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SHORT COMMUNICATION

Short communication articles are short scientific entities often dealing with methodological problems or with byproducts of larger research projects. The style is the same as in original articles

Initial effects of reintroduced wolves *Canis lupus* on bighorn sheep *Ovis canadensis* dynamics in Yellowstone National Park

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Wolves *Canis lupus* may naturally achieve densities that contribute to significant changes in prey populations and entire ecosystems. We analyzed a time series of counts, index of recruitment, and estimates of survival for bighorn sheep *Ovis canadensis* during 1995-2005 to evaluate the prediction that sheep numbers would decrease in the northern portion of Yellowstone National Park, Montana and Wyoming, USA, owing to lower survival and recruitment following wolf reintroduction. The number of wolves residing in the northern range increased from 21 to a maximum of 106 in response to an abundant elk *Cervus elaphus* population and legal protection. Counts of bighorn sheep decreased following the severe winter of 1997, but then increased by 7% annually during 1998-2005 (95% CI: 2-11%). Recruitment followed a similar temporal pattern, decreasing to 7-11 lambs/100 ewes during the severe winter of 1997 and the following winter, but then increasing to 21-34 lambs/100 ewes during 1998-2005. Annual estimates of survival for 14 adult females and four males 1-3 years old were high (0.94; 95% CI: 0.89-0.97) and indicative of an increasing or constant population. Thus, the presence of wolves did not prevent the bighorn sheep population from increasing slowly during the decade following reintroduction. However, sheep counts remain low compared to the 487 sheep observed before an outbreak of keratoconjunctivitis caused 60% mortality during 1982, suggesting that other factors limited the recovery of this relatively isolated, high-elevation, native sheep population. Increases in abundance and recruitment of bighorn sheep during 1998-2005 were concurrent with a 50% decrease in the numbers of northern Yellowstone elk after wolf reintroduction. Thus, the potential effects of decreased competition for resources between elk and bighorn sheep on lamb recruitment and sheep population growth merit further investigation.

Key words: bighorn sheep, Canis lupus, Ovis canadensis, population dynamics, recruitment, survival, wolves, Yellowstone

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Public support to restore large predators to landscapes that can sustain viable populations is growing (Breitenmoser et al. 2001, Carroll et al. 2003). Such proposals are highly controversial, with much of the debate focused on the potential for predators to substantially change ecosystems or reduce sport-hunting opportunities (Garrott et al. 2006). Wolves *Canis lupus* may naturally achieve densities that contribute to significant changes in prey populations and ecosystems (Smith et al. 2003). Wolves were reintroduced to Yellowstone National Park in the western United States during 1995-1996 and exceeded predicted equilibrium levels (i.e. ~100 wolves in 10 packs) in 5-6 years (U.S. Fish & Wildlife Service 2005). Elk *Cervus elaphus* were the preferred prey of wolves (Smith 2005) and experienced decreased recruitment and adult survival, as well as changes in their spatial and temporal distribution, during the decade following wolf reintroduction (Creel et al. 2005, Mao et al. 2005, White & Garrott 2005, Garrott et al. 2006). Such effects have significant implications for natural resource managers because a reduction in ungulate abundance can lead to alterations in species abundance and community composition, nutrient concentrations of plants and the physical structure of the vegetation and the environment (Hebblewhite et al. 2005). Decreased ungulate abundance and recruitment can also result in fewer hunting opportunities (White & Garrott 2005).

The initial numerical response of wolves to an abundant elk population in Yellowstone raised concerns that wolves would also affect the population dynamics of less abundant, alternate prey (i.e. bighorn sheep *Ovis canadensis*, moose *Alces alces*, mule deer *Odocoileus hemionus* and pronghorn *Antilocapra americana*). Bighorn sheep in the northern range of Yellowstone are organized into 10-13 bands that appear to function as a metapopulation with periodic movements and gene flow among groups (Houston 1982, Keating 1982, Legg 1996, Ostovar 1998). Most sheep are migratory, wintering in lower-elevation areas along the Yellowstone, Lamar, and Gardner rivers and then migrating to higher-elevation summer ranges during May through October. Aerial counts of 471 and 487 sheep were reported during 1978 and 1981; however, an outbreak of infectious keratoconjunctivitis or 'pinkeye' (caused by the protozoan *Chlamydia* sp.) resulted in the mortality of at least 60% of these sheep during the winter of 1982 (Meagher et al. 1992). Counts did not increase significantly during the next 13 years prior to wolf reintroduction, even though there was no sign of *Chlamydia* in sheep (Lemke 2005a).

We analyzed a time series of counts, index of recruitment, and estimates of survival for bighorn sheep in northern Yellowstone, along with numbers of wolves, elk, and environmental covariates (drought, snow) to evaluate the prediction that wolf predation would reduce survival and recruitment of bighorn sheep and, thus, cause a decline in sheep numbers. Alternatively, wolves could enable an increase in sheep numbers by contributing to decreased elk abundance and changes in elk distribution, thereby decreasing competition for resources between elk and sheep.

Material and methods

The northern range of Yellowstone consists of approximately 1,500 km^2 of foothills and valley bottoms along the Gardner, Lamar, and Yellowstone rivers in the northern portion of the park and adjacent areas of Montana (Lemke et al. 1998). Descriptions of the climate, topography, vegetation, and diverse predator-prey complex of this range during our study were provided in White & Garrott (2005) and the references cited therein. We used helicopters to conduct counts and classifications (ewes, lambs, rams) of bighorn sheep in their winter ranges during April or May each year during 1995-2005 (Lemke 2005a). Due to visibility bias, these counts provided a variable underestimate of actual abundance, the extent of which was unknown because sightability was not quantified. However, helicopter surveys consistently provided counts of 30-370% more sheep than December-January ground counts in these areas. No count was conducted during 2004 because early spring 'green-up' and migration from winter ranges resulted in poor survey conditions. We interpolated a count of 214 bighorn sheep for that year using the polynomial method of Eberhardt (1987:7) to estimate the relative changes in total population size during 2003-2004.

We first estimated the independent effects of drought, snow pack, elk and wolves on year-to-year changes in population size and recruitment. We considered 1-year lags, squared terms and log-transformed terms because analyses for northern Yellowstone elk indicated these transformations greatly improved model fit (Coughenour & Singer 1996, Taper & Gogan 2002, White & Garrott 2005). We used the Palmer Drought Severity Index (PDSI; Palmer 1968) from the National Climatic Data Center as our warm-season climate covariate because it incorporates multiple environmental factors and is used to gauge growing conditions across the United States. We averaged PDSI over the growing season (1 May through 31 July) across Region 1 of Wyoming. We predicted a positive correlation between PDSI and relative population change because dry years (i.e. low PDSI) would decrease plant production, thereby decreasing fat reserves for sheep entering winter and resulting in lower lamb survival. We used the accumulated daily value of snow water equivalent (SWE_{acc}) during 1 October to 30 April as our cold-season climate covariate because it integrates the depth, density and duration of the snow pack (Garrott et al. 2003). We used SWE_{acc} estimates from the Tower Falls climatological station located in the mid-elevation zone (1,909 m a.s.l.) of the winter range (Farnes et al. 1999). We predicted a negative correlation between SWE_{acc} and relative population change because deep snows would result in less digestible energy intake and more energy expenditure, thereby contributing to lower survival of lambs. We used aerial counts of wolves residing in the northern range each year, including outside the park, compiled by the U.S. Fish & Wildlife Service (2005). Counts during September-December were advanced one year to reflect abundance that winter (e.g. count in December 2005 equals winter 2006). We predicted a negative correlation between wolf numbers and relative population change due to predation and lower sheep survival. Alternatively, a positive correlation between wolf numbers and relative population change could occur if wolves substantially reduced elk numbers and/or distribution because fewer elk would result in less competition for resources and higher digestible energy intake by sheep, thereby contributing to higher survival of lambs. Fewer elk could also result in lower predator densities and less predation on bighorn sheep (Ostovar & Irby 1998). We used aerial counts of elk residing in the northern range each winter and added harvests of elk occurring 1-2 months before the count (White & Garrott 2005; Montana Fish, Wildlife and Parks, unpubl. data).

During 1995-2005, only 1-4 mature rams were harvested each autumn outside the park in the Gallatin and Absaroka Mountains (Montana Fish, Wildlife and Parks, unpubl. data). We ignored these few removals and fit a regression line using least squares procedures on logarithms of the bighorn sheep counts. We then took the exponent of the slope of the regression line to estimate the growth rate of the population following wolf reintroduction (Eberhardt 1985). We also evaluated the relative change in total population size (r_t) during 1995-2005 using basic models for density independence (exponential growth, random walk) and density dependence (Ricker, Gompertz), as described in Jacobson et al. (2004). We used program R version 2.0.0 (R Development Core Team 2004) to fit

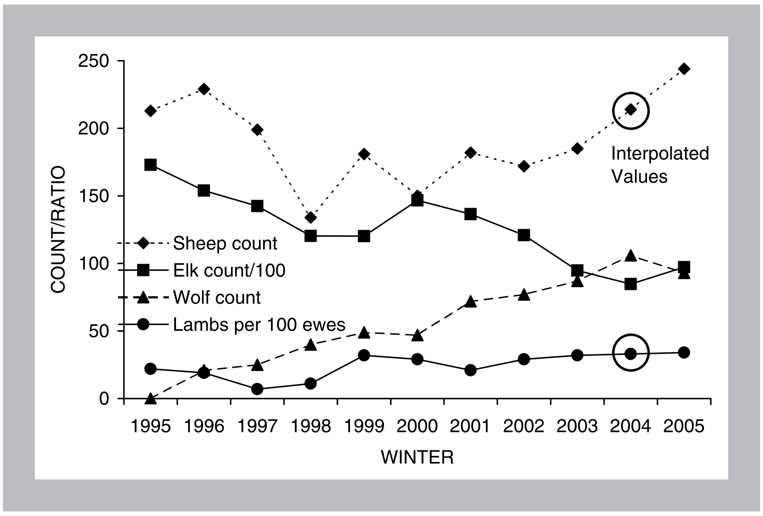

Figure 1. Annual counts of total bighorn sheep, lambs per 100 ewes, elk (divided by 100) and wolves in the northern range of Yellowstone National Park, Montana and Wyoming, USA, during 1995-2005. No count or classification of bighorn sheep occurred during 2004 and circled values for that winter are interpolations.

these population models and Akaike's Information Criteria corrected for small sample size (AIC_c) as model-selection criterion (Burnham & Anderson 1998).

During 1997, we captured 14 adult female and four young (1-3 years old) male bighorn sheep from a primary breeding, wintering and lambing area (Mt. Everts) using net guns from helicopters or ground chemical immobilization with carfentanil (Ostovar 1998). Captured animals were fitted with a radio collar equipped with a motion-sensitive mortality sensor. Telemetry was used to monitor the survival status of radio-collared bighorn sheep every 1-4 months (Ostovar 1998; Yellowstone Center for Resources, unpubl. data). When a mortality signal was detected, the animal was located and cause of death was evaluated. We used program MARK (White & Burnham 1999) to obtain maximum likelihood estimates of survival for radio-collared bighorn sheep between May 1997 and April 2002 under a known fate model with two monitoring intervals (May-October and November-April). We examined the strength of evidence in the data for the following *a priori* survival models: (1) no variation in survival by year or season; (2) survival varied by year, but not season; (3) survival varied by season, but not year; and (4) survival varied by year and season. We used AIC_c as model-selection criterion (Burnham & Anderson 1998).

Results

The number of wolves residing in the northern range, including outside the park, increased from 21 in winter 1996 to 106 by winter 2004 and then decreased to 93 in winter 2005 (Fig. 1). Elk counts during the pre-wolf years of 1982-1995 were consistently high and ranged mostly between 15,000 and 20,000 animals (see Fig. 1). After wolf reintroduction in 1995-1996, the count decreased to approximately 12,000 elk in 1998 following a substantial winterkill and harvests of >3,300 elk outside the park during the severe winter of 1997. Counts increased to 15,000 elk by 2000, but then decreased to 9,000-10,000 elk in 2004-2005. Severe, sustained drought conditions existed during the study, with mean PDSI (May-July) decreasing from 0.9 to -9.0 during 1996-2005 compared to a mean PDSI of -1.0 during 1969-1995 (range: -6.4 - 2.9). The winter of 1997 was severe, with $SWE_{acc} = 1{,}845$ cm being the second highest recorded during 1969-2005 (mean = 951, range: 335-1,931). The winters of 2001-2005 were relatively mild ($SWE_{acc} = 467\text{-}901$ cm).

Counts of bighorn sheep decreased following the severe winter of 1997 and then increased by 7% annually (95% CI: 2-11) during 1998-2005 ($R^2 = 0.72$, $P = 0.02$, df = 6; see Fig. 1). Due to the influential winter of 1997, the relative change in total population size was significantly correlated with the square of SWE_{acc} ($R^2 = 0.38$, $P = 0.06$, df = 9). The relative change in total population size during 1995-2005 provided little support for exponential ($\Delta AIC_c = 3.18$, Akaike weight (w_i) = 0.14, K = 2) or density-dependent models (Gompertz: $\Delta AIC_c = 4.01$, $w_i = 0.09$, K = 3; Ricker: $\Delta AIC_c = 4.41$, $w_i = 0.08$, K = 3). Parameter estimates for the Gompertz ($\hat{a} = 3.53$ (SE = 1.94), $\hat{b} = -0.67$ (SE = 0.37)) and Ricker models ($\hat{a} = 0.68$ (SE = 0.40), $\hat{b} = -0.004$ (SE = 0.002)) were not significantly different from zero, suggesting no density-dependent feedbacks on population growth during 1995-2005. However, values approached significance (P = 0.11 and 0.13, respectively) and suggested a carrying capacity (-a/b) of approximately 190 bighorn sheep, which was identical to the mean count during 1995-2005.

Table 1. Annual variation in counts, ratios of lambs per 100 ewes, relative change in population size and summer and winter climate covariates for bighorn sheep, as well as counts of elk and wolves in the northern winter range of Yellowstone National Park, Montana and Wyoming, during 1995-2005.

Year	Bighorn sheep count[a]	Lambs/ 100 adult females	Change in population size (r^t)[b]	Numbers of		Winter SWE[e] at time t	Drought index[f] at time t-1
				Wolf[c]	Elk[d]		
1995	213	22	0.072	0	17290	1187	-1.64
1996	229	19	-0.140	21		646	0.87
1997	199	7	-0.395	25		1845	-0.13
1998	134	11	0.301	40	12029	721	1.40
1999	181	32	-0.188	49	12018	1066	-2.11
2000	150	29	0.193	47	14663	1109	-3.84
2001	182	21	-0.057	72	13650	467	-4.17
2002	172	29	0.073	77	12096	656	-7.29
2003	185	32	0.146	87	9471	541	-7.48
2004			0.131	106	8471	901	-5.97
2005	244	34		93	9724		-8.92

[a] No count was conducted during 2004, but we interpolated a count of 214 bighorn sheep for that year to estimate the relative changes in total population size during 2003-2004.

[b] Values reflect the relative change in population size (r^t) during time t to time t+1.

[c] Wolf abundance was estimated at the end of each calendar year during September-December. We advanced each count by one year to reflect abundance during the following year. Thus, the count of 106 wolves during December 2003 was used to reflect wolf abundance during the winter and summer of 2004 (i.e. October 2003 - September 2004).

[d] Aerial counts of elk residing in the northern range each winter, with harvests occurring 1-2 months before the count added. No counts were conducted in 1996 and 1997.

[e] Cumulative daily snow water equivalent (SWE) from October through April estimated from temperature and precipitation records at Tower Falls CLIM station. No estimate was available for winter 2005.

[f] The Palmer Drought Severity Index averaged over the growing season (May through July) across Region 1 of Wyoming.

The most supported model in our candidate set was the random walk model ($\Delta AIC_c = -1.8$, $w_i = 0.69$, $K = 1$) owing to the substantial variation in annual growth rates (-0.4 to 0.3) during 1995-2002, despite a relatively small variance in counts (134-244; Table 1).

Recruitment followed a similar temporal pattern, decreasing to 7-11 lambs/100 ewes during the severe winter of 1997 and the following winter, but then increasing to 21-34 lambs/100 ewes during 1998-2005 (slope = 0.030, 95% CI: 0.005-0.056;$R^2 = 0.59$, $P = 0.03$, df = 6). Recruitment was not significantly correlated with SWE in year t or t-1 ($R^2 < 0.18$, $P > 0.22$, df = 8), but was negatively correlated with PDSI in year t and t-1 ($R^2 = 0.62$, $P = 0.007$, df = 9). Bighorn sheep recruitment was also positively correlated with wolf numbers ($R^2 = 0.38$, $P = 0.06$, df = 9), though the 95% confidence intervals (-0.008, 0.38) spanned zero. However, bighorn sheep recruitment was not significantly correlated with decreasing elk numbers ($R^2 = 0.19$, $P = 0.28$, df = 7), and neither elk or wolf numbers were significantly correlated with bighorn sheep numbers during 1995-2005 ($R^2 < 0.06, P > 0.49$).

Causes of death during May 1997 through April 2002 for the 14 adult female and four young (1-3 years old) male bighorn sheep radio-collared during 1997 (Ostovar 1998) were lightning strike (1), mountain lion *Puma concolor* predation (1), natural causes (1), poaching (1) and unknown (4). Three additional animals died during autumn 2002, including two lion predations and one unknown cause. Wolves did not kill any radio-collared sheep. There was considerable support for survival variation by season ($AIC_c = 61.1$, $w_i = 0.79$, $K = 2$) with maximum likelihood estimates equal to 0.91 for May-October (95% CI: 0.82-0.95) and 0.99 for November-April (95% CI: 0.90-1.0). We found less support for the model assuming constant survival (0.94; 95% CI: 0.89-0.97) for all radio-collared bighorn sheep ($\Delta AIC_c = 2.75$, $w_i = 0.20$, $K = 1$). Models assuming survival variation by year ($\Delta AIC_c = 9.46$, $w_i = 0.01$, $K = 5$), and season and year ($\Delta AIC_c = 12.80$, $w_i = 0.001$, $K = 10$), had virtually no support.

Discussion

Wolves in the northern range of Yellowstone exhibited a rapid numerical increase in response to abundant prey (primarily elk) and their protected status during 1995-2005, with densities inside the park reaching one of the highest recorded in the scientific literature (> 50 wolves/1,000 km^2; Smith et al. 2003). However, evidence suggests that the presence of wolves did not prevent the bighorn sheep population from increasing slowly during the decade following reintroduction. Decreased counts and recruitment for bighorn sheep during 1997-1998 were associated with a severe winter in 1997, which led to substantial winterkill of deer and elk (Lemke 1997) and, also, likely contributed to poor maternal condition and high lamb mortality the following year (Ostovar & Irby 1998). During 1998-2005, however, recruitment increased to an average of 30 lambs/100 ewes and there was a slow to moderate rate of increase (95% CI: 2-11) in bighorn counts. Moreover, maximum likelihood estimates of survival for adult bighorn sheep were relatively high (0.94; 95% CI: 0.89-0.97) in the presence of wolves and comparable to the survival of adult ungulates in Europe and areas of North America where predation was minimal (Eberhardt et al. 1982, Eberhardt 1985, Garrott & Taylor 1990, Gaillard et al. 1993, Loison et al. 1994, Skogland 1985, Eberhardt et al. 1996, Toigo et al. 1997, Sibly & Smith 1998).

These findings likely reflect the strong selection of elk as prey by wolves. Elk comprised 89% of wolf kills in winter and roughly 70% of diet biomass during summer, while bighorn sheep comprised < 0.5% of wolf kills during winter and an insignificant portion of their summer diet (Smith et al. 2004, Smith 2005). Small populations of 150-300 bighorn sheep, such as the one we studied, likely cannot support robust populations of large predators, unless those predators rely mostly on other ungulates (Jorgenson et al. 1997). Thus, bighorn sheep in northern Yellowstone may escape attention by wolves because they are much less abundant than elk and inhabit steep, rugged terrain where they are relatively difficult to capture. Despite a 50% decrease in elk counts during 1995-2005, elk are still an abundant source of prey at densities of 7-8 elk/km^2 in the northern range (White & Garrott 2005). There are similar parallels between bighorn sheep and mule deer as alternate prey species for Yellowstone wolves. Wolf recovery seemed to have little influence on mule deer numbers and recruitment (Lemke 2005b).

Our findings may also reflect the comparatively lower density of wolves (< 20 wolves/1,000 km^2) on major sheep winter ranges along the northwest park boundary and outside the park used by 75-85% of northern Yellowstone sheep during 1995-2005 (Lemke 2005a, Smith 2005). Wolves are at much lower densities in these areas where human-induced mortalities (e.g. vehicle strikes) are more frequent and wolves can be culled if they prey on livestock. For example, 26 wolves were removed during 1999-2004 from the Sheep Mountain pack near the Paradise Valley of Montana owing to livestock depredation (U.S. Fish & Wildlife Service 2005). As a result, bighorn sheep wintering in the boundary area and outside the park are less likely to face intense wolf predation.

Bighorn sheep numbers have not recovered from the pinkeye outbreak in 1982 and factors other than wolf predation appear to be limiting recruitment and population growth. Many bighorn sheep populations wintering at high elevations are small, slow growing and low in productivity; despite their high reproductive potential (Beuchner 1960, Stevens & Goodson 1993, Wishart et al. 1998). Adult survival is little affected by changes in population density and, as a result, year-to-year variations in lamb and yearling survival profoundly affect population dynamics (Jorgenson et al. 1997). Thus, low recruitment due to density independent factors can limit the ability of high-elevation populations to respond to drastic decreases in abundance caused by disease epizootics, severe stochastic weather events or removals.

Interspecific competition with the high densities of elk (14-16/km^2) in the northern range during 1982-1995 may have limited the ability of the northern Yellowstone bighorn sheep population to recover from the pinkeye outbreak, especially during severe winters. Singer & Norland (1994) reported substantial overlap in diets and spatial use by elk and bighorn sheep on the northern range during this period, which possibly resulted in decreased *per capita* intake rates and increased risks of predation for sheep during foraging. Also, Ostovar & Irby (1998) suggested that large numbers of elk wintering along the northern boundary of Yellowstone provided a source of carrion for high densities of coyotes *Canis latrans*, golden eagles *Aquila chrysaetos* and mountain lions that switched to preying on bighorn sheep in summer. Thus, decreased elk numbers due to their avoidance of, or predation by, a recovered wolf population could actually benefit sheep by reducing competition for resources and the risk of predation; thereby enabling an increase in sheep recruitment.

During the decade following wolf reintroduction, elk numbers decreased by 50% while counts of bighorn sheep indicated a fairly consistent, slow rate of increase after the severe winter of 1997. Thus, it is enticing to suggest that the positive correlation between wolf numbers and bighorn sheep recruitment during 1995-2005 reflects decreased competition for resources between elk and sheep due to decreased elk abundance and changes in elk distribution following wolf reintroduction. However, we strongly caution against inferring or predicting the possible effects of decreased elk numbers on bighorn sheep following wolf reintroduction based on a short time series of observations interrupted by a major stochastic event (i.e. severe winter of 1997). Annual variation in population growth was substantial and was affected by latent factors, which limited insights that could be gained via formal analysis. Also, we did not detect significant relationships between numbers of bighorn sheep or recruitment and numbers of elk, similar to Ostovar & Irby (1998) who could not detect a causal relationship between increasing elk numbers and low bighorn sheep numbers on the Mt. Everts winter range during the 1980s and 1990s. Continued monitoring across a greater range of bighorn sheep densities should enable a more rigorous evaluation of critical influential factors and autocorrelation effects (i.e. time lags) on the population growth and recruitment of Yellowstone bighorn sheep.

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