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Research Article

Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming

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ABSTRACT Wolf (*Canis lupus*) predation on livestock and management methods used to mitigate conflicts are highly controversial and scrutinized especially where wolf populations are recovering. Wolves are commonly removed from a local area in attempts to reduce further depredations, but the effectiveness of such management actions is poorly understood. We compared the effects of 3 management responses to livestock depredation by wolf packs in Montana, Idaho, and Wyoming: no removal, partial pack removal, and full pack removal. We examined the effectiveness of each management response in reducing further depredations using a conditional recurrent event model. From 1989 to 2008, we documented 967 depredations by 156 packs: 228 on sheep and 739 on cattle and other stock. Median time between recurrent depredations was 19 days following no removal ($n = 593$), 64 days following partial pack removal ($n = 326$), and 730 days following full pack removal ($n = 48$; recurring depredations were made by the next pack to occupy the territory). Compared to no removal, full pack removal reduced the occurrence of subsequent depredations by 79% (hazard ratio [HR] = 0.21, $P < 0.001$) over a span of 1,850 days (5 years), whereas partial pack removal reduced the occurrence of subsequent depredations by 29% (HR = 0.71, $P < 0.001$) over the same period. Partial pack removal was most effective if conducted within the first 7 days following depredation, after which there was only a marginally significant difference between partial pack removal and no action (HR = 0.86, $P = 0.07$), and no difference after 14 days (HR = 0.99, $P = 0.93$). Within partial pack removal, we found no difference in depredation recurrence when a breeding female (HR = 0.64, $P = 0.2$) or $\geq$1-year-old male was removed (HR = 1.0, $P = 0.99$). The relative effect of all treatments was generally consistent across seasons (spring, summer grazing, and winter) and type of livestock. Ultimately, pack size was the best predictor of a recurrent depredation event; the probability of a depredation event recurring within 5 years increased by 7% for each animal left in the pack after the management response. However, the greater the number of wolves left in a pack, the higher the likelihood the pack met federal criteria to count as a breeding pair the following year toward population recovery goals. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Canis lupus*, depredation, Idaho, lethal control, livestock, Montana, recovery, removal, wolf, Wyoming.

Depredation on livestock has put wolves in conflict with humans for centuries and continues to be a major issue facing their recovery and persistence in agricultural areas around the world (Mech 1995, Fritts et al. 2003). Conflicts with livestock were partly responsible for the heavy persecution of wolves in the contiguous United States that led to their near complete extirpation by the late 1930s (Young and Goldman 1944, Curnow 1969). Through protection under the Endangered Species Act (ESA), gray wolf (*Canis lupus*) populations have been recovering in the Great Lakes region and in the northwestern and southwestern United States (Wydeven et al. 2009, U.S. Fish and Wildlife Service [USFWS] et al. 2014).

In the northern Rocky Mountains (NRM), the wolf population grew rapidly as a result of natural recovery via dispersal of wolves from Canada and reintroduction into

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Yellowstone National Park and Central Idaho in 1995 and 1996 (Bangs and Fritts 1996, Bangs et al. 1998). By 2012, 26 years after the first wolf den was documented in the western United States since listing (Ream et al. 1989), wolves in the NRM were removed from ESA protections. States and Tribes are currently responsible for most wolf management. In Montana, Idaho, and Wyoming, wolf conflicts are managed primarily through lethal removal by agencies and public harvest to manage wolf numbers and distribution (USFWS et al. 2014).

Reducing depredation on livestock has been a critical focus of wolf recovery efforts in the NRM. Wolf depredation has composed a small fraction of total livestock mortality each year, but in some cases, individual livestock producers have experienced significant losses (Bangs et al. 1995, 1998, 2005). In 2010 federal agencies spent $4,566,000 to restore and manage the NRM wolf population. Of that, $1,103,000 was spent by the United States Department of Agriculture Wildlife Services (USDA WS) to investigate reports of suspected wolf damage and to kill problem wolves. In 2010, private and state compensation programs paid $453,741 for livestock damage caused by wolves in the NRM (USFWS et al. 2011).

Managing wolf conflicts in a manner that allowed wolf population growth was important in attempts to encourage local tolerance while working toward federal ESA recovery goals (Bangs et al. 1995). Application of wolf removal generally trended from more conservative actions, such as removing small numbers of wolves and translocation in earlier years toward larger removals and more full pack removals after wolf numbers exceeded recovery goals. Lethal removal is considered a necessary component of wolf management (Mech 1995) but is controversial (Cluff and Murray 1995, Reiter et al. 1999, Bruskotter et al 2009).

Wolf removal is primarily used as a short-term strategy designed to reduce further livestock depredations in the local area where they occurred. However, most research aimed at evaluating the effectiveness of lethal wolf removal to date has focused on wolf removal and depredation patterns at a regional level. Wielgus and Peebles (2014) evaluated wolf depredation and removal data from interagency annual reports for the NRM from 1987 to 2012 (USFWS et al. 2013) by examining the relationship between total numbers of depredations and wolves removed 1 year to total numbers of livestock depredations the following year across the region. They found that depredations increased each year despite wolf removals until wolf mortality exceeded 25% and suggested that lethal removal of wolves is related to increased depredations. However, the wolf population was growing rapidly during most of the years of the study and they also found a correlation between numbers of depredations and numbers of wolves in the region (Wielgus and Peebles 2014). Musiani et al. (2005) analyzed the same dataset in the NRM from 1987 to 2003 and additional data from Alberta and also found that wolf removal did not decrease livestock depredations at the regional scale, acknowledging these removal actions were not designed to do so. In Minnesota, Harper et al. (2008) found similar results; wolf removals were generally ineffective in reducing depredations when evaluated at the statewide level.

Local and more fine-scale data on the effects of wolf removal on livestock depredations are sparse. Wolf removal appeared to reduce local livestock losses in northwestern Alberta and British Columbia (Bjorge and Gunson 1983, 1985; Tompa 1983). Methods of wolf removal in both cases included poisoning, and in some cases aerial gunning, which removed most of the wolves in the study area in northwestern Alberta (Bjorge and Gunson 1983, 1985) but an unknown proportion of the local wolf population in British Columbia (Tompa 1983). In Minnesota, Harper et al. (2008) looked at local farm clusters and found little effect of wolf removal on recurrence of depredations within the clusters except at sheep farms and when ≥ 1 adult male was removed. They found that total number of wolves removed had no effect on depredation recurrence; however, there was no information on the number and size of the packs in these areas and how much removal occurred relative to the size of the local wolf population. To date no researchers have looked at individual wolf packs and examined the effects of removing wolves from these packs on their subsequent depredation behavior. Many packs were radio-collared in the NRM during the years of wolf recovery, especially those near livestock. This provided a unique opportunity to identify and follow individual depredating wolf packs, and to study the effects of management actions on these packs through time.

We examined data on livestock depredations and wolf removal in Montana, Idaho, and Wyoming conducted under authority of the USFWS and state agencies from 1989 to 2008. We focused our analysis on depredations by known wolf packs. Our first objective was to evaluate the relative effects of 3 management responses to livestock depredation: no removal, partial pack removal, and full pack removal. We tested the following hypotheses: 1) there would be differences in depredation recurrence by wolf packs after different management responses, and 2) the effects of each management action would differ between grazing seasons and type of livestock. Our second objective was to evaluate partial pack removal independently and test the following hypotheses: 1) the effects of partial pack removal would differ based on wolf pack size, and 2) the effects of partial pack removal would differ based on whether a breeding female or adult male was removed. Third, we tested the hypothesis that depredation recurrence in local areas would increase as the wolf population grew in the NRM. Our fourth objective was to evaluate the effects of wolf removal for livestock depredation on wolf recovery. We tested the hypothesis that partial pack removal would affect a pack's breeding pair status the following year.

STUDY AREA

The states of Montana, Idaho, and Wyoming were divided into 3 wolf recovery areas (USFWS 1987): central Idaho, the Greater Yellowstone area (GYA), and northwest Montana (Fig. 1). Wolves naturally recolonized northwest Montana in the 1980s via dispersal from Canada (Ream et al. 1991) and were managed as endangered. Wolves were reintroduced into central Idaho and Yellowstone National Park in 1995 and 1996 (Bangs and Fritts 1996, Fritts et al. 1997) and were managed as

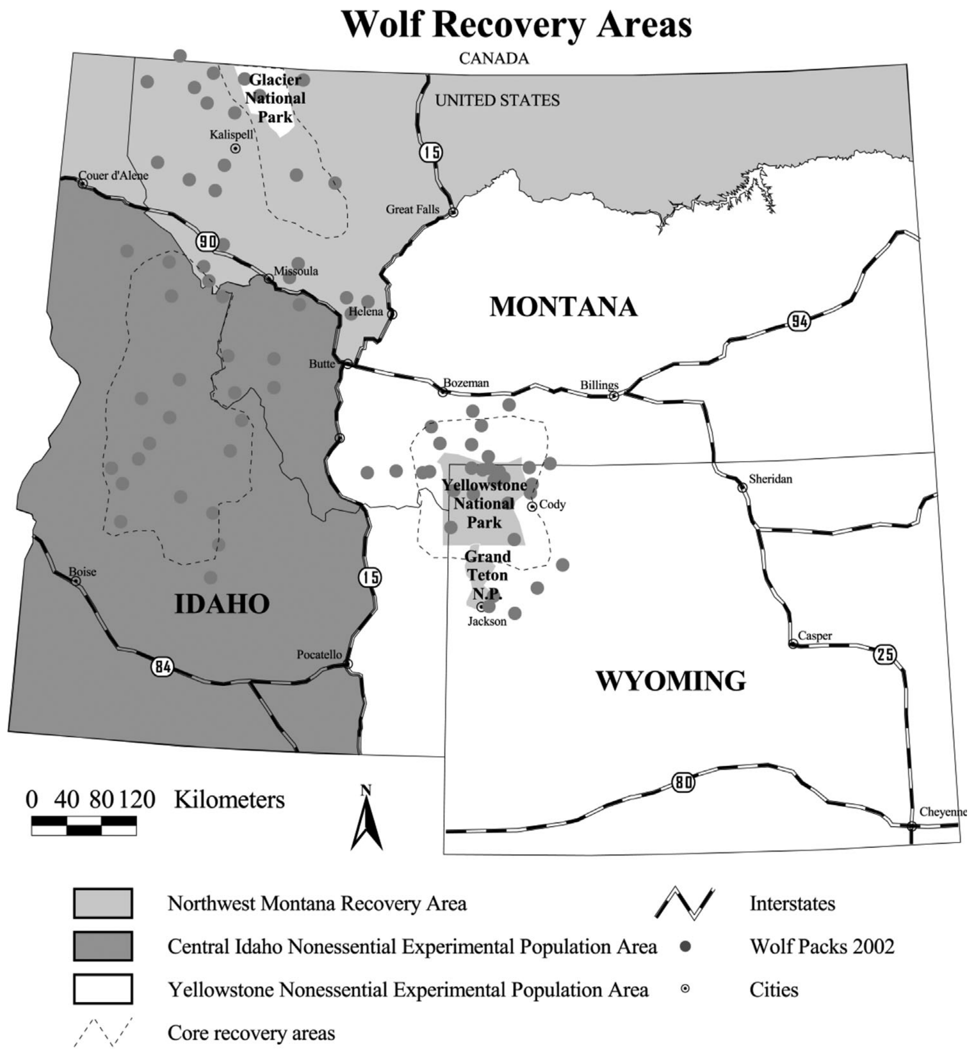

Figure 1. Wolf pack locations in Montana, Idaho, and Wyoming, USA, at the time the wolf population reached federal recovery goals in 2002.

a nonessential experimental population under section 10(j) of the ESA to allow for more flexibility in addressing conflicts with livestock (USFWS 1994*a*). Wolves were federally listed for all but a short duration of this study in 2008.

The wolf population grew rapidly in the NRM and increased each year between 1989 and 2008. At the end of 2008 there were at least 1,645 wolves inhabiting the 3 recovery areas: 914 in central Idaho, 449 in the GYA, and 282 in northwest Montana (USFWS et al. 2009). Recovery goals were met at the end of 2002 (>663 individuals) when there were ≥30 breeding pairs and >300 wolves across the 3 recovery areas for 3 consecutive years (USFWS et al. 2009). A breeding pair of wolves was defined as an adult male and an adult female wolf with ≥2 pups surviving through the end of the calendar year (USFWS 1994*b*). Montana, Idaho, and Wyoming must each continue to hold a minimum of 10 breeding pairs to meet ESA recovery goals (USFWS 2009).

METHODS

We compiled data from 1989 to 2008 on all confirmed wolf depredation events and associated management responses in Montana, Idaho, and Wyoming. Depredations were confirmed by USDA WS personnel using standard protocols (Roy and Dorrance 1976, Paul and Gipson 1994) and represent minimum numbers of livestock killed. Other depredations were not reported or found, or lacked enough evidence to confirm (Bangs et al. 1998, Oakleaf et al. 2003). Initial depredations were often followed by an increase in monitoring, which likely helped increase detection of further depredations.

We used depredation and removal data on packs, which we defined as groups of ≥2 wolves with established territories. Wolf packs were often radio-collared either before or during control operations. Pack involvement in depredations was determined by proximity of the pack based on radio-telemetry locations, documented return of pack members to the depredation site, or both.

Lethal removal was the primary method used to remove wolves from packs and was conducted by USDA WS by request of the USFWS or state agencies. Lethal removal methods included trapping and euthanizing, ground shooting, and aerial gunning. Larger removals were usually accomplished with the use of aerial gunning. Some wolves were legally killed by landowners or their agents with agency-issued kill permits or under applicable federal or state defense of property laws. Landowner removals were less than 10% of all yearly removals and never eliminated a pack (USFWS et al. 2009). In the early years of wolf recovery, the USFWS translocated some wolves away from depredation sites, but this practice was halted by the end of 2002 (Bradley et al. 2005). Translocated wolves were counted as removed if they did not return to their original territory.

We examined the effects of 3 management responses to livestock depredation: no removal, partial pack removal, and full pack removal. Management responses where no removal occurred were either by design or from failure to capture or kill wolves in a reasonable time frame. Partial pack removal events included those where part of the pack was removed, but some pack members remained in the pack territory. Full pack removal events included those where all pack members were killed or in a few cases, where remaining pack members disbanded and vacated the territory. In many cases nonlethal preventative methods were employed prior to and during depredations (Bangs et al 2006), but removal was the primary tool attempted once depredations occurred. We could not evaluate effectiveness of preventative methods, such as modification of livestock management practices, fencing, and scare devices, because of the wide diversity of methods, the inconsistency of their application, and sparse record keeping.

Recurrent depredations can occur in 2 ways, first in the same territory by the same pack, and secondly in the same territory by a different pack. For this reason we conducted our analyses either from the perspective of the individual wolf pack or pack territory. Often, there were multiple depredation events caused by the same pack. For analyses conducted from the pack perspective, we measured time between depredations by the same pack. From the territory perspective, there were sometimes different packs inhabiting those territories over the years of this study. For these analyses, we measured the time between depredations in a territory, regardless of what pack was involved. Pack territories were defined by yearly telemetry locations of radio-collared pack members. Each pack or pack territory entered the dataset each time a depredation occurred by that pack or in that area. For example, one pack may have depredated multiple times and had several no removal or partial removal management actions leading up to a final full pack removal. To account for this correlation among observations, we clustered our analysis based on wolf pack or pack territory depending on the perspective used (Lin and Wei 1989). For those packs that had multiple depredations, we stratified our observations based on the order of the depredation and then tested for an interaction between these multiple events, or strata, and management action to determine whether there was a change in efficacy of the action for an individual pack over time (i.e., is a management action less effective after a pack's fifth depredation than after its first).

We divided depredations into 2 broad categories: 1) sheep, and 2) all other stock including cattle. Only $<3\%$ of depredations in our dataset involved livestock other than cattle or sheep, but we did not exclude these events because they were tied to our perspective of analysis: wolf pack or pack territory. For example, over the course of a year a particular pack of wolves may kill both cattle and llamas. If llama depredations are excluded then we miss a management response tied to that depredation that may have affected that pack's probability of attacking cattle again. We tested for a difference in the seasonal distribution of these 2 depredation types using a Spearman rank correlation across months. We broke seasons into winter (15 Oct to 1 Feb), spring calving and lambing (1 Feb to 15 June), and summer grazing (15 June to 15 Oct) to reflect varying vulnerability of livestock throughout the year. Winter season is believed to be the period of least vulnerability when livestock are larger bodied and living in more contained areas. The spring calving and lambing season reflects a period when livestock are vulnerable based on size. The summer grazing period reflects a period when livestock are vulnerable based on both size and wide distribution across the landscape.

We examined the effect of grazing season (spring, summer grazing, winter), livestock type (sheep and cattle or other), 3 management response levels (no removal, partial pack removal, and full pack removal), year, and pack-related characteristics (pack size, and whether a breeding female or adult male was removed) on depredation using a conditional recurrent event, or gap time, model (Prentice et al. 1981, Hosmer et al. 2008). The model is conditional in that observations are stratified by their failure order and the risk set at time t for event k is limited to subjects that have had event k-1 (Prentice et al. 1981). In this form of the Cox proportional hazards model, subjects (i.e., wolf packs or pack territory) enter the analysis following their first event (in this analysis a depredation), with analysis time being the number of days from one depredation event to the subsequent depredation event, or censoring. The response variable, therefore, is a depredation interval, measured in days. No new packs were added to the analysis after 2008; however, packs already being monitored were followed until 31 December 2010, the end of the study period. Packs that had not committed a recurrent depredation by the end of the study period or were no longer monitored were right censored (i.e., included in the risk set until censored). All covariates were considered enduring fixed variables (i.e., constant across the segment interval). We limited follow-up time to approximately 5 years (1,850 days) to limit the effect of small sample sizes at the end of the period. We performed all analyses using the statistical software package Stata 11 (StataCorp, College Station, TX).

We ran the first analysis with the 3 management response variables (no removal, partial pack removal, and full pack removal), livestock type, and grazing season. We conducted this analysis from the perspective of the wolf pack territory to compare the 3 management response variables. Full pack removal can be examined only from the pack territory perspective because the response variable (depredation interval) represents the time between the last depredation by a removed pack and the next depredation that occurs in that pack territory by a new pack. The other 2 variables, livestock type and grazing season, were clearly attributes of the pack territory rather than of a particular pack.

The effects of partial pack removal may potentially vary depending on the number and type of wolves that are removed. Therefore, we ran a second analysis restricting the data to cases of partial pack removal and included 3 covariates: 1) pack size following removal (continuous variable), 2) whether a breeding female was removed, and 3) whether a yearling or male (≥1-year-old) was removed (indicator variables). We conducted this analysis from the perspective of the wolf pack because all variables were attributes of individual packs. Breeding determination was based on physical characteristics. Breeding males were sometimes difficult to identify so we classified the removal of breeding females and ≥1-year-old males as separate covariates. Pack sizes were estimated based on aerial or ground observations, and in some cases, snow tracking.

We ran a third analysis to examine whether there were any differences in depredation recurrence at the territory scale as the wolf population in the region increased by using the annual minimum population for each year of the study as a predictor variable. A minimum count of the wolf population in the NRM is estimated and reported by federal and state personnel at the end of each year; the minimum count increased from 12 wolves in 1989 to 1,645 in 2008 (USFWS et al. 2009). We ran the analysis on all treatment levels together and while restricting the data to full pack removals to examine potential effects of regional population growth on depredation occurrence and to more specifically look at whether population growth affected depredation recurrence after pack removal (i.e., whether vacant territories filled faster and therefore depredations resumed sooner).

To evaluate the effects of partial pack removal on wolf recovery, we compared the relative hazard of pack size after removal on the probability of depredation recurrence and on the probability a pack would contain a breeding pair the following year. We ran a Cox proportional hazard model on pack size while restricting the data to partial pack removals only, and limiting the time period to 1 year (365 days). If a second event had not occurred within 1 year, the remainder of the observations from that pack were right censored. As with previous analyses, we stratified the analysis by event number and clustered on pack to account for the correlation among observations (Lin and Wei 1989). We then predicted the relative hazard, $\exp(x_j\widehat{\beta}_j)$, where β_j is the coefficient for pack size. We used a logistic regression to model the effect of observed pack size on whether or not a pack contained a breeding pair the following year. Similar to the Cox model, we predicted breeding probability based on the coefficient for pack size: $\exp(y + x_j\widehat{\beta}_j)/[1 + \exp(y + x_j\widehat{\beta}_j)]$. We graphed both predicted probabilities over a single x axis, pack size.

RESULTS

From 1989 through 2008 we documented 967 wolf depredations by 156 packs: 228 on sheep and 739 on cattle and other livestock (5 goat, 15 llama, and 8 horse depredation events). There were 593 management responses with no removal actions (61%), 326 partial pack removals (34%), and 48 full pack removals (5%). Partial removals averaged 2.2 wolves (range 1–10, SD = 1.43). Depredations occurred in all months with cattle and sheep depredations distributed similarly across the year ($r_s = 0.88$, $P \leq 0.001$; Fig. 2). Recurrent depredations were significantly more likely to occur during summer grazing (15 Jun to 15 Oct) than spring (hazard ratio [HR] = 1.27, SE = 0.116, $Z = 2.59$, $P = 0.009$), whereas risk of recurrent depredation did not differ between winter and spring (HR = 1.00, SE = 0.126, $Z = 0.00$, $P = 0.997$). Management actions followed this same general distribution with full pack removal being somewhat more constant across the year (Fig. 3).

Median period between recurrent depredations was 19 days ($\bar{x} = 115$ days) following no removal, 64 days ($\bar{x} = 170$ days) following partial pack removal, and 730 days ($\bar{x} = 753$ days) following full pack removal and subsequent refilling of the home range and depredation by the recolonizing pack. When compared to no removal, full pack removal reduced the occurrence of subsequent depredations by 79% over a span of 1,850 days (HR = 0.205, SE = 0.033, $Z = -9.77$, $P = 0.00$), whereas partial pack removal reduced the occurrence of subsequent depredations by 29% over the same period (HR = 0.707, SE = 0.056, $Z = -4.4$, $P = 0.00$). However, there was only a marginal difference between partial pack removal and no removal if the partial pack removal was not conducted in the first 7 days following depredation (HR = 0.86, $P = 0.08$), and there was no difference if conducted after 14 days (HR = 0.99, $P = 0.95$). When no removal occurred following a depredation there was a 50% chance of recurrence at 18 days. With partial pack removal, that 50% probability was extended to 63 days. Full pack removal offered a 729-day window where the probability of a recurrent depredation was less than 50% (Fig. 4). We found no significant season × action interactions, which suggested there was no difference in efficacy between seasons. We also found no strata×action interactions, which suggested that partial pack removal or no removal did not increase or decrease in efficacy with repeated depredations or repeated actions. Finally, we found no significant species × action

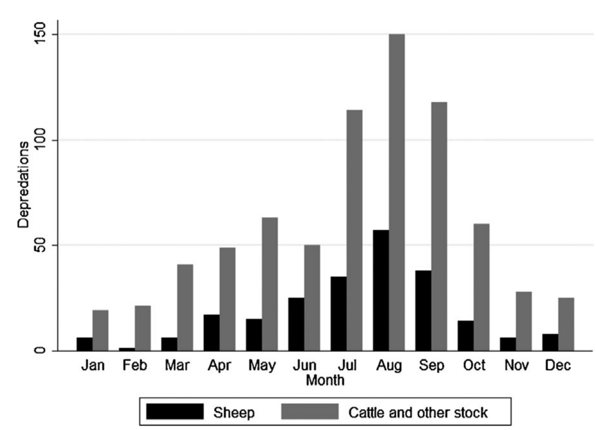

Figure 2. Monthly occurrence of sheep and cattle or other livestock depredation events by wolf packs in Idaho, Montana, and Wyoming, USA, 1989–2008.

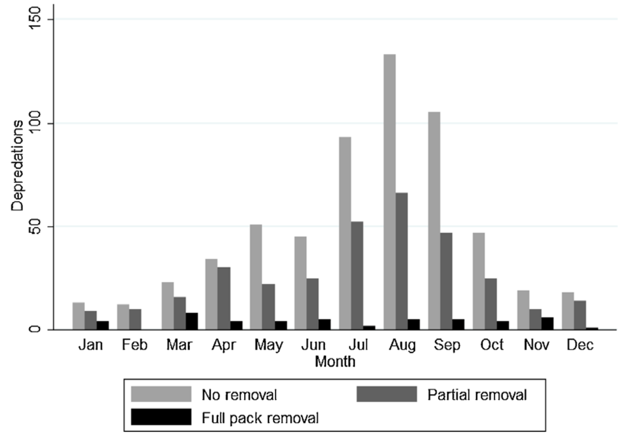

Figure 3. Monthly distribution of management actions taken in response to livestock depredation events by wolf packs in Idaho, Montana, and Wyoming, USA, 1989–2008.

interaction, which suggested efficacy was similar whether the depredation occurred on sheep or other livestock.

The number of wolves in the pack following partial pack removal was the best predictor of a recurrent event. In a model containing pack size, and whether or not a ≥1-year-old male or breeding female was removed, only pack size was significant (Table 1). Univariate analysis of pack size alone suggested a 7% increase in the probability of a recurrent event within 5 years for each animal left in the pack ($HR = 1.068$, $P < 0.01$).

The probability of depredation recurrence did not increase after full pack removals as the wolf population grew ($HR = 1$, $P = 0.52$). When combining all management response treatments together, there was no relationship between minimum wolf counts and depredation recurrence ($HR = 0.99$, $P = 0.35$).

The probability of a pack containing a breeding pair the year following partial pack removal increased with pack size ($x = -1.801 + 0.223 \times$ pack size, $P < 0.001$) and probability of depredation recurrence increased 5% for each wolf left in the pack for ≤1 year after removal ($HR = 1.05$, $P < 0.001$; Fig. 5). Of 169 non-lethal actions, 89 (53%) packs were counted as breeding pairs the following year. Of 140 partial pack removals, 43 (31%) were counted as breeding pairs the following year.

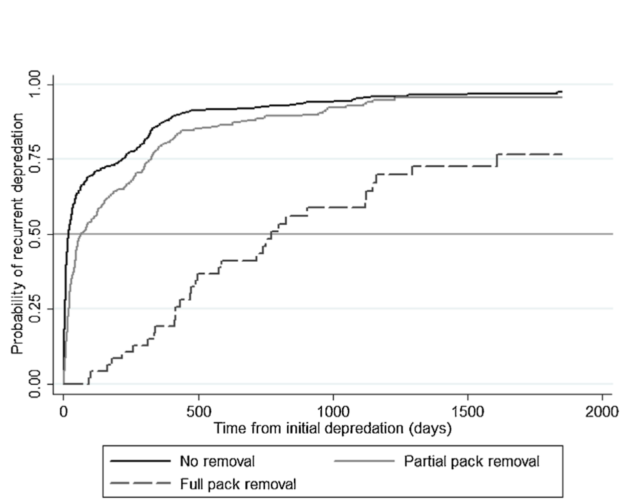

Figure 4. Probability of recurrent wolf depredation on livestock following 3 management actions in Wyoming, Idaho, and Montana, USA, 1989–2008.

Table 1. Hazard ratios of a multivariate model for the effects of wolf pack characteristics on the probability of recurrent depredations within 5 years following partial pack removal in Wyoming, Idaho, and Montana, USA from 1989–2010. Hazard ratios are relative to all other partial removal events that did not include breeding female or adult male removal. For pack size the hazard ratio reflects the probability of a recurrent event for every one-unit increase in pack size.

Management action	Hazard ratio	SE	*Z*	*P*
Breeding F removed	0.6428	0.2214	−1.28	0.200
≥1-yr-old M removed	1.000	0.1828	0.00	0.998
Pack size following action	1.087	0.0353	2.59	0.010

DISCUSSION

The wolf population grew rapidly in the NRM during the period of this study and increased every year after reintroduction through 2009 (USFWS et al. 2011). Wolf depredation had to be addressed to achieve wolf restoration and to reduce economic impacts on ranchers. The goal of wolf removal was to stop depredations in local areas while still promoting large-scale population growth (USFWS 1994*a*). As wolf recovery progressed, wolves filled the most suitable habitat. Bradley (2004) found that in 1987 through 2002 an average of 22% of all packs in the NRM depredated on livestock annually. Having core areas without livestock such as the central Idaho wilderness and Yellowstone National Park helped the population grow and expand despite agency removal of depredating wolves outside these areas. To date, no wolf packs have persisted in open habitat types used for intensive agriculture (Oakleaf et al. 2006, USFWS et al. 2014).

Human tolerance is recognized as one of the most important issues affecting long-term persistence of wolves (Boitani 1995, Fritts and Carbyn 1995, Fritts et al. 2003). As wolf populations increase throughout the western United States, most packs will occur outside of protected areas, will

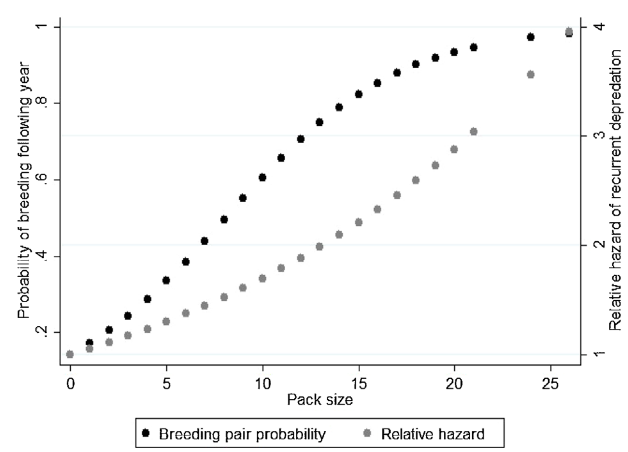

Figure 5. Hazard ratio for recurrence of wolf depredation on livestock and probability of a wolf pack containing a breeding pair the following year, both as a function of pack size following partial pack removal in Montana, Idaho, and Wyoming, USA, 1989–2008.

have territories that overlap with livestock, and will have an opportunity to depredate. Removing depredating wolves is thought to result in fewer illegal killings by the general public and increased local tolerance for non-depredating wolves (Bangs et al. 1995, 1998; Treves and Naughton-Treves 2005). Wolf removal, therefore, will continue to be an important management tool for most wildlife management agencies.

Of the wolf-related variables we examined, we found that pack size was the most important predictor of depredation recurrence in the NRM. Harper et al. (2008) found that total number of wolves removed did not appear to affect depredation recurrence, but in contrast we looked at remaining pack size, which may explain the difference. Larger packs may be more likely to depredate again sooner simply because of higher energy requirements. Large packs are also likely to have higher encounter rates with livestock, especially during summer months when packs are less cohesive and livestock are distributed more widely. Other variables, such as livestock density, natural prey density, livestock husbandry, ranch management practices, and proximity of pup rearing sites (Mech et al. 2000, Bradley and Pletscher 2005) certainly could have affected depredation recurrence in certain places, but we were unable to look at these factors consistently across our dataset.

Partial pack removal was only slightly more effective in reducing depredation recurrence than no removal, and then only if it occurred within the first 7 days after the depredation. Partial pack removal resulted in a median of only 45 days additional time without depredations compared to no removal. However, caution should be used in generalizing the effects of partial pack removal. In this study, partial pack removals averaged 2.2 individuals, thus most of our data represented small removals. Partial pack removals were more effective the more wolves removed.

Not surprisingly, removal of the entire pack decreased depredation recurrence the most (median = 2 years). In Alberta, Bjorge and Gunson (1985) found that vacant wolf territories filled within 1 through 2 years. Brainerd et al. (2008) found that when 1 or both breeding wolves were lost from a pack, replacement time was affected by surrounding wolf population size. Larger recolonizing and saturated populations had quicker replacement times than smaller recolonizing populations. The data used in our study spans a period of time when wolves were recolonizing the NRM and the population was growing rapidly in number and distribution. Therefore, it would seem likely that recolonization time of vacant territories could have been affected by dynamics of the surrounding wolf population. However, we did not find a relationship between wolf population size and depredation recurrence in territories where packs were removed. Perhaps we were limited because of small sample size of pack removals ($n = 48$), or minimum wolf counts across the NRM may not relate well with wolf density, especially on a smaller scale.

Our findings differed from other research that examined the effects of wolf removal on livestock depredation recurrence at large, regional scales (Musiani et al. 2005, Harper et al. 2008, Wielgus and Peebles 2014). Whereas previous studies found no effect, or even a positive correlation between wolf removal and subsequent depredations, we found that scale matters. Our ability to examine individual packs and pack territories revealed that wolf removal did appear to reduce recurrence of depredations at the local level, depending on the number of wolves remaining in the pack. We therefore recommend caution in selecting the appropriate scale of analysis and suggest that depredation management is most appropriately studied at the wolf pack-level or local scale.

Harper et al. (2008) found that the overall rate of recurrence of wolf depredation in the same year was quite low. Using 365-day recurrences, at 250 days post-depredation the recurrence rate was estimated to be 23%, much lower than our finding of approximately 70% (Fig. 4). Fritts et al. (1992) recognized numerous differences in landscape and livestock management practices between western states and Minnesota, and suggested higher depredation rates in the West as a result. Our divergent findings confirm differences between the 2 areas and that caution should be used in extrapolating our findings to different areas and time periods.

Some depredations ceased at farms in Minnesota whether wolves were removed or not. Furthermore, regardless of success, trapping at farms appeared more successful at reducing depredations than not trapping, suggesting that human activity may play a role in reducing depredations (Fritts 1982, Harper et al. 2008). Such data suggest that at some farms in Minnesota depredations could be reduced without the need for lethal control. We were unable to look at removal effort; however, we found very little difference between partial pack removal and no removal, which suggests there was very little to be gained by removing a small number of wolves. Our depredation recurrence rate was much higher than in Minnesota suggesting that choosing to not remove wolves would have been less successful in reducing depredations in the NRM than in Minnesota.

Discerning whether entire packs or individuals are involved in depredations is difficult (Fritts et al. 1992) but is important for managers deciding which animals should be removed. Wolf depredation on livestock is a learned behavior and therefore may be difficult to stop if all individuals in a pack are involved (Harper et al. 2005). Problem individuals, if they exist, may still be difficult to target (Linnell et al. 1999). Unless individual offenders could be identified, removal was generally non-selective. Breeders, as dominant leaders of a pack, are known to often lead hunts on wild prey (Mech and Boitani 2003, MacNulty et al. 2012) and could reasonably be expected to lead livestock depredations (Fritts et al. 1992). Breeding males are more difficult to identify than breeding females, and yearling males can be difficult to discern from adult males, especially later in the year; therefore, we looked at potential effects of breeding females and $\geq$1-year-old males. We found no evidence that removing a breeding female curbed depredation any more than removing a non-breeder, which was consistent with findings in Minnesota (Fritts et al. 1992, Harper et al. 2008). However, contrary to our findings, Harper et al. (2008) found that removing adult males decreased depredation recurrence. This difference may in part be due to our inability to break out adult males from yearling males in our dataset.

Harper et al. (2008) found that depredations actually increased at localized farm clusters, despite more wolves being removed each year. In such cases, they suggested either the possibility there were more wolves in these areas to begin with or that the entire pack had learned to prey on livestock and removal of some pack members may have increased the remaining packs' dependence on livestock. Removal of wolves, either from public hunting, livestock depredation management, or other causes, can cause changes in a pack's social structure and in some cases may result in dissolution of a pack, especially if breeders are lost (Brainerd et al. 2008). However, we found that depredations either decreased after partial pack removal or remained at levels similar to when no removal occurred, suggesting that social disruption from wolf removal did not increase depredations by packs in the NRM.

Similar to Mitchell et al. (2008), we found that pack size was an important predictor of whether a pack qualified as a breeding pair toward federal recovery goals the following year. Therefore, managers must be aware of the reduced probability of meeting the breeding pair requirements associated with wolf recovery. We found that 31% of packs that were partially removed counted as breeding pairs the following year compared to 53% of packs with no removal. The most obvious explanation is that packs that have lost 1 or more breeding individuals are less likely to reproduce the following season (Brainerd et al. 2008, Borg et al. 2014). Validation of breeding pairs can be difficult by field staff, especially in the absence of radio-telemetry (Mitchell et al. 2008). Therefore, there was some uncertainty in breeding pair status of packs, especially in later years when monitoring became more challenging with increasing numbers of packs and limited field staff (USFWS 2014). As such, there was a potential bias in the data in that larger packs were easier to find and document their reproduction. However, packs causing conflicts with livestock were often monitored more intensively and were more likely to be radio-collared (Bangs et al. 2006).

Radio-collars played an integral role in our study in that they gave the ability to effectively identify, follow, and target depredating packs. Most full pack removals or larger partial pack removals that occurred in the NRM during our study were accomplished by aerial gunning (usually via helicopter) of radio-collared packs. Full pack removals, in particular, were very difficult to accomplish otherwise. Both radio-collaring and aerial gunning are expensive management tools, but in many situations helped facilitate quick and effective removal. Ground-based removal methods such as trapping or ground shooting were more likely to remove fewer wolves, and often took longer to achieve. However, ground-based methods are sometimes the only methods available because of lack of funding, bad weather, difficult terrain for flying, or the absence of a radio-collared member of the pack. Radio-collars may become increasingly challenging to maintain in wolf packs with the advent of public harvest and consequent increased mortality.

Managers making decisions in response to wolf depredation need to consider economic, social, and biological issues. Reducing pack size, for example, can be achieved (and at lower agency cost) through public harvest. Wolf harvest is controversial with much of the public but may be partly judged by its effectiveness in reducing wolf and livestock conflicts (Mech 2010). A 2012 survey of Montana residents showed strong support for wolf hunting, and although hunting did not appear to increase general tolerance of wolves, it did appear to increase tolerance for overall wolf management in that state after the 2011 hunt (Lewis et al. 2012). Average pack sizes have decreased in Montana since public harvest commenced, from 7.03 to 4.86 wolves/pack (Bradley et al. 2014). Consistent with our predictions, livestock depredations and agency wolf removals have also decreased, despite little change in overall wolf population size (Bradley et al. 2014). Further information is needed however, to determine whether and how wolf harvest plays a role in reducing depredations. Such information will be important for managers in developing effective harvest programs and reaching wolf management objectives.

MANAGEMENT IMPLICATIONS

In the NRM, full pack removal was the most effective management response to reduce future livestock depredations in a local area. Removing entire packs may not always be feasible though, for logistical, social, or economic reasons. We found pack size was the most important wolf-related predictor of recurring depredations; therefore, managers should aim to reduce pack size as much as is practical to prevent future depredations following an initial depredation event. Radio-collars were a helpful tool during the years of wolf recovery in the NRM to help identify, locate, and target depredating packs. Managers should consider the benefits and increased challenges of maintaining radio-collars in recovered and harvested populations. Partial pack removals that remove a small number of wolves, such as those achieved through ground-based methods, should be implemented in the first 7 days following a depredation event and no later than 14 days to minimize further depredations. In the absence of knowledge pertaining to problem individuals, managers can be non-selective in their removal of individual wolves while still reducing the probability of a future depredation event. However, managers seeking to recover wolf populations or managing a wolf population close to a recovery threshold must consider the trade-offs between preserving larger packs (and therefore breeding pairs) and reducing depredations on livestock.

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