

Optimal predator management for mountain sheep conservation depends on the strength of mesopredator release

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Large predators often suppress ungulate population growth, but they may also suppress the abundance of smaller predators that prey on neonatal ungulates. Antagonistic interactions among predators may therefore need to be integrated into predator–prey models to effectively manage ungulate–predator systems. We present a modeling framework that examines the net impact of interacting predators on the population growth rate of shared prey, using interactions among wolves *Canis lupus*, coyotes *Canis latrans* and Dall sheep *Ovis dalli dalli* as a case study. Wolf control is currently employed on approximately 16 million ha in Alaska to increase the abundance of ungulates for human harvest. We hypothesized that the positive effects of wolf control on Dall sheep population growth could be counteracted by increased levels of predation by coyotes. Coyotes and Dall sheep adult females (ewes) and lambs were radiocollared in the Alaska Range from 1999–2005 to estimate fecundity, age-specific survival rates, and causes of mortality in an area without wolf control. We used stage-structured population models to simulate the net effect of wolf control on Dall sheep population growth (λ). Our models accounted for stage-specific predation rates by wolves and coyotes, compensatory mortality, and the potential release of coyote populations due to wolf control. Wolves were the main predators of ewes, coyotes were the main predators of lambs, and wolves were the main source of mortality for coyotes. Population models predicted that wolf control could increase sheep λ by 4% per year in the absence of mesopredator release. However, if wolf control released coyote populations, our models predicted that sheep λ could decrease by up to 3% per year. These results highlight the importance of integrating antagonistic interactions among predators into predator–prey models, because the net effect of predator management on shared prey can depend critically on the strength of mesopredator release.

Populations of large carnivores have been eliminated or greatly reduced in many areas due to habitat loss and conflicts with humans, and the consequential weakening of top–down effects has triggered trophic cascades throughout the world (Estes et al. 2011). Despite a long history of persecution, the distributions of large predators such as wolves *Canis lupus* and cougars *Puma concolor* are expanding, fueling heated clashes among scientists, policy makers and the public about how to best manage these species. The ability of large predators to suppress populations of their ungulate prey has been well demonstrated (Gasaway et al. 1983, White and Garrott 2005). Large predators may also suppress the abundance of mesopredators (Crooks and Soulé 1999, Ritchie and Johnson 2009, Levi and Wilmers 2012), but evidence of suppression and cascading effects on prey is often circumstantial (Prugh et al. 2009). Because mesopredators such as coyotes *Canis latrans* also prey on neonatal ungulates, the net effect of large predator abundance on shared ungulate prey is difficult to predict. Successful wildlife conservation in these changing landscapes therefore requires a better understanding of the interactions among large predators, mesopredators, and their shared prey.

Triangular interaction motifs such as intraguild predation and apparent competition are common in food webs and can strongly influence community structure and stability (Polis and Strong 1996). Unlike apparent competition theory, which has been applied extensively to wildlife management and conservation (DeCesare et al. 2010), intraguild predation theory has remained largely in the theoretical realm with few empirical tests or applications (Novak 2013). In a review of mesopredator release, Brashares et al. (2010) found that 40% of documented apex–mesopredator–prey interactions were triangular (involving shared predation) rather than classic linear cascades. When large predators and mesopredators share prey, intraguild predation theory predicts that extirpation of the large predator could negatively impact prey because the mesopredator should be a more efficient consumer (Polis et al. 1989). Despite the potential for intraguild predation to strongly affect ungulate–predator dynamics, no studies have examined the effect of intraguild predation on populations of shared ungulate prey.

Current models of intraguild predation ignore prey age structure and implicitly assume that all prey individuals are subject to identical predation regimes (Vance-Chalcraft

et al. 2007). However, nearly all animal species have different predation regimes on juveniles and adults. In an analysis of four predators preying on two ungulate species in Scandinavia, Gervasi et al. (2012) found the age composition of targeted prey was more important than overall kill rates in predicting predator impacts on prey population growth. When the main predators of different life stages interact, stage-structured models that account for these interactions are needed to accurately predict the response of prey to changes in predator abundance. In this paper, we use empirical data and stage-structured population models to examine the potential direct and indirect effects of reducing wolf abundance (hereafter, 'wolf control') on Dall sheep *Ovis dalli dalli* population growth, accounting for stage-specific predation and mesopredator release (Fig. 1).

Wolves are now considered fully recovered in parts of the western United States and subject once again to harvest (Way and Bruskotter 2012). In Alaska, eight wolf control programs are currently active, covering 165 736 km² (Alaska Dept of Fish and Game, <www.adfg.alaska.gov/index.cfm?adfg=intensivemanagement.programs>, accessed 9 September 2013). These programs are intended to increase designated populations of moose *Alces alces* and caribou *Rangifer tarandus* by reducing wolf abundance to specified levels, and past efforts have generally succeeded (Gasaway et al. 1983, Boertje et al. 1996, Keech et al. 2011). However, the broader impacts of wolf control on mesopredator populations and other prey species, such as Dall sheep, remain unknown.

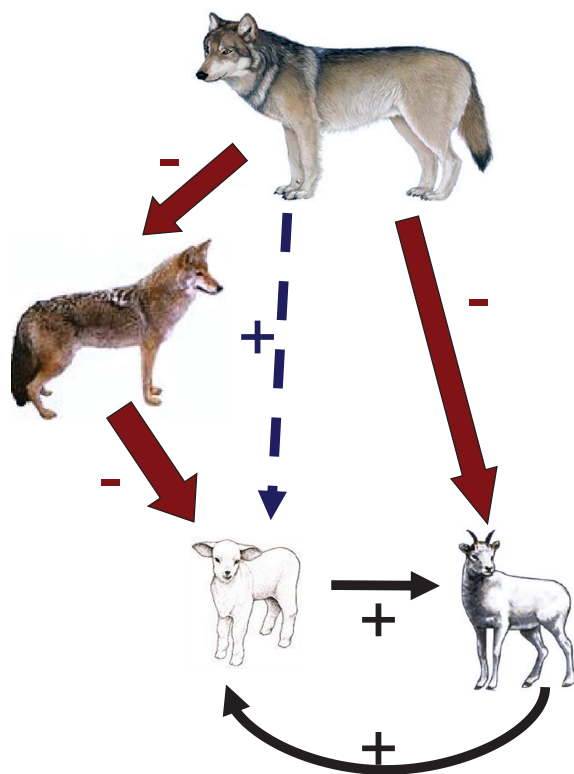


Figure 1. Hypothesized relationships among wolves (top), coyotes (middle), Dall sheep lambs (lower left), and adult Dall sheep (lower right). Negative arrows indicate negative effects on population growth and positive arrows indicate positive effects. The dashed arrow from wolves to lambs indicates an indirect positive effect through suppression of coyotes.

Gasaway et al. (1983) reported that lamb survival rates decreased during a wolf control program in central Alaska and did not decline as sharply in nearby Denali National Park (where wolves are protected), but the net effect of wolf control on Dall sheep population growth was not assessed. Likewise, Hayes et al. (2003) found that moose and caribou responded positively to wolf control in the Yukon Territory, but Dall sheep did not.

Mountain sheep have a K-selected life history strategy, with high adult survival rates, low reproductive rates, and highly variable juvenile survival rates (Loison et al. 1999, Coulson et al. 2005). Structured population models generally show that population growth rates (λ) of K-selected ungulates are highly sensitive to changes in adult survival and less sensitive to changes in juvenile survival (Rubin et al. 2002), but juvenile survival rates generally are more variable and thus have a greater capacity for increase (Mills et al. 1999, Johnson et al. 2010). Our previous work and other studies have found that wolves are important predators of adult Dall sheep and coyotes are important predators of lambs (Murie 1944, Hoefs and Cowan 1979, Arthur and Prugh 2010). We therefore used a life stage simulation analysis to determine whether Dall sheep λ would be affected more by changes in predation by wolves or coyotes, taking into account differences in both the mean and variation of cause-specific mortality rates (Wisdom et al. 2000). Because the response of coyote populations to wolf control has not been documented, we evaluated a range of scenarios to identify conditions under which wolf control would lead to net increases or decreases in sheep λ . More generally, we present a modeling framework that can be used to examine the net impact of interacting predators on the population growth rate of shared prey while accounting for stage-specific differences in predation rates.

Methods

Study area

Fieldwork for this study was conducted from 1999–2005 in the central Alaska Range (63°57'N, 147°18'W). The study area encompassed 1300 km² of mountains and foothills on the northern edge of the range. Topography was rugged, with elevation ranging from 500–2400 m. Dall sheep habitat consisted of alpine meadows and bare rock at higher elevations (1000–2100 m), which made up 41% of the study area.

Wolf control programs were conducted in our study area and adjacent lowlands during the 1950s, 1976–1982 and 1993–1994 (Gasaway et al. 1983, Boertje et al. 1996, Valkenburg et al. 2004). The wolf population was reduced to 40% of pre-control density during the winters of 1993 and 1994 but rebounded to 91% of pre-control density by 1995 (Valkenburg et al. 2004). Coyote density in our study area was estimated to range from 1.4–2.5 per 100 km² from 1999–2002 (Prugh et al. 2005), an order of magnitude lower than estimates in the Rocky Mountains (Berger and Gese 2007). Wolf density was estimated to be 11.7 per 1000 km² in our study area during winter 2000–2001 (Young 2003). Density of Dall sheep ranged from 0.94–1.3 per km² during our study, well below peak densities of 1.9–2.4 sheep

per km² recorded from 1967–1984 in the study area (Arthur and Prugh 2010).

Radiocollaring

We fitted adult female sheep (ewes ≥ 3 years old), lambs (0–3 days old), and coyotes with VHF radiocollars. Lamb collars were expandable with a battery life of 1–1.5 years, and collars for ewes and coyotes had a battery life of 3–4 years. For details of capture and collaring methods, see Arthur and Prugh (2010). Mortalities were investigated to determine cause of death based on predator tracks, feces, tooth marks, blood on collars, and other signs. When kills were visited by more than one predator, or if signs were inconclusive regarding species of predator, we classified the cause as unknown predation. Capture and handling procedures followed animal care standards recommended by the American Society of Mammalogists (Sikes et al. 2011).

Estimation of Dall sheep demographic parameters

Annual estimates of fecundity were derived from pregnancy rates of collared ewes. Pregnancy status was determined by progesterone assay of serum samples (Brundige et al. 1988). Because samples were obtained during the final two months of pregnancy, we assumed pregnancy and birth rates were identical (i.e. there were no fetal losses). Twinning in Dall sheep is extremely rare (Hoefs 1978, Simmons et al. 1984) and was never observed in our study, so we assumed all pregnant ewes produced a single lamb. We examined pregnancy rates in relation to age and found no evidence of reproductive senescence. For example, the 10 oldest ewes (12–14 years old) in our sample were pregnant each year.

Our sample of young ewes was insufficient to determine the age of first reproduction. Previous studies reported first reproduction at 2–4 years, but cases of two-year olds giving birth were rare (Nichols 1978, Bunnell and Olsen 1981, Hoefs and Nowlan 1993). Thus, we set the age of first reproduction at three years. We used a constant fecundity rate for 3+ year old ewes, defined as the number of female offspring per ewe per year. We assumed an equal sex ratio at birth (Simmons et al. 1984) and multiplied pregnancy rates of collared ewes by 0.5 to estimate fecundity.

Ewe survival rates were estimated from our sample of collared animals. The numbers and ages of at-risk ewes were recorded each year, along with the numbers, ages, and causes of death of ewes that died. Our previous analyses indicated that survival rates did not differ significantly among years (Arthur and Prugh 2010). We therefore pooled data for each age class over the 6-year study to calculate age-specific survival rates using the Kaplan–Meier method (Kaplan and Meier 1958). Kaplan–Meier is a non-parametric survival estimator that accounts for staggered entry of animals into the collared sample and censoring of animals from the sample (e.g. due to collar failure). Following Loison et al. (1999), we fit a quadratic curve to the estimated age-specific survival rates. This curve fit the data well ($R^2 = 0.77$, Fig. 2) and was similar to the curves for five ungulate populations reported in Loison et al. (1999).

We used a cumulative incidence function (CIF) model of competing risks to calculate cause-specific mortality rates

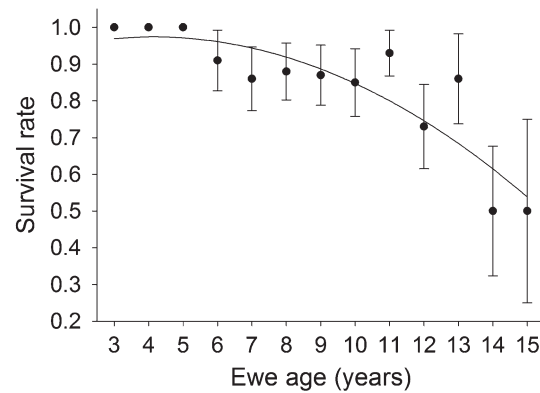


Figure 2. Age-specific survival rates of adult female Dall sheep (ewes) in the Alaska Range. Rates were calculated from a sample of 31 ewes monitored from 1999–2005, for a total of 117 ewe-years. Standard error bars are shown.

(Heisey and Patterson 2006). The CIF model is a type of Kaplan–Meier analysis that calculates separate mortality rates for each cause of death. This method is preferable to simple binomial estimates (i.e. dividing numbers dying of each cause by the collared sample size) because the CIF model accounts for staggered entry and censoring, resulting in more accurate and precise estimates of mortality rates (Heisey and Patterson 2006). Cases in which cause of death could not be definitively assigned were censored ($n = 7$ ewes and 17 lambs). Censoring reduces precision of estimates but should not result in bias, assuming the causes of mortality for censored animals were proportional to known causes. The proportions of unknown-caused deaths with coyote or wolf sign present were similar to the proportions of sheep known to have been killed by these predators.

Ewe mortality data were too sparse to use a fully age-structured CIF model. The age-structured Kaplan–Meier survival model showed that survival decreased non-linearly with age (Fig. 2), and we therefore grouped ewes into ‘young’ and ‘old’ age classes. We sequentially increased the age cut-off for ‘old’ ewes from 7–12 years and found that mortality rates did not change appreciably until the cutoff reached 12 years (Supplementary material Appendix 1 Fig. A1). Cause-specific mortality rates were therefore estimated for lambs (age < 1 year), ‘young’ ewes (age 3–11), and ‘old’ ewes (age 12+), with causes classified as wolf, coyote, or other (e.g. other predator, disease, accident). CIF models were run using the ‘etm’ package in R, which allows for right and left censoring (Allignol et al. 2011).

Dall sheep population model

We constructed a female-only post-birth-pulse matrix with four stages: lambs (age 0–1), pre-breeding ewes (ages 1–2), young ewes (age 3–11), and old ewes (age 12+):

$$\begin{bmatrix} 0 & 0 & f * s_y & f * s_o \\ s_j & (1 - t_y) * s_y & 0 & 0 \\ 0 & t_y * s_y & (1 - t_o) * s_y & 0 \\ 0 & 0 & t_o * s_y & s_o \end{bmatrix}$$

Where f = fecundity, s_j = survival of lambs, s_y = survival of pre-breeding and young ewes, s_o = survival of old ewes,

t_y = probability of transitioning from a pre-breeding ewe to a young ewe, and t_o = probability of transitioning from a young to an old ewe. Transition probabilities were calculated as the inverse of the number of years that ewes remained in multi-year stages ($t_y = 0.5$, $t_o = 0.11$). Survival rates were calculated as a function of the cause and stage-specific mortality rates obtained from the CIF model:

$$s_i = 1 - \text{wolf}_i - \text{coyote}_i - \text{other}_i$$

Where i = stage class of sheep ($i = j$ for lambs, y for young ewes, and o for old ewes) and wolf, coyote, and other refer to the causes of mortality. We used an additive rather than a multiplicative equation (sensu Gervasi et al. 2012) because multiplying mortality risks from competing causes overestimates survival when mortality rates are high (Lebreton 2005). The population growth rate, λ , was calculated as the dominant eigenvalue of the matrix.

Monte Carlo simulations were used to estimate the mean and variance of λ . For each simulation, parameter values for fecundity and mortality were obtained by drawing random values from the beta distribution with means and standard deviations obtained from annual estimates of fecundity and the CIF model of cause-specific mortality (Table 1). Morris and Doak (2002) recommend removing sampling variance prior to simulations. However, this procedure requires dividing data among years, and our data were too sparse because we modeled separate causes of mortality as well as age classes. Our variance estimates therefore included both sampling and process variance. The Leslie matrix was constructed using the randomly drawn parameter values and simulations were run 10 000 times. Scripts were written to conduct these analyses using the 'popbio' package in Program R (Stubben and Milligan 2007). This model served as the baseline population model for Dall sheep under conditions of light human harvest (limited to mature males) and unmanaged predator populations (also subject to light human harvest).

Simulating effects of wolf control

Because the density of wolves was stable during our study, we could not empirically examine the effects of wolf control on coyotes or Dall sheep. We therefore created a

Table 1. Parameter estimates and associated standard deviations used to construct the baseline stage-structured Leslie matrix model of a Dall sheep population in Alaska. Fecundity = no. females born per ewe per year. Coyote, wolf, other = proportion of sheep killed by coyotes, wolves, and other causes each year within each sheep stage class.

Stage class	Parameter	Mean	SD
Young and old ewes (3 + years)	fecundity	0.44	0.036
	coyote	0.26	0.044
	wolf	0.02	0.013
	other	0.38	0.058
Young ewes (3-11 years)	coyote	0	–
	wolf	0.05	0.024
	other	0.02	0.015
	coyote	0	–
Old ewes (12 + years)	wolf	0.18	0.080
	other	0	–
	coyote	0	–

range of plausible scenarios by constructing models where wolf and coyote-caused predation rates were changed by varying amounts.

Wolf-caused mortality

Wolf control programs typically reduce wolf densities by 50–80% (Gasaway et al. 1992, Keech et al. 2011). Our scenarios assumed an 80% reduction in wolf density to simulate the maximum potential benefit of wolf control to Dall sheep. However, wolf-caused mortality may be partially compensatory (i.e. some sheep that would have been killed by wolves may instead die of other causes). To determine the likelihood that wolf predation was compensatory, we examined the mortality risk of collared ewes in relation to body condition at the start of each year. During March captures and recaptures, ewe body condition was assigned a score based on subjective classification of body fat thickness assessed by palpating the shoulders, ribs and hips (Gerhart et al. 1996). This index ranged from 1 (poor: no detectible subcutaneous fat, bones easily palpable on ribs, hips, and shoulders), to 5 (excellent: thick padding of fat in all three regions). We ran a Cox proportional hazards model using the 'Surv' function in program R to test for an effect of body condition on risk of wolf-caused mortality. Based on these results and the fact that most wolf-killed sheep were 12 + years old, our wolf control scenarios assumed half the sheep that would have been killed by wolves would instead have died from other causes. Our scenarios therefore reduced wolf-caused mortality by 80% and re-allocated half of the wolf kills to 'other' mortality (i.e. 40% of wolf mortality was assigned to 'other' mortality and 40% was eliminated) to simulate compensatory mortality. We did not re-allocate any wolf-caused mortality to coyotes because wolves and coyotes preyed almost exclusively on different life stages of sheep.

Coyote-caused mortality

The degree to which coyote predation rates may increase due to wolf control depends on relationships between: 1) coyote and wolf density, and 2) coyote density and predation rates on sheep. We used data from our study and Berger and Gese (2007) to create scenarios for these indirect effects. Although wolf density was stable during our study, coyote density decreased by 43% (from 2.5 to 1.4 per 100 km²) due to a six-fold decline in snowshoe hare abundance (Prugh et al. 2005). The annual proportion of collared lambs killed by coyotes decreased by 58% during this period (from 36% to 22%; Arthur and Prugh 2010). These changes were similar to patterns of coyote abundance and pronghorn *Antilocapra americana* fawn mortality in relation to wolf abundance in Wyoming, where coyote density was 40% lower in wolf-abundant compared to wolf-free sites and coyote predation on pronghorn fawns was 52% lower where wolves were abundant (Berger and Gese 2007, Berger and Conner 2008). Based on these results, we examined scenarios where our observed coyote predation rates were increased by 0, 20, 40, 60 or 80%. This range represents realistic limits to the magnitude of mesopredator release and reflects the high degree of uncertainty due to sparse empirical data.

Our five wolf control scenarios combined the altered coyote predation rates with the altered wolf and other predation rates described above. Dall sheep population models were

run as described for the baseline population model, with new mortality rates based on each scenario (Supplementary material Appendix 1).

Life-stage simulation analysis

We conducted a life-stage simulation analysis to examine the impact of changes to cause-specific predation rates on sheep λ , while accounting for variability and correlations among rates (Wisdom et al. 2000). We calculated correlations among each of the 'vital' rates used in the matrix model (i.e. fecundity and causes of mortality) during our six-year study. Because our sample sizes within individual years were limited, these correlations should be interpreted with caution. We therefore ran all models both with and without correlation among rates. We used the method described in Morris and Doak (2002, p. 282–286) to convert random uncorrelated beta values into correlated beta values for use in the Leslie matrix. The sensitivity and elasticity of λ to each matrix element was calculated using the 'eigen.analysis' function in popbio during each of the 10 000 simulation runs, and means and variances were calculated. We also calculated the elasticity of λ to each cause of mortality to test the hypothesis that λ would be more sensitive to changes in wolf predation than coyote predation. Elasticity to lower-level factors (i.e. causes of mortality) were calculated using the 'vitalsens' function in popbio during each simulation run, and means and variances were calculated. Elasticity values for wolf and coyote-caused mortality were summed across stage classes to estimate the total impact of each predator on sheep λ (Gervasi et al. 2012). The variation in λ explained by each 'vital' rate was estimated by calculating R^2 values from simple linear regressions of each rate and λ across the 10 000 simulation runs (Wisdom et al. 2000). Analyses were conducted for the baseline sheep model and the five wolf control scenarios.

Results

Rates and causes of mortality

We radiocollared a total of 31 adult female Dall sheep (ewes) and maintained annual samples of 15–24 at-risk ewes from 1999–2005, for a total of 117 ewe-years. Survival rates declined with age, and no mortalities were observed among collared ewes age 3–5 years (Fig. 2). A total of 18 ewes died during the study, and wolves were responsible for 82% of known-caused mortality (Table 2). Wolf sign was present at all six kill sites where the cause of predation could not be definitively assigned. Coyotes did not kill any collared ewes, and coyote presence was not detected at any kills attributed to unknown predators. On average, wolves killed 5% of young (age 3–11) ewes and 18% of old (age 12+) ewes per year (Table 2). Ewes with poorer body condition indices had a higher risk of wolf-caused mortality ($z = -2.07$, $p = 0.039$, $n = 79$; Fig. 3), indicating that wolf predation may have been partially compensatory.

We monitored the survival of 17–21 radiocollared lambs per year from 1999–2004 (total $n = 119$). A total of 82 lambs died, and 90% of deaths were attributed to

Table 2. Causes of mortality for radiocollared Dall sheep lambs and ewes in the Alaska Range, 1999–2005. Numbers of individuals are shown.

Cause of death	Lambs	Ewes
Coyote	29	0
Golden eagle	22	0
Wolf	3	9
Wolverine	5	1
Grizzly bear	0	1
Accident/disease	6	0
Unknown cause	2	1
Unknown predator	15	6
Total mortality	82	18
No. collared	119	31

predation (Table 2). Coyotes were the main predator of lambs, responsible for 45% of known-caused mortality (29 deaths), whereas wolves were responsible for 4.6% of known-caused mortality (3 deaths; Table 1). Coyote sign was present at seven of the 15 lamb deaths attributed to unknown predators. On average, coyotes killed 26% and wolves killed 2% of collared lambs each year (Table 2).

We monitored a total of 17 radiocollared coyotes and maintained annual samples of 5–11 at-risk coyotes from 1999–2005, for a total sample of 52 coyote-years. Annual survival rates ranged from $0.68–1.0 = 0.83$, $SE = 0.04$). A total of eight coyotes died during the study. Three were killed by wolves, two died from unknown causes (wolf or bear predation was suspected), one pregnant female died from septicemia resulting from a ruptured uterus, one emaciated coyote died from injuries related to ingestion of porcupine quills, and one was trapped.

Simulated effects of wolf control

The population growth rate (λ) of Dall sheep estimated from our baseline model was 1.005 (95% $CI = 0.93–1.07$), indicating the population was stable during our study. Including correlations among vital rates had negligible effects on results despite strong correlations among some rates (Table A1). For example, λ for the baseline model without including correlations was 1.002 (95% $CI = 0.92–1.07$). Elasticity analyses

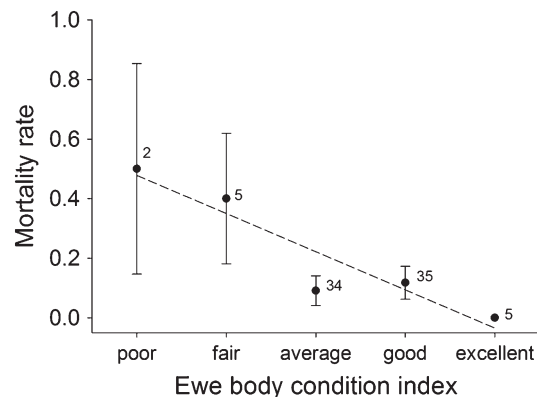


Figure 3. Effect of body condition on the probability of wolf-caused mortality for adult female Dall sheep (ewes) in the Alaska Range, 1999–2005 ($n = 79$ ewe-years). Numbers indicate sample sizes for each condition index. Standard error bars are shown.

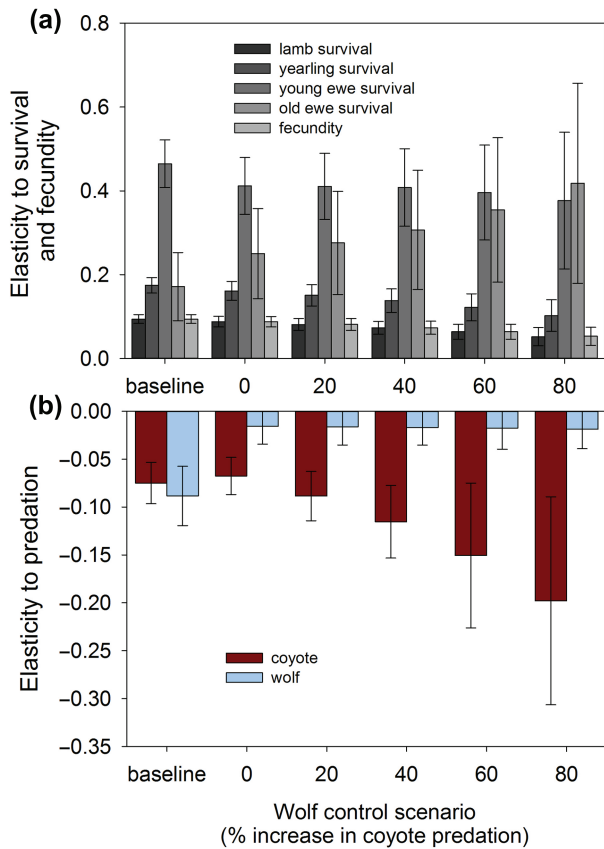


Figure 4. Elasticity of Dall sheep population growth (λ) to (a) changes in survival of sheep stage classes and fecundity, and (b) changes in cause-specific mortality rates summed across stage classes. The baseline scenario used average rates observed without wolf control in the Alaska Range, 1999–2005. All wolf control scenarios decreased baseline wolf predation rates across all stage classes by 80% and allocated half of the reduced wolf predation to ‘other’ predation (to account for compensatory mortality). Wolf control scenarios increased coyote predation rates by 0–80%. Standard error bars are shown.

indicated that λ was most strongly affected by changes in young ewe survival and least affected by changes in lamb survival and fecundity (Fig. 4a). Elasticity to survival of old ewes increased and elasticity to survival of lambs decreased as levels of coyote predation increased in the wolf control scenarios (Fig. 4a). Elasticity analysis of lower-level factors revealed that wolf and coyote predation had similar effects on λ in the baseline scenario (summed elasticity = -0.09 and -0.07 for wolves and coyotes, respectively), and elasticity to coyote predation increased and became more variable as levels of coyote predation increased in wolf control scenarios (Fig. 4b). Wolf predation on young ewes explained the greatest amount of variation in λ in the baseline scenario ($R^2 = 0.38$) despite low variability in young ewe survival and low rates of wolf predation. In contrast, coyote predation on lambs explained only 11% of variation in λ despite high variability in lamb survival and high rates of coyote predation (Table 3). Across all wolf control scenarios, variation in mortality by wolves and other causes explained more variation in λ than did variation in coyote-caused mortality (Table 3).

Simulations indicated that wolf control would lead to a net increase in sheep λ if release of coyote popula-

tions resulted in $\leq 40\%$ increase in coyote predation. A net decrease in sheep λ was predicted if coyote predation increased by $\geq 60\%$ (Fig. 5). Without mesopredator release, wolf control was predicted to increase in sheep λ by 4% (Fig. 5). With mesopredator release, wolf control could reduce sheep λ by up to 3% assuming the maximum (80%) increase in coyote predation. Limited empirical data suggest that a 50–60% increase in coyote predation due to wolf control may be the most realistic scenario, and our models suggest mesopredator release in this case would roughly cancel out the benefits of wolf control, leading to no net change or a slight decline in sheep λ (Fig. 6).

Discussion

Our study indicates that reducing the abundance of large predators to increase population growth of ungulates could produce opposite results if control efforts release mesopredator populations and lead to increased predation on neonates (Fig. 1). Wolf management is among the most controversial of wildlife management issues worldwide, with implications for management of other large predators. Using a range of realistic scenarios, we found that wolf control could lead to net increases or declines in Dall sheep population growth (λ), depending on the strength of mesopredator release. These findings highlight the importance of considering stage-specific differences in predation regimes and the potential for mesopredator release when evaluating predator management plans. Our models also highlight the importance of quantifying the strength of mesopredator release, as the response of coyotes to weakened top-down control was a key unknown that critically impacted the net effect of simulated wolf control on Dall sheep populations (Fig. 5). Confidence intervals were wide in all scenarios, indicating the ability to predict the effect of wolf control on sheep λ in any given year would be poor (Fig. 5, 6). These scenarios are therefore most useful in exploring how different levels of mesopredator release would likely affect the long-term trend in sheep λ .

In general, the triangular intraguild predation motif should weaken the impact of fluctuations in large predator abundance on prey, because the direct effects of large predators are counteracted by opposing indirect effects via mesopredators (Fig. 1). As expected, our simulations showed that mesopredator release has the potential to reduce the benefit of wolf control to Dall sheep populations. Intraguild predation is widespread in ecosystems (Arim and Marquet 2004) and may increase the resistance of prey populations to predator management.

Consistent with predictions of intraguild predation theory (Polis et al. 1989), coyotes were more efficient predators than wolves, killing three times as many sheep during our study as did wolves. Despite this efficiency, we expected stage-specific predation to reduce the relative importance of coyote predation because ungulate λ is thought to be more sensitive to changes in adult female (ewe) survival than neonate survival (Rubin et al. 2002). Conversely, lamb survival was more variable among years than ewe survival was (Arthur and Prugh 2010), indicating that lamb survival had greater potential to respond strongly to predator management. Modeling survival as a function of cause-specific mortality directly in

Table 3. Variation in Dall sheep population growth (λ) explained by each 'vital' rate in the matrix model. R^2 values from regressing each rate against λ across the 10 000 Monte Carlo runs for each scenario are shown. Predation by coyotes, wolves, and other predators on each stage class of sheep as well as the total effect across age classes are shown. Coyotes preyed on lambs only. The baseline scenario used average mortality rates observed without wolf control in the Alaska Range, 1999–2005. All wolf control scenarios decreased baseline wolf predation rates across all stage classes by 80% and allocated half of the reduced wolf predation to "other" predation (to account for compensatory mortality). Wolf control scenarios increased coyote predation rates by 0–80%.

Scenario	Coyote Lambs	Wolf				Other				Fecundity Ewes	Grand total
		Lambs	Young ewes	Old ewes	Total	Lambs	Young ewes	Old ewes	Total		
Baseline	0.11	0.01	0.38	0.08	0.47	0.20	0.18	0	0.38	0.003	0.97
0%	0.13	0.01	0.26	0.11	0.38	0.22	0.19	0.05	0.45	0.001	0.97
20%	0.14	0.02	0.23	0.12	0.37	0.25	0.15	0.05	0.45	0.002	0.95
40%	0.15	0.01	0.17	0.14	0.32	0.28	0.15	0.05	0.49	0.001	0.96
60%	0.18	0.03	0.11	0.14	0.28	0.32	0.11	0.05	0.49	0.001	0.95
80%	0.21	0.02	0.07	0.16	0.25	0.36	0.07	0.06	0.49	0.0003	0.95

the population matrix allowed us to directly compare the effects of wolf and coyote predation on sheep λ using a life-stage simulation analysis (LSA; Wisdom et al. 2000). Results of the LSA were mixed. Regressions showed that wolf predation rates explained more variation in sheep λ than did coyote predation. However, the elasticity of λ to predation by coyotes and wolves was similar under baseline conditions, and elasticity to coyote predation was substantially higher than elasticity to wolf predation in all wolf control scenarios (Fig. 4b). Sheep λ was most sensitive to changes in young ewe survival, which was the life stage least impacted by predation. Wolf predation was concentrated primarily on older ewes, thereby reducing the importance of wolf predation to sheep λ . Large predators often selectively prey on very young and very old individuals, with lower predation rates on 2–10 year old ungulates (Loison et al. 1999, Hayes et al. 2000). The sensitivity of ungulate λ to predation on adults can therefore be overestimated if young and old adults are not differentiated.

In addition to examining the magnitudes of stage-specific mortality rates, the degree of additivity of each rate is an

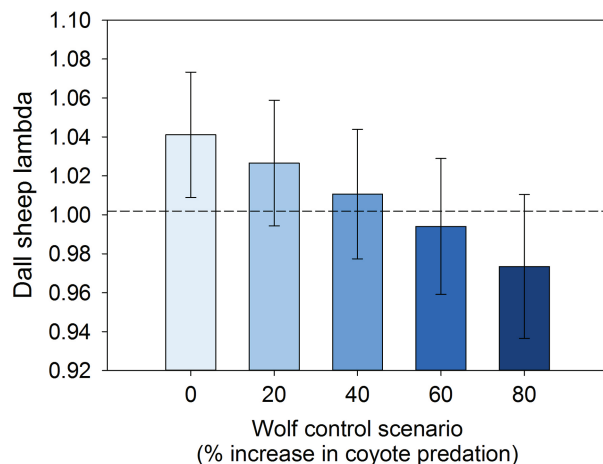


Figure 5. Simulated effects of wolf control on the population growth rate (λ) of Dall sheep. Dashed line shows the baseline λ (1.005) in the absence of wolf control. All wolf control scenarios decreased baseline wolf predation rates across all stage classes by 80% and allocated half of the reduced wolf predation to 'other' predation (to account for compensatory mortality). Wolf control scenarios increased coyote predation rates by 0–80%. Standard error bars are shown.

important consideration in determining the net impact of multiple predators on shared prey populations. The impact of each mortality source on stage-specific survival rates and λ depends partially on the degree to which each source is additive (Sandercock et al. 2011). We found that ewes in poorer body condition were at higher risk of mortality, and wolf predation was concentrated on ewes age 12 and older. These results support other studies indicating that wolf predation can be largely compensatory (Tveraa et al. 2003, Vucetich et al. 2005; but see Hayes et al. 2003).

Wolves are important predators of moose, caribou and elk *Cervus canadensis* neonates (Valkenburg et al. 2004, White and Garrott 2005, Keech et al. 2011), but we found they preyed infrequently on Dall sheep lambs. Lambs may be so small, rare, and difficult to catch in steep terrain that they are of little value as prey for wolves. In contrast to wolves, coyote predation was concentrated on lambs. Coyote-caused lamb mortality decreased by 58% during our study because coyote populations declined in response to the snowshoe hare cycle

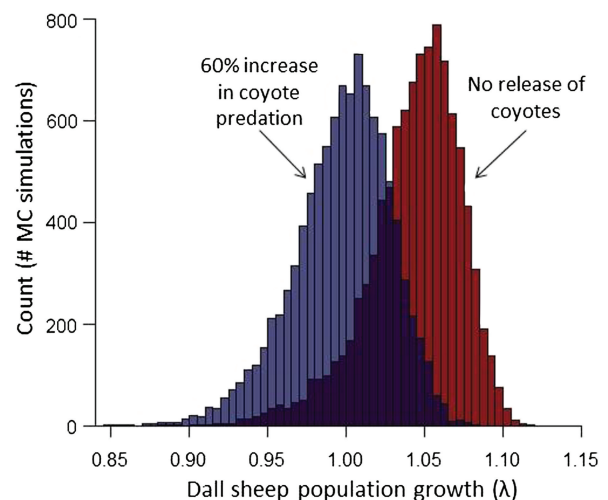


Figure 6. Histograms of estimated Dall sheep population growth (λ) from 10 000 Monte Carlo simulations of Leslie matrix models. Results from two wolf control scenarios are shown: 60% increase in coyote predation on sheep due to mesopredator release (left histogram), and no mesopredator release (right histogram). Both scenarios decreased baseline wolf predation rates across all stage classes by 80% and allocated half of the reduced wolf predation to 'other' predation (to account for compensatory mortality).

(Arthur and Prugh 2010). Survival rates of lambs doubled during this period, indicating that coyote predation was largely additive. In prey populations near carrying capacity, predation on neonates can be compensatory because neonates often starve in the absence of predation (Bartmann et al. 1992). The Dall sheep population during our study was approximately half the densities observed from 1967–1984 (Arthur and Prugh 2010). Thus, the population was likely below carrying capacity, which may explain why predation on lambs appeared to be additive. Examining the response of survival rates to changes in cause-specific mortality rates may be a useful way of estimating the degree of additivity when direct experimentation is not an option.

Our models did not include density dependence in estimation of Dall sheep mortality rates. If predators have a strong functional response to prey, kill rates may vary as a function of prey density or the ratio of predators to prey (Gasaway et al. 1992, Vucetich et al. 2011). In such cases, a modeling framework that accounts for these relationships may improve predictions of predator–prey dynamics (Gervasi et al. 2012). However, a recent analysis found that predation rates (i.e., proportion of prey population killed) were more useful in predicting prey growth rates than were kill rates (i.e., number of prey killed per predator; Vucetich et al. 2011). In our study, there was no evidence that kill rates or predation rates of coyotes or wolves varied as a function of Dall sheep density or predator–prey ratios (unpublished analyses). We did not expect to find a strong functional response of coyotes or wolves to Dall sheep density, because Dall sheep comprised minor components of the diet of both predators (Gasaway et al. 1983, Prugh 2005). Wolves have clear functional and numeric responses to moose in our system, whereas coyotes respond to hare abundance (Gasaway et al. 1983, O'Donoghue et al. 1997), and both predators appear to prey on sheep only incidentally. In systems where the ungulate populations of interest fluctuate closer to carrying capacity and are primary prey for the predators, density-dependence in fecundity or mortality rates may need to be considered (Houston and Stevens 1988).

Although the strength of mesopredator release due to wolf control was a key unknown that we explored, the return of wolves to the intermountain west has shown that wolves likely do suppress some coyote populations (Berger and Gese 2007). The wolf-caused mortality rate in our study was similar to rates in other areas where coyotes and wolves are sympatric. Excluding deaths from unknown causes, wolves killed 13% of radiocollared coyotes ($n = 15$) in Glacier National Park, Montana (Arjo 1999), 16% of coyotes ($n = 32$) in Wyoming (Berger and Gese 2007), 24% of coyotes ($n = 9$) in the Kenai Peninsula, Alaska (Thurber et al. 1992), and 20% of coyotes ($n = 15$) in this study. Although larger carnivores often kill smaller ones (Palomares and Caro 1999), the impact of intraguild predation on demographic rates of mesopredators is rarely assessed. Mesopredators may compensate for reduced survival by increased reproduction or immigration, leading to little net change in population growth (Karki et al. 2007, Swanson et al. 2014). Mesopredators may also benefit from the presence of large predators by scavenging their kills (Wilmers et al. 2003). Conversely, non-lethal effects of larger predators may reduce foraging efficiency or increase physiological stress, which could

amplify the effects of direct mortality (Lima and Dill 1990, Creel 2011, Clinchy et al. 2013).

The magnitude of suppression and factors that influence the strength of suppression remain poorly understood for many sympatric carnivores (Roemer et al. 2009). Our results suggest that a better understanding of intraguild interactions among predators may be critical to the successful conservation of shared prey species.

The abundance of other prey species is an important consideration when predicting the impact of predator management on sensitive prey populations. Because Dall sheep are secondary prey for both of their main predators, asymmetric apparent competition with snowshoe hares and other ungulates may have especially strong effects on Dall sheep population dynamics (Arthur and Prugh 2010, DeCesare et al. 2010). Mesopredator abundance often varies strongly in response to fluctuations in prey abundance, and yet large predators can suppress mesopredator populations despite strong bottom-up effects (Prugh et al. 2009, Ritchie and Johnson 2009, Roemer et al. 2009). For example, coyotes responded strongly to snowshoe hare abundance in our study, but coyote abundance in our study area was lower than is typical in areas without wolves, even when hares were abundant. A recent continental-scale analysis reports that wolves do indeed limit coyote abundance throughout Alaska, indicating joint bottom-up and top-down control of coyote density (Newsome and Ripple 2014). We expect the strength of top-down effects may vary as a function of bottom-up forces, such that large carnivores may prevent mesopredators from achieving high densities when prey is abundant, but mesopredators may be limited by prey availability rather than top-down forces when prey is scarce (Elmhagen and Rushton 2007, Elmhagen et al. 2010). We were not able to account for this complexity in our models, and examining the interactive effects of bottom-up and top-down forces on mesopredator abundance would be a fruitful avenue for future work.

Our models highlight two critical factors in determining the net effect of control of a top predator on shared prey: 1) the strength of mesopredator release, and 2) the relative rates of additive predation by each predator. The impact of top predator loss on shared prey via mesopredator release has rarely been examined in detail, and general predictions about conditions under which prey populations should increase or decline are therefore difficult to make. The extirpation of feral cats *Felis catus*, an exotic top predator on many islands, led to declines in bird populations via release of an exotic mesopredator, Pacific rats *Rattus exulans* (Rayner et al. 2007). However, rates of predation were not measured, so it is difficult to generalize these results to other systems in which relative predation rates on shared prey may differ. In another study, wolf recovery was found to benefit pronghorn antelope populations by suppressing coyote populations in Wyoming (Berger and Conner 2008). Wolves rarely depredate pronghorn, however, so these results may not apply to other ungulates that are preyed on by both large and smaller predators. For example, the net effect of predator management on bighorn sheep *Ovis canadensis* and deer *Odocoileus* spp., which are preyed upon by wolves, cougars, and coyotes (Shackleton et al. 1999, Ballard et al. 2001), may depend critically on the strength of intraguild aggression and stage-specific predation rates.

In conclusion, we found that control of a large predator could lead to either increased or decreased population growth of shared prey, depending on the strength of mesopredator release. We therefore recommend that wildlife managers consider the possibility of mesopredator release or suppression when planning predator control or reintroduction programs. The most realistic scenarios, in which wolf predation was partially compensatory and coyote predation increased by 40–60%, indicated that wolf control could lead to no net change or declines in sheep populations. We therefore recommend close monitoring of Dall sheep populations in areas where wolf control is implemented and coyotes are present. Likewise, bighorn sheep and deer populations should be closely monitored as wolf management policies evolve in western states. Estimates of the strength of mesopredator release and stage-specific predation rates are sorely needed in a variety of predator–prey systems. Expansions of large predator populations into new areas, as well as the patchwork of areas where predators are either controlled or protected in Alaska and elsewhere, offer unprecedented opportunities to quantify these parameters.

Acknowledgements – Funding for this work was provided by the Alaska Dept of Fish and Game and Federal Aid in Wildlife Conservation grants W-27-2 through W-33-10, projects 6.13 and 6.14. Field data was collected with the assistance of P. Del Vecchio, K. Whitten, B. Minor, K. Seaton, T. Seaton, M. McNay and S. Szepanski and the piloting skills of T. Cambier, R. Swisher, M. Webb, D. Miller, S. Hamilton, P. Valkenburg, and C. Gardner. S. Brainerd, K. Titus, D. James and B. Borg provided valuable comments on an earlier version of this manuscript. R. Taylor provided helpful advice and R code.

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Supplementary material (available online as Appendix oik.02017 at <www.oikosjournal.org/readers/appendix>). Appendix 1. R code for matrix model simulations of Dall sheep under baseline conditions and wolf control scenarios. Table A1. Matrix of within-year correlations among vital rates used in the Dall sheep stage-structured matrix model ($n = 6$ years). Figure A1. Wolf-caused mortality rates for 'young' and 'old' ewes as the cutoff between stages is increased from 7–12 years old.