



# Effects of Wolf Mortality on Livestock Depredations

Robert B. Wielgus, Kaylie A. Peebles

Published: December 3, 2014 • DOI: 10.1371/journal.pone.0113505

## Abstract

Predator control and sport hunting are often used to reduce predator populations and livestock depredations, – but the efficacy of lethal control has rarely been tested. We assessed the effects of wolf mortality on reducing livestock depredations in Idaho, Montana and Wyoming from 1987–2012 using a 25 year time series. The number of livestock depredated, livestock populations, wolf population estimates, number of breeding pairs, and wolves killed were calculated for the wolf-occupied area of each state for each year. The data were then analyzed using a negative binomial generalized linear model to test for the expected negative relationship between the number of livestock depredated in the current year and the number of wolves controlled the previous year. We found that the number of livestock depredated was positively associated with the number of livestock and the number of breeding pairs. However, we also found that the number of livestock depredated the following year was positively, not negatively, associated with the number of wolves killed the previous year. The odds of livestock depredations increased 4% for sheep and 5–6% for cattle with increased wolf control - up until wolf mortality exceeded the mean intrinsic growth rate of wolves at 25%. Possible reasons for the increased livestock depredations at  $\leq 25\%$  mortality may be compensatory increased breeding pairs and numbers of wolves following increased mortality. After mortality exceeded 25%, the total number of breeding pairs, wolves, and livestock depredations declined. However, mortality rates exceeding 25% are unsustainable over the long term. Lethal control of individual depredating wolves may sometimes necessary to stop depredations in the near-term, but we recommend that non-lethal alternatives also be considered.

**Citation:** Wielgus RB, Peebles KA (2014) Effects of Wolf Mortality on Livestock Depredations. PLoS ONE 9(12): e113505. doi:10.1371/journal.pone.0113505

**Editor:** Joseph K. Bump, Michigan Technological University, United States of America

**Received:** July 28, 2014; **Accepted:** October 24, 2014; **Published:** December 3, 2014

**Copyright:** © 2014 Wielgus, Peebles. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data Availability:** The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are within the Supporting Information files.

**Funding:** Funding for this research was provided solely by a research grant from the Washington Department of Fish and Wildlife. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing interests:** The authors have declared that no competing interests exist.

## Introduction

Predator control and sport hunting are often used to reduce predator populations, livestock depredations, and increase social acceptance of large carnivores such as brown bears (*Ursus arctos*) [1], wolves (*Canis lupus*) [2], cougars (*Puma concolor*) [3], jaguars (*Panthera onca*) [4], lions (*Panthera leo*) [5], leopards (*Panthera pardus*) [6], and others [7].

Gray wolves (our model animal) are currently being hunted in Idaho, Wyoming and Montana, in part, to reduce livestock depredations [8]. However, to our knowledge, the long-term effectiveness of lethal wolf control to reduce livestock depredations has not yet been rigorously tested. For example, Bradley and Pletscher [9] predicted that breeding pairs are responsible for most livestock depredations because they are bound to the den site, not natural prey distribution [10]. Brainerd et al. [11] predicted that increased wolf mortality could result in fracture of pack structure and increased breeding pairs. If this is the case, increased mortality of wolves could result in increased breeding pairs and livestock depredations following lethal control. In other species,

Collins et al. [12] and Treves et al. [13] found increased damages by black bears (*Ursus americanus*) following high remedial mortality and Peebles et al. [14] found that increased mortality of cougars resulted in increased livestock depredations because of social disruption. In this paper we test the widely accepted, but untested, hypothesis that increased lethal control decreases wolf livestock depredations in a large scale (tri-state) long-term (25 year) quasi-experimental [15]. The “remedial control” hypothesis predicts that livestock depredations will decrease following increased lethal control.

**Methods**

We obtained the confirmed number of cattle (*Bos primigenius*) and sheep (*Ovis aries*) depredated, wolf population estimates, number of breeding pairs, and the number of wolves killed in the wolf-occupied area of each state for each year between 1987–2012 from United States Fish and Wildlife Services Interagency Annual Wolf Reports [16] (Table S1). The number of wolves killed were wolves that were killed through control methods including wolves killed legally by livestock owners or through government control methods, these numbers do not include other sources, including natural mortality. Only the total numbers of livestock killed, not the number of confirmed livestock depredation incidents, were available from the USFW database.

Numbers of livestock were similarly obtained from United States Department of Agriculture National Agricultural Statistics Service for counties where wolves are present [17] (Table S1). Livestock numbers for individual properties were not available so livestock tallies were made across the tri-state area using counts from wolf occupied counties.

Following Peebles et al. [14], we used forward selection, negative binomial general linearized models to assess the relationship between livestock depredations and numbers of livestock, wolves, breeding pairs, and wolves killed. We used this method because depredations were over-dispersed and consisted of 0 to positive integer count data with a variance exceeding the mean [18]. The best statistical model was then selected using the lowest AIC (Akaike Information Criterion) and highest log-likelihood [19]. The rate ratio, analogous to odds-ratio, was computed from the coefficients to aid in interpreting the results [20]. For example, a rate ratio of 1.0 for any independent variable means the effect on the dependent variable is unchanged. A rate ratio of 1.5 means the odds are increased by 50%.

To establish directionality, we analyzed the effect of independent variables in year 1 on number of livestock depredated in year 2. This one year time-lag between control kills and depredations removes the directional effect of depredations causing kills. After assessing the models, we plotted and interpreted the most important independent variables against depredations to provide a visual representation of model terms. Only the independent variables that had a rate ratio larger than 1.01 or smaller than 0.99, meaning the change in the mean number of livestock depredated was increased or decreased by at least 1%, were examined further. We conducted our regressions on the entire tri-state area and the 3 separate states- but only report the larger tri-state area here because the results were basically the same in all cases (Figures S1 and S2).

**Results**

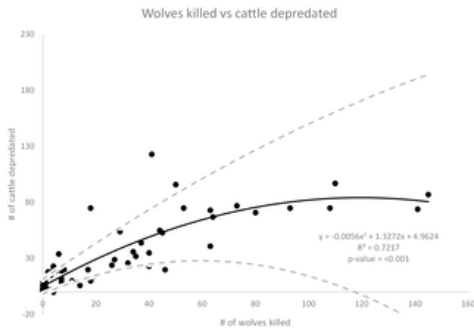
The total number of livestock depredated between January 1987- December 2012 in the tri-state area was 5670; 1853 were cattle and 3723 were sheep. Sample size for paired depredations in year 2 and wolf and cattle numbers and wolves killed in year 1 was: 17 years for Idaho, 17 years for Wyoming, and 25 years for Montana (N total = 59).

All of the well performing models (AIC<466) for cattle depredated included the # wolves killed, # of breeding pairs and the # of wolves killed by # breeding pairs interaction (Table 1) - and the coefficients for these terms were very similar across models. The best models were #10, #12 and #13. The 1<sup>st</sup> model was  $g(y) = \exp [1.307 + 0.05078(\text{wolves killed through control methods}) + 0.07979(\# \text{ of breeding pairs}) + 2.116 \times 10^{-8}(\# \text{ of cattle}) - 1.343 \times 10^{-3}(\# \text{ breeding pairs} * \text{wolves killed}) - 2.980 \times 10^{-8}(\# \text{ of cattle} * \text{wolves killed})]$ . The 2<sup>nd</sup> model was  $g(y) = \exp [1.142 + 0.05293(\text{wolves killed through control methods}) + 0.08791(\# \text{ of breeding pairs}) + 2.674 \times 10^{-7}(\# \text{ of cattle}) - 0.001377(\text{wolves killed} * \# \text{ of breeding pairs}) - 1.701 \times 10^{-8}(\# \text{ of cattle} * \# \text{ of breeding pairs})]$ . The 3<sup>rd</sup> model was  $g(y) = \exp [1.182 + 0.05795(\text{wolves killed through control methods}) + 0.07783(\# \text{ of breeding pairs}) + 2.112 \times 10^{-7}(\# \text{ of cattle}) - 0.001378(\text{wolves killed} * \# \text{ of breeding pairs}) - 7.804 \times 10^{-9}(\# \text{ of cattle} * \# \text{ of wolves killed})]$

Model #	Main Effects	Interaction Effects	AIC	2 * log-likelihood
1	Cattle	N/A	528.19	-522.188
2	# of breeding pairs	N/A	496.13	-490.132
3	wolves killed	N/A	454.11	-448.111
4	cattle + breeding pairs	N/A	488.08	-482.079
5	cattle + wolves killed	N/A	489.96	-481.957
6	breeding pairs + wolves killed	N/A	464.61	-458.610
7	cattle + breeding pairs + wolves killed	N/A	465.43	-457.387
8	cattle + breeding pairs + wolves killed	cattle * breeding pairs	467.36	-459.360
9	cattle + breeding pairs + wolves killed	cattle * wolves killed	467.34	-459.336
10	cattle + breeding pairs + wolves killed	breeding pairs * wolves killed	464.02	-452.018
11	cattle + breeding pairs + wolves killed	cattle * breeding pairs, cattle * wolves killed	468.8	-474.803
12	cattle + breeding pairs + wolves killed	cattle * breeding pairs, breeding pairs * wolves killed	465.67	-451.668
13	cattle + breeding pairs + wolves killed	cattle * wolves killed, breeding pairs * wolves killed	465.39	-451.362
14	cattle + breeding pairs + wolves killed	cattle * breeding pairs, cattle * wolves killed, wolves killed * breeding pairs	467.36	-451.358

**Table 1. AIC and log-likelihood values for forward selection of main effects and interaction effects models of cattle depredations**  
doi:10.1371/journal.pone.0113505.t001

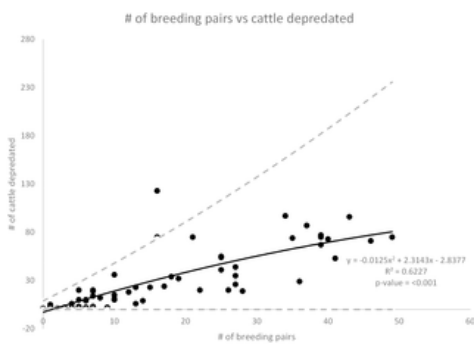
In both models all of the main effects and some two way interactions were found to be statistically significant (Table 2). The number of wolves killed in year one was positively related to the number of cattle depredated the following year (rate ratios = 1.05, 1.05 and 1.06,  $z = 5.67$  and  $5.66, 4.69, P < 0.001$ ) (Figure 1). For each additional wolf killed the estimated mean number of cattle depredated the following year increased by 5 to 6%. The number of breeding pairs was also positively related to the number of cattle depredated (rate ratios = 1.08, 1.09 and 1.08,  $z = 6.28, 4.87$  and  $6.04, P = 0.0336$  and  $< 0.001$ ) (Figure 2). For each additional breeding pair on the landscape the estimated mean number of cattle depredated the following year increased by 8 to 9%. Breeding pairs were highly correlated with numbers of wolves (Table S2).



**Figure 1. Wolves killed vs cattle depredated.**

Number of wolves killed through control methods the previous year versus the number of cattle depredated the following year. The dashed lines show the upper and lower limits of the 95% confidence interval for the best fit line.

doi:10.1371/journal.pone.0113505.g001



**Figure 2. Number of breeding pairs vs cattle depredated.**

Number of breeding pairs present on the landscape the previous year versus the number of cattle depredated the following year. The dashed lines show the upper and lower limits of the 95% confidence interval for the best fit line.

doi:10.1371/journal.pone.0113505.g002

Dependent Variable	Independent Variable	Estimated Coefficient	Standard Error	VF (variance inflation factor)	Z value	p-value	AIC
Cattle Depredated	Cattle	$2.116 \times 10^{-6}$	$3.701 \times 10^{-7}$	1.38	0.057	0.954	404.02
	# of breeding pairs	.07079	.01270	3.87	6.281	<0.001	
	# of wolves killed	.05078	$8.925 \times 10^{-3}$	3.41	5.688	<0.001	
	# of breeding pairs*# of wolves killed	$-1.343 \times 10^{-3}$	$2.460 \times 10^{-4}$		-5.308	<0.001	
Cattle Depredated	Cattle	$2.074 \times 10^{-7}$	$5.493 \times 10^{-7}$		0.487	0.628	405.67
	# of breeding pairs	.05795	.01084		4.872	<0.001	
	# of wolves killed	.05293	$9.354 \times 10^{-3}$		5.698	<0.001	
	Cattle*# of breeding pairs	$-1.701 \times 10^{-6}$	$2.809 \times 10^{-7}$		-6.005	0.045	
Cattle Depredated	Cattle	$-1.377 \times 10^{-3}$	$2.511 \times 10^{-4}$		-5.485	<0.001	
	Cattle	$2.112 \times 10^{-7}$	$4.477 \times 10^{-7}$		0.472	0.637	405.39
	# of breeding pairs	.07183	.01289		6.036	<0.001	
	# of wolves killed	.05795	.01236		4.689	<0.001	
Cattle*# of wolves killed	Cattle*# of wolves killed	$-7.804 \times 10^{-3}$	$9.805 \times 10^{-4}$		-7.971	0.029	
	# of breeding pairs*# of wolves killed	$-1.378 \times 10^{-3}$	$2.498 \times 10^{-4}$		-5.515	<0.001	

**Table 2. Summary of best model for cattle depredated.**

doi:10.1371/journal.pone.0113505.t002

There was also one important 2-way negative interaction for the relationship between the increasing numbers of wolves killed and decreasing breeding pairs on livestock depredations (rate ratios = 0.99,  $z = -5.39, -5.49$  and  $-5.12, P < 0.001$ ). In our models, the

main effects of wolves killed was increased depredations. But the negative interaction effect in the model shows that depredations ultimately declined with increased wolf kills as number of breeding pairs decreased. These conflicting effects on livestock depredations are represented here as proportion of wolves killed vs. cattle depredations in (Figure 3). Depredations increased with increasing wolf mortality up to about 25% mortality but then depredations declined when mortality exceeded 25%.

**Figure 3. The proportion of wolves killed vs cattle depredated.**

Proportion of wolves killed the previous year versus the number of cattle depredated the following year. The dashed lines show the upper and lower limits of the 95% confidence interval for the best fit line.

doi:10.1371/journal.pone.0113505.g003

One model out of 53 (Table 3) was also selected for determining which factors may influence the number of sheep depredated the following year (Table 4). The model was  $g(y) = \exp [-10.499 + 0.05539(\text{minimum wolf population}) + 0.03883(\text{wolves killed through control methods}) + 3.058 \times 10^{-5}(\text{cattle}) + 2.077 \times 10^{-4}(\text{sheep}) - 5.116 \times 10^{-4}(\text{wolves killed} * \text{wolf population}) - 4.932 \times 10^{-7}(\text{wolves killed} * \text{cattle}) - 1.159 \times 10^{-7}(\text{wolf population} * \text{cattle}) - 3.712 \times 10^{-6}(\text{wolves killed} * \text{sheep}) - 6.827 \times 10^{-7}(\text{wolf population} * \text{sheep}) - 3.408 \times 10^{-10}(\text{cattle} * \text{sheep}) + 6.532 \times 10^{-10}(\text{wolves killed} * \text{wolf population} * \text{cattle}) + 4.819 \times 10^{-9}(\text{wolves killed} * \text{wolf population} * \text{sheep}) + 3.682 \times 10^{-12}(\text{wolves killed} * \text{cattle} * \text{sheep}) - 4.336 \times 10^{-15}(\text{wolves killed} * \text{wolf population} * \text{cattle} * \text{sheep})]$ .

Model #	Main Effects	Interaction Effects	AIC	2x log-likelihood
1	Wolves killed	N/A	575.92	-568.925
2	Cattle	N/A	581.06	-573.058
3	Sheep	N/A	582.08	-564.077
4	Wolf population	N/A	583.81	-567.805
5	Wolves killed + cattle	N/A	573.4	-565.401
6	Wolves killed + sheep	N/A	581.86	-553.861
7	Wolves killed + cattle + sheep	N/A	585.19	-557.192
8	Cattle + sheep	N/A	581.81	-553.809
9	Cattle + wolf population	N/A	585.20	-557.205
10	Sheep + wolf population	N/A	588.89	-550.889
11	Wolves killed + cattle + sheep	N/A	583.51	-553.513
12	Wolves killed + sheep + wolf population	N/A	580.43	-550.432
13	Cattle + sheep + wolf population	N/A	580.88	-550.882
14	Wolves killed + cattle + sheep + wolf population	N/A	582.41	-550.406
15	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle	584.33	-550.334
16	Wolves killed + cattle + sheep + wolf population	Wolves killed*sheep	583.79	-538.780
17	Wolves killed + cattle + sheep + wolf population	Wolves killed*wolf population	586.00	-542.004
18	Wolves killed + cattle + sheep + wolf population	Cattle*sheep	549.98	-536.978
19	Wolves killed + cattle + sheep + wolf population	Cattle*wolf population	583.62	-543.622
20	Wolves killed + cattle + sheep + wolf population	Sheep*wolf population	581.13	-537.127
21	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep	583.70	-537.698
22	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*wolf population	587.64	-541.643
23	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, cattle*sheep	548.16	-532.159
24	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, cattle*wolf population	583.36	-547.365
25	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, sheep*wolf population	548.38	-532.378
26	Wolves killed + cattle + sheep + wolf population	Wolves killed*sheep, wolves killed*wolf population	585.78	-538.778
27	Wolves killed + cattle + sheep + wolf population	Wolves killed*sheep, cattle*sheep	551.82	-535.819
28	Wolves killed + cattle + sheep + wolf population	Wolves killed*sheep, cattle*wolf population	584.61	-538.608
29	Wolves killed + cattle + sheep + wolf population	Wolves killed*sheep, sheep*wolf population	583.10	-537.089
30	Wolves killed + cattle + sheep + wolf population	Wolves killed*wolf population, cattle*sheep	581.38	-536.376
31	Wolves killed + cattle + sheep + wolf population	Wolves killed*wolf population, cattle*wolf population	587.98	-541.981
32	Wolves killed + cattle + sheep + wolf population	Wolves killed*wolf population, sheep*wolf population	583.12	-537.120
33	Wolves killed + cattle + sheep + wolf population	Cattle*sheep, cattle*wolf population	548.34	-532.342
34	Wolves killed + cattle + sheep + wolf population	Cattle*sheep, sheep*wolf population	581.11	-535.115
35	Wolves killed + cattle + sheep + wolf population	Cattle*wolf population, sheep*wolf population	549.75	-533.754
36	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, wolves killed*wolf population	585.40	-537.401
37	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, cattle*sheep	549.67	-531.675
38	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, cattle*wolf population	585.39	-537.391
39	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, sheep*wolf population	580.30	-532.304
40	Wolves killed + cattle + sheep + wolf population	Wolves killed*sheep, wolves killed*wolf population, cattle*sheep	583.09	-535.090
41	Wolves killed + cattle + sheep + wolf population	Wolves killed*sheep, wolves killed*wolf population, cattle*wolf population	586.36	-538.360
42	Wolves killed + cattle + sheep + wolf population	Wolves killed*sheep, wolves killed*wolf population, sheep*wolf population	585.00	-537.003
43	Wolves killed + cattle + sheep + wolf population	Wolves killed*wolf population, cattle*sheep, cattle*wolf population	549.86	-531.863
44	Wolves killed + cattle + sheep + wolf population	Wolves killed*wolf population, cattle*sheep, sheep*wolf population	583.06	-535.059
45	Wolves killed + cattle + sheep + wolf population	Cattle*sheep, cattle*wolf population, sheep*wolf population	548.20	-530.203
46	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, wolves killed*wolf population, cattle*sheep	581.60	-531.602
47	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, wolves killed*wolf population, cattle*wolf population	587.22	-537.216
48	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, wolves killed*wolf population, sheep*wolf population	582.26	-532.258
49	Wolves killed + cattle + sheep + wolf population	Wolves killed*wolf population, cattle*sheep, cattle*wolf population, sheep*wolf population	583.62	-533.622
50	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, wolves killed*wolf population, cattle*sheep, cattle*wolf population	583.53	-531.534
51	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, wolves killed*wolf population, cattle*sheep, sheep*wolf population	581.27	-529.273
52	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, wolves killed*wolf population, cattle*sheep, cattle*wolf population, sheep*wolf population	583.20	-529.200
53	Wolves killed + cattle + sheep + wolf population	Wolves killed*cattle, wolves killed*sheep, wolves killed*wolf population, cattle*sheep, cattle*wolf population, sheep*wolf population, Wolves killed*cattle*wolf population, Wolves killed*sheep*wolf population, Wolves killed*wolf population, Wolves killed*cattle*sheep*wolf population, Wolves killed*cattle*wolf population, Wolves killed*sheep*wolf population, Wolves killed*wolf population, Wolves killed*cattle*sheep*wolf population	544.05	-510.052

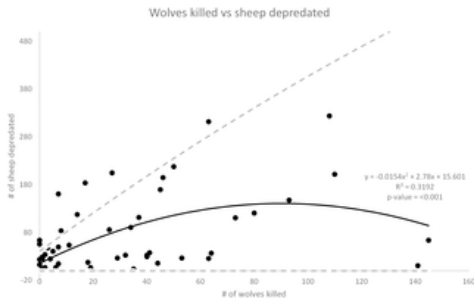
**Table 3. AIC and log-likelihood values for forward selection of main effects and interaction effects models of sheep depredations.**  
doi:10.1371/journal.pone.0113505.t003

Dependent Variable	Independent Variable	Estimated Coefficient	Standard Error	z/P	2x log-likelihood	p-value	AIC
Sheep Depredated	Wolves killed	0.0383	0.0171	3.26	2.218	0.026	544.05
	Minimum wolf population	0.05539	0.01720	4.29	3.220	0.001	
	Cattle	3.058 × 10 <sup>-4</sup>	6.481 × 10 <sup>-4</sup>	1.67	4.718	<0.001	
	Sheep	2.077 × 10 <sup>-4</sup>	6.255 × 10 <sup>-5</sup>	2.66	3.320	0.001	
	Wolves killed*wolf population	-5.118 × 10 <sup>-4</sup>	2.703 × 10 <sup>-4</sup>	-1.893	0.058		
	Wolves killed*cattle	-4.832 × 10 <sup>-4</sup>	2.707 × 10 <sup>-4</sup>	-1.822	0.068		
	Wolf population*cattle	-1.159 × 10 <sup>-7</sup>	3.687 × 10 <sup>-8</sup>	-3.170	0.001		
	Wolves killed*sheep	-3.712 × 10 <sup>-8</sup>	2.087 × 10 <sup>-8</sup>	-1.770	0.077		
	Wolf population*sheep	-8.827 × 10 <sup>-7</sup>	2.610 × 10 <sup>-7</sup>	-2.616	0.009		
	Cattle*sheep	-3.426 × 10 <sup>-10</sup>	7.444 × 10 <sup>-10</sup>	-4.678	<0.001		
	Wolves killed*wolf population*cattle	6.532 × 10 <sup>-10</sup>	5.772 × 10 <sup>-10</sup>	1.132	0.256		
	Wolves killed*wolf population*sheep	4.819 × 10 <sup>-8</sup>	4.247 × 10 <sup>-8</sup>	1.135	0.256		
	Wolves killed*cattle*sheep	3.882 × 10 <sup>-10</sup>	3.216 × 10 <sup>-10</sup>	1.145	0.252		
	Wolf population*cattle*sheep	1.834 × 10 <sup>-10</sup>	6.035 × 10 <sup>-10</sup>	2.722	0.006		
	Wolves killed*wolf population*cattle*sheep	-4.338 × 10 <sup>-10</sup>	8.803 × 10 <sup>-10</sup>	-0.483	0.622		

**Table 4. Summary of best following year sheep depredated models.**  
doi:10.1371/journal.pone.0113505.t004

Both of the main effects and one interaction effect were significant in this model. Once again, the number of wolves killed was positively related to the number of sheep depredated the following year (rate ratio = 1.04, z = 2.218, P = 0.026) (Figure 4). For each additional wolf killed the estimated mean number of sheep being depredated the following year increased by 4%. The minimum wolf population was also positively related to the number of sheep depredated the following year (rate ratio = 1.06, z = 3.220, P = 0.001) (Figure 5). For each additional wolf on the landscape the estimated mean number of sheep being depredated the following year increased by 6%. The number of cattle and sheep were found to be positively related to the number of sheep depredated but the coefficient was negligible (rate ratios = 1.00 and 1.00, z = 4.718 and 3.320, P = <0.001 and 0.001) which results in an increase

of sheep depredated the following year by 1.00 or less than 1%. However, as with cattle, there was an important 2-way negative interaction. Sheep depredations increased with increasing wolf mortality rate up until about 25%, then depredations began to decline after mortality exceeded 25% (Figure 6).



**Figure 4. Wolves killed vs sheep depredated.**

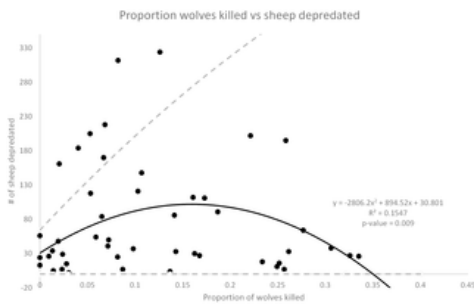
Number of wolves killed through control methods the previous year versus the number of sheep depredated the following year. The dashed lines show the upper and lower limits of the 95% confidence interval for the best fit line.

doi:10.1371/journal.pone.0113505.g004

**Figure 5. Minimum wolf population vs sheep depredated.**

Minimum year end wolf population the previous year versus the number of sheep depredated the following year. The dashed lines show the upper and lower limits of the 95% confidence interval for the best fit line.

doi:10.1371/journal.pone.0113505.g005



**Figure 6. Proportion of wolves controlled versus the number of sheep depredated.**

Proportions of wolves killed through control methods the previous year versus the number of sheep depredated the following year. The dashed lines show the upper and lower limits of the 95% confidence interval for the best fit line.

doi:10.1371/journal.pone.0113505.g006

## Discussion

Our results do not support the “remedial control” hypothesis of predator mortality on livestock depredations the following year. However, lethal control of wolves appears to be related to increased depredations in a larger area the following year. Our results are supported by the findings of Harper et al. (2008) in Minnesota where they found that across the state (large scale) none of their correlations supported the hypothesis that killing a high number of wolves reduced the following year’s depredations. Harper et al also found that trapping and not catching wolves decreased depredations more than no trapping at all, suggesting that a mere increase in human activity at depredation sites reduced further depredations by those wolves in their study area. By contrast, Bjorge and Gunson (1985) found reducing the population from 40 to 3 wolves in 2 years in Alberta (a 10 fold reduction to near extirpation) resulted in a decline of livestock depredations for two years - followed by subsequent recolonization and increased depredations thereafter. Tompa (1983) also found that lethal control prevented conflict for more than a year in some areas of British Columbia. It should be noted that these 2 studies examined wolf control and livestock depredations at a fine scale (grazing allotment or wolf pack territory or management zone). They did not examine wolf control and livestock depredations at a larger

scale (wolf occupied areas) as was done by Harper et al. (2008) and us (this study). It appears that wolf control is associated with reduced depredations at the local wolf pack scale but increased depredations at the larger wolf population scale. This appears consistent with Treves et al. (2005) prediction that the removal of carnivores generally only achieves a temporary reduction in livestock depredations locally when immigrants can rapidly fill the vacancies.

There were several different factors that influenced the number of livestock depredated the following year by wolves. In order of importance, based on the values of the rate ratios, these include: the number of wolves removed through control methods, the number of breeding pairs, the minimum wolf population, and the number of livestock on the landscape. Consistent with expectations, each additional breeding pair on the landscape increased the expected mean number of cattle depredated by 8 to 9% and each additional wolf on the landscape increased the expected mean number of sheep depredated by 6%. Cattle were most affected by breeding pairs and sheep by wolves – perhaps because it takes more than one wolf (a pack) to kill a relatively larger cow and only one wolf to kill a smaller sheep. However, contrary to the “remedial control” hypothesis, each additional wolf killed increased the expected mean number of livestock depredated by 5–6% for cattle and 4% for sheep. It appears that lethal wolf control to reduce the number of livestock depredated is associated with increased, not decreased, depredations the following year, on a large scale – at least until wolf mortality exceeds 25%. Why 25%? The observed mean intrinsic growth rate of wolves in Idaho, Wyoming, and Montana is about 25% [21]. Therefore, once anthropogenic mortality exceeds 25%, the numbers of breeding pairs and wolves must decline – resulting in fewer livestock depredations.

Below 25% mortality, lethal control may increase breeding pairs and wolves through social disruption and compensatory, density dependent effects. For example, wolf control efforts occur year round and often peak during grazing season in areas with livestock depredations [22], [23]. However, if control takes place during the breeding season and a member of the breeding pair is removed it may lead to pack instability and increased breeding pairs [24], [10]. Furthermore, loss of a breeder in a pack during or near breeding season can result in dissolution of territorial social groups, smaller pack sizes and compensatory density dependent effects – such as increased per-capita reproduction [11], [25], [26]. Culling of wolves may also cause frequent breeder turnover [11] and related social disruption – which can result in reduced effective prey use (through loss of knowledge of prey sources and ability to subdue prey) which may also result in increased livestock depredations [27], [28]. All of these effects could potentially result in increased livestock depredations.

We would expect to see increased depredations, wolves killed, and breeding pairs as the wolf population grows and recolonizes the area - but our data suggest that lethal control exacerbates these increases. The secondary effects of time, wolf population growth rate, wolf occupied area, and wolf population size on depredations were already subsumed in the primary main effect terms of breeding pairs (cattle) and wolves (sheep), so those secondary effects cannot account for the positive effects of wolf kills on depredations. We do not yet know the exact mechanism of how increased wolf mortality up to  $\leq 25\%$  results in increased livestock depredations, but we do know that increased mortality is associated with compensatory increased breeding pairs, compensatory numbers of wolves, and depredations [24], [10], [27], [28], [11], [26]. Further research is needed to determine the exact causal mechanism(s). Annual mortality in excess of 25% will reduce future depredations, but that mortality rate is unsustainable and cannot be carried out indefinitely if federal relisting of wolves is to be avoided. Furthermore, a 5% (sheep) and 5% (cattle) kill rate of wolves yields the same number of cattle and sheep depredations as a 35% (cattle) and 30% (sheep) kill rate (Figures 3 & 6), but the 30% or 35% rate is unsustainable for wolf population persistence and the 5% rate is not. The worst possible case appears to be a high mortality rate at about 20–25%, since this corresponds to a “standing wave” of the highest livestock depredations. Further research is needed to test if this high level of anthropogenic wolf mortality (25%) is associated with high levels of predation on natural prey such as deer and elk.

Further research is also needed to account for the limitations of our data set. The scale of our analysis was large (wolf occupied areas in each state in each year) and the scale of some other studies were small (wolf packs). Simultaneous, multi-scale analysis (individual wolf packs, wolf management zones, and wolf occupied areas) may yield further insights.

Although lethal control is sometimes a necessary management tool in the near-term, we suggest that managers also consider testing non-lethal methods of wolf control [29] because these methods might not be associated with increased depredations in the long-term.

#### Supporting Information

**Figure S1.**  
**Proportion of wolves harvested vs cattle depredated.** Proportion of wolves harvested the previous year in each state (Montana, Idaho and Wyoming) versus the number of cattle depredated the following year.  
 doi:10.1371/journal.pone.0113505.s001  
 (TIF)

**Figure S2.**  
**Proportion of wolves harvested vs sheep depredated.** Proportion of wolves harvested the previous year in each state (Montana, Idaho and Wyoming) versus the number of sheep depredated the following year.  
 doi:10.1371/journal.pone.0113505.s002  
 (TIF)

**Table S1.**

**Data by state, 1987–2012.** Data for all variables used in the analysis grouped by state from 1987–2012.

doi:10.1371/journal.pone.0113505.s003

(DOCX)

**Table S2.**

**Pearson correlation matrix.** Pearson correlation matrix for independent variables: cattle, sheep, minimum wolf population, wolves harvested and number of breeding pairs.

doi:10.1371/journal.pone.0113505.s004

(DOCX)

**Acknowledgments**

This analysis and paper benefitted from the insights and comments of Hilary Cooley (U.S. Fish and Wildlife Service), and John Pierce, Donny Martorello, Brian Kertsen, Ben Maletzke, and Stephanie Simick (Washington Department of Fish and Wildlife).

**Author Contributions**

Conceived and designed the experiments: RBW KAP. Performed the experiments: RBW KAP. Analyzed the data: RBW KAP. Contributed reagents/materials/analysis tools: RBW KAP. Wrote the paper: RBW KAP.

**References**

- Zimmerman B, Wabbakken P, Dotterer M (2003) Brown bear – livestock conflicts in a bear conservation zone in Norway: are cattle a good alternative to sheep? *Ursus* 14 (1):72–83.  
View Article • PubMed/NCBI • Google Scholar
- Creel S, Rotella JJ (2010) Meta-Analysis of Relationships between Human Offtake Total Mortality and Population Dynamics of Gray Wolves (*Canis lupus*). *PloS ONE* doi:10.1371/journal.pone.0012918.
- Lambert C, Wielgus RB, Robinson HS, Katnik DD, Cruickshank HS, et al. (2006) Cougar population dynamics and viability in the Pacific Northwest. *Journal of Wildlife Management* 70:246–254. doi: 10.2193/0022-541x(2006)70[246:cpdavi]2.0.co;2  
View Article • PubMed/NCBI • Google Scholar
- Rabinowitz A (2005) *Jaguars and livestock: living with the world's third largest cat. People and wildlife: conflict or coexistence.* Cambridge University Press, The Zoological Society of London. Pages 278–285.
- Packer C, Kosmala M, Cooley HS, Brink H, Pintea L, et al. (2009) Sport hunting, predator control and conservation of large carnivores. *PloS ONE* 4(6):e5941. doi: 10.1371/journal.pone.0005941  
View Article • PubMed/NCBI • Google Scholar
- Balme GA, Batchelor A, De Woronin Britz N, Seymour G, Grover M, et al. (2012) Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. *Mammal Review* doi: 10.1111/j.1365-2907.2012.00219.x.
- Treves A (2009) Hunting for large carnivore conservation. *Journal of Applied Ecology* 46:1350–1356. doi: 10.1111/j.1365-2664.2009.01729.x  
View Article • PubMed/NCBI • Google Scholar
- U.S. Fish and Wildlife Service, Idaho Department of Fish and Game, Montana Fish Wildlife & Parks, Nez Perce Tribe, National Park Service, et al. (2012) Northern Rocky Mountain Wolf Recovery Program 2011 Interagency Annual Report. M.D. Jimenez and S.A. Becker, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana, 59601.
- Bradley EH, Pletscher DH (2005) Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. *Wildlife Society Bulletin* 33:1256–1265. doi: 10.2193/0091-7648(2005)33[1256:aftrwd]2.0.co;2  
View Article • PubMed/NCBI • Google Scholar
- Mech LD (2010) Consideration for developing wolf harvesting regulations in the contiguous United States. *Journal of Wildlife Management* 74:1421–1424. doi: 10.1111/j.1937-2817.2010.tb01268.x  
View Article • PubMed/NCBI • Google Scholar
- Brainerd SM, Andren H, Bangs EE, Bradley EH, Fontaine JA, et al. (2008) The effects of breeder loss on wolves. *Journal of Wildlife Management* 72:89–



98. doi: 10.2193/2006-305  
View Article • PubMed/NCBI • Google Scholar
12. Collins GH, Wielgus RB, Koehler GM (2002) Effects of sex and age on American black bear conifer damage and control. *Ursus* 13:231–236.  
View Article • PubMed/NCBI • Google Scholar
13. Treves A, Kapp KJ, MacFarland D (2010) American black bear nuisance complaints and hunter take. *Ursus* 21(I):30–42. doi: 10.2192/09gr012.1  
View Article • PubMed/NCBI • Google Scholar
14. Peebles KA, Wielgus RB, Maletzke BT, Swanson ME (2013) Effects of remedial sport hunting on cougar complaints and livestock depredations. *PLoS ONE*. DOI: 10.1371/journal.pone.0079713.
15. Biondi F (2014) Paleoecology grand challenge. *Frontiers in Ecology and Evolution* DOI: 10.3389/fevo.2014.00050.
16. U.S. Fish and Wildlife Service, Idaho Department of Fish and Game, Montana Fish Wildlife & Parks, Nez Perce Tribe, National Park Service, et al. (2013) Northern Rocky Mountain Wolf Recovery Program 2012 Interagency Annual Report. M.D. Jimenez and S.A. Becker, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana, 59601.
17. United States Department of Agriculture (2012) Washington Livestock Statistics. National Agricultural Statistics Service, U.S. Department of Agriculture, Washington D.C., USA.
18. Agresti A (1996) An introduction to categorical data analysis. John Wiley and Sons, New York.
19. Burnham KP, Anderson DR (2010) Model Selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
20. Mosteller F (1968) Association and estimation in contingency tables. *Journal of American Statistical Association* 63:1–28. doi: 10.1080/01621459.1968.11009219  
View Article • PubMed/NCBI • Google Scholar
21. Wiles GJ, Allen HL, Hayes GE (2011) Wolf conservation and management plan for Washington. Washington Department of Fish and Wildlife, Olympia, Washington.
22. Musiani M, Mamo C, Boitani L, Callaghan C, Gates CC, et al. (2003) Wolf depredation trends and the use of fladry barriers to protect livestock in western North America. *Conservation Biology* 17:1538–1547. doi: 10.1111/j.1523-1739.2003.00063.x  
View Article • PubMed/NCBI • Google Scholar
23. Fritts SH, Stephenson RO, Hayes RD, Boitani L (2003) Wolves and humans. *Wolves: behavior, ecology, and conservation*. The University of Chicago Press, Chicago. pp. 289–316.
24. Haber GC (1996) Biological, conservation, and ethical implications of exploiting and controlling wolves. *Conservation Biology* 10:1068–1081. doi: 10.1046/j.1523-1739.1996.10041068.x  
View Article • PubMed/NCBI • Google Scholar
25. VonHoldt BM, Stahler DR, Smith DW, Earl DA, Pollinger JP, et al. (2008) The genealogy and genetic variability of reintroduced Yellowstone grey wolves. *Molecular Ecology* 17:252–274. doi: 10.1111/j.1365-294x.2007.03468.x  
View Article • PubMed/NCBI • Google Scholar
26. Murray DL, Smith DW, Bangs EE, Mack C, Oakleaf JK, et al. (2010) Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biological Conservation* 143(11):2514–2524. doi: 10.1016/j.biocon.2010.06.018  
View Article • PubMed/NCBI • Google Scholar
27. Sand H, Wikenros C, Wabakken P, Liberg O (2006) Effects of hunting on group size snow depth and age on the success of wolves hunting moose. *Animal Behavior* 72:781–789. doi: 10.1016/j.anbehav.2005.11.030  
View Article • PubMed/NCBI • Google Scholar
28. Stahler DR, Smith DW, Guernsey DS (2006) Foraging and feeding ecology of the gray wolf (*Canis lupus*): lessons from Yellowstone national park, Wyoming, USA. *Journal of Wildlife Nutrition* 36:1923s.  
View Article • PubMed/NCBI • Google Scholar

29. Wielgus RB (2014) Minimizing and mitigating wolf/livestock conflicts in Washington. Statement of Work. Washington State University. College of Agriculture, Human, and Natural Resource Sciences. 10 pp.