Native prey distribution and migration mediates wolf predation on domestic livestock in the Greater Yellowstone Ecosystem

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Native prey distribution and migration mediates wolf predation on domestic livestock in the Greater Yellowstone Ecosystem


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ABSTRACT

Little research has evaluated how the migration and distribution of native prey influence patterns of livestock depredation by large carnivores. Previous research suggests that the presence of native prey can increase depredation rates by attracting predators (Prey Tracking Hypothesis). Alternatively, the absence of native prey may facilitate predation on livestock (Prey Scarcity Hypothesis). In this study, we evaluated support for these competing hypotheses through analysis of four years of cattle (Bos taurus L., 1758) depredation data ($n = 39$ kills), two years of summer and fall wolf (Canis lupus L., 1758) predation and tracking data ($n = 4$ wolves), and three years of elk (Cervus elaphus L., 1758) movement data ($n = 70$ elk). We used logistic regression to compare the relative influence of landscape features and elk distribution on the risk of livestock depredation in areas with migratory and resident elk. Cattle depredations occurred in habitats with increased encounter rates between wolves and livestock. In resident elk areas, depredation sites were associated with elk distribution, and open roads. In migratory elk areas, depredation sites were associated with wolf dens, streams, and open habitat. Patterns of carnivore-livestock conflicts are complex, and using ungulate distribution data can predict and minimize such instances.

Key words: large carnivore conservation; livestock conflict; elk; wolves; Canis lupus, Greater Yellowstone Ecosystem; partial migration; ungulate migration
INTRODUCTION

Wolves (*Canis lupus*), grizzly bears (*Ursus arctos horribilis* Ord 1815), spotted hyena (*Crocuta crocuta* Erxleben 1777) and tigers (*Panthera tigris* L., 1758), are examples of large carnivores that roam widely across vast home ranges to hunt seasonal prey (MacDonald 1983). These large-scale movements often bring predators into conflict with humans (Woodroffe and Ginsberg 1998). Worldwide, the conflict associated with depredations of domestic livestock is a major limitation for the conservation, restoration, and viability of large carnivore populations. Attempting to managing both human and wildlife components of such conflicts requires an understanding of the ecological factors underlying patterns of depredation.

In the northern Rocky Mountains, USA, approximately 94% of wolf packs now exist outside national parks (U.S. Fish and Wildlife Service 2013) on land-use types ranging from wilderness areas to public and private rangelands (Oakleaf et al. 2006). Expansive wolf populations have come into conflict with domestic livestock, and although livestock do not typically dominate wolf diets (Bangs et al. 2005), wolf depredation can be locally chronic for particular livestock producers (Mech et al. 2000). Although government agencies and non-governmental organizations attempt to alleviate conflicts through lethal and non-lethal wolf control, financial compensation, and other preventative methods (Mech 1995), many livestock producers remain frustrated (see Steele et al. 2013). Often the removal of depredating packs is a short-term solution, because dispersing individuals recolonize the area quickly (Musiani et al. 2005).

Prior studies indicate that the distribution and abundance of native prey can strongly influence where wolves kill livestock, but these studies have found surprisingly disparate effects of prey distribution on livestock depredation by wolves (Gunson 1983; Treves et al.
A study in Montana and Idaho found that elk presence was a strong predictor of cattle depredations in study pastures (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* Zimmerman, 1780) 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 attracted to native prey, but kill co-occurring livestock, as the “Prey Tracking Hypothesis.”

In contrast, wolves also kill cattle when native prey is scarce. 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). For example, a study in northern Portugal found that wolves preyed almost exclusively on domestic goats when native prey abundance was low (Vos 2000). Garrott et al. (2005) hypothesized that the timing of the spring migration of elk with the beginning of cattle grazing may influence some patterns of depredations. In such situations, wolves shift to hunting livestock when native prey become scarce through seasonal changes or long-term declines, and the amount of livestock in the diet is 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 (Vos 2000). 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). On the Northern Range of Yellowstone National Park (YNP), wolves increased deer (*Odocoileus hemionus* Rafinesque,
1817) in their diets from 7% in May to 14% of their diet in June and July (Metz et al. 2011). However, whether this diet shift was driven by changes in elk and deer vulnerability or availability is unclear, because both can influence shifts in prey selection (Garrott et al. 2007). The extent to which wolves exploit either domestic livestock or alternate, native prey may increase when wolves’ preferred prey become scarce, or less vulnerable.

In addition to prey distribution, landscape features also influence where wolves tend to kill cattle. For example, Treves et al. (2011) found livestock kills to occur in open areas, while Dorrance (1982) showed depredations to occur in remote areas with forest cover. Additionally wolf-livestock conflicts have been associated with other features such as den or rendezvous areas (Bradley and Pletscher 2005), calving locations, and dead livestock (Fritts 1982). 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 landscape factors that influence the encounter stage of an interaction between wolves and cattle.

Whether the Prey Tracking or Prey Scarcity Hypothesis holds (not mutually exclusive), is relevant to understanding the implications of current changes in native prey distribution for wolf management. In several areas of the Northern Rockies, partially migratory populations of elk are increasingly dominated by resident individuals that remain year-round in mixed-use landscapes (Hebblewhite et al. 2006; Middleton et al. 2013). The likely causes of these shifts include increased predation on migrants (Hebblewhite et al. 2006), disproportionate drought effects on the high-elevation summer ranges of migrants (Middleton et al. 2013), and low levels of harvest and predation pressure on resident elk that seek out private land refuges (Haggerty and Travis 2006; Hebblewhite et al. 2006). Because wolf distribution can track native prey (Garrott et al. 2005; Nelson et al. 2012) and resident
elk subpopulations often commingle with cattle in mixed-use landscapes (Middleton et al. 2013), these recent shifts in native prey could conceivably lead to increased rates of wolf-cattle conflict. Whether the changing demography and distribution of elk will mediate livestock depredations by wolves hinges on understanding how native prey distribution influences wolf hunting of livestock.

We studied the interactions among wolves, elk, 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) wolf depredations of cattle should be associated with elk distribution; and 2) the number of depredations should increase during time periods when elk and cattle spatially comingle. We were unable to formally test the second prediction, however a qualitative summary of this hypothesis is presented in figure S1. We also used the comparison of wolves hunting migrant vs. resident elk as a means of evaluating aspects of the Prey Scarcity Hypothesis. Primarily, we sought to evaluate whether the spring migration of elk away from wolf denning areas forced wolves to shift to hunting alternative prey (e.g. cattle or deer) during summer compared to the hunting patterns of wolves in resident elk areas. We tracked four GPS-collared wolves and used agency-generated data on livestock kills to identify the location and timing of livestock depredations and prey selection in areas where elk are either migratory or resident. Clarifying whether native prey distribution influences patterns of wolf-cattle conflict may help illuminate ecologically-driven solutions to manage carnivore populations.
MATERIALS AND METHODS

Study area

Our study area was located in northwest Wyoming, spanning from the eastern limit of YNP to the town of Cody (Fig. 1). Land jurisdiction was primarily US 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* (Mirb.) Franco) forests (11%), and sagebrush (*Artemisia*) 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, with a mean spring migration start date of May 26 and fall migration start date of October 16 (A.D. Middleton, unpublished data (2015)). The winter range of the migratory elk subpopulation (Fig. 2; red polygon) showed the vast majority of winter elk GPS locations within the cattle pasture polygon designated as the migratory area. In summer, these elk migrated out essentially vacating the area of analysis except for a small group available for wolves to kill in the western part of the study area. The migratory habits of this elk herd are well studied (Middleton et al. 2013 and Nelson et al. 2012) but not the focus of this paper. In summer, cattle and elk were exposed to the Sunlight, Beartooth, and Crandall. 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, 300-400 whitetail deer, 200-300 pronghorn (*Antilocapra Americana* Ord 1815), and a small number of moose (*Alces alces* L., 1758; D.E.M., unpublished data). Over the span of four years, the study area contained three to four wolf packs in a given year (2007 included the Sunlight, Beartooth and Absaroka packs, and 2008 – 2010 included Sunlight, Beartooth, Crandall and Absaroka packs), all of whom had some interaction with the livestock depredations recorded for our analysis. Grizzly bear, black bear (*Ursus americanus* Pallas 1780), cougar (*Puma concolor* L. 1771) and coyote (*Canis latrans* Say 1823) were also present. Public and private rangelands in our study area also support several thousand head of cattle that spatially overlap with at least part of the range of all four wolf packs we tracked.

**Capture and collaring**

To collect data on wolf predation events, we tracked GPS collared wolves, however the majority of cattle kills for the main analysis were recorded through agency depredation records (*n*=36) from 2007 – 2010. Several were also located using wolf GPS collars through cluster searching methods (*n*=3).

We captured wolves using leg-hold 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 (Kreeger and Arnemo 2007). 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). 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. Animal captures were conducted using 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) from July 1 – October 26 (2007 and 2008) which included the seasonal peak in depredations for the area (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, defined as at least three locations within 100 m of each other, were identified in GIS (ArcMAP 9.2) and searched by field crews. We visited 96\% of 594 clusters within an average of 8.6 days \( (\pm 5.2 \text{ SD}) \) after wolves left the site. Clusters associated with a den or rendezvous site were searched after the wolves left the area.

Searching techniques described here are similar to those described in Metz et al. (2011). We searched a radius of 35 m around each individual location (20 minute GPS fix rate) 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. 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. 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.

**Analysis of factors influencing cattle depredations**

In evaluating multiple drivers of wolf kills, we sought primarily to test the prediction from the Prey Tracking Hypothesis that elk distribution would positively influence the location of wolf-killed cattle. We also sought to evaluate the influence of landscape features, including distance to stream, distance to road, distance to forest edge and distance to wolf den. We derived GIS covariate rasters (100 m cell size) to index these landscape attributes.

To index elk distribution, we created a fixed kernel density estimate using location data from 86 elk GPS collars during summer months based on the median date of elk migration in the migratory elk area (May 27). To index proximity to stream, we used a high resolution National Hydrology Dataset (NHD 1999) stream polyline layer. As a proxy for human activity, we estimated a primary road layer using polylines from U.S. Detailed Streets (2002), and edited 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. Similarly, we created a distance to den raster, including known natal dens for each of the study packs.

We used a resource selection function (RSF) with a use vs. availability design (Manly 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). Used locations consisted of confirmed or probable 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 occurring either in the migratory or resident elk area, using a dividing line consistent with the WGFD elk herd unit ecologically delineating migratory or resident elk (Middleton et al. 2013). Available points were randomly placed (20 per used location) in the study area with a 200 m buffer within which GIS covariates were averaged. A 200 meter buffer was designated to represent the characteristics of the area involved with the predation sequence and was based on observations of the attack and kill site of livestock depredations. 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 found that there was enough variation in summer elk distribution (both in the migratory and resident areas) to detect a difference using the logistic regression framework between the random and kill site locations (Fig. 2). 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 potential bias. We used separate logistic regression (Minitab Inc, State College, PA) analyses in migratory and resident elk areas to evaluate the influence of landscape features and elk distribution 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 in the resident elk area. Though difficult to generalize across different livestock operations, cattle generally were grazed farther away from elk in early summer (Fig. 3A), and moved up in
elevation closer to, and in some cases comingling with, elk by late summer (Fig. 3B). We attempted to assess whether the frequency of depredations occurring within two week intervals throughout the summer increased or decreased as summer progressed (4-year depredation dataset (2007-2010)). We plotted the number of kills occurring against these ordered time periods throughout the summer for the migratory and resident areas. Because of small sample size and the lethal removal of depredating wolves soon after they began killing cattle, we view this analysis as largely descriptive, and it is described in the supplementary materials.

To identify differences in composition of wolf-killed prey species in migratory and resident elk areas, we compared the frequency of wild ungulate prey killed by wolves identified through cluster searching. We sought to evaluate differences that might result from wolves living in migratory elk areas switching to alternate prey as predicted by the Prey Scarcity Hypothesis, or conversely, following migratory elk. Because most prey remains were elk and deer, we conducted a binomial proportion test (Minitab 16, State College, PA) to evaluate differences in the proportion of deer and elk in the kills of wolves from each area.

RESULTS

Analysis of factors influencing cattle depredations

Analysis of 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 distribution ($Z = 3.18, P = 0.001$). Depredations in this area also occurred closer to roads than the available habitat ($Z = -2.61, P = 0.009$), which was contrary to our predictions. 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 ($Z = 2.47$, $P = 0.014$). We assessed goodness of fit for the migratory and resident areas (Hosmer-Lemeshow), which respectively had $P$-values of 0.956 and 0.222, neither low enough to cause concern. In contrast to the resident area, elk distribution in the migratory elk area did not influence the location of cattle depredations (Table 1).

Prey selection

Binomial proportion analysis indicated differences in the composition of wild ungulate prey between wolves living in migratory and resident areas ($Z = -3.22$, $P = 0.001$; Fig.4), suggesting the use of deer instead of livestock as alternative prey by wolves in the migratory elk area. Wild ungulate composition of wolf kills 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). Cluster searching revealed too few cattle depredation events ($n=3$) to estimate cattle as a proportion of total kills documented.

DISCUSSION

We found that depredations on cattle were strongly associated with groups of summering elk 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 (Kauffman et al. 2007); however, they had a stronger influence on cattle kills in the migratory area, in the absence of elk. 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 provide support for the Prey Tracking Hypothesis.

Although we did not have enough cattle kill data to adequately test the Prey Scarcity Hypothesis, we found support for the importance of alternative prey in the migratory elk area.
Wolf kills in the migratory elk area suggest that wolves prey on elk, but also hunt deer to a greater degree than in the resident elk area, possibly because of seasonally low densities of elk in the migratory elk area. The availability of deer as alternative prey may have reduced the frequency with which wolves in the migratory area killed cattle. Acknowledging the small sample size, the few cattle kills located in the migratory elk area through cluster searching methods ($n=3$) support the notion that, of all other ungulates killed, cattle predation is mostly incidental, in this context where wolves are often immediately removed from the population following depredations. Overall, these findings in both the migratory and resident areas imply that seasonally variable native prey distribution can mediate the location and occurrence of livestock depredations, suggesting the importance of co-managing livestock, wolves, and growing resident elk populations.

In the resident area, we found that wolves tend to kill cattle in locations where cattle comingle with elk groups (Fig. 3C), which is consistent with the observation that wolves have higher encounter rates with large elk groups (Hebblewhite and Pletscher 2002). The strong association between wolves and elk (Nelson et al. 2012) seems to provide a benefit to cattle when they are nearby, but not comingling with elk. Wolves killed relatively few cattle in pastures separate from elk, and depredations tended to increase when cattle were moved into higher elevation elk-rich habitat (see figure S1A). Spatial patterns of native ungulate kills generally 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. 3A and 3B). These results are consistent with the finding that elk abundance in pastures increases the likelihood of wolf depredations (Bradley and Pletscher 2005).

By contrast, landscape attributes other than elk distribution had a strong influence on the location of cattle kills in the migratory areas, suggesting that in the absence of native
prey, other attributes that influence encounter rates between wolves and cattle become more important. Wolves in Idaho that had high spatial overlap with cattle also had higher rates of depredation (Oakleaf et al. 2003), possibly driven by encounter rates. 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. Due to their dampened anti-predator behavior (Linnell et al. 1999; Muhly et al. 2009) and dispersed distribution throughout pastures, domestic livestock may be highly vulnerable to attack wherever they encounter wolves. We suspect that wolf capture success of cattle is higher than the success rate of wolves that target elk, which has been estimated at ≈ 21% (Smith et al. 2000).

Landscape attributes associated with cattle kill sites may facilitate 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; Bradley and Pletscher 2005). Cattle kills in the migratory elk area were also associated with habitat distant from forest edge, or in open areas, where wolves often travel (Oakleaf et al. 2003). A caveat to finding kills in open areas, however, is that our method of collecting depredation reports could include a bias towards open areas, as 36 of 39 cattle kills were derived exclusively from human reporting, and only a few kills (n=3) were also located through GPS cluster searches. However, if this were a significant influence on the analysis we feel it would mask the ecological differences detected between the two areas (not the case). The association of cattle kills with streams highlights the importance of encounters, as cattle tend to use riparian habitat (Oakleaf et al. 2003) and wolves often use such drainages to travel (Kunkel and Pletscher 2001). Our results support the notion that, in the absence of native prey, landscape
attributes that facilitate predator-prey encounters strongly influence spatial patterns of wolf-livestock kills.

In the migratory area, we found that wolves selected deer as an alternate prey resource in summer when elk became scarce (Fig. 4). Prey switching can occur in response to changing availability or vulnerability of preferred prey (Garrott et al. 2007). We did not test differences in seasonal prey selection, however, wolves in our study area appear to respond to declines in abundance of elk by killing a greater proportion of deer than was found in an adjacent study area during winter in YNP studies (96% elk; Smith et al. 2004) and in the resident elk area we studied (Fig. 4). While some studies have found that low abundance of native prey is associated with more frequent cattle depredations (Gunson 1983), our findings suggest that availability of deer as alternative prey, in the context of effective lethal control of problem wolves, can mediate wolf depredation on cattle.

Cattle depredations in the resident area generally occurred in greater numbers in late summer and fall (Fig. S1A), and no cattle were confirmed as killed by wolves in winter and spring of the study period. In YNP, wolf consumption of vulnerable neonate ungulates declined after the start of July, when biomass consumption reaches a year-round low (Metz et al. 2011), which suggests a decline in availability of vulnerable prey. Cattle tend to be moved up in elevation in resident elk areas as the summer progresses; such pastures have high elk numbers (Nelson et al. 2012) and are far from human activity. Both remoteness and the presence of elk have been associated with higher wolf depredations (Dorrance 1982; Bradley and Pletscher 2005).

Management implications

The relative proportions of migrant and resident elk are changing in many herds in the Rocky Mountains (Hebblewhite et al. 2006; Middleton et al. 2013). Our research suggests
that a shift in the distribution of ungulate biomass towards front country landscapes, may increase wolf depredation rates, livestock-related removal of wolves, and spatially influence the dynamics of regional wolf populations (Garrott et al. 2005). Growing resident elk populations increasingly exist year-round on private land that is at times characterized by restricted hunting access and livestock grazing. On these multiple-use landscapes, wolves will typically encounter cattle at some point while hunting elk, and wolves that chronically kill livestock have historically been lethally removed (Jimenez et al. 2010). Changing patterns of elk distribution could slow pack re-establishment following control actions where migratory prey are scarce (see Musiani et al. 2005), or create an attractant for wolf establishment in areas with abundant resident prey.

Harvest is currently an important tool to manage wolf populations under the state plans for Montana, Wyoming (when delisted) and Idaho. Livestock conflicts tend to peak in September and October often warranting entire pack removals, which, in combination with pre-established harvest quotas, may drive populations close to minimum allowable thresholds. The states of WY, ID and MT are currently aware of this and model harvest including a proxy for average or prior lethal removal numbers. Our findings support the efforts of management agencies to reconcile management removals with harvest quotas and population objectives, and the efforts of cattle producers to consider pasture rotations that can reduce comingling of cattle and elk. Additionally, human activity, such as that generated by a hunters (and now wolf hunters), may temporarily displace wolves (Treves 2009; Nelson et al. 2012) and elk in areas with livestock conflict, which could prove useful in the early fall when depredation rates appear to increase in our study area. In addition to reducing crop depredations, forage competition, and disease transmission to cattle, when targeting ungulate
harvest across landscapes shared with cattle production, our study suggests that reducing elk density or displacing elk away from cattle may also reduce livestock depredations by wolves.

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Figure legends:

**Figure 1.** Study area located in northwestern Wyoming, including the eastern boundary of Yellowstone National Park. Summer movements (July 1 – October 22, 2007-2008) of four GPS-collared wolves (*Canis lupus* L., 1758) are shown. Wolf packs occupying migratory elk (*Cervus elaphus* L., 1758) 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.

**Figure 2.** Pastures that were considered available for wolves (*Canis lupus* L., 1758) to kill cattle (*Bos taurus* L., 1758) in resident (black outline) and migratory (gray outline) prey areas. Cattle depredation locations (black triangles) were positively associated with areas of core summer elk (*Cervus elaphus* L., 1758) use (grey filled polygons) in the resident elk areas (*n*=20), but showed no association with the distribution of elk in the migratory elk area (*n*=19). Cattle depredation data was gathered year-round through agency reporting (2007-2010) and GPS data (2007-2008) from collared wolves.

**Figure 3** (A) In early summer (May 1 – August 15), there were few cattle (*Bos taurus* L., 1758) depredations (red circles) and they occurred somewhat randomly with respect to elk (*Cervus elaphus* L., 1758) distribution. (B) In late summer (August 15 – October 31), wolves (*Canis lupus* L., 1758) tended to kill more cattle (red dots) as pasture rotations brought cattle to comingle with elk (B). Cattle kill data represented in this figure and used for the logistic regression analysis were collected using a combination of agency reports (2007-2010) and GPS data.
collar data (2007-2008). Wolf movements (black dots) in the resident elk area were closely associated with upper 50% of resident elk distribution (striped polygon) throughout summer, and they tended to kill ungulates (July – mid-August; blue circles) in areas with large elk groups.

**Figure 4.** Proportion of ungulate prey species killed by wolves (*Canis lupus* L., 1758) 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 (*Odocoileus hemionus* Rafinisque, 1817) or elk calf (*Cervus elaphus* L., 1758) remains that were present with signs of predation but too inconclusive to determine species.
Figure 1.
Figure 2.
Figure 3 (Panels A, B & C)

Legend
- Ungulate kills
- Livestock kill
- Open_roads
- Wolf locations
- 50% elk use
- Used cattle pastures

Cody, WY
Figure 4.
Table 1. Resource selection function coefficients that influence the location of wolf (*Canis lupus* L., 1758) -killed cattle in areas where elk (*Cervus elaphus* L., 1798) are resident (n = 19 kills) or migratory (n = 20). Significant variables are in bold.

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