Rates and Spatial Patterns of Decline in Historical Cougar and Wolf Populations in Montana

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Abstract

We characterized spatial patterns of decline of cougar (*Puma concolor*) and wolf (*Canis lupus*) in response to exploitation at the county level and estimated rates of decline using generalized linear models derived from historical bounty data collected in early 20th century Montana. Cougar bounty payments (n = 1457) declined at a rate of 7 percent/year from 1902 to1920. Wolf bounty payments (n = 33,121) declined at a rate of 15 percent/year from 1902 to1910 and 33 percent/year from 1911 to 1920. Spatially, cougar populations declined in equal proportions across Montana with remnant populations located in areas of rugged, mountainous terrain in the northwest. Cougars may have avoided extirpation in Montana because remnant populations continue to survive in these rugged, mountainous areas far from areas of high human population density and agricultural expansion. In contrast, wolves initially declined directionally toward the eastern prairie. However, in the decade before their extirpation, wolf populations collapsed in equal proportions across Montana. Increased economic incentives between 1911 and 1920, and higher real and perceived conflict with humans and livestock may have increased hunter effort to kill the last remaining wolves.

Keywords: Bounty, *Canis lupus*, carnivore, exploitation, generalized linear models, Montana, *Puma concolor*.

Introduction

Knowledge of population response to exploitation is a vital component of large carnivore management and conservation (Musiani and Paquet 2004). Historically, many large carnivores took decades or longer to recover from exploitation coincident with the westward expansion of European settlers across North America (Weaver et al. 1996). Wolves and cougars were once widely distributed across the continent, but both species were nearly driven to extinction in the western U.S. due to predator control programs and habitat destruction (Young and Goldman 1944, Mech 1970). Given current uncertainty over the response of recovering carnivore populations to potential management actions, a deeper understanding of the historical response of wolf and cougar populations to predator control programs may benefit conservation efforts. However, few suitable records of large carnivore harvest from the early 1900s have survived.

A previous study used historical bounty payment records to describe general patterns of regional population collapse of cougars and wolves in early 20th century Montana (Riley et al. 2004). Although cougars and wolves once occupied most regions of Montana, intense exploitation, prey loss, and habitat destruction nearly eradicated

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cougars and wolves by 1930 (Curnow 1969, Riley et al. 2004). Statewide cougar bounty payments declined from almost 200/year in the early 1900s to 2/year by 1930; statewide wolf bounty payments declined from over 4000/year in the early 1900s to 0/year by 1928. Cougars were most abundant in the mountainous western region of Montana; in contrast, wolves were most productive and most abundant in the flat, eastern prairie (Riley et al. 2004). Over time, the relative concentration of wolves and cougars appears to have changed, indicating that each species exhibited different spatial responses to exploitation. The exact pattern of collapse, however, for cougars and wolves in Montana, and the implications of those patterns have not been previously investigated. Rates of decline and the potential contribution of anthropogenic factors to those patterns of decline also have not been estimated.

To further elucidate the rate and spatial patterns of decline in Montana wolf and cougar populations in response to exploitation, we modeled spatial and temporal trends in historical bounty payments. Our objectives were to 1) estimate and compare rates of decline in cougar and wolf populations as both species neared extirpation, 2) compare small-scale (county) spatial patterns of decline between cougars and wolves, 3) examine the ability of anthropogenic data to explain variability in wolf and cougar bounty harvest data, and 4) identify conservation implications for modern large carnivores.

Study area

Montana has a land area of 381,086 km^2, and averages approximately 870 km from east to west and 450 km from north to south. The western third of Montana is mountainous and the eastern two–thirds are a mix of undulating prairie interspersed with rivers, breaks, and isolated mountain ranges of the Missouri and Yellowstone watersheds. Elevations range from 546 m where the Kootenai River exits the state in the northwest corner to 3898 m in the Beartooth Mountains of south central Montana.

Methods

We used several data sources to model cougar and wolf bounty payments including landscape feature, European settlement, and bounty program data (see full descriptions below). Bounty payment records were collected at the county scale (Riley et al. 2004), so we included data sources in our models that could also be represented at the county scale. Statewide data on prey abundance were not available from the early 1900s; however, increases in human population size and number of farms (data included in our analyses) likely accounted for major statewide declines in prey abundance given that range contraction and population collapse of many ungulates has been attributed to exploitation and settlement of Europeans in North America (Mussehl and Howell 1971, Laliberte and Ripple 2004).

Bounty harvest records from 1902 to 1923 and 1925 to 1930, initially recorded by county clerks, were transcribed from surviving ledgers (Riley et al. 2004). Records report number of bounty payments for adult cougar and wolf pelts submitted by individuals in the county where animals were killed. Complete accounts of Montana's bounty programs and associated records appear in Curnow (1969) and Riley et al. (2004). Reported number of wolves killed may be somewhat inaccurate because bounty hunters occasionally attempted to substitute cheaper coyote pelts for wolf pelts, and many cougars and wolves killed by humans were not claimed for their bounties (Curnow 1969). However, we do not believe that either of these issues poses serious problems for interpretation of the data. We restricted our analysis to records collected prior to 1920 because excessive zeros obscured spatial patterns of range collapse in later years as wolves approached extirpation and cougars became scarce.

We used a measure of terrain ruggedness to account for regional variation in habitat suitability that might have affected wolf and cougar rates of decline. This allowed us to determine if cougars and wolves declined at different rates in areas with different amounts of suitable habitat. Terrain ruggedness was chosen because the physical landscape of Montana has not changed markedly since the early 1900s and because no data on the land cover or prey abundance were available from that period. In addition, terrain ruggedness reliably predicts modern (1975-1995) cougar abundance in Montana (Riley and Malecki 2001). Cougars, being solitary ambush predators, prefer highly rugged terrain. In addition, previous analysis of Montana bounty harvest records indicated that density of cougars was likely highest in the mountainous west and wolf densities were highest in the flat, eastern prairie (Riley et al. 2004). Using a 1:24,000 digital elevation map, Riley et al. (1999) created a terrain ruggedness index that represented the average difference in elevation between each 1-km^2 pixel and its 8 neighboring pixels within a county. We calculated the mean terrain ruggedness index value for each county in Montana in each U.S. census period (Fig. 1) and used this value as a covariate, *Tri* (Table 1), in our models. High *Tri* indicated largely mountainous terrain, whereas low *Tri* indicated flat, prairie terrain.

We included the covariate *Year* (Table 1) in our analysis to account for overall decreases in wolf and cougar abundance and to represent the rate of decline in the population over time. We assumed that, on average, wolf and cougar populations experienced an exponential decline in population size in each county, which seemed reasonable given the pattern of decline in bounty payments described by Riley et al. (2004).

We included the area of each county as a covariate, *Area* (Table 1), in our analyses to standardize the number of bounty payments for differences in county size. Also, about 75 percent of Montana counties changed size with redrawing of county boundaries after the 1910 census of which most decreased in area.

To capture potential changes in hunter effort due to economic incentives, we included bounty price as a covariate, *Bountyprice* (Table 1), in our cougar models. Cougar bounty prices changed from $7 in 1902 to $10 in 1905. Adult wolf bounty prices changed from $5 in 1902 to $10 in 1906 and $15 in 1912. However, this variable was highly correlated with *Year* and *Decade* factors and ultimately was not incorporated into our wolf models because of multicolinearity issues. The effect of increasing bounty price was confounded with *Year* and *Decade* and could not be separated. Total value of wolf bounty payments made in Montana between 1902 and 1920 was calculated and plotted against changes in bounty price/pelt to explore changes in economic incentives over time.

We included human population by county and U.S. decennial census period (Forstall 1995) as a covariate, *Humanpopsize* (Table 1), in our models as a potential indicator of hunter effort and habitat change due to human development. We represented population size during 1902–1910 with the value from the 1900

Table 1. Definitions of cougar and wolf model factors and range of values of the factor.

Variable	Variable definition	Range
Wbounty	Annual number of wolf bounty payments in a county	0-1209
Cbounty	Annual number of cougar bounty payments in a county	0-115
Tri	Mean terrain ruggedness index value for each county by census period (100 m)	1.1-11.5
Year	Year of data	2-20
Area	Area of each county by census period (100 km^2)	18.2-419.5
Bountyprice	Dollar value of cougar and wolf pelts in each year	7-10 5-15
Humanpopsize	Human population size by county from the U.S. census (in 1000s)	2.0-60.3
Farms	Number of farms by county from the U.S. census (100s)	1.0-42.3
Decade	Decade of data, 1902–1910 or 1911–1920	0 or 1

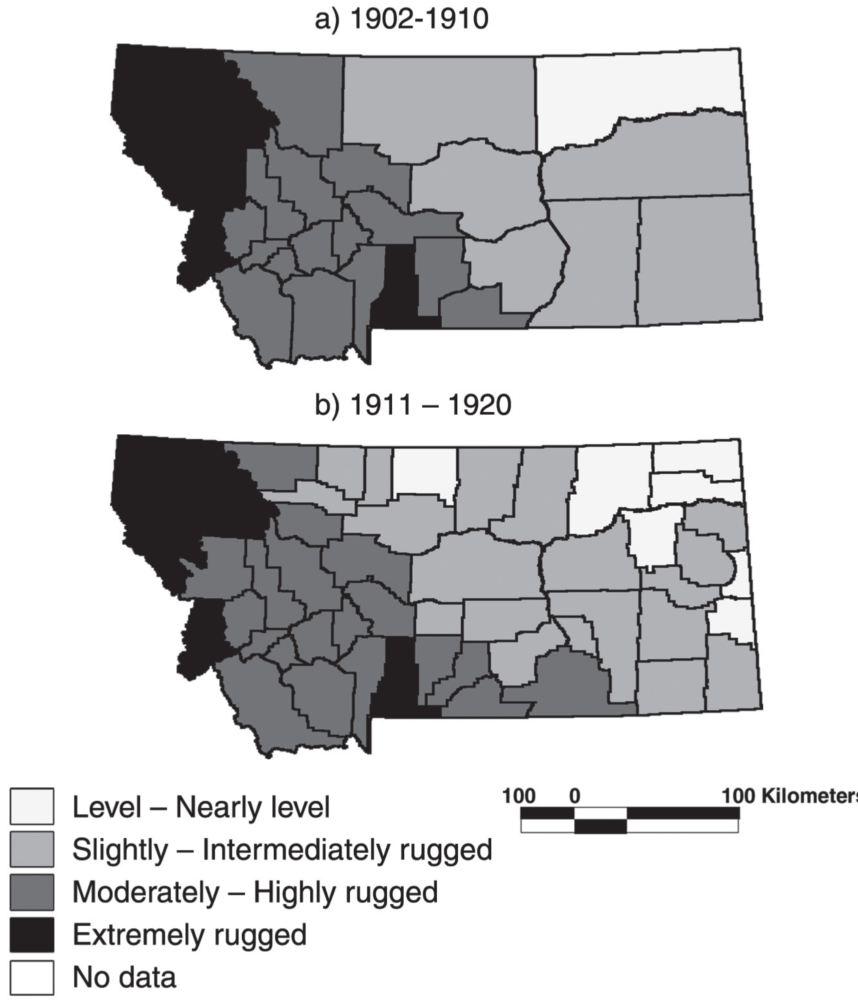

Figure 1. Mean terrain ruggedness index value for each county by census period (a. 1902–1910, and b. 1911–1920).

census and 1911–1920 from the 1910 census. We also included the number of farms (all types) in each county and census period, *Farms* (Table 1), as another potential index of human–carnivore conflicts. We included a dummy variable, *Decade* (Table 1), in our models to represent census periods 1902–1910 and 1911–1920 and account for changes in scale of data collection, i.e., changing county boundaries. Also, this dummy variable allowed us to estimate separate model intercepts for the first and second decades.

We examined four first order interactions: *Tri* by *Year*, and *Tri* by *Decade* allowed the effect of terrain ruggedness to change over time; *Tri* by *Area* accounted for the possibility that larger counties contained more microhabitats than smaller counties; *Year* by *Decade* allowed for different rates of decline between the first and second decades.

Model Development

We developed a series of generalized linear models to predict the mean number of bounty payments reported in each county and year. This approach was ideal for modeling count data with extensive zero occurrences (McCullagh and Nelder 1989). For each species, the full model contained eight main covariates (Table 1) and four interaction terms. Every model included an intercept, year, and area, and a parameter that described the overdispersion. We considered all possible subsets of the remaining main covariates. Models containing interaction terms were only considered if the factors included in those interaction terms were also present as main factors in the model, e.g., *Tri* by *Year* was only included if the model already contained *Tri* and *Year*. Altogether, we fitted 368 models to cougar bounty payments (*Cbounty*) and 184 models to wolf bounty payments (*Wbounty*). Model fitting was performed using SAS® Version 9.1 for PC (SAS Institute Inc., Cary, NC, USA) PROC GENMOD with a negative binomial distribution and a log link function. We used a negative binomial distribution because variances of the models were higher than expected under the assumption of a Poisson distribution (McCullagh and Nelder 1989). One would expect overdispersion for these data because cougars maintain territories and are unlikely to be distributed randomly across the landscape; also wolves, live in packs and may be captured in groups. The best model was chosen by comparing quasi–Akaike Information Criterion values (QAIC, Burnham and Anderson 2002). We estimated the overdispersion parameter for the full model and used that estimate to calculate the QAIC values and standard errors for all subsequent models (Burnham and Anderson 2002).

Correlations among model factors ranged from $R = 0.01$ between *Wbounty* and *Cbounty* to $R = 0.9$ between *Bountyprice* (for wolves) and *Year* (Appendix 1). Due to high correlations between *Wbounty* and *Year* and *Wbounty* and *Decade*, we did not consider *Wbounty* in our models. Most pairs of variables were correlated at $R < 0.5$, and most variables exhibited tolerances > 0.4 (Appendix 2), indicating multicolinearity was not a serious problem in our analyses (Allison 1991). We expected moderately low tolerances for *Year* and *Decade* (0.222 and 0.240, respectively) because these factors were fairly highly correlated. However, we kept both factors in our analyses to account for overall declining trends in cougar and wolf bounty payments. Multicolinearity between *Year* and *Decade* did not affect estimated values or standard errors of other model parameters.

Results

Year, *Area*, and *Tri* explained much of the variation in wolf and cougar bounty payments. However, our best generalized linear models for these large carnivores differed in two important ways: 1) direction of influence of *Tri* on number of bounty payments, and 2) inclusion of anthropogenic explanatory factors and interaction terms. We did not find evidence of interspecific competition between wolves and cougars in our models as suggested by Riley et al. (2004).

Patterns of cougar decline.—The best cougar model included five factors and one interaction term (Table 2). The effect of each model factor can be inferred by examining

Table 2. Parameter estimates and standard errors for the best models describing the mean number of cougar and wolf bounty payments in Montana, 1902–1920.

	Cougar model		Wolf model	
Name	Value	Standard error	Value	Standard error
Intercept	–2.558	0.395	7.817	0.569
Tri	0.220	0.055	–0.579	0.088
Year	–0.073	0.016	–0.403	0.032
Area	-0.002	0.002	0.004	0.002
Farms	0.077	0.013	–	–
Decade	–	–	–3.263	0.497
Tri by Area	0.002	0.0004	0.002	0.0005
Tri by Year	–	–	0.029	0.005
Year by Decade	–	–	0.241	0.047
Dispersion	2.476	0.299	2.457	0.147

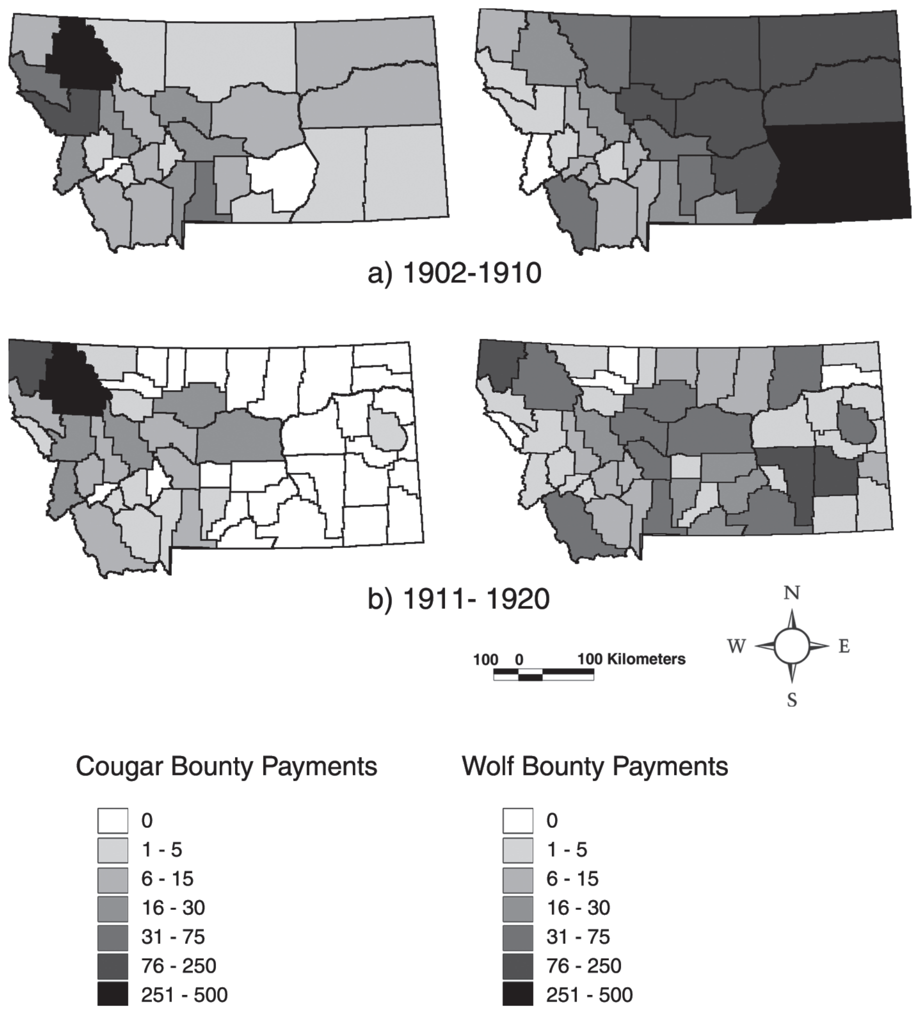

Figure 2. Total wolf and cougar bounty payments reported in Montana by county and census period (a. 1902–1910, and b. 1911–1920).

the coefficient sign and coefficient estimate compared to its standard error (Burnham and Anderson 2002). Mean number of cougar bounty payments declined over time as indicated by the negative coefficient for *Year* and the large effect relative to the standard error. Cougar bounty payments (n = 1457) declined at a rate of 7 percent/year throughout the study period.

Spatially, cougar bounty payments declined across the state in proportion to their abundance at the beginning of the study period as indicated by the positive effect of *Tri* on mean number of cougar bounty payments made in each county and year. Thus, higher numbers of cougar bounty payments were reported in the more rugged (western) counties where cougars were in higher abundance. Cougar populations were rapidly extirpated in the eastern prairie regions where initial populations were low (Fig. 2); remnant populations were restricted to the mountainous western third of the state. Because of the positive interaction between *Tri* and *Area*, larger counties had higher numbers of predicted cougar bounty payments than smaller counties with similar mean terrain ruggedness index values. Mean number of bounty payments also was higher in counties with a high number of farms (*Farms*).

The QAIC difference between the best model and the second best model was 1.52 (Appendix 3) that indicated moderate evidence favoring the best model. Other models with QAIC values close to the best model did not indicate qualitatively different patterns of range collapse than the best model (Appendix 3).

Patterns of wolf decline.—Our best wolf model consisted of five covariates and three interaction terms (Table 2). Mean number of wolf bounty payments declined through time as indicated by the negative coefficient for *Year*. However, decline was less rapid during 1902–1910 than during 1911–1920 as indicated by the positive interaction between *Year* and *Decade*. Wolf bounty payments (n = 33,121) declined at a rate of 15 percent/year from 1902-1910 and 33 percent/year from 1911-1920.

In contrast to cougars, declines in wolf bounty payments were disproportionate across the Montana landscape. High numbers of wolf bounty payments were associated with flat terrain in the beginning of the time series, but the effect of terrain ruggedness lessened through time (Fig. 2). *Tri* had an overall negative effect on the mean number of wolf bounty payments made in each county and year indicating that the number of wolf bounty payments was higher in counties with low terrain ruggedness than in counties with high terrain ruggedness. Yet, the effect of terrain ruggedness on number of bounty payments decreased over time as indicated by the positive interaction between *Tri* and *Year*. By 1920, the effect of terrain ruggedness was nearly zero. The negative effect of terrain ruggedness on the number of wolf bounty payments was lower in large counties than in small counties as indicated by the positive interaction between *Tri* and *Area*.

The QAIC difference between the best model and the next best model was 0.7 (Appendix 4). The top two models were the same except that the second best model contained the factor *Humanpopsize*. Other models that had QAIC values close to the best model did not indicate qualitatively different spatial patterns of collapse than the best model (Appendix 4).

Discussion

Plausible reasons why wolves were extirpated in Montana although cougars were not include 1) regions of Montana with high wolf abundance were also heavily used by humans for settlement and agriculture, increasing their vulnerability to harvest and habitat destruction, 2) higher real and perceived conflict between carnivores and humans (and their livestock) was higher for wolves than for cougars, and 3) economic incentives for bounty hunters to harvest wolves were greater than for cougars.

Our analyses indicated that resilient, remnant cougar populations occupied favorable habitat (high terrain ruggedness); such rugged terrain likely provided additional protection from human disturbance. Our models showed that cougars declined proportionately across their range such that small prairie populations were extirpated first whereas larger remnant populations persisted in the rugged, sparsely settled, western region of the state (Table 2, Fig. 2). That cougar populations persisted in areas not easily accessed by humans likely afforded enough protection to survive exploitation and eventually recover after World War II (Mussehl and Howell 1971). Thus, cougars were less vulnerable to hunters than wolves in which highest abundance occurred in the more flat, open riverine habitats of the prairie. In addition, cougars may have been more resilient than the highly social wolf to demographic problems that arose from low population size (Allee effects). The cougar's natural tendency toward solitary behavior, low productivity, and dispersal may have better equipped them to deal with low remnant population size in the early 1900s and rebound as predator control subsided after World War II.

In contrast, wolves thrived in the flatter, prairie habitats (Riley et al. 2004), which put them in direct conflict with humans who also preferred the prairie for ranching and farming. Following extirpation of bison from the prairie, wolf depredation on livestock likely increased, thus creating greater economic incentives for humans to kill wolves than cougars in agricultural areas. Compared with cougars that preferred rugged terrain, wolves likely were easier to find and kill than cougars given their preference for less rugged terrain and their easily accessed dens along the banks of rivers. Also, scavenging behavior of wolves left them vulnerable to widespread use of poison and disease as predator control tools (Young 1942).

Another factor that may have led to a disproportionately higher harvest pressure on wolves than cougars was wolves higher perceived conflict with humans and livestock. Specialized cougar bounty hunters existed (Curnow 1969), and humans likely could have harvested enough cougars from western Montana to cause extirpation. However, contemporary studies indicate wolves are generally perceived a greater threat to humans and agriculture than cougars (Kellert 1985, Kellert et al. 1996) despite higher livestock depredation rates by cougars and higher incidences of cougar–caused human fatalities (Curnow 1969, Beier 1991). Historical human attitudes were likely similar as indicated by stories of famous wolves that appeared in the popular press of the late 1800s and early 1900s (Gipson et al. 1998); as wolves became more rare and difficult to catch, these stories may have provided additional incentive to remove remaining animals. Overall, lower exposure to humans and less negative human attitudes towards cougars may have prevented their extirpation in Montana.

Finally, we believe that economic incentives in the form of increased bounty prices likely served as the final driving force extirpating wolves. Our models indicated that wolves collapsed directionally toward areas of highly suitable habitat in the eastern prairie at first and then declined to extirpation in a fragmented manner across the entire state (Table 2, Fig. 2). We speculate bounty hunters sought areas of high wolf abundance in the eastern prairie first to achieve highest profits and then hunted other regions of the state as bounty prices increased in the second decade of our study, i.e., it became profitable to bounty hunt everywhere. Myers and Worm (2003) observed a similar pattern in decline of the world's large fish species in that declines were briefly directional (toward the Indian Ocean), then occurred more evenly across the world's oceans.

Also, increased rates of wolf decline in the second decade (33% decline/year, 1911–1920 versus 15% decline/year, 1902–1910) might indicate that increased hunter effort driven by increased bounty price led to more rapid wolf declines in the second decade. Although wolf bounty programs began in Montana in the 1880s, the number of wolves harvested did not decline precipitously until the price/wolf pelt reached $15 (Fig. 3). A bounty price of $15 represents a tripling of the original bounty price that would be worth nearly $300 today accounting for inflation (U.S. Department of Labor, Bureau of Labor Statistics). Additionally, five of our 10 best-fit models included human population size as a factor. This was likely due to the fact that human population and settlement of the prairie nearly doubled in the second decade of this study, which likely increased demand for wolf control.

A large increase in rate of decline was not apparent in our models of cougar bounty payments despite an increase in bounty price from $7 to $10 in 1905. Economic incentives for bounty hunters may not have been high enough to induce eradication of cougars in Montana. Bounty hunters likely recognized the benefits of pursuing wolves as opposed to cougars, which are more difficult to capture than wolves without specialized dogs, given that the total value of the cougar harvest (sum of annual total values during 1902-1920) was only $13,631 compared with $158,670 for wolves. Several recent fisheries studies have also demonstrated that economic incentives promote exploitation and population collapse in commercial fisheries (Myers et al. 1996, Baum et al. 2003, Myers and Worm 2003, Safina et al. 2005). Even highly fecund fishes have experienced population collapse in response to intense fishing pressure (Sadovy 2001, Myers and Worm 2003).

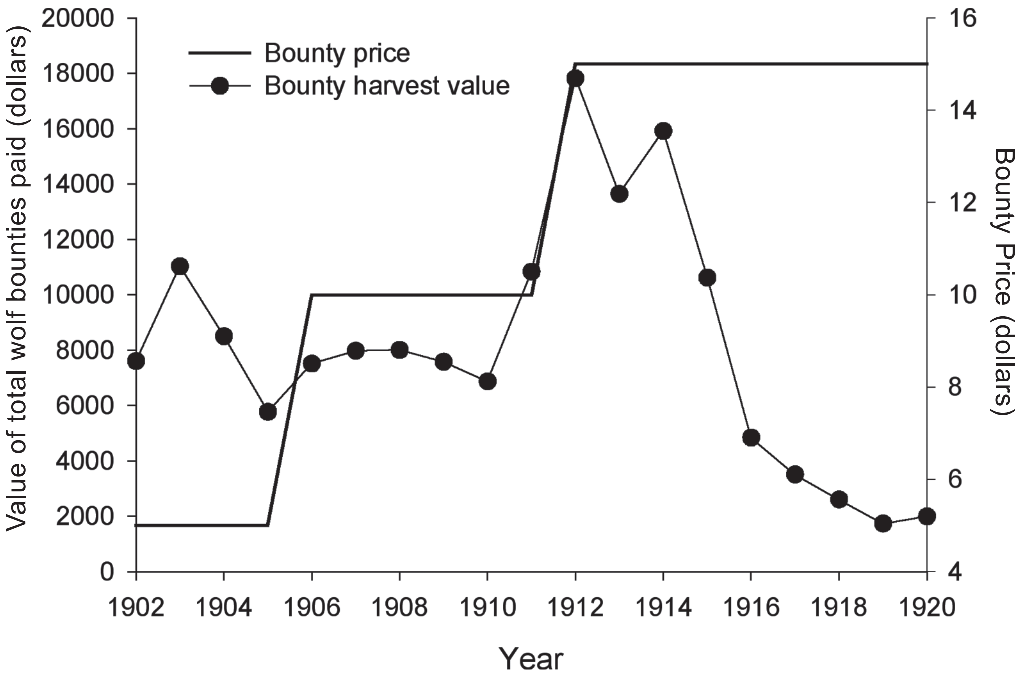

Figure 3. Total value of wolf bounty payments made in Montana between 1902 and 1930 is shown on the left ordinate. Temporal correspondence of wolf bounty payments with changes in bounty price per pelt is shown on the right ordinate. Note the sharp decline in wolf bounty payments with the increase in bounty price from $10 to $15 in 1912.

Conservation Implications

In general, Weaver et al. (1996) considers wolf populations more resistant to exploitation relative to other large carnivores because of high annual productivity and capabilities for long-distance dispersal. Populations have recovered from intense harvests as high as 80 percent (Hayes and Harestad 2000). In contrast, cougar populations are generally thought to be less resilient to disturbance than wolves (Weaver et al. 1996) because they are solitary predators and require large areas of rugged terrain for hunting (Riley and Malecki 2001). Also, cougars are poor competitors with other carnivores such as wolves (White and Boyd 1989, Boyd and Neale 1992, Bangs and Fritts 1996, Kunkel et al. 1999) and have lower productivity than many other carnivores (Weaver et al. 1996).

That cougars persisted in Montana while wolves were extirpated implies cougars may be better able to withstand exploitation than wolves. However, our results complicate this interpretation because overall depletion of wolves was much greater than that of cougars. Without considering private bounty programs and unreported kills (Curnow 1969), in < 20 years a minimum of 1457 and 33,121 bounty payments were made for cougars and wolves, respectively, in Montana as part of the state's predator control program. Wolf populations declined at a much higher rate than cougars throughout the study period (15-33 percent/year for wolves vs. 7 percent/year for cougars). Given these rates of decline, we estimated that in 1920 cougar populations were at 25 percent of the 1902 levels and wolf populations were at 0.5 percent of the 1902 levels. Yet, Riley et al. (2004) reported evidence that wolves maintained high reproduction in the face of exploitation even in the final years before extirpation as indicated by the ratio of pups to adult wolves (>1 from 1902-1920). Even high apparent productivity (Riley et al. 2004) could not prevent their extirpation.

Cougar survival and recovery may be attributed to the fact that rugged regions of northwestern Montana provided refuge from harvest pressure. Weaver et al. (1996) argued for the need in conservation plans for refugia for both wolves and cougars. Ideally, refugia (either man-made or natural) help sustain source populations (Weaver et al. 1996). In Montana, wolves were not afforded refugia because their preferred habitat (undulating/flat prairies of eastern Montana) was also preferred for ranching and other agricultural development.

Wildlife managers in North America have traditionally believed bounty harvest programs cannot cause extirpation of species (Wilman 1996, Pauly et al. 2002). Yet, this study and others (Woodroffe 2000, Logan and Sweanor 2001, Laliberte and Ripple 2004, Riley et al. 2004) present evidence that bounty programs have contributed greatly to the extirpation of wolves and cougars in many regions of North America. The case of wolf extirpation in Montana demonstrates how even a highly productive terrestrial species can succumb to exploitation if economic incentives and negative human attitudes are strong enough. Until most government–sponsored bounty programs ceased and human attitudes toward large carnivores became more favorable (Kellert et al. 1996, Woodroffe 2000), wolves did not begin their recovery in Montana or elsewhere.

Acknowledgements

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Appendix 1. Correlations among variables used to model wolf and cougar bounty payments made in Montana, 1902-1920. Variable names and descriptions are listed in Table 1. Due to high correlations among *Wbounty*, *Decade*, and *Year*, *Wbounty* was not included in our models.

Variable	*Year*	*Cbounty*	*Wbounty*	*Tri*	*Area*	*Humanpopsize*	*Farms*	*Bountyprice (c)*	*Bountyprice (w)*	*Decade*
Year	*1.00*									
Cbounty	-0.13	1.00								
Wbounty	-0.28	0.01	1.00							
Tri	-0.20	0.32	-0.15	1.00						
Area	-0.32	0.12	0.46	-0.25	1.00					
Humanpopsize	-0.10	0.12	0.05	0.09	0.09	1.00				
Farms	0.11	0.05	0.14	-0.46	0.48	0.28	1.00			
Bountyprice (cougars)	0.63	-0.08	-0.25	-0.12	-0.19	-0.06	0.06	1.00		
Bountyprice (wolves)	0.90	-0.14	-0.26	-0.20	-0.33	-0.10	0.11	0.70	1.00	
Decade	-0.85	0.14	0.22	0.24	0.38	0.12	-0.13	-0.50	-0.86	1.00

Appendix 2. Tolerances for variables in Montana wolf and cougar bounty payments model, 1902-1920.

Variable	Tolerance
Intercept	—
Tri	*0.694*
Year	*0.222*
Area	*0.464*
Decade	*0.240*
Humanpopsize	*0.835*
Farms	*0.503*
Bountyprice (cougars)	*0.598*
Bountyprice (wolves)	*0.736*

Appendix 3. Ten best models of cougar bounty payments in Montana, 1902-1920. Parameter estimates, standard errors, log-likelihood, quasi-Akaike Information Criterion (QAIC) values, and QAIC differences between each model and the best model are presented. Variable names and descriptions are listed in Table 1.

Rank	Intercept	*Year*	*Area*	*Tri*	*Decade*	*Human popsize*	*Farms*	*Bounty price*	*Wbounty*	*Tri* Year*	*Tri* Decade*	*Tri* Area*	Dispersion	Log Likelihood	QAIC	QAIC diff
1	-2.55813 (±0.404)	-0.073 (±0.016)	-0.002 (±0.002)	0.220 (±0.056)			0.077 (±0.014)					0.002 (±0.0005)	2.531 (±0.305)	2207.575	-596.459	0.000
2	-3.28557 (±0.567)	-0.028 (±0.029)	-0.002 (±0.002)	0.215 (±0.056)	0.608 (±0.326)		0.079 (±0.014)					0.002 (±0.0005)	2.504 (±0.302)	2209.310	-594.939	1.520
3	-1.87841 (±0.678)	-0.121 (±0.042)	-0.003 (±0.002)	0.119 (±0.097)			0.084 (±0.015)			0.007 (±0.006)		0.003 (±0.0005)	2.530 (±0.305)	2208.354	-594.675	1.784
4	-2.61898 (±0.41)	-0.070 (±0.016)	-0.002 (±0.002)	0.223 (±0.056)			0.079 (±0.014)		0.002 (±0.002)			0.002 (±0.0005)	2.529 (±0.305)	2208.037	-594.587	1.872
5	-2.38565 (±0.9)	-0.070 (±0.02)	-0.002 (±0.002)	0.219 (±0.056)			0.077 (±0.014)	-0.021 (±0.096)				0.002 (±0.0005)	2.531 (±0.305)	2207.598	-594.466	1.994
6	-2.548 (±0.407)	-0.073 (±0.016)	-0.002 (±0.002)	0.221 (±0.056)		-0.002 (±0.009)	0.078 (±0.015)					0.002 (±0.0005)	2.532 (±0.305)	2207.593	-594.464	1.995
7	-3.85708 (±0.363)	-0.075 (±0.017)	0.005 (±0.002)	0.505 (±0.031)			0.099 (±0.015)						3.039 (±0.339)	2193.106	-594.458	2.001
8	-3.39463 (±0.577)	-0.029 (±0.029)	-0.006 (±0.002)	0.230 (±0.567)	1.611 (±0.015)		0.090 (±0.079)				-0.143 (±0.057)	0.003 (±0.0005)	2.487 (±0.3)	2211.772	-593.620	2.839
9	-1.84656 (±0.386)	-0.042 (±0.015)	0.001 (±0.002)	0.097 (±0.051)								0.003 (±0.0005)	2.820 (±0.337)	2189.531	-593.470	2.990
10	-2.54247 (±0.758)	-0.080 (±0.047)	-0.004 (±0.002)	0.096 (±0.098)	0.661 (±0.328)		0.087 (±0.015)			0.008 (±0.006)		0.003 (±0.0005)	2.501 (±0.301)	2210.383	-593.236	3.223

Appendix 4. Ten best models of wolf bounty payments in Montana, 1902-1920. Parameter estimates, standard errors, log-likelihood, quasi–Akaike Information Criterion (QAIC) values, and QAIC differences between each model and the best model are presented. Variable names and descriptions are listed in Table 1.

Rank	Intercept	*Year*	*Area*	*Tri*	*Decade*	*Human popsize*	*Farms*	*Cbounty*	*Tri* Year*	*Tri* Decade*	*Tri* Area*	*Year* Decade*	Dispersion	Log Likelihood	QAIC	QAIC diff
1	7.817	-0.403	0.004	-0.579	-3.263				0.029		0.002	0.241	2.498	55254.346	-37441.915	0.000
	(± 0.575)	(±0.033)	(±0.002)	(±0.089)	(±0.503)				(±0.005)		(±0.0005)	(±0.048)	(±0.149)			
2	7.655	-0.401	0.004	-0.582	-3.242	0.012			0.029		0.002	0.234	2.483	55256.268	-37441.218	0.697
	(±0.581)	(±0.033)	(±0.002)	(±0.089)	(±0.502)	(±0.006)			(±0.005)		(±0.0005)	(±0.048)	(±0.148)			
3	5.993	-0.282	0.004	-0.135	-2.179					-0.301	0.002	0.294	2.503	55253.183	-37441.127	0.788
	(±0.457)	(±0.027)	(±0.002)	(±0.555)	(±0.073)					(±0.049)	(±0.0005)	(±0.048)	(±0.149)			
4	7.154	-0.356	0.003	-0.416	-2.630				0.018	-0.149	0.002	0.262	2.483	55255.962	-37441.011	0.904
	(±0.674)	(±0.041)	(±0.002)	(±0.128)	(±0.602)				(±0.008)	(±0.082)	(±0.0005)	(±0.049)	(±0.148)			
5	7.041	-0.357	0.003	-0.428	-2.649	0.011			0.019	-0.140	0.002	0.255	2.469	55257.717	-37440.201	1.715
	(±0.676)	(±0.041)	(±0.002)	(±0.6)	(±0.006)	(±0.008)			(±0.09)	(±0.127)	(±0.0005)	(±0.049)	(±0.147)			
6	5.851	-0.281	0.004	-0.138	-2.188	0.011				-0.296	0.002	0.288	2.491	55254.738	-37440.181	1.734
	(±0.465)	(±0.027)	(±0.002)	(±0.553)	(±0.006)	(±0.073)				(±0.049)	(±0.0005)	(±0.048)	(±0.149)			
7	7.799	-0.401	0.004	-0.579	-3.269			-0.008	0.028		0.002	0.241	2.496	55254.530	-37440.040	1.875
	(±0.575)	(±0.033)	(±0.002)	(±0.089)	(±0.503)			(±0.012)	(±0.005)		(±0.0006)	(±0.048)	(±0.149)			
8	7.810	-0.403	0.004	-0.579	-3.256		0.001		0.029		0.002	0.240	2.498	55254.350	-37439.918	1.997
	(±0.58)	(±0.033)	(±0.002)	(±0.089)	(±0.508)		(±0.01)		(±0.005)		(±0.0005)	(±0.048)	(±0.149)			
9	7.685	-0.396	0.004	-0.577	-3.321	0.016	-0.012		0.027		0.002	0.237	2.479	55256.775	-37439.562	2.353
	(±0.579)	(±0.033)	(±0.002)	(±0.089)	(±0.507)	(±0.007)	(±0.012)		(±0.005)		(±0.0005)	(±0.048)	(±0.148)			
10	7.621	-0.398	0.003	-0.581	-3.248	0.012		-0.011	0.028		0.002	0.234	2.479	55256.617	-37439.455	2.460
	(±0.581)	(±0.033)	(±0.002)	(±0.089)	(±0.502)	(±0.006)		(±0.012)	(±0.005)		(±0.0006)	(±0.048)	(±0.148)			