Research Article

Wolf-Livestock Conflict and the Effects of Wolf Management

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ABSTRACT Wolf (*Canis lupus*) depredations of livestock are a ubiquitous source of conflict in every country where wolves and livestock overlap. We studied the spatial and temporal variation of wolf depredations of livestock in Montana during 2005–2015, including evaluations of targeted control efforts and public harvest as potential means to reduce depredations. During this time we collected spatial data for all confirmed wolf-livestock depredations, tallied the annual number of depredation events within hunting districts, and collected data for variables potentially predictive of depredation events. We decomposed variation in depredation data into 2 distinct components: the binary presence or absence of depredation events in each district-year, and the count of depredation events in district-years with $\geq$1 event. We found that presence-absence of depredations increased with wolf presence and wolf density, increased with livestock density, were highest at intermediate proportionate areas of agricultural land, and were a recurrent phenomenon such that districts with depredations the previous year were more likely to continue having them. Targeted removal, but not public harvest, significantly reduced the recurrent presence of depredations. The number of conflicts in district-years with $\geq$1 depredation event was positively correlated with wolf density, cattle density, intermediate proportionate areas of forested land, and the number of events during the previous year. Public harvest reduced the counts of depredation events in areas where conflict reoccurred, though with a modest predicted effect size of 0.22 fewer depredations/district-year, or 5.7 fewer depredation events statewide/year (8% of the annual average). Minimizing livestock losses is a top priority for wolf management. These results shed light on the broad-scale patterns behind chronic problems and the effectiveness of wolf management practices in addressing them. © 2018 The Wildlife Society.

KEY WORDS *Canis lupus*, cattle, harvest, human-wildlife conflict, hunting, lethal control, livestock depredation, wolves.

Wolf (*Canis lupus*) depredations of livestock are a ubiquitous source of conflict in every country where wolves and livestock overlap (Fritts et al. 2003). Eliminating depredation was a primary reason behind historical efforts to exterminate wolves, and their subsequent recovery in portions of North America and Europe has brought familiar challenges of understanding, reducing, and mitigating conflicts with livestock (Bangs et al. 2009, Boitani and Ciucci 2009).

Wolf-livestock conflicts, in particular, can be difficult to explain or predict with statistical approaches relative to other forms of human-wildlife interactions (Mabille et al. 2015), yet some consistent patterns have emerged. The risk of livestock depredation has increased in areas with greater numbers of both wolves and livestock and with higher spatial overlap among them (Bradley and Pletscher 2005, Gula 2008, Kaartinen et al. 2009, Treves et al. 2011). Depredations have been positively associated with particular land cover types, including forested or agricultural vegetation or a mix of both (Bradley and Pletscher 2005, Kaartinen et al. 2009). Densities

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of wild ungulate prey have been linked to wolf-livestock conflicts in some regions, though results have included positive (Bradley and Pletscher 2005, Imbert et al. 2016, Nelson et al. 2016) and negative (Gula 2008, Kaartinen et al. 2009) correlations. Studies of temporal patterns of wolf-livestock conflict have shown strong seasonality, with monthly depredation totals peaking during late summer in North American and European study areas (Ciucci and Boitani 1998, Harper et al. 2008, Bradley et al. 2015). Also apparent from previous studies is a predictable pattern of recurrence of depredations in areas with prior conflicts (Karlsson and Johansson 2010, Bradley et al. 2015).

Efforts to reduce the occurrence of carnivore depredations of livestock have included 2 suites of widely applied tools: non-lethal deterrents such as visual or auditory deterrents, barriers, enclosures, or guardian animals, and lethal removal of carnivores, including targeted removal following depredation events and non-targeted reduction of populations through public harvest (Miller et al. 2016). Studies of targeted lethal control have been controversial regarding its effectiveness for reducing depredations by wolves (Harper et al. 2008, Wielgus and Peebles 2014, Poudyal et al. 2016, Treves et al. 2016, Kompaniyets and Evans 2017). Detailed assessments accounting for the autocorrelated nature of depredations have typically shown a significant effect of targeted removals in reducing future depredations by wolves (Harper et al. 2008, Bradley et al. 2015, Poudyal et al. 2016).

Little is known about the effects of public harvest on wolf-livestock conflicts, though studies in other carnivore-livestock systems suggest a range of possible outcomes (Treves 2009, Treves et al. 2016). Harvest can reduce sheep depredations by Eurasian lynx (*Lynx lynx*) primarily by reducing the overall abundance of lynx at broad spatial scales (Herfindal et al. 2005). To the contrary, hunter harvest of black bears (*Ursus americanus*) does not affect numbers of nuisance bear complaints (Treves et al. 2010) or bear-related depredation costs (Huygens et al. 2004). Regulated public hunter harvest of wolves began in portions of the western United States in 2009. Although harvest in this region significantly affects population dynamics of wolves (Gude et al. 2012, Ausband et al. 2015), it is unclear whether these effects or other behavior-mediated effects of harvest (Imbert et al. 2016) translate to changes in the rates at which the wolf population depredates livestock.

Efforts to reduce wolf-livestock conflicts in Montana have included a host of non-lethal practices implemented cooperatively by individual livestock producers, non-governmental organizations, and public agency staff (e.g., Wilson et al. 2017). Management to reduce conflicts also has included lethal removal of wolves by public agencies, permitted landowner take, and most recently public harvest, beginning in 2009 (Bradley et al. 2015). Despite these practices, depredations negatively affect some livestock producers, and the economic effects of these are partially mitigated through compensation programs. In Montana, financial reimbursements of >\$300,000 were paid during 1987–2008 for confirmed wolf-caused livestock depredations by a private fund administered by a non-government organization (i.e., Defenders of Wildlife; K. Paul, Defenders of Wildlife, unpublished data). Since 2008, compensation payments and funding for prevention efforts have been administered by the Montana Livestock Loss Board (MLLB), a state legislature-created panel of governor-appointed members. Payments for confirmed livestock losses to wolves from the MLLB have averaged \$96,245/year to producers within Montana during 2009–2015 (G. Edwards, MLLB, unpublished data).

Minimizing and mitigating livestock depredations are key priorities for wolf management and conservation in Montana and other jurisdictions, and future management will benefit from continued reassessment of and subsequent improvements to actions geared to minimize conflicts. Our objective was to summarize the spatial and temporal patterns of wolf-livestock conflict over the past decade within Montana and evaluate the influence of hypothesized predictors of conflict in local areas. We hypothesized that spatio-temporal factors influencing conflict in Montana during this period would be like those reported in previous studies, and we included a novel assessment of public harvest as a potential management strategy for reducing conflict.

STUDY AREA

Our study was in Montana, USA during 2005–2015. Montana is 380,832 km^2 in area and ranges in elevation from 555–3,904 m. The western portion of the state consists predominately of a portion of the Rocky Mountains, whereas the eastern portion includes large expanses of prairie-badlands and prairie-agricultural lands mixed with timbered river drainages and island mountain ranges. January temperatures average -12° to -6°C and July temperatures average 18° to 23°C. Precipitation varies widely depending on location and elevation, with average annual precipitation ranging from 17–88 cm/year. Most wolves and wolf-livestock conflicts occur in western Montana, where land cover includes a mix of coniferous forest-dominated mountains separated by large valleys containing grassland, rangeland, or agricultural vegetation types. Major wild prey species for wolves in Montana include elk (*Cervus canadensis*), deer (*Odocoileus* spp.), moose (*Alces alces*), and other species.

METHODS

Confirmed Wolf-Livestock Depredations

We briefly reviewed the time series of depredation events during 1985–2015 but restricted our spatio-temporal summaries and analyses to 2005–2015 to focus on contemporary patterns. We recorded depredations of livestock by wolves as events, such that the injuring or killing of $\geq$1 livestock at a given place and time was 1 event. The United States Department of Agriculture Wildlife Services staff confirmed depredation events following standardized protocols (Roy and Dorrance 1976). The number of depredation events and the number of livestock injured or killed per event represented minimum numbers of actual livestock loss given the occurrence of additional, unconfirmed depredations (Oakleaf et al. 2003). We restricted our analyses solely to confirmed events, and removed events from the data that included only animals deemed to be probable or possible cases of wolf-caused injury or mortality (3.6% of events).

Overall, 786 confirmed depredation events occurred during 2005–2015. To study spatial and temporal patterns of depredations at broad scales, we treated administrative hunting districts (districts) as polygonal sample units and assigned each depredation to 1 of 162 districts across the state. Sufficient spatial information (e.g., recording of spatial coordinates or district) were available to assign 760 (97%) of the 786 depredations to a specific district. We then counted the number of depredation events occurring within each district for each calendar year. District boundaries followed topographic and anthropogenic features, which led to variable sizes with a median area of 1,280 km^2 ($\bar{x} = 2{,}198 \pm 2{,}779$ [SD]; range = 44–18,688). To control for the influence of differences in area among districts when counting depredation events, we calculated standardized counts by adjusting counts according to the relative area of districts. We adjusted the raw counts (x_{raw}) to standardized counts (x_{adj}) for each hunting district (i) relative to the median district area by multiplying them by an adjustment factor (a_i) where,

$$a_i = \frac{\mathrm{area}_i}{\mathrm{area}_{\mathrm{median}}}, \text{ and}$$

$$x_{\mathrm{adj},i} = x_{\mathrm{raw},i} \times a_i. \quad (1)$$

We used the median district area instead of the mean because the distribution of district areas is right-skewed by relatively few large-area districts in the eastern portion of the state.

Potential Explanatory Variables

Wolf abundance, removals, and harvest.—We tallied the numbers of wolves and packs within each district at the end of each calendar year, and used values at the end of a given year to predict the subsequent year's depredation responses. Thus, for the 2005–2015 study of depredations, we counted wolves at the end of each year during 2004–2014. We monitored the number of wolves and wolf packs (defined as groups of ≥ 2 wolves with established territories) statewide using a combination of capture and radio-telemetry, direct observational counts, howling and snow-track surveys, remote cameras, and public wolf reports (Coltrane et al. 2016). Each year we sought to document pack size, determine pack territories, and verify wolf activity in new areas, indicating new packs. Counts of wolves were minimum counts and not population estimates (Coltrane et al. 2016). These efforts resulted in the documentation of 1,071 pack-years and 5,170 wolf-years across the state during the study period. We captured and handled wolves in accordance with Montana Fish, Wildlife and Parks' (MFWP) biomedical protocol for free-ranging wolves, which has been approved by the MFWP animal care and use committee (MFWP 2005).

We estimated spatial locations of packs using minimum convex polygon home range estimates from very high frequency (VHF) and global positioning system (GPS)-based radio-telemetry (39% of pack-years) and using survey and observational data to estimate the centroids of pack home ranges (61% of pack-years), which we then buffered to be circular home ranges equal in area to the statewide average home range size of 599.8 km^2 (Rich et al. 2012, Coltrane et al. 2016). We then estimated the annual numbers of wolves and packs within each district by summing pack home ranges and pack sizes contained within districts. When home ranges spanned multiple districts, we assigned counts of packs and wolves proportionately to each overlapping district according to the proportion of the home range area contained by each. To account for the differences in area among districts when monitoring wolves, we converted total counts of packs and wolves to densities of each per 1,000 km^2 by dividing the total counts by the district area (in thousands of km^2).

The numbers of wolves killed through targeted lethal removals and public harvest were also reported annually during the study period and tallied annually for each district. The United States Department of Agriculture—Wildlife Services (USDA-WS) conducted targeted removal efforts and methods included trapping and shooting from the ground or aircraft. We used pack identification information from each targeted removal to assign removals to hunting districts according to the district(s) overlapped by the packs' home range. Targeted removals were conducted by USDA-WS under statutory authority according to the Animal Damage Control Act of 1931 and in cooperation with the Montana Department of Livestock under statutory authority according to MCA 81-7-102. During the 2009 and 2011–2015 public wolf hunting and trapping seasons (there was no such season in 2010), MFWP monitored wolf harvest using a mandatory reporting requirement for all wolves harvested by hunters and trappers. Only hunting was allowed during the 2009 and 2011 seasons, and hunting and trapping were allowed during 2012–2015. Public harvest of wolves was regulated under the auspices of legal hunting and trapping seasons defined by the Montana Fish & Wildlife Commission, under the authority granted to them in statute MCA 87-1-301. Reporting requirements included a legal description (i.e., township, range, section) of the harvest location, which allowed us to spatially assign each harvested wolf to a district. Harvest totals were 72 wolves during the 2009–2010 season, 166 during the 2011–2012 season, 225 during the 2012–2013 season, 230 during the 2013–2014 season, and 207 during the 2014–2015 season, and location descriptions were available for 97% of wolves harvested. To account for the differences in area among districts when monitoring wolf mortality, we converted total counts of removals and harvest per district to densities of each per 1,000 km^2 by dividing the counts by the district area (in thousands of km^2). Like our treatment of pack and wolf densities, we tested the densities of removals and harvest for a given calendar year on the subsequent years' variation in depredation events.

Agricultural land cover and livestock density.—We estimated the proportionate area of rural agricultural land (including irrigated and non-irrigated grazing lands) within each district using property type attributes of each private land parcel provided by the Montana Cadastral Mapping Project of the Montana State Library (Montana State Library 2015). We then estimated the proportionate area of forested land within each district using Montana Land Cover Framework data from the Montana Natural Heritage Program (Montana Natural Heritage Program 2013).

We obtained annual head counts per county during 2004–2015 for livestock (cattle and domestic sheep) in Montana from the United States Department of Agriculture National Agricultural Statistics Service (USDA-NASS 2015). We estimated the proportion of agricultural land within each county that was contained within each hunting district and used these values to divide the total numbers of livestock per county among overlapping hunting districts. Lastly, we estimated the density of cattle, sheep, and livestock (cattle and sheep) per hunting district in 2 ways: density per area as head count divided by district area, and density per agricultural area as the head count divided by area of agricultural land per district. We conducted all spatial analyses using ArcGIS 10.1 (ESRI, Redlands, CA, USA).

Statistical Modeling of Spatial and Temporal Patterns in Wolf-Livestock Depredations

We used descriptive statistics and maps to summarize patterns of livestock depredations across the state and over time. These included characterizations of the annual numbers of depredation events over time, number of individual livestock killed per event, and spatial patterns of depredation events per unit area. We assessed spatial variation among districts first in terms of the proportion of years during which $\geq$1 depredation occurred within each district. This characterized the degree to which depredations were a chronic problem within a district. We also evaluated the average annual count of depredations within each district to characterize the within-year frequency at which depredations occurred. We then used statistical modeling to ask 3 questions about variation in depredation events over space and time.

Presence-absence versus number of depredations.—Our first question was if annual variation in the statewide number of depredation events was influenced by changes in the presence–absence of depredations among varying numbers of districts or by changes in the number of depredations per district in areas where they occur. In other words, was a year with high overall depredations characterized by numerous places with conflict, or instead by higher numbers of conflicts in the same typical places? During subsequent analyses (questions 2 and 3), we sought to understand the factors influencing each of these 2 processes. Initially asking about the relative contribution of each process to the statewide totals established a basis for us to interpret how much emphasis should be placed on the factors influencing each process.

To address our first question, our response variable was the annual count of depredation events statewide, during 2005–2015 ($n = 11$ annual counts). We used multiple linear regression to regress the extent to which 1) the annual number of districts with $\geq$1 depredation event and 2) the average number of depredation events per district with $\geq$1 explained variation in the overall statewide total. We then used estimates of the average semi-partial correlations of each component to assess how much of the total variance was explained by each (Kim 2015).

Factors affecting presence-absence and number of depredations.—To study the spatial and temporal factors influencing depredations across Montana during 2005–2015, we followed a form of hurdle modeling wherein we distinctly modeled covariates of the presence-absence of depredations in a given district-year (question 2) and the count of depredations in a district-year given $\geq$1 event (question 3; Bolker et al. 2012). The approach is called hurdle modeling because the user first models what variables describe the likelihood of clearing a hurdle, in this case having $\geq$1 depredation. Then, among those districts with $\geq$1 depredation, a second model is fit to describe the relative frequency, in terms of the count of depredation events per year. In a framework of generalized linear mixed-effects models (GLMMs), we used logistic regression to develop binary models of the initial presence of depredations (zero vs. non-zero) and a truncated negative binomial regression to develop count models for the subsequent number of depredations when present. Preliminary comparisons among Poisson, negative binomial (NB), and truncated negative binomial distributions (with NB1 and NB2 variance parameterizations; Bolker et al. 2012) concluded the latter with an NB1 variance parameterization best fit the data for counts of depredations. We screened sets of predictor variables included in multivariable models to avoid having correlated ($r > 0.6$) variables together within models, and we checked models for error inflation or coefficient changes due to multicollinearity. We conducted all statistical analyses using Program R, version 3.1.1 (R Core Team 2014), and the packages ppcor version 1.1 (Kim 2015) and glmmADMB version 0.8.3.2 (Bolker et al. 2012).

We developed models assessing patterns of variation in presence and count of depredations over space (among districts within a given year) and over time (among years within a given district). We treated each district-year as a sample unit and included a random intercept for year to treat each year as a new trial comparing variation among districts. This approach parameterized a spatial comparison of variation in depredations among districts within each year and with respect to spatially varying covariates concerning wolf and livestock densities and land cover types measured per district. In addition to measuring the effect of wolf density, we also included a binary covariate for the presence or absence of wolves, as determined at the end of the previous year. We recognize that the presence of wolves is an innate component of a depredation event in real-time, yet our minimum count data instead represented an imperfect depiction (including false negatives) of wolf presence during the prior year. We used this covariate to control for spatial variance in the annual statewide presence of wolves while testing for the effects of other covariates on spatial variance in livestock depredations.

To additionally study the temporal rate of change in depredations within a given district over the 11 years of study, we also included a covariate characterizing the presence or count of depredations in the previous year. This approach tested whether depredations were a temporally autocorrelated phenomenon, such that the presence or number of depredations in any one year could be predicted by that of the previous year. We then included additional variables that interacted with the previous year's presence or count, which allowed us to test whether other variables such as targeted removals or public harvest had any effect on the recurrence of depredations over time.

We used Akaike's Information Criterion (AIC) to evaluate the relative support for both binary and count models, and conducted comparisons among models in batches using a mix of *a priori* groupings of candidate models and manual forward stepping comparisons (Arnold 2010). We first evaluated different covariates characterizing wolf populations in each district, including wolf presence, pack density, and wolf density. Upon selecting a best model with the lowest AIC from this suite of variables, we then evaluated new models including suites of candidate variables characterizing livestock densities. We next evaluated models including land cover variables, using quadratic terms to accommodate non-linear relationships. Next, we tested for temporal autocorrelation by adding to the model a variable characterizing the previous years' presence-absence or count of depredations within each district. This evaluated whether patterns of the previous year were predictive of the current year, which would imply temporal autocorrelation. We then tested interactions of public harvest and targeted removals with this autocorrelation parameter to assess whether harvest or removals had any effect on the trend in depredations from year to year within a given district. We tested the binary presence-absence of any level of harvest or removals and the number and proportion of wolves harvested or removed within each district. When evaluating the effects of public harvest, we restricted analyses to a subset of depredation data during years that followed harvest (2010, 2012–2015). In using AIC to evaluate model support, we followed recommendations of Arnold (2010), which included using additional information (e.g., values of β/SE) to identify and remove models with non-informative parameters when comparing nested models.

RESULTS

Descriptive Statistics and Maps of Wolf-Livestock Depredations

With natural recolonization of wolves into northwest Montana came an initially small number of livestock depredation events, ranging from 0 to 5 annually during 1987–1995 (Fig. 1a). Following the 1995 reintroductions of wolves into Yellowstone National Park and central Idaho, USA annual numbers of wolves and depredations in

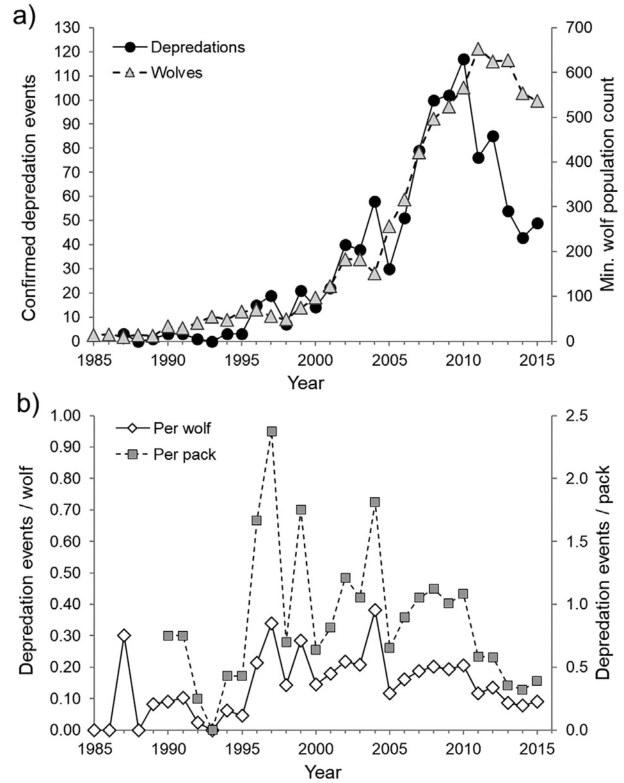

Figure 1. Annual numbers of a) confirmed livestock depredations by wolves and minimum wolf counts and b) depredations per known wolf and pack statewide, Montana, USA, 1985–2015.

Montana rose gradually, from 15 confirmed depredations in 1996 to a peak of 117 in 2010. However, as the minimum population counts for wolves leveled off during 2011–2015, numbers of depredation events showed a disproportionate decline. For comparison, annual *per capita* depredation events during 1995–2010 appeared relatively stable, averaging 0.20 ± 0.08 events/wolf, but decreased during the subsequent 5 years, averaging 0.10 ± 0.02 events/wolf (Fig. 1b).

During our 2005–2015 study period, there were 786 confirmed depredation events of livestock, 80% of which were attacks on cattle, 15% on sheep, and 5% on other domestic animals including (in order of abundance) horses, llamas, and goats. We excluded 26 additional events during which dogs were killed or injured without harm to livestock from these analyses. Among confirmed cattle depredation events, 13% involved injury to livestock but no deaths, 74% were lethal to a single animal, and 12% were lethal to more than one animal; the mean deaths per event involving cattle was 1.03 animals (median = 1, SD = 0.66, range = 0–6). Among sheep depredation events, 1% involved injury to livestock but no deaths, 33% were lethal to a single animal, and 66% were lethal to more than one animal; the mean deaths per event involving sheep was 5.03 animals (median = 2, SD = 8.49, range = 0–82). Depredation events occurred primarily on private land (83%) but also on public (14%) and tribal lands (3%).

Comparison of the cumulative proportion of statewide depredations with cumulative area covered by districts showed a notable concentration of events in relatively few districts. For example, 95% of depredation events occurred in 22% of the state. Spatial display of the proportionate presence of livestock depredation events across the 11-year period revealed several regions of Montana where depredations were chronic (Fig. 2a). After adjusting counts of depredation events for each district to be relative to the median district area (eq. 1), 16% of district-years included $\geq$1 depredation event. For those districts with $\geq$1 event during the 11-year study period, there was on average an event in 35% of years, and the maximum was 100% of years (11 of 11 years), which occurred in 2 districts. Among districts with $\geq$1 depredation event, the raw number of events for a given district-year varied from 1–19, though adjusting these data to a standardized median area resulted in an adjusted range of 1–21 depredation events/district-year. Average annual numbers of depredation events followed a similar spatial pattern to their proportionate presence (Fig. 2b).

Statewide Annual Depredation Totals

The annual totals of wolf-livestock conflicts mathematically reflect changes in both the number of districts with depredations and the number of depredations per district in affected districts. Multiple linear regression analysis of the average semi-partial correlations for each component indicated that approximately 48% of the variation was influenced by changes in the number (or proportion) of districts with depredations, whereas 51% of the variation was influenced by variation in the average number of depredations per district when and where they occurred (Fig. 3). This result establishes the equal importance of understanding the factors influencing the presence-absence of depredations and the number of depredations where and when present.

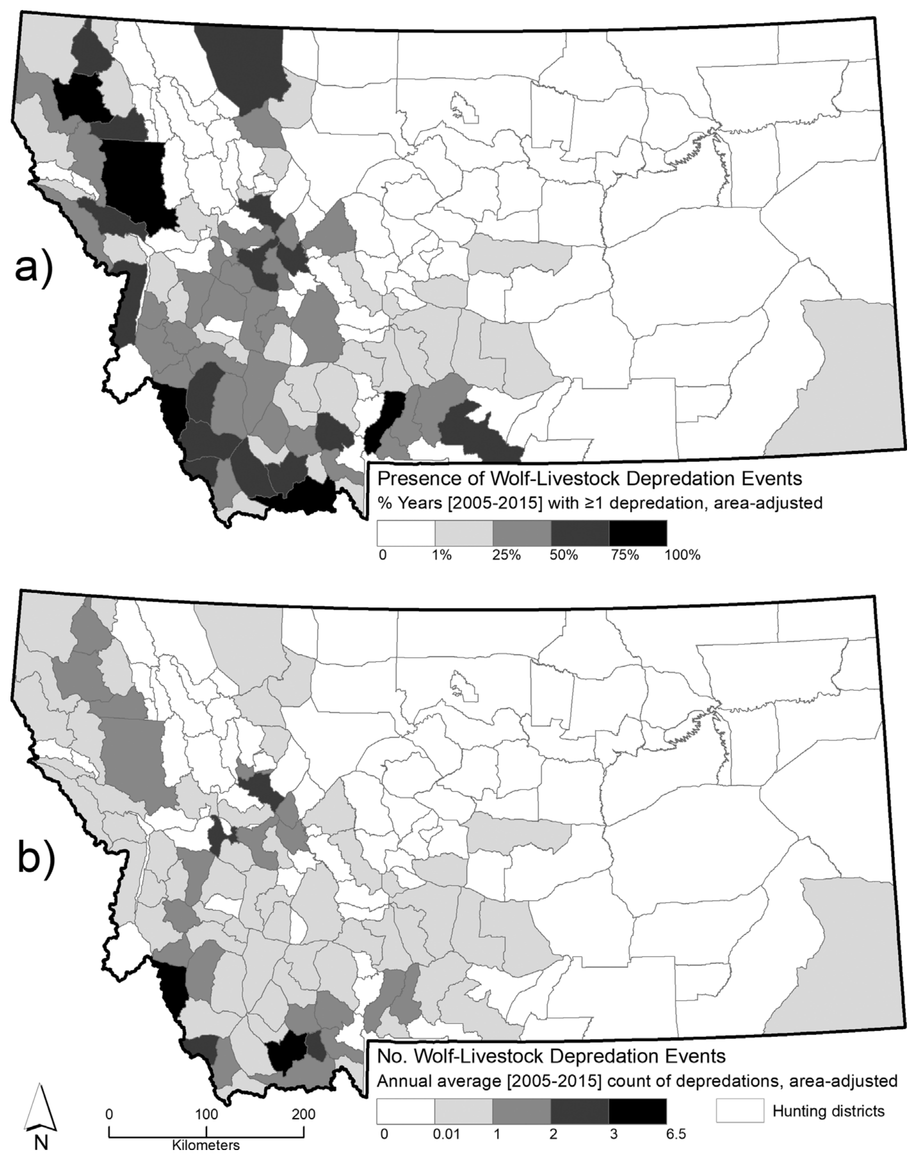

Figure 2. Spatial variation in wolf-livestock conflicts as measured by a) percent of years with $\geq$1 confirmed depredation event and b) average annual count of depredation events, each standardized by the area of each district relative to the median area of 1,280 km^2, Montana, USA, 2005–2015.

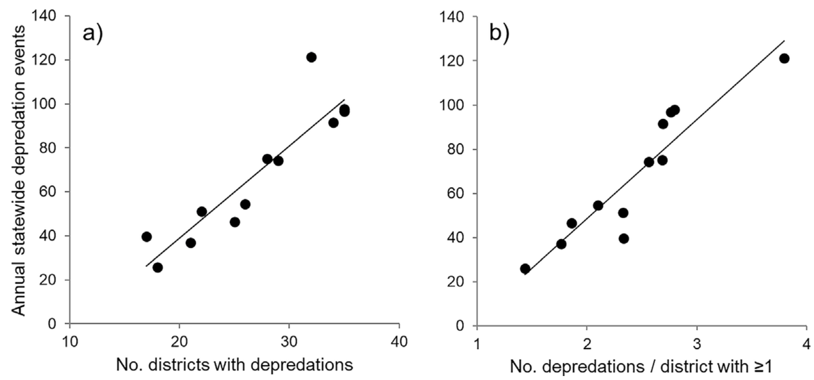

Figure 3. Linear regression showing positive relationships between the statewide annual total of wolf-livestock depredation events (*y*-axis) and annual variations in a) the number of districts with depredations and b) the average number of depredation events occurring in districts with $\geq$1 event, Montana, USA, 2005–2015.

Factors Affecting Presence–Absence of Depredations

We used GLMMs to study the presence-absence of wolf depredation events for a data set of 1,782 district-years over 162 districts and 11 years. Model selection of candidate logistic regression models yielded several statistically significant predictors of the presence or absence of wolf depredations of livestock (Tables 1 and 2). Depredations were more likely to occur in districts where wolves were documented as present during the previous year, and with greater densities of wolves (Table 2 and Fig. 4). The density of wolves (the product of pack density and the number of wolves per pack) was more predictive than that of packs, though both were statistically significant in univariate models. The density of livestock (cattle and sheep), measured per unit of agricultural land within each district, was also positively related to the probability of depredations (Table 2 and Fig. 4). The proportionate area of agricultural land showed a significant quadratic relationship with the presence of depredations, such that the peak probability of a depredation occurring with respect to this variable occurred at 48% agricultural land within a district.

Table 1. Sequential model selection results for 5 steps comparing batches of multiple logistic regression models of the probability of $\geq$1 wolf-livestock depredation event occurring in each hunting district and year, including model log-likelihoods (ll), degrees of freedom (df), and Akaike's Information Criterion (AIC), Montana, USA, 2005–2015. We carried the best model (ΔAIC = 0) from each step to the next modeling step.

Step	Variables	ll	df	AIC	ΔAIC
1	Wolf presence + wolf density	−654.7	4	1317.3	0.0
	Wolf presence + pack density	−657.4	4	1322.7	5.4
	Wolf presence	−658.7	3	1323.4	6.1
	Wolf density	−741.6	3	1489.1	171.8
	Pack density	−748.9	3	1503.9	186.6
	Intercept only	−787.6	2	1579.1	261.8
2	Step 1 + livestock density (per agricultural area)	−629.7	5	1269.4	0.0
	Step 1 + cattle density (per agricultural area)	−630.1	5	1270.2	0.8
	Step 1 + cattle density (per agricultural area) + sheep density (per agricultural area)	−629.5	6	1271.1	1.7
	Step 1 + sheep density (per agricultural area)	−634.0	5	1278.1	8.7
	Step 1 + livestock density (per total area)	−635.3	5	1280.5	11.1
	Step 1 + cattle density (per total area)	−637.4	5	1284.7	15.3
	Step 1 + cattle density (per total area) + sheep density (per total area)	−636.7	6	1285.5	16.1
	Step 1 + sheep density (per total area)	−644.4	5	1298.8	29.4
	Step 1	−654.7	4	1317.3	47.9
3	Step 2 + proportionate agricultural land + proportionate agricultural land^2	−606.7	7	1227.5	0.0
	Step 2 + proportionate forested land + proportionate forested land^2	−615.2	7	1244.3	16.8
	Step 2 + proportionate agricultural land	−625.2	6	1262.4	34.9
	Step 2	−629.7	5	1269.4	41.9
	Step 2 + proportionate forested land	−629.7	6	1271.4	43.9
4	Step 3 + depredations$_{t-1}$ + (depredations$_{t-1}$ × targeted removal density)	−559.5	9	1136.9	0.0
	Step 3 + depredations$_{t-1}$	−562.3	8	1140.7	3.8
	Step 3 + depredations$_{t-1}$ + (depredations$_{t-1}$ × targeted removal proportion)	−561.9	9	1141.9	5.0
	Step 3 + depredations$_{t-1}$ + (depredations$_{t-1}$ × targeted removal presence)	−562.3	9	1142.7	5.8
	Step 3	−606.7	7	1227.5	90.6
5[a]	Step 4	−269.4	9	556.8	0.0
	Step 4 + (depredations$_{t-1}$ × public harvest density)	−269.2	10	558.4	1.6
	Step 4 + (depredations$_{t-1}$ × public harvest presence)	−269.4	10	558.8	2.0
	Step 4 + (depredations$_{t-1}$ × public harvest proportionate)	−269.4	10	558.8	2.0

[a] We used a subset of data for this final step to include only those years following an administrated wolf harvest; thus, AIC values are not comparable with models from previous steps.

Table 2. Coefficients (β), standard errors, Wald test statistics (Z), and significance values (P) of the best multiple logistic regression model characterizing predictors of the probability of ≥1 wolf-livestock depredation event occurring in each hunting district and year in Montana, USA, 2005–2015.

Variable	β	SE	Z	P
(Intercept)	−5.61	0.417	−13.5	<0.001
Wolf presence	2.22	0.300	7.40	<0.001
Wolf pack density (wolves/km^2)	0.048	0.017	2.84	0.005
Livestock density (head/km^2 of agricultural land)	0.036	0.008	4.56	<0.001
Proportionate agricultural land	5.96	1.31	4.55	<0.001
Proportionate agricultural land^2 (quadratic term)	−6.17	1.49	−4.14	<0.001
Prior depredations, t−1	1.72	0.181	9.50	<0.001
Wolf removals (count) × prior depredations, t−1	−0.116	0.050	−2.32	0.021

Depredation events were autocorrelated over time, such that districts with depredations the previous year were more likely to keep having them (Table 2 and Fig. 5). However, this effect was dampened by a significant negative effect of targeted removals on the probability of repeated depredations (Table 2 and Fig. 5). Removing a greater number of wolves through targeted removal in 1 year significantly decreased the probability of having any depredations during the subsequent year. Contrary to targeted removals, hunter harvest did not significantly reduce the probability of repeated depredations. When restricting analyses to a subset of years following public harvest of wolves by hunting or trapping, there was no evidence that spatial variation in either the presence of public harvest ($P = 0.874$) nor the number of wolves harvested ($P = 0.515$) had significant effects on the probability of repeated depredations within districts.

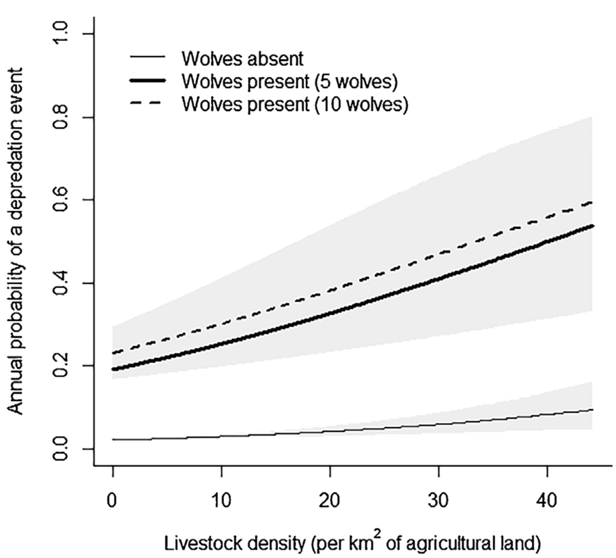

Figure 4. Predicted probabilities and 95% confidence intervals (shaded area) of ≥1 wolf-livestock depredation event occurring in a given hunting district and year as a function of livestock density, the presence or absence of wolves and the number of wolves present based on logistic regression modeling of depredations in Montana, USA, 2005–2015.

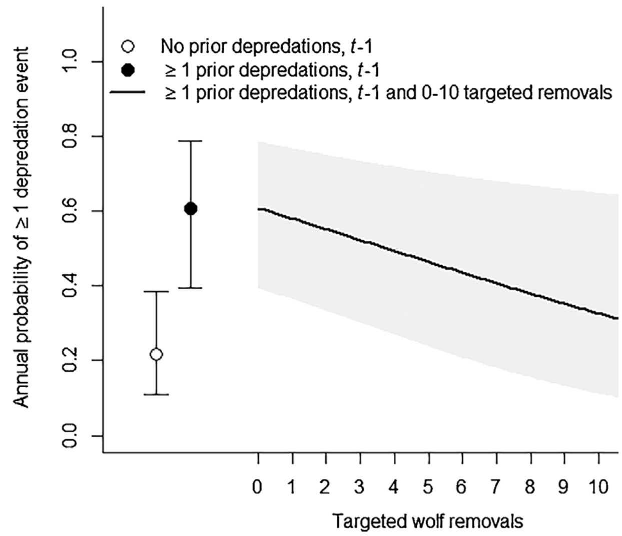

Figure 5. Predicted probabilities and 95% confidence intervals (error bars and shaded area) of ≥1 wolf-livestock depredation event occurring in each hunting district and year as a function of the prior occurrence of a depredation event in the same district during the previous year and as mediated by targeted lethal removal of wolves in districts with prior depredations, based on logistic regression modeling of depredations in Montana, USA, 2005–2015.

Factors Affecting Counts of Depredations When Present

We used GLMMs to study the count of wolf depredation events where and when they occurred for a restricted data set of 288 district-years. Model selection results from truncated negative binomial GLMMs showed a suite of variables that were predictive of the count of depredation events when and where at least 1 occurred (Tables 3 and 4). Higher counts of depredations occurred in district-years with higher density of wolves, and the total density of wolves was more predictive than the density of packs, though both were statistically significant in univariate models (Table 4). The density of cattle, measured per unit of agricultural land within each district, was also positively related to the number of depredations (Table 4). The proportionate area of forested land showed a significant quadratic relationship with the count of depredations, such that the peak predicted count of depredations with respect to this variable occurred at 44% forested land.

There was autocorrelation in the depredation count data like that in the presence-absence data, such that the count of depredations for a given year was positively correlated with the count of depredations during the previous year. In other words, areas with high numbers of depredations were more likely to continue having high numbers of depredations. Unlike models for presence-absence of depredations, the recurrence of depredations occurring in districts that had ≥1 was not significantly affected by targeted removal of wolves during 2005–2015. However, there was a significant reduction in the recurring number of depredations in districts where a large proportion of the known wolf population was harvested (Table 4 and Fig. 6). A plot of the predicted values of this relationship shows that the magnitude of this effect was small at the level of the district, with the average predicted number of depredation events per district decreasing by 0.8 depredations (from 2.1 to 1.3) as

Table 3. Sequential model selection results for 6 steps comparing batches of truncated negative binomial (NB) models of the number of wolf-livestock depredation events given at least 1 in each hunting district and year, including model log-likelihoods (ll), degrees of freedom (df), and Akaike's Information Criterion (AIC), Montana, USA, 2005–2015. We carried the best model ($\Delta AIC = 0$) from each step to the next modeling step, and used models in step 0 to select an appropriate distribution.

Step	Variables	ll	df	AIC	ΔAIC
0	Intercept only, truncated negative binomial distribution, NB1 formulation[a]	−485.0	3	975.9	0.0
	Intercept only, truncated negative binomial distribution, NB2 formulation[b]	−497.7	3	1001.5	25.6
	Intercept only, negative binomial distribution, NB2 formulation[b]	−567.1	3	1140.2	164.3
	Intercept only, negative binomial distribution, NB1 formulation[a]	−569.4	3	1144.7	168.8
	Intercept only, Poisson distribution	−595.5	2	1194.9	219.0
1	Step 0 + wolf density	−482.0	4	972.0	0.0
	Step 0 + wolf presence + wolf density	−481.4	5	972.8	0.8
	Step 0 + pack density	−483.3	4	974.5	2.5
	Step 0 + wolf presence + pack density	−482.6	5	975.2	3.2
	Step 0 + wolf presence	−483.7	4	975.3	3.3
	Step 0	−485.0	3	975.9	3.9
2	Step 1 + cattle density (per agricultural area)	−470.1	5	950.3	0.0
	Step 1 + livestock density (per agricultural area)	−471.0	5	952.0	1.7
	Step 1 + cattle density (per total area)	−474.0	5	957.9	7.6
	Step 1 + cattle density (per total area) + sheep density (per total area)	−473.8	6	959.6	9.3
	Step 1 + livestock density (per total area)	−470.1	5	963.8	13.5
	Step 1 + sheep density (per agricultural area)	−477.3	5	964.6	14.3
	Step 1 + sheep density (per total area)	−477.6	5	965.2	14.9
	Step 1	−482.0	4	972.0	21.7
	Step 1 + cattle density (per agricultural area) + sheep density (per agricultural area)	NA[c]	6	NA[c]	NA[c]
3	Step 2 + proportionate forested land + proportionate forested land ^{2}	−461.4	7	936.9	0.0
	Step 2	−470.1	5	950.3	13.4
	Step 2 + proportionate agricultural land	−469.8	6	951.6	14.7
	Step 2 + proportionate forested land	−470.0	6	952.0	15.1
	Step 2 + proportionate agricultural land + proportionate agricultural land^2	−469.7	7	953.4	16.5
4	Step 3 + depredations$_{t-1}$	−450.4	8	916.8	0.0
	Step 3 + depredations$_{t-1}$ + (depredations$_{t-1}$ × targeted removal density)	−449.8	9	917.5	0.7
	Step 3 + depredations$_{t-1}$ + (depredations$_{t-1}$ × targeted removal presence)	−450.1	9	918.1	1.3
	Step 3 + depredations$_{t-1}$ + (depredations$_{t-1}$ × targeted removal proportion)	−450.3	9	918.6	1.8
	Step 3	−461.4	7	936.9	20.1
5[d]	Step 4 + (depredations$_{t-1}$ × public harvest proportionate)	−208.5	10	435.0	0.0
	Step 4 + (depredations$_{t-1}$ × public harvest presence)	−209.2	10	436.3	1.3
	Step 4 + (depredations$_{t-1}$ × public harvest density)	−210.5	10	439.1	4.1
	Step 4	−212.0	8	440.0	5.0

[a] NB1 formulation: variance = $\phi\mu$.
[b] NB2 formulation: variance = $\mu(1 + [\mu/k])$.
[c] Model excluded because of coefficient sign-switching effect of multicollinearity.
[d] We used a subset of data for this final step to include only those years following an administrated wolf harvest; thus, AIC values are not comparable with models from previous steps.

the percent of known wolves were harvested increased from 0% to 100% (which does not necessarily mean that all wolves in the local area were harvested because not all wolves present are always known or detected). This negative effect of harvest was specific to districts where $\geq$1 event still occurred, whereas the modeling procedures for factors affecting presence-absence of depredations showed that public harvest would not be expected to prevent depredations altogether within a given area. To scale the predicted effect of public harvest up to an estimate of the net change in depredations statewide, we first calculated that an average of 22.8% of the known wolves were harvested each year during 2011–2015 from the 26 districts with $\geq$1 depredation. An average public harvest of 22.8% of known wolves would achieve an average predicted decrease of 0.22 depredations/district, or a combined decrease of 5.7 depredation events statewide/year.

DISCUSSION

Factors Influencing Wolf-Livestock Conflict

The strongest predictor of wolf depredations of livestock was the occurrence of depredations in the previous year. This result mirrors that of a study by Karlsson and Johansson (2010), who reported that the risk of depredation by wolves, lynx, and bears (*Ursus arctos*) in Sweden was 55 times higher in areas with depredations within the preceding 12 months. These findings suggest that there are additional mechanisms outweighing the spatial factors measured in our analysis in terms of predicting areas and times with particularly high risk of conflicts. Such mechanisms may include the conceptualization of livestock depredation as learned behavior by particular individual carnivores that become repeat offenders, differences in animal husbandry practices by livestock producers that create unmeasured differences in susceptibility to depredations (Miller et al. 2016), or additional unmeasured spatial mechanisms that put carnivores and livestock in close proximity.

There is some evidence to suggest that livestock depredations are a learned behavior by particular wolves, who become more likely to target livestock after an initial event (Harper et al. 2008, Bradley et al. 2015). Linnell et al. (1999) reviewed the concept of problem individuals and formulated 2 categories: type 1 individuals are any given carnivore that is likely to depredate livestock if found in the wrong place and time, and type 2 individuals are those that are more prone to depredate than others under similar conditions. Our finding that both presence and count of depredations in districts equally predicted statewide

Table 4. Coeffecients (β), standard errors, Wald test statistics (Z), and significance values (P) for the best truncated negative binomial regression model characterizing predictors of the number of wolf-livestock depredation events occurring, given the occurrence of at least 1 event, in a given hunting district and year in Montana, USA, 2005–2015.

Variable	β	SE	Z	P
(Intercept)	−0.461	0.284	−1.63	0.104
Wolf density (area-adjusted/mean-sized district)	0.021	0.009	2.30	0.021
Cattle density (head/km^2)	0.015	0.005	2.96	0.003
Proportionate forested land	3.77	1.20	3.14	0.002
Proportionate forested land^2 (quadratic term)	−4.31	1.29	−3.35	0.001
Number of prior depredations, $t-1$	0.069	0.013	5.14	<0.001
Proportionate wolf harvest[a] × prior depredations, $t-1$	−0.375	0.143	−2.62	0.009

[a] We estimated the coefficient and test statistics for the wolf harvest parameter separately by applying this model to a different subset of data consisting of only those years of data following harvest (2010, 2012–2015).

depredation numbers (Fig. 3) may be indicative of a roughly equal split between type 1 and type 2 depredations in Montana. Extrinsic conditions (e.g., animal husbandry practices, other preventative management practices, spatial proximity between wolves, and livestock) could dictate type 1 depredations by the general wolf population, but the intrinsic learning of this behavior by particular individuals may result in type 2 problem wolves that are more likely to depredate again.

As found elsewhere, wolf density and livestock density were significant predictors of the presence of depredations and their relative frequency (Gula 2008, Kaartinen et al. 2009, Treves et al. 2011). Mixed cover types, or intermediate proportions of agricultural (typically private) or forested (typically public) land, have been related to increased conflict likelihood in other areas (Bradley and Pletscher 2005, Kaartinen et al. 2009).

Effects of Public Harvest

We found no evidence that removing wolves through public harvest affected the year-to-year presence or absence of livestock depredations by wolves. In other words, public harvest did not effectively turn off depredations in areas with reoccurring conflict. However, we did find evidence that public harvest of a greater proportion of the known wolves in a district reduced the number of depredations, within the subset of districts with conflicts. Although statistically significant, our estimate of the effect size of this relationship (5.7 fewer depredation events statewide/year) would amount to only an 8% reduction from the average annual total of statewide depredations during the 2005–2015 study period.

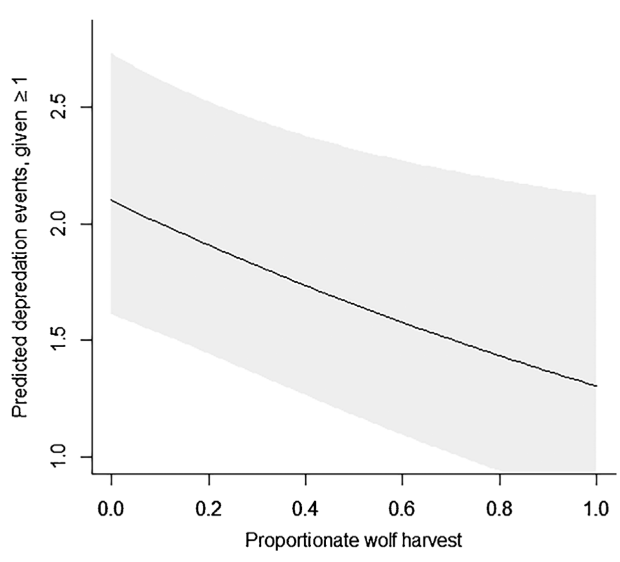

Figure 6. Predicted number and 95% confidence interval (shaded area) of wolf-livestock depredations in a hunting district, given at least 1 event, as a function of the proportion of the known wolf population that was harvested by the general public during the previous year, Montana, USA, 2010, 2012–2015.

Prior research reported that partial pack targeted removals in the Northern Rocky Mountains ($\bar{x} = 2.2$ wolves killed/pack) were relatively ineffective as a response to wolf-livestock depredations compared to removal of the entire pack (Bradley et al. 2015). Public harvest in Montana has achieved a similar numerical effect to partial pack removals, averaging 1.6–2.2 harvested wolves/pack experiencing harvest during 2009–2014. Thus, in areas with recurrent conflicts, removing a relatively low number of wolves, whether through targeted control or public harvest, may do little to prevent future depredations.

Our results showed that 83% of depredations occurred on private land, yet a cursory look at harvest locations during the study period suggested that only 41% of public wolf harvest occurred on private lands (MFWP, unpublished data). Wolf home ranges in Montana are large enough (median area = 600 km^2; Rich et al. 2012) to span multiple ownership types, but further research may be warranted concerning the accessibility to problem wolves by a public constrained to predominately public lands.

We tested for direct effects of harvest in terms of a reduction in the prevalence or magnitude of depredations with increasing harvest. We might also expect a variety of indirect effects of harvesting wolves on levels of conflict with livestock. Wolf density is a consistent predictor of wolf-livestock conflict, and public harvest can negatively affect wolf population dynamics (Gude et al. 2012, Ausband et al. 2015). We conducted a *post hoc* analysis testing for an indirect effect of harvest as mediated by harvest effects on the wolf density covariate. We re-analyzed our best models with 2 treatments of wolf density including harvested wolves within the estimated wolf density versus excluding harvested wolves from the estimated wolf density. Excluding harvested wolves from the measure of wolf density marginally reduced model fit for predicting presence-absence of depredations (ΔAIC = 0.4) but significantly improved model fit for predicting the number of depredations in affected districts (ΔAIC = −4.6).

In the latter but not the former case, there may be some evidence that harvest-mediated reductions in wolf density may further reduce conflicts. In addition to numerical effects, there may be other behavior-mediated indirect effects for which we could not account. Effects of harvest on wolf behavior would have been captured by our analysis only to the extent that the magnitude of those effects is correlated to the magnitude of harvest. Lastly, there is potential that the advent of public harvest has affected public perception or practices enough to change reporting rates of depredations and thus confound our measurement of depredations. Reporting rates can be variable or low in some cases (Lee et al. 2017), and it is unclear whether adding public harvest to carnivore management would necessarily affect public attitudes or responses (Treves 2009).

Effects of Targeted Removals

Increasing levels of targeted lethal removal of wolves following depredations reduced the probability of their recurrence (Fig. 5), which mirrored results of another recent study at the scale of individual wolf packs (Bradley et al. 2015). Although targeted removals did not appear to significantly affect the frequency of depredations in places where they did reoccur, it seemed the primary effect was in reducing the probability that any depredation event occurred, effectively reducing the subsequent frequency of depredations to 0 as more wolves were removed.

Wielgus and Peebles (2014) recently reported a positive correlation between lethal removal of wolves and subsequent depredations using annual statewide totals in the western United States. However, 2 independent studies later reanalyzed their data with increased attention to autocorrelation and the growing wolf population during that time series and found, instead, negative effects of lethal removal on subsequent depredations (Poudyal et al. 2016, Kompaniyets and Evans 2017). In our study, we accounted for autocorrelation by testing targeted controls as an interaction variable with the previous year's depredation patterns, yielding additional support to the conclusions of the latter 2 studies (Fig. 5).

The results of our analyses do not account for potential differences in the application of targeted control according to how, where, and when it was employed. It can be practically difficult to target offending individuals, particularly for group-living carnivores (Gipson 1975, Linnell et al. 1999). In cases where the risk of recurring depredations hinges on 1 or few individuals with a learned behavior, the success of targeted removals may be tied to the removal of those specific individuals rather than the removal of a higher quantity of individuals overall. We were not able to distinguish between these 2 scenarios, and thus our results may reflect either an additive effect of removing each wolf or a higher probability of removing the problem individuals with each animal removed. Lastly, we wish to highlight the correlative nature of our results and acknowledge that unmeasured spatio-temporal factors were likely at play. We agree with recent calls for rigorous study of carnivore-livestock conflicts (Miller et al. 2016, Treves et al. 2016), yet also hold our own study up as a valuable example of evaluating the effects of ongoing management practices. In jurisdictions where management practices are used to address human-wildlife interactions, we encourage an adaptive management approach (Nichols et al. 2007).

MANAGEMENT IMPLICATIONS

In accordance with our result that depredation totals were equally influenced by depredations in new areas and the severity of recurring depredations (Fig. 3), we recommend an equal split between preventative efforts to reduce the propensity for conflicts in places where they are less common and reactive efforts to reduce the severity or number of conflicts in places where they are more common. Our results also uphold the use of targeted lethal removals to reduce recurrent depredations (Fig. 5). Our findings are mixed with regards to the management utility of prescribing public harvest to reduce wolf-livestock conflict. Although we did find a significant effect of harvest in certain situations, the predicted magnitude of this effect was modest (5.7 events/year). Statewide depredation totals have decreased substantially in Montana since the advent of public harvest (from 119 in 2010 to 44 in 2014), yet we were unable to support a hypothesis that public harvest has been a primary factor influencing these decreases.

Depredation of livestock by wolves is a relatively rare phenomenon, making it likely that many additional and fine-scale factors are at play when prescribing preventative and reactive management approaches. We therefore advocate a case-by-case approach to deciding how each situation is managed with regards to the use of non-lethal or lethal tools. Managers are required to consider trade-offs between wolf population recovery goals and efforts to minimize conflict with livestock when managing North American wolves in the current era. Lastly, we acknowledge that there are other ethical and value-based aspects to management of wolves that are not reviewed here but require thorough consideration as components of effective and sound wolf management and conservation (Haber 1996, Nie 2002).

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