict.

Another important factor that may influence wolves' ability to follow migrating elk is the need to regularly deliver food to their pups at den and rendezvous sites throughout the summer months (Thurston 2002). Reproducing packs can exhibit central place foraging behaviors during summer, while adopting nomadic territorial behavior during other parts of the year (Malikovic et al. 2011). In turn, in systems where prey migrate away during the denning period, wolves may fail to numerically track the reproduction and growth of the herd especially in multiple-prey systems (Mech and Peterson 2003). In Alaska, increased litter size in areas with high levels of ungulate biomass (Boertje and Stephenson 1992) and increased pup survival close to caribou migration routes in Canada (Frame et al. 2009) suggest a strong role of prey distribution during the time when wolves attend homesites. For wolves that rely on migratory prey, the importance of making large movements to access prey (Walton et al. 2001) may weaken their association with the natal den. For example, Scott and Shackleton (1982) found that wolves moved away from natal dens in summer to rendezvous sites closer to the seasonal range of black tailed deer (*Odocoileus hemionus columbianus*). In Alaska, where wolves are generally non-territorial in the season preceding whelping, they select their dens close to tree line, presumably to maximize their access to migratory caribou (Heard and Williams 1992). Wolves in some areas, however, can be strongly territorial during the winter months preceding den selection (Peters and Mech 1975), which can limit their flexibility in selecting natal den locations. For wolves that prey on elk in the northern Rockies, the timing of den selection often occurs while elk are congregated on winter range. Because of its influence on wolf movements, the den may be an important constraint on the ability of wolves to follow migratory prey.

Whereas much prior theoretical and empirical study points to the likely influence of ungulate migration strategies and den location in determining seasonal wolf movements, other lines of evidence highlight the importance of human activity and infrastructure. Human-caused mortality has historically threatened many large carnivore species (Woodroffe and Ginsberg 1998, Treves and Karanth 2003), and wolf avoidance of human structures and activity is well-documented (Mladenoff et al. 1995, Potvin et al. 2005, Oakleaf et al. 2006). For example, wolves in south-central Alaska use closed pipeline roads as travel corridors, but avoid oilfield access roads with higher traffic levels (Thurber et al. 1994). In Spain and Italy, wolves that live in disturbed areas are more active at night than day (Vila et al. 1995), and in Minnesota, wolves use cattle pastures more frequently at night, when human activity is low (Chavez and Gese 2006). In addition, the nocturnal activity of wolves has been shown to increase with road density and the availability of anthropogenic food resources (Theuerkauf 2009). Such dynamic tradeoffs between obtaining food resources and avoiding the risk of human-caused mortality complicate our understanding of wolf habitat selection, especially when the foraging costs and benefits for wolves change seasonally. As wolves expand their range into more developed areas of the northern Rockies, an important task is to reconcile the countervailing influences of such factors as prey migration with that of contemporary human development patterns.

In this study, we evaluated the seasonal habitat use of wolves in the GYE whose core winter territories encompassed either migratory or resident elk subpopulations. Our study area in northwest Wyoming is typical of many landscapes in the western US where expansive wilderness areas adjoin private ranches and public grazing allotments. The wolf packs we studied were characterized by high turnover rates due to lethal removals by management agencies in response to livestock depredations, followed by re-establishment by dispersing wolves (see also Musiani et al. 2005). In addition, resident elk are growing steadily more numerous in front-country habitats (Middleton et al., in press) that are managed for livestock grazing. These are often the same landscapes where hunter access and elk harvest on private ranch lands are limited, which provides a robust prey base for re-establishing wolves. We sought to evaluate the influence of elk distribution and human disturbance on seasonal wolf habitat use by using fine-scale GPS movement data from four wolf packs over three years. We took a comparative approach, contrasting habitat use in both summer and winter for three wolf packs living with limited summer availability of migratory elk and one wolf pack living with year-round availability of resident elk. Understanding how wolf movements are influenced by shifting prey distribution in such mixed-use landscapes can aid in efforts to integrate the often disparate goals of managing large carnivores, ungulates, and domestic livestock.

METHODS

Study area

We studied wolf habitat use in the Absaroka Mountains of northwest Wyoming, including habitats just inside the eastern border of YNP and east to the town of Cody, Wyoming (Fig. 1). Land ownership was primarily US Forest Service, with a mix of public, private and state land. The dominant vegetation types include alpine, subalpine, and montane meadows (≈ 40%), subalpine deciduous shrubland (20%), subalpine spruce-fir forests (13%), Douglas fir (*Pseudotsuga menziesii*) forests (11%), and sagebrush (*Artemesia spp.)* steppe (6%). The elevation of the study area ranges from 1,738 to 3,734 m. The Clarks Fork elk herd is partially migratory and consists of distinct subpopulations of migratory and resident elk. Migratory elk winter primarily in low-elevation valleys and migrate to the upper reaches of the Lamar River inside YNP during summer. These elk are preyed upon by three wolf packs (Sunlight, Beartooth and Hoodoo packs), and typically at least one additional pack in YNP during summer. The resident elk subpopulation is associated with front-country habitats, which are outlying areas of the ecosystem characterized by lower elevation, and a greater proportion of private land close to human development. The resident elk occupy the Absaroka foothills year-round within 16 km of the town of Cody, WY, and are preyed upon by one wolf pack (Absaroka pack). Wolf packs were almost entirely linked to either migratory or resident elk, which overlap relatively little (10%-15%) on winter range (Middleton et al. in press). During the years of 2007 – 2009, the study area encompassed the summer and winter range of approximately 4,000-5,000 elk in the Clarks Fork and Cody herds, 4,000-6,000 mule deer, 300-400 whitetail deer (*Odocoileus virginianus*), 200-300 pronghorn, and a small number of moose (*Alces alces*) (D.E.M., unpublished data). The study area contained three to five wolf packs each year, and grizzly bears (*Ursus arctos horribilus*), black bears (*Ursus americanus*), cougars and coyotes (*Canis latrans*) were also present. Several thousand head of cattle were grazed on public and private rangelands within the study area.

Capture and collaring

We captured 14 wolves between 2007 and 2009 by aerial darting in winter (n = 12) and leghold trapping in summer (n = 2). Four wolves were captured in the resident elk area (Absaroka pack) and 10 wolves were captured in the migratory elk area (Sunlight pack: n = 4, Hoodoo pack: n = 3, Beartooth pack: n=3). Each wolf was immobilized with 10 mg/kg Telozol for trapping efforts and 17 mg/ kg for helicopter capture (Kreeger and Arnemo 2007), delivered by a dart gun (Cap-Chur, Powder Springs, GA, USA); all wolves were fitted with GPS collars. Twelve wolves were fitted with Argos GPS collars (Model TGW-3580, Telonics Inc., Mesa, AZ), programmed to acquire a fix once every three hours, and three wolves were fitted with remotely downloadable collars (4400s Lotek Wireless, Newmarket, Ontario) that recorded one fix every 20 minutes during the summer months only (July-October). Argos collars were deployed for one full year, and Lotek collars were deployed for one to three months. Wolf data used in this analysis was modeled by individual wolf, which either had a 20 minute fix rate or a 3 hour fix rate, but not both.

Adult female elk were captured via helicopter netgunning and fitted with GPS collars (Telonics TGW-3600) in January 2007 and 2008 (n = 81), and the resulting movement data were used to create a seasonal elk density covariate. Collars were programmed to record a fix every 3 hours on summer and winter range, and every 8 and 24 hours respectively for the duration of migratory periods of September - October and April - June. The elk collars were programmed to drop off after 3.25 years. The effects of habitat-induced fix-rate bias were assumed to be minimal because of high mean fix rates (Whittington et al. 2011). Fix success of wolf collars were 91.6%

(+/- 1.2%) and elk collars 97.9% (+/- 0.4%). All animal captures were conducted according to protocols approved by the University of Wyoming's Institutional Animal Care and Use Committee.

Analysis of habitat use

To estimate the influence of landscape variables on seasonal wolf habitat use we employed the approach suggested by Marzluff et al. (2004), which uses kernel methods to translate point locations into a continuous estimate of intensity of use (i.e., the height of the kernel). We used each collared wolf in each season as the sampling unit, estimating a unique set of coefficients for each individual in each season. We characterized summer and winter seasons based on median elk migration dates of winter range departure and arrival for a subsample of elk collars that were retrieved in spring 2009 (n=9). Based on these criteria, we defined summer as May 27 - October 27 and winter as October 28 - May 26 in both migratory and resident elk areas.

We were primarily interested in how wolf habitat use was influenced by elk distribution, distance to den, roads, and other landscape features, including distance to forest edge and elevation. For each wolf, in each season, we delineated the available habitat in summer and winter by creating a 99% volume contour from a fixed kernel density estimate (Hawth's Tools; Beyer et al. 2005). We used 80% of the optimum bandwidth as a smoothing factor for each dataset (Kie et al. 2002, 2010), which we calculated for each wolf's dataset using the Animal Space Use Tool (Horne and Garton 2007). The 99% volume contour with 80% optimum smoothing factor appeared to effectively represent habitat available to wolves for a third-order analysis of habitat use (Buskirk and Millspaugh 2006). We felt a third-order analysis that compared habitat use within seasonal home ranges was the most appropriate scale to test the degree to which seasonal wolf habitat use did or did not shift to encompass distant areas of summering migratory elk. While we conducted our analysis at the home range scale, we did observe a number of extraterritorial forays, whereby wolves in the migratory elk area made trips toward the summer range of migratory elk (Appendix A).

To evaluate our use of the individual wolf (not pack) as the sampling unit, we examined the distance between collared pack members when two or more collars were simultaneously deployed in a pack. To explore temporal variation in 'pack cohesion', we averaged the distance between pairs of wolves during the summer (June – October) and winter (November – May) months. We observed an average distance between two pack members of 2668 m (+/-1660 m) in summer, and 2278 m (+/- 1448) in winter. Although wolves generally travel in cohesive packs, the variation around these estimates supports the use of individual wolves as the sampling unit for the purposes of this study. Because of our small sample size (n = 6 within-pack pairs), we considered this an evaluation of the association between pack members in our sample – not an analysis of population-level social behavior.

Seasonal elk distribution covariate

Generally, we predicted that wolves in both resident and migratory elk areas would increase their use of habitats with high elk density (their preferred prey in this system; Messier 1984) when territorial constraints allowed. However, we expected the influence of elk on wolf habitat use in the migratory elk area to diminish during summer, when wolves are constrained by the den and elk move outside of winter wolf territories to remote high-elevation habitat within YNP. Additionally, the option of preying on an alternate available prey species such as mule deer, might allow wolves living in the migratory area to avoid taking prolonged trips away from their den (Ballard et al. 1997). All GIS covariates and response kernel rasters were created using a 100-m cell size. To estimate elk distribution, we created fixed kernel density estimates using location data from 81 elk within the study area for summer and winter. Contribution of elk locations to the dataset varied by individual from 103 to 6423 locations, with an average of 4129 (CI 439). The majority of elk collars were deployed for the same time period, and all were pooled in creating the kernel.

Human activity covariate

Wolves respond differently to roads with different levels of human use (Thurber et al. 1994), so we estimated a primary road layer consisting of any roads receiving daily traffic, year round. Road polylines (U.S. Detailed Streets, ESRI, Redlands CA, USA 2002) were edited using satellite imagery. We then created a distance to nearest road raster using the Spatial Analyst distance function (linear). Although many studies conducted at a larger scale use road density as an index of wolf response to human activity (e.g. Mladenoff et al. 1995), our fine-scale GPS data warranted examining wolf response to particular road features. Generally, wolves tend to avoid human activity but will sacrifice road avoidance when preferred prey occur close to roads (Potvin et al. 2005). Thus, we expected wolves to use habitats close to roads more often in winter when elk concentrate at low elevations near roads, than in summer when elk disperse at higher elevations.

Other landscape feature covariates

Elevation was described with a digital elevation model (DEM) obtained from the US Geological Survey (http://seamless.usgs.gov/). The distance to den covariate raster was created using the Spatial Analyst distance function (linear) of known natal den locations. To calculate distance to forest edge, we reclassified the REGAP vegetation layer (GAP Ecological Systems, USGS, Moscow, ID, USA 2007) into forest and non-forest classes before creating a distance to forest edge raster.

Sampling spatial data

To relate wolf use to explanatory GIS variables, we created a sampling grid of 500 m x 500 m cells, created around regularly spaced center points that were clipped to the 99% volume contour for each wolf in each season. For each individual cell in the sampling grid, we estimated mean wolf utilization (height of the kernel) and the mean of each GIS covariate using Spatial Analyst zonal statistics tool (ArcMAP 2009). We then standardized values for each covariate by subtracting the measured covariate value from the mean and dividing by the standard deviation of that wolf's measured covariate dataset.

Habitat selection model

Analyzing each individual wolf in each season separately, we modeled probability of use as a function of habitat variables using PROC GLIMMIX in SAS 9.2, with a log link and a Gaussian error term. We modeled spatially correlated residuals using a spherical decay function by wolf, thereby addressing the error in model coefficient estimates that would otherwise be biased low (Marzluff et al. 2004). PROC GLIMMIX was configured to fit a unique sill and range value for each wolf (SAS Institute INC 2006) with no input parameters. Using kernel methods to estimate habitat use as the continuous response variable provided better biological accuracy and fewer problems with convergence than did our earlier efforts modeling counts directly (see also Hebblewhite and Merrill 2008).

Mixed-effects modeling techniques have recently been used to estimate hierarchical responses (e.g., wolves and packs) and individual responses to habitat covariates (Hebblewhite and Merrill 2008). Because the wolves in our study varied widely in the degree of spatial correlation in their use patterns, and because we could not achieve model convergence in models that included all wolves and seasons, we estimated model coefficients for each wolf separately in each season. This approach of modeling wolf habitat use provided a readily transparent means to characterize differential habitat associations of individual wolves. This approach yielded n = 8 sets of model coefficients in the migratory elk area and n = 3 sets of model coefficients in the resident elk area in each season. Using a functional data analysis approach (Zhao et al. 2004), we sought to evaluate the influence of each habitat variable on intensity of use (i.e., whether coefficients were different from zero) and to determine if each variable's influence differed between wolves in migrant or resident elk areas in each season. Functional data analysis draws inference by first generating summary statistics and then analyzing summary results (e.g., evaluating selection for each wolf, then comparing among groups). To evaluate model coefficients for migratory and resident elk areas in each season, we estimated bootstrapped confidence intervals by first randomly sampling with replacement from the wolves in each area, then drawing a bootstrap coefficient at random from a normal distribution using the coefficient as the mean and the variance estimate produced by GLIMMIX (n=1000 bootstrap samples). Significant influence of a variable on habitat use was determined by evaluating if 95% bootstrapped confidence intervals overlapped zero. To test for differences in the influence of variables on habitat use between seasons and between migratory and resident elk areas, we conducted a similar bootstrap procedure, except that we used the bootstrapped differences and drew randomly from the distribution of normally distributed differences between model coefficients of compared groups.

Nocturnal activity and human use

Because nocturnal and diurnal habitat selection patterns often differ in wolves due to lower levels of human activity at night (Vila et al. 1995, Hebblewhite and Merrill 2008), we sought to examine the difference in distance to road between day and night wolf locations.

Wolves exhibit more nocturnal activity near human development (Theuerkauf 2009), so we expected wolves in our study area to be closer to roads during night time, and that the difference between day and night would be most pronounced during winter when prey aggregate near roads. We identified daylight hours by monthly averages calculated by mean sunrise and sunset times (http://aa.usno.navy.mil), and assigned each wolf location to day or night time periods. We then calculated an average distance to road measure during day and night, paired for each pack in each season, and tested for differences between day and night use of road habitat using a paired t-test.

RESULTS

Winter

Wolves in both resident and migratory elk areas showed significant use of elk-rich habitat in winter (Fig. 2), supporting our predictions. In the migratory elk area, elk had a stronger influence on wolf use ($\beta_{MIG} = 0.0274$) than in the resident elk area ($\beta_{RES} = 0.0085$) although this difference was not significant (95% CIs were highly overlapping: Table 2; Fig. 3). As we expected, wolves in migratory elk areas were attracted to road habitat ($\beta_{MIG} = -0.1861$), however, contrary to our predictions, wolves in resident elk areas avoided roads in winter ($\beta_{RES} = 0.0618$, Table 1; Fig. 4).

Wolves in both areas showed significant use of habitats close to the den ($\beta_{MIG} = -0.4887$, $\beta_{RES} = -0.1950$, Table 1) in winter, but such use was stronger for wolves in the migratory elk area than in the resident elk area (Fig. 5, Table 2). This relationship could be driven by movements in the months of April – May when wolves tend to localize around the den (our winter time period ended May 27); inspection of wolf locations indicated that they spend time near their dens throughout winter. Wolves in the migratory elk area showed stronger use of lower elevation habitats than did wolves living in resident elk areas (Table 2), likely due to the more rugged topography in the migratory elk area. In contrast with other studies (Bergman et al. 2006), forest edge habitat did not influence wolf habitat use patterns (Table 1).

*Summe*r

Although we predicted the influence of elk density to taper off in summer months for wolves in the migratory elk area, areas of high wolf use still had a positive association with elk-rich habitat in summer (β_{MIG} = 0.0152, Table 1). Wolves in the resident elk area were more strongly influenced by elk (β_{RES} = 0.0711) than wolves in the migratory elk area, and the influence of elk was also stronger in summer than winter (Table 2; Fig. 4). In the migratory elk area, wolves were not influenced by roads in summer (β_{MIG} = 0.0092), while wolves consistently avoided roads in the resident elk area (β_{RES} = 0.1704, Table 1; Fig. 6). In the resident elk area, wolf use of habitats close to dens was stronger in summer (β_{RES} = -0.4166) than winter (β_{RES} = -0.1950, Table 1). This pattern was different for wolves living in migratory elk areas, which showed similar levels of use of habitats close to their den between seasons (Fig. 5). Although we expected wolves in the migratory elk areas to spend less time at the den compared with the resident elk area, there was no difference in the influence of the den between areas during summer (Table 2). Contrary to what we predicted for the summer, wolves in both prey areas showed use of low elevation habitats, likely because they only occasionally used high elevation habitat with elk but spent more time at moderate elevations close to their homesites. Wolves' habitat use was random with respect to forest edge habitat in summer (Table 1).

Wolves living in both migratory and resident elk areas showed similar differences in their use of road habitat in day compared to night. As expected, pairing mean day and night locations within each pack and season, we found that wolves used habitat closer to roads at night compared to day. This effect differed between seasons, with an average 392 m (SE = 163, P=0.004) difference in winter and a 134 m difference in summer (SE = 37, P = 0.013; Fig. 7).

DISCUSSION

Wolves in adjacent habitats dominated by migratory and resident elk differed in their use of elk-rich areas and their avoidance of roads. These findings affirmed the importance of interactions between prey migration and human activity as predictors of seasonal wolf movements. It was unclear if wolves in the migratory elk area would maintain use for elk-occupied habitats through spring and summer. An important finding is that wolves living in the migratory elk area appeared to behaviorally adjust throughout the summer to access elk distant from their den sites, by moving to rendezvous sites, accessing nearby resident elk, and taking extraterritorial forays towards summering migratory elk (Appendix A). While we expected wolves in the resident elk area to use elk-rich habitat in summer, unexpectedly, the difference in influence of elk on wolf habitat use between summer and winter was much greater among wolves in the resident elk area, than the migratory elk area.

In the resident elk area, the weaker influence of elk in winter was likely caused by wolf avoidance of human activity associated with the main north-south highway that bisects the elk winter range (Figs. 4 & 6). A county road also bisects the winter range of migratory elk, but this road was not avoided by wolves (Fig. 2a), likely because the wintering elk were tightly associated with the valley bottom where the low-traffic road is located. Nevertheless, wolf avoidance of roads in the resident elk area appeared to more strongly disassociate wolf movements from elk-rich habitat than did the 40-60 km seasonal shift in prey distribution experienced by wolves in the migratory prey area. We also found that wolves in both areas use habitats close to human development more frequently during the night than the day (Vila et al. 1995, Chavez and Gese 2006). Such a strategy may allow wolves to access elk that aggregate in areas of high human activity (i.e., by using the cover of darkness to hunt). Although we found considerable variation between individuals and packs, likely constrained by age, sex and territoriality, our findings suggest that the migratory habits of elk can influence wolf habitat use in predictable ways. These findings bear on several aspects of wolf ecology and management, particularly with respect to the expanding distribution of wolves, the changing migratory patterns of elk, and the growth of human development.

Wolf response to human activity

Wolves in the migratory and resident elk areas responded to human activity (i.e., roads and traffic) in disparate ways that appear to be driven by different patterns in the distribution of their prey and the intensity of human activity. Wolves generally avoid areas with high road density (Mladenoff et al. 1995), except in cases where they might access prey-rich areas close to roads (Potvin et al. 2005), or use low-traffic roads for travel (Thurber et al. 1994). We found that in winter, wolves in the resident elk area failed to access the most elk-rich habitat immediately adjacent to a major highway (Fig. 2b), and wolf locations away from the road were consistent with known distributions of bull elk during winter (D.E.M., unpublished data). The high abundance of elk within the resident elk area (Middleton et al. in press) may have alleviated the need for wolves to access prey close to roads that they perceive as risky. In the migratory elk area, wolves showed significant use of habitat near roads (and associated housing) that run through the core of their winter range. There exist few other habitats where wolves in migratory elk areas can predictably locate large groups of prey outside of these valley bottoms in winter. Despite differences in avoidance or use of road habitat, all wolves used habitat closer to roads at night, and differences in nocturnal activity were strongest in winter when elk are close to roads (Fig. 7). These results suggest that 1) wolves frequent human-dominated areas to a greater degree when high prey density provides a strong incentive (Treves et al. 2004); and 2) where prey exist close to humans, wolves reduce their risk of human-caused mortality by increasing their nocturnal behavior (Theuerkauf 2009). For example, Hebblewhite and Merrill (2008) showed that wolf packs with home ranges farther from human development have a decreasing tendency for human-driven nocturnal activity, while our results suggest the same effect for wolves existing farther from roads in summer compared to winter (Fig. 6). Together, these findings indicate that wolves respond dynamically to human disturbance as they seek prey (Vila et al. 1995, Theuerkauf 2009), which allows them to tolerate and use areas with low levels of human development.

Wolves occupying the resident elk area appear to have a potential advantage, because they can maximize access to prey while minimizing risk of human-caused mortality on a year-round basis (Fig. 8a, b). In contrast, wolves living in the migratory elk area can only simultaneously use elk-rich habitats and avoid roads in summer (Fig. 8b). Optimizing the tradeoff between avoiding humans and acquiring prey (Whittington et al. 2005) may allow wolves in the resident elk area to achieve greater fitness than wolves in the migratory elk area (Messier 1984). However, higher rates of lethal wolf removal associated with chronic livestock depredation (Middleton et al. in press) in the front-country habitats of resident elk may ultimately negate such benefits. Nevertheless, our habitat use results do suggest that even in the face of high rates of lethal removal, wolves will continue to be attracted to – and even intermittently productive within – these front-country landscapes with abundant resident elk populations.

Do wolves follow migratory prey?

In migratory elk areas, we expected the influence of elk on wolf use to weaken once elk departed on their migration to summer range (Garrott et al. 2005). However, the influence of elk in the migratory elk area did not differ between seasons (Table 2), despite considerable change in the seasonal distribution of migratory elk (Figs. 3a & 4a). Wolves appeared to use four discernible strategies in summer to cope with seasonal shifts in elk availability. First, some wolves in the migratory elk area did not alter their distribution seasonally and showed weak or a negative association with elk, which could have been facilitated by the availability of alternate prey (similar to Northwest Alaska, Ballard et al. 1997). Predation data from our study area indicate that wolves may subsist partly on mule deer as an alternate prey source, killing about 50% each of deer and elk in summer months (Nelson 2011). Second, the Sunlight pack, which occupies a migratory elk territory adjacent to the resident elk area, killed elk in the periphery of the nearby resident elk herd during the summer months (Nelson 2011). We also documented extraterritorial forays towards the summer range of the migratory elk (n = 3 animals, 7 total trips; Appendix A), a behavior typical of wolves considered to be ‘partially migratory’ (Ballard et al. 1997). Finally, the Hoodoo and Sunlight packs appeared to shift their rendezvous sites closer to the summer ranges of migratory and resident elk, respectively. These latter behaviors, extraterritorial forays and rendezvous site shifts, seem to allow wolves to track migrating elk relatively well – largely explaining the unexpectedly consistent use of prey-rich habitat that we observed.

These patterns suggest that in our study system, the response of wolves to shifts in the distribution of their preferred prey - foray behaviors, hunting alternate prey and accessing nearby resident elk - may buffer them against the large fitness costs that have been observed in areas with a single migratory prey species that migrates long distances (Frame et al. 2009). In southwest Quebec, Canada, wolves living in areas amid low prey densities had higher adult and pup mortality compared to those living in high prey areas (Messier 1984), and wolves in Alaska had larger litters in habitats with high levels of ungulate biomass (Boertje and Stephenson 1992). In the absence of alternative prey, we might expect wolves in our study area to make trips more commonly and uniformly to groups of summering elk, despite their remoteness from den sites (see Cook et al. 1999). The availability of mule deer as an alternate prey resource may allow wolves the flexibility to respond to seasonal changes in abundance of migratory elk by shifting their diet (Garrott et al 2007) without significantly shifting their distribution. For example, Milakovic et al. (2011) hypothesized that in a multiple-prey system, the lack of association between wolves and distribution indices for single ungulate prey indices occur because wolves select easily traveled pathways to maximize encounter rates with multiple potential prey species. Our results and the findings of others suggest there are likely benefits to accessing elk-rich habitat despite the costs of travel, and that variation in response to elk migration is supported by the presence of alternate prey. Further study is required, however, to assess the threshold distance at which such advantages outweigh the potential costs of traveling and of territorial trespass during these time periods.

Consistent with our expectations, wolves in the resident elk area spent more time near their den during summer (Table 2, Fig. 5) than winter. The ability of wolves living in the resident elk area to tend their young at the den while accessing abundant prey may confer fitness benefits, similar to higher rates of pup survival observed in wolf packs that denned close to caribou migration routes in Alaska (Frame et al. 2009). Wolves in the GYE establish dens in late winter (Thurston 2002), when migratory elk remain densely aggregated on low-elevation winter ranges. Thus, when prey migrate away during summer (as in other systems), wolves may be forced to travel long distances from the den to locate prey (Walton et al. 2001), whereas wolves with resident prey can access an abundance of prey close to their den (Fig. 3b). Such patterns, whereby migratory elk depart for high-elevation summer range, have been hypothesized to decouple wolves from the distribution of elk in summer, in much of the GYE (Garrott et al. 2005). However, our observations indicate strategies wolves may use to cope with this challenge. One strategy that wolves might employ is moving rendezvous sites closer to summering groups of elk. We documented one of three packs in the migratory area showing this behavior: the Hoodoo pack ceased activity at their natal den after July 23rd and moved to a rendezvous site 5.5 km closer to summering migratory elk. Indeed, wolves can move their pups to rendezvous sites that are within 1- 8 km from the den as summer progresses (Mech and Boitani 2003), distances which may be related to seasonal changes in distribution of prey (Packard 2003). There has been a lack of consensus about whether large carnivores can effectively follow the migrations of their prey. Our work suggests that in the GYE, where elk migration is common in summer, wolves use several different behavioral strategies to effectively cope with this seasonal challenge.

MANAGEMENT IMPLICATIONS

Migratory prey, resident prey and livestock depredations

In the GYE, and other areas of the northern Rockies, wolf populations are expanding into areas with high livestock densities. In this study we did not assess wolf response to cattle distribution. However, our finding that elk are a strong attractant for wolves in the resident elk area suggests that the risk of encounter between wolves and livestock may be elevated in pastures where elk and cattle comingle. On the other hand, we also found evidence that this elevated risk of encounter may be counterbalanced in pastures that are close to roads and human activity that can serve to deter wolves. Prior study in the northern Rocky Mountains found that elk presence in pastures increases the risk of wolf-cattle conflicts (Bradley and Pletscher 2005). Thus, obtaining and disseminating information about the timing of comingling between elk and cattle may help livestock producers to increase the level of attention (e.g., range riders) that ranchers give cattle in remote areas during key times of the summer. Wildlife management agencies may also seek to reduce the density of elk that comingle with these livestock, which has proven complicated when ranch owners are reluctant to allowing high levels of hunter access (Haggerty and Travis 2006).

In migratory elk areas, our study yielded two findings that could help predict wolf-livestock encounters in areas with low human density. Wolves in both prey areas used elk-rich habitat in winter (despite its close proximity to people) and habitat close to their natal den year round (Fig. 2a). Thus, livestock that graze in areas of low human activity among wintering elk may encounter wolves commonly, especially at night. Dens and rendezvous sites are known to be hotspots for conflicts with cattle (Oakleaf et al. 2003, Bradley and Pletscher 2005), and our results support the possibility of increased wolf-cattle encounters when cattle are close to den areas irrespective of the migratory behavior of prey. When livestock producers must use pastures with elk or close to dens, it may prove beneficial to do so when calves are older and less vulnerable, and with a greater amount of human attention (and activity).

Human-induced predation refugia for elk populations

Wolf pack avoidance of human activity - and specifically, roads - may translate to demographic benefits for the resident elk subpopulation we studied. Wolves are a primary predator of adult elk in the GYE (Smith et al. 2004) and an important secondary predator of elk calves (Barber-Meyer et al. 2008). Thus, wolf avoidance of human activity may create refuge areas for prey. In Banff National Park, elk thrived in and around the townsite of Banff, a pattern attributed to wolf avoidance of human activity in the area (Hebblewhite and Merrill 2007). A similar pattern has been observed in the Madison Valley of YNP, where White et al. (2009) suggested that elk have begun to favor areas of high visitor traffic in winter following wolf establishment. In our study, resident elk that cross a two-lane highway (i.e., WY Highway 120) escaped almost entirely from wolves, probably because wolves during our study avoided the highway. High rates of calf recruitment among resident elk in this area support the idea that resident elk are benefiting from lower rates of predation by bears and wolves alike (Middleton et al. in press). As carnivore populations are restored to the Rocky Mountain West, human-induced refugia may become an increasingly important driver of demographic differences among prey populations living amid varying levels of human development.

Growing resident front-country populations of elk

Amid growing tension in the northern Rockies between the interests of producing cattle and harboring robust wildlife populations on public and private rangelands (Haggerty and Travis 2006), there is a pressing need to better integrate the management of livestock and wildlife. A key finding of our study – that wolves' use of elk-dense areas can draw them into close contact with cattle operations – highlights these challenges. Livestock losses on private and public lands can reduce the tolerance for living with carnivores (Bangs et al. 2005). In turn, the lethal removal of wolves associated with livestock losses was the most common cause of death outside protected areas prior to wolves' de-listing from the Endangered Species Act, and such actions influence wolf demography in the northern Rockies (Smith et al. 2010). This challenge is likely to grow if the ratio of migratory to resident elk continues to decrease in the region, providing "attractive sinks" to wolves that seek prey in the front-country agricultural matrix (Hebblewhite and Merrill 2008). Some management options are now emerging that may help reduce spatial overlap of elk and cattle in front-country habitats with high rates of wolf conflict. In northwest Wyoming, including within our study area, the Wyoming Game and Fish Department (WGFD) works cooperatively with landowners to reduce elk densities on private ranches, and employs personnel to intensively coordinate and manage hunter access on specific private lands. Following wolf de-listing, Montana Fish Wildlife and Parks works with cattle producers and hunters to provide wolf depredation hunts following confirmed livestock loss, which may help displace both wolves and elk from a close proximity to cattle (Treves 2009) on these landscapes where all three species comingle. Sustaining viable wolf populations while also reducing wolf-livestock conflicts into the future is likely to require creative solutions that integrate knowledge of cattle management, predator resource selection, and prey demography and movements.

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LITERATURE CITED

Ballard, W. B., L. A. Ayres, P. R. Krausman, D. J. Reed, and S. G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs: 3-47.

Bangs, E. E., J. Fontaine, M. Jimenez, T. J. Meier, E. H. Bradley, C. C. Niemeyer, D. W. Smith, C. M. Mack, V. J. Asher, and J. K. Oakleaf. 2005. Managing wolf-human conflict in the northwestern United States. Pages 340 - 356 *in* R. Woodroffe, S. Thirgood and A. Rabinowitz, editors. People and Wildlife: Conflict or Coexistence? Cambridge University Press, Cambridge, UK.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169:1-30.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18: 320-331.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications 16:273-284.

Boertje, R. D., and R. O. Stephenson. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. Canadian Journal of Zoology 70:2441-2443.

Bradley, E. H., and D. H. Pletscher. 2005. Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. Wildlife Society Bulletin 33:1256-1265.

Buskirk, S. W., and J. J. Millspaugh. 2006. Metrics for studies of resource selection. Journal of Wildlife Management 70:358-366.

Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. Science 295:2273-2276.

Chavez, A. S., and E. M. Gese. 2006. Landscape use and movements of wolves in relation to livestock in a wildland-agriculture matrix. Journal of Wildlife Management 70:1079-1086.

Ciucci, P., M. Masi, and L. Boitani. 2003. Winter habitat and travel route selection by wolves in the northern Apennines, Italy. Ecography 26:223-235.

Cook, S.J., R. Norris, and J. Theberge. 1999. Spatial dynamics of a migratory wolf population in winter, south - central Ontario (1990-1995). Canadian Journal of Zoology 77: 1740-1750.

Frame, P., D. H. Cluff, and D. S. Hik. 2009. Wolf reproduction in response to caribou migration and industrial development on the central barrens of mainland Canada. Arctic 61:134-142.

Fryxell, J. M.,J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? The American Naturalist 131:781-798.

Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3:237-241.

Garrott, R. A., J. A. Gude, E. J. Bergman, C. Gower, P. J. White, and K. L. Hamlin. 2005. Generalizing wolf effects across the Greater Yellowstone Area: a cautionary note. Wildlife Society Bulletin 33:1245-1255.

Garrott, R.A., J.E. Bruggeman, M.S. Becker, S.T. Kalinowski, and P.J. White. 2007. Evaluating prey switching in wolf-ungulate systems. Ecological Applications 17: 1588 -1597.

Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. Geoforum 37:816-830.

Harrington, F.H. and L. D. Mech, 1982. Patterns of homesite attendance in two Minnesota wolf packs. Pages 81-105 *in* F.H. Harrington and P.C. Paquet, editors. Wolves of the world: perspectives of behavior, ecology and conservation. Noyes, Park Ridge, New Jersey, USA.

Heard, D. C., and T. M. Williams. 1992. Distribution of wolf dens on migratory caribou ranges in the Northwest Territories, Canada. Canadian Journal of Zoology 70:1504-1510.

Hebblewhite, M., and E. H. Merrill. 2008. Modeling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834-844.

Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152:377-387.

Hebblewhite, M., E. H. Merrill, L. E. Morgantini, C. A. White, and J. R. Allen, Eldon Bruns, L. Thurston and T. E. Hurd. 2006. Is the migratory behavior of montane elk herds in peril? The case of Alberta’s Ya Ha Tinda elk herd. Wildlife Society Bulletin 34:1280-1294.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135-2144.

Hofer, H., and M. L. East. 1993. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. I. Social organization. Animal Behaviour 46:547-557.

Horne, J. S., and E. O. Garton. 2007. Animal space use tool. (http://www.cnr. uidaho.edu/population_ecology/animal_space_use).

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530-544.

Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J.-M. Gaillard, and P. R. Moorcroft. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society B: Biological Sciences 365:2221-2231.

Kreeger, T. J., and J. M. Arnemo. 2007. Handbook of Chemical Immobilization, 3rd edition. Sunquest, Laramie, USA.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85:1411-1427.

Massolo, A., and A. Meriggi. 1998. Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. Ecography 21:97-107.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1-34 *in* L.D. Mech and L Boitani, editors. Wolves: Behavior, ecology, and conservation. University of Chicago Press, Chicago, IL, USA.

Mech, L. D., and R.O. Peterson. 2003. Wolf-prey relations. Pages 131-160 *in* L.D. Mech and L Boitani, editors. Wolves: Behavior, ecology, and conservation. University of Chicago Press, Chicago, IL, USA.

Messier, F. 1984. Social organization, spatial distribution, and population density of wolves in relation to moose density. Canadian Journal of Zoology 63:1068-1077.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. In press. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology.

Milakovic, B., K.L. Parker, D.D. Gustine, R.J. Lay, A.B.D. Walker, and M.P. Gillingham. 2011. Habitat selection by a focal predator (Canis lupus) in a multiprey ecosystem of the northern Rockies. Journal of Mammalogy 92: 568-582.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9:279-294.

Musiani, M., T. Muhly, C. C. Gates, C. Callaghan, M. E. Smith, and E. Tosoni. 2005. Seasonality and reoccurrence of depredation and wolf Control in western North America. Wildlife Society Bulletin 33:876-887.

Nelson, A. 2011. The influence of migratory and resident elk movements on seasonal wolf habitat selection and depredation patterns. M.Sc. Thesis.

Oakleaf, J. K., C. Mack, and D. L. Murray. 2003. Effects of wolves on livestock calf survival and movements in central Idaho. Journal of Wildlife Management 67:299-306.

Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection by recolonizing wolves in the northern Rocky Mountains of the United States. Journal of Wildlife Management 70:554-563.

Packard, J. 2003. Wolf behavior: reproductive, social, and intelligent. Pages 35-65 *in* L.D. Mech and L Boitani, editors. Wolves: Behavior ecology and conservation. University of Chicago Press, Chicago, USA.

Peters, R.P. and L.D. Mech. 1975. Scent marking in wolves: Radio - tracking of wolf packs has provided definite evidence that olfactory sign is used for territory maintenance and may serve for other forms of communication within the pack as well. American Scientist 63:628:637.

Pierce, B. M., V.C. Bleich, J. D. Wehausen and R. T. Bowyer, 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986-992.

Potvin, M. J., T. D. Drummer, J. A. Vucetich, D. E. Beyer, R. O. Peterson, and J. H. Hammill. 2005. Monitoring and habitat analysis for wolves in upper Michigan. Journal of Wildlife Management 69:1660-1669.

Reynolds, J. C., and S. C. Tapper. 1996. Control of mammalian predators in game management and conservation. Mammal Review 26:127-155.

Sawyer, H., F. Lindzey and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin 33: 1266-1273.

Scott, B., and D. M. Shackleton. 1982. A preliminary study of the social organization of the Vancouver Island wolf. Pages 12-25 *in* F.H. Harrington and P.C. Paquet, editors. Wolves of the world: perspectives of behavior, ecology and conservation. Noyes Publications, New Jersey, USA.

Sidorovich, V.E., L.L. Tikhomirova, and B. Jedrzejewska. 2003. Wolf Canis lupus numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. Wildlife Biology 9:103-111.

Smith, D. W., E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of colonizing wolves in the northern Rocky Mountains of the United States, 1982-2004. Journal of Wildlife Management 74:620-634.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. Journal of Wildlife Management 68:153-166.

Theuerkauf, J. 2009. What drives wolves: fear or hunger? Humans, diet, climate and wolf Activity Patterns. Ethology 115:649-657.

Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin 22:61-68.

Thurston, L. 2002. Homesite attendance as a measure of alloparental and parental care by gray wolves (*Canis lupus*) in Northern Yellowstone National Park. M.Sc. Thesis.

Treves, A. 2009. Hunting for large carnivore conservation. Journal of Applied Ecology 46:1350-1356.

Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:1491-1499. .

Treves, A., L. Naughton-Treves, E. K. Harper, D. J. Mladenoff, R. A. Rose, T. A. Sickley, and A. P. Wydeven. 2004. Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. Conservation Biology 18:114-125.

Vila, C., V. Urios, and J. Castroviejo. 1995. Observations on the daily activity patterns in the Iberian wolf. Pages 335-340 *in* L. N.Carbyn , S. H. Fritts, and D. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Canada.

Walton, L. R., H. D. Cluff, P. C. Paquet, and M. A. Ramsay. 2001. Movement patterns of barren-ground wolves in the central Canadian arctic. Journal of Mammalogy 82:867.

White, P. J., R. A. Garrott, S. Cherry, F. Watson, C. Gower, M. Becker, and E. Meredith. 2009. Changes in elk resource selection and distribution within the reestablishment of wolf predation risk. Pages 451-476 *in* Garrott, R. A., P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone. Elsevier, San Diego, USA.

Whittington, J.C., M. Hebblewhite, N.J. Decesare, L. Neufeld, M. Bradley, J. Wilmhurst and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to event approach. Journal of Applied Ecology 48:1535-1542.

Whittington, J. C., C. S. Clair, and G. Mercer. 2005. Spatial Responses of Wolves to Roads and Trails in Mountain Valleys. Ecological Applications 15:543-553.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126-2128.

Zhao, Xin. J. S. Marron and M. T. Wells. 2004. The functional data analysis view of longitudinal data. Statistica Sinica 14: 780- 80.

FIGURES AND TABLES

Table 1. Habitat use coefficients averaged among collared wolves for summer and winter models in the migratory (n = 10 wolves) and resident (n = 4 wolves) elk areas. Confidence intervals are bootstrapped among individual wolf coefficients and significance ($P < 0.05$) denoted by bold text.

	WINTER MODEL						SUMMER MODEL					
	Migratory area			Resident area			Migratory area			Resident area		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI	
elk$^{\Psi\dagger}$	**0.0274**	0.0029	0.0573	**0.0085**	0.0006	0.0179	**0.0152**	0.0025	0.0283	**0.0711**	0.0522	0.0906
road $^{\Psi\dagger\Phi\text{ί}}$	**-0.1861**	-0.2659	-0.1156	**0.0618**	0.0310	0.0933	0.0092	-0.085	0.1204	**0.1704**	0.1372	0.2052
forest edge	0.0007	-0.003	0.0053	-0.0019	-0.0043	0.0004	0.0002	-0.002	0.0029	-0.0025	-0.0082	0.0026
elevation$^{\Phi}$	**-0.0424**	-0.06	-0.027	-0.007	-0.0145	0.0024	**-0.0296**	-0.0459	-0.0134	**-0.0334**	-0.0573	-0.0103
den$^{\dagger\Phi}$	**-0.4887**	-0.735	-0.29	**-0.195**	-0.3101	-0.091	**-0.422**	-0.6753	-0.2075	**-0.4166**	-0.4838	-0.3572

Ψ = Use coefficients are different between migratory and resident elk areas in summer.
† = Use coefficients in the resident elk area are different in summer and winter.
Φ = Use coefficients are different between resident and migratory elk areas in winter.
Ί = Use coefficients are different between summer and winter in the migratory elk area.

Figure 1. Study area map showing the year-round distribution of wolf study packs using areas with migratory and resident elk in northwest Wyoming. Year-round elk locations from GPS collars are indicated for migratory (black dots) and resident (white dots) subpopulations. The three wolf packs living in the migratory elk area (white 95% use contour, Sunlight, Hoodoo, and Beartooth packs) overlapped slightly with one another and the one wolf pack (Absaroka) living in the resident elk area (black 95% use contour).

Figure 2. In winter, locations of wolf packs living in the migratory elk area (Panel A) were strongly associated with elk (60% kernel contour), whereas wolf packs living in resident elk area (panel B) were weakly associated with elk that winter near a major highway.

Figure 3. Individual wolf habitat use coefficients for elk density with the population means (hollow circle) and bootstrapped confidence intervals for wolves living in the migratory and resident areas in winter (panel A) and summer (panel B). Packs using the migratory elk area included Hoodoo (X), Beartooth (diamond), and Sunlight (triangle) packs, with the Absaroka pack (square) using the resident area. Wolves were associated with elk-rich habitat across areas, but the strength of association is stronger for wolves in the resident elk area in summer, and the migratory elk area in winter.

Figure 4. Wolf packs living in the migratory elk area (panel A) accessed some areas of summering migratory and resident elk (60% kernel contour), whereas wolf packs living in resident elk area (panel B) were strongly associated with the summer range of resident elk.

Figure 5. Individual wolf habitat use coefficients for proximity to natal den were different in winter (panel A) between wolves living in migratory and resident elk areas. In the resident prey area, use of habitat close to natal den also differed between summer (panel B) and winter.

Population means (hollow circle) and bootstrapped confidence intervals are shown for wolves living in the migratory and resident elk areas. Negative habitat use coefficient indicates affinity for the den, and a positive coefficient indicates avoidance. Packs using the migratory prey area included Hoodoo (X), Beartooth (diamond), and Sunlight (triangle) packs, with the Absaroka pack (square) using the resident area.

Figure 6. Wolf use of habitat close to roads varied by season and by area. Individual wolf habitat use coefficients for open roads are given with the population means (hollow circle) and bootstrapped confidence intervals for wolves living in the migratory and resident areas in winter (panel A) and summer (panel B). Negative habitat use coefficients indicate strong use of road habitats, and positive coefficients indicate avoidance. Packs using the migratory prey area included Hoodoo (X), Beartooth (diamond), and Sunlight (triangle) packs, with the Absaroka pack (square) using the resident area.

Figure 7. Wolves used landscapes closer to roads at night than during the day. Mean differences of day vs. night paired locations by pack are shown for each season (n = four packs and 14 individual wolves).

Figure 8. Wolves in the resident elk area benefited from selecting for elk and avoiding roads (square marker; shaded quadrant in upper right) in both winter (panel A) and summer (panel B). Wolves in the migratory elk area, which included the Hoodoo (X), Sunlight (triangle) and Beartooth (diamond) packs, appeared to trade off these two resources to some degree, especially in winter when migratory elk move to low-elevation valleys close to human settlements. Positive coefficients for roads indicate avoidance.

Figure 1.

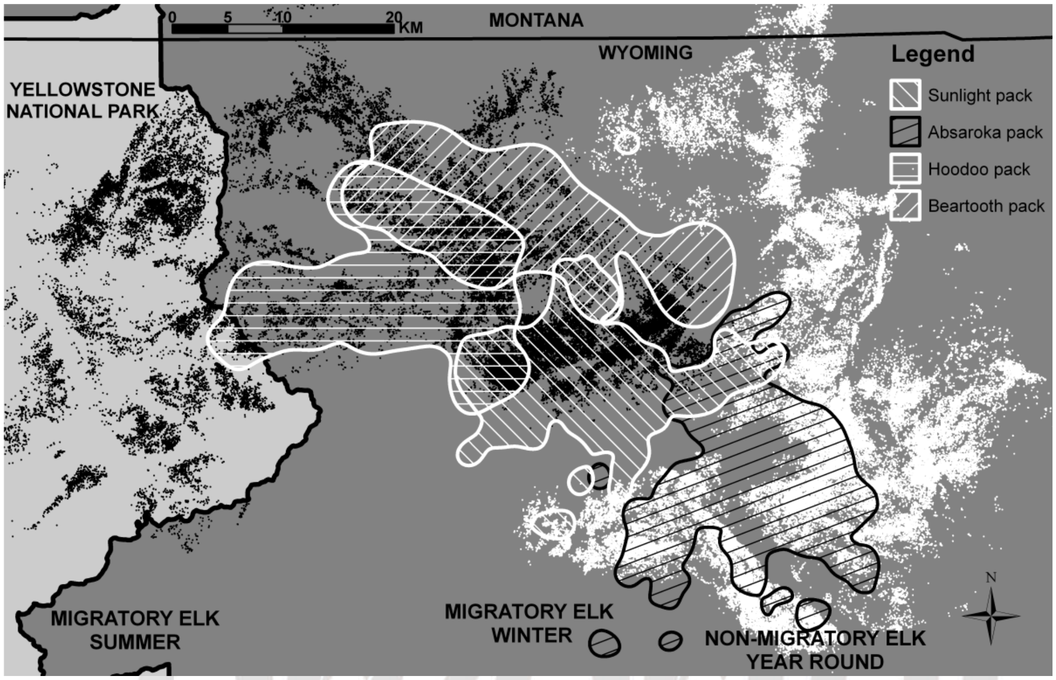

0 5 10 20 KM
MONTANA
WYOMING
YELLOWSTONE NATIONAL PARK
Legend
Sunlight pack
Absaroka pack
Hoodoo pack
Beartooth pack
MIGRATORY ELK SUMMER
MIGRATORY ELK WINTER
NON-MIGRATORY ELK YEAR ROUND
N

Figure 2.

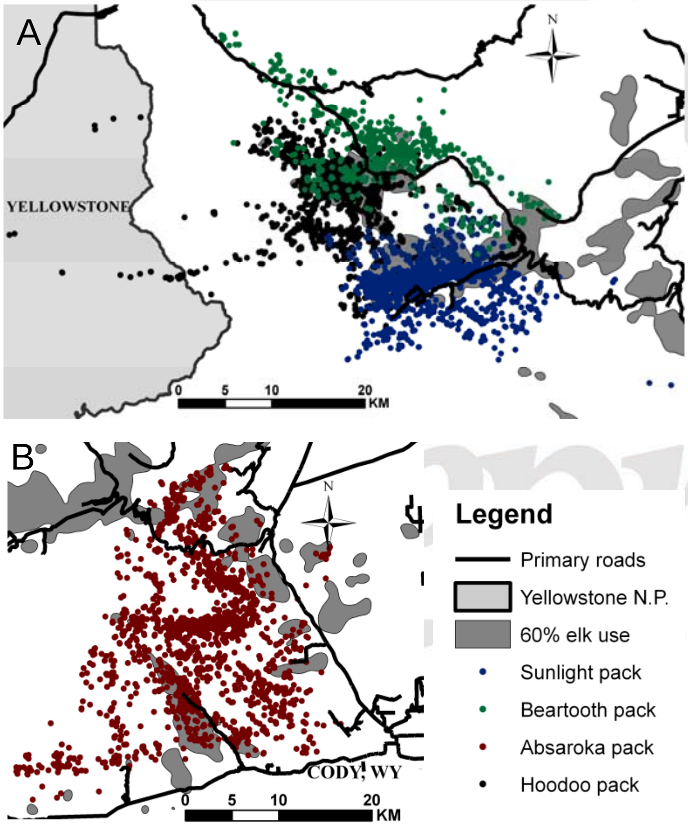
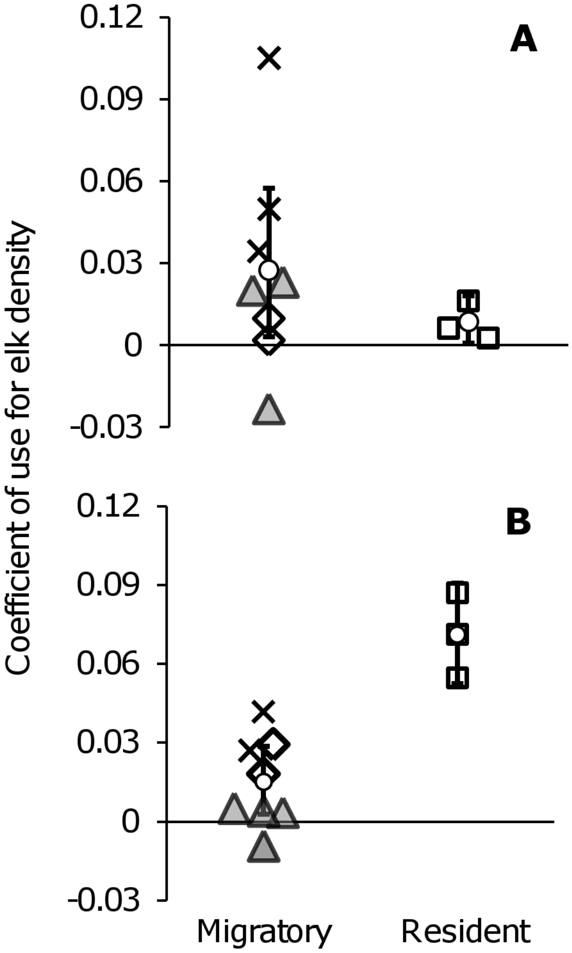

A
N
YELLOWSTONE
0
5
10
20
KM
B
N
CODY, WY
0
5
10
20
KM
Legend
Primary roads
Yellowstone N.P.
60% elk use
Sunlight pack
Beartooth pack
Absaroka pack
Hoodoo pack

Figure 3.



A
B
Coefficient of use for elk density
0.12
0.09
0.06
0.03
0
-0.03
Migratory
Resident

Figure 4.

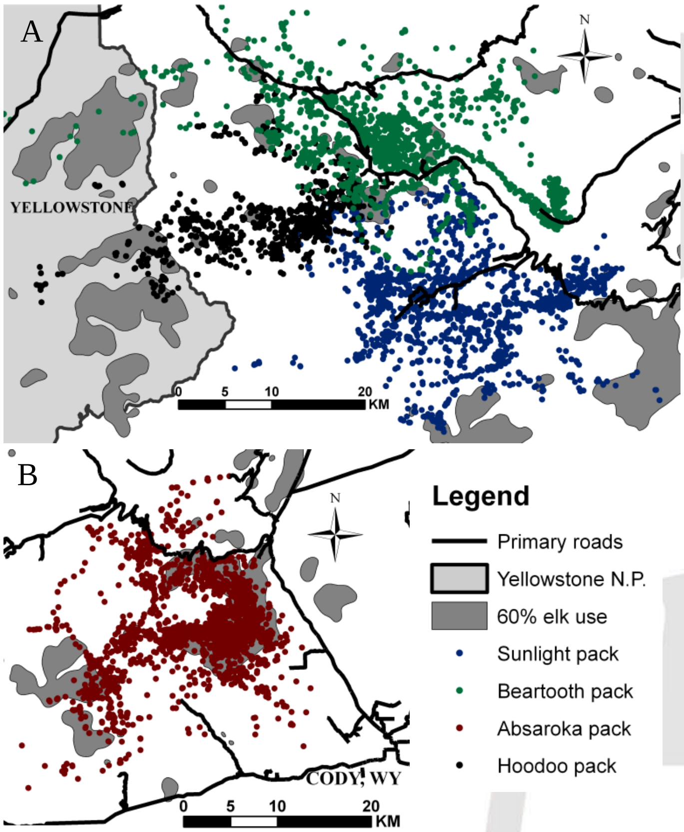

A
N
YELLOWSTONE
0 5 10 20
KM
B
N
CODY, WY
0 5 10 20
KM
Legend
Primary roads
Yellowstone N.P.
60% elk use
Sunlight pack
Beartooth pack
Absaroka pack
Hoodoo pack

Figure 5.

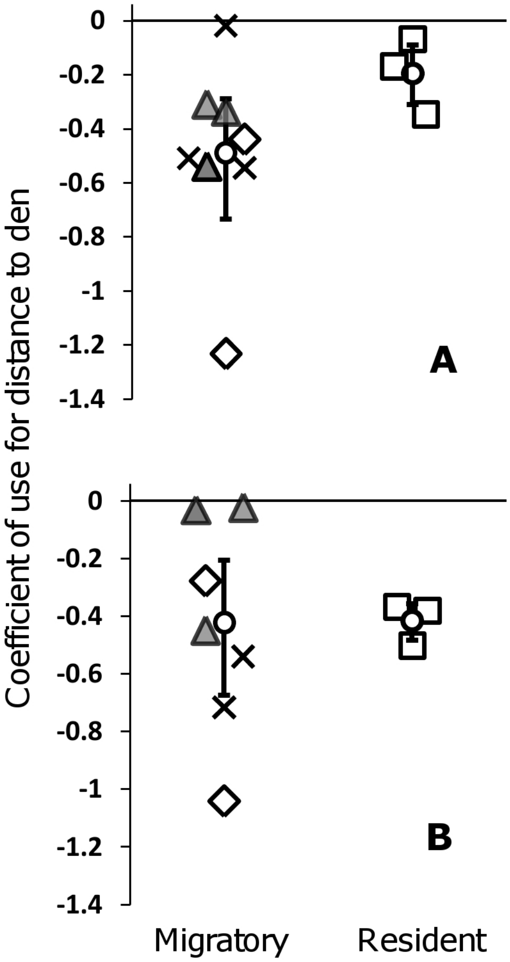

Coefficient of use for distance to den
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
-1.4
A
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
-1.4
B
Migratory
Resident

Figure 6.

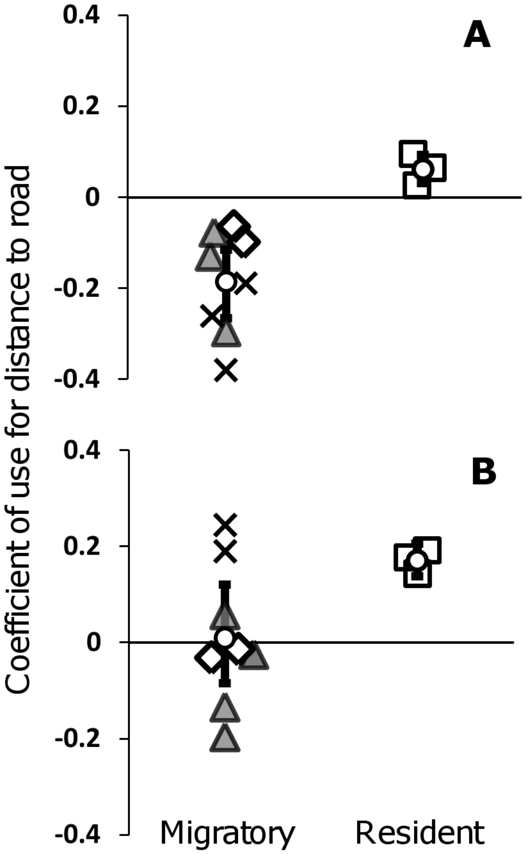

Coefficient of use for distance to road
0.4
0.2
0
-0.2
-0.4
A
0.4
0.2
0
-0.2
-0.4
B
Migratory
Resident

Figure 7.

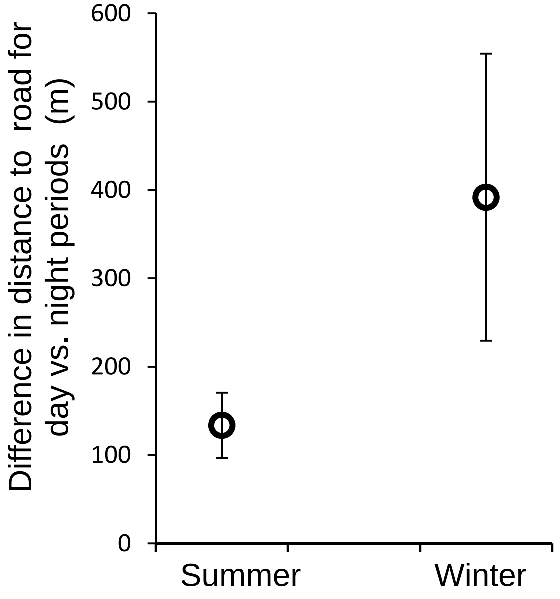
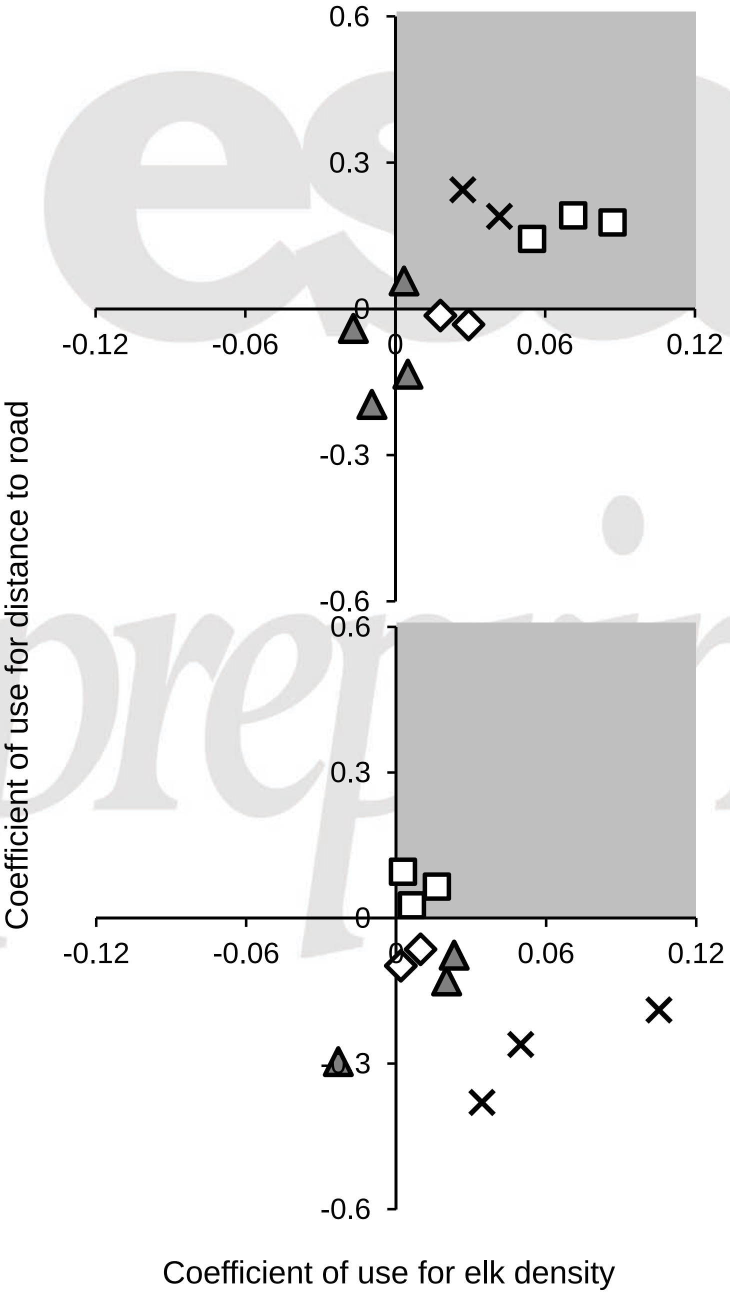

Difference in distance to road for day vs. night periods (m)
600
500
400
300
200
100
0
Summer
Winter

Figure 8.


0.6
0.3
0
-0.3
-0.6
-0.12
-0.06
0
0.06
0.12
Coefficient of use for distance to road
Coefficient of use for elk density