

RECOLONIZING WOLVES AND MESOPREDATOR SUPPRESSION OF COYOTES: IMPACTS ON PRONGHORN POPULATION DYNAMICS

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Abstract. Food web theory predicts that the loss of large carnivores may contribute to elevated predation rates and, hence, declining prey populations, through the process of mesopredator release. However, opportunities to test predictions of the mesopredator release hypothesis are rare, and the extent to which changes in predation rates influence prey population dynamics may not be clear due to a lack of demographic information on the prey population of interest. We utilized spatial and seasonal heterogeneity in wolf distribution and abundance to evaluate whether mesopredator release of coyotes (*Canis latrans*), resulting from the extirpation of wolves (*Canis lupus*) throughout much of the United States, contributes to high rates of neonatal mortality in ungulates. To test this hypothesis, we contrasted causes of mortality and survival rates of pronghorn (*Antilocapra americana*) neonates captured at wolf-free and wolf-abundant sites in western Wyoming, USA, between 2002 and 2004. We then used these data to parameterize stochastic population models to heuristically assess the impact of wolves on pronghorn population dynamics due to changes in neonatal survival. Coyote predation was the primary cause of mortality at all sites, but mortality due to coyotes was 34% lower in areas utilized by wolves ($P < 0.001$). Based on simulation modeling, the realized population growth rate was 0.92 based on fawn survival in the absence of wolves, and 1.06 at sites utilized by wolves. Thus, wolf restoration is predicted to shift the trajectory of the pronghorn population from a declining to an increasing trend. Our results suggest that reintroductions of large carnivores may influence biodiversity through effects on prey populations mediated by mesopredator suppression. In addition, our approach, which combines empirical data on the population of interest with information from other data sources, demonstrates the utility of using simulation modeling to more fully evaluate ecological theories by moving beyond estimating changes in vital rates to analyses of population-level impacts.

Key words: *Allee effect; Antilocapra americana; Canis latrans; Canis lupus; coyotes; population management; predation; projection model; pronghorn; simulation modeling; wolves.*

INTRODUCTION

Large carnivore populations are declining, or have been eliminated, in many ecosystems around the world (Weber and Rabinowitz 1996, Woodroffe and Ginsberg 1998, Woodroffe 2001). Food web theory predicts that the loss of large carnivores may contribute to elevated predation rates and, hence, declining prey populations, through the process of mesopredator release (Soulé et al. 1988). Opportunities to test predictions of the mesopredator release hypothesis are rare, however, due to both a lack of spatial and temporal controls, as well as logistical and ethical difficulties associated with large-scale manipulations of terrestrial communities (Polis et

al. 2000, Steneck 2005). Furthermore, the management implications associated with large carnivore removal or restoration can be difficult to discern, as the extent to which changes in predation rates influence prey population dynamics may not be clear due to a lack of demographic information on the prey population of interest. Faced with incomplete data, stochastic population models, which combine empirical data on the population of interest with information gleaned from other data sources, can be a useful heuristic tool to compare the relative impact of different management scenarios on prey population dynamics (Beissinger 2002). In addition, these models can serve as a powerful method to assess the extent to which outcomes of field manipulations support or refute predictions based on ecological theory.

Predation represents an important source of mortality for neonatal ungulates. Neonatal mortality rates of temperate ungulates average 47% at sites where predators occur, vs. 19% in areas lacking predators (Linnell et al. 1995). Although disease, hypothermia, starvation,

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and abandonment contribute to juvenile mortality, predation is often cited as the primary cause of death and accounts for an average of 67% of total neonatal mortality (Linnell et al. 1995). However, for mule deer (*Odocoileus hemionus*; Lingle 2000) and pronghorn (*Antilocapra americana* [see Plate 1]; Gregg et al. 2001, O'Gara and Yoakum 2004), predation rates as high as 85% of total mortality have been reported.

Pronghorn have high reproductive potential and populations can generally withstand considerable neonatal losses (Byers 1997). Still, in cases where populations have already been reduced by severe winter weather or overharvesting by humans, poor recruitment resulting from sustained levels of elevated predation can maintain ungulate densities at low levels or even threaten local populations with extirpation (Gasaway et al. 1983).

The mesopredator release hypothesis (Soulé et al. 1988) attributes the expansion in the coyote population, and concomitant increase in predation rates, to the extirpation of gray wolves (*Canis lupus*) throughout much of the United States by the 1930s. For instance, in parts of northeastern North America, coyotes have replaced wolves as an important predator of white-tailed deer (*Odocoileus virginianus*; Gompper 2002). Because of their relatively smaller size (10 kg for coyotes vs. 39 kg for wolves), coyotes consume a greater proportion of smaller sized prey (1–10 kg; Gittleman 1985) and may thus be a more effective predator of mule deer, white-tailed deer, and pronghorn neonates, which typically weigh ≤ 5 kg at birth.

The reintroduction of wolves to the Greater Yellowstone Ecosystem, USA (Bangs and Fritts 1996), provided an opportunity to assess the extent to which the extirpation of wolves contributes to high rates of neonatal mortality in pronghorn. Berger et al. (2008) observed an inverse relationship between coyote densities and survival of neonatal pronghorn, and a direct relationship between wolf densities and survival of neonatal pronghorn. Here we report cause-specific mortality of neonatal pronghorn captured at wolf-free and wolf-abundant sites. In addition, we demonstrate the value of using demographic modeling to heuristically assess the potential impact of wolf recolonization on pronghorn population dynamics as a result of changes in neonatal survival rates due to mesopredator suppression of coyotes.

METHODS

Study sites

The study was conducted in Grand Teton National Park (GTNP; 43°39' N, 110°40' W), Wyoming, USA, and on the adjacent Bridger Teton National Forest (BTNF), from June 2002 through August 2004. Two wolf-abundant sites and one wolf-free site were selected to exploit spatial and seasonal variation in wolf distribution and abundance. Wolf-abundant sites were located at Elk Ranch, an area used extensively by wolves during denning and pup rearing (May–September) and periodically throughout the winter (October–April), and the

Gros Ventre River drainage, which was used by wolves only during winter (Fig. 1). In contrast, the Antelope Flats site was not used by wolves during either season. Over the course of the study, wolf densities ranged from 0.053 to 0.061 wolves/km² at the Elk Ranch site and from 0.028 to 0.033 wolves/km² at the Gros Ventre site during the winter; in summer, wolf densities at the Elk Ranch site varied from 0.015 to 0.030 wolves/km² (Berger et al. 2008). Total coyote densities (i.e., resident plus transient; means \pm SE) at the wolf-abundant sites (0.272 ± 0.018 coyotes/km²) were 33% lower than densities at the wolf-free site (0.406 ± 0.039 , $P = 0.012$; Berger et al. 2008). This disparity in coyote densities was primarily due to differences in the transient segment of the coyote population (0.039 ± 0.005 /km² vs. 0.188 ± 0.019 /km² at the wolf-abundant and wolf-free sites, respectively, $P < 0.001$), resulting from increased mortality and dispersal rates of transient coyotes in wolf-abundant areas (Berger and Gese 2007). All sites were characterized by shrub-steppe habitat dominated by big sagebrush (*Artemisia tridentata*), low sagebrush (*A. arbuscula*), antelope bitterbrush (*Purshia tridentata*), and associated understory grasses of the genera *Stipa*, *Bromus*, and *Poa*.

Fawn captures and monitoring

To locate fawns for radio-collaring, we monitored solitary, adult females with udder development, or those showing signs of imminent parturition (Byers 1997), with binoculars and 15–45 power telescopes. To minimize the risk of abandonment, neonates were not handled until ≥ 4 hours after birth to allow mother/young imprinting to occur (Autenrieth and Fichter 1975). Fawns were captured by hand or with long-handled nets, blindfolded to discourage bleating, weighed using a canvas sling hung from a spring scale, and aged based on observation of birth or the degree of desiccation of the umbilicus (Byers and Moodie 1990). The sex of each fawn, as well as evidence of dehydration, disease, physical injuries, or deformities, was recorded. Fawns were fitted with expandable, breakaway VHF radio collars with four-hour mortality sensors (~ 60 g; Advanced Telemetry Systems, Isanti, Minnesota, USA). Following processing, fawns were released at their capture sites.

Using handheld telemetry equipment and a vehicle-mounted antenna, we monitored fawns daily from the ground during the first two months of life and then weekly thereafter until the fall migration. Aerial telemetry was used to locate missing fawns. When a mortality signal was detected, the carcass was recovered and necropsied immediately to determine the cause of death. Kill sites were also examined for predator sign. We classified cause of mortality as (1) predation when sufficient remains were recovered to determine that the fawn had been alive at the time it was attacked, (2) likely predation when tracks, scats, hair, and caching behavior were adequate to identify the predator involved but we could not irrefutably rule out the possibility of scavenging, (3) disease, and (4) other (e.g., starvation,

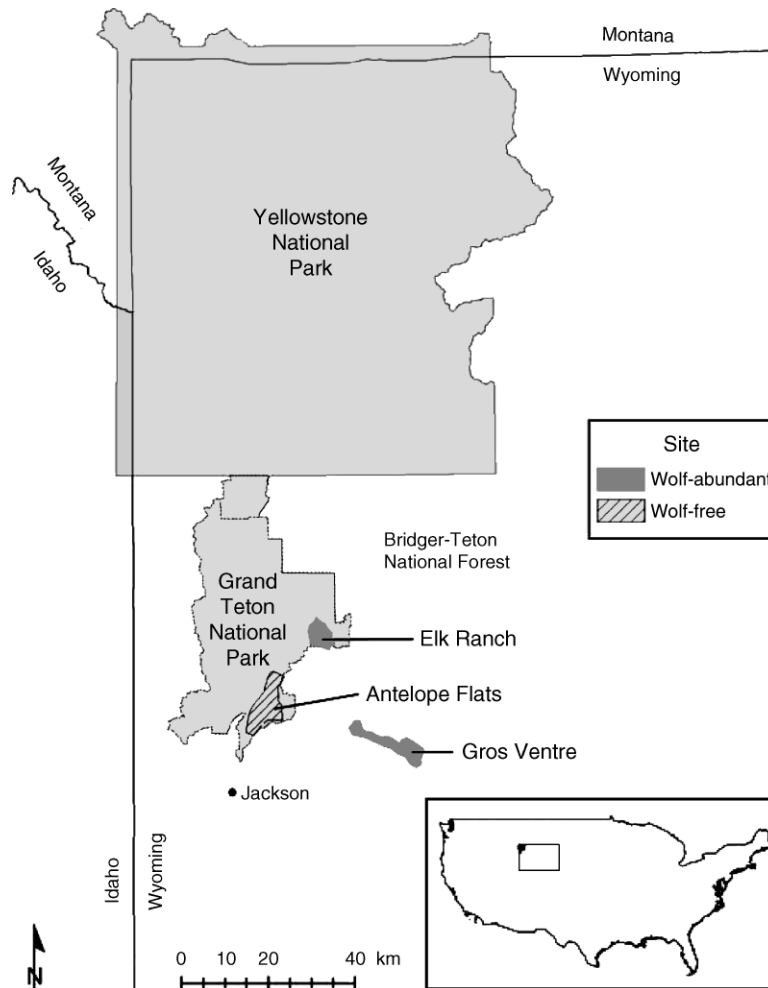


FIG. 1. Map showing the location of the Greater Yellowstone Ecosystem (GYE) in the western United States, the locations of study sites, and place names.

accidents). Predation-caused mortalities were further classified by type of predator based on differential characteristics of predator kills (O’Gara 1978).

Analysis of neonatal survival

We estimated summer survival of neonates using a known fate model in Program MARK (White and Burnham 1999). The analysis was based on individual encounter histories with two encounters per cohort that indicated whether the fawn survived or died during the first two months of life. We estimated survival rates for the first and second months of life separately because previous studies suggest most mortality occurs during the first few weeks of life (Byers 1997, O’Gara and Yoakum 2004, Zimmer 2004); thus, we expected survival rates during the first month of life to be much lower than during the second. We evaluated 22 models (Berger 2007) to assess the effects of month, site, gender, and birthweight on fawn survival. For fawns that were not newborns at capture, we calculated mass at birth from the following relationship (modified from Byers 1997):

$$\text{birthweight} = \text{weight at capture} - 0.2446 \times \text{age in days.} \tag{1}$$

The most global model we could parameterize with our data was $S_{N(s+m+g+w)}$, where S_N was estimated summer survival of neonates, s was site, m was month, g was gender, and w was weight at birth. Because our initial analysis did not support differences in fawn survival rates between the two wolf-abundant sites (Berger 2007), we pooled the data for fawns captured in areas used by wolves. We used Akaike’s Information Criterion adjusted for small sample sizes (AIC_c) and Akaike weights to rank models (Burnham and Anderson 2002).

Model construction and parameterization

To investigate the impact of differential neonatal survival on pronghorn population dynamics, we used a stochastic, stage-structured matrix model with a post-reproductive census (Lefkovich 1965). We utilized a post-reproductive census to be consistent with the

TABLE 1. Comparison of neonatal survival rates observed in radio-collared pronghorn (*Antilocapra americana*) fawns and estimated from young:female ratios during fall classification counts.

Year	Observed survival†	Estimated survival‡
2002	0.222	0.227
2003	0.186	0.319
2004	0.311	0.311

† Total number of surviving fawns divided by total number of collared fawns.

‡ Estimated from classification count data; see Appendix.

monitoring approach used by the Wyoming Game and Fish Department (WGF), which bases pronghorn management on classification surveys (i.e., surveys to record the distribution of animals by age and sex) conducted each fall. Our model was based on females and utilized vital rates for five biological stage classes and seven parameter estimates. The biological stage classes were neonates (N), juveniles (J), yearlings (Y), prime-age adults (A_{PA}), and “senescent” adults (A_S). The model included seven parameter estimates: adult fertility (F_A), neonatal survival at the wolf-free site (S_{NWF}), neonatal survival at the wolf-abundant sites (S_{NWA}), overwinter juvenile survival (S_J), yearling survival (S_Y), survival of prime age adults (S_{APA}), and a transition probability between prime age and senescent adults (T_{AS}). We included the latter stage class to eliminate potentially immortal animals that result in the absence of a terminal stage (Mollet and Cailliet 2002).

Fertility data were not available for the population of interest. In general, annual reproductive effort for female pronghorn is high relative to that of other ungulates and shows little annual variation (O’Gara and Yoakum 2004). Females typically reach estrus at age 15 months, produce their first offspring at age two, and bear twins each year thereafter until death (Byers 1997). Although reproduction in yearlings has been recorded, early sexual maturation is rare and often results in reduced litter size or low birthweight fawns with poorer than average survival (Mitchell 1967, Byers 1997). Litter size averaged 1.89 ± 0.017 (mean \pm SE) fetuses per female ($n = 327$), including pregnant yearlings, for nine studies in the western United States (O’Gara and Yoakum 2004). Similarly, mean litter size was 1.90 ± 0.019 fetuses per adult female ($n = 235$) in Wyoming and Colorado (Zimmer 2004; T. Gerlach and M. R. Vaughan, *unpublished manuscript*). Thus, assuming 100% pregnancy rates for adult females and an even sex ratio for fawns (Byers 1997, Zimmer 2004), we estimated adult fertility as

$$F_A = \frac{1.9 \text{ fawns/adult female}}{2} \\ = 0.950 \text{ female fawns/adult female.} \quad (2)$$

Fertility of yearling females was assumed to be zero.

We estimated survival rates with demographic data obtained from the following sources. For neonatal

survival at the wolf-free (S_{NWF}) and wolf-abundant (S_{NWA}) sites, we used data from 125 fawns captured in GTNP between 2002 and 2004 (as previously discussed). In addition, to generate a more realistic estimate of long-term variation in neonatal survival, we used a 24-year data set based on classification surveys conducted in GTNP each August between 1981 and 2005 (Wyoming Game and Fish, *unpublished data*). We used a procedure modified from Firchow (1986) to generate annual estimates of neonatal survival from the count data (Appendix).

Bonenfant et al. (2005) suggest the young:female ratio is not a reliable proxy of juvenile recruitment because detection of young is influenced by behavioral changes during the first year of life, and because changes in ratios over time may be a reflection of differences in juvenile survival rates, pregnancy rates, or both. We consider our use of young:female ratios a reasonable method for estimating neonatal survival in most years because (1) the time frame between births (June) and the classification counts (August) is short; thus, the ratios are not likely to be impacted by adult mortality; (2) the detection of fawns is not dependent upon maternal/offspring behavior, as both females and young join groups when fawns are approximately three weeks old (Byers 1997); and (3) pregnancy rates of adult females are uniformly high and relatively invariant over time, except in cases of extreme winter weather or drought when reabsorption of fetuses can occur (O’Gara and Yoakum 2004, Byers et al. 2005). The survival rates projected from count data agreed well with observed survival rates of radio-collared fawns in two out of the three years of our study (Table 1).

We estimated overwinter juvenile survival from the fates of fawns radio-collared in GTNP that survived the summer in 2002 ($n = 6$) and 2003 ($n = 7$). Fawns captured in the summer of 2004 were excluded from this analysis because we did not follow them closely enough during the winter of 2004 to accurately assess their fates. We pooled fawns captured at the wolf-free and wolf-abundant sites for the analysis of overwinter juvenile survival because all pronghorn that summer in the vicinity of GTNP migrate to the same wintering area (Sawyer et al. 2005).

For adult survival, data were obtained from telemetry studies conducted in GNTNP between 1998 and 2001 and from 2002 to 2003 (Sawyer and Lindzey 2000; K. M. Berger, *unpublished data*). We used 43 marked females in the analysis of adult survival (33 from 1998–2001 and 10 from 2003–2004). Data on yearling survival were not available for either the population of interest or pronghorn in other areas. Although survival of yearlings is often lower and more variable than that of adults in large ungulates (Gaillard et al. 2000), no differences in survival of adult and yearling females have been reported for pronghorn (Byers 1997). Thus, we used the same estimates of survival for both S_Y and S_{APA} .

TABLE 2. Pronghorn stage classes, ages, and vital rates used to construct the demographic models.

Class	Age (months)	Vital rate	Description	Mean (variance)
Neonate	0–2	S_{NWA}	summer survival of fawns captured at wolf-abundant sites	0.070 (0.006)
Neonate	0–2	S_{NWF}	summer survival of fawns captured at the wolf-free site	0.354 (0.006)
Juvenile	2–12	S_J	winter survival	0.836 (0.005)
Yearling	12–24	S_Y	annual survival	0.872 (0.005)
Adult	24+	S_A	annual survival	0.872 (0.005)
Adult	24+	F_A	fertility	0.95 (0.0003)

We estimated the transition probability from prime age to senescent adults following Crouse et al. (1987):

$$T_{AS} = \frac{S_{APA}^{d_i}(1 - S_{APA})}{1 - S_{APA}^{d_i}} \quad (3)$$

where d_i represents the oldest individuals in the population. Based on survivorship of 840 female pronghorn at the National Bison Range, Montana, pronghorn females survive to a maximum age of 14; thus, we assumed $d_i = 14$, and that survival of animals in the senescent stage class was zero (Byers 1997).

To obtain parameter estimates for the population model, we first analyzed the survival data for each stage class in Program MARK with a known fate model in which time was not constrained (White and Burnham 1999, White et al. 2001). However, the parameter estimates obtained from fixed-effects models contain both process ($\sigma_{process}^2$) and sampling variance. Because inclusion of sampling error inflates variance estimates and negatively biases population viability (White 2000, Morris and Doak 2002), we then used random effects models in the variance components module of Program MARK to distinguish process variation from sampling variation and generate shrinkage estimators of the parameter estimates (White et al. 2001). We report the resulting shrinkage estimators (also called empirical Bayes estimators; Burnham et al. 1987, Johnson 1989) and estimates of process variance used to parameterize the demographic models (Table 2). Because overall variation in reproduction among years and individuals was low, we were unable to partition the variance into sampling and process components. Therefore, the fertility estimate used in the demographic models includes both process and sampling variance. We used $\hat{\sigma}_{process}^2$ obtained from the analysis of neonatal survival based on count data as the variance estimate for neonatal survival at both the wolf-free and wolf-abundant sites, and $\hat{\sigma}_{process}^2$ obtained from the analysis of adult survival as the variance estimate for juvenile survival, because the sample sizes and sampling durations used to generate these estimates were greater. Thus, we considered these values a better reflection of long-term variation in neonatal and juvenile survival.

Correlation in vital rates

Values of different vital rates typically covary over time because the same environmental factors similarly

affect all rates (Doak et al. 1994). Positive correlation between vital rates increases variability in population growth rates, thereby decreasing population viability, whereas negatively correlated vital rates dampen variability in population growth and, thus, enhance population viability (Morris and Doak 2002). Consequently, the decision to incorporate or exclude correlation among vital rates in a population model can have a substantial effect on predicted population viability (Ferson and Burgman 1995), as well as the estimated contribution of different demographic rates to population growth (Coulson et al. 2005).

Data from which to estimate correlation among vital rates were not available for pronghorn in GTNP because, with the exception of a single year, studies of adults and juveniles have not been conducted contemporaneously. Because severe winter weather has been identified as an important factor contributing to high rates of pronghorn mortality in Wyoming and Montana, USA, and Canada in some years (O’Gara and Yoakum 2004), we estimated correlation in winter survival rates using published estimates from concurrent studies of adults and juveniles (Table 3). Based on our analysis of these data, we estimated the correlation between S_A and S_J as $r = 0.880$. Note that for adults and yearlings, mortality exclusive of hunting-related deaths occurs primarily during winter (Pyrah 1987). We did not include correlation among other vital rates because data were lacking from which to estimate these parameters. However, we expect that correlations among other vital rates should generally be lower than for overwinter survival rates due to spatial and seasonal differences in the occurrence of these life-history events. Consequently, we expect that their omission from the model should have less of an impact on population growth than correlation in winter survival. We tested the extent to which correlation in winter survival rates influenced our results by comparing simulations run both with and without the imposed correlation structure.

Density dependence

Although we did not include density dependence in our model, we did use ordinary least squares regression analysis, based on data obtained from classification counts (WGF, unpublished data) to evaluate the extent to which density dependence might be important for neonatal survival. In addition to a linear model, we also tested a logarithmic model and a second-order polyno-

TABLE 3. Pronghorn survival rates for adults and juveniles used to estimate correlation in overwinter survival.

State	Adult survival	Juvenile survival	Reference
Colorado	0.950	0.935	T. Pojar (<i>unpublished data</i>)
Montana	0.850	0.802	Martinka (1967)
Montana	0.870	0.800	Pyrah (1987)
Montana	0.934	0.890	Byers (1997)
Utah	0.920	0.850	Smith and Beale (1980)
Wyoming	0.925	0.836	Sawyer and Lindzey (2000); K. M. Berger (<i>unpublished data</i>)

mial, because a scatterplot of the data suggested a possible inflection point at population sizes near 300.

Stochastic population simulations

We used the parameter estimates to construct two projection matrices that differed only in their estimate of neonatal survival (Table 4). Using these projection matrices, we assessed potential effects of differences in neonatal survival on pronghorn population dynamics as follows: (1) Start with an initial population vector (N_0) that specifies the number of individuals in each stage class. (2) For each vital rate, use parametric bootstrapping to select a random value from a β -distribution corresponding to the mean and variance specified for the parameter from the random effects model and the desired correlation structure (Morris and Doak 2002). (3) Use these randomly drawn vital rates to populate the projection matrix. (4) Multiply the projection matrix by the population size in year t (N_t) to estimate the population size in year $t + 1$ (N_{t+1}). Record the new population size. (5) Repeat this process to project the population over $T = 20$ years (the total number of years over which the population dynamics were projected). (6) At the end of each simulation of T years, record the log of the average annual population growth rate as

$$\log(\lambda_t) = \frac{1}{T} \times \log\left(\frac{N_T}{N_0}\right). \quad (4)$$

(7) Repeat this process 8000 times (White et al. 2002).

(8) At the end of 8000 simulations, record the median population size for each year and the mean log of the population growth rate ($\log(\lambda_t)$).

All simulations were performed with MATLAB 6.5 (MathWorks 2002). The initial population vector was derived from count data for 2005 and consisted of 109 juveniles, 25 yearlings, 115 adults, and 4 senescent adults (WGF, *unpublished data*). Because WGF does not distinguish adult from yearling females in the classification counts, we used our calculation of the percentage of reproductive females in the population (82%; Appendix) to determine the number of adult females and yearlings in the initial population vector. In addition, we ran trials in which we varied the percentage of yearlings from 10% to 25%, and results were robust to the number of yearlings in the initial population vector (Berger 2007). We estimated the number of adults in the senescent stage class by multiplying the number of yearlings in the initial population vector by the proportion expected to survive to age 14 (i.e., S_Y^{14}). For each year, we recorded the effect of wolf reintroduction on the population growth rate (sensu Ellner and Fieberg 2003) as

$$\Delta \log(\lambda_t) = [\log(\lambda_t)|\text{wolves}, \boldsymbol{\theta}_t] - [\log(\lambda_t)|\text{no wolves}, \boldsymbol{\theta}_t] \quad (5)$$

where $\boldsymbol{\theta}_t$ represents the vector of bootstrapped vital rates. Although we allowed the demographic models to project population dynamics over 20 years, we present estimates of the realized population growth rates and effect sizes using a 10-year window. While the former is a useful time horizon for heuristic purposes, we consider the latter a more likely time frame over which management plans are likely to be implemented.

We used a parametric bootstrap to compute 95% confidence intervals on N_t , $\log(\lambda_t)$, and $\Delta \log(\lambda_t)$. Using the values of $\log(\hat{\lambda}_t)$, $\text{SE}(\log(\hat{\lambda}_t))$, and $\hat{\sigma}_{\text{process}}$ from our initial simulations, we modeled $\log(\lambda_t)$ with a normal distribution possessing mean $\log(\hat{\lambda}_t)$ and standard deviation $\text{SE}(\log(\hat{\lambda}_t))$, and process variance as a multiple of a χ^2 distribution as follows (Morris and Doak 2002, Blakesley et al. 2006):

TABLE 4. Average population projection matrices for pronghorn based on differences in survival rates of neonates at wolf-free and wolf-abundant sites in Grand Teton National Park (GTNP), Wyoming, USA.

Stage class	Wolf-free site				Wolf-abundant site			
	N	Y	A_{PA}	A_S	N	Y	A_{PA}	A_S
N	0	0	0.829†	0	0	0	0.829	0
Y	0.059‡	0	0	0	0.296	0	0	0
A_{PA}	0	0.872	0.872	0	0	0.872	0.872	0
A_S	0	0	0.022§	0	0	0	0.022	0

Note: Abbreviations are: N , neonate; Y , yearling; A_{PA} , prime adult; A_S , senescent adult.

† Annual reproductive rate = $S_A \times F_A = 0.872 \times 0.950 = 0.829$.

‡ Neonate and juvenile stage classes are combined in the projection matrix. Thus, the transition probability from the neonate stage class to the yearling stage class for fawns captured at the wolf-free site = $S_N \times S_J = 0.070 \times 0.836 = 0.059$.

§ Transition probability to senescent stage class.

TABLE 5. Sample sizes (number of fawns, n) and percentages of radio-collared pronghorn fawns dying by various causes during the first 60 days of life in Grand Teton National Park.

Cause of mortality	Wolf-free site						Wolf-abundant sites					
	2002		2003		2004		2002		2003		2004	
	n	%	n	%	n	%	n	%	n	%	n	%
Predation												
Coyote	6	32	7	41	2	13	5	29	6	22	9	30
Dog	0	0	0	0	0	0	1	6	1	4	0	0
Raptor	0	0	0	0	0	0	1	6	0	0	0	0
Unidentified	0	0	0	0	0	0	0	0	0	0	1	3
Likely predator												
Coyote	7	37	5	29	8	53	4	24	5	19	4	13
Other												
Trauma†	1	5	0	0	0	0	1	6	0	0	0	0
Abandonment	1	5	0	0	0	0	0	0	0	0	2	7
Unknown	2	11	5	29	3	20	1	6	6	22	2	7
Censored	0	0	0	0	0	0	0	0	1	4	0	0
Survived	2	11	0	0	2	13	4	24	8	30	12	40
Total	19	100	17	100	15	100	17	100	27	100	30	100

Note: “Censored” indicates that fawns were excluded from the analysis if their fate could not be determined because their collar signal disappeared.

† Trauma includes drowning ($n = 1$) and exertion myopathy ($n = 1$).

$$\frac{df \times \hat{\sigma}_{process}^2}{\sigma_{process}^2} \sim \chi_{df}^2 \tag{6}$$

We used $df = T$ to approximate the confidence interval of $\hat{\sigma}_{process}$. To estimate the confidence intervals, we generated 1000 bootstrap data sets consisting of 8000 population trajectories for each treatment group over a 20-year period. For each trajectory, we used randomly selected values of $\log(\hat{\lambda}_t)$ and $\hat{\sigma}_{process}$ for each year to estimate the population size as

$$\hat{N}_{t+1} = e^{\log(\hat{\lambda}_t)} \hat{N}_t \tag{7}$$

and $\Delta \log(\hat{\lambda}_t)$ as in Eq. 4. From each bootstrap dataset, we selected the 2.5 and 97.5 percentile values for N_t , $\log(\lambda_t)$, and $\Delta \log(\lambda_t)$. The 95% confidence intervals were then estimated as the expected values for these parameters from the 1000 bootstrap replicates.

RESULTS

Fawn captures and causes of mortality

We radio-collared 36 fawns in 2002, 44 fawns in 2003, and 45 fawns in 2004. Mean handling time was 4.25 ± 0.18 minutes, and mean age of captured fawns was 1.40 ± 0.15 days (means \pm SE). At the time of capture, three fawns showed signs of abandonment. Although we knew prospects for survival of these fawns were poor, we included them in our sample so as not to bias our results. All other fawns were in good physical condition and showed no evidence of illness, injury, or deformity.

The distribution was 74 captured fawns at the wolf-abundant sites (17 in 2002, 27 in 2003, and 30 in 2004) and 51 fawns at the wolf-free site (19 in 2002, 17 in 2003, and 15 in 2004). The sex ratio of captured fawns did not differ from parity (1:1.05 in favor of females), and was

similar between wolf-abundant (1:1.06 in favor of females) and wolf-free (1:1.04 in favor of females) sites. Although birthweights did not differ among years (one-way ANOVA, $P = 0.203$) or between sexes (Student’s t test, $P = 0.085$), there was an apparent trend toward slightly heavier birthweights for males ($\bar{X} = 3.90 \pm 0.09$ kg) than for females ($\bar{X} = 3.76 \pm 0.05$ kg).

Causes of mortality were similar among years and between wolf-free and wolf-abundant areas. Predation/likely predation was the primary cause of death in all three years and accounted for the deaths of 68%, 71%, and 67% of fawns captured at the wolf-free site, and 65%, 44%, and 47% of fawns at the wolf-abundant sites, in 2002, 2003, and 2004, respectively (Table 5). Note that in 2003, the cause of death could not be determined in 25% of cases (29% at the wolf-free site and 22% at the wolf-abundant site) because carcasses were not recovered promptly due to a malfunction in the mortality sensors. Coyotes predation (verified plus likely) accounted for 100% of predation-related deaths at the wolf-free site in all years, and 82%, 92%, and 93% of predation-related deaths at the wolf-abundant sites in 2002, 2003, and 2004, respectively. Wolves did not kill any radio-collared fawns during the first two months of life, but did kill one 99-day-old fawn in 2003. The onset of mortality occurred two days after the first fawn was captured at the wolf-free site, whereas there was a seven-day delay between the first capture at the wolf-abundant sites and the first recorded death (Fig. 2). Seventy-five percent of all mortality at both sites occurred during the first three weeks of life (Fig. 2).

Neonatal survival

We included 125 marked individuals in the analysis of fawn survival. On the basis of minimum AIC_c , the best

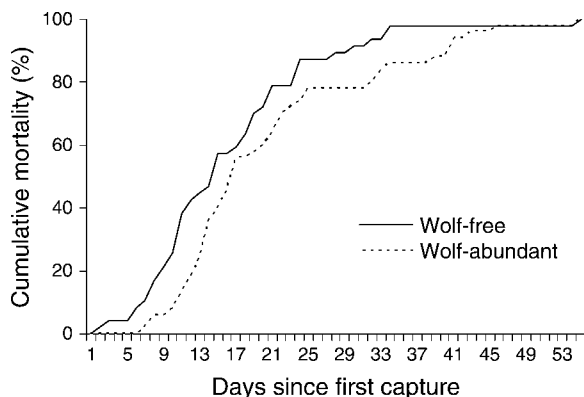


FIG. 2. Cumulative mortality during the first two months of life of pronghorn (*Antilocapra americana*) fawns captured at wolf-free and wolf-abundant sites in Grand Teton National Park, Wyoming, USA, 2002–2004.

model of fawn survival contained parameters for site and gender, plus an even–odd parameter that suggested that survival differed during the first and second month of life, but not among years (Table 6). Based on the parameter estimates from the top-ranked model, neonatal survival was lower at the wolf-free site than the wolf-abundant sites (Wald test, $P < 0.001$), and was lower for male fawns than for females (Wald test, $P = 0.04$; Table 7). Two-month survival of female fawns was more than three times higher than for male fawns at the wolf-free site, and nearly twice as high as for male fawns at the wolf-abundant sites (Table 7). Survival during the first month of life was considerably lower than during the second (Wald test, $P < 0.001$; Table 7). Although the second-ranked model suggested that survival was positively correlated with birthweight, the confidence interval on the coefficient overlapped zero, indicating there was no clear effect of birthweight on fawn survival (Wald test, $P = 0.332$). Together, the top two models accounted for 75% of the Akaike weights (Table 6).

Density dependence

There was some support for positive density dependence in neonatal survival rates at current population densities (Fig. 3). Although a second-order polynomial maximized the proportion of the variance explained ($r^2 = 0.301$) relative to either a linear model ($r^2 = 0.220$) or a logarithmic model ($r^2 = 0.257$), the improvement in fit was not sufficient to compensate for the additional parameter ($F_{1,21} = 1.33$, $P > 0.25$). While a logarithmic model (neonatal survival = $-0.433 = 0.1275 \times \ln[\text{pronghorn population size}]$; $P = 0.004$) is clearly not biologically realistic in that it suggests neonatal survival approaches an asymptote near 1.0 as population size increases, it is still more biologically reasonable than a linear model, which indicates that neonatal survival increases indefinitely at a constant rate with increasing population size. The appearance of a positive relationship between population size and neonatal survival should be interpreted cautiously; as there is considerable variation in neonatal survival at population sizes near 200, there are few years in which the population size was >300 upon which to base the curve (Fig. 3), and the count data have not been corrected for detection probability.

Demographic modeling

Results from simulations run with and without correlation in overwinter survival were virtually identical; confidence intervals were slightly wider for the model that included correlation (Berger 2007). Thus, we present only the results from the model that included correlation.

At the end of 10 years, the realized population growth rate was 0.92 (95% CI = 0.85 to 0.99) based on fawn survival rates in the absence of wolves, and 1.06 (95% CI = 0.98 to 1.14) based on survival rates of neonates captured at sites utilized by wolves (Fig. 4). Thus, based on a 10-year window, the projected effect of wolf recolonization was a 14% annual increase in the

TABLE 6. Model selection results from analysis of neonatal pronghorn survival.

Model	k	AIC_c	ΔAIC_c	Akaike weights	Model likelihood	Deviance
S_{s+EO+g}	4	173.475	0.000	0.480	1.000	165.216
$S_{s+EO+g+w}$	5	174.664	1.189	0.265	0.552	164.272
S_{s+EO}	3	175.927	2.452	0.141	0.294	169.772
S_{s+EO+w}	4	177.652	4.177	0.059	0.124	169.393
S_{s+m+g}	8	179.314	5.839	0.026	0.054	162.354
$S_{s+m+g+w}$	9	180.145	6.669	0.017	0.036	160.936
S_{s+m}	7	182.301	8.825	0.006	0.012	167.559
S_{s+m+w}	8	183.787	10.311	0.003	0.006	166.827
S_{EO+g}	3	184.987	11.512	0.002	0.003	178.832
S_{EO+g+w}	4	186.292	12.817	0.001	0.002	178.033
S_{EO}	2	186.683	13.208	0.001	0.001	182.606

Notes: Akaike weights scale from 0 to 1 and indicate the relative support for each model. Although we tested 22 models, we present only the results for models with Akaike weights >0 . Abbreviations are: k , the number of estimable parameters; AIC_c , Akaike's Information criterion adjusted for small sample sizes; ΔAIC_c , the difference in AIC_c values between the i th model and the top-ranked model; s, site; EO, an even–odd effect for the first and second months of life; g, gender; w, birthweight; and m, month.

TABLE 7. Comparison of estimated survival rates (\hat{S}) with upper and lower 95% confidence limits (LCL and UCL, respectively) for male and female fawns based on parameter estimates from the top-ranked model.

Site and age	Males			Females		
	\hat{S}	95% LCL	95% UCL	\hat{S}	95% LCL	95% UCL
Wolf-free site						
First month of life	0.082	0.056	0.117	0.168	0.123	0.227
Second month of life	0.429	0.336	0.528	0.631	0.541	0.712
Two-month survival	0.035	0.019	0.062	0.106	0.066	0.161
Wolf-abundant site						
First month of life	0.292	0.217	0.379	0.484	0.393	0.576
Second month of life	0.777	0.701	0.838	0.888	0.845	0.920
Two-month survival	0.227	0.152	0.318	0.429	0.332	0.530

pronghorn population growth rate ($\Delta\lambda_t = 0.14$, 95% CI = -0.01 to 0.28; Fig. 5a), corresponding to an overall increase in the pronghorn population of 355 animals (95% CI = -24 to 957; Fig. 5b).

From an initial population size of 249 pronghorn, the most likely population trajectory based on fawn survival at the wolf-free site was a 33% decline in the population within five years to 166 animals, a 56% reduction within 10 years to 109 animals, and an 81% decrease over 20 years to 47 animals (Fig. 6a). However, confidence intervals on the predicted population size ranged from 100 to 276 pronghorn within five years, 50 to 239 pronghorn within 10 years, and 13 to 169 pronghorn at 20 years, indicating that both a modest decrease in the population, as well as near extinction of the population, were consistent with the available data. Conversely, the mostly likely population trajectory given neonatal survival at the wolf-abundant sites was a 33% increase within five years to 331 animals, a 73% increase within 10 years to 432 animals, and a 196% increase in 20 years to 767 animals (Fig. 6b). The 95% confidence intervals suggest that an increase in the population over the next 20 years is likely, but indicate that both a slight decline (221 animals) and a 10-fold increase (2455 animals) are reasonably likely outcomes.

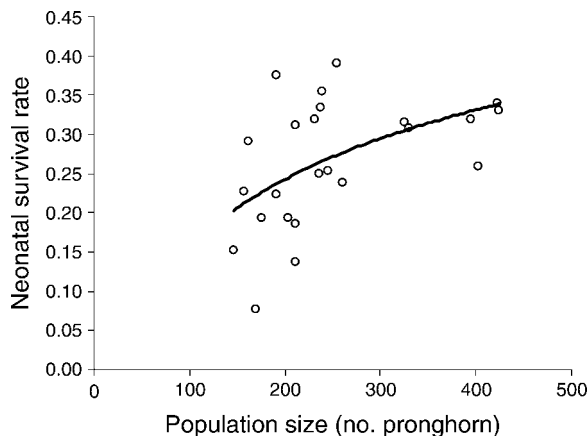


FIG. 3. Test for density dependence in pronghorn neonatal survival in Grand Teton National Park, 1981–2005.

DISCUSSION

Our results provide strong support for the hypothesis that mesopredator release of coyotes contributes to high rates of coyote predation on neonatal ungulates observed in some areas of western North America. Although causes and timing of mortality in our study were generally consistent with results reported for populations elsewhere (Byers 1997, O’Gara and Yoakum 2004, Zimmer 2004), mortality rates due to coyotes were 34% lower in areas utilized by wolves ($P < 0.001$).

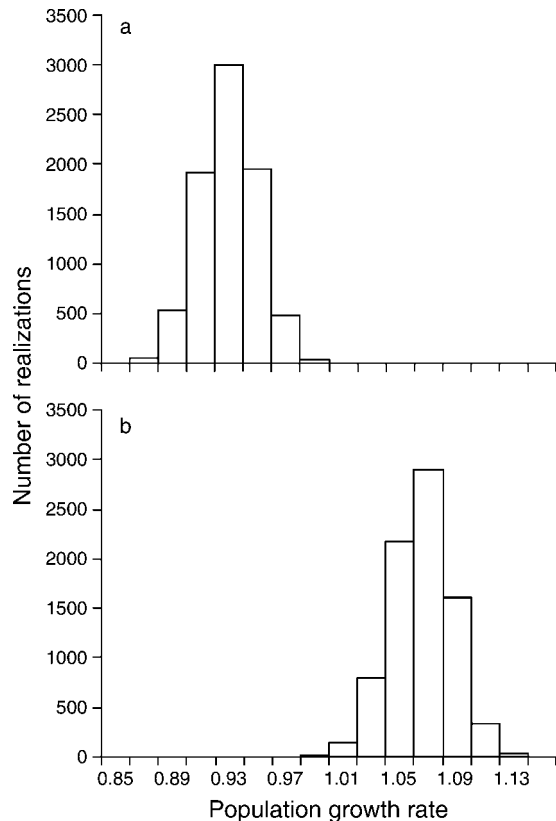


FIG. 4. Realized population growth rates from the demographic model based on survival of fawns captured at (a) wolf-free and (b) wolf-abundant sites.

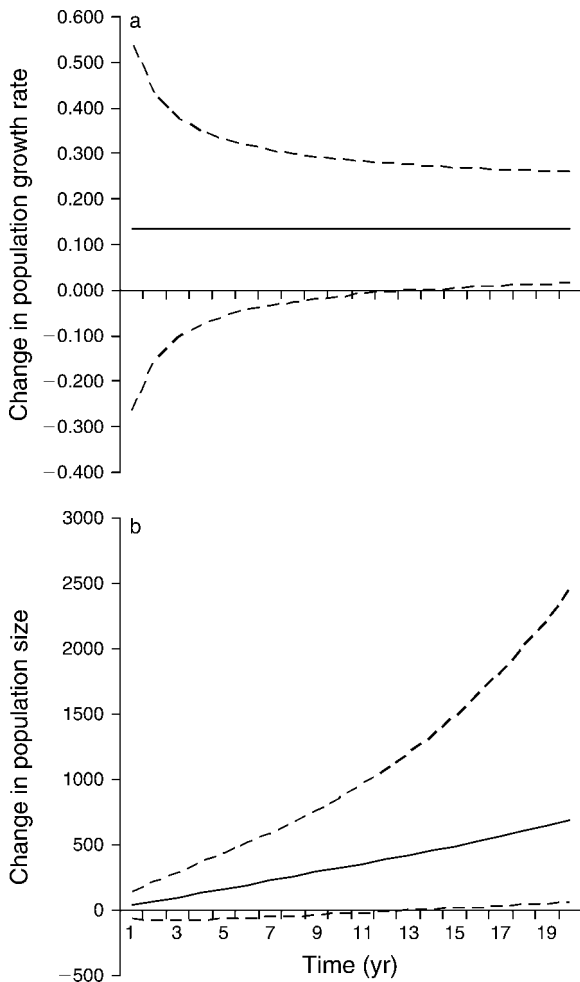


FIG. 5. Average annual effect of recolonizing wolves on (a) pronghorn population growth rate and (b) pronghorn population size, based on demographic modeling. Dashed lines represent 95% confidence intervals.

This disparity in predation rates corresponds to a 33% difference ($P = 0.012$) in coyote densities in wolf-abundant areas of GTNP, which has been attributed to direct mortality of coyotes by wolves and higher dispersal rates of transient coyotes (Berger and Gese 2007). We found no evidence that disease or malnutrition were important sources of neonatal mortality or contributed to an increased risk of coyote predation. In the process of conducting our fieldwork, we commonly observed radio-collared fawns in the days prior to their deaths, and all fawns appeared healthy and vigorous. The lack of compensatory mortality at the wolf-abundant sites from disease, starvation, or predators other than coyotes suggests that mortality due to coyotes is additive and that wolf restoration can increase survival of pronghorn neonates through mesopredator suppression of coyotes.

The results of the survival analysis support sex-differential survival, with female fawns surviving better

than males at both wolf-free and wolf-abundant sites (Table 7). Evidence of sex-biased survival in favor of female fawns has previously been reported in pronghorn, but the results were not definitive (Fairbanks 1993, Byers 1997). Whereas female survival was four times higher at sites utilized by wolves, survival of male fawns was more than six times higher, suggesting that males may benefit disproportionately from wolf recolonization. Given that the increase in survival of both male and female fawns stemmed from a reduction in predation-related mortality, our finding contradicts the results of previous studies that suggest that female fawns tend to be more active than males and are thus more vulnerable to detection by predators (Byers and Moodie 1990).

Our results also tentatively suggest the existence of positive density dependence, a potential Allee effect, in fawn survival (Fig. 3; Allee 1951). Although reproductive synchrony should be less important for ungulates that utilize a hiding strategy to protect neonates from predators (Ims 1990), survival rates of pronghorn fawns

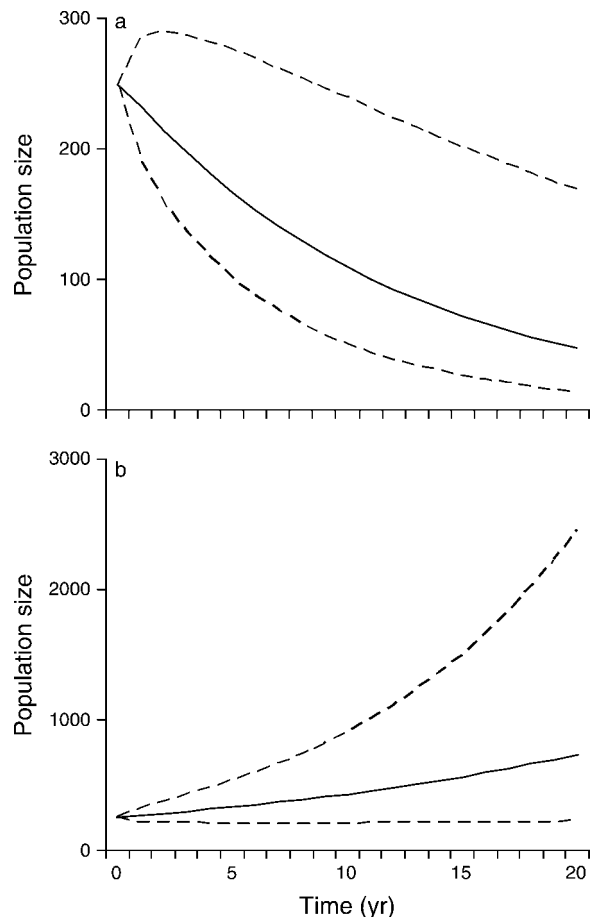


FIG. 6. Results of the demographic model showing median changes in pronghorn population size over time based on survival of fawns captured at (a) wolf-free and (b) wolf-abundant sites. Dashed lines represent 95% confidence intervals.

born during the peak of fawning are higher than those born during non-peak periods (Gregg et al. 2001). Given the large number of reproducing coyote packs in the vicinity of our study sites (Berger and Gese 2007), and the energetic demands of coyote packs during the denning/pup-rearing period, it appears that coyotes could conceivably consume nearly all of the estimated ~150 pronghorn fawns produced in GTNP each summer (i.e., 13 known reproducing coyote packs \times 1 fawn consumed every other day = 137 fawns within the first three weeks of life, alone). Thus, relatively high densities of coyotes coupled with relatively low densities of pronghorn may contribute to the existence of an Allee effect driven by predation (sensu Gascoigne and Lipcius 2004).

Demographic modeling indicates that wolf recolonization will likely have a substantial impact on the demography of pronghorn in GTNP. The pronghorn population growth rate (λ_t) based on the survival of fawns at the wolf-abundant sites was consistently greater than 1.0 (Fig. 4b). In addition, the model projected a likely 73% increase in population size within 10 years (Fig. 6b), and the confidence intervals on $\Delta\lambda_t$ were ≥ 0 for all time horizons beyond 13 years (Fig. 5a). Thus, there is considerable evidence that wolf recolonization will have a positive effect on pronghorn population dynamics, resulting in a larger population size and reduced probability of extinction.

Model advantages and further applications

Elasticity analysis is frequently used to assess potential impacts of alternative management scenarios, and the technique has proven useful for identifying the vital rate to which population growth is most sensitive (e.g., Crouse et al. 1987, Wisdom and Mills 1997, Crooks et al. 1998). However, the ability to predict potential changes in population growth is often hampered by uncertainty regarding the extent to which the identified vital rate can be manipulated through management action (Mills et al. 1999). Furthermore, long-lived species that produce numerous offspring typically have high adult survival elasticities (Heppell et al. 2000), which may lead wildlife managers to conclude that juvenile survival has little impact on population growth. Conversely, our simulation model projects that differences in neonatal survival rates between wolf-free and wolf-abundant areas are sufficient to alter the trajectory of the pronghorn population from a declining to an increasing trend. Thus, while we do not advocate using simulation models to make absolute predictions about future population numbers, approaches such as ours are useful for making relative comparisons of the effects of ecological factors or alternative management actions on population growth.

Many studies have used well-designed field experiments to evaluate changes in vital rates, especially survival (Murray and Patterson 2006), in response to ecological factors (e.g., Johnson et al. 2006), or



PLATE 1. A female pronghorn (*Antilocapra americana*) grooms her fawn prior to nursing. In Grand Teton National Park, Wyoming (USA), the increase in fawn survival rates at sites recolonized by wolves (*Canis lupus*) was sufficient to alter the trajectory of the pronghorn population from a declining to an increasing trend. Photo credit: Irene Greenberg.

management actions (e.g., Clutton-Brock and Loneragan 1994). The population growth rate, which incorporates all vital rates and thus is a more robust measurement of population-level impacts, has also been used to evaluate population response to ecological and management changes (e.g., Anthony et al. 2006). These analyses are retrospective approaches that test whether the treatment or ecological factor had a population-level effect. In contrast, population projection models use previously collected data to project future changes in population size. Here we combined both approaches by using vital-rate data from a designed field experiment to project future effects on the pronghorn population growth rate and population size under wolf-free and wolf-abundant scenarios. Although population viability analyses provide predictions of extinction probability or population size over a given time frame under different management scenarios (e.g., Linkie et al. 2006), they rarely allow for statistical comparisons between scenarios or produce confidence intervals on their predictions (Morris and Doak 2002). In contrast, our modeling approach allows for direct estimation of both the effect size and confidence interval associated with competing scenarios. This offers an advantage to wildlife managers who wish to know how much population size might differ in the future under alternate management scenarios, by providing a measure of confidence in that effect.

Model limitations and uncertainty

We have attributed the increase in neonatal survival and concomitant impact on pronghorn population dynamics to mesopredator suppression of coyotes. However, field studies of this nature all suffer from inherent limitations due to an inability to randomly assign treatments (i.e., wolf presence or absence), a lack of replication, and a failure to control potentially confounding variables (Diamond 1986). Thus, we acknowledge that factors other than mesopredator suppression of coyotes may have contributed to differences in coyote densities and coyote predation rates between wolf-free and wolf-abundant areas. For instance, coyote densities at the Gros Ventre site are likely impacted by human hunting, as the site is located beyond the protected boundaries of GTNP (Fig. 1; Berger and Gese 2007). In addition, the presence of large numbers of white-tailed jackrabbits (*Lepus townsendii*) at the Gros Ventre site during the summer of 2004 (K. Berger, *personal observations*), coupled with the recent functional extinction of white-tailed jackrabbits inside the Park, may have contributed to higher fawn survival rates at the Gros Ventre site in 2004 due to prey switching by coyotes (Berger et al. 2008). Although neither of these factors can be discounted, they do not adequately explain the congruence in coyote densities and neonatal survival rates at the two wolf-abundant areas.

We also acknowledge that increases in the pronghorn population size represented by the upper confidence interval (Fig. 6b) are unlikely to be observed for several reasons. First, our model does not incorporate negative density dependence in population growth. Although there is no evidence of negative density dependence at current populations levels (Fig. 3), declines in the population growth rate would likely occur long before a population size of ~2500 is reached (Fig. 6b). The threshold at which density dependence might be important is unclear, however, as the number of pronghorn that summer in the Park is currently far below the historical level of "a few thousand" during the 1800s (Deloney 1948). Furthermore, high population levels might not be achieved because habitat loss resulting from development of gas wells and attendant infrastructure on pronghorn winter range has the potential to substantially decrease overwinter survival rates of all stage classes (Berger et al. 2006). Consequently, any increase in the population growth rate due to improvements in neonatal survival may be more than offset by human-induced compensatory increases in overwinter mortality.

Conclusions

Our model represents a heuristic tool to evaluate pronghorn population response to an ecological perturbation resulting from wolf reintroduction. As such, the results should not be viewed as predictive of future population numbers, but rather as a relative assessment of the population-level impact that may result due to

changes in neonatal survival following wolf recolonization.

Sensitivity analyses performed for long-lived species with high adult survival rates typically indicate that juvenile survival has relatively little impact on population growth (Heppell et al. 2000). However, our simulation model projects that differences in neonatal survival rates between wolf-free and wolf-abundant areas are sufficient to alter the trajectory of the pronghorn population from a declining to an increasing trend. Thus, our results demonstrate the utility of simulation modeling to move beyond changes in vital rates to assess potential population-level impacts associated with different management scenarios. This approach may also be useful to ecologists who wish to compare outcomes of field manipulations against predictions based on ecological theories.

Our results support the hypothesis that mesopredator release of coyotes, resulting from the extirpation of wolves throughout much of North America, contributes to poor recruitment of pronghorn fawns observed in some systems. Thus, wolf restoration holds promise for enhancing ungulates populations by reducing coyote predation rates on neonates of species such as pronghorn, mule deer, and white-tailed deer. This finding may be of particular relevance to wildlife managers affiliated with national parks, which operate under the paradigm of natural regulation (Huff and Varley 1999). Consequently, lethal control of mesocarnivores, a controversial but commonly employed method in attempts to enhance ungulate survival rates, is likely to be deemed incompatible with management philosophy.

Finally, given the apparent disproportionate improvement in the survival rates of male fawns, wolf recolonization may enhance the number of male pronghorn available to human hunters. Thus, our findings have important applications for both wildlife management and conservation. To the extent that large carnivores exert top-down forces on systems, our results suggest that their loss or removal may result in unanticipated effects on ecological communities that may lead to further decreases in biodiversity.

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APPENDIX

A method to estimate the number of reproductive females in the population and neonatal survival rates from count data (*Ecological Archives* A018-019-A1).