To the University of Wyoming:

The members of the Committee approve the thesis of Abigail A. Nelson presented on 5/26/2011.

Matthew J. Kauffman, Chairperson

Ken Gerow, External Department Member

Steve Buskirk

Dan Doak

APPROVED:

Frank Rahel, Program Chair, Department of Zoology and Physiology.

B. Oliver Walter, College Dean

Nelson, Abigail A., Master of Science, M.S., Deparment of Zoology and Physiology, August 2011.

Human conflict is a unique and persistent driver of management and conservation of large mammalian carnivores. Understanding these conflicts in space and time can assist in appropriate decision-making as managers seek to balance the population viability of carnivore species with management that curbs carnivore impacts on human livelihoods. The patchy distribution of prey-rich habitat across landscapes influences abundance and movements of wolves; however, many ungulate populations are partially migratory, and it is unclear how wolves respond behaviorally to the seasonal movements of migratory versus nonmigratory prey. In this context, wolf selection for prey-rich habitat can influence seasonal encounter rates and thus depredation rates on domestic livestock. In this study, conducted in Northwest Wyoming, USA, we use three years of fine-scale wolf (n = 14) and elk (n = 70) movement information to evaluate the influence of elk distribution and other landscape features on wolf habitat selection and patterns of depredation on domestic livestock.

THE INFLUENCE OF MIGRATORY AND RESIDENT ELK MOVEMENTS ON SEASONAL WOLF HABITAT SELECTION AND DEPREDATION PATTERNS

By

Abigail A. Nelson

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ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

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CHAPTER 1: THE INFLUENCE OF MIGRATORY AND RESIDENT PREY ON THE SEASONAL HABITAT SELECTION OF WOLVES IN NORTHWEST WYOMING

ABSTRACT*:* Identifying ecological dynamics that drive human-wildlife conflicts can help manage and conserve wildlife populations. Although it is well known that the distribution and density of ungulate prey determines the distribution of terrestrial carnivores, many ungulate populations migrate seasonally, complicating our understanding of their influence on carnivore movements. There has been little empirical research that links carnivore distribution to large-scale movements of their prey. In this study, we use three years of fine-scale wolf (n = 14) and elk (n=70) movement information to evaluate the influence of elk distribution and other landscape features on wolf habitat selection in an area of chronic wolf-livestock conflicts in the northern Rocky Mountains, USA. We compared the seasonal habitat selection of wolves living in an area dominated by migratory elk with that of wolves living in a nearby area dominated by resident elk. Wolves occupying the migratory elk area faced large-scale seasonal shifts in elk distribution (migration = 40-55 km), whereas wolves occupying the resident elk area had year-round access to abundant prey. We used a generalized linear mixed model to compare relative probability of wolf use as a function of GIS-based habitat covariates in the migratory elk area and the resident elk area. Wolves in the resident elk area selected for elk-rich habitat in both summer and winter, but selection for elk was stronger in summer. Wolves in migratory elk areas did not vary their selection for elk-rich habitat summer to winter, indicating various strategies to cope with summer departure of elk. Wolves differed in their associations with roads. In winter months, wolves in the migratory elk area selected for roads, while wolves in the resident elk area avoided roads. In summer, migratory elk area wolves were indifferent to roads, while wolves in resident elk areas strongly avoided roads, presumably due to a greater amount of traffic, and the location of dens. Although we observed differences in seasonal wolf habitat selection related to patterns of elk movement, our findings suggest that wolf avoidance of human activity plays an equally important role. Study findings can help managers anticipate the habitat use and establishment of wolf packs as they expand into areas with migratory or resident prey populations and varying levels of human activity.

INTRODUCTION

Understanding drivers of carnivore habitat selection as they relate to abundance and distribution of seasonal food resources may help predict variation in rates and locations of conflict. The density of large carnivore species that prey on ungulates is often determined by the abundance and distribution of prey (Carbone and Gittleman 2002), and thus prey distribution may mediate the spatial and temporal arrangement of conflicts between large carnivores and humans. These species require nuanced management because they can kill domestic livestock (Sillero-Zubiri and Laurenson 2001), compete with humans for ungulate prey (Reynolds and Tapper 1996), and range widely across landscapes that are increasingly human-dominated (Woodroffe and Ginsberg 1998, Brashares 2003, Treves and Karanth 2003). A remaining challenge is for ecologists and managers to understand how carnivores select habitat based on seasonal changes in distribution of migratory and non-migratory prey in ecosystems with varying levels of human use.

In many systems, the distribution of large ungulates changes seasonally due to annual migrations. Well known, long-distance migrants such as African wildebeest (*Connochaetes taurinus*) and barren-ground caribou (*Rangifer tarandus*) can move as far as 4,000 km, and species such as elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), and bison (*Bison bison*) move 40-400 km (Berger 2004, Sawyer et al. 2005). Such movements are primarily driven by the seasonal availability of high-quality forage and may reduce the exposure of prey to denning predators (Fryxell and Sinclair 1988). The degree to which carnivores follow migrating prey is highly variable. Some carnivores do not move seasonally with 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 even fully migrating with their prey. The extent to which a carnivore tracks migrating prey has implications for migratory ungulates and carnivore populations, as their associated predation patterns may induce dramatic changes in partially migratory prey populations (Hebblewhite et al. 2006; Middleton et al. unpublished ms.).

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 of Yellowstone National Park (YNP), the low-elevation valleys where many ungulates winter are typically dominated by private land, much of which is used to graze livestock. Conflict between wolves and livestock can be locally chronic in these areas (Bangs et al. 2005). The coincidence of summer grazing and the departure of migratory elk (i.e., the 'replacement' of native with domestic prey) has been hypothesized as a driver of wolf-livestock conflict in the GYE (Garrott et al. 2005), but this notion has not been empirically evaluated. Migration is likely to play an important role in seasonal wolf habitat selection patterns, in as much as wolf distribution range-wide is tightly 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 can be 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).

Dramatic reductions in the proportion of migrants to residents in partially migratory elk populations have recently been documented in the US (Middleton et al., unpublished ms.) and Canada (Hebblewhite et al. 2005, Hebblewhite et al.2006). The declining proportion of migrants in these populations has been caused partly by higher predation inside reserves where large carnivores are protected and recovering. As ungulate populations shift, the growing abundance of residents that remain year-round on low–elevation areas of mixed land-use (Hebblewhite et al. 2006; Middleton et al. *unpublished ms.*), may bring wolves into closer contact with domestic livestock and heighten conflict rates.

Wolves also alter their behavior to avoid the risk of human-related mortality while acquiring prey (Hebblewhite and Merrill 2008). Wolf avoidance of human disturbance is well-studied (Mladenoff et al. 1995, Potvin et al. 2005, Oakleaf et al. 2006) and mortality associated with humans has historically threatened large terrestrial carnivores (Woodroffe and Ginsberg

1998, Treves and Karanth 2003). For example, wolves in south-central Alaska use closed pipeline roads as travel corridors, but avoid oilfield access roads that have more traffic (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 were found to select more strongly for cattle pastures at night, when human activity was low (Chavez and Gese 2006). The level of nocturnal activity among wolf populations also increases with anthropogenic food resources and road density (Theuerkauf 2009). The tradeoffs inherent in such foraging behaviors are perhaps best evaluated within the framework of predation risk (Whittington et al. 2005). Thus it is possible that wolves drawn into close contact with human activity by resident prey can adaptively balance their own risk of mortality with their need to forage. Such dynamic tradeoffs between food resources and risk complicate our understanding of wolf habitat selection.

In this study, we evaluated seasonal habitat selection of wolves whose winter territories encompass either migratory or resident elk subpopulations. Our study area in northwest Wyoming is typical of many landscapes in the western US where private ranches and public grazing allotments abut expansive wilderness areas. The wolf population we studied was characterized by high turnover rates due to lethal removals of problem wolves or packs by management agencies, often followed by re-establishment by dispersing wolves (see Musiani et al. 2005). In addition, the resident elk subpopulation is growing more numerous on front country ranchlands (Middleton et al. unpublished ms.), which are managed for both domestic livestock grazing and often only light harvest of elk herds focusing on trophy bulls. Understanding how wolf movements are influenced by shifting prey distribution in such mixed-use landscapes can aid in the effort to integrate the management of large carnivores, ungulates, and domestic livestock. We sought to evaluate the influence of elk distribution and human disturbance on seasonal wolf habitat selection by using fine-scale GPS movement data from four wolf packs over three years. We took a comparative approach, by contrasting the habitat selection in both summer and winter for a wolf pack living with year-round availability of resident elk and three wolf packs living with limited summer availability of migratory elk.

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. 1.1). Land jurisdiction is 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)* steppe (6%). The elevation of the study area ranges from 1,738 to 3,734 m. The Clarks Fork and Cody elk herds consist of partially migratory elk. The migratory elk subpopulation winters in low-elevation valleys and migrates 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 occupies the Absaroka foothills year-round within 16 km of the town of Cody, WY, and is preyed upon by the Absaroka pack. 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, 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.

METHODS

Capture and collaring

We captured 14 wolves between 2007 and 2010 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 with10 mg/kg Telozol for trapping efforts and 17 mg/ kg for helicopter capture (Kreeger and Arnemo 2007), delivered by a Cap-Chur Palmer dart gun; 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 remote-downloadable collars were deployed for one to three months.

Adult female elk were captured via helicopter netgunning and fitted with GPS collars (Telonics TGW-3600) in January 2007 (n = 60) and 2008 (n = 10). 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. All animal captures were conducted according to protocols approved by the University of Wyoming's Institutional Animal Care and Use Committee.

Habitat selection analysis

To estimate the influence of landscape variables on seasonal wolf habitat use we used 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 selection 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.

For each wolf, 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 and Boroski 1996, 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 selection analysis (Buskirk and Millspaugh 2006).

We were primarily interested in how wolf habitat use was influenced by elk distribution, roads, distance to den, and other landscape features, including distance to forest edge, and elevation. We predicted that wolves in both resident and migratory elk areas would select strongly for elk, except for wolves in the migratory elk area in summer, when elk move to remote high-elevation habitat within YNP. 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 80 elk within the study area for summer and winter. Elevation was described with a digital elevation model (DEM) obtained from the US Geological Survey (http://seamless.usgs.gov/). Wolves respond differently to roads that experience 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, 2002) were edited using satellite imagery (NAIP Digital Ortho Photo Image 2007). We then created a distance to nearest road raster using the Spatial Analyst distance function (linear). We expected wolves to avoid roads less in winter when elk were concentrated at low elevations near road corridors, a pattern that has been observed elsewhere (Potvin et al. 2005). To relate wolf use to explanatory GIS variables, we created a sampling grid of 500m x 500m 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 per wolf.

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 (2009), with a log link, and a Gaussian error term. We modeled spatially correlated residuals using a spherical decay function as a random effect by wolf, thereby addressing the error in selection coefficient estimates that would otherwise be biased low (Marzluff et al. 2004). PROC GLIMMIX fit a unique sill and range value for each wolf (SAS Institute INC 2006) with no input parameters, consistent with the methods described by (Kleinschmidt et al. 2001). 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 selection 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 selection coefficients in the migratory elk area and n=3 sets of selection coefficients in the resident elk area in each season. We sought to evaluate selection or avoidance for each habitat variable (i.e., whether coefficients were different from zero) and to determine if the strength or direction of selection differed between wolves in migrant or resident elk areas in each season, thereby using a functional data analysis approach (Zhao et al. 2004). To evaluate selection 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 selection coefficient as the mean and the variance estimate produced by GLIMMIX. Significant selection was determined by evaluating if 95% bootstrapped confidence intervals overlapped zero. To test for differences in the strength of selection 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 selection coefficients of compared groups.

Because nocturnal and diurnal 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 locations. Because wolves exhibit more nocturnal activity near human development (Theuerkauf 2009), 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 selection for elk-rich habitat in winter (Fig. 1.2), supporting our predictions. In the migratory elk area, wolves showed stronger selection for elk (β_{MIG} = 0.0274) than those in the resident elk area (β_{RES} = 0.0085) although this difference was not significant (95% CIs were highly overlapping: Table 2; Fig. 1.3). As we expected, wolves in migratory elk areas were attracted to road habitat (β_{MIG} = -0.1861), however, contrary to our predictions, wolves in resident elk areas avoided roads in winter (β_{RES} = 0.0618, Table 1; Fig. 1.4).

Wolves in both areas showed significant selection for habitats close to the den (β_{MIG} = -0.4887, β_{RES} = -0.1950, Table 1) in winter, but such selection was stronger for wolves in the migratory elk area than in the resident elk area (Fig. 1.5, 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 selection for 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

In contrast with our prediction, wolves in the migratory elk area showed selection for elk-rich habitat in summer (β_{MIG} = 0.0152, Table 1) despite most elk migrating away from wolf den areas (Fig. 1.3). Wolves in the resident elk area selected more strongly for elk (β_{RES} = 0.0711) than wolves in the migratory elk areas, and their selection for elk was also stronger in summer than winter (Table 2; Fig. 1.4). In the migratory elk areas, wolves neither selected nor avoided roads in summer (β_{MIG} = 0.0092), while wolves consistently avoided roads in the resident elk area (β_{RES} = 0.1704, Table 1; Fig. 1.6). In the resident elk area, wolves selected for their dens more strongly 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 selection for habitats close to their den between seasons (Fig. 1.5). 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 between areas in selection for den in summer (Table 2). Contrary to what we predicted, wolves in both prey areas selected lower elevation habitats than available, likely because they use high elevation habitat with elk but spend more time at moderate elevations. Wolves used habitat randomly with respect to forest edge habitat in summer (Table 1). Trips to high elevation summering elk likely caused this result, as wolves may spend more time at comparatively lower elevations close to the den. Several wolves in migratory elk areas took extraterritorial forays in summer in the direction of summering migratory elk (n = 3 animals, total 7 trips; Table 2), but wolves in the resident elk area did not exhibit this behavior .

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. 1.7).

DISCUSSION

Wolf habitat selection patterns differed between adjacent areas that were dominated by migratory versus resident elk, affirming the importance of prey migration as a predictor of wolf movements. We predicted that wolves in the migratory elk area would not select for elk-rich habitat in summer, due to den-related movement constraints and availability of alternate prey;

however, both migratory and resident elk area wolves selected for elk in summer. While we expected wolves in the resident elk area to select for elk-rich habitat in summer, the difference in strength of selection for elk between summer and winter was much greater among wolves in the resident elk area, than the migratory elk area. Contrary to our main prediction, we also found that wolves living in the migratory elk area appear to adjust behaviorally 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. In the resident elk area, the weaker selection for 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. 1.4 & 1.6). A county road also bisects the winter range of the migrant elk, but this road was not avoided by wolves (Fig. 1.2A), likely because the wintering elk were tightly associated with the valley bottom where the road is located. Wolf avoidance of roads appeared to have more significant impacts on disassociating wolf movements from elk-rich habitat than the 40-55 km seasonal prey migration. 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 selection in predictable ways, and the variation among packs likely contributes to our understanding of how these effects may play out in different systems. These findings bear on several aspects of wolf ecology and management, particularly with respect to the expanding distribution of wolves, the changing migratory habitats of elk, and the continual progression of human development.

Variation in human activity

Wolves in the migratory and resident elk areas responded to human activity (e.g., roads and traffic) in disparate ways that appear to be related to the density and distribution of their prey and the intensity of human use. Wolves have often been observed to 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. 1.2b), 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 pack's territory (Middleton et al. unpublished ms.) may have facilitated such a weak association between wolves and collared cow elk. In the migratory elk area, wolves showed significant selection for 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 selection of roads, 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. 1.7). These results confirm that 1) wolf use of human-dominated landscapes occurs 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 adjust by using a greater degree of nocturnal behavior (Theuerkauf 2009), which decays with distance to road (Hebblewhite and Merrill

2008). For example, (Hebblewhite and Merrill 2008) show 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. 1.6). Together, these findings indicate that wolves respond dynamically to human disturbance as they seek prey (Vila et al. 1995, Theuerkauf 2009), which might allow them to tolerate or even use areas with low levels of human development.

Wolves in the resident elk area appear to have a distinct advantage in selecting for elk-rich habitat while avoiding roads on a year- round basis (Fig. 1.8a, b). However, wolves living in the migratory elk area both select for elk and avoid roads to a greater extent only in summer (Fig. 1.8b). Presumably these tradeoffs between avoiding humans and the associated risk of mortality while acquiring food (Whittington et al. 2005) would cause wolves in the resident elk area to have greater fitness than wolves in the migratory elk area (Messier 1984). Ultimately, however, given immigration, high quality habitat patches with growing available resident elk will likely result in continued high densities of wolves via turnover and reestablishment (Musiani et al. 2005) despite mortality. Of even greater consequence to population dynamics in this system is whether or not wolves are involved with livestock depredations and then undergo subsequent lethal removal. However, our wolf habitat selection results indicate wolves will continue to be attracted to these landscapes with resident elk.

Do wolves follow migratory prey?

In migratory elk areas, we expected wolf selection for elk to weaken once elk completed their spring migration (Garrott et al. 2005). However, the strength of wolf selection for elk in the migratory elk area did not differ between seasons (Table 2), despite considerable change in the seasonal distribution of migratory elk (Figs. 1.3A & 1.4A). This result would suggest that some individual wolves may follow migratory prey (Table 3); however, wolves appear to use four discernible strategies in summer to cope with seasonal shifts in prey availability. First, some wolves in the migratory elk area did not alter their distribution seasonally and showed weak or negative selection for elk, which could have been afforded given availability of alternate prey, similar to Northwest Alaska described by Ballard et al. (1997). In this system, predation data that we have collected indicate that wolves may be able to hunt sufficiently by using local deer as an alternate prey source, killing about 50% each of deer and elk in summer months (A. Nelson, Chapter 2). 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 (A. Nelson, Chapter 2). Third, some animals made extraterritorial forays towards the summer range of the migratory elk (n = 3 animals, 7 total trips), behavior typical of wolves considered to be partially migratory (Ballard et al. 1997). And fourth, the Hoodoo and Sunlight packs appeared to shift their rendezvous sites closer to the elk summer range – for the Hoodoo pack in the direction of summering migratory elk, and for the Sunlight pack close to summering resident elk. These data suggest that while wolves may spatially respond to the shifts in density of their preferred prey, encountering other alternate prey and having nearby resident elk may buffer them from more extreme fitness costs that wolves denning in areas with a single migratory prey species experience (Frame et al. 2009). In Southwest Quebec, Canada, wolves living in low prey areas had higher adult and pup mortality compared to those living in high prey areas (Messier 1984), and wolves had larger litters in habitats with high levels of ungulate biomass (Boertje and Stephenson 1992). Our results, and the results of others, suggest there are distinct rewards to accessing prey-rich habitat despite the costs of travel. Further study would be required, however, to assess the threshold distance at which such advantages outweigh the cost of traveling long distances.

Whether or not wolves follow migrating elk is mediated by the constraints placed on wolves as they regularly deliver food to young at den and rendezvous sites throughout the summer months (Thurston 2002). Consistent with our expectations, wolves in the resident elk area spent more time near their den during summer (Table 2, Fig. 1.5). 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 Yellowstone area establish dens in late winter (Thurston 2002) when migratory elk remain densely aggregated on low-elevation winter ranges. Thus, in other systems, when prey migrate away during summer, 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. 1.3b). Such a pattern, whereby migratory elk departure for high-elevation summer range decouples wolves from the distribution of elk in summer, has been hypothesized to occur in much of the GYE (Garrott et al. 2005). However, our observations indicate strategies wolves may use to cope with this dilemma. One strategy that may explain why wolf selection for elk remained positive after elk dispersed from winter range is moving centers of activity or rendezvous sites closer to summering groups of elk. We documented in one of three packs in the migratory area show this behavior: the Hoodoo pack ceased activity at their natal den after July 23rd, presumably moving 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). For example, Scott and Shackleton (1982) found that wolves moved to rendezvous sites in the direction of the seasonal range of black tailed deer (*Odocoileus hemionus columbianus*). This type of shift in homesite location likely explains some selection for elk during the summer. In Alaska, where wolves are generally non-territorial in the season preceding whelping, they select their dens close to tree line to maximize the time they can hunt migratory caribou (Heard and Williams 1992). In our study area, however, wolves are strongly territorial during winter months preceding den selection and may have limited flexibility in selecting natal den sites. There has been a lack of consensus about whether large carnivores can effectively follow the migrations of their prey. Our work suggests that wolves use several different behavioral strategies to cope with seasonal fluctuations in the distribution of their prey.

MANAGEMENT IMPLICATIONS

Migratory prey, resident prey and livestock depredations

In the resident elk area, our results suggest that encounters between wolves and livestock may be more frequent in pastures where elk and cattle comingle and relatively uncommon in pastures that are close to roads and human activity, during the day. Although we did not directly measure the depredation rates of wolves on cattle, our findings are consistent with prior studies in the northern Rocky Mountains that found elk density in pastures increases the risk of wolf-cattle conflicts (Bradley and Pletscher 2005). For livestock producers and wildlife managers, separation of wildlife (in this case elk) and livestock is a topic of increasing management importance for disease concerns; however, our results suggest that there may be additional benefits to maintaining separation to decrease livestock predator encounters. Additionally, such knowledge of the timing of cattle and elk comingling could be used to increase the level of attention (i.e., range riders) that ranchers provide their cattle during key times of the summer. However, these options can be expensive and at times may require much effort with limited success. An alternative management consideration may be the augmentation of efforts to reduce the density of elk that comingle with these livestock, which has proven complicated when ranch owners or managers are averse to allowing high levels of hunter access (Haggerty and Travis 2006). Several agencies in the region are attempting to address this issue through improved partnerships and hunter access programs.

In migratory elk areas, our study yielded two findings that could help predict wolf-livestock encounters in areas with migratory prey and low human density. Wolves in both prey areas selected for elk-rich habitat in winter (despite its close proximity to people) and habitat close to their natal den year round (Fig. 1.2a). Thus, livestock that graze in areas of low human density among wintering elk may encounter wolves commonly, especially at night. In our study area, livestock in the migratory elk area generally spend winters elsewhere, and do not overlap with wintering elk during the most vulnerable period of calving. However, in other parts of the GYE, producers calve in winter months among wintering elk, and this may partially explain winter and spring depredations that happen in these areas. 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 likelihood of increased wolf-cattle encounters around dens irrespective of the migratory behavior of prey. Because den selection is known to be related to predictable, aggregated food sources (Ciucci and Mech 1992), and appears to be related to wintering elk in our system, knowledge of prey distribution may assist in predicting where wolves den and hunt on the landscape, zones which may be high risk for conflict once cattle are turned out. Most producers are not afforded the flexibility of altering pasture use patterns due to consideration of grass phenology and the peak of poisonous plants among other restrictions. However, if necessary to use pastures with elk or close to dens, it may prove beneficial to do so when calves are older and less vulnerable.

Human-induced predation refugia for elk populations

Wolf pack avoidance of human activity - and specifically, roads - may translate to fitness benefits for the resident elk subpopulation we studied. Wolves are a primary predator of adult elk in the GYE (Smith et al. 2004), an important secondary predator of elk calves (National Research Council 1997, Barber-Meyer et al. 2008), and their predation pressure can influence lifetime reproductive contribution in ungulates (Kjellander et al. 2004). Thus, wolves' avoidance of human activity may effectively generate refuge areas for prey. In Banff National Park, elk prospered in and around the townsite of Banff, which was avoided by wolves (Hebblewhite and Merrill 2007). A similar pattern has been observed elsewhere 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 (White et al. 2009). In our study, resident elk that cross a two-lane highway (i.e., WY Highway 120) experience very low levels of exposure to wolves, which is likely caused by wolf avoidance of the highway. Recent changes in the demography of migratory and resident elk support the notion that resident elk are benefiting from lower rates of predation (Middleton et al. unpublished ms.). It is likely this is especially significant with respect to calf production; wolves are a predator of elk calves in YNP (Barber-Meyer et al. 2008, Metz et al. 2011 *in press*). The resident subpopulation currently experiences calf: cow ratios around 40 per 100, whereas the migratory subpopulation has declined to calf ratios of 15 per 100 cows, although poor summer habitat quality is also an important contributing factor (Middleton et. al. unpublished ms.). 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 along a gradient of human development.

Growing resident front country populations of elk

There is growing tension in the northern Rockies between the interests of producing cattle and harboring wildlife populations on private and public rangelands (Haggerty and Travis 2006), and thus a growing need for integrative wildlife and domestic species management. A key finding of our study, that wolf selection for elk is likely to draw wolves into close contact with cattle operations, highlights these challenges. Livestock loss due to the co-occurrence of wolves, elk, and cattle on private and public lands (Bradley and Pletscher 2005) can reduce the tolerance for living with carnivores (Bangs et al. 2005). In turn, lethal removal of wolves associated with domestic sheep and cattle influences wolf demography throughout the Northern Rocky Mountain region, as it is the most common cause of death for wolves outside protected areas (Smith et al. 2010). These consequences of comingling among elk, cattle and wolves are likely to become particularly acute if the ratio of migratory to resident prey continues to diminish in the region, providing “attractive sinks” to wolves outside of wilderness areas into the agricultural matrix (Hebblewhite and Merrill 2008). However management actions play out, our results suggest areas of congregating prey populations will remain important attractants to the fine-scale habitat use patterns of wolves. Some management options exist that seek to prevent elk and cattle from comingling. In the Paradise Valley of Montana just outside of YNP, Montana Fish, Wildlife and Parks employs an elk herder to keep elk and cattle separate during the winter season when elk are driven down onto low elevation ranchlands, mainly for disease reasons. Treves (2009) suggested managers increase hunter access and potentially reduce the spatial overlap of wolves and cattle by displacing wolves with hunters and reducing elk populations in these areas through hunter harvest. Managing wolves into the future is likely to require creative solutions such as these and others involving knowledge of prey demography and movements that can sustain wolf populations while reducing wolf-livestock conflicts.

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Table 1.1. Selection 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 mig	95%Cl-mig		β res	95%Cl-res		β mig	95% Cl-mig		β res	95%Cl-res	
elk[Ψ†]	**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 [Ψ† Φ 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[Φ]	**-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[† Φ]	**-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 = Selection coefficients different between migratory and resident elk areas in summer.
† = Selection coefficients in the resident elk area are different in summer and winter.
Φ = Selection coefficients different between resident and migratory elk areas in winter.
Ί = Selection coefficients different are different between summer and winter in the migratory elk area.

Table 1.2. Wolves in study area that took extraterritorial forays lived in the migratory elk area and generally travelled long distances towards migratory prey**.** This table does not include dispersal resulting in death (n = 2). Forays typically began either at a den or rendezvous (RV) site.

Wolf ID	Age	Start	End	Start	Destination	Dist. (km	Num. days
608M	3	6/17/2007	6/24/2007	den	YNP: Specimin ridge	155.8	7
608M	3	10/11/2007	10/14/2007	RV	YNP: Cache cr.	65.3	3
608M	3	10/21/2007	10/23/2007	RV	Republic cr.	55.1	2
664M	4	7/4/2008	7/15/2008	den	YNP:Lamar x Soda Butte cr.	231.4	11
664M	4	7/17/2008	8/2/2008	den	YNP: Hellroaring	444.8	16
673F	1.5	10/15/2008	10/28/2008	Crandall cr.	YNP: Jasper bench	158.4	13
697M	2	4/17/2009	4/27/2009	den	YNP: Lamar	83.7	10
					Average	170.6	8.9

Figure 1.1. 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) overlap slightly with one another and the one wolf pack (Absaroka) living in the resident elk area (black 95%use contour).

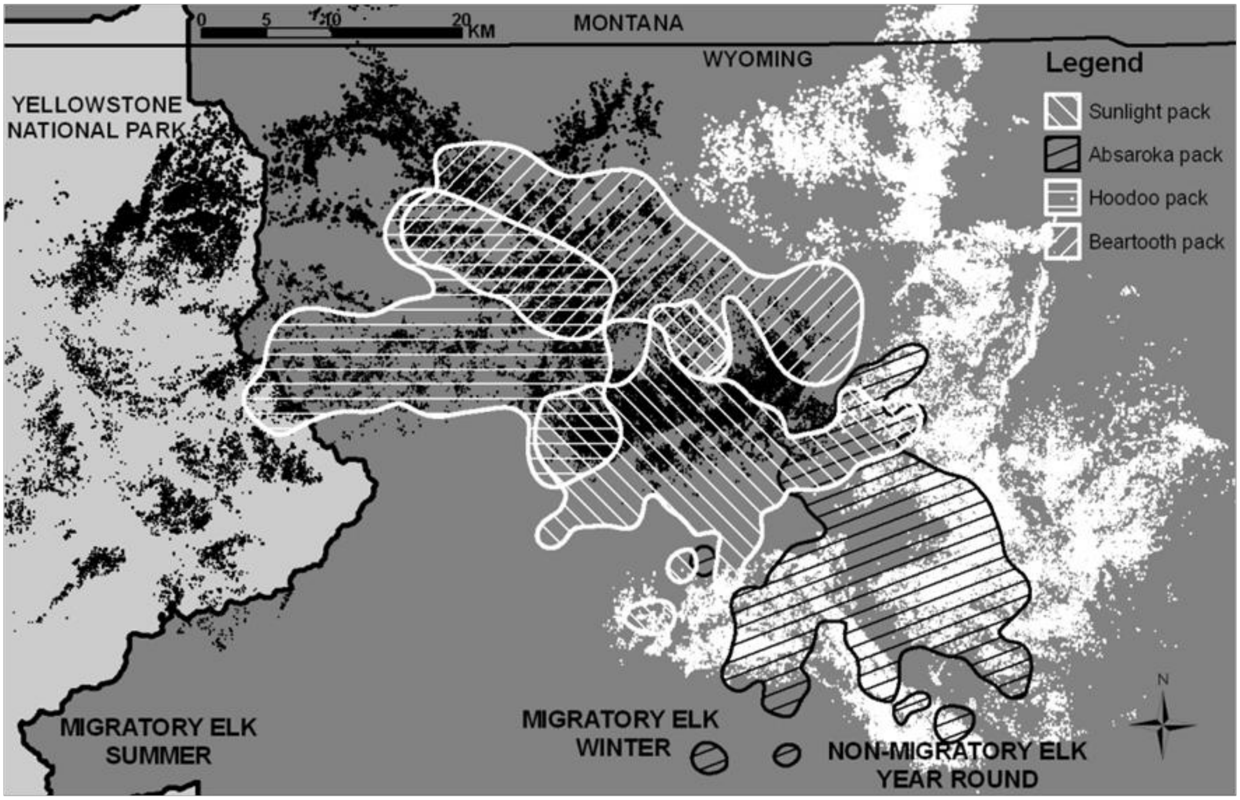


Figure 1. 2. Locations of wolf packs living in the migratory elk area (Panel A) are strongly associated with the wintering elk (60% kernel contour), whereas wolf packs living in resident elk area (panel B) are weakly associated with resident elk that winter near a major highway.

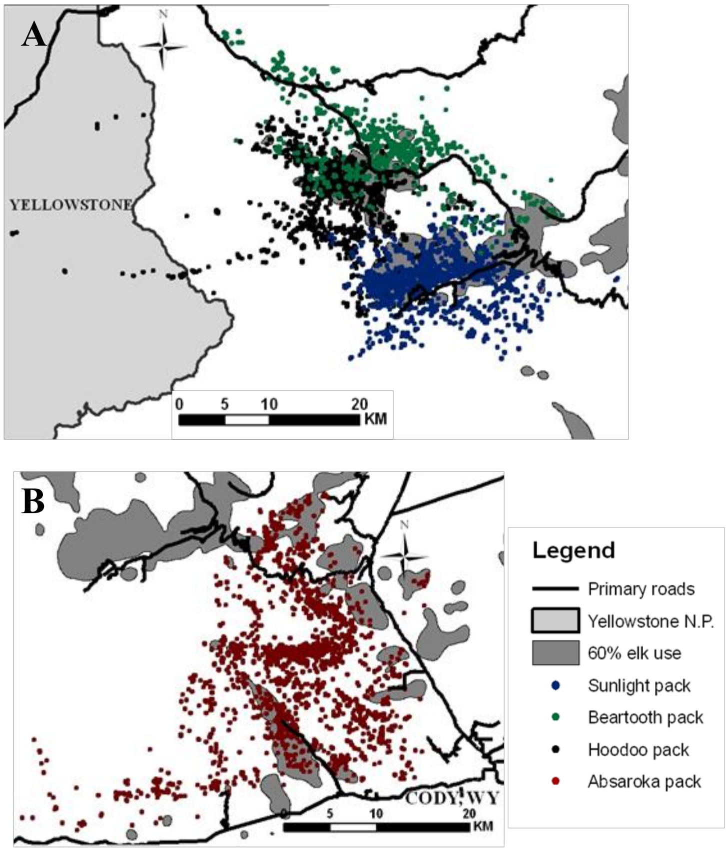


Figure 1.3. Wolves are associated with elk- rich habitat across areas, but the strength of association is mediated by seasonal migratory patterns of elk. Individual wolf selection coefficients for elk density with the population means (hollow circle) and bootstrapped confidence intervals for wolves living 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.

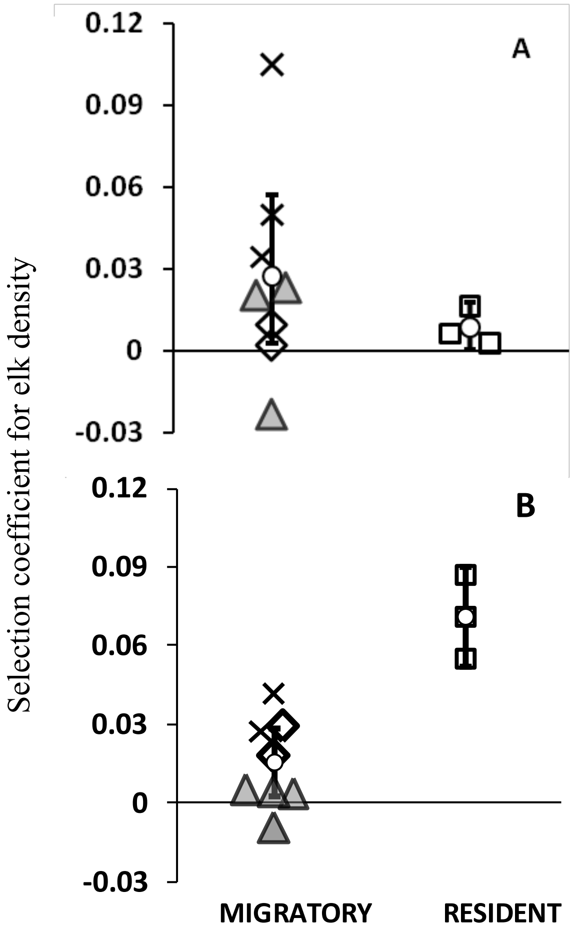


Figure 1.4. Locations of wolf packs living in the migratory elk area (Panel A) access some areas of summering migratory and resident elk (60% kernel contour), whereas wolf packs living in resident elk area (panel B) are strongly associated with resident elk on summer range.

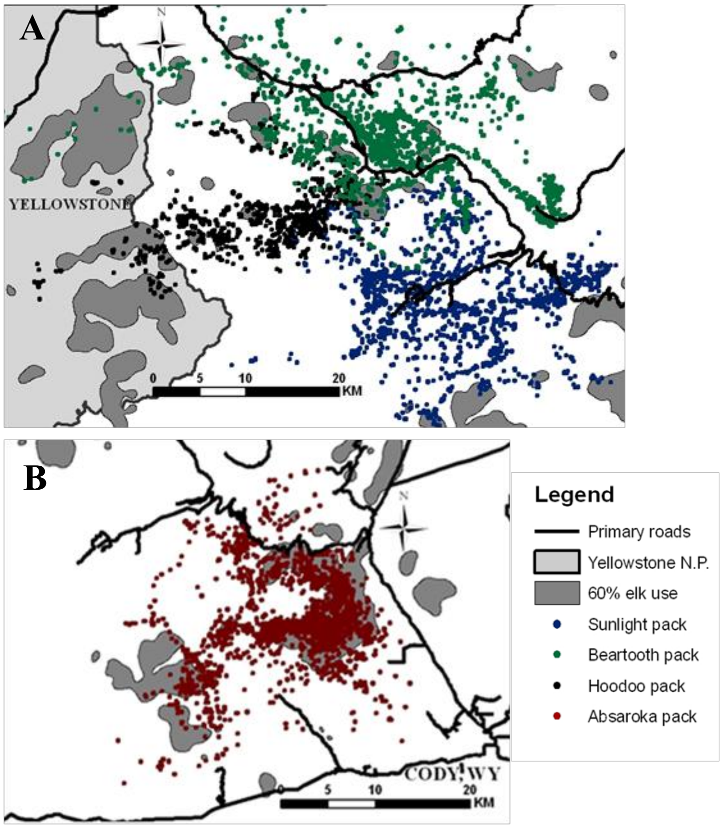


Figure 1.5. Individual wolf selection coefficients for proximity to natal den are different in winter between wolves living in migratory and resident elk areas (A); and between summer (B) and winter (A) for resident elk area wolves. The population means (hollow circle) and bootstrapped confidence intervals shown for wolves living in the migratory and resident elk areas. Negative selection coefficient indicates selection for feature, and 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.

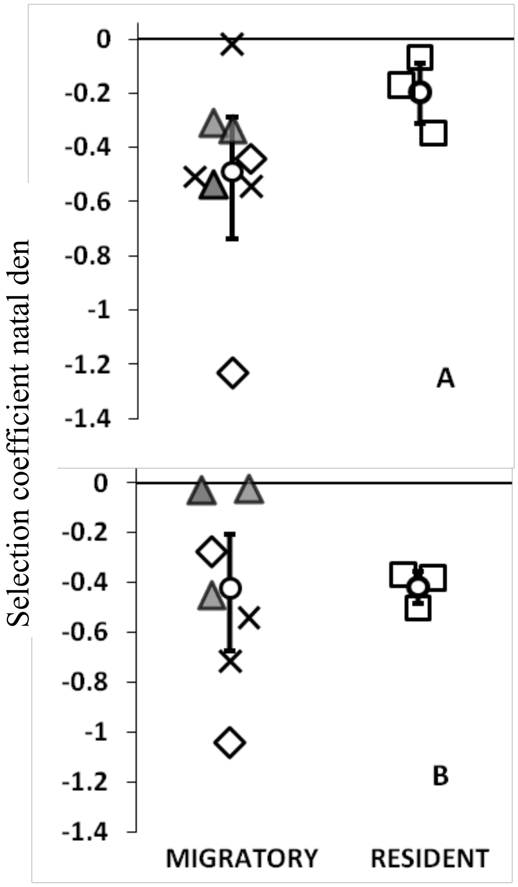


Figure 1.6. Wolf selection for habitat close to roads varied by season and by area. Individual wolf selection coefficients for open roads with the population means (hollow circle) and bootstrapped confidence intervals for wolves living in the migratory and resident areas in winter (panel A) and summer (panel B). Negative selection coefficient indicates selection for feature, and 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.

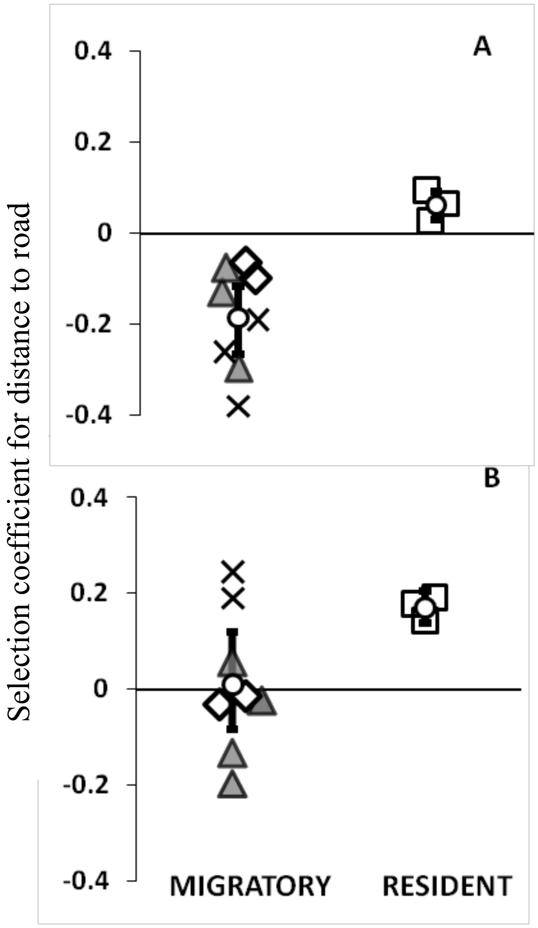


Figure 1.7. Wolves used landscapes closer to roads at night than during the day. Mean differences of day vs. night paired locations by pack are shown by open circles (n = four packs and 14 individual wolves).

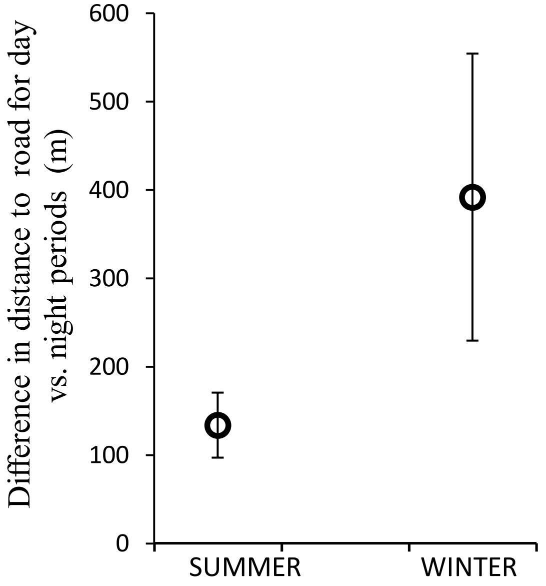
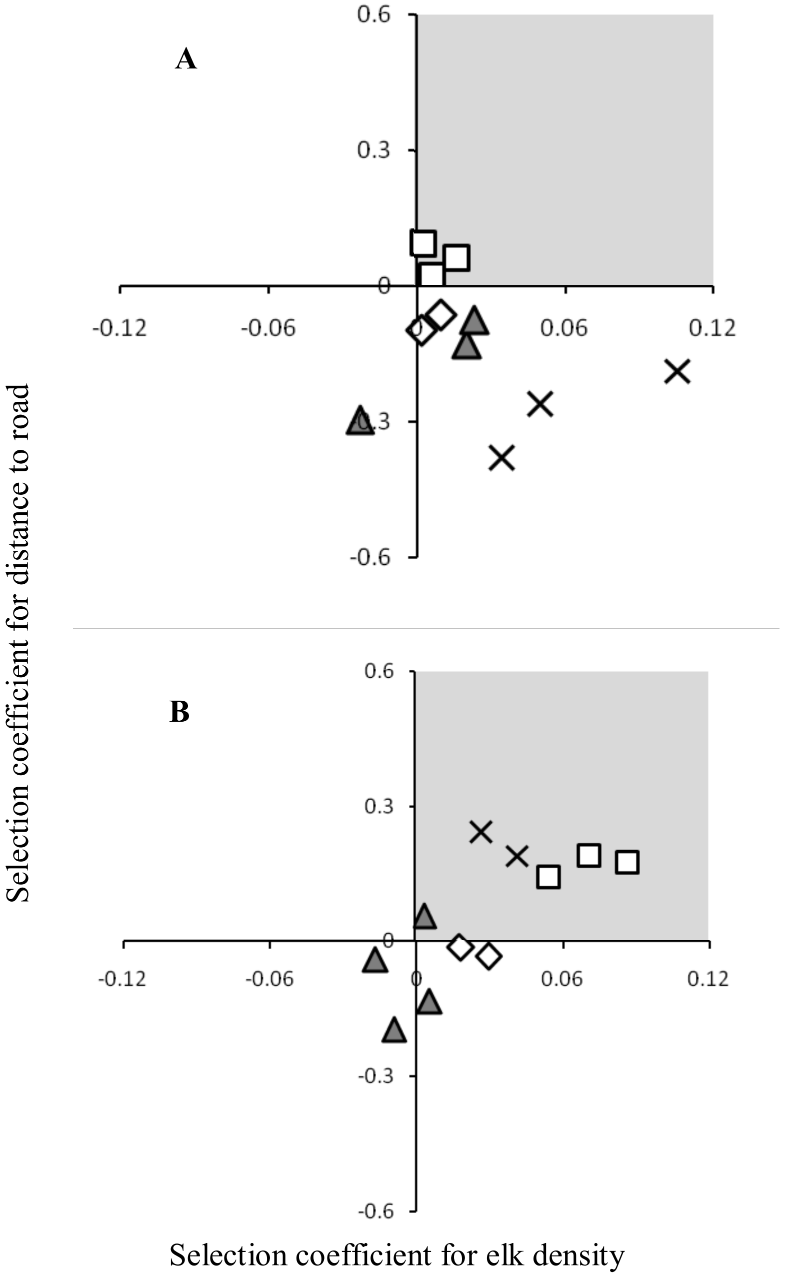


Figure 1.8. Individual wolves varied in the strength of selection for elk and their avoidance of roads. Wolves living in the resident elk area were able to select for elk and avoid roads (square marker; shaded quadrant in upper right) in both winter (panel A) and summer (panel B). Wolves in the migratory elk area, which included the Hoodoo (X), Sunlight (triangle) and Beartooth (diamond) packs, appeared to tradeoff 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.



CHAPTER 2: LANDSCAPE PATTERNS OF WOLF DEPREDATIONS OF CATTLE IN NORTHWEST WYOMING: A COMPARISION BETWEEN AREAS WITH MIGRATORY AND RESIDENT ELK

ABSTRACT: As large carnivores recover in many wilderness areas, wildlife management agencies must seek ways to minimize private property damage while maintaining viable populations, and the success of these efforts can influence public tolerance for carnivores. Although much is known about carnivore-livestock conflicts, our knowledge of what drives these processes in the Northern Rocky Mountains is still emerging amid the dynamic conditions of recovering predator populations (gray wolves [*Canis lupus*] and grizzly bears [*Ursus arctos horribilis*]), declining elk productivity, and the re-distribution of migratory and resident elk subpopulations. There has been little research to date that examines the influence of fine-scale elk distribution and movements on patterns of livestock depredation. In this study, we analyze four years of cattle depredation data, two years of summer and fall wolf predation data (n = 4 wolves), and three years of elk movement data (n = 70 elk) to assess the influence of migratory and resident prey on the location and occurrence of wolf depredations on cattle. Wolves living in migratory elk areas face low densities of their preferred prey in summer, when elk depart for higher elevations inside Yellowstone National Park (YNP), while wolves living in the resident elk area have access to abundant elk year-round. Wolves living in both areas have the potential to interact with several thousand head of cattle. We used logistic regression to compare the relative influence of landscape features on the risk of livestock depredation in the migratory and resident elk areas. We also evaluated the role of migration and native prey availability on wolf diet by comparing the composition of wolf kills in the migratory and resident elk areas. Wolf-

killed cattle were associated with areas that increased encounter rates between wolves and livestock, and these areas were different for cattle living in the migratory elk area and the resident elk area. Depredation sites in the resident elk area were associated with habitats closer to roads and with high elk density, while depredation sites in the migratory elk area were associated with dens, streams, and open habitat away from the forest edge. Our findings indicate that knowledge of ungulate distributions and migration patterns can help understand and predict hotspots of wolf conflict with livestock.

INTRODUCTION

Understanding the factors that drive patterns of wolf depredation of livestock is important to reduce and manage conflicts. Large carnivores inhabit vast homeranges, bringing them into contact with human settlements where they can cause conflicts (Woodroffe and Ginsberg 1998). Wolf-cattle conflicts are associated with a number of landscape features, such as prey distribution, den and rendezvous sites, and forest cover (Dorrance 1982, Oakleaf et al. 2003, Bradley and Pletscher 2005), but a general understanding has yet to emerge. In the Northern Rockies, wolf packs occupy a variety of land-use types, including National Parks, wilderness areas, and private or agricultural land (Oakleaf et al. 2006). Although depredations by wolves represent only a small percentage of livestock losses in the western US (Bangs et al. 2005), they tend to be locally chronic, with some producers carrying a high proportion of re-occurring losses (Mech et al. 2000). Tolerance is often promoted through methods like financial compensation to producers and lethal control of problem wolves (Mech 1995). Often the removal of depredating packs is a temporary solution, however, as it generally results in recolonization by dispersing individuals in subsequent years (Musiani et al. 2005). A better understanding of the landscape attributes that influence wolf-livestock conflicts may enhance the ability of wildlife managers to maintain target levels of wolf numbers while minimizing livestock losses.

The distribution and abundance of native prey is a critical factor influencing where wolves kill livestock on the landscape. Prior studies have found surprisingly divergent patterns, with either a positive or negative influence of prey density on livestock depredation by wolves (Gunson 1983, Treves et al. 2004). A study in Montana and Idaho found that elk presence was a strong predictor of whether or not pastures had cattle depredations (Bradley and Pletscher 2005), and a 25-year study from Wisconsin and Minnesota found that wolves killed cattle more often in townships with higher deer (*Odocoileus virginianus*) densities (Treves et al. 2004). These studies suggest that as wolves seek out native prey, they may learn to hunt cattle (Harper et al. 2005), or kill them incidentally (Treves et al. 2004) where cattle and native prey comingle. We refer to this hypothesis, wherein wolves are strongly attracted to – and tend to kill livestock that co-occur with – the distribution of their native prey, as the Prey Tracking Hypothesis.

Additional considerations in the context of changing native prey distribution are needed to understand the implications of the Prey Tracking Hypothesis. Throughout the range of wolves, the migratory patterns of elk, a primary prey species, are shifting in ways that favors resident (i.e., non-migratory) herds (Hebblewhite et al. 2006). There are several causes for these changes, including increased predation on migrants (Hebblewhite et al. 2006), drought on high-elevation range of migrants (Middleton et al. unpublished ms.), and a low level of hunting pressure and predation on residents that occupy private land refuges (Haggerty and Travis 2006, Hebblewhite et al. 2006). Prior work that we have conducted has shown that patterns of elk migration, especially their summer distribution, influence seasonal wolf habitat selection and may alter wolf travel patterns and encounters with livestock (A. Nelson, Chapter 1.). Despite the importance of elk migration to patterns of wolf habitat selection, little empirical work has examined whether such seasonal dynamics of elk density also influence patterns of cattle depredation on the landscape. As some elk populations shift to favor resident subpopulations existing alongside cattle in mixed-use landscapes (Middleton et al., unpublished ms.), it has been hypothesized that wolf distribution may track such shifts in native prey (Garrott et al. 2005) and lead to more wolf cattle conflicts where elk and cattle comingle. Reconciling whether such changes in ungulate migration will exacerbate or dampen livestock depredations by wolves hinges on understanding the degree to which native prey distribution influences wolf hunting of livestock.

In contrast, wolves also kill cattle when native prey are scarce, a pattern likely caused by declines in native prey availability. In systems with multiple ungulates, declines in preferred prey can result in diet shifts reflective of a change in relative prey abundance, or true prey switching, where preference changes (Garrott et al. 2007). A synthesis of 15 studies conducted in southern Europe found that when prey abundance declines, wolves tend to include a greater amount of livestock as the main component of their diet (Meriggi and Lovari 1996). In an extreme example of this pattern, a study in northern Italy found that wolves preyed almost exclusively on domestic goats when native prey abundance was low (Vos 2000). Regarding seasonal changes in native prey, Garrott et al. (2005) hypothesized that the departure of wolves preferred prey (elk) during summer when cattle grazing begins, may explain some patterns of depredations. In these situations, wolves shift to hunting livestock when native prey become scarce, with the amount of livestock in the diet mediated by availability of alternate prey. We refer to this as the Prey Scarcity Hypothesis.

The manner in which wolves respond to scarcity of native prey is varied and may include: following groups of migrating prey (Forbes and Theberge 1996), using local alternate native prey (Ballard et al. 1997), or killing livestock (Meriggi and Lovari 1996). In Alaska, the degree to which wolves extended their search distance to follow migratory prey depended on the annual availability of alternate prey (Ballard et al. 1997). In northwest Montana, wolves responded to diminishing elk numbers by switching to deer, apparently because hunting wintering deer was more predictable and profitable than dispersed groups of elk (Kunkel et al. 2004). Some studies have shown that depredations occur on ranches with larger groups of cattle (Mech et al. 2000), perhaps due to a high degree of predictability in locating groups of cattle compared to hunting dispersed native prey. In addition to changes in availability, vulnerability of native prey also can shift seasonally (Smith et al. 2004). On the Northern Range of YNP, wolves increased their use of deer from 7% of the diet in May to 14% of the diet in June and July (Metz 2011). However, whether this diet shift is driven by changes in elk and deer vulnerability or availability is unclear. The relative availability and vulnerability of prey species are two key factors that influence shifts in prey selection (Garrott et al. 2007). These factors would predict that with seasonal shifts in prey availability, the extent to which wolves seasonally rely on domestic livestock – or other native alternate prey - may increase, as described by the Prey Scarcity Hypothesis.

Patterns of wolf encounters and kills of native ungulate prey may also inform where wolves kill livestock. There is some debate regarding whether native prey are most vulnerable where wolves travel (Bergman et al. 2006) or where landscape features increase wolf capture success (see Hebblewhite et al. 2005). Kauffman et al. (2007) suggested that landscape attributes mediate the outcome of interactions between wolves and elk, causing elk to be more vulnerable in areas where wolves can best target and capture them. Similarly, Hebblewhite et al. (2005) suggested that topography and openness facilitated wolf-elk encounters, whereas low elevation pine stands increased the likelihood of a successful kill once an encounter had occurred. Because of domestication, antipredator behaviors are generally not as strong in cattle compared to wild prey (Linnell et al. 1999, Muhly et al. 2009), perhaps increasing the importance of factors that influence wolf-cattle encounters alone. The post-encounter success rate of wolves killing elk and bison in Yellowstone is quite low, approximately 21% and 7% respectively (Smith et al. 2000). While this difference is likely due to both prey abundance and ease of killing, we hypothesize that encounters with cattle likely have a greater potential to lead to a successful kill due to diminished antipredator behaviors (Linnell et al. 1999) and the ability of wolves to kill novel or weak prey when the incentive exists (Smith et al. 2000).

Many studies have now revealed the factors that influence vulnerability of native prey to wolf predation (Kunkel et al. 1999, Smith et al. 2004, Gude et al. 2006, Kauffman et al. 2007, Hebblewhite and Merrill 2009). Similar quantitative evaluations of how landscape attributes influence high-risk areas for livestock depredations have been conducted, though at larger scales, and without fine-scale native prey distribution data (Treves et al. 2004; Edge et al. 2011; Treves et al. 2011). In addition to native prey distribution, landscape factors also play a role in the habitats where wolves tend to kill cattle. For example, in Wisconsin, livestock kills occurred in open areas (Treves et al. 2011) and wolf-livestock conflicts have been positively associated with other attributes such as den or rendezvous areas (Bradley and Pletscher 2005), forest cover and remote areas (Dorrance 1982; Bjorge 1983), calving locations, and dead livestock (Fritts 1982). Indeed, an influence of landscape features may account for the difficulty in generalizing the influence of native prey distribution across systems.

We have been studying the interactions among wolves, native prey, and livestock in an area of chronic wolf-livestock conflict in the Greater Yellowstone Ecosystem, where wolf packs generally hunt either resident or migratory populations of elk, their primary prey. We sought to evaluate two predictions that follow from the Prey Tracking Hypothesis. If wolves are strongly associated with native prey during the grazing season, 1) elk distribution should predict wolf depredations of cattle; and 2) depredation rates should increase during time periods when elk and cattle comingle. We also used the comparison of wolves hunting migrant vs. resident elk as a means of evaluating aspects of the Prey Scarcity Hypothesis. First, we sought to evaluate whether the spring migration of elk forced wolves to shift to hunting alternative prey during summer compared to the hunting patterns of wolves in resident elk areas. Next, we asked whether the inclusion of deer in the summer diets of wolves in migratory elk areas mediated their consumption of livestock. We tracked four GPS-collared wolves to identify the location and timing of livestock depredations and prey selection in areas where elk where are migratory or resident. Clarifying how native prey influence where wolves cause chronic livestock conflicts may enhance our understanding of regional control-driven population dynamics (Smith et al. 2010) involving depredating and non-depredating wolf packs.

Study area

Our study area was located in the Absaroka Mountains of northwest Wyoming and consists of habitats just inside the eastern border of YNP, and east to the town of Cody, Wyoming (Fig. 2.1). Land jurisdiction is primarily USDA National Forest Service, with a mix of public, private and state land. The eastern front of the Absaroka Mountains is characterized by rugged topography, prominent rocky peaks, and a patchwork of forest and grasslands. 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)* steppe (6%). The average elevation of the study area was 2,404 m and ranged from 1,738 to 3,734 m. The migratory elk subpopulation wintered in low-elevation valleys formed by Sunlight and Crandall Creeks and the Clark's Fork of the Yellowstone River, and summered in the upper reaches of the Lamar River inside YNP. These elk were preyed upon by the Sunlight, Beartooth and Hoodoo packs. The resident elk herd moved only short distances seasonally, occupying overlapping summer and winter ranges in the Absaroka foothills within 10 miles of the town of Cody, WY; they were preyed upon by the Absaroka pack. During the years of 2007 – 2009, the study area encompassed the summer and winter range of approximately 3,500 elk in the Clarks Fork and Cody herds, 4,000 - 6,000 mule deer (*Odocoileus hemionus)*, 300-400 whitetail deer (*Odocoileus virginianus*), 200-300 pronghorn (*Antilocapra americana)*, and a small number of moose (*Alces alces*) (D.E.M., unpublished data). The study area contained three to five wolf packs in a given year, and grizzly bear (*Ursus arctos horribilis)*, black bear (*Ursus americanus*), cougar (*Puma concolor*) and coyote (*Canis latrans*) were also present. Public and private rangelands support several thousand head of cattle that spatially overlap with at least part of the range of all four wolf packs we studied.

METHODS

Capture and collaring

To determine the identity, location, and timing of wolf predation events, we tracked GPS collared wolves. We captured four wolves using leghold traps in the summers of 2007 (n=2) and 2008 (n=2). One wolf was captured in the resident elk area (Absaroka pack) and three wolves were captured in the migratory elk area, with one wolf each in the Sunlight, Crandall, and

Beartooth packs. Each wolf was immobilized with 10 mg/kg Telazol during trapping efforts and 17 mg/kg Telazol/ Kg during helicopter capture (Kreeger and Arnemo 2007). Telazol was delivered by a Cap-Chur Palmer dart gun. Wolves were fitted with remotely downloadable collars (4400s, Lotek Wireless, Newmarket, Ontario) that recorded one fix every 20 minutes during the summer months (July-October) to generate data to locate kill sites. Collars were deployed for durations of 1- 3 months. Adult female elk were captured via helicopter netgunning and fitted with GPS collars (Telonics TGW-3600) in January 2007 (n = 60) and 2008 (n = 10). Elk collars were programmed to record a fix every 3 hours on summer and winter range, and every 8 and 24 hours respectively for migration periods of September – October and April – June. The collars were programmed to drop off after 3.25 years. All animal captures were conducted in compliance with protocols approved by the University of Wyoming's Institutional Animal Care and Use Committee.

Locating and identifying wolf kills

We located wolf-killed native ungulate and cattle carcasses using cluster searching methods (Anderson and Lindzey 2003, Sand et al. 2005) from July 1 – October 26, which included the seasonal peak in depredations by Wyoming wolves that occurs in August (Jimenez et al. 2011). We remotely downloaded GPS data from collared wolves every 7-10 days on foot or from aircraft. Distinct clusters of locations were identified in GIS (ArcMAP 9.2) and searched by field crews. Clusters, which were defined as being within 100 m of at least two other points, identified all areas where wolves spent > 40 minutes within a 100 m radius. We visited 96% of 594 clusters within an average of 8.6 days (± 5.2 SD) after wolves left the site.

Most clusters associated with a den or rendezvous site were searched after the wolves left the area. The majority of cattle kills were recorded through agency depredation records (n=39) from 2007 - 2010, a small proportion of which were also located through cluster searching methods (n=3).

Searching techniques described here are similar to those described in (Metz et al. *in press*). We searched a radius of 35 m around each individual location within a cluster (Webb et al. 2008), and we conducted a final search that included a 30-40 m buffer around the perimeter of the cluster. We searched individual clusters for an average of 34 minutes (± 28 SD). Once a carcass was located, the approximate date of death was estimated and cross-checked with the date of first GPS location at the site. The scene was assessed for signs of predation (e.g., broken vegetation, blood splatter), and the remains of the carcass were assessed for hemorrhaging consistent with a wolf attack or other forms of predation (Bjorge and Gunson 1983, Clucas 2005). We categorized each carcass as: unknown cause of death, possible wolf kill, probable wolf kill, definite wolf kill, or other. Presence of bears and other scavengers was documented. To ensure documentation of multiple carcasses if appropriate, we searched all locations within clusters in this manner regardless of whether we located a carcass or not. We identified and catalogued prey by species, approximate age (yearling, young of year, or adult) and sex. Livestock kills were confirmed by USDA Wildlife Services or Wyoming Game and Fish Department personnel according to similar protocols developed for agency purposes.

Analyzing factors influencing wolf kill locations

We were primarily interested in the influence of elk distribution on wolf-killed cattle, but we also sought to evaluate the influence of distance to stream, distance to road, distance to forest edge and distance to den on the locations of cattle kills. We derived GIS covariate rasters (100 m cell size) to index these landscape attributes across the study area. To index elk distribution, we created a fixed kernel density estimate using location data from 80 elk GPS collars within the study area for summer months based on the median date of elk migration in the migratory elk area (May 27th). To investigate the proximity of cattle kills to streams, we used a high resolution NHD stream polyline layer (National Hydrology Dataset 1999) to develop a raster that served as an index for proximity to stream, using the Spatial Analyst linear distance tool. We were interested in location of cattle kills in relation to human activity, so as a proxy for human development, we estimated a primary road layer. For this layer, we edited polylines from U.S. Detailed Streets (2002) using satellite imagery (NAIP Digital Ortho Photo Image 2007) to include all roads receiving daily traffic, year-round. Roads were ultimately characterized as a raster of linear distance to the nearest road using the Spatial Analyst distance function. Similarly, we created a distance to den raster, including known natal dens for each of the study packs. We did not include rendezvous sites in the analysis because association of pups to GPS collared wolves was not always clear.

Cattle depredation analysis

We used a resource selection function (RSF) with a use vs. availability design (Manley et al. 2002) to evaluate the factors that influence cattle kill sites in migratory vs. resident elk areas. The domain of availability was defined as cattle pastures where depredations had the potential to occur, which included all pastures where wolves were known (via GPS collar data) or suspected (from sightings) to occur during May – October in the resident and migratory elk areas (Fig.

2.2). Used locations consisted of confirmed, probable, or definite wolf-killed cattle locations found through GPS clusters in addition to carcasses found by ranchers and state and federal agency personnel. We classified kills as either occurring in the migratory or resident elk area, using a dividing line consistent with the WGFD elk herd unit. Available points were randomly placed (20 per used location) in the study area with a 200 m buffer within which the GIS covariates were averaged. There were a few occasions where wolves in the migratory elk area travelled east to make kills in the resident elk area. In this case we classified these kills as belonging to the resident elk area. We suspect that because most of the cattle depredations were obtained through the reports of ranchers and agency personnel, these locations were likely biased towards open areas and roads, although we had no means to correct for this. Thus, this is a potential unaccounted for bias in our analysis. We used separate logistic regression (Minitab Inc, State College, PA) analyses in migratory and resident elk areas to evaluate the influence of habitat coefficients on kill-site locations.

Timing of kills and prey selection

We sought to test the prediction from the Prey Tracking Hypothesis that the rate of cattle kills increased over the course of summer due to increased comingling of cattle and elk, which is known to occur in the resident area. We assessed the frequency of depredations occurring within two week intervals throughout the summer with a 4-year depredation dataset (2007-2010). We regressed the number of kills occurring against these ordered time periods throughout the summer. Because of small sample size and the lethal removal of problem wolves soon after they began killing cattle, we view this analysis as largely descriptive. We did not have a large enough sample of kills to evaluate temporal trends separately for each area.

To identify differences in composition of wolf-killed prey species between wolves in migratory and resident elk areas, we compared the frequency of wild ungulate prey identified through cluster searching. We sought to evaluate differences between wolves in migrant and resident areas that might result from wolves living in migratory elk areas switching to alternate prey, or following elk migration. The available prey included cattle, mule deer, moose, white tailed deer and elk, along with pronghorn and bison for wolves that took extraterritorial forays into YNP (see A. Nelson, Chapter 1.). Because most prey remains were elk and deer, we conducted a binomial proportion test to evaluate differences in the proportion of deer and elk in the diets of wolves from each area.

RESULTS

Cattle kill resource selection function

Landscape attributes associated with 20 cattle kills in the migratory area and 19 cattle kills in the resident area support the Prey Tracking Hypothesis, as cattle depredations in resident areas were positively associated with elk-rich habitat (Z = 3.18, P = 0.001). Depredations in this area also occurred closer to roads than what was available (Z = -2.61, P = 0.009), which was contrary to our predicted results. There was no relationship between resident cattle kills and the remaining landscape variables (Table 1). In the migratory area, landscape attributes played a stronger role, with kills occurring close to the den (Z = -2.36, P = 0.018) and streams (Z = -2.66, P=0.008) and farther from the forest edge (Z = 2.47, P = 0.014). In contrast to the resident area, elk distribution in the migratory elk area did not influence the location of cattle depredations (Table 1).

Timing of kills and prey selection

The number of cattle kills in combined resident and migratory areas showed a modest increase over the course of the summer ($F_{1,9}$ = 11.8, *P* = 0.009, r^2 = 54.6; Fig. 2.4). Binomial proportion analysis indicated differences in the composition of wild ungulate prey between wolves living in migratory and resident area (Z = -3.22, P = 0.001; Fig. 2.5), suggesting the use of deer as alternative prey by wolves in the migratory elk area. Wild ungulate composition of kills made by wolves living in resident elk areas was 92% (11/12) elk and 8% (1/12) deer, while wolves in migratory areas consumed equal proportions of elk (50%; 12/24) and deer (50%; 12/24). In the migratory area, results show that of all kills found at clusters, 3% were domestic cattle, suggesting that wolves do not rely heavily on domestic cattle as an alternate prey resource when elk migrate away during the grazing season. The radio collared wolf in the resident elk area dispersed late August 2007, and although we discovered depredations through rancher and agency reports from the Absaroka pack following dispersal, we did not locate any cattle kills at GPS cluster sites prior to dispersal.

DISCUSSION

We found that depredations on cattle were strongly associated with elk density in the resident elk area but not in the migratory elk area. We expected that landscape attributes would influence cattle depredations in both areas as they do for native ungulates; however, they had a stronger influence on cattle kills in the migratory area. The timing of depredations in both areas showed a tendency for the frequency of cattle depredations to increase over the course of the summer. Although based on a small number of kills, this finding appears consistent with pasture rotations that bring cattle to higher elevation where they comingle with elk (in the resident area), or in some instances, closer to den locations as summer progresses (in the migratory area). These two findings in the resident elk area indicate that the close spatial association between wolves and elk appears to influence the incidence of cattle depredations and provides support for the Prey Tracking Hypothesis. Although we did not have enough cattle kill data to test the Prey Scarcity Hypothesis, we did find support for the importance of alternative prey in the migratory elk area. Prey composition of wolf kills in the migratory elk area suggests that wolves still prey on elk, but also shift to hunting deer when elk densities became seasonally low. The availability of deer as alternative prey may have influenced the tendency of migratory wolves to kill cattle in a somewhat incidental manner, as encountered close to dens, in the open, and close to streams. Although our sample size is small, the few cattle kills located in the migratory elk area (10% of killed animals at GPS clusters) support the notion of incidental cattle predation. Overall, these finding suggest the seasonal variability in native prey distribution can mediate the location and occurrence of livestock depredations, indicating an increasing importance of co-managing livestock, wolves, and growing resident elk populations.

Consistent with the observation that wolves have higher encounter rates with large elk groups (Hebblewhite and Pletscher 2002), we found, in the resident area, that they tend to kill cattle in locations with high elk density. The strong association between wolves and elk (A. Nelson, Chapter 1.) seems to provide a benefit to cattle when they are nearby, but not comingling with elk. Cattle in our system are grazed within reach of wolves (less than 1 mile) for much of the grazing season. Wolves killed relatively few cattle in pastures separate from elk, yet depredations tended to increase when cattle were moved into higher elevation elk-rich habitat (Fig. 2.3C). Wolf predation of elk was also tightly associated with elk distribution in the resident elk area (Fig. 2.3A). Gude et al. (2006) suggested that areas where predation occurs are different from areas of frequent wolf presence. Although we did not test this directly, spatial patterns of native ungulate kills overlapped with livestock depredation locations, suggesting that areas of high predation, or "hunting zones" (e.g., Gude et al. 2006), could carry over from native prey to livestock (Fig. 2.3A & 2.3C). These results are also consistent with studies conducted at a larger scale that found that elk abundance in pastures increases the likelihood of wolf depredations (Bradley and Pletscher 2005). In the migratory area, elk only occur in small diffuse pockets in summer, which did not influence the location of cattle kills, suggesting that threshold levels of elk density that facilitate increased encounter rates with livestock may exist.

In the resident elk area, we expected elk density and landscape attributes to influence the location of cattle kills, but only elk density and proximity to roads were important. By contrast, landscape attributes had a stronger influence on the location of cattle kills in the migratory areas. These findings suggest that in the absence of strong wolf association with native prey, other attributes that influence encounter rates between wolves and cattle become important drivers. Wolves in Idaho that had high spatial overlap with cattle also had higher rates of depredation (Oakleaf et al. 2003), which supports the importance of encounter rates between wolves and cattle. This differs from Kauffman et al. (2007) who suggested that when wolves are hunting native prey, landscape attributes influence the ability of wolves to successfully kill their prey after the initial encounter, e.g., by hindering prey escape (Hebblewhite et al. 2005). Due to dampened anti-predator behavior (Linnell et al. 1999, Muhly et al. 2009), domestic livestock may be highly vulnerable where they encounter wolves. Although we do not have rates of capture success for wolf-cattle encounters, we suspect that it is higher than the success rate of wolves that encounter elk, which has been estimated at ≈ 21% (Smith et al. 2000).

Most landscape attributes associated with cattle kill sites were consistent with the mechanism of increased rates of encounter between wolves and cattle. Kills in the migratory areas were associated with dens, which are seasonal centers of activity for wolves (Mech 1970). This is clearly a factor that increases encounters between wolves and cattle and was also found by Bradley and Pletscher (2005) to increase likelihood of cattle depredations in Montana and Idaho. The lack of any association between kills and dens in the resident area may be a function of these dens being somewhat equally spaced throughout the available habitat. Cattle kills in the migratory elk area were associated with habitat distant from forest edge. Some studies have shown that depredations are more common in forested areas (Fritts 1982, Gunson 1983) or near forest edge (Treves et al. 2004). However, cattle depredations have also been associated with open habitats in some systems such as Wisconsin which may be due to either wolves tracking their native prey (Treves wt al. 2011) or the visual attractant of cattle congregating in large groups in open areas (Oakleaf et al. 2003). A caveat to this finding, however, is that our method of collecting depredation reports includes a likely bias towards open areas, as 36 of 39 cattle kills were derived exclusively from human reporting; only a few kills (n=3) were also located through GPS cluster searches. These three kills, however, were located in open areas as well. Our finding of depredations close to streams also supports the importance of wolf-cattle encounters, because cattle tend to use riparian habitat close to a consistent water source (Yeo et al. 1993, Oakleaf et al. 2003) and wolves often travel along easiest travel routes (Kunkel and Pletscher 2001), which was also evident in our study area on trails along steep drainages. Our results support the notion that landscape attributes that facilitate predator-prey encounters may have the strongest influence on the spatial patterns of wolf-livestock kills.

We found that wolves selected deer as an alternate prey resource when elk became scarce due to seasonal migration (Fig. 2.5). Prey switching can occur in response to changing availability or vulnerability of preferred prey (Garrott et al. 2007). Although we cannot confirm true switching, wolves appear to respond to declines in abundance of elk by killing a greater proportion of deer than was found during winter in YNP studies (96% elk; Smith et al. 2004) and in the resident elk area we studied (Fig. 2.5). Morehouse (2010) suggested that cattle may replace ungulates as a prey source during the summer grazing season, although the role of wolf prey selection is unclear. For example, elk were the predominant prey item in scats (42.6%; Morehouse 2010) during the non-grazing season, while cattle were the dominant prey item in scats (58.9%; Morehouse (2010)) during the grazing season. While some studies have found that low abundance of native prey is associated with more frequent cattle depredations (Gunson 1983, Meriggi and Lovari 1996), our findings suggests that availability of deer as alternative prey may reduce wolf depredation on cattle. An important caveat, however, is that we studied an effectively managed wolf population whereby lethal removal slowed or stopped the behavior of wolves that killed cattle once they were detected. This management appeared to yield remaining wolves that relied predominantly on deer and elk in the migratory area. We note that prey selection is known to change throughout the summer and by individual (Metz et al. *in press*), indicating that a larger sample of wolves followed over a longer time frame might reveal predation patterns different than those we have reported.

Depredations of cattle within our study area occurred at an increasing rate throughout the summer, and not at all during the winter and spring months. These findings are consistent with some other areas in the GYE, and may be driven by changes in prey vulnerability and pasture rotations that bring cattle close to elk groups or wolf dens. In British Columbia, the highest frequency of cattle depredations occurred in July and August (Tompa 1983), and in Minnesota, wolf depredation of sheep and turkeys typically peaks in August, presumably due to the increased food needs of pups. In YNP, wolf consumption of vulnerable neonate ungulates declines after the start of July, and biomass consumption reaches a year-round low (Metz et al. *in press*). Changing vulnerability of prey may have influenced patterns in the migratory area, but we did not have an adequate sample size to evaluate the timing of depredations between the migratory and resident areas (Fig. 2.4). Cattle tend to move up in elevation in resident areas as the summer progresses; such pastures have high elk numbers (A. Nelson, Chapter 1) and are remote from human activity. Both remoteness and the presence of elk have been associated with wolf depredations (Dorrance 1982, Bradley and Pletscher 2005). Some research has suggested moving cattle closer to human settlements in late summer (Dorrance 1982), but this is likely not possible for most ranchers in our study area due to concerns with optimizing phenology of grasses and the timing of the emergence of poisonous plants.

MANAGEMENT IMPLICATIONS

Our research suggests that as resident elk subpopulations grow and migratory subpopulations decline, the redistribution of ungulate biomass towards front country multiple-use landscapes is likely to increase wolf depredation rates, wolf lethal removal, and potentially influence regional wolf population dynamics (Garrott et al. 2005). Growing resident elk populations increasingly exist year-round on private land that is often characterized by restricted hunting access and livestock grazing. We found that the strong association of wolves with resident elk during summer (A. Nelson, Chapter 1) appears also to elevate depredation rates when cattle are allowed to comingle with elk late summer. However, while wolves have abundant, easily accessible prey, it is possible that strong associations with native prey groups may take pressure off nearby cattle that are not comingling with elk. On these multiple-use landscapes, wolves typically encounter cattle at some point alongside elk, and wolves that chronically kill livestock can be lethally removed (Jimenez et al. 2010). It is unclear whether changing patterns of elk distribution and migratory patterns will slow pack re-establishment following control actions in areas with declining migratory prey (see Musiani et al. 2005), or create an attractant for wolf establishment in areas with abundant resident prey.

Study findings may also be relevant to several aspects of wolf management as wolves are now considered recovered and jurisdiction is shifting from federal to state management. Wolf harvest is an important management tool for delisted wolf populations under the state plans for Montana, Wyoming and Idaho. Creating harvest quotas that accurately reflect current wolf population numbers prior to the start of the harvest will be necessary to maintain minimum wolf numbers, as states may manage closer to the minimum population sizes than has been allowed under federal management. Our research shows that depredations and subsequent lethal removal may often peak in September and October, after harvest quotas have been established for most areas. The timing of the most severe periods of livestock conflicts in areas such as those we studied often warrant entire pack removals, which, in combination with a pre-established harvest quotas may drive populations to below desired levels. This suggests a need for management agencies to establish an overall mortality objective for the year within which they can flexibly adjust harvest quotas during or immediately prior to the season opening, depending on the extent of livestock- related lethal removal, or find other creative means to reconcile managed harvest with lethal removal of problem packs. Additionally, human activity, such as that generated by a hunting season, may temporarily displace wolves (Treves 2009) and elk following livestock conflict, which could prove useful in the early fall when depredation rates appear to increase in our study area. Our results suggest that when managing for ungulate harvest and cattle production across large rangelands, managed separation of cattle and elk will likely decrease conflicts with wolves and livestock. Though such notions may currently seem impractical, they may become more important as the distributions of elk, both migrant and resident, and wolves continue to change.

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Table 2.1. Landscape attributes and resource selection function coefficients that influence the location of wolf-killed cattle in areas where elk are resident (n = 19 kills) or migratory (n = 20). Significant variables are in bold.

	RESIDENT AREA				MIGRATORY AREA			
Predictor	Coef	SE	Z	P value	Coef	SE	Z	P value
den	-0.01	0.01	-1.45	0.148	-0.03	0.02	-2.36	**0.018**
roads	-0.04	0.02	-2.59	**0.010**	0.00	0.02	0.18	0.859
forest	-0.11	0.07	-1.49	0.137	0.67	0.27	2.47	**0.014**
elk	1634.67	513.63	3.18	**0.001**	-6099.13	4578.04	-1.33	0.183
stream	-0.17	0.22	-0.75	0.453	-0.95	0.36	-2.66	**0.008**

Figure 2.1 Study area located in northwestern Wyoming, including the eastern boundary of Yellowstone National Park. Summer movements (July 1 – October 22) of four GPS-collared wolves where cluster searches were conducted are shown. Wolf packs occupying migratory elk areas are shown in green, red and blue (Beartooth, Crandall, and Sunlight packs respectively), and the resident Absaroka pack is shown in black. Core summer use areas for migratory (grey stipple polygon) and resident elk (grey polygon) are also shown, which were derived from 50% use contours of fixed kernel density estimates. Crandall pack male 664M took two extraterritorial forays, 11 and 16 days in length, before killing a beef calf in the resident elk area (see Table 2, Chapter 1).

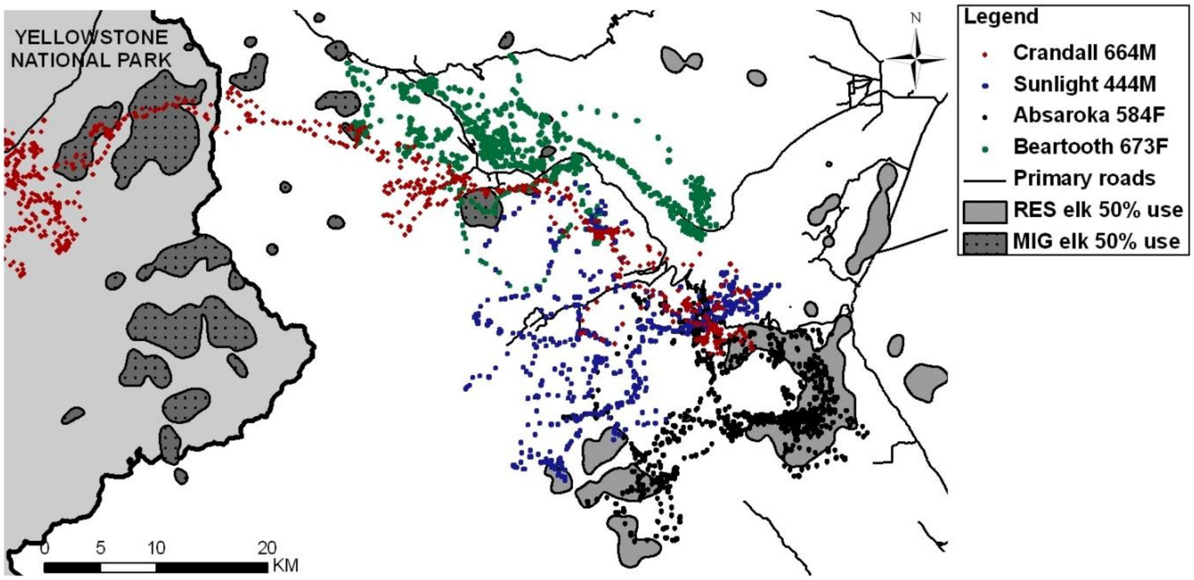


Figure 2.2. Pastures that were considered available for wolves to kill cattle in resident (blue outline) and migratory (red outline) prey areas. Cattle depredation locations (black triangles) were positively associated with areas of core summer elk use (grey polygons) in the resident elk areas, but showed no association with elk density in the migratory elk area.

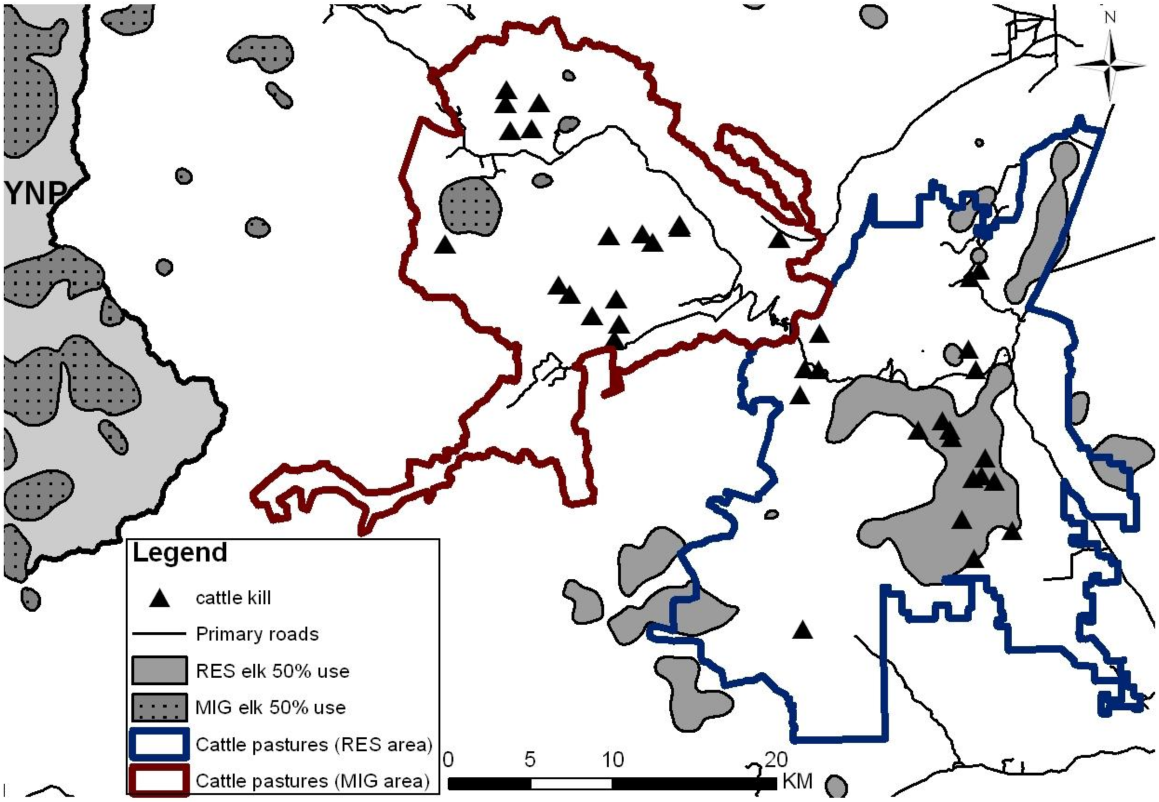


Figure 2.3. (A) Wolf movements (black dots) were closely associated with resident elk density (striped polygon) throughout summer, and they tended to kill ungulates (July – mid-August; blue circles) in areas with large elk groups. (B) In early summer (May 1 – August 15), there were few cattle depredations (red circles) and they occurred somewhat randomly with respect to elk distribution. (C) In late summer (August 15 – October 31), wolves tended to kill more cattle (red dots) as pasture rotations brought cattle to comingle with elk (C).

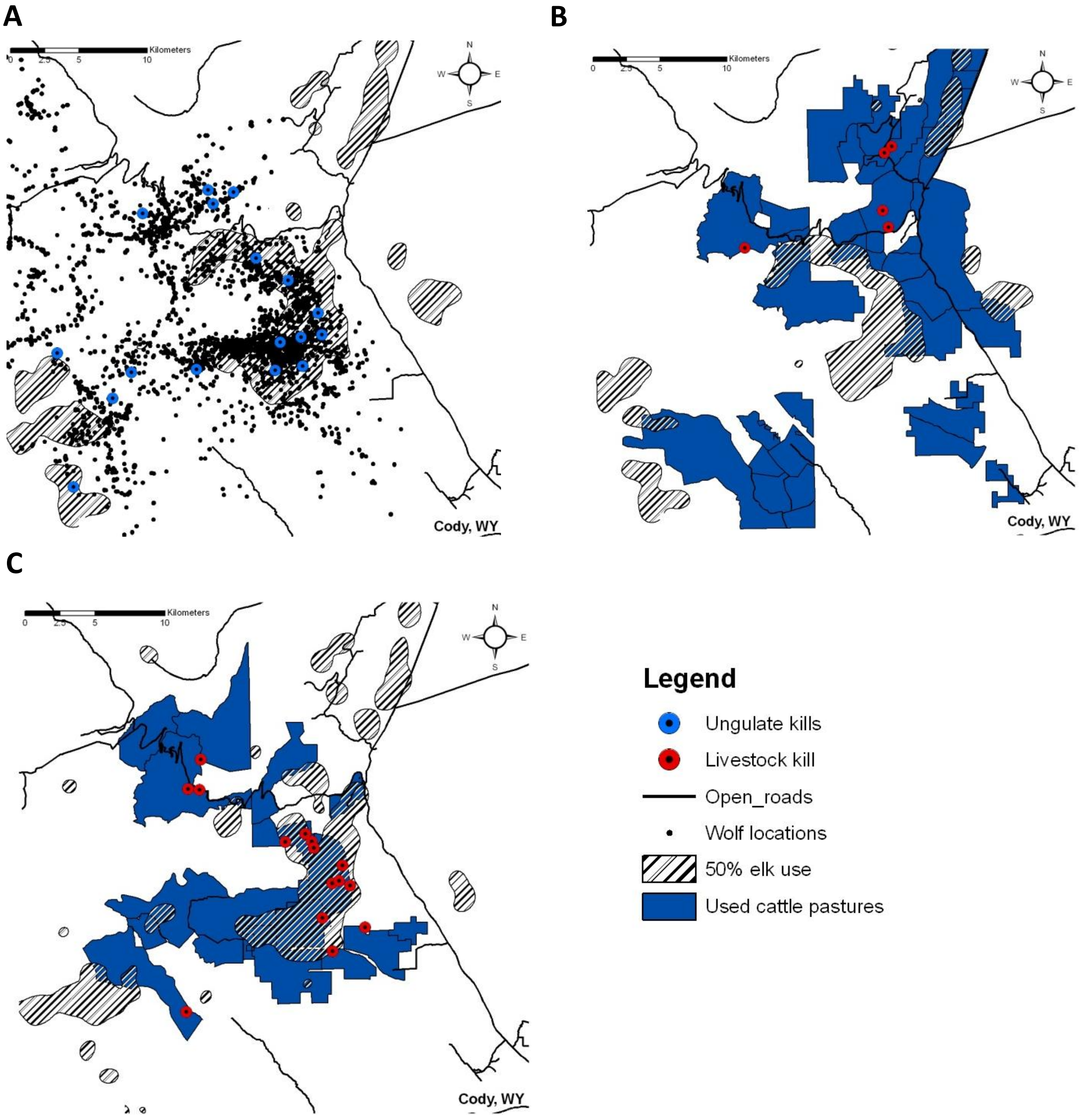


Figure 2.4 The number of cattle depredations (per two-week intervals) increased over the summer period (2007-2010). Due to small sample size, depredations from both resident (black) and migratory (white) elk areas were combined. Considerable variability between years existed, however the timing of depredation appears to be consistent with increased comingling of elk and cattle in late summer.

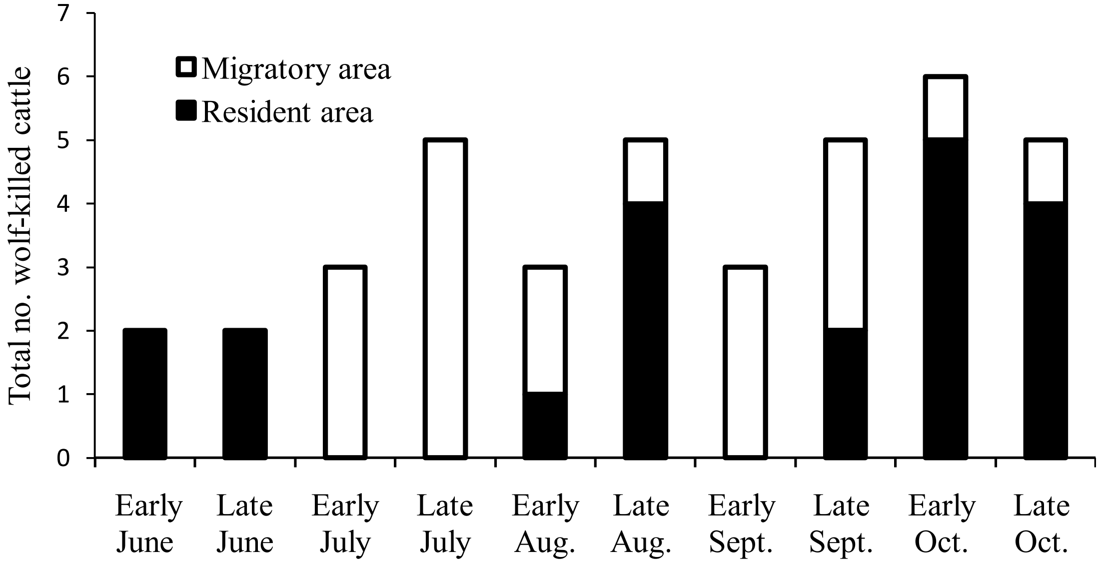
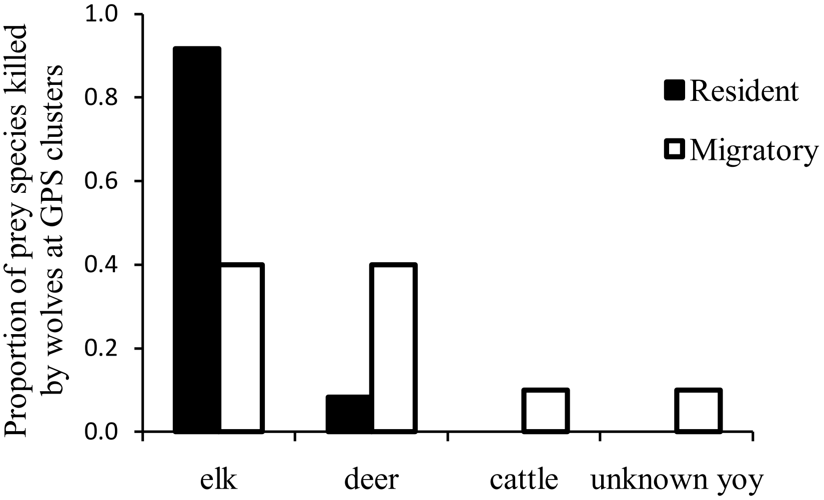


Figure 2.5. Proportion of ungulate prey species killed by wolves at GPS clusters for wolves living in resident (black; n = 12 kills) and migratory (white; n = 30 kills) prey areas. Young of year (yoy) refers to deer fawn or elk calf remains that were present with signs of predation but too inconclusive to determine species.



Appendix A. Wolves fitted with GPS collars used for this research. ID numbers given by management authority (USFWS).

GPS collared wolves that contributed to research

ID	Color	Age	Breeder?	Pack	Area	Chapter	Collar start	Collar end	Fate
584F	Black	3	N	Absaroka	Res.	1,2	7/1/2007	8/22/2007	Dispersal, unknown mort.
585F	Grey	2	Unk.	Absaroka	Res.	1	1/26/2007	12/27/2007	Dropped collar
683F	Black	3	Y	Absaroka	Res.	1	1/10/2009	1/3/2010	Collar replaced
583M	Grey	4	Unk.	Absaroka	Res.	1	1/26/2007	3/8/2007	Intraspecific mort.
608M	Black	3	Unk.	Beartooth	Mig.	1	3/6/2007	11/2/2007	Dropped collar
673F	Black	1	N	Beartooth	Mig.	1,2	8/4/2008	10/27/2008	Dropped collar
717F	Black	3	Y	Beartooth	Mig.	1	2/24/2009	6/22/2009	Collar replaced
664M	Black	3	Unk.	Crandall	Mig.	2	7/1/2008	8/10/2008	Lethal removal
525F	Black	5	Y	Hoodoo	Mig.	1	1/12/2009	1/1/2010	Collar replaced
681M	Black	4	Y	Hoodoo	Mig.	1	1/12/2009	11/30/2009	Dropped collar
697M	Black	1	N	Hoodoo	Mig.	1	1/12/2009	12/29/2009	Dispersal, intraspec. mort.
444M	Black	7	Unk.	Sunlight	Mig.	1,2	7/20/2007	8/27/2007	Collar malfunction
581M	Black	3	Unk.	Sunlight	Mig.	1	1/26/2007	1/15/2008	Dropped collar
582M	Black	3	Unk.	Sunlight	Mig.	1	1/26/2007	8/20/2007	Dropped collar
649F	Black	1.5	N	Sunlight	Mig.	1	2/19/2008	9/20/2008	Dropped collar