CONSERVATION IMPLICATIONS OF FOOD WEBS INVOLVING WOLVES, COYOTES, AND PRONGHORN

by

Kim Murray Berger

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

UTAH STATE UNIVERSITY
Logan, Utah

2007

ABSTRACT

Conservation Implications of Food Webs Involving Wolves, Coyotes, and Pronghorn

by

Kim Murray Berger, Doctor of Philosophy

Utah State University, 2007

Major Professor: Eric M. Gese
Department: Wildland Resources

Coyote (*Canis latrans)* predation is an important factor in the mortality of neonatal pronghorn (*Antilocapra americana)*. It has been suggested that the extirpation of gray wolves (*Canis lupu*s) contributed to an overall increase in coyote densities and a concomitant rise in predation rates on pronghorn fawns, a process known as trophic cascades. To test this hypothesis we contrasted cause-specific mortality and survival rates of fawns captured at wolf-free and wolf-abundant sites; used demographic modeling to assess the impact of wolves on pronghorn population dynamics; and evaluated coyote survival rates, causes-specific mortality, and spatial segregation with wolves, to identify mechanisms by which wolves limit coyote densities. Fawn survival rates were 400% higher, and coyote densities 33% lower, at sites used by wolves. Wolves killed 56% of transient coyotes, and dispersal rates of transients were 117% higher at the wolf-abundant site; thus, differential effects on solitary coyotes may be an important mechanism by which wolves reduce coyote densities. Our results support the hypothesis that the extirpation of wolves contributes to high rates of coyote predation on pronghorn fawns, and add to a growing body of evidence demonstrating the importance of top-down forces in structuring the dynamics of consumer-resource interactions.

(169 pages)

ACKNOWLEDGMENTS

Funding for this research was provided by Grand Teton National Park and the Biological Resources Division of the U.S. Geological Survey under Cooperative Agreement No. 01CRAG0031, with additional support from the Wildlife Conservation Society, National Wildlife Research Center at Utah State University, NatureFlight Foundation, and Earth Friends Foundation. I thank Noah Weber, Renee Wulff, Mike Nordell, Jana Martinez, Sonja Berger, and the pronghorn capture team volunteers for field assistance, and Jim Pehringer (Wildlife Services) for assistance with coyote captures. Grand Teton National Park, the Wyoming Game & Fish Department, the U.S. Fish & Wildlife Service, and the U.S. Forest Service granted necessary permits. Mike Jimenez, Sarah Dewey, and Lisa Robertson provided wolf locations. I am indebted to Mary Conner for her infinite patience and assistance with issues related to Program MARK, simulation modeling, and statistical analysis, and Gary White for indulging all my "true or false" questions about random effects models and variance components. John Fieberg graciously provided code for the analysis of home-range overlap. I thank Eric Gese for his professionalism throughout the graduate school process, for allowing me to pursue my intellectual interests while still providing guidance when I needed it, and for somehow finding time to assist with field work every year. John Bissonette, Mary Conner, Dan Rosenberg, and Phaedra Budy provided thoughtful comments on my manuscripts. Lastly, I thank Joel for being a source of inspiration, for his patience during my long absences from home, and for being my biggest fan.

Kim Murray Berger

PREFACE

Chapter 2, Does Interference Competition with Wolves Limit the Distribution and Abundance of Coyotes?, will be submitted to the *Journal of Animal Ecology*. The sole co-author will be Eric M. Gese. Chapter 3, Evidence of a Species-Level Trophic Cascade in a Terrestrial Food Web Involving Wolves, Coyotes, and Pronghorn, will be submitted to *Ecology*. Coauthors will be Eric M. Gese and Joel Berger. Chapter 4, Recolonizing Wolves and Mesopredator Suppression of Coyotes: Impacts on Pronghorn Population Dynamics, will be submitted to *Ecological Applications*. The sole co-author will be Mary M. Conner.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

JUSTIFICATION AND BACKGROUND

Research on ungulate population size and behavior provides a scientific basis for managing these species and the ecosystems upon which they depend. Much less is known, however, about the roles played by carnivores such as wolves (*Canis lupus*) and coyotes (*Canis latrans*), especially their involvement in ecosystem function. Recent studies suggest that wolves have the capacity to limit elk (*Cervus elaphus*), moose (*Alces alces*), and bison (*Bison bison*) calf survival (Smith et al. 2000), and thus have the potential to shape the demography, behavior, and prevalence of these species. Less understood, however, are indirect ecosystem-level effects of recolonizing wolves. For example, where wolves have been extirpated for >75 years, such as in Grand Teton National Park (GTNP), moose occur at higher densities and have reduced both willow communities and the diversity and abundance of neotropical songbirds dependent upon them (Berger et al. 2001).

Wolves were reintroduced to Yellowstone National Park (YNP) in the spring of 1995 (Smith et al. 2003). Verified sightings of wolves in the Jackson Hole area emerged during the winter of 1997, and documented kills of elk first occurred in May of 1997 (U.S. Fish and Wildlife Service, *unpublished data*). During the winter of 1997-98, three wolf packs visited areas in and around GTNP. Since then, four wolf packs (Gros Ventre, Teton, Delta, and Nez Percé) have visited the Jackson Hole area. In 1999 and again from 2001-2004, the Teton wolf pack denned at Elk Ranch in the northeastern part of GTNP.

In 2002, the Teton wolf pack grew to 23 members with the addition of 11 pups; however, the subsequent dispersal of 9 yearlings in 2003 reduced the pack size to 14 individuals. In 2004, the Teton wolf pack numbered 17 individuals, including 9 pups.

Changes in the number of one carnivore species can lead to an increase or decrease in the abundance of another carnivore (mesopredator release or suppression; Soulé et al. 1988, Crooks and Soulé 1999), with resulting complex changes in prey populations. For instance, in the absence of wolves, coyote populations are thought to expand (Peterson 1995). Coyotes, which are both predators and scavengers, exert ecological effects through competition with other mesocarnivores, such as red foxes (*Vulpes vulpes*; Sovada et al. 1995). More importantly, in the absence of wolves, high densities of coyotes may threaten the persistence of species such as pronghorn (*Antilocapra americana*) by limiting fawn recruitment (Byers 1997).

Pronghorn in the Greater Yellowstone Ecosystem (GYE) have experienced recent population declines in both Yellowstone and Grand Teton national parks (Clark 2001). The number of pronghorn summering in Grand Teton and on adjacent Forest Service lands in the Gros Ventre River Drainage (GVRD) reached a peak of 424 animals in 1991, and has since declined to 212 as of August 2004 (Wyoming Game and Fish, *unpublished data*). In Yellowstone, coyote predation on fawns is an important factor in the population decline (J. Byers, *personal communications*); however, little is known about the cause of the decline in GTNP. It may stem from changes in habitat, weather, disease, predation, or from factors related to residential and energy development on pronghorn winter range.

Fall classification counts (i.e., surveys to record the distribution of animals by age and sex) indicate fawn recruitment in the Jackson Hole area is low (Wyoming Game and

Fish, *unpublished data*). However, the observed low fawn:doe ratios could arise as a consequence of poor fawn survival or low fecundity. Factors responsible for the consistently lower fawn:doe ratios in GTNP relative to the GVRD are also not known. Differential predation rates may exist in these two areas, or perhaps pregnant females are simply unable to reach the Park prior to parturition.

The motivation for this study was twofold. First, pronghorn that summer in GTNP are of particular conservation interest because they have the longest migration (> 193 km) of any terrestrial mammal between central Canada and Argentina (Berger 2004). A better understanding of the forces driving pronghorn population dynamics, especially factors that may be limiting juvenile recruitment, is needed to assist the Park in developing effective management strategies to preserve this unique population.

Second, the return of wolves to Grand Teton represents a natural experiment (*sensu* Diamond 1986) by which to assess some of the ecosystem-level effects associated with restoration of an apex carnivore. It provides an opportunity to evaluate the extent to which various densities of one carnivore species may alter the abundance or distribution of another, as well as how these changes may affect species at lower trophic levels. Specifically, wolf recolonization may have implications for pronghorn persistence because wolves are thought to compete with coyotes (Peterson 1995), a primary predator of neonate pronghorn.

The purpose of this study was to investigate the effects of recolonizing wolves on pronghorn population persistence, as mediated by changes in the distribution and abundance of coyotes. Specific questions addressed were: 1) Are coyotes limited by competition with wolves? 2) If so, by what mechanism(s) do wolves alter coyote densities? 3) What effects do changes in coyote densities have on pronghorn fawn survival? and 4) What are the implications for changes in fawn survival on pronghorn population dynamics?

LITERATURE CITED

Berger, J. 2004. The last mile: how to sustain long-distance migrations in mammals. Conservation Biology **18**:320-331.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications **11**:947-960.

Byers, J. A. 1997. American pronghorn: social adaptations & the ghosts of predators past. University of Chicago Press, Chicago, Illinois, USA.

Clark, W. E. 2001. History and management of Yellowstone National Park pronghorn. Proceedings Pronghorn Antelope Workshop **19**:107.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563-566.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 *in* J. Diamond and T. Case, editors. Community ecology. Oxford University Press, New York, New York, USA.

Peterson, R. O. 1995. Wolves as interspecific competitors in canid ecology. Pages 315-324 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves. Circumpolar Press, Edmonton, Alberta, Canada.

Smith, D. W., L. D. Mech, M. Meagher, W. E. Clark, R. Jaffe, M. K. Phillips, and J. A. Mack. 2000. Wolf-bison interactions in Yellowstone National Park. Journal of Mammalogy **81**:1128-1135.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. Bioscience **53**:331-340.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wrights, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology **2**:75-92.

Sovada, M. A., A. B. Sargeant, and J. W. Grier. 1995. Differential effects of coyotes and red foxes on duck nest success. Journal of Wildlife Management **59**:1-18.

CHAPTER 2

DOES INTERFERENCE COMPETITION WITH WOLVES LIMIT THE DISTRIBUTION AND ABUNDANCE OF COYOTES?[1]

Abstract. Interference competition with wolves (*Canis lupus*) is hypothesized to limit the distribution and abundance of coyotes (*Canis latrans*), and the extirpation of wolves is often invoked to explain the expansion in coyote range throughout much of North America. We used spatial and seasonal heterogeneity in wolf distribution and abundance to test the hypothesis that interference competition with wolves limits the distribution and abundance of coyotes. From August 2001 to August 2004, we gathered data on cause-specific mortality and survival rates of coyotes radio-collared at wolf-free and wolf-abundant sites in Grand Teton National Park (GTNP), Wyoming, to determine whether mortality due to wolves is sufficient to reduce coyote densities. We examined whether spatial segregation limits the local distribution of coyotes by evaluating home-range overlap between resident coyotes and wolves, and by contrasting dispersal rates of transient coyotes captured in wolf-free and wolf-abundant areas. Finally, we analyzed data on population densities of both species at three study areas across the Greater Yellowstone Ecosystem (GYE) to determine whether an inverse relationship exists between coyote and wolf densities. Although coyotes were the numerically dominant predator across the GYE, densities varied spatially and temporally in accordance with wolf abundance. Mean coyote densities were 33% lower at wolf-abundant sites in

---

[1] Coauthored by Kim Murray Berger and Eric M. Gese

GTNP, and densities declined 39% in Yellowstone National Park following wolf reintroduction. A strong negative relationship between coyote and wolf densities ($\beta = -3.988$, $P < 0.005$, $r^2 = 0.54$, $n = 16$), both within and across study sites, supports the hypothesis that competition with wolves limits coyote populations. Overall mortality of coyotes resulting from wolf predation was low, but wolves were responsible for 56% of transient coyote deaths ($n = 5$). In addition, dispersal rates of transient coyotes radio-collared at wolf-abundant sites were 117% higher than for transients in wolf-free areas. Our results support the hypothesis that coyote abundance is limited by competition with wolves, and suggest that differential effects on survival and dispersal rates of transient coyotes are important mechanisms by which wolves reduce coyote densities.

INTRODUCTION

Interspecific competition among large carnivores has important implications for the structure and function of carnivore communities (Palomares and Caro 1999, Caro and Stoner 2003). Among carnivores, interactions often occur directly in the form of interference competition (Ricklefs 1979), which involves harassment, kleptoparasitism, or outright killing, and may result in spatial or temporal avoidance, reductions in the density of the subordinate species, or even competitive exclusion from certain habitats or regions (Linnell and Strand 2000). In more extreme cases, the victim may be consumed by the dominant species, an interaction known as intraguild predation that results in complex trophic interactions exhibiting characteristics of both competition and predation (Polis and Holt 1992).

Although numerous studies have focused on the effects of interspecific competition on the persistence of threatened carnivores (Caro 1994, Laurenson 1995, Creel and Creel 1996, Durant 1998, 2000), interference competition may also have implications for the management of abundant native species. In particular, because the loss of top carnivores often results in increases in mesocarnivore abundance and concomitant impacts on prey populations (Soulé et al. 1988, Crooks and Soulé 1999, Chapter 3), ecosystem restoration has been suggested as an alternative to traditional methods such as lethal control as a means to reduce overabundant species (Goodrich and Buskirk 1995).

In North America, interference competition with wolves (*Canis lupus*) is hypothesized to be an important factor influencing the distribution and abundance of coyotes (*Canis latrans*; Thurber et al. 1992, Peterson 1995). Coyotes increased their range during the past two centuries following the extirpation of wolves from much of the contiguous Unites States (Parker 1995, Peterson 1995). In addition, coyotes went extinct on Isle Royale following wolf colonization in the late 1940s (Krefting 1969). Incidents of wolves killing coyotes are commonly reported (Berg and Chesness 1978, Carbyn 1982, Paquet 1992, Thurber et al. 1992, Arjo 1998); however, the extent to which coyote distribution and abundance are reduced as a consequence is poorly understood.

In this study, we used spatial, seasonal, and temporal heterogeneity in wolf distribution and abundance, resulting from the recent reintroduction of wolves to the Greater Yellowstone Ecosystem (GYE), to test the hypothesis that interference competition with wolves limits the distribution and abundance of coyotes. We assessed cause-specific mortality and survival rates of coyotes radio-collared at wolf-free and wolf-abundant sites in Grand Teton National Park (GTNP), Wyoming, USA, to determine whether mortality due to wolves is sufficient to reduce coyote densities. Next, we looked for evidence that spatial segregation between coyotes and wolves limits the local distribution of coyotes by evaluating the degree of home-range overlap between resident coyotes and wolves, and by contrasting dispersal rates of transient coyotes radio-collared in wolf-free and wolf-abundant areas. Finally, we analyzed data on population densities of both species at three study areas in the GYE that have been recolonized by wolves since the mid-1990s to determine whether an inverse relationship exists between coyote and wolf densities.

METHODS

Study site

The field component of the study took place in GTNP (43˚ 39' N, 110˚ 40' W) between August 2001 and August 2004. Field sites were selected to exploit spatial and seasonal variation in wolf distribution and abundance. The wolf-abundant site was located at Elk Ranch, an area used extensively by wolves during denning and pup rearing (May - September) and periodically throughout the winter (November-April; Fig. 2-1). In contrast, the Antelope Flats site was not used by wolves during either season. Because the sites were located within the boundaries of GTNP (Fig. 2-1), human harvest of coyotes was not legally permitted in either area. Vegetation at both sites is characterized by shrub-steppe habitat dominated by big sagebrush (*Artemesia tridentata*), low sagebrush (*A. arbuscula),* Antelope bitterbrush *(Purshia tridentata*), and associated understory grasses of the genera *Stipa*, *Bromus,* and *Poa*. Common forbs include lupine (*Lupinus caudatus*) and arrowleaf balsamroot (*Balsamorrhiza sagitata*).

Capture and monitoring of coyotes

We monitored the survival and movements of coyotes radio-collared at the wolf-free and wolf-abundant sites. Coyotes were captured using padded foothold traps with offset jaws and attached tranquilizer tabs (Balser 1965), or by a net-gun fired from a helicopter (Gese et al. 1987), and were fitted with VHF radio collars with 8-hour mortality sensors (Advanced Telemetry Systems Inc., Isanti, Minnesota, USA). We recorded the sex and weight of each animal and estimated age based on tooth wear (Gier 1968).

The territorial status of each coyote was classified as either a resident or a transient (Bowen 1981, Gese et al. 1988). Resident coyotes were members of packs that actively defended well-defined territories, whereas transients showed weak fidelity to large areas that encompassed the home ranges of several resident packs, but were not associated with a particular pack or territory.

Survival and cause-specific mortality of coyotes

When mortality signals from radio-collared coyotes were detected, carcasses were recovered and necropsied to evaluate cause-specific mortality. We classified cause of death as human, predation, disease, other, or unknown. Differential characteristics of predator kills such as wounds, hemorrhaging, carcass consumption, and caching behavior, as well as tracks and signs at carcass sites, were used to assign kills to a specific predator species (O'Gara 1978). When disease was suspected, carcasses were frozen and shipped to the Wyoming State Veterinary Laboratory (Laramie, Wyoming) for further evaluation.

Survival rates of coyotes were estimated using a known fate model in Program MARK (White and Burnham 1999). The analysis was based on monthly encounter histories where encounters represented either initial captures or relocations by radio-telemetry during subsequent months. We evaluated 18 models to assess the effects of site (wolf-free or wolf-abundant), season (summer [May - September] or winter [October - April]), year, and covariates (sex and territorial status) on coyote survival. The most global model we could parameterize with our data included parameters for site, territorial status, season, sex, and year ($S_{site+status+season+sex+year}$), where S was the estimated monthly survival rate of coyotes. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and Akaike weights to assess model fit (Burnham and Anderson 2002). Model averaging (Burnham and Anderson 2002) was used to estimate monthly survival rates of coyotes. Seasonal and annual survival estimates were calculated from monthly survival estimates following Burnham et al. (1987), and standard errors and 95% confidence intervals were approximated using the Delta method (Seber 1982). Means and associated standard errors are reported throughout.

Home-range analysis and spatial segregation

Coyotes were monitored using a hand-held receiver from a vehicle, on foot, and from a fixed-wing aircraft. Point and sequential locations ($\bar{x} = 78 \pm 17$ per pack) obtained by ground and aerial telemetry were used to develop annual coyote and seasonal wolf home ranges (Gese et al. 1990). Relocations were attempted at least weekly and were obtained throughout the 24-hour period to reduce bias in home-range estimates (Smith et al. 1981). For ground locations, ≥ 3 compass bearings with intersecting angles between 20° and 160° were used (White and Garrott 1990). Locations were estimated using the program Locate II (Pacer Ltd., Truro, N.S.), and home ranges by the fixed-kernel (FK) density method (Worton 1989). To estimate home ranges, we used an *ad hoc* smoothing parameter ($h_{ad\ hoc}$) designed to prevent over- or under-smoothing. This method involves choosing the smallest increment of the reference bandwidth (h_{ref}) that results in a contiguous 95% kernel home-range polygon that contains no lacuna (i.e., $h_{ad\ hoc} = 0.9*h_{ref}, 0.8*h_{ref}, 0.7*h_{ref}$, etc.; J. G. Kie, *unpublished manuscript*). Home-range analyses were performed with the ‘adehabitat’ package (Calenge 2006) in program R (R Development Core Team 2006).

Overlap of coyote and wolf pack home ranges (95% FK) and core areas (60% FK; Shivik et al. 1996) was evaluated using two complementary methods to look for evidence of spatial segregation. For each coyote pack-wolf pack pair, overlap in home ranges and core areas was measured as:

$$\text{Percentage overlap} = \frac{\text{coyote pack home range} \cap \text{wolf pack home range}}{\text{coyote pack home range}} \times 100.$$

Although interpretation of this index is straightforward, percentage overlap provides only a crude index of spatial segregation because it does not consider the extent to which overlap areas are used by either species (Powell 2000). Consequently, this measure may result in a large estimate of overlap between coyote and wolf pack home ranges even though the probability of finding the two species in the same area is relatively low

(Fieberg and Kochanny 2005). Therefore, we also measured home-range overlap by assessing the extent to which overlap areas were used by the two species using the utilization distribution overlap index (UDOI) proposed by Fieberg and Kochanny (2005):

$$\text{UDOI} = A_{i,wolf} \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \hat{\text{UD}}_i(x,y) \times \hat{\text{UD}}_{wolf}(x,y)\,dxdy$$

where $A_{i,wolf}$ is the area of overlap between the coyote pack and wolf pack home ranges, and $\hat{\text{UD}}_i$ and $\hat{\text{UD}}_{wolf}$ are the estimated utilization distributions for the *i*th coyote pack and wolf pack, respectively. Values of UDOI <1 indicate less overlap relative to uniform space use, whereas values >1 indicate higher than normal overlap relative to uniform space use (Fieberg and Kochanny 2005). Calculations of percentage overlap and UDOI were performed in program R (R Development Core Team 2006). Because transient coyotes use large areas and do not have well-defined home ranges, we contrasted dispersal rates of transient coyotes radio-collared at wolf-free and wolf-abundant sites to look for evidence of spatial segregation between transient coyotes and wolves. We classified a coyote as dispersing if it permanently emigrated from the study site at which it had been captured and radio-collared.

Coyote and wolf densities

To evaluate the relationship between coyote and wolf densities, we summarized data on population densities of coyotes and wolves at three study areas across the GYE: 1) GTNP, 2) the Lamar River Valley (LRV), and 3) the Northern Madison Study Area (NMSA). For GTNP, we included data from the Elk Ranch and Antelope Flats sites, as well as a second wolf-abundant site located on Forest Service land adjacent to GTNP in the Gros Ventre River drainage (Fig. 2-1). Unlike the Elk Ranch and Antelope Flats sites, coyotes are subject to human harvest at the Gros Ventre site, as the area is located outside Park boundaries and the State of Wyoming permits unregulated hunting of coyotes year-round.

The LRV study area (70 km^2) is located in Yellowstone National Park (YNP) in northwestern Wyoming (Fig. 2-1). Following a more than 50-year absence, wolves were translocated to YNP from western Canada in 1995-96 (Smith et al. 2003). Within 5 years of reintroduction, 65 wolves comprising four packs were utilizing the area surrounding the LRV (Smith et al. 2004). Because the site is located within the protected boundaries of YNP, coyotes are not subject to legal harvest at the LRV.

The NMSA (680 km^2) is located on a private ranch in southwestern Montana, approximately 50 km northwest of YNP (Fig. 2-1). A single wolf pack recolonized the NMSA during the winter of 2002 (Atwood 2006). Coyotes are subjected to extensive culling on the NMSA, with an estimated 50 individuals removed each year during late winter (T. C. Atwood, *personal communications*).

At all study areas, wolf and coyote densities included juveniles born during the prior summer. No effort was made to adjust coyote or wolf densities for disparities introduced by methodological differences in home-range calculations. However, because coyote densities reported for YNP (Gese et al. 1996a, 1996b, Allen et al. 1999, S. Grothe, *unpublished data*, T. A. Switalski, *unpublished data*) reflected residents only, we increased the reported densities by the average percentage of transients in the coyote population (6.4% ± 3.9%; E. M. Gese, *unpublished data*) from 1991-1993. Although the assumption that transients comprised a constant proportion of the YNP coyote population was likely invalid, this adjustment should produce better estimates for comparative purposes than simply presuming transient densities were zero for all years.

We evaluated the relationship between coyote and wolf densities by ordinary least-squares regression using both linear and non-linear models (Bates and Watts 1988). Examination of residuals was used to assess the extent to which the assumptions of regression were met. Because coyotes were subject to human harvest at the NMSA and the Gros Ventre site, we included a dummy variable to distinguish protected from unprotected areas.

RESULTS

Coyote captures

We radio-collared 38 coyotes at the wolf-abundant ($n = 15$) and wolf-free ($n = 23$) sites. The percentage of coyotes classified as residents and transients was 51% ($n = 18$) and 49% ($n = 17$), respectively, and did not differ between the wolf-free (41% residents and 59% transients) and wolf-abundant (54% residents and 46% transients) sites (Likelihood ratio test, $P = 0.458$). In three cases the animal died too soon after capture for territorial status to be determined. Two coyotes initially classified as residents subsequently became transients when pack members died, and two transient coyotes became residents shortly before the end of the study.

At the time of capture, the mean ages of animals classified as residents and transients did not differ and were 3.17 ± 0.36 and 2.41 ± 0.46 years, respectively (Student's *t* test, $P = 0.202$). The mean ages of residents and transients at the time of death also did not differ and were 4.10 and 3.56 years, respectively (Student's *t* test, $P = 0.564$). The sex ratio of captured coyotes was 1:1.533 in favor of females, but did not differ from parity (Binomial, $P = 0.324$). Mean pack size did not differ between years and was 3.18 ± 0.18 ($n = 11$) in 2003 and 3.22 ± 0.22 ($n = 9$) in 2004 (Student's *t* test, $P = 0.89$). Although mean pack size did not differ significantly between the wolf-free (3.27 ± 0.18, $n = 15$) and wolf-abundant (3.00 ± 0.00, $n = 5$) sites, there was evidence of a trend toward slightly smaller pack sizes in areas used by wolves (Student's *t* test, $P = 0.164$).

Coyote survival rates and cause-specific mortality

We included 28 marked individuals in the analysis of coyote survival. Seven animals were excluded from the survival analysis because they dispersed to areas beyond our study sites, and three were omitted because their territorial status was unknown at the time of death. On the basis of minimum AIC_c, the model of coyote survival that best fit our data contained parameters for territorial status and season (Table 2-1). The parameter estimates from the top-ranked model suggested survival of resident coyotes was higher than for transients ($\beta = 0.483 \pm 0.249$; Wald test, $P = 0.052$), and survival rates were higher during summer than during winter ($\beta = -1.236 \pm 0.645$; Wald test, $P = 0.055$). The second- ($\Delta AIC_c = 1.334$) and third-ranked ($\Delta AIC_c = 1.556$) models suggested that survival rates also differed among years and were higher at the wolf-free site (Table 2-1). However, the confidence intervals on the coefficients for the year and site variables overlapped zero, indicating there was no clear effect of site or year on survival rates. The fourth-ranked model ($\Delta AIC_c = 1.685$) indicated that season alone was the best predictor of coyote survival. Together, the top four models accounted for 63% of the Akaike weights (Table 2-1).

Seasonal model-averaged survival estimates for coyotes were lowest at the wolf-abundant site during the winter of 2004 ($\hat{S} = 0.680 \pm 0.129$), and highest at the wolf-free site during the summer of 2002 ($\hat{S} = 0.913 \pm 0.053$), but did not differ statistically between sites or among years (Table 2-2). Annual model-averaged survival estimates for coyotes were also lowest at the wolf-abundant site in 2004 ($\hat{S} = 0.601 \pm 0.166$), and highest at the wolf-free site in 2002 ($\hat{S} = 0.681 \pm 0.140$), but did not differ statistically between sites or among years (Table 2-2). Over the course of the study, survival of resident coyotes ($\hat{S} = 0.746 \pm 0.044$) was significantly higher (58%, $P = 0.052$) than that of transients ($\hat{S} = 0.471 \pm 0.113$; Fig. 2-2).

Cause-specific mortality of coyotes did not differ between sites (Fig. 2-3a; one-way ANOVA, $P = 1.00$). Human-related deaths accounted for 45% of total coyote mortality at both sites, followed by predation (30%), other (10%), and disease (5%). In 10% of cases, cause of death could not be determined because we either did not recover a carcass or the condition of the carcass was too poor for an accurate assessment. Although the percentage of coyote deaths attributable to various factors did not differ between wolf-free and wolf-abundant sites (Fig. 2-3a), mortality factors differed significantly based on territorial status (one-way ANOVA, $P = 0.001$). Whereas humans were responsible for 88% of all resident coyote deaths, 67% of transient coyote deaths resulted from predation (Fig. 2-3b). Wolves accounted for 83% ($n = 5$) of predation-related mortality and mountain lions (*Puma concolor*) for 17% ($n = 1$).

Spatial segregation of coyotes and wolves

Percentage overlap of coyote and wolf home ranges was 100% (95% FK: $\bar{x} = 100 \pm 0\%$, *n* = 4; Table 2-4), as the home ranges of all coyotes packs at the Elk Ranch site were completely subsumed within the wolf pack's home range. Percentage overlap of coyote and wolf core areas was considerably lower (60% FK: $\bar{x} = 48 \pm 4\%$, *n* = 4), however, and no locations of radio-collared resident coyotes were recorded in the vicinity of the wolf pack's den site, the location of greatest wolf activity within the wolf core area.

Based on the UDOI, coyote and wolf use of overlap areas was not uniform and the intensity with which specific areas were used differed between the two species. The UDOI ranged from 0.03 to 0.23 for home ranges (95% FK: $\bar{x} = 0.13 \pm 0.05$, *n* = 4; Table 2-4), and from 0.00 to 0.17 for core areas (60% FK: $\bar{x} = 0.08 \pm 0.04$, *n* = 4).

Dispersal rates of transient coyotes at the wolf-free (*n* = 6) and wolf-abundant (*n* = 13) sites were not statistically different (Likelihood ratio test, *P* = 0.140); however, there was an apparent trend towards markedly higher dispersal rates for transients captured at the wolf-abundant site (67%, *n* = 4), relative to the wolf-free site (31%, *n* = 4). No resident coyotes dispersed from either the wolf-free or wolf-abundant sites.

Relationship between coyote and wolf densities

Coyote densities were highest in areas lacking wolves, but showed considerable temporal variation independent of wolf densities (Table 2-3). Densities ranged from a low of 0.345 coyotes/km^2 at the wolf-free site (Antelope Flats) in GTNP in 2002, to a high of 0.726 coyotes/km^2 prior to wolf reintroduction at the LRV study area in 1994 (Table 2-3). Based on ordinary least squares regression, a linear model ($\mathit{coyote\ density} = 0.345 - 4.102 \times \mathit{wolf\ density} + 0.192 \times \mathit{protected\ status}$, $r^2 = 0.58$, $F_{2,14} = 9.49$, $P = 0.002$, $n = 16$; Fig. 2-4a) fit the data slightly better than a negative exponential model ($\mathit{coyote\ density} = e^{-1.001 - 15.921 \times \mathit{wolf\ density}} + 0.170 \times \mathit{protected\ status}$, $r^2 = 0.56$, $F_{2,14} = 8.76$, $P = 0.003$, $n = 16$; Fig. 2-4b), in terms of the proportion of the variance explained. However, the latter is a more biologically realistic model because coyote densities are bounded by zero. Both models suggest a strong negative relationship between coyote and wolf densities (linear model: $\beta = -4.102$, $P = 0.003$; negative exponential model: $\beta = -15.921$, $P = 0.030$), and a strong positive relationship between coyote densities and protected area status (linear model: $\beta = 0.192$, $P = 0.019$; negative exponential model: $\beta = 0.170$, $P = 0.031$). Note that heteroskedasticity in the residuals exists because coyote densities vary more widely in the data set when wolf densities are zero than at higher wolf densities (Figs. 4a,b). Consequently, although the estimated regression is not affected, the standard errors and confidence intervals represent a biased estimate of the true variance (Barreto and Howland 2006).

DISCUSSION

Effects of interference competition with wolves on coyote abundance

Coyotes were the numerically dominant predator across the GYE, but densities varied both spatially and temporally in accordance with wolf abundance (Table 2-3).

Mean coyote densities in the LRV declined by 39% following wolf reintroduction, and densities were 33% lower at wolf-abundant sites in GTNP compared to the wolf-free site (Table 2-3). This finding is consistent with previous observations that coyote densities appear higher in areas and years in which wolf densities are reduced (Carbyn 1982, Dekker 1989). Furthermore, the negative relationship between coyote and wolf densities, based on regression analysis, supports the hypothesis that competition with wolves limits coyote abundance. Alternatively, the inverse relationship in densities might simply reflect differential habitat selection by the two species based on the distribution of preferred prey. However, the latter explanation would not account for temporal reductions in coyote densities in the LRV following wolf reintroduction, unless natural shifts in the distribution of coyote prey simply coincided with the reintroduction of wolves.

Coyote populations fluctuate widely independent of the presence of wolves in relation to factors such as disease, food resources, and human persecution (Knowlton and Stoddart 1992, O'Donoghue et al. 1997). For instance, coyote densities at the LRV increased by 31% between 1991 and 1994, and densities at the wolf-free site in GTNP fluctuated by an average of 29% per year over the three-year study (Table 2-3). However, although the magnitude of fluctuations in coyote densities was similar, mean coyote densities in the LRV were significantly higher prior to wolf reintroduction ($\bar{x} = 0.639 \pm 0.050$) than following wolf reintroduction ($\bar{x} = 0.389 \pm 0.052$, Student's *t* test, $P = 0.014$), and mean densities were significantly higher in GTNP in wolf-free ($\bar{x} = 0.406 \pm 0.039$) versus wolf-abundant ($\bar{x} = 0.272 \pm 0.018$) areas (Student's *t* test, $P = 0.012$). Interestingly, coyote densities were lowest at NMSA even though wolf densities in the area were negligible (Table 2-3). This may result from the extensive harvest of coyotes by humans at the NMSA during the winter months (T. C. Atwood, *personal communications*).

Although our sample size is small ($n = 3$), the negative relationship between coyote and wolf densities does not appear to hold outside protected areas, as either no discernable pattern, or perhaps even a positive relationship, is evident from an analysis of these data points ($\beta = 3.80 \pm 1.73$, $P = 0.272$, $r^2 = 0.828$). If this pattern is indicative of the actual relationship outside protected areas, it may reflect that wolves can only persist outside reserves in areas where the potential for conflict with humans and livestock is low, and that these same factors also favor coyote populations. Anthropogenic factors can have a strong impact on coyote mortality rates, even within the purportedly protected boundaries of national parks. For instance, poisonous baits distributed illegally in GTNP during fall 2003 resulted in the deaths of 21% of all radio-collared coyotes, contributing to the reduction in coyote densities that occurred between 2003 and 2004 (K. M. Berger, *unpublished data*).

Despite early recognition of an apparent inverse relationship between coyote and wolf densities (Berg and Chesness 1978, Fuller and Keith 1981, Carbyn 1982, Dekker 1989), the mechanisms by which wolves reduce coyote populations have not been clear. Although wolves were reportedly responsible for a 50% reduction in the coyote population in the LRV between 1996 and 1998 (Crabtree and Sheldon 1999), rates of coyote predation by wolves reported in telemetry studies have consistently been low. For instance, based on our analysis of data in Arjo (1998) and Atwood (2006), wolves were responsible for the deaths of just 13% and 3% of radio-collared coyotes in northwestern

Montana and the NMSA, respectively. In contrast, cougars killed 40% of radio-collared coyotes in northwestern Montana (Arjo 1998) and 14% of coyotes at the NMSA (Atwood 2006). It is worth noting, however, that telemetry studies tend to focus on the fates of adult coyotes (>1 year) because of the propensity for juveniles to disperse from study sites. As there is evidence to suggest that juvenile coyotes are more vulnerable to attacks by wolves (e.g., 90% [$n = 20$] of mortalities recorded in Riding Mountain National Park were <1 year old; Paquet 1992), mortality rates attributed to wolves based on telemetry studies are likely biased low. However, as survival rates of juvenile coyotes are comparatively low independent of the presence of wolves (Gese et al. 1989), juvenile mortality due to wolves may be compensatory and thus have little impact on overall recruitment and coyote population dynamics.

Mortality of coyotes resulting from predation by wolves was similarly low in this study, with wolves accounting for the deaths of just 16% ($n = 5$) of all radio-collared coyotes. Notably, although wolves have not been previously reported to consume coyotes, we did document one instance during late winter in which a coyote carcass appeared to have been fed upon by wolves. Thus, intraguild predation of coyotes by wolves may occur during periods of food scarcity (Polis and Holt 1992, Palomares and Caro 1999). Although coyote hunting is not permitted in GTNP, humans were the primary cause of death of radio-collared coyotes (29%, $n = 9$). While some of these deaths occurred legally when coyotes left the protected boundaries of the Park ($n = 3$), the majority of human-related deaths (67%, $n = 6$) resulted from poaching.

While overall mortality of coyotes in GTNP attributable to wolves was low, the impact of wolves on coyotes differed significantly based on territorial status. Whereas humans were responsible for 88% (*n* = 7) of all resident coyote deaths (Fig. 2-3b), 67% (*n* = 6) of transient coyote deaths (representing 42% of all radio-collared transients) resulted from predation, with wolves accounting for 83% of predation-related mortality. In addition, although no coyotes were killed by wolves at the wolf-free site, three transients collared at the wolf-free site were killed by wolves in separate incidents when they ventured into areas frequented by wolves. The differential vulnerability of transients was further supported by the deaths of two former resident animals that were killed by wolves shortly after they became transients when other pack members died. Annual survival of transient coyotes was 58% lower than that of residents (Fig. 2-2). Although survival of transient coyotes is typically lower than that of residents independent of the presence of wolves, survival rates of transients in GTNP were lower than those reported for transients in other areas (Andelt 1982, Gese et al. 1989), suggesting that wolves may represent an additive source of mortality for transient coyotes. Thus, the extent to which wolves reduce coyote abundance through direct killing may vary with the proportion of transient individuals in the coyote population.

Several explanations could account for the observed differential vulnerability of transient coyotes to predation by wolves. Transients may have been unfamiliar with the terrain and thus less knowledgeable about the locations of refuges and escape routes (Gese 2001), or they may have been less able to avoid agonistic encounters because they were unaware of the hunting and ranging patterns of local wolves. A similar pattern has been reported in both vervet monkeys (*Cercopithecus aethiops)* and white-footed mice (*Peromyscus leucopus*), as individuals in novel surroundings (i.e., transients) suffer higher predation rates than those of residents (Metzgar 1967, Isbell et al. 1990).

Alternatively, due to their solitary nature, transients may have been more vulnerable if group size or vigilance is a deterrent to attacks by wolves. For instance, adolescent cheetahs (*Acinonyx jubatus*) in groups are more effective at deterring spotted hyenas (*Crocuta crocuta*) than singletons (Caro 1994), and both dwarf mongooses (*Helogale parvula*; Rasa 1986) and suricates (*Suricata suricatta*; Clutton-Brock et al. 1999) experience lower predation rates with increasing group size. In coyotes, the importance of group size is supported by an observed increase in the percentage of coyotes traveling in pairs or groups following wolf recolonization in both northwestern Montana and the LRV (Arjo 1998, Crabtree and Sheldon 1999). Atwood (2006) notes that numerically superior groups of coyotes are able to displace wolves from carcasses. Hence, the benefits of numerical superiority may extend to aversion of attacks by wolves. However, it is not known whether group size acts as an actual deterrent to wolf attacks, or whether group vigilance (Pulliam 1973) simply reduces the risk of surprise encounters.

Effects of interference competition with wolves on the distribution of coyotes

Based on the results of an early study (Fuller and Keith 1981), it is often suggested that resident coyotes avoid encounters with wolves by occupying the borders of wolf pack territories. However, with the exception of the immediate area surrounding the wolf pack's den site, we found no evidence that spatial segregation was an important mechanism facilitating coexistence of resident coyotes and wolves. Annual home ranges of all coyote packs at the wolf-abundant site were completely subsumed within the boundaries of the wolf pack's territory (Table 2-4). And, although mean overlap of coyote and wolf core areas was considerably lower (48 ± 28%), the core areas of the two coyote packs in closest proximity to the wolf core area still overlapped by nearly 100% ($\bar{x}$ = 97 ± 0.5%).

To our knowledge, no telemetry study has reported a high degree of spatial segregation between the two species. At the NMSA, overlap of coyote and wolf winter home ranges and core areas averaged 78 ± 5.54% and 82 ± 6.69%, respectively (Atwood 2006). In northwestern Montana, overlap of winter home ranges averaged 72%, while overlap of core areas averaged 8% (Arjo 1998). Although estimates of percentage overlap are not available for YNP, overlap of coyote and wolf home ranges in the LRV appears extensive based on the depicted locations of coyote home ranges within the boundaries of wolf pack territories (see Fig. 2-1 in Switalski 2002). In addition, Atwood (2006) notes that both the level of wolf activity and sites of wolf-killed prey were proportionally greater in coyote core areas than in coyote home ranges. Thus, rather than orienting home ranges to avoid encounters with wolves, coyote core areas may actually be configured to exploit wolf activity centers (Atwood 2006). A similar pattern of apparent attraction to wolves was also previously reported for coyotes in Riding Mountain National Park, Canada (Paquet 1992).

Although percentage overlap of coyote and wolf home ranges and core areas was extensive based on area alone, the UDOI for all packs was low, indicating differential use of these overlap areas by the two species. Thus, although wolves have not excluded coyotes from broad areas in GTNP, finer-scale spatial partitioning within coyote home ranges may mitigate agonistic encounters with wolves and facilitate coexistence.

As with cause-specific mortality, evidence of differential vulnerability of residents and transients based on spatial segregation was apparent when dispersal rates of transient coyotes were examined. Whereas only 31% of transient coyotes captured at the wolf-free site dispersed to other areas, 63% of transients captured at the wolf-abundant site dispersed to wolf-free regions of the Park, including 33% (n = 2) that moved from the wolf-abundant to the wolf-free site. Although the effect size in dispersal rates was large (117% higher at the wolf-free site) and likely had a biologically significant impact on site-specific coyote densities, our ability to detect a statistically significant difference was hampered by the small number of transient coyotes captured at the wolf-abundant site (n = 6). However, evidence suggests that the observed trend is indicative of actual differences in transient dispersal patterns between wolf-free and wolf-abundant areas. Most notably, in both cases in which transients failed to disperse from the wolf-abundant site, the animal was killed by wolves within months ($\bar{x} = 3.62 \pm 3.25$) of capture.

Previous studies have demonstrated that spatial segregation is an important mechanism facilitating persistence of subordinate species such as African wild dogs (*Lycaon pictus*) and cheetahs with lions (*Panthera leo*) and spotted hyenas (Laurenson 1995, Creel and Creel 1996, Durant 2000). As mortality rates of adult coyotes due to wolves are comparable to, or exceed, those reported for wild dogs and cheetahs due to lions and spotted hyenas (Creel and Creel 1996, Durant 2000), the failure of coyotes to exhibit similar patterns of spatial segregation with wolves may appear incongruous. However, whereas wild dogs and cheetahs kill most, or all, of the prey they consume (Kruuk 1972, Caro 1994), coyotes are both predators and scavengers. Thus, wolves represent not only a cost to coyotes in terms of the risk of a lethal attack, but also a potential energetic benefit, as scavenging from wolf-kills represents an important food resource for coyotes (Paquet 1992, Atwood 2006), especially during mild winters when winter-kills are scarce (Wilmers and Getz 2005). The need to balance these potential costs and benefits may account for the relatively low degree of spatial segregation between resident coyotes and wolves compared to that exhibited by wild dogs and cheetahs with lions and spotted hyenas (Sih 1992, Durant 2000). Furthermore, neither the energetic benefits nor associated risks are likely to be uniformly distributed among all coyotes. Access to carcasses is a function of both relative pack size and dominance rank within the pack (Gese et al. 1996a, Gese 2001, Atwood 2006), and vulnerability to attack may also vary with group size (Rasa 1986, Caro 1994, Clutton-Brock et al. 1999). Thus, due to their solitary nature, transient coyotes should be differentially vulnerable to attacks by wolves, and least able to scavenge from wolf carcasses, resulting in the greater degree of spatial segregation exhibited by transient coyotes.

Conclusions

Our results support the hypothesis that coyote abundance is limited by competition with wolves, and that the extirpation of gray wolves contributes to high densities of coyotes observed in some areas. Although mortality from wolves alone appears insufficient to drastically suppress coyote populations throughout the GYE, our results suggest that interference competition with wolves has resulted in localized population reductions. For instance, differential effects of wolves on survival and dispersal rates of transient coyotes likely accounts for the considerable disparity in transient coyote densities (0.188 ± 0.019/km^2 versus 0.039 ± 0.005/km^2; Chapter 4), and thus overall coyote densities (0.406 ± 0.039/km^2 versus 0.272 ± 0.018/km^2; Table 2-3), between wolf-free and wolf-abundant sites in GTNP.

Our results also suggest that the impact of wolves on coyote densities may extend to adjacent areas that are not directly used by wolves. Specifically, 67% of transient coyotes captured at the wolf-abundant site dispersed to wolf-free areas of the Park, including two transient coyotes that emigrated to the wolf-free study site. Thus, efforts by transient coyotes to balance costs of intra- and inter-specific aggression may result in an increase in coyote densities in adjacent wolf-free areas. Conversely, three transient coyotes that predominantly used the wolf-free site were killed when they ventured into areas intermittently used by wolves, underscoring the potential for wolves to reduce coyote densities in adjacent wolf-free areas. Although the net effect of wolves on transient densities at the wolf-free site was negative, our sample size ($n = 5$) was too small for definitive conclusions to be drawn.

Finally, our results do not support the hypothesis that competition with wolves limits the distribution of coyotes. Unlike Isle Royale, localized extirpation of coyotes in the GYE appears improbable as coyote mortality rates, even with additional mortality from wolves, do not approach levels projected to lead to extirpation (Connolly 1978, Gese 2005). Rather, regression analysis indicates that coyote populations in wolf-abundant areas of the GYE may simply fluctuate around a reduced mean density (i.e., perhaps a mean density of ~ 0.3 coyotes/km^2 in wolf-abundant areas versus ~ 0.5 coyotes/km^2 in areas lacking wolves; Fig. 2-4). The failure of wolves to exclude coyotes is not surprising, as unlike Isle Royale (Krefting 1969, Mech 1966), the GYE is not spatially closed and spatial heterogeneity in both habitat and wolf distribution creates refugia that likely facilitate coyotes persistence even in close proximity to wolves (*sensu* Durant 1998). Thus, human alteration of landscapes due to agriculture, logging, livestock grazing, and development may be a more parsimonious explanation for the increase in coyote distribution throughout North America than the extirpation of gray wolves from much of their former range.

LITERATURE CITED

Allen, J. J., M. Bekoff, and R. L. Crabtree. 1999. An observational study of coyote (*Canis latrans*) scent-marking and territoriality in Yellowstone National Park. Ethology **105**:289-302.

Andelt, W. F. 1982. Behavioral ecology of coyotes in south Texas. Wildlife Monograph **94**.

Arjo, W. M. 1998. The effects of recolonizing wolves on coyote populations, movements, behaviors, and food habits. Dissertation. University of Montana, Missoula, Montana, USA.

Atwood, T. C. 2006. Wolves, coyotes, elk, and mule deer: predator-prey behavioral ecology in southwest Montana. Dissertation. Utah State University, Logan, Utah, USA.

Balser, D. S. 1965. Tranquilizer tabs for capturing wild carnivores. Journal of Wildlife Management **29**:438-442.

Barreto, H., and F. M. Howland. 2006. Introductory econometrics: using Monte Carlo simulations with Microsoft Excel. Cambridge University Press, New York, New York, USA.

Bates, D. M., and D. G. Watts. 1988. Nonlinear regression analysis and its applications. John Wiley & Sons, New York, New York, USA.

Berg, W. E., and R. A. Chesness. 1978. Ecology of coyotes in northern Minnesota. Pages 229-248 *in* M. Bekoff, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.

Bowen, W. D. 1981. Variation in coyote social organization: the influence of prey size. Canadian Journal of Zoology **59**:639-652.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph **5**.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling **197**:516-519.

Carbyn, L. N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. Canadian Field Naturalist **96**:176-183.

Caro, T. M. 1994. Cheetahs of the Serengeti plains: group living in an asocial species. University of Chicago Press, Chicago, Illinois, USA.

Caro, T. M., and C. J. Stoner. 2003. The potential for interspecific competition among African carnivores. Biological Conservation **110**:67-75.

Clutton-Brock, T. H., D. Gaynor, G. M. McIlrath, A. D. C. Maccoll, R. Kansky, P. Chadwick, M. Manser, J. D. Skinner, and P. N. M. Brotherton. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. Journal of Animal Ecology **68**:672-683.

Connolly, G. E. 1978. Predator control and coyote populations: a review of simulation models. Pages 327-345 *in* M. Bekoff, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.

Crabtree, R. L., and J. W. Sheldon. 1999. The ecological role of coyotes on Yellowstone's northern range. Yellowstone Science **Spring**:15-23.

Creel, S., and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. Conservation Biology **10**:526-538.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563-566.

Dekker, D. 1989. Population fluctuations and spatial relationships among wolves, *Canis lupus*, coyotes, *Canis latrans*, and red foxes, *Vulpes vulpes*, in Jasper National Park, Alberta. Canadian Field Naturalist **103**:261-264.

Durant, S. M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology **67**:370-386.

Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. Behavioral Ecology **11**:624-632.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management **69**:1346-1359.

Fuller, T. K., and L. B. Keith. 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. Journal of Mammalogy **62**:403-405.

Gese, E. M. 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: who, how, where, when and why. Canadian Journal of Zoology **79**:980-987.

Gese, E. M. 2005. Demographic and spatial responses of coyotes to changes in food and exploitation. Proceedings of the Wildlife Damage Management Conference **11**: 271-285.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1987. Manual and net-gun capture of coyotes from helicopters. Wildlife Society Bulletin **15**:444-445.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. Journal of Wildlife Management **52**:640-646.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1989. Population dynamics of coyotes in southeastern Colorado. Journal of Wildlife Management **53**:174-181.

Gese, E. M., D. E. Andersen, and O. J. Rongstad. 1990. Determining home-range size of resident coyotes from point and sequential locations. Journal of Wildlife Management **54**:501-505.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996a. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. Canadian Journal of Zoology **74**:769-783.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996b. Social and nutritional factors influencing the dispersal of resident coyotes. Animal Behaviour **52**:1025-1043.

Gier, H. T. 1968. Coyotes in Kansas. Kansas State College Agricultural Experiment Station Bulletin No. **393**.

Goodrich, J. M., and S. W. Buskirk. 1995. Control of abundant native vertebrates for conservation of endangered species. Conservation Biology **9**:1357-1364.

Isbell, L. A., D. L. Cheney, and R. M. Seyfarth. 1990. Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. Behavioral Ecology and Sociobiology **27**:351-358.

Knowlton, F. F., and L. C. Stoddart. 1992. Some observations from two coyote-prey studies. Pages 101-121 *in* H. H. Boer, editor. Ecology and management of the eastern coyote. Wildlife Research Unit, University of New Brunswick, Fredericton, Canada.

Krefting, L. W. 1969. The rise and fall of the coyote on Isle Royale. Naturalist **20**:25-31.

Kruuk, H. 1972. The spotted hyaena: a study of predation and social behavior. University of Chicago Press, Chicago, Illinois, USA.

Laurenson, M. K. 1995. Implications of high offspring mortality for cheetah population dynamics. Pages 385-399 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: research, conservation, and management of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Linnell, J. D., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions **6**:169-176.

Mech, L. D. 1966. The wolves of Isle Royale. U.S. Government Printing Office, Washington, D.C., USA.

Metzgar, L. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). Journal of Mammalogy **48**:387-391.

O'Donoghue, M., S. Boutin, C. J. Krebs, and E. J. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos **80**:150-162.

O'Gara, B. W. 1978. Differential characteristics of predator kills. Proceedings of the Biennial Pronghorn Antelope Workshop **8**:380-393.

Palomares. F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. American Naturalist **153**:492-508.

Paquet, P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy **73**:337-343.

Parker, G. 1995. Eastern coyote, the story of its success. Nimbus Publishing, Halifax, Nova Scotia, Canada.

Peterson, R. O. 1995. Wolves as interspecific competitors in canid ecology. Pages 315-324 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves. Circumpolar Press, Edmonton, Alberta, Canada.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution **7**:151-153.

Powell, R. A. 2000. Animal home ranges and territories. Pages 65-110 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York, USA.

Pulliam, H. R. 1973. On the advantages of flocking. Journal of Theoretical Biology **38**:419-422.

R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasa, J .P. 1986. The costs and effectiveness of vigilance in the dwarf mongoose: implications for fitness and optimal group size. Ethology, Ecology and Evolution **1**:265-282.

Ricklefs, R. E. 1979. Ecology. Chiron Press, New York, New York, USA.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. C. Griffin & Co., London, UK.

Shivik, J. A., M. M. Jaeger, and R. H. Barrett. 1996. Coyote movements in relation to the spatial distribution of sheep. Journal of Wildlife Management **60**:422-430.

Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. American Naturalist **139**:1052-1069.

Smith, G. J., J. R. Cary, and O. J. Rongstad. 1981. Sampling strategies for radio-tracking coyotes. Wildlife Society Bulletin **9**:88-93.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. Bioscience **53**:331-340.

Smith, D. W., D. R. Stahler, and D. S. Guernsey. 2004. Yellowstone wolf project: annual report, 2003. National Park Service, Yellowstone Center for Resources, Mammoth Hot Springs, Wyoming, USA.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wrights, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology **2**:75-92.

Switalski, T. A. 2002. Coyote foraging ecology, vigilance, and behavioral cascades in response to gray wolf reintroduction in Yellowstone National Park. Thesis. Utah State University, Logan, Utah, USA.

Thurber, J. M., R. O. Peterson, J. D. Woolington, and J. A. Vucetich. 1992. Coyote coexistence with wolves on the Kenai Peninsula, Alaska. Canadian Journal of Zoology **70**:2494-2498.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Supplement **46**:120-138.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio tracking data. Academic Press, London, UK.

Wilmers, C. C., and W. M. Getz. 2005. Gray wolves as climate change buffers in Yellowstone. PLoS Biology **3**:571-576.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology **70**:164-168.

TABLE 2-1. Model selection results for survival of coyotes at two study sites in Grand Teton National Park, Wyoming, 2001-2004.

Model	*K*	AIC$_c$	ΔAIC$_c$	Akaike weight	Model Likelihood	Deviance
$S_{status+season}$	3	144.805	0.000	0.261	1.000	138.755
$S_{status+season+year}$	5	146.139	1.334	0.134	0.513	136.012
$S_{site+status+season}$	4	146.361	1.556	0.120	0.460	138.276
S_{season}	2	146.490	1.685	0.112	0.431	142.465
S_{status}	2	147.359	2.554	0.073	0.279	143.334
$S_{site+status+season+sex}$	5	147.695	2.890	0.061	0.236	137.568
$S_{status+year}$	4	147.818	3.013	0.058	0.222	139.734
$S_{site+season}$	3	148.516	3.710	0.041	0.156	142.465
$S_{status+sex}$	3	148.678	3.873	0.038	0.144	142.628
$S_{.}$	1	148.979	4.173	0.032	0.124	146.970
$S_{site+status+sex}$	4	150.112	5.307	0.018	0.070	142.028
$S_{site+season+sex}$	4	150.515	5.710	0.015	0.058	142.431
S_{sex}	2	150.971	6.166	0.012	0.046	146.946
S_{site}	2	150.994	6.188	0.012	0.045	146.968
$S_{site+status+year}$	5	152.450	7.644	0.006	0.022	142.323
$S_{site+sex}$	3	152.996	8.191	0.004	0.017	146.946
$S_{site+status+season+sex+year}$	7	153.187	8.382	0.004	0.015	138.950
$S_{site+status}$	3	167.583	22.777	0.000	0.000	161.532

TABLE 2-2. Seasonal and annual estimates of coyote survival at two study sites in Grand Teton National Park, Wyoming, 2002-2004.

Parameter	Year	$\hat{S}$	SE	95% LCL	95% UCL
Wolf-free Site – Antelope Flats					
Summer survival	2002	0.913	0.053	0.741	0.975
Winter survival	2002	0.746	0.107	0.493	0.899
Annual survival	2002	0.681	0.140	0.376	0.883
Summer survival	2003	0.912	0.051	0.750	0.973
Winter survival	2003	0.742	0.099	0.512	0.888
Annual survival	2003	0.677	0.129	0.397	0.870
Summer survival	2004	0.898	0.061	0.707	0.970
Winter survival	2004	0.704	0.112	0.453	0.872
Annual survival	2004	0.632	0.147	0.333	0.856
Wolf-abundant Site – Elk Ranch					
Summer survival	2002	0.906	0.061	0.718	0.973
Winter survival	2002	0.725	0.112	0.407	0.910
Annual survival	2002	0.657	0.147	0.294	0.898
Summer survival	2003	0.900	0.058	0.712	0.970
Winter survival	2003	0.719	0.137	0.423	0.899
Annual survival	2003	0.647	0.175	0.305	0.884
Summer survival	2004	0.885	0.059	0.659	0.968
Winter survival	2004	0.680	0.129	0.375	0.883
Annual survival	2004	0.601	0.166	0.247	0.874

TABLE 2-3. Population densities of coyotes and wolves at three study areas in the Greater Yellowstone Ecosystem, 1991-2005.

Study Area	Period	Coyotes/ km^2	Wolves/ km^2
Sites without wolves			
Yellowstone National Park – Lamar River Valley [a,b]	1991	0.499	0.000
Yellowstone National Park – Lamar River Valley [a,b]	1992	0.636	0.000
Yellowstone National Park – Lamar River Valley [a,b]	1993	0.694	0.000
Yellowstone National Park – Lamar River Valley [b,c]	1994	0.726	0.000
Grand Teton National Park – Antelope Flats [d]	2002	0.345	0.000
Grand Teton National Park – Antelope Flats [d]	2003	0.479	0.000
Grand Teton National Park – Antelope Flats [d]	2004	0.394	0.000
Sites with wolves			
Yellowstone National Park – Lamar River Valley [b,e,f]	1997	0.477	0.032
Yellowstone National Park – Lamar River Valley [b,f,g]	1998	0.332	0.042
Yellowstone National Park – Lamar River Valley [b,f,g]	1999	0.477	0.035
Yellowstone National Park – Lamar River Valley [b,f,g]	2000	0.270	0.065
Grand Teton National Park – Elk Ranch [d]	2002	0.279	0.053
Grand Teton National Park – Elk Ranch [d]	2003	0.308	0.061
Grand Teton National Park – Gros Ventre [d]	2003	0.312	0.033
Grand Teton National Park – Elk Ranch [d]	2004	0.215	0.053
Grand Teton National Park – Gros Ventre [d]	2004	0.247	0.028
Northern Madison Study Area [h]	2003-05	0.194	0.008

[a] Gese et al. 1996a,b

[b] Coyote densities adjusted to include transient coyotes ($\bar{x}$ = 0.064 ± 0.039 of total coyote numbers; E. M. Gese, *unpublished data*)

[c] S. Grothe, *unpublished data*

[d] Chapter 3

[e] Allen et al. 1999

[f] Smith et al. 2003, Smith et al. 2004

[g] T. A. Switalski, *unpublished data*

[h] T. C. Atwood, *unpublished data*

TABLE 2-4. Overlap between coyote and wolf annual home ranges and core areas as measured by percentage of area and utilization distribution overlap index (UDOI) in Grand Teton National Park, Wyoming, 2002-2004.

	Area of Overlap		UDOI	
Pack	Home range (%)	Core area (%)	Home range	Core area
Elk Ranch North	100	0	0.03	0.00
Elk Ranch South	100	0	0.04	0.00
Uhl Hill	100	96	0.21	0.13
Eynon Draw	100	97	0.23	0.17
Mean	100	48	0.13	0.08
SE	0	28	0.05	0.04

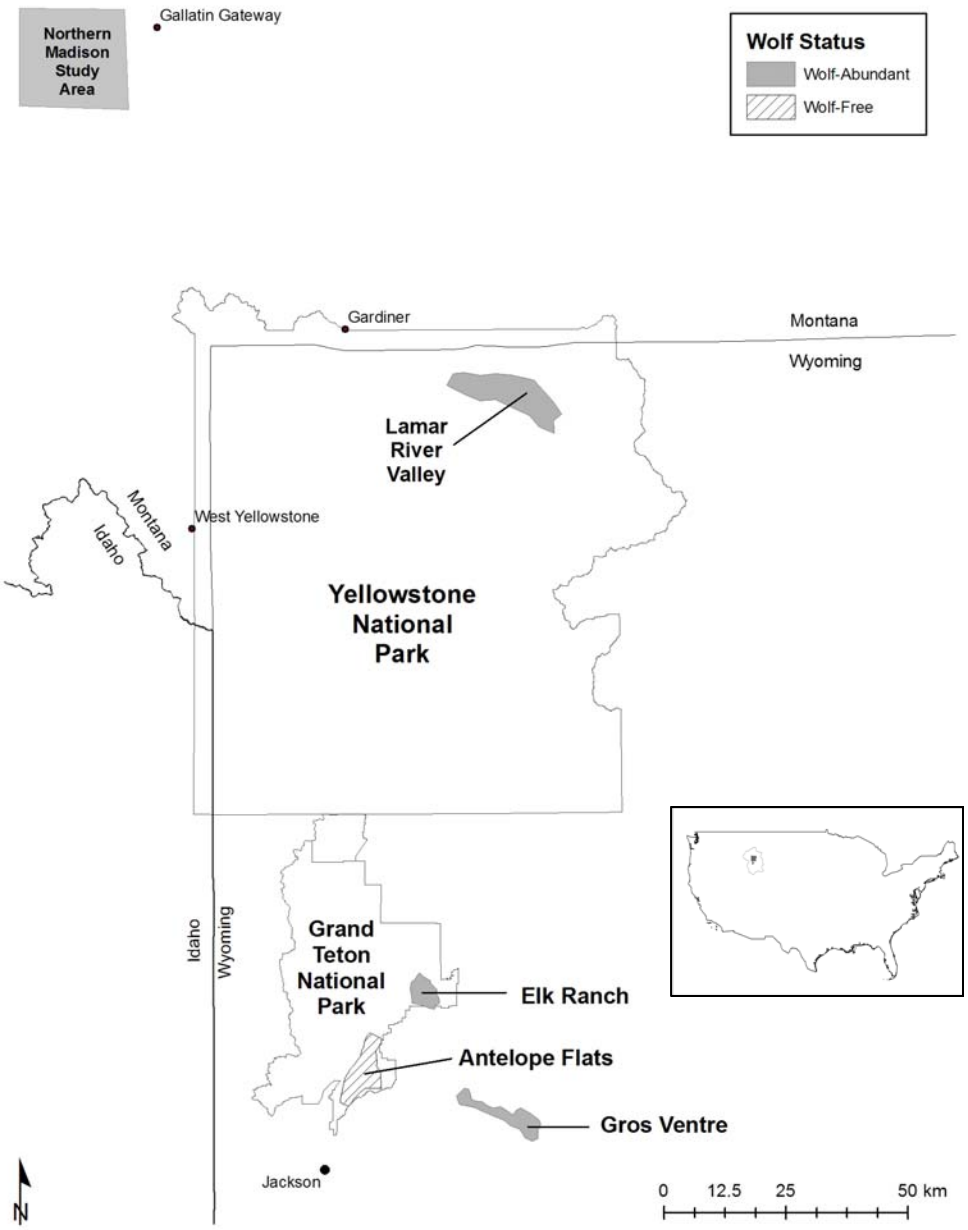


FIG. 2-1. Map showing the location of the Greater Yellowstone Ecosystem (GYE) in the western United States (inset), the locations of study areas, and place names referred to in the text. "Wolf status" refers to the distribution of wolves within the GYE during the 1997-2005 period.

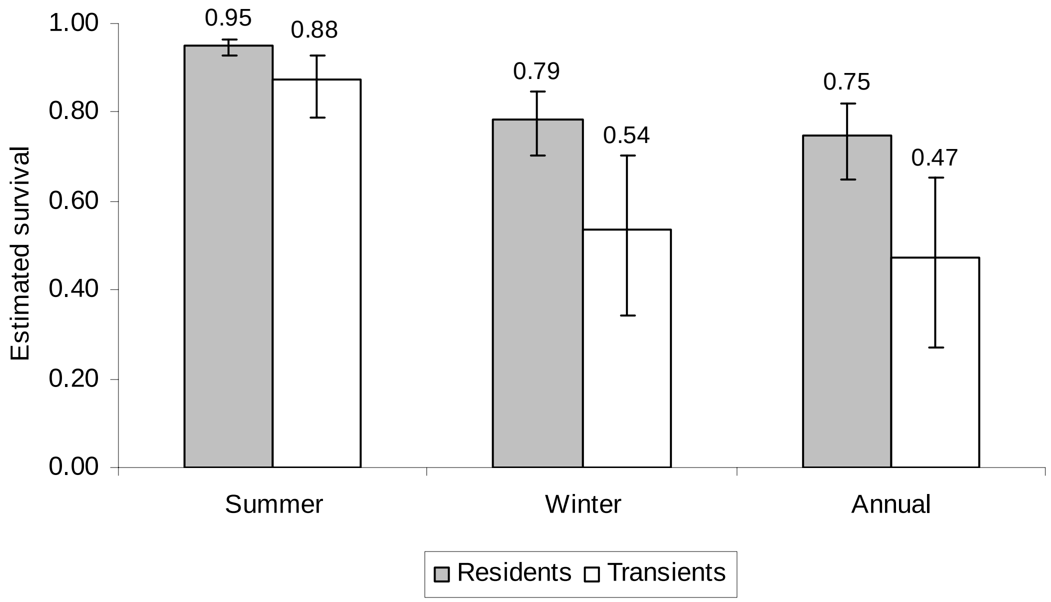


FIG. 2-2. Seasonal and annual differences in survival rates estimated by Program MARK for resident and transient coyotes in Grand Teton National Park, Wyoming, 2002-2004.

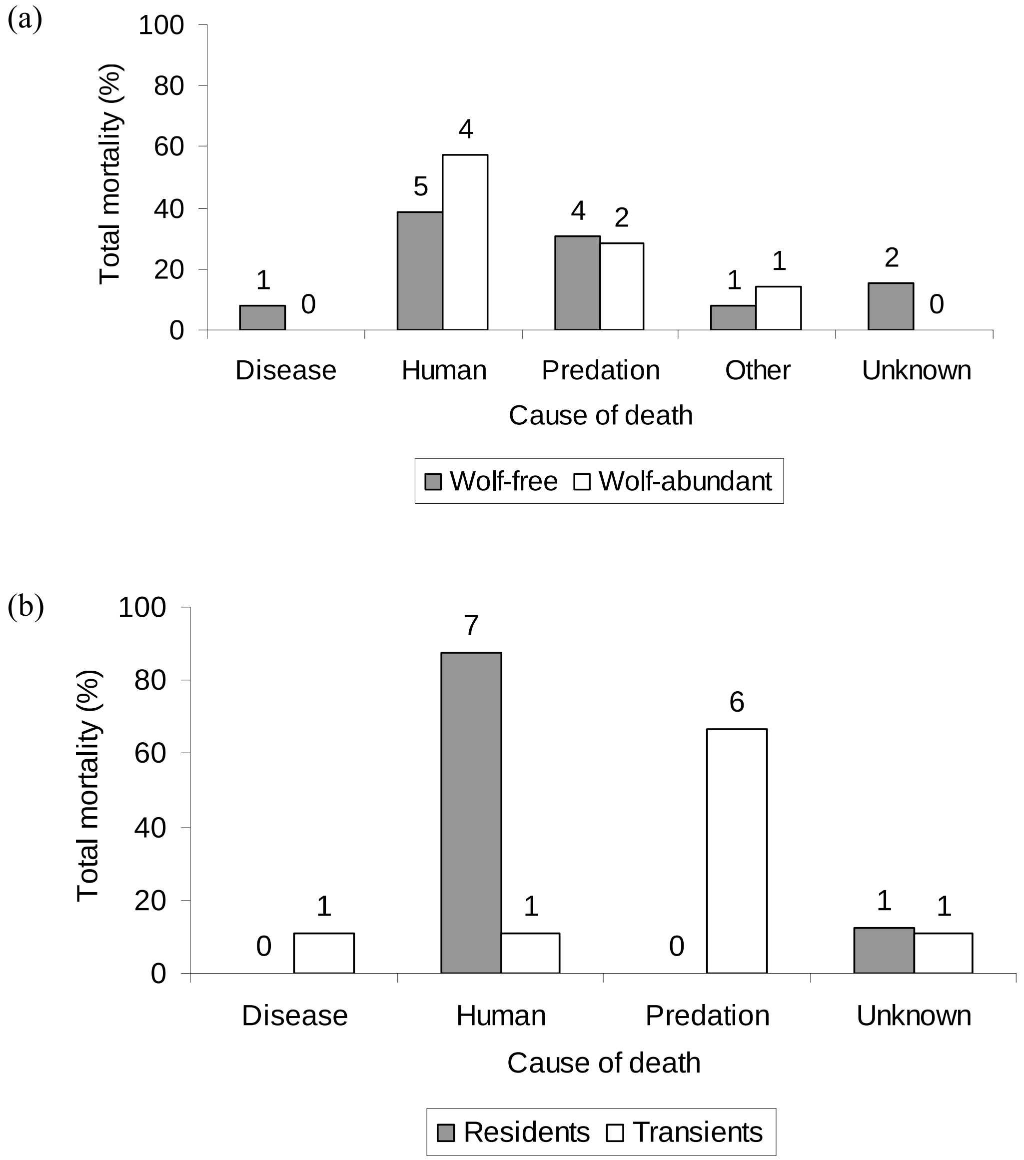


FIG. 2-3. Percentage of total mortality of radio-collared coyotes attributable to various causes (a) in wolf-free versus wolf-abundant sites, and (b) by territorial status, Grand Teton National Park, Wyoming, 2002-2004. The numbers above each bar indicate the actual number of deaths. Note that 3 deaths (1 human and 2 other) were excluded from the bottom panel because the territorial status of the animal was unknown.

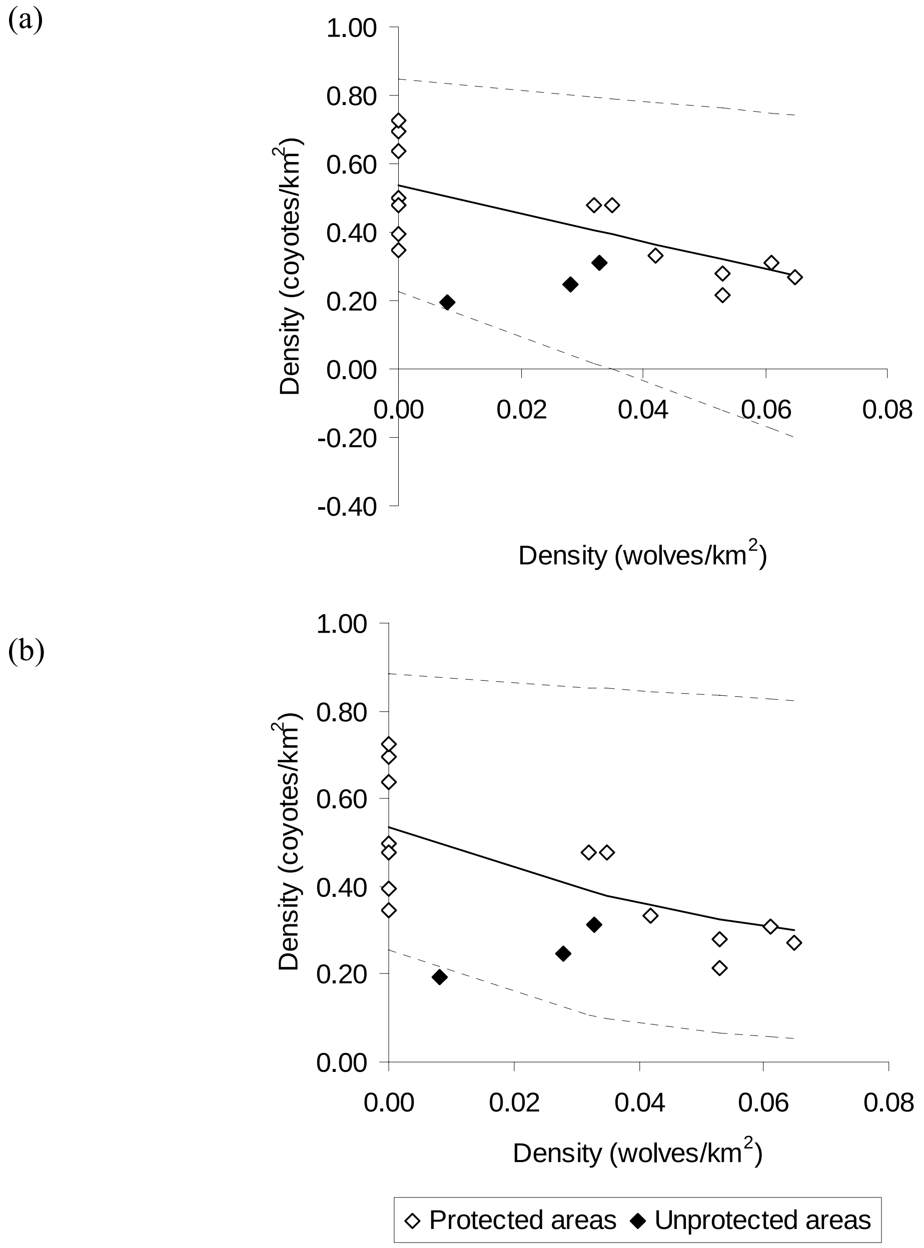


Fig. 2-4. Linear (a) and negative exponential (b) models of the relationship between coyote and wolf densities within protected areas for three study areas (GTNP, LRV, and NMSA) in the Greater Yellowstone Ecosystem, 1991-2005. For reference, actual coyote and wolf densities in both protected (←) and unprotected (⇦) areas are shown.

CHAPTER 3

EVIDENCE OF A SPECIES-LEVEL TROPHIC CASCADE IN A TERRESTRIAL FOOD WEB INVOLVING WOLVES, COYOTES, AND PRONGHORN[2]

Abstract. The trophic cascades hypothesis was proposed to explain observed patterns of population control in terrestrial ecosystems, but to date the model has been most successfully applied to aquatic environments. From September 2001 to August 2004, we used spatial and seasonal heterogeneity in wolf distribution and abundance in the southern Greater Yellowstone Ecosystem to evaluate whether mesopredator release of coyotes (*Canis latrans*), resulting from the extirpation of wolves (*Canis lupus*), accounts for high rates of coyote predation on pronghorn (*Antilocapra americana*) fawns observed in some areas of the western U.S. Results of this ecological perturbation in wolf densities, coyote densities, and pronghorn neonatal survival at wolf-free and wolf-abundant sites support the existence of a species-level trophic cascade. Wolves apparently precipitated a trophic cascade as evidenced by fawn survival rates that were four-fold higher at sites used by wolves. Negative correlations between coyote and wolf densities ($r = -0.740$, $n = 7$, $P = 0.036$), and between coyote density and fawn survival ($r = -0.882$, $P = 0.009$), support the hypothesis that interspecific competition facilitated the increase in fawn survival. Whereas densities of resident coyotes were similar between wolf-free and wolf-abundant sites ($\bar{x} = 0.251 \pm 0.025/\mathrm{km}^2$ and $\bar{x} = 0.232 \pm 0.029/\mathrm{km}^2$, respectively, $P = 0.687$), the abundance of transient coyotes was

---

[2] Coauthored by Kim Murray Berger, Eric M. Gese, and Joel Berger

significantly lower in areas used by wolves ($\bar{x} = 0.188 \pm 0.019/\text{km}^2$ vs. $\bar{x} = 0.039 \pm 0.005/\text{km}^2$, $P < 0.001$). Thus, differential effects of wolves on solitary coyotes may be an important mechanism by which wolves limit coyote densities. Our results suggest that the extirpation of wolves from some areas of North America may contribute to high rates of coyote predation on pronghorn fawns, and support a growing body of evidence demonstrating the importance of top-down forces in structuring the dynamics of consumer-resource interactions in terrestrial systems.

INTRODUCTION

Large carnivores can shape the structure and function of ecological communities (Ray et al. 2005), yet few ecosystems still harbor apex predators (Schaller 1996). Most large carnivores are declining globally due to habitat loss, fragmentation, disease, and human persecution (Weber and Rabinowitz 1996, Woodroffe and Ginsberg 1998, Woodroffe 2001), the latter often due to livestock depredation (Johnson et al. 2001, Ogada et al. 2003, Berger 2006). In addition to threatening the survival of these species, the loss of large carnivores carries broader implications for the maintenance of biodiversity as a result of indirect effects at lower trophic levels (Crooks and Soulé 1999, Henke and Bryant 1999). For instance, in the absence of grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*), moose (*Alces alces*) in the southern Greater Yellowstone Ecosystem (GYE) expanded resulting in a reduction in both willow communities and attendant diversity of neotropical songbirds (Berger et al. 2001). Similarly, the extirpation of vertebrate predators led to a 10- to 100-fold increase in herbivore densities and a concomitant decrease in the number of seedlings and saplings of canopy trees on islands in Venezuela (Terborgh et al. 2001).

Trophic cascades have been defined as predation-related effects resulting in inverse patterns of abundance or biomass across multiple trophic levels in a food web (Micheli et al. 2001). Although the classic cascade is based on a three-tiered system consisting of predators, herbivores, and plants (Hairston et al. 1960), cascades can involve more than three trophic levels and apply to any multilink linear food-web interaction (Polis et al. 2000). In systems with top-down control, the pattern of biomass that emerges depends on the number of trophic levels (Fig. 3-1). In even-numbered food chains with four or more trophic levels, herbivores can expand and overgraze plant communities because mesocarnivores are held in check by apex carnivores (Fig. 3-1; Oksanen et al. 1981, Fretwell 1987). The loss of primary carnivores from a four-tiered food chain shifts the trophic structure to a three-tiered system in which populations of secondary carnivores can increase (Fig. 3-1). This process, termed mesopredator release (Soulé et al. 1988), affects the persistence of both ground- and scrub-nesting birds through increased nest-predation by striped skunks (*Mephitis mephtis*), raccoons (*Procyon lotor*), and grey foxes (*Urocyon cinereoargenteus*; Rogers and Caro 1998, Crooks and Soulé 1999).

Efforts to experimentally test predictions of the mesopredator release hypothesis using large carnivores have been hampered by an absence of appropriate baselines against which to measure changes, the complexity of terrestrial food-webs which makes discerning effects problematic, a lack of spatial and temporal controls, and logistical and ethical difficulties associated with large-scale manipulations of terrestrial communities

(Polis et al. 2000, Steneck 2005). As a consequence, natural experiments involving the reintroduction or recolonization of large carnivores to systems where they have been absent, offer important opportunities to evaluate the effects of apex predators (Gittleman and Gompper 2001). The recolonization of wolves to Grand Teton National Park (GTNP), Wyoming, USA, is a case in point. Wolves were extirpated from northwestern Wyoming by the 1930s and were absent for nearly 70 years until their reintroduction to Yellowstone National Park (YNP) in 1995 (Smith et al. 2003). During late 1998, dispersing wolves from YNP recolonized GTNP, and the first litter of pups was born there in April 1999 (U.S. Fish and Wildlife Service, *unpublished data*).

We investigated potential direct and indirect effects of recolonizing wolves on pronghorn (*Antilocapra americana*) neonatal survival, as mediated by changes in the distribution and abundance of a mesocarnivore, coyotes (*Canis latrans*), a major predator of neonate pronghorn (Fig. 3-1). Because wolves are suspected competitors with coyotes (Peterson 1995a), in the absence of wolves, coyote populations may expand and threaten the persistence of pronghorn populations by limiting fawn recruitment. Following from the mesopredator release hypothesis, we tested three primary predictions: 1) survival of pronghorn fawns is positively associated with wolf density; 2) survival of pronghorn fawns is negatively associated with coyote density; and 3) an inverse relationship characterizes coyote and wolf densities.

METHODS

Study area and field sites

The study took place in Grand Teton National Park (GTNP), Wyoming, USA, and on the adjacent Bridger Teton National Forest (BTNF), from September 2001 to August 2004 (Fig. 3-2). The Park is bordered to the southeast by the National Elk Refuge (NER), a 100 km^2 area established in 1912 to provide secure winter habitat for elk (Fig. 3-2; Smith et al. 2004). Elevation ranges from 1900 m to >4000 m. Within this broad array of protected lands, we selected three sites to exploit spatial and temporal variation in wolf distribution and abundance. The Elk Ranch site (ER) was used extensively by wolves when denning and pup rearing occurred (May-September) and periodically throughout the winter (November-April), whereas the Gros Ventre site (GV) was used by wolves only during winter (Fig. 3-2). In contrast, the Antelope Flats (AF) site was not used by wolves during either season. All sites are characterized by shrub-steppe habitat dominated by big sagebrush (*Artemesia tridentata*), low sagebrush (*A. arbuscula),* Antelope bitterbrush *(Purshia tridentata*), and associated understory grasses of the genera *Stipa*, *Bromus,* and *Poa*. Common forbs include lupine (*Lupinus caudatus*) and arrowleaf balsamroot (*Balsamorrhiza sagitata*). The Antelope Flats and Elk Ranch sites are periodically used for livestock grazing; consequently, some native vegetation at both sites has been replaced with smooth brome (*Bromus inermis* Leyss).

Handling and monitoring of coyotes

We monitored the movements of coyotes captured at the Elk Ranch and Antelope Flats sites. No coyotes were captured at the Gros Ventre site because restrictions on access during winter precluded recovery of coyote carcasses during the period when mortality due to wolf predation was most likely to occur (Peterson 1995a). We captured coyotes with padded foothold traps or with a net-gun fired from a helicopter (Gese et al. 1987). Coyotes were equipped with VHF collars with 8-hour mortality sensors (Advanced Telemetry Systems Inc., Isanti, Minnesota, USA). Point and sequential locations obtained by ground and aerial telemetry were used to monitor survival and develop coyote home ranges (Gese et al. 1990). For ground locations, ≥ 3 compass bearings with intersecting angles between 20° and 160° were used (White and Garrott 1990). Locations were estimated using the program Locate II (Pacer Ltd., Truro, N.S.), and home ranges by the fixed-kernel density method (Worton 1989) with the 'adehabitat' package (Calenge 2006) in program R (R Development Core Team 2006). To estimate home ranges, we used an *ad hoc* smoothing parameter ($h_{ad\ hoc}$) designed to prevent over- or under-smoothing. This method involves choosing the smallest increment of the reference bandwidth (h_{ref}) that results in a contiguous 95% kernel home-range polygon that contains no lacuna (i.e., $h_{ad\ hoc} = 0.9*h_{ref}$, $0.8*h_{ref}$, etc.; J.G. Kie, *unpublished manuscript*).

Estimation of coyote densities

We classified all coyotes as either residents or transients. Resident coyotes actively defended well-defined territories, whereas transients were not associated with a particular pack or territory. Densities of resident coyotes were assessed using a combination of spring (pre-whelping) pack sizes of known (i.e., radio-collared) individuals and indices of coyote abundance based on scat deposition surveys. Scat transects were located along ~ 7.5 km of unimproved road at each site. Transects were initially cleared of all scats and then walked once/week for three weeks each spring and fall (Gese 2001). For known individuals, we determined pack sizes based on aerial and ground-based observations of animals displaying affiliative behaviors such as traveling, hunting, and resting together, or territorial maintenance (Camenzind 1978). For 2003 and 2004, we calculated resident coyote densities at the Elk Ranch and Antelope Flats sites by dividing the number of adult (>1 year old) coyotes in each pack by the size of the pack's home-range using the 95% probability contour. Estimates for all packs at a site were then averaged to determine a site-specific mean and variance. We estimated transient coyote densities at the Elk Ranch and Antelope Flats sites based on the ratio of radio-collared transients to total radio-collared coyotes in 2003. We used 2003 as the baseline because we conducted extensive helicopter captures of coyotes that year and had the largest number of collars (n = 26) deployed. Densities of resident and transient coyotes were combined to produce estimates of total coyote density for both sites. Because we had radio-collars on coyotes in too few packs to estimate numbers directly for 2002, we estimated coyote densities at the Elk Ranch and Antelope Flats sites based on the following relationship between coyote densities at both sites in 2003 and 2004 and assessments of relative abundance determined by scat deposition surveys (regression through the origin, $r^2 = 0.912$, $P = 0.011$; Appendix A):

$$\text{Coyote density} = 1.644 \times \text{scat deposition index}. \tag{1}$$

For 2003 and 2004, coyote densities at the Gros Ventre site were estimated using Eq. 1. No estimate of coyote density was available for the Gros Ventre site in 2002 because we did not conduct scat deposition surveys there until the spring of 2003.

Estimation of wolf densities

Capture and collaring of wolves was handled by the U.S. Fish and Wildlife Service. Radio-tracking of wolves followed the same procedures as for coyotes. Seasonal wolf densities were based on known pack sizes for the summer (May - September) and winter (November - April) periods (U.S. Fish and Wildlife Service 2004). These periods corresponded to seasonal shifts in centers of activity between the wolf pack's den site in GTNP and the state-run elk feed grounds in the BTNF. Summer density estimates were based on the number of adults in the pack, whereas winter estimates were based on the number of adults and pups. Pups were included in the latter estimates because their presence would increase competition at kills and thus might make wolves less tolerant of coyotes at carcasses. To calculate seasonal wolf densities, we divided the number of wolves in the pack each season by the size of the pack's seasonal home range. Seasonal home ranges for wolves were estimated using the same procedures as for coyotes.

Capture and monitoring of neonate pronghorn

We monitored the survival of pronghorn fawns captured at the Antelope Flats site during June 2002-2004, and at the Gros Ventre and Elk Ranch sites during June 2003-2004. All fawns were equipped with expandable, breakaway VHF radio-collars with 4-hour mortality sensors (weight ~ 60g; Advanced Telemetry Systems Inc., Isanti, Minnesota, USA), 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). Fawns were monitored daily for the first 60 days of life, and then weekly until the fall migration.

Statistical analysis

We evaluated the relationships between coyote density and pronghorn fawn survival, wolf density and fawn survival, and coyote density and wolf density using correlation analysis. We used correlation analysis rather than simple linear regression or multivariate regression because for each bivariate comparison, values of the independent variable were subject to measurement error; thus, we did not meet the assumptions of regression analysis (Gotelli and Ellison 2004). Furthermore, the hypothesized relationship between wolf density and fawn survival was indirect and mediated by changes in coyote density; thus, we expected that the relationship between wolf density and fawn survival would be confounded by the coyote variable in a multivariate analysis (Cohen et al. 2003).

We estimated survival of pronghorn fawns for the first 60 days of life using a known fate model in Program MARK (White and Burnham 1999). The analysis was based on individual encounter histories, with a single encounter for each cohort that indicated whether the fawn survived or died during the 60-day period. We evaluated 37 models to assess the effects of individual covariates (gender and birthweight) and group covariates (coyote density, summer wolf density, and winter wolf density) on fawn survival (Table 3-1). For fawns that were not newborns at capture, we calculated mass at birth based on the following relationship (modified from Byers 1997):

$$\text{birthweight} = \text{weight at capture} - 0.2446 \times \text{age in days}. \qquad (2)$$

The global model considered was ($\hat{S}_{g+m+c+sw+ww}$), where $\hat{S}$ was estimated survival probability, *g* was gender, *m* was birthweight, *c* was coyote density, *sw* was summer wolf density, and *ww* was winter wolf density. We also tested models that included dummy variables for site (*s*), wolf-free site (*wf*), and year (*y*) to examine possible differences in fawn survival among sites and years that were not captured by the group covariates. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and Akaike weights to rank models (Burnham and Anderson 2002). Using the top-ranked (i.e., minimum AIC_c) model from the initial analyses, we fit one additional model to assess whether an irruption in white-tailed jackrabbits (*Lepus townsendii*) at the Gros Ventre site might account for an observed increase in fawn survival in 2004.

RESULTS

Coyote captures

We radio-collared 38 coyotes at the Elk Ranch and Antelope Flats sites. The percentage of coyotes classified as residents and transients was 51% ($n = 18$) and 49% ($n = 17$), respectively. In three cases the animal died too soon after capture for its status to be determined. In addition to the three coyotes of unknown status, seven coyotes were censored from all analyses because they dispersed to areas outside our field sites.

Coyote and wolf densities

Coyote densities were highest at the Antelope Flats site in 2003 (0.479 ± 0.065 coyotes/km^2) and lowest at the Elk Ranch site in 2004 (0.215 ±0.002 coyotes/km^2; Fig. 3-3). Densities of resident coyotes at the Antelope Flats site ($\bar{x} = 0.251 \pm 0.025$) were similar to those at the Elk Ranch site ($\bar{x} = 0.232 \pm 0.029$, Student's *t* test, $P = 0.687$) whereas transient densities were significantly lower at Elk Ranch (Fig. 3-4; $\bar{x} = 0.188 \pm 0.019$ vs. $\bar{x} = 0.039 \pm 0.005$, Student's *t* test, $P < 0.001$). With respect to wolves, densities were highest at the Elk Ranch site during the winter of 2003 (0.061 wolves/km^2), and lowest at the Elk Ranch site during the summers of 2003 (0.015 wolves/km^2; Fig. 3-5). Wolves made only rare visits to the Antelope Flats site, thus wolf density at this site was effectively zero for all years.

Relationship between carnivore densities and pronghorn neonatal survival

We included 108 marked individuals (19 in 2002, 44 in 2003, and 45 in 2004) in the analysis of fawn survival, distributed by site as follows: ER - 27, GV - 30, and AF - 51. On the basis of minimum AIC_c, the best model of fawn survival contained parameters for gender, birthweight, and coyote density (Table 3-2). However, the top-ranked model had just 13.7% of the Akaike weights (Table 3-2), indicating there was considerable uncertainty as to which of the highly-ranked candidate models was actually the best predictor of fawn survival (Burnham and Anderson 2002). Coyote density appeared in all nine of the top-ranked models, with a cumulative Akaike weight of 62.4% (Table 3-2). Thus, the overall importance of this single variable likely contributed to model-selection uncertainty, as a model that included only coyote density was nearly as good ($\Delta AIC_c = 1.311$) at predicting fawn survival as one that also included both gender and birthweight (Table 3-2). Models that included variables for coyote and wolf densities outperformed comparable models that suggested that fawn survival differed among the sites independent of coyote and wolf densities (Table 3-2).

Model-averaged survival estimates (Burnham and Anderson 2002) during the first 60 days of life ranged from a low of $\hat{S} = 0.049$ at the Antelope Flats site in 2003, to a high of $\hat{S} = 0.440$ at the Elk Ranch site in 2004 (Table 3-3). Based on the parameter estimates from the top-ranked model, fawn survival was negatively correlated with coyote density ($\beta = -12.313 \pm 3.875$, Wald test, $P = 0.002$) and positively correlated with birthweight ($\beta = 0.413 \pm 0.263$, Wald test, $P = 0.116$). Survival of male fawns was lower than for females (β = -0.496 ± 0.266, Wald test, P = 0.062). Based on the results of correlation analysis, fawn survival was negatively correlated with coyote density ($r = -0.882$, $P = 0.009$; Fig. 3-6a) and positively correlated with winter wolf density (r = 0.791, P = 0.034; Fig. 3-6b), and the relationship between coyote and winter wolf densities was negative (r = -0.740, P = 0.036; Fig. 3-6c). Summer wolf density was also positively correlated with fawn survival (r = 0.447, P = 0.314), and negatively correlated with coyote density (r = -0.521, P = 0.185), but neither relationship was statistically significant.

DISCUSSION

Did wolves precipitate a trophic-level interaction?

Although the trophic cascades hypothesis was proposed to explain observed patterns of population control in terrestrial systems (Hairston et al. 1960), the model has been most successfully applied in marine (Paine 1966, Estes et al. 1998) and freshwater (Power 1990) environments. This has led some ecologists to suggest trophic cascades may play a less important role in structuring terrestrial communities (Strong 1992, Polis 1999).

That wolves precipitated a species-level trophic cascade (*sensu* Polis 1999) is evidenced by more than a four-fold difference in neonatal pronghorn survival at sites that are used by wolves during either the winter, or both winter and summer (Table 3-3). The corresponding negative correlation between coyote and wolf densities supports the hypothesis that interspecific competition between these species facilitated the observed increase in pronghorn fawn survival. Whereas mean densities of resident coyotes were similar between wolf-free and wolf-abundant sites (Fig. 3-4; Student's *t* test, $P = 0.687$), the mean abundance of transient coyotes was significantly lower in areas used by wolves (Fig. 3-4; Student's *t* test, $P < 0.001$). Thus, differential effects of wolves on solitary coyotes may be an important mechanism by which wolves limit coyote populations (Chapter 2). This hypothesis is further supported by differences in mortality rates and cause-specific mortality of resident and transient coyotes in GTNP between 2001 and 2004. Annual mortality rates of resident and transient coyotes were 25% and 53%, respectively (Chapter 2). And, whereas no resident coyotes were killed by wolves, 67% of transient coyote deaths resulted from predation, with wolves accounting for 83% of predation-related mortality (Chapter 2).

Despite the strong correlations between coyote densities, winter wolf densities, and pronghorn fawn survival, the variable for winter wolf density did not appear in any of the highest ranked models (i.e., models with $AIC_c < 2$; Table 3-2; Burnham and Anderson 2002). This supports the hypotheses that the effect of wolves on pronghorn fawn survival is largely indirect and mediated by differences in coyote densities among the sites, as inclusion of the winter wolf density variable in the model explained no additional variation in fawn survival beyond that already captured by the coyote density variable.

Reductions in coyote densities in GTNP have not been as large as those documented elsewhere. For instance, coyote densities were allegedly reduced by 50% in YNP following wolf reintroduction, and coyotes were extirpated from Isle Royale within 8 years of the arrival of wolves in the late 1940s (Krefting 1969, Smith et al. 2003). In contrast, coyote abundance in GTNP has declined by approximately 33% based on differential population densities at sites with and without wolves.

Several factors likely contributed to the lesser reduction in coyote densities we detected. For instance, the small size of the area (2,314 km^2) and corresponding lack of refugia are thought to have contributed to the rapid extirpation of coyotes from Isle Royale (Peterson 1995b). In contrast, GTNP is not spatially closed and a single wolf pack occupied only a small portion of the Park during the course of this study. Thus, it is likely the coyote population in GTNP will experience additional reductions as the wolf population continues to increase and wolves expand into areas of the Park from which they are currently absent. Furthermore, competition between wolves and coyotes may have been mediated by a relative abundance of prey. Elk densities in GTNP are in the neighborhood of 6/km^2, rising to approximately 76/km^2 during winter when elk are concentrated on feed grounds (based on data from Smith et al. 2004). As elk are the primary prey of wolves (Smith et al. 2003), their relative abundance may increase wolf tolerance of coyotes at carcasses where agonistic encounters are most likely to occur (Switalski 2003).

Effects of changes in neonatal survival on pronghorn population density

For increases in summer survival of pronghorn fawns to result in an increase in the pronghorn population in GTNP, several conditions must be met. First, mortality from coyote predation must be additive and not compensatory (Boyce et al. 1999). We found no evidence of any compensatory predation-related mortality in radio-collared fawns

(Chapter 4), and prospects for compensatory density-dependent mortality appear unlikely given that the current pronghorn population in the Park is less than 10% of its historical size (Berger 2003). Second, fawns surviving the summer must also survive their first winter to be recruited into the population as yearlings. Whereas prospects for density-dependent population regulation appear unlikely on the summer range, conditions on the winter range, located on lands managed by the Bureau of Land Management some 190 km beyond Park borders, strongly differ. Habitat designated “crucial winter range” for pronghorn (Wyoming Game and Fish Department, Cheyenne, WY) is currently undergoing rapid conversion due to development of natural gas wells. As overwinter survival rates of juvenile ungulates are typically lower than those of adults (Gaillard et al. 1998), this age class is likely to be differentially susceptible to any reductions in carrying capacity stemming from habitat loss. Thus, increases in summer survival of fawns may be offset by increases in over-winter mortality, resulting in no net change, or even a decrease, in the pronghorn population. Third, fawns surviving their first winter must complete the return migration the following spring to be recruited into the Park population. Telemetry data indicate that approximately 80-85% of fawns return to the Park each year, with the remainder dispersing to other summer ranges (K. M. Berger, *unpublished data*). Although competition for forage could alter the proportion of fawns showing philopatry to their natal range, this possibility appears unlikely given the low population density.

Contributing factors

The detection of trophic cascades in terrestrial systems has often been elusive because interactions between species can be weak and diffuse (Polis et al. 2000). Although the food web in Greater Yellowstone is complex due to a large number of sympatric carnivores and herbivores (Berger and Smith 2005), the focal chain we studied was relatively simple in structure. Adult pronghorn are effectively predator-free owing to their speed (Byers 1997), and while bobcats (*Lynx rufus*) and golden eagles (*Aquila chrysaetos*) are important predators of pronghorn fawns in some areas (Beale and Smith 1973, Byers 1997), both species occur at low densities at our field sites (K. M. Berger *personal observations*). Wolves do kill pronghorn fawns opportunistically, but their large body mass (18-80 kg) relative to coyotes (11-18 kg) makes it energetically inefficient for wolves to hunt systematically for pronghorn neonates (3-4 kg) with the same intensity as coyotes (Gittleman 1985, Byers 1997). Consequently, coyotes accounted for 71% of total mortality, and 97% of predation-related mortality, of pronghorn fawns in our system (Chapter 4). Thus, effects of changes in coyote predation on fawn survival may have been easier to discern due to a lack of compensatory predation.

Anthropogenic changes in pronghorn population densities may have contributed to the strength of the interaction between coyotes and pronghorn. Specifically, populations that have been reduced by severe winter weather or over-harvesting by humans may experience poor recruitment resulting from sustained levels of predation (Gasaway et al. 1983). Although a few thousand pronghorn historically summered in the

Park (Deloney 1948), the population was reduced in the late 1800s as a consequence of market hunting. Since the turn of the 20th century, the population has never numbered more than the low 400s and is currently ~200 animals (Berger 2003). Thus, relatively high coyote densities coupled with relatively low densities of pronghorn may allow coyotes to consume nearly all of the estimated ~ 150 pronghorn fawns produced in the Park each summer (Chapter 4).

Populations of migratory ungulates may be regulated by bottom-up forces when carnivore densities are determined by the supply of resident herbivores (Sinclair 1995). However, alternative prey may maintain stable predator populations or enable high densities (Polis 1999). Because pronghorn females rely on reproductive synchrony and predator swamping to maximize fitness (Gregg et al. 2001), low pronghorn densities relative to the number of coyotes sustained by resident herbivores such as elk may allow coyotes to effectively regulate the pronghorn population by consuming a large proportion of the fawns produced each year (i.e., a predator-pit; Holling 1965). The possibility of a predator-pit is suggested by a positive relationship between fawn survival and pronghorn population density ($r^2 = 0.257$, $P = 0.004$) in GTNP between 1981 and 2004 (Chapter 4).

The strength of the interaction between coyotes and pronghorn may also be enhanced by a lack of alternative prey. Notably, although jackrabbits are an important component of coyote diets in some areas (Clark 1972), black-tailed jackrabbits (*Lepus californicus)* do not occur in northwestern Wyoming (Best 1996), and white-tailed jackrabbits are functionally, if not ecologically, extinct in GTNP (Berger et al. 2006). Jackrabbits and pronghorn neonates are similarly-sized (3-4 kg), and the absence of alternative prey may increase coyotes’ dependence on pronghorn fawns at a critical juncture when adult coyotes are experiencing energetic demands associated with provisioning pups.

An irruption in the jackrabbit population at the Gros Ventre site in 2004 provided an opportunity to explore this idea. Specifically, we included a dummy variable representing the jackrabbit irruption in the model of estimated fawn survival to test for evidence of additional variation in survival that was not adequately explained by the top-ranked model. The model that included the jackrabbit variable accounted for 5.6% of the Akaike weights (Table 3-2), suggesting some support for our hypothesis (Burnham and Anderson 2002). However, this model had a similar deviance to the top-ranked model and the $\Delta AIC_c \approx 2$ was a result of adding another parameter to the model that explained little additional variation (Burnham and Anderson 2002). Thus, we concluded there was weak evidence that an irruption in the jackrabbit population contributed to an increase in fawn survival at the GV site in 2004.

Finally, the strength of the interaction between coyotes and pronghorn may be enhanced by changes in coyote densities resulting from human alteration of resource availability. Specifically, whereas most elk migrated out of GTNP and the surrounding area prior to human settlement, currently an average of 7,500 elk now winter just south of GTNP on the National Elk Refuge (Smith et al. 2004). Overwinter mortality of elk on the NER averages 2-3% (Smith 1991), resulting in an estimated 41,000 kg of gross carcass biomass during a typical winter (i.e., 7,500 elk x 2% mortality x 273 kg/elk = 40,950 kg). Coyotes are opportunistic, generalist predators and scavengers and their densities are limited by the availability of prey during winter (Gese 2004). Thus, the availability of abundant elk carcasses on the NER is likely to subsidize the winter diets of coyotes and maintain the population in GTNP at artificially-elevated densities. Furthermore, because elk feeding suppresses temporal variation in elk mortality associated with mild and harsh winters, carcasses on the NER provide a stable food supply that may buffer the coyote population from weather-dependent fluctuations. That elk carrion is an important resource for coyotes is suggested by the "aggregations" that form on the NER each winter (Camenzind 1978). Indeed, the availability of this seasonal food subsidy results in the seasonal migration of transient and resident coyotes from both the ER and AF sites (K. M. Berger, *unpublished data*).

Limitations of the study

We have attributed the increase in neonatal pronghorn survival to mesopredator suppression of coyotes by wolves, resulting from direct mortality of transient coyotes by wolves, and a disparity in dispersal rates of transient coyotes between wolf-free and wolf-abundant areas. 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 wolves may have contributed to differences in coyote densities 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. 3-1; Chapter 2). Furthermore, the inverse relationship between coyote and wolf densities might simply reflect differential habitat selection by the two species based on the distribution of preferred prey. For example, jackrabbits are an important component of coyote diets in many areas

(Clark 1972) and the presence of large numbers of white-tailed jackrabbits at the Gros Ventre site during the summer of 2004 (K. Berger, *personal observations*) may have contributed to site-specific differences in coyotes densities. However, in the absence of wolves, coyote densities should be higher in areas with a greater abundance of prey, and higher prey densities should also facilitate fawn survival by encouraging prey switching by coyotes (Stoddart et al. 2001). Thus, differences in prey densities do not adequately explain the coyote density patterns we observed in GTNP, as coyote densities were highest at the Antelope Flats site where jackrabbits were absent. Furthermore, coyote predation rates on fawns were also highest at the Antelope Flats site, suggesting that alternative prey were not more abundant at this site, as prey switching did not occur.

Conclusions

In contrast with previous studies, the changes in herbivore populations we observed resulted not from direct predation by a top carnivore, but rather as a result of indirect effects mediated by changes in mesocarnivore abundance. The strong, negative correlations between coyote and wolf densities, and coyote densities and fawn survival, support the hypothesis that mesopredator release of coyotes, resulting from the extirpation of wolves throughout much of North America, contributes to high rates of coyote predation on pronghorn fawns observed in some areas. Thus, from both management and conservation perspectives wolf restoration holds promise for reducing coyote predation rates on neonatal ungulates such as pronghorn, mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*) in areas where wolves prey primarily on elk (*Cervus elaphus*). In particular, we expect that similar cascades should emerge in places such as YNP where the pronghorn population has declined precipitously in recent years, coyote predation on pronghorn fawns is high, and wolves have reportedly reduced the coyote population by as much as 50% (Goodman 1996; Smith et al. 2003). Our results provide strong evidence of a species-level trophic cascade precipitated by wolf recolonization in the southern GYE, and support a growing body of research demonstrating the importance of top-down forces in structuring the dynamics of consumer-resource interactions in terrestrial systems (McLaren and Peterson 1994, Berger et al. 2001, Ripple et al. 2001, Terborgh et al. 2001, Fortin et al. 2005).

LITERATURE CITED

Beale, D. M., and A. D. Smith. 1973. Mortality of pronghorn antelope fawns in western Utah. Journal of Wildlife Management **37**:343-352.

Berger, J., and D. W. Smith. 2005. Restoring functionality in Yellowstone with recovering carnivores: gains and uncertainties. Pages 100-109 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press Washington, D.C., USA.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications **11**:947-960.

Berger, J., K. M. Berger, P. F. Brussard, R. Gibson, J. Rachlow, and A. Smith. 2006. Where have all the rabbits gone? Summary and Recommendations from a Workshop Held in Grand Teton National Park – September 23-24, 2005. Wildlife Conservation Society, Bozeman, Montana, USA.

Berger, K. M. 2003. Pronghorn in peril. Wildlife Conservation **August**:38-41.

Berger, K. M. 2006. Carnivore-livestock conflicts: effects of subsidized predator control and economic correlates on the sheep industry. Conservation Biology **20**:751-761.

Best, T. L. 1996. Lepus californicus. Mammalian Species **530**:1-10.

Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos **87**:419-426.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd edition. Springer-Verlag, New York, New York, USA.

Byers, J. A. 1997. American pronghorn: social adaptations & the ghosts of predators past. University of Chicago Press, Chicago, Illinois, USA.

Byers, J. A., and J. D. Moodie. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. Behavioral Ecology and Sociobiology **26**:157-164.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling **197**:516-519.

Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 *in* M. Bekoff, editor. Coyote: biology, behavior, and management. Academic Press, New York, New York, USA.

Clark, F. W. 1972. Influence of jackrabbit density on coyote population change. Journal of Wildlife Management **36**: 343-356.

Cohen, J., P. Cohen, S. G. West, and L. S. Aiken. 2003. Applied multiple regression/correlation analysis for the behavioral sciences. Lawrence Erlbaum, Mahwah, New Jersey, USA.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563-566.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 *in* J. Diamond and T. Case, editors. Community ecology. Oxford University Press, New York, New York, USA.

Deloney, W. C. 1948. Passing of the antelope in the Jackson Hole. Jackson Hole Courier February 12 edition.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science **282**:473-476.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320-1330.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? Oikos **50**:291-301.

Gaillard, J. -M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution **13**:58-63.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs **84**.

Gese, E. M. 2001. Monitoring of terrestrial carnivore populations. Pages 372-396 *in* J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, London, UK.

Gese, E. M. 2004. Coyotes in Yellowstone National Park: the influence of dominance on foraging, territoriality, and fitness. Pages 271-283 *in* D. W. Macdonald and C. Sillero-Zubiri, editors. Biology and conservation of wild canids. Oxford University Press, New York, New York, USA.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1987. Manual and net-gun capture of coyotes from helicopters. Wildlife Society Bulletin **15**:444-445.

Gese, E. M., D. E. Andersen, and O. J. Rongstad. 1990. Determining home-range size of resident coyotes from point and sequential locations. Journal of Wildlife Management **54**:501-505.

Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. Oecologia **67**:540-554.

Gittleman, J. L., and M. E. Gompper. 2001. The risk of extinction – what you don't know will hurt you. Science **29**:997-999.

Goodman, D. 1996. Viability analysis of the antelope population wintering near Gardiner, Montana. National Park Service, Yellowstone Center for Resources, Mammoth Hot Springs, Wyoming, USA.

Gotelli, N. J., and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Inc. Sunderland, Massachusetts, USA.

Gregg, M. A., M. Bray, K. M. Kilbride, and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. Journal of Wildlife Management **65**:19-24.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**: 421-425.

Henke, S. E., and F. C. Bryant. 1999. Effects of coyote removal on the faunal community in western Texas. Journal of Wildlife Management **63**:1066-1081.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada **45**:3-60.

Johnson, W. E., E. Eizirik, and G. M. Lento. 2001. The control, exploitation, and conservation of carnivores. Pages 196-219 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, UK.

Krefting, L. W. 1969. The rise and fall of the coyote on Isle Royale. Naturalist **20**:24-31.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science **266**:1555-1558.

Micheli, F., G. A. Polis, P. D. Boersma, M. A. Hixon, E. A. Norse, P. V. R. Snelgrove, and M. E. Soulé. 2001. Human alteration of food webs: research priorities for conservation and management. Pages 31–57 *in* M. E. Soulé and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, D.C., USA.

Ogada, M. O., R. Woodroffe, N. O. Oguge, and L. G. Frank. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. Conservation Biology **17:**1521-1530.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240-261.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65-75.

Peterson, R. O. 1995a. Wolves as interspecific competitors in canid ecology. Pages 315-324 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves. Circumpolar Press, Edmonton, Alberta, Canada.

Peterson, R. O. 1995b. The wolves of Isle Royale. Willow Press Creek, Minocqua, Wisconsin, USA.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos **86**:3-15.

Polis G. A., A. L. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? Trends in Ecology and Evolution **15**:473-475.

Power, M. E. 1990. Effects of fish in river food webs. Science **250**:811-814.

R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, J. C., K. H. Redford, J. Berger, and R. Steneck. 2005. Is large carnivore conservation equivalent to biodiversity conservation and how can we achieve both? Pages 400-427 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C., USA.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range. Biological Conservation **102**:227-234.

Rogers, C. M., and M. J. Caro. 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. Oecologia **116**:227-233.

Schaller, G. B. 1996. Carnivores and conservation biology. Pages 1-10 *in* J. L. Gittleman, editor. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, New York, USA.

Sinclair, A. R. E. 1995. Population limitation of resident herbivores. Pages 194-219 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Smith, B. L. 1991. Jackson Hole elk. Bugle **Fall**:2-15.

Smith, B. L., E. K. Cole, and D. S. Dobkin. 2004. Imperfect pasture: a century of change at the National Elk Refuge in Jackson Hole, Wyoming. U.S. Fish and Wildlife Service, Jackson, Wyoming, USA.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. Bioscience **53**:331-340.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wrights, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology **2:**75-92.

Steneck, R. S. 2005. An ecological context for the role of large carnivores in conserving biodiversity. Pages 9-33 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C., USA.

Stoddart, L. C., R. E. Griffiths, and F. F. Knowlton. 2001. Coyote responses to changing jackrabbit abundance affect sheep predation. Journal of Range Management **54**:15-20.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73**:747-754.

Switalksi, T. S. 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. Canadian Journal of Zoology **81**:985-993.

Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science **294**:1923-1926.

Weber, W., and A. Rabinowitz. 1996. A global perspective on large carnivore conservation. Conservation Biology **10**:1046-1054.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, London, UK.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Supplement **46**:120-138.

Woodroffe, R. 2001. Strategies for carnivore conservation: lessons learned from contemporary extinctions. Pages 61-92 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, UK.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science **280**:2126-2128.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology **70**:164-168.

TABLE 3-1. Descriptions of variables included in the analysis of pronghorn fawn survival.

Variable	Description
.	No effect
c	An additive coyote density effect
wf	An additive wolf-free site effect
g	An additive gender effect
j	An additive effect for jackrabbit presence
m	An additive birthweight effect
s	An additive site effect
sw	An additive summer wolf density effect
ww	An additive winter wolf density effect
y	An additive year effect

TABLE 3-2. Model selection results for survival of pronghorn fawns during the first 60 days of life at three study sites in northwestern Wyoming, 2002-2004.

Model	*K*	AIC$_c$	ΔAIC$_c$	Akaike weight	Model Likelihood	Deviance
S_{g+m+c}	4	107.003	0.000	0.137	1.000	98.611
S_{g+c}	3	107.357	0.353	0.115	0.838	101.124
S_{c}	2	108.314	1.311	0.071	0.519	104.198
S_{m+c}	3	108.566	1.563	0.063	0.458	102.333
$S_{g+m+c+j}$	5	108.804	1.800	0.056	0.407	98.209
$S_{g+m+c+sw}$	5	109.014	2.011	0.050	0.366	98.420
$S_{g+m+c+ww}$	5	109.122	2.119	0.048	0.347	98.528
S_{g+c+sw}	4	109.282	2.278	0.044	0.320	100.889
S_{g+c+ww}	4	109.431	2.428	0.041	0.297	101.039
S_{wf+g+m}	4	109.729	2.725	0.035	0.256	101.336
S_{wf+g}	3	109.772	2.769	0.034	0.250	103.539
S_{wf}	2	109.829	2.826	0.033	0.243	105.714
S_{c+sw}	3	109.873	2.870	0.033	0.238	103.640
S_{c+ww}	3	110.364	3.360	0.026	0.186	104.131
$S_{g+m+c+ww+sw}$	6	110.590	3.587	0.023	0.166	97.750
$S_{wf+y+g+m}$	6	110.728	3.725	0.021	0.155	97.888
$S_{g+c+ww+sw}$	5	110.737	3.734	0.021	0.155	100.143
$S_{c+ww+sw}$	4	110.897	3.894	0.020	0.143	102.505
$S_{wf+g+m+c+ww}$	6	111.151	4.148	0.017	0.126	98.311
$S_{m+c+ww+sw}$	5	111.302	4.298	0.016	0.117	100.708
S_{s+g+m}	5	111.910	4.906	0.012	0.086	101.315
S_{s+g}	4	111.921	4.917	0.012	0.086	103.528
S_{s}	3	111.921	4.918	0.012	0.086	105.688
S_{g+m+ww}	4	112.300	5.297	0.010	0.071	103.908
S_{s+m}	4	112.311	5.308	0.010	0.070	103.919

[a] Although we tested 37 models, we present results only for models with Akaike weights ≥ 0.01.

[b] *g* = gender, *m* = birthweight, *c* = coyote density, *j* = an irruption in the population of white-tailed jackrabbits, *sw* = summer wolf density, *ww* = winter wolf density, *wf* = wolf-free site, *s* = site, *y* = year.

TABLE 3-3. Model-averaged estimates of pronghorn fawn survival during the first 60 days of life at three study sites in northwestern Wyoming, 2002-2004.

Site	$\hat{S}$	SE	95% LCL	95% UCL
Sites with coyotes and wolves				
Gros Ventre 2003	0.255	0.071	0.141	0.417
Gros Ventre 2004	0.390	0.094	0.228	0.581
Elk Ranch 2003	0.259	0.085	0.127	0.454
Elk Ranch 2004	0.440	0.112	0.244	0.657
Site with coyotes and no wolves				
Antelope Flats 2002	0.149	0.055	0.070	0.291
Antelope Flats 2003	0.049	0.037	0.011	0.193
Antelope Flats 2004	0.097	0.043	0.040	0.218

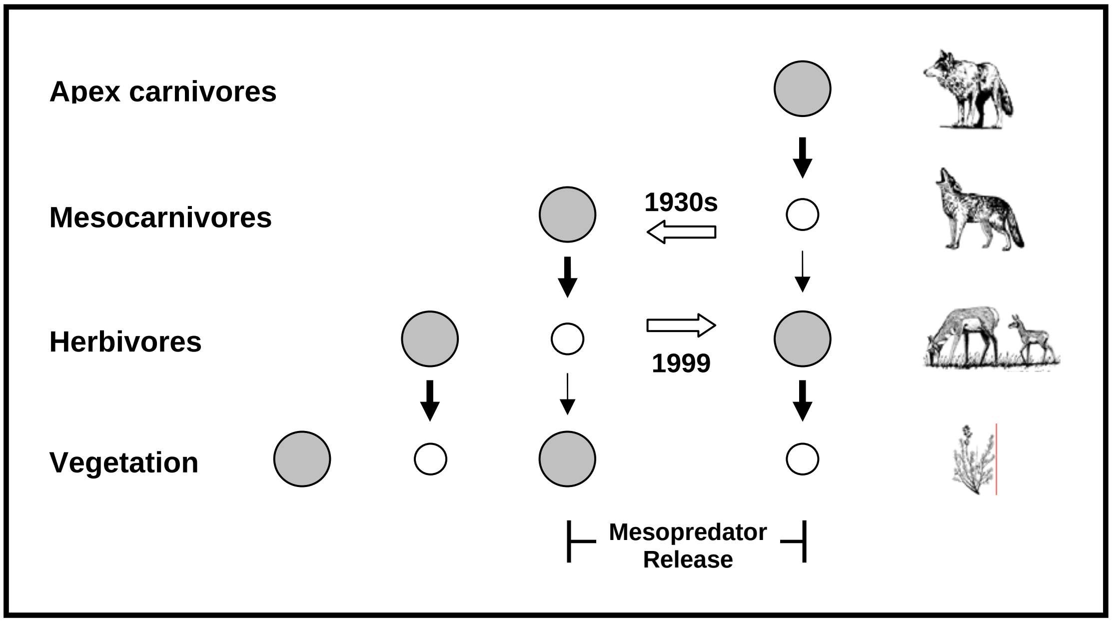


FIG. 3-1. Hypothesized relationships among trophic levels and changing trophic structure in Grand Teton National Park, Wyoming. The weight of the arrow indicates the strength of the effect. Relative abundance of organisms at each trophic level is indicated by the size of the circles. Mesocarnivore release in coyotes is thought to have occurred between the 1930s and 1999 as a consequence of the extirpation of wolves in northwestern Wyoming.

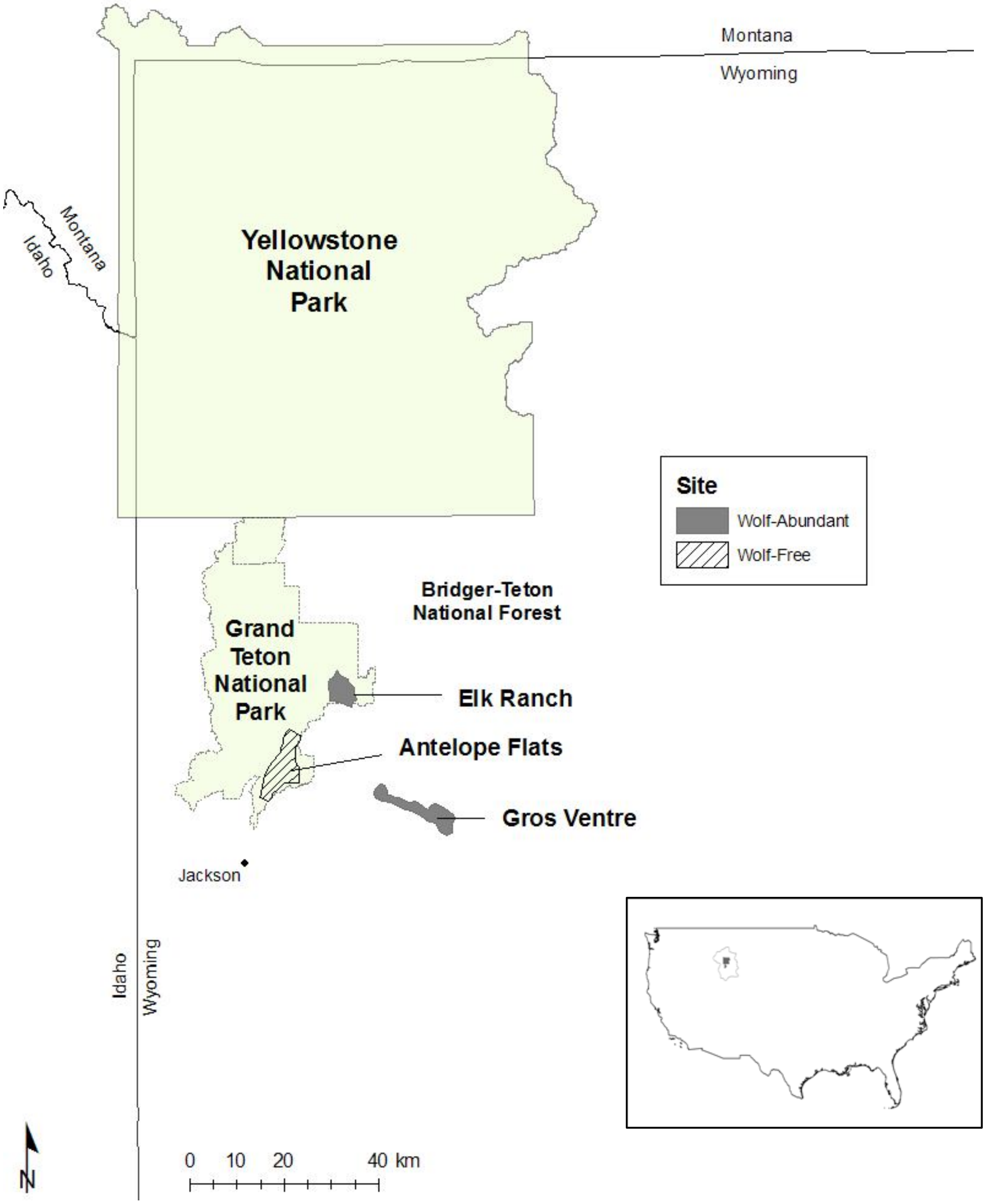


FIG. 3-2. Map showing the location of the Greater Yellowstone Ecosystem (GYE) in the western United States (inset), the locations of study sites, and place names referred to in the text.

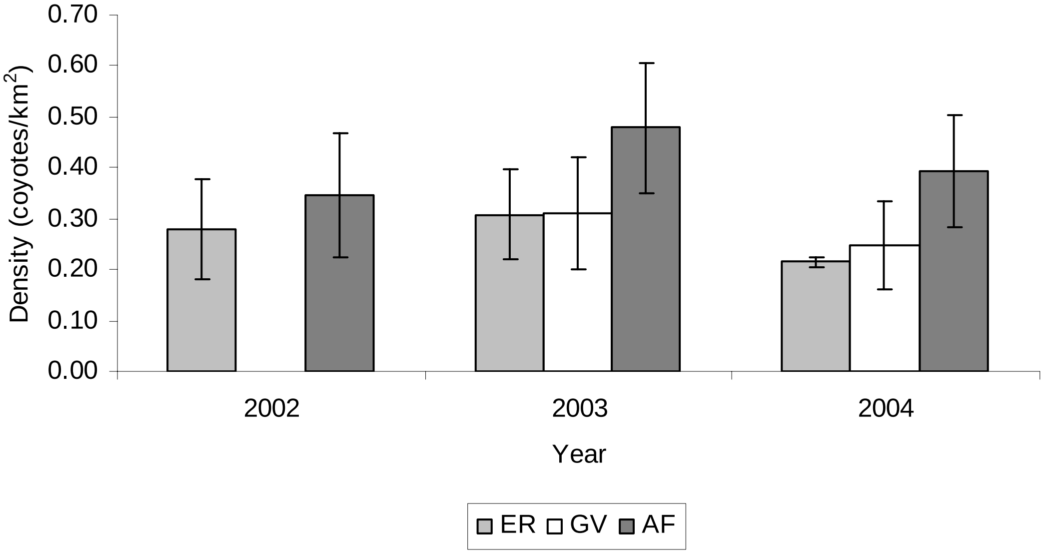


FIG. 3-3. Pre-whelping coyote densities (resident and transient combined) at three field sites in northwestern Wyoming, 2002-2004.

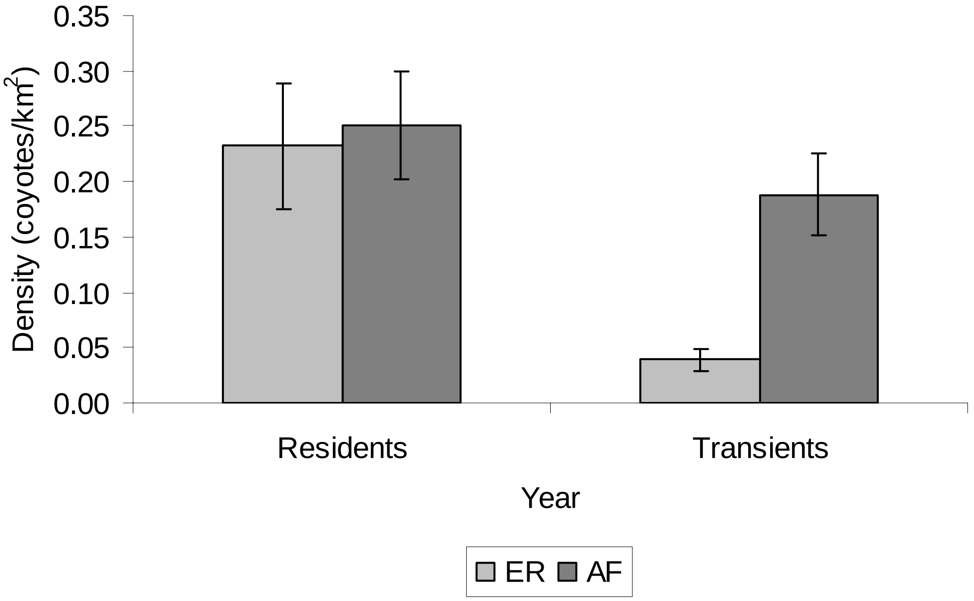


FIG. 3-4. Comparison of pre-whelping resident and transient coyote densities at sites with radio-collared coyotes in northwestern Wyoming, 2003-2004.

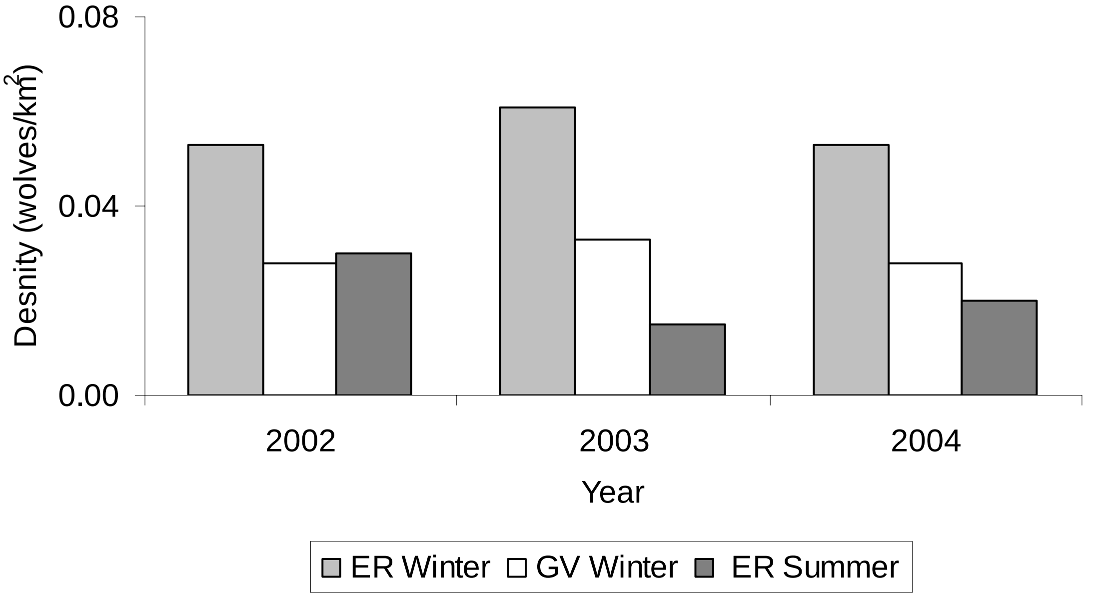


FIG. 3-5. Seasonal wolf densities at two sites in northwestern Wyoming, 2002-2004. The Antelope Flats site is not shown because wolves did not use the site.

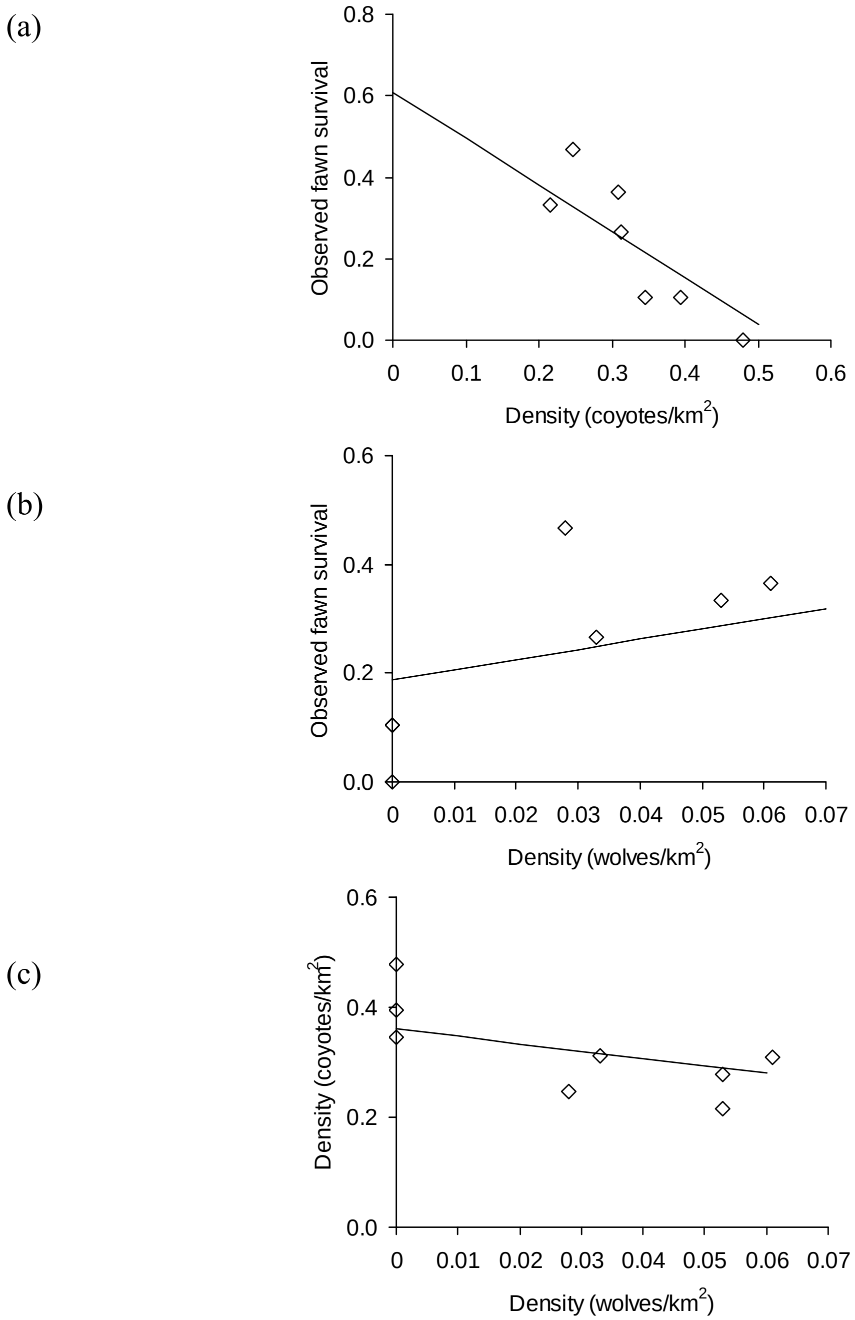


FIG. 3-6. Correlations between (a) observed pronghorn fawn survival and pre-whelping coyote density, (b) observed pronghorn fawn survival and winter wolf density, and (c) pre-whelping coyote and winter wolf densities at three sites in northwestern Wyoming, 2002-2004.

CHAPTER 4

RECOLONIZING WOLVES AND MESOPREDATOR SUPPRESSION OF COYOTES: IMPACTS ON PRONGHORN POPULATION DYNAMICS[3]

Abstract. The mesopredator release hypothesis predicts that an increase in coyote (*Canis latrans*) densities, resulting from the extirpation of wolves (*Canis lupus*) throughout parts of the United States, contributes to high rates of neonatal mortality in pronghorn. 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 between 2002 and 2004. Further, we used stochastic 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 rates and cause-specific mortality attributable to coyotes were markedly lower in areas utilized by wolves. Based on simulation modeling, the realized population growth rate was 0.95 based on fawn survival in the absence of wolves, and 1.09 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. Neonatal survival was positively correlated with pronghorn population size, suggesting the existence of an Allee effect driven by predation may contribute to the high rate of neonatal morality observed in this system. Our results suggest that reintroductions of large carnivores may influence biodiversity through effects on prey populations mediated by mesopredator

---

[3] Coauthored by Kim Murray Berger and Mary M. Conner

suppression, and demonstrate the utility of using simulation modeling to move beyond changes in vital rates to population-level impacts.

INTRODUCTION

The importance of predation as a source of mortality for neonatal ungulates has been well documented. Neonatal mortality rates of temperate ungulates average 47% at sites where predators occur, versus 19% in areas lacking predators (Linnell et al. 1995). Although disease, hypothermia, starvation, 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;* 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 over-harvesting 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).

Several factors unrelated to predators may contribute to the high levels of predation observed in some systems. Habitat degradation due to fire suppression, livestock grazing, or conversion of native vegetation to livestock forage may predispose neonates to predation if they are dependent upon adequate hiding cover for protection against searching predators (Barrett 1981). Concentration of hiding neonates at artificially high densities due to fencing or a lack of suitable fawning habitat may increase the efficiency of searching predators (Byers 1997). A lack of alternative prey, especially during periods when carnivores are provisioning young, may increase hunting intensity on neonatal ungulates (Byers and Byers 1983). Furthermore, changes in prey densities may reduce the effectiveness of anti-predator strategies such as reproductive synchrony (Ims 1990).

In addition, factors contributing to enhanced predator densities may facilitate high levels of predation. For instance, despite sustained efforts during the past century to reduce coyote numbers (Berger 2006), densities have increased in many areas and their distribution, once limited to the midwestern United States, now extends from Alaska to Central America (Parker 1995). The increase in coyote densities has been ascribed to various causes including food subsidies provided by humans in the form of garbage, agricultural crops, and livestock, as well as alteration of habitat through logging and livestock grazing which may promote densities of native prey (Gompper 2002).

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 (Gompper 2002). Because of their relatively smaller size (10.6 kg for coyotes versus 33.2 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 (*Odocoileus virgianus*), and pronghorn neonates, which typically weigh ≤ 5 kg at birth.

The reintroduction of wolves to the Greater Yellowstone Ecosystem provided an opportunity to assess the extent to which the extirpation of wolves contributes to high rates of neonatal mortality in pronghorn. An inverse relationship between coyote densities and survival of neonatal pronghorn, and a direct relationship between wolf densities and survival of neonatal pronghorn, was previously described (Chapter 3). Here we report cause-specific mortality of neonatal pronghorn captured at wolf-free and wolf-abundant sites. In addition, we use demographic modeling to 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 in this area.

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 (November - April), and the Gros Ventre River drainage, which was used by wolves only during winter (Fig. 4-1). In contrast, the Antelope Flats site was not used by wolves during either season. All sites are characterized by shrub-steppe habitat dominated by big sagebrush (*Artemesia 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 4-hour mortality sensors (weight ~ 60g; Advanced Telemetry Systems Inc., Isanti, Minnesota, USA). Following processing, fawns were released at their capture sites.

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 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) suspected predation when tracks, scats, hair, or caching behavior indicated that a predator was involved, but sufficient remains were not recovered to rule out scavenging, 3) disease, and 4) other (e.g., starvation, 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 or second month of life. We evaluated 22 models (Appendix B) to assess the effects of month of life (i.e., first or second), 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):

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

The most global model we could parameterize with our data was $S_{N(m+s+g+w)}$, where S_N was estimated summer survival of neonates, *m* was month, *s* was site, *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 (Appendix C), we pooled the data for fawns captured in areas used by wolves. We used Akaike's Information Criterion adjusted for small sample sizes ($\mathrm{AIC_c}$) 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 (Lefkovitch 1965). Our model was based on females and utilized vital rates for four biological stage classes -- neonates (*N*), juveniles (*J*), yearlings (*Y*), and adults (*A*), and six 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), and adult survival (S_A).

Fertility

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 ± SE) fetuses per female (*n* = 327), including pregnant yearlings, for nine studies in the western U.S. (O'Gara and Yoakum 2004). Similarly, mean litter size was 1.90 ± 0.019 fetuses per adult female (*n* = 235) in Wyoming and Colorado (Gerlach and Vaughan 1990, Zimmer 2004). Thus, assuming 100% pregnancy rates for adult females and an even sex-ratio for fawns (Byers 1997, Zimmer 2004), we estimated adult fertility as

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

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 (discussed above). 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 counts (i.e., surveys to record the distribution of animals by age and sex) conducted in GTNP each August between 1981 and 2005 (Wyoming Game and Fish [WG&F], *unpublished data*). We used a procedure modified from Firchow (1986) to generate annual estimates of neonatal survival from the count data (Appendix D).

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 re-absorption 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 4-1).

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 GNTP 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_A.

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). However, the parameter estimates obtained from fixed effects models contain both process ($\sigma^2_{process}$) 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 4-2). 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 $\hat{\sigma}^2_{process}$ 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 $\hat{\sigma}^2_{process}$ 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 co-vary over time because the same environmental factors similarly affect all rates (Doak et al. 1994). Positive correlation in vital rate 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).

Correlations among vital rates were not available for pronghorn in GTNP because, with the exception of a single year, studies of adults and juveniles were not conducted contemporaneously. Because severe winter weather has been identified as an important factor contributing to high rates of pronghorn mortality in Wyoming, Montana, 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 4-3). 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 (WG&F, *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 polynomial, 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 4-4). 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; 6) At the end of each simulation of *T* years, record the log of the average annual population growth rate as

$$\log(\lambda_t) = \frac{1}{T} \times \log\left(\frac{N_T}{N_0}\right). \tag{3}$$

7) Repeat this process 8,000 times (White et al. 2002); 8) At the end of 8,000 simulations, record the median population size for each year and the mean log of the population growth rate $\left(\overline{\log(\lambda_t)}\right)$.

All simulations were performed with MALAB 6.5 (The MathWorks, Inc., Natick, MA). The initial population vector was derived from count data for 2005 (WG&F, *unpublished data*). Because WG&F does not distinguish adult from yearling females in the classification counts, we used our calculation of the proportion of reproductive females in the population (82%; Appendix D) to determine the number of adult females and yearlings in the initial population vector. In addition, we ran trials in which we varied the proportion of yearling from 10-25%, and results were robust to the number of yearlings in the initial population vector (Appendix E). For each year we recorded the effect of wolf reintroduction on the population growth rate (*sensu* Ellner and Fieberg 2003) as

$$\Delta \log(\lambda_t) = \left(\log(\lambda_t) \mid \text{wolves}, \underline{\theta_t}\right) - \left(\log(\lambda_t) \mid \text{no wolves}, \underline{\theta_t}\right) \tag{4}$$

where $\underline{\theta_t}$ 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 $\overline{\log(\hat{\lambda}_t)}$, $\mathrm{SE}\left(\overline{\log(\hat{\lambda}_t)}\right)$, and $\hat{\sigma}_{process}$ from our initial simulations, we modeled $\log(\lambda_t)$ with a normal distribution possessing mean $\overline{\log(\hat{\lambda}_t)}$ and standard deviation $\mathrm{SE}\left(\overline{\log(\hat{\lambda}_t)}\right)$, and process variance as a multiple of a χ^2 distribution as

$$\frac{df \times \hat{\sigma}^2_{process}}{\sigma^2_{process}} \sim \chi^2_{df} \text{ (Morris and Doak 2002, Blakesely et al. 2006).} \qquad (5)$$

We used $df = T$ to approximate the confidence interval of $\hat{\sigma}_{process}$. To estimate the confidence intervals, we generated 1,000 bootstrap data sets consisting of 8,000 population trajectories for each treatment group over a 20-year period. For each trajectory, we used randomly selected values of $\overline{\log(\hat{\lambda}_t)}$ and $\hat{\sigma}_{process}$ for each year to estimate the population size as

$$\hat{N}_{t+1} = e^{\log(\hat{\lambda}_t)} \hat{N}_t \qquad (6)$$

and $\Delta\log(\hat{\lambda}_t)$ as in (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 1,000 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. 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 of captured fawns was 74 at the wolf-abundant sites (17 in 2002, 27 in 2003, and 30 in 2004) and 51 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/suspected 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 4-5). 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. Coyote predation (verified plus suspected) 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. 4-2). Seventy-five percent of all mortality at both sites occurred during the first three weeks of life (Fig. 4-2).

Neonatal survival

We included 125 marked individuals in the analysis of fawn survival. On the basis of minimum AIC_c, the best 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 4-6). 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 (Table 4-7, Wald test, $P = 0.04$). 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 4-7). Survival during the first month of life was considerably lower than during the second (Table 4-7, Wald test, $P < 0.001$). 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 4-6).

Density dependence

There was some support for positive density dependence in neonatal survival rates at current population densities (Fig. 4-3). 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 × ln[*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, however, as there is considerable variation in neonatal survival at population sizes near 200, there are few years in which the population size was above 300 upon which to base the curve (Fig. 4-3), 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 (Appendix F). Thus, we present only the results from the model that included correlation.

At the end of 10 years, the realized population growth rate was 0.949 (95% CI = 0.884 to 1.019) based on fawn survival rates in the absence of wolves, and 1.086 (95% CI = 1.015 to 1.163) based on survival rates of neonates captured at sites utilized by wolves (Fig. 4-4). Thus, wolf recolonization could result in a 14% annual increase in the pronghorn population growth rate ($\Delta\lambda_t$ = 0.137, 95% CI = -0.004 to 0.279, Fig. 4-5a), corresponding to an overall increase in the pronghorn population of 422 animals (95% CI = -13 to 1,051, Fig. 4-5b).

From an initial population size of 249 pronghorn, the most likely population trajectory based on fawn survival at the wolf-free site was a 23% decline in the population within 5 years to 192 animals, a 37% reduction within 10 years to 148 animals, and a 65% decrease over 20 years to 88 animals (Fig. 4-6a). However, confidence intervals on the predicted population size ranged from 121-304 within 5 years, 73-302 within 10 years, and 28-281 at 20 years, indicating that both a slight increase 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 51% increase within 5 years to 377 animals, a 111% increase within 10 years to 570 animals, and a 383% increase at 20 years to 1,305 animals (Fig. 4-6b). The 95% confidence intervals suggest that an increase in the population over the next 20 years is likely, but indicate that both a relatively modest increase (432 animals) and a sixteen-fold increase (3,943 animals) are reasonably likely outcomes.

DISCUSSION

Our results support the hypothesis that mesopredator release of coyotes contributes to high rates of coyote predation on neonatal pronghorn 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), both overall mortality rates and coyote predation intensity were markedly lower in areas utilized by wolves. This disparity in predation rates corresponds to a 33% reduction 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 in wolf-abundant areas (Chapter 2). 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 field work, 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 4-7). 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 which 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. 4-3; 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 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 (Chapter 3), 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 × 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. 4-4b). In addition, the model projected a likely 111% increase in population size within 10 years (Fig. 4-6b), and the confidence intervals on $\Delta\lambda_t$ were ≥ 0 for all time horizons beyond 10 years (Fig. 4-5a). Thus, there is considerable evidence that wolf recolonization will have a positive effect on pronghorn population dynamics.

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 management actions (e.g., Clutton-Brock and Lonergan 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

The validity of population projections based on any demographic model hinges on the adequacy of the underlying mean vital rates, as well as the extent to which variability and correlation in these rates are accurately characterized over time (Morris and Doak 2002). Importantly, although the vital rates in our demographic model vary stochastically between time periods, the underlying stochastic processes that produce the vital rates are assumed to be stationary (Caswell 2001). To the extent that future variation in vital rates differs from that incorporated in the model, actual population dynamics may diverge considerably from model predictions. With respect to vital rates used to parameterize our model, the estimate of juvenile overwinter survival, though consistent with winter survival rates reported in long-term studies of other juvenile ungulates (Gaillard et al. 2000), was based on a small sample ($n = 13$) and just two years of data. This also necessitated the use of $\hat{\sigma}^2_{process}$ in adult survival as the variance estimate for juvenile overwinter survival. Furthermore, our model did not incorporate correlation between fertility and survival rates of adult females, which could have a strong, negative impact on population size during droughts or severe winters (Byers et al. 2005). Thus, a detailed demographic study of pronghorn in GNTP that focuses on obtaining improved vital rate and variance estimates for each stage class, as well as elucidating co-variation among the vital rates, could improve model performance.

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. 4-1; Chapter 2). 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 (Chapter 3). While 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 (Figure 4-6b) 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. 4-3), declines in the population growth rate would likely occur long before a population size of ~ 4,000 is reached (Fig. 4-6b). 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). Second, 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.

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. In addition, 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. In particular, 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.

LITERATURE CITED

Allee, W. C. 1951. The social life of animals. Beacon Press, Boston, Massachusetts, USA.

Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. Gutiérrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and trends in demography of northern spotted owls, 1985-2003. Wildlife Monographs **163.**

Autenrieth, R. E., and E. Fichter. 1975. On the behavior and socialization of pronghorn fawns. Wildlife Monographs **42**.

Barrett, M. W. 1981. Environmental characteristics and functional significance of pronghorn fawn bedding sites in Alberta. Journal of Wildlife Management **45**:120-131.

Berger, J., K. M. Berger, and J. P. Beckmann. 2006. Wildlife & energy development: pronghorn of the Upper Green River Basin. Wildlife Conservation Society, New York, New York, USA.

Berger, K. M. 2006. Carnivore-livestock conflicts: effects of subsidized predator control and economic correlates on the sheep industry. Conservation Biology **20**:751-761.

Blakesely, J.A., M. E. Seamans, M. M. Conner, A. B. Franklin, G. C. White, R. J. Gutiérrez, J. E. Hines, J. D. Nichols, T. E. Munton, D. W. H. Shaw, J. J. Keane, G. N. Steger, B. R. Noon, T. L. McDonald, and S. Britting. 2006. Demography of the California Spotted Owl in the Sierra Nevada. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Bonenfant, C., J. -M. Gaillard, F. Klein, and J. -L. Hamann. 2005. Can we use the young:female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. Journal of Applied Ecology **42**:361-370.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph Number **5**.

Byers, J. A. 1997. American pronghorn: social adaptations & the ghosts of predators past. University of Chicago Press, Chicago, Illinois, USA.

Byers, J. A., and K. Z. Byers. 1983. Do pronghorn mothers reveal the locations of their hidden fawns? Behavioral Ecology and Sociobiology **13**:147-156.

Byers, J. A., and J. D. Moodie. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. Behavioral Ecology and Sociobiology **26**:157-164.

Byers, J. A., A. A. Byers, and S. J. Dunn. 2005. A dry summer diminishes mate search effort by pronghorn females: evidence for a significant cost of mate search. Ethology **112**:74-80.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Clutton-Brock, T. H., and M. E. Lonergan. 1994. Culling regimes and sex ratio biases in highland red deer. Journal of Applied Ecology **31**:521-527.

Coulson, T., J. -M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology **74**:789-801.

Crooks, K. R., M. A. Sanjayan, and D. F. Doak. 1998. New insights on cheetah conservation through demographic modeling. Conservation Biology **12**:889-895.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412-1423.

Deloney, W. C. 1948. Passing of the antelope in the Jackson Hole. Jackson Hole Courier February 12 edition.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 *in* J. Diamond and T. Case, editors. Community ecology. Oxford University Press, New York, New York, USA.

Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. Ecological Applications **4**:446-460.

Ellner, S. P., and J. Fieberg. 2003. Using PVA for management despite uncertainty: effects of habitat, hatcheries, and harvest on salmon. Ecology **84**:1359-1369.

Fairbanks, W. S. 1993. Birthdate, birthweight, and survival in pronghorn fawns. Journal of Mammalogy **74**:129-135.

Ferson, S., and M. A. Burgman. 1995. Correlations, dependency bounds and extinction risks. Biological Conservation **73**:101-105.

Firchow, K. M. 1986. Ecology of pronghorn on the Piñon Canyon Manuever Site, Colorado. Thesis. Virginia Polytechnic Institute, Blacksburg, Virginia, USA.

Gaillard, J. -M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation of fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31**:367-393.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs **84**.

Gascoigne, J. C., and R. N. Lipcius. 2004. Allee effects driven by predation. Journal of Applied Ecology **41**:801-810.

Gerlach, T., and M. R. Vaughan. 1990. Guidelines for the management of pronghorn on the Piñon Canyon Maneuver Site, Colorado. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. Oecologia **67**:540-554.

Gompper, M. E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of northeastern North America by coyotes. BioScience **52**:185-190.

Gregg, M. A., M. Bray, K. M. Kilbrade, and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. Journal of Wildlife Management **65**:19-24.

Heppell, S. S., H. Caswell, and L. B Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology **81**:654-665.

Ims, R. A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. American Naturalist **136**:485-498.

Johnson, M. D., T. W. Sherry, R. T. Holmes, and P. P. Marra. 2006. Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. Conservation Biology **20**:1433-1444.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics **21**:1-18.

Lingle, S. 2000. Seasonal variation in coyote feeding behaviour and mortality of white-tailed deer and mule deer. Canadian Journal of Zoology **78**:85-99.

Linkie, M., G. Chapron, D. J. Martyr, J. Holden, N. Leader-Williams. 2006 Assessing the viability of tiger subpopulations in a fragmented landscape. Journal of Applied Ecology **43**:576–586.

Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biology **1**:209-223.

Martinka, C. J. 1967. Mortality of northern Montana pronghorns in a severe winter. Journal of Wildlife Management **31**:159-164.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology **13**:815-829.

Mitchell, G. J. 1967. Minimum breeding age of female pronghorn antelope. Journal of Mammalogy **48**:489-490.

Morris, W. F., and D. K. Doak. 2002. Quantitative conservation biology. Sinauer and Associates, Inc., Sunderland, Massachusetts, USA.

Murray, D. L., and B. R. Patterson. 2006. Wildlife survival estimation: recent advances and future directions. Journal of Wildlife Management **70**:1499-1503.

O'Gara, B. W. 1978. Differential characteristics of predator kills. Proceedings of the Biennial Pronghorn Antelope Workshop **8**:380-393.

O'Gara, B. W., and J. D. Yoakum. 2004. Pronghorn ecology and management. University Press of Colorado, Boulder, Colorado, USA.

Parker, G. 1995. Eastern coyote: the story of its success. Nimbus Publishing Limited, Halifax, Nova Scotia.

Pyrah, D. B. 1987. American pronghorn antelope in the Yellow Water Triangle, Montana. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.

Sawyer, H., and F. Lindzey. 2000. Jackson Hole Pronghorn Study. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, Wyoming, USA.

Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin **33**:1266-1273**.**

Smith, A. D., and D. M. Beale. 1980. Pronghorn Antelope in Utah: some research and observations. Utah Division of Wildlife Resources, Salt Lake City, Utah, USA.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wrights, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology **2**:75-92.

White, G. C. 2000. Population viability analysis: data requirements and essential analysis. Pages 288 - 331 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology – controversies and consequences. Columbia University Press, New York, New York, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Supplement **46**:120-138.

White, G. C., K. P. Burnham, and D. R. Anderson. 2001. Advanced features of program MARK. Pages 368-377 *in* R. Field, R. J. Watten, H. Okarma, and P. R. Sievert, editors. Wildlife, land, and people: priorities for the 21st century. The Wildlife Society, Bethesda, Maryland, USA.

White, G. C., A. B. Franklin, and T. M. Shenk. 2002. Estimating parameters of PVA models from data on marked animals. Pages 169-190 *in* S. R. Beissinger and D. R. McCullough, editors. Population viability analysis. University of Chicago Press, Chicago, Illinois, USA.

Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. Journal of Wildlife Management **61**:302-312.

Zimmer, J. E. 2004. Pronghorn productivity and fawn survival in central and southeastern Wyoming. Thesis. University of Wyoming, Laramie, Wyoming, USA.

TABLE 4-1. Comparison of observed neonatal survival rates of radio-collared fawns and neonatal survival rates estimated from young:female ratios during fall classification counts.

Year	Observed survival[a]	Estimated survival
2002	0.222	0.227
2003	0.186	0.319
2004	0.311	0.311

[a] Total number of surviving fawns divided by total number of collared fawns.

[b] Estimated from classification count data (see Appendix D).

TABLE 4-2. Stage classes, ages, and vital rates used to construct the demographic models.

Class	Age (months)	Vital rate	Description	Mean (variance)
Neonate	0-2	S_{NE}	Summer survival of fawns captured at wolf-abundant sites	0.070 (0.006)
	0-2	S_{NC}	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)
		F_A	Fertility	0.95 (0.0003)

TABLE 4-3. Survival rates for adults and juveniles used to estimate correlation in overwinter survival.

Site	Adult survival	Juvenile survival	Reference
Colorado	0.950	0.935	T. Pojar, *unpublished data*
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, *unpublished data*

TABLE 4-4. 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, Wyoming.

	Wolf-free site			Wolf-abundant sites		
Stage class	Neonate	Yearling	Adult	Neonate	Yearling	Adult
Neonate	0	0	0.829[b]	0	0	0.829
Yearling	0.059[a]	0	0	0.296[a]	0	0
Adult	0	0.872	0.872	0	0.872	0.872

[a] 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 = $S_N * S_J$ = 0.070 * 0.836 = 0.059.

[b] Annual reproductive rate = $S_A * F_A$ = 0.872 * 0.950 = 0.829.

TABLE 4-5. Sample sizes (*n*) and percentages of radio-collared pronghorn fawns dying by various causes during the first 60 days of life in Grand Teton National Park, Wyoming.

	Wolf-free site						Wolf-abundant sites					
	2002		2003		2004		2002		2003		2004	
Cause	*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
Suspected predation												
Coyote	7	37	5	29	8	53	4	24	5	19	4	13
Other												
Trauma[a]	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

[a] Trauma includes drowning (*n* = 1) and exertion myopathy (*n* = 1).

TABLE 4-6. Model selection results from analysis of neonatal pronghorn survival at wolf-free and wolf-abundant sites in Grand Teton National Park, Wyoming.[a]

Model[b]	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

[a] Although we tested 22 models, we present only the results for models with Akaike weights >0.

[b] s = site, EO = an even-odd effect for the first and second months of life, g = gender, w = weight at birth, m = month.

TABLE 4-7. Comparison of estimated survival rates for male and female fawns based on parameter estimates from the top-ranked model.

	Males			Females		
Site	$\hat{S}$	95% LCL	95% UC	$\hat{S}$	95% LCL	95% UC
Wolf-free site						
1st month of life	0.082	0.056	0.117	0.168	0.123	0.227
2nd 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						
1st month of life	0.292	0.217	0.379	0.484	0.393	0.576
2nd 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

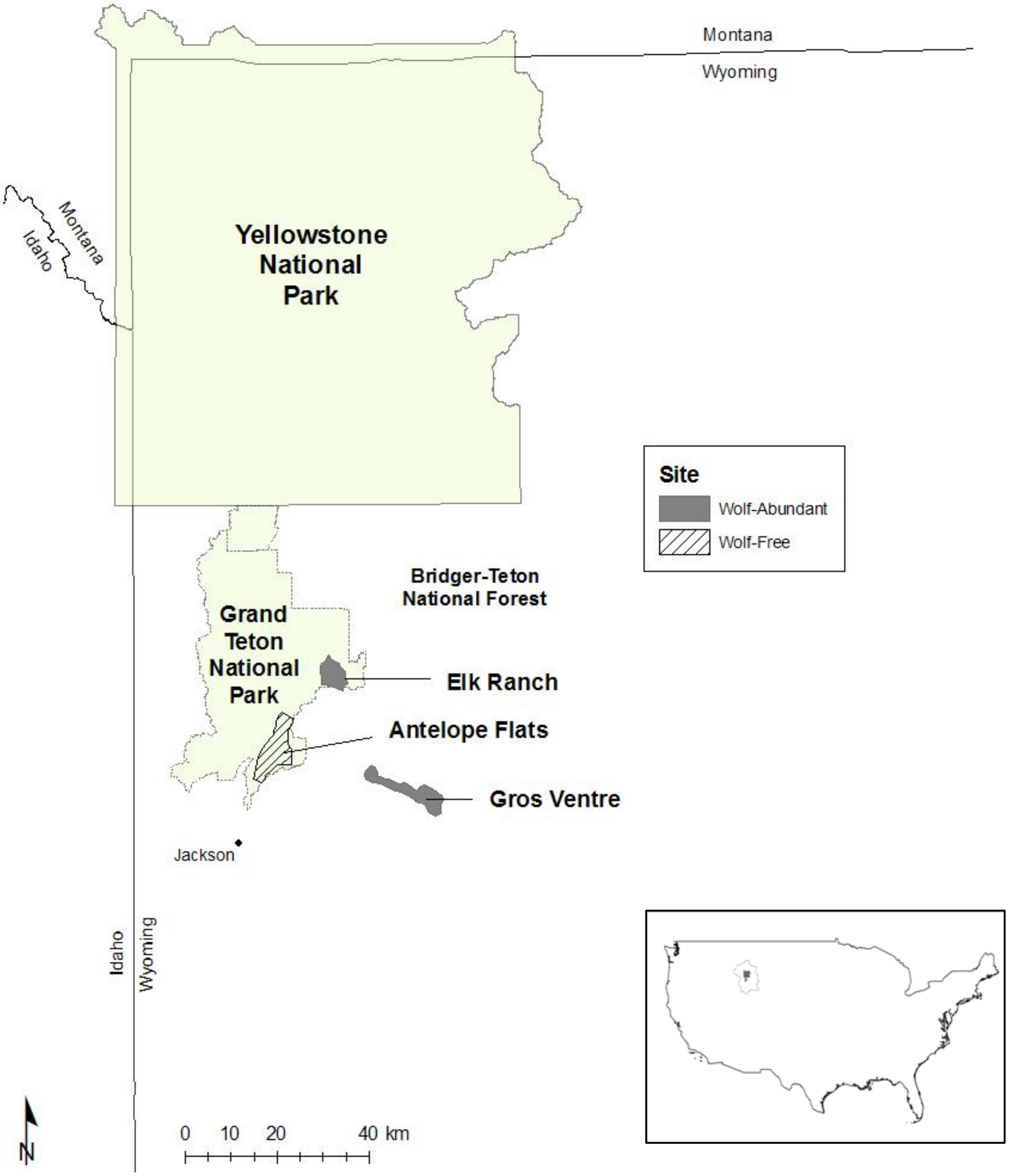


FIG. 4-1. Map showing the location of the Greater Yellowstone Ecosystem (GYE) in the western United States (inset), the locations of study sites, and place names referred to in the text.

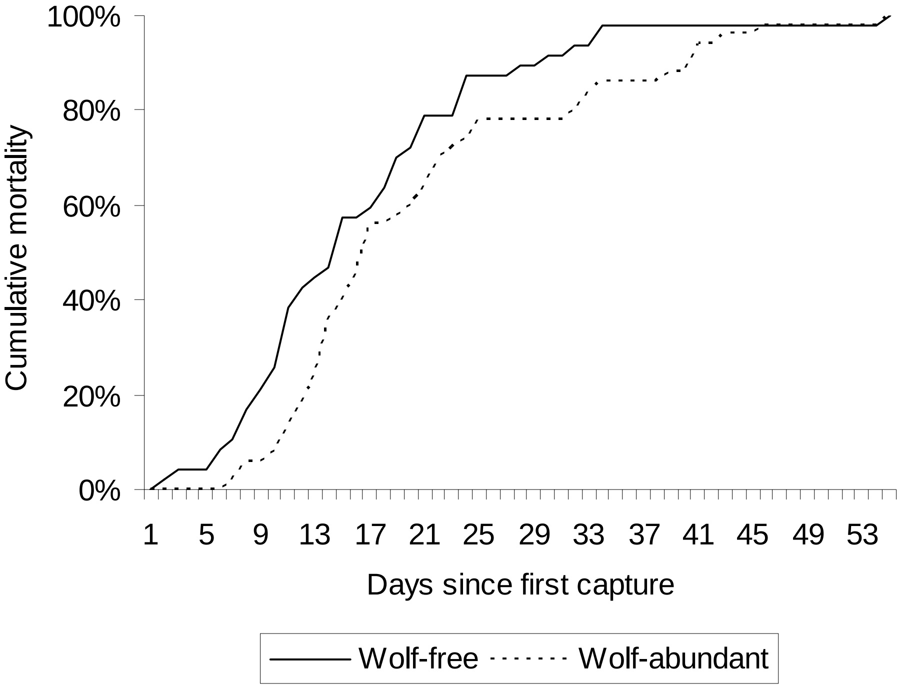


FIG. 4-2. Cumulative mortality during the first two months of life of pronghorn fawns captured at wolf-free and wolf-abundant sites in Grand Teton National Park, Wyoming, 2002-2004.

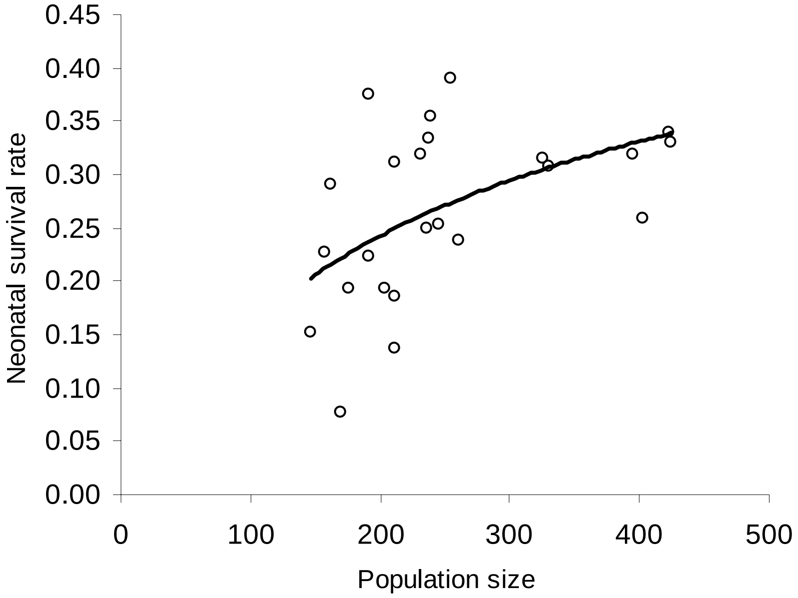
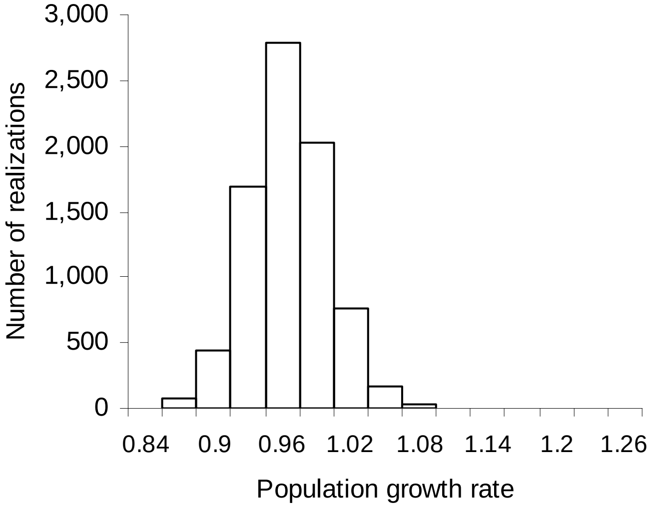


FIG. 4-3. Test for density dependence in pronghorn neonatal survival in Grand Teton National Park, Wyoming, 1981-2005.

(a)



(b)

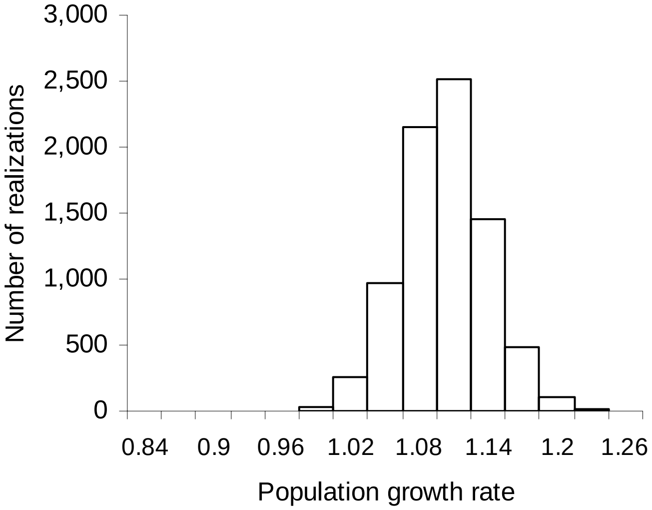
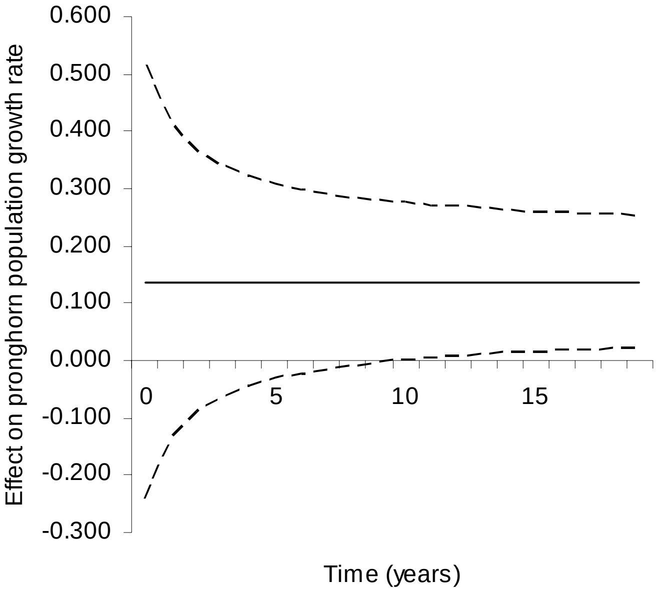


FIG. 4-4. Realized population growth rates from the demographic model based on survival of fawns captured at (a) wolf-free and (b) wolf-abundant sites.

(a)



(b)

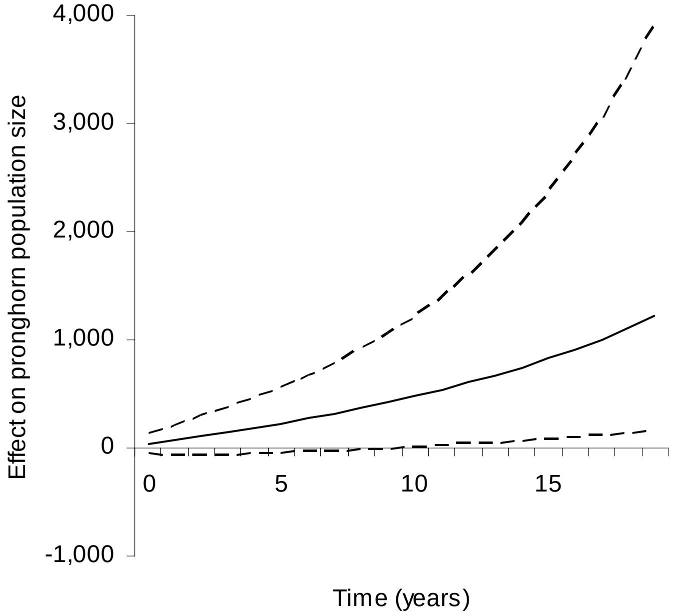
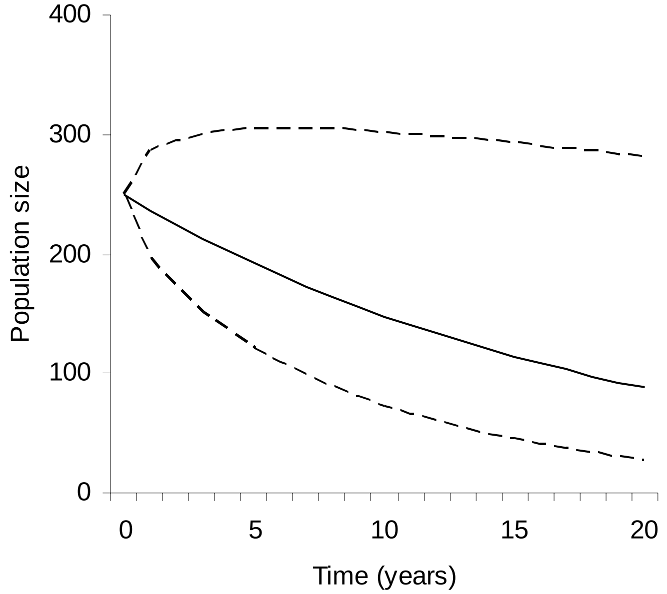


FIG. 4-5. Average annual effect of recolonizing wolves on (a) the pronghorn population growth rate, and (b) pronghorn population size, based on demographic modeling. Dashed lines represent 95% confidence intervals.

(a)



(b)

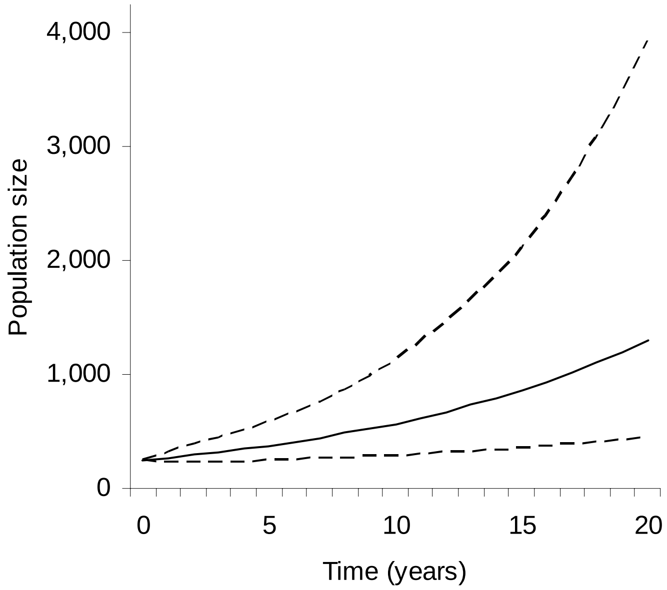


FIG. 4-6. Results of the demographic model showing median changes in pronghorn population size over time based on survival of fawns captured at (a) wolf-free, and (b) wolf-abundant sites. Dashed lines represent 95% confidence intervals.

CHAPTER 5

CONCLUSIONS

Trophic cascades are predation-related effects that result in inverse patterns of abundance or biomass across multiple trophic levels in a food web (Micheli et al. 2001). In four-tiered food chains, the loss of primary carnivores shifts the trophic structure to a three-tiered system in which populations of mesocarnivores can increase. This process, termed mesopredator release (Soulé et al. 1988), has been shown to affect the persistence of both ground- and scrub-nesting birds through increased nest-predation by striped skunks (*Mephitis mephtis*), raccoons (*Procyon lotor*) and grey foxes (*Urocyon cinereoargenteus*; Rogers and Caro 1998, Crooks and Soulé 1999).

The mesopredator release hypothesis predicts that an expansion in the coyote (*Canis latrans*) population, resulting from the extirpation of gray wolves (*Canis lupus*) throughout much of the United States, accounts for high rates of neonatal mortality in pronghorn (*Antilocapra americana*) observed in some areas. However, although interspecific competition with wolves is often suggested as an important factor limiting coyote populations (Thurber et al. 1992, Peterson 1995), the actual mechanisms by which wolves reduce coyote densities are poorly understood. The recolonization of wolves in Grand Teton National Park (GTNP) in the late 1990s provided an opportunity to test the hypotheses that a) competition with wolves limits coyote abundance, and b) mesopredator release of coyotes by wolves facilitates high rates of neonatal mortality in pronghorn.

That wolf recolonization precipitated a species-level trophic cascade (*sensu* Polis 1999) was evidenced by more than a four-fold difference in neonatal survival of pronghorn at sites used by wolves (32.4 ± 0.063%), relative to neonatal survival in the wolf-free area (6.5 ± 0.083%). The corresponding negative relationship between coyote and wolf densities, both within GTNP ($r^2 = 0.55$, $n = 7$, $P = 0.036$) and at study areas across the Greater Yellowstone Ecosystem ($r^2 = 0.54$, $n = 16$, $P < 0.005$), supports the hypothesis that interspecific competition between these species facilitated the observed increase in pronghorn fawn survival. Notably, whereas densities of resident coyotes in GTNP were similar between wolf-free and wolf-abundant sites ($\bar{x} = 0.251 \pm 0.025/\text{km}^2$ and $\bar{x} = 0.232 \pm 0.029/\text{km}^2$, respectively, $P = 0.687$), the abundance of transient coyotes was significantly lower in areas used by wolves ($\bar{x} = 0.188 \pm 0.019/\text{km}^2$ vs. $\bar{x} = 0.039 \pm 0.005/\text{km}^2$, $P < 0.001$). Thus, differential effects of wolves on solitary coyotes may be an important mechanism by which wolves limit coyote densities. This hypothesis was further supported by differences in survival rates and cause-specific mortality of resident and transient coyotes in GTNP. Between 2001 and 2004, annual survival rates of resident and transient coyotes were 74.6 ± 4.4% and 47.1 ± 11.3%, respectively. And, whereas no resident coyotes were killed by wolves, 67% of transient coyote deaths resulted from predation, with wolves accounting for 83% of predation-related mortality. In addition, although no coyotes were killed by wolves at the wolf-free site, three transients collared at the wolf-free site were killed by wolves in separate incidents when they ventured into areas frequented by wolves. Two former resident coyotes were also killed by wolves shortly after they became transients when other pack members died.

Although it is often suggested that resident coyotes avoid encounters with wolves by occupying the borders of wolf pack territories (Fuller and Keith 1981, Thurber et al. 1992, Peterson 1995, Arjo 1998), we found little evidence that spatial partitioning was an important mechanism facilitating coexistence of resident coyotes and wolves. Annual home ranges of all coyote packs at the wolf-abundant site were completely subsumed within the boundaries of the wolf pack's territory. These finding are consistent with results reported elsewhere (Arjo 1998, Atwood 2006), as no telemetry study conducted to date has documented a high degree of spatial partitioning between the two species. In particular, it has been suggested that rather than orienting home ranges to avoid encounters with wolves, coyote core areas may actually be configured to exploit wolf activity centers (Atwood 2006). Whereas percentage overlap of coyote and wolf home ranges and core areas was extensive based on area alone, the utilization distribution overlap index for all packs was low, indicating differential use of these overlap areas by the two species. Thus, although wolves have not excluded coyotes from broad areas in GTNP, finer-scale spatial partitioning within coyote home ranges may mitigate agonistic encounters with wolves and facilitate coexistence.

Evidence of differential vulnerability of resident and transients coyotes based on spatial segregation was apparent when dispersal rates of transient coyotes were examined. Whereas only 31% (*n* = 4) of transient coyotes captured at the wolf-free site in GTNP emigrated from the area, 67% (*n* = 4) of transients captured at the wolf-abundant site dispersed to wolf-free regions of the Park. And notably, in both cases in which transient coyotes failed to disperse from the wolf-abundant site, the animal was killed by wolves within months ($\bar{x}$ =3.62 ± 3.25). No resident coyotes dispersed from either the wolf-free or wolf-abundant sites.

Mortality from wolves alone appears insufficient to substantially suppress coyote populations in the GYE, but our results suggest that interference competition with wolves contributes to localized population reductions. Specifically, differential effects of wolves on survival and dispersal rates of transient coyotes likely account for the considerable disparity in transient coyote densities, and thus overall coyote densities, between wolf-free and wolf-abundant sites in GTNP.

Results of demographic modeling indicate that wolf recolonization will likely have a considerable impact on the demography of pronghorn in GTNP. Population projections over a 10-year period result in a realized annual population growth rate of 0.949 based on fawn survival rates in the absence of wolves, versus 1.086 based on survival rates of neonates captured in wolf-abundant areas. Thus, on average, wolf restoration could result in a 14% annual increase in the pronghorn population growth rate. Importantly, these differences in neonatal survival rates between wolf-free and wolf-abundant areas were sufficient to alter the trajectory of the pronghorn population from a declining to an increasing trend.

Several factors likely contributed to the significant increase in survival rates of neonatal pronghorn we observed including: 1) the relative simplicity of the focal food chain in our study, 2) anthropogenic changes in resource availability that have resulted in an increase in coyote densities, and 3) a lack of alternative prey stemming from the recent functional extinction of white-tailed jackrabbits (*Lepus townsendii*) in the Park. In particular, 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 facilitate survival of pronghorn neonates through mesopredator suppression of coyotes. In addition, as fawn survival in GTNP between 1981 and 2004 was positively related to pronghorn population density ($r = 0.51$, $P = 0.004$), our results tentatively suggest the existence of positive density dependence in fawn survival. Although it has been observed that reproductive synchrony is less important for ungulates that utilize a hiding strategy to protect neonates from predators (Ims 1990), survival rates of pronghorn fawns born during the peak of fawning are higher than those of fawns born during non-peak periods (Gregg et al. 2001). Given the large number of coyote packs in the vicinity of our study sites, and the energetic demands of coyote packs during the denning/pup-rearing period, it appears likely that coyotes may consume nearly all of the estimated ~ 150 pronghorn fawns produced in the Park each summer. 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).

Our results suggest that restoration of ecological functionality through reintroductions of large carnivores may have implications for the maintenance of biodiversity in areas where mesocarnivore populations have expanded due to mesopredator release. In addition, given the apparent disproportionately higher survival of male fawns at wolf-abundant sites, wolf recolonization has the potential to increase the number of adult male pronghorn available to human hunters. Thus, our findings have important applications for the management of game species as well as the designation and management of protected areas. In particular, 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.

LITERATURE CITED

Arjo, W. M. 1998. The effects of recolonizing wolves on coyote populations, movements, behaviors, and food habits. Dissertation. University of Montana, Missoula, Montana, USA.

Atwood, T. C. 2006. Wolves, coyotes, elk, and mule deer: predator-prey behavioral ecology in southwest Montana. Dissertation. Utah State University, Logan, Utah, USA.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563-566.

Fuller, T. K., and L. B. Keith. 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. Journal of Mammalogy **62**:403-405.

Gascoigne, J. C., and R. N. Lipcius. 2004. Allee effects driven by predation. Journal of Applied Ecology **41**:801-810.

Gregg, M. A., M. Bray, K. M. Kilbrade, and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. Journal of Wildlife Management **65**:19-24.

Ims, R. A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. American Naturalist **136**:485-498.

Micheli, F., G. A. Polis, P. D. Boersma, M. A. Hixon, E. A. Norse, P. V. R. Snelgrove, and M. E. Soulé. 2001. Human alteration of food webs: research priorities for conservation and management. Pages 31–57 *in* M. E. Soulé and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, D.C., USA.

Peterson, R. O. 1995. Wolves as interspecific competitors in canid ecology. Pages 315-324 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves. Circumpolar Press, Edmonton, Alberta, Canada.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos **86**:3-15.

Rogers, C. M., and M. J. Caro. 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. Oecologia **116**:227-233.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wrights, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology **2**:75-92.

Thurber, J. M., R. O. Peterson, J. D. Woolington, and J. A. Vucetich. 1992. Coyote coexistence with wolves on the Kenai Peninsula, Alaska. Canadian Journal of Zoology **70**:2494-2498.

APPENDICES

Appendix A.

Coyote Densities Predicted by Scat Deposition Index

TABLE A-1. Results of regression analysis to estimate coyote densities as a function of scat deposition index at the Elk Ranch and Antelope Flats sites, 2003-2004.

Parameter	Mean	*SE*	LCL	UCL
β_1	1.644	0.295	1.066	2.222

TABLE A-2. Coyote densities predicted by scat deposition index at the Antelope Flats and Elk Ranch sites in 2002, and the Gros Ventre site in 2003-2004.

Site	Year	Scat Deposition Index	Estimated Density[a]	95% LCL	95% UCL
Antelope Flats	2002	0.21	0.345	0.224	0.467
Elk Ranch	2002	0.17	0.279	0.181	0.378
Gros Ventre	2003	0.19	0.312	0.203	0.422
Gros Ventre	2004	0.15	0.240	0.160	0.333

[a] Estimated density = 1.644 × scat deposition index.

Appendix B.

Description of Known Fate Models Examined in the Analysis of Neonatal Pronghorn Survival

TABLE B-1. Description of known fate models examined in the analysis of neonatal survival (*S*) of pronghorn at wolf-free and wolf-abundant sites in Grand Teton National Park, Wyoming, 2002-2004.

Model[a]	Description of structure
$S_{(s+EO+g)}$	Study site and gender effects with an additive even-odd effect for the first and second months of life
$S_{(s+EO+g+w)}$	Study site, gender, and birthweight effects with an additive even-odd effect for the first and second months of life
$S_{(s+EO)}$	Study site with an additive even-odd effect for the first and second months of life
$S_{(s+EO+w)}$	Study site and birthweight effects with an additive even-odd effect for the first and second months of life
$S_{(s+m+g)}$	Study site and gender effects with an additive month effect
$S_{(s+m+g+w)}$	Study site, gender, and birthweight effects with an additive month effect
$S_{(s+m)}$	Study site with an additive month effect
$S_{(s+m+w)}$	Study site and birthweight with an additive month effect
$S_{(EO+g)}$	Gender effect with an additive even-odd effect for the first and second months of life
$S_{(EO+g+w)}$	Gender and birthweights effects with an additive even-odd effect for the first and second months of life
$S_{(EO)}$	Even-odd effect for the first and second months of life
$S_{(m+g)}$	Gender effect plus an additive month effect
$S_{(m+g+w)}$	Gender and birthweight effects with an additive month effect
$S_{(m)}$	Month effect
$S_{(m+w)}$	Birthweight effect with an additive month effect
$S_{(s+g)}$	Study site with an additive gender effect
$S_{(s+g+w)}$	Study site and gender effects with an additive birthweight effect
$S_{(s)}$	Study site effect
$S_{(s+w)}$	Study site with an additive birthweight effect
$S_{(g)}$	Gender effect
$S_{(.)}$	No effect
$S_{(w)}$	Birthweight effect

[a] *s* = site, *EO* = an even-odd effect for the first and second months of life, *g* = gender, *w* = weight at birth, *m* = month.

Appendix C.

Model-Selection Results Comparing the Performance of Models by Site and Treatment and Resulting Estimates of Neonatal Survival

TABLE C-1. Model selection results from analysis of neonatal pronghorn survival comparing the performance of models by site and treatment.

Model[a]	*k*	AIC_c	ΔAIC_c	Akaike weights	Model likelihood	Deviance
$S_{(tmt+EO+sex)}$	4	173.475	0.000	0.342	1.000	165.216
$S_{(tmt+EO+sex+mass)}$	5	174.664	1.189	0.189	0.552	164.272
$S_{(site+EO+sex)}$	5	175.282	1.807	0.138	0.405	164.890
$S_{(tmt+EO)}$	3	175.927	2.452	0.100	0.294	169.772
$S_{(site+EO+sex+mass)}$	6	176.291	2.816	0.084	0.245	163.739
$S_{(tmt+EO+mass)}$	4	177.652	4.177	0.042	0.124	169.393
$S_{(site+EO)}$	4	177.930	4.455	0.037	0.108	169.670
$S_{(tmt+time+sex)}$	8	179.314	5.839	0.018	0.054	162.354
$S_{(site+EO+mass)}$	5	179.618	6.143	0.016	0.046	169.226
$S_{(tmt+time+sex+mass)}$	9	180.145	6.669	0.012	0.036	160.936
$S_{(site+time+sex)}$	6	176.291	2.816	0.084	0.245	163.739
$S_{(site+time+sex+mass)}$	9	181.303	7.827	0.007	0.020	162.095
$S_{(tmt+time)}$	10	182.078	8.603	0.005	0.014	160.591
$S_{(tmt+time+mass)}$	7	182.301	8.825	0.004	0.012	167.559
$S_{(site+time)}$	8	183.787	10.311	0.002	0.006	166.827
$S_{(EO+sex)}$	8	184.498	11.023	0.001	0.004	167.538
$S_{(site+time+mass)}$	3	184.987	11.512	0.001	0.003	178.832
$S_{(EO+sex+mass)}$	9	186.001	12.526	0.001	0.002	166.793
$S_{(EO)}$	4	186.292	12.817	0.001	0.002	178.033
$S_{(time+sex)}$	2	186.683	13.208	0.000	0.001	182.606
$S_{(time+sex+mass)}$	7	189.725	16.249	0.000	0.000	174.983
$S_{(time)}$	8	190.416	16.941	0.000	0.000	173.456
$S_{(time+mass)}$	6	191.778	18.303	0.000	0.000	179.226
$S_{(tmt+sex)}$	7	193.137	19.662	0.000	0.000	178.396
$S_{(tmt+sex+mass)}$	3	194.441	20.966	0.000	0.000	188.286
$S_{(site+sex+mass)}$	4	194.684	21.209	0.000	0.000	186.424
$S_{(site+sex)}$	5	195.616	22.140	0.000	0.000	185.223
$S_{(tmt)}$	4	195.837	22.361	0.000	0.000	187.577
$S_{(tmt+mass)}$	2	198.264	24.789	0.000	0.000	194.187
$S_{(site)}$	3	199.431	25.956	0.000	0.000	193.276
$S_{(site+mass)}$	3	200.077	26.602	0.000	0.000	193.922
$S_{(sex)}$	4	201.104	27.628	0.000	0.000	192.844
$S_{(.)}$	2	212.467	38.992	0.000	0.000	208.390
$S_{(mass)}$	1	215.547	42.072	0.000	0.000	213.522
$S_{(tmt+EO+sex)}$	2	216.695	43.219	0.000	0.000	212.618

[a] *tmt* = wolf-free or wolf-abundant site; *EO* = an even-odd effect for the first or second month of life; *sex* = fawn's gender; *mass* = birthweight; *site* = Gros Ventre, Elk Ranch, or Antelope Flats; *time* = month.

TABLE C-2. Model-averaged estimates of pronghorn neonatal survival by site and treatment.

Site/Month	$\hat{S}$ [a]	SE	95% LCL	95% UCL
Antelope Flats site (*wolf-free*)				
June 2002	0.122	0.044	0.058	0.237
July 2002	0.528	0.143	0.267	0.774
June 2003	0.120	0.044	0.057	0.236
July 2003	0.530	0.143	0.268	0.777
June 2004	0.123	0.045	0.059	0.241
July 2004	0.538	0.143	0.274	0.782
Gros Ventre site (*wolf-abundant*)				
June 2002	0.364	0.070	0.240	0.509
July 2002	0.821	0.076	0.625	0.927
June 2003	0.359	0.071	0.234	0.506
July 2003	0.823	0.075	0.629	0.928
June 2004	0.366	0.071	0.241	0.513
July 2004	0.828	0.073	0.638	0.929
Elk Ranch site (*wolf-abundant*)				
June 2002	N/A	N/A	N/A	N/A
July 2002	N/A	N/A	N/A	N/A
June 2003	0.421	0.096	0.252	0.611
July 2003	0.859	0.067	0.674	0.947
June 2004	0.429	0.095	0.260	0.616
July 2004	0.862	0.065	0.682	0.948
Wolf-free sites (*Gros Ventre and Elk Ranch pooled*)				
June 2002	0.122	0.044	0.059	0.235
July 2002	0.531	0.142	0.270	0.776
June 2003	0.120	0.044	0.057	0.234
July 2003	0.535	0.142	0.273	0.779
June 2004	0.123	0.045	0.059	0.240
July 2004	0.543	0.142	0.280	0.785
Wolf-abundant site				
June 2002	0.386	0.059	0.278	0.507
July 2002	0.837	0.066	0.664	0.930
June 2003	0.381	0.060	0.272	0.504
July 2003	0.840	0.064	0.672	0.930
June 2004	0.390	0.060	0.281	0.511
July 2004	0.844	0.063	0.681	0.932

[a] N/A indicates fawns were not captured at this site until 2003.

Appendix D.

A Technique to Estimate the Number of Reproductive Females in the Population and Neonatal Survival Rates from Count Data

To determine the number of reproductive females in the current population, we multiplied the number of juveniles from the classification survey in the prior year ($N_{J(t-1)}$) by the proportion of fawns that are female (J_F) to estimate the number of juvenile females in the prior year ($N_{JF(t-1)}$). Next, we multiplied $N_{JF(t-1)}$ by the juvenile overwinter survival rate (S_J) to estimate the number of juvenile females recruited into the population as yearlings in the current year ($N_{Y(t)}$). We subtracted $N_{Y(t)}$ from the total number of females recorded in the classification survey in the current year ($N_{F(t)}$) to determine the number of reproductive (i.e., adult) females in the population ($N_{AF(t)}$). Thus, the estimated number of reproductive females in the current year was

$$N_{AF(t)} = N_{F(t)} - \left(N_{J(t-1)} \times J_F \times S_J\right) = N_{F(t)} - N_{Y(t)} .$$

Next, we multiplied $N_{AF(t)}$ by the adult fertility rate (F_A; Note that F_A has previously been divided by two to reflect an assumed even sex ratio) to estimate the number of female neonates produced in the current year ($N_{NF(t)}$). Finally, we multiplied the actual number of juveniles recorded in the classification survey in the current year ($N_{J(t)}$) by J_F to estimate the number of juvenile females in the current year ($N_{JF(t)}$), then divided this number by $N_{NF(t)}$ to determine $S_{N(t)}$. Thus, estimated neonatal survival for the current year was

$$S_{N(t)} = \frac{N_{J(t)} \times J_F}{N_{AF(t)} \times F_A} = \frac{N_{JF(t)}}{N_{NF(t)}} .$$

Appendix E.

Effect of Percentage Yearlings in the Initial Population Vector on the Results of Demographic Modeling

TABLE E-1. Effect of percentage yearlings in initial population vector on population size in time periods 0 through 10.

	Time Period										
Description	0	1	2	3	4	5	6	7	8	9	10
Wolf-abundant sites											
10% yearlings in initial population vector											
95% UCL	249	324	382	443	510	585	669	764	871	991	1,127
95% LCL	249	226	227	231	237	244	252	261	271	281	292
Median	249	271	294	320	348	378	411	446	485	527	573
15% yearlings in initial population vector											
95% UCL	249	324	382	443	510	585	669	764	871	991	1,128
95% LCL	249	226	227	231	237	244	252	261	271	281	292
Median	249	271	294	320	348	378	411	446	485	527	573
20% yearlings in initial population vector											
95% UCL	249	324	382	443	510	585	669	764	870	991	1,127
95% LCL	249	226	227	231	237	244	252	261	270	281	292
Median	249	271	294	320	348	378	411	446	485	528	573
25% yearlings in initial population vector											
95% UCL	249	324	382	443	510	585	669	764	871	991	1,127
95% LCL	249	226	227	231	237	244	252	261	270	281	291
Median	249	271	294	320	348	378	411	446	485	527	573
Wolf-free site											
10% yearlings in initial population vector											
95% UCL	249	286	295	300	303	305	305	305	305	304	303
95% LCL	249	196	171	152	135	122	110	99	89	81	73
Median	249	236	225	213	203	192	183	174	165	157	149
15% yearlings in initial population vector											
95% UCL	249	286	295	300	303	305	305	305	305	304	302
95% LCL	249	196	171	152	135	122	109	99	89	81	73
Median	249	237	225	213	203	192	183	174	165	157	149
20% yearlings in initial population vector											
95% UCL	249	286	295	300	303	305	305	305	305	304	302
95% LCL	249	196	171	152	135	122	109	99	89	81	73
Median	249	236	225	213	203	192	183	174	165	157	149
25% yearlings in initial population vector											
95% UCL	249	286	295	300	303	304	305	305	304	304	302
95% LCL	249	196	171	152	135	122	109	99	89	81	73
Median	249	237	225	213	203	192	183	174	165	157	149

TABLE E-2. Effect of percentage yearlings in initial population vector on population size in time periods 11 through 20.

	Time Period									
Description	11	12	13	14	15	16	17	18	19	20
Wolf-abundant sites										
10% yearlings in initial population vector										
95% UCL	1,281	1,456	1,652	1,874	2,125	2,410	2,735	3,099	3,512	3,981
95% LCL	303	315	328	342	356	371	387	403	421	439
Median	623	677	736	800	870	945	1,028	1,117	1,214	1,320
15% yearlings in initial population vector										
95% UCL	1,282	1,454	1,652	1,875	2,125	2,409	2,729	3,092	3,501	3,965
95% LCL	303	315	328	342	356	371	387	404	421	439
Median	623	677	736	800	870	946	1,028	1,118	1,215	1,320
20% yearlings in initial population vector										
95% UCL	1,281	1,455	1,652	1,873	2,124	2,410	2,733	3,096	3,507	3,972
95% LCL	303	316	329	342	356	371	387	404	421	439
Median	623	678	737	801	871	946	1,028	1,118	1,215	1,321
25% yearlings in initial population vector										
95% UCL	1,281	1,455	1,652	1,873	2,123	2,408	2,732	3,095	3,509	3,975
95% LCL	303	315	328	342	355	371	386	403	420	438
Median	623	677	736	800	870	945	1,028	1,117	1,214	1,320
Wolf-free site										
10% yearlings in initial population vector										
95% UCL	301	300	298	296	294	292	289	287	285	282
95% LCL	66	60	55	50	45	41	37	34	31	28
Median	141	134	127	121	115	109	104	98	93	89
15% yearlings in initial population vector										
95% UCL	301	300	298	296	294	292	290	287	285	282
95% LCL	66	60	55	50	45	41	37	34	31	28
Median	141	134	127	121	115	109	104	98	93	89
20% yearlings in initial population vector										
95% UCL	301	299	297	295	294	291	289	287	285	283
95% LCL	66	60	55	49	45	41	37	34	31	28
Median	141	134	127	121	115	109	104	98	93	89
25% yearlings in initial population vector										
95% UCL	301	299	298	296	294	292	289	287	285	282
95% LCL	66	60	55	50	45	41	37	34	31	28
Median	141	134	127	121	115	109	104	98	93	89

Appendix F.

Effect of Correlation in Overwinter Survival Rates on the Results of Demographic Modeling

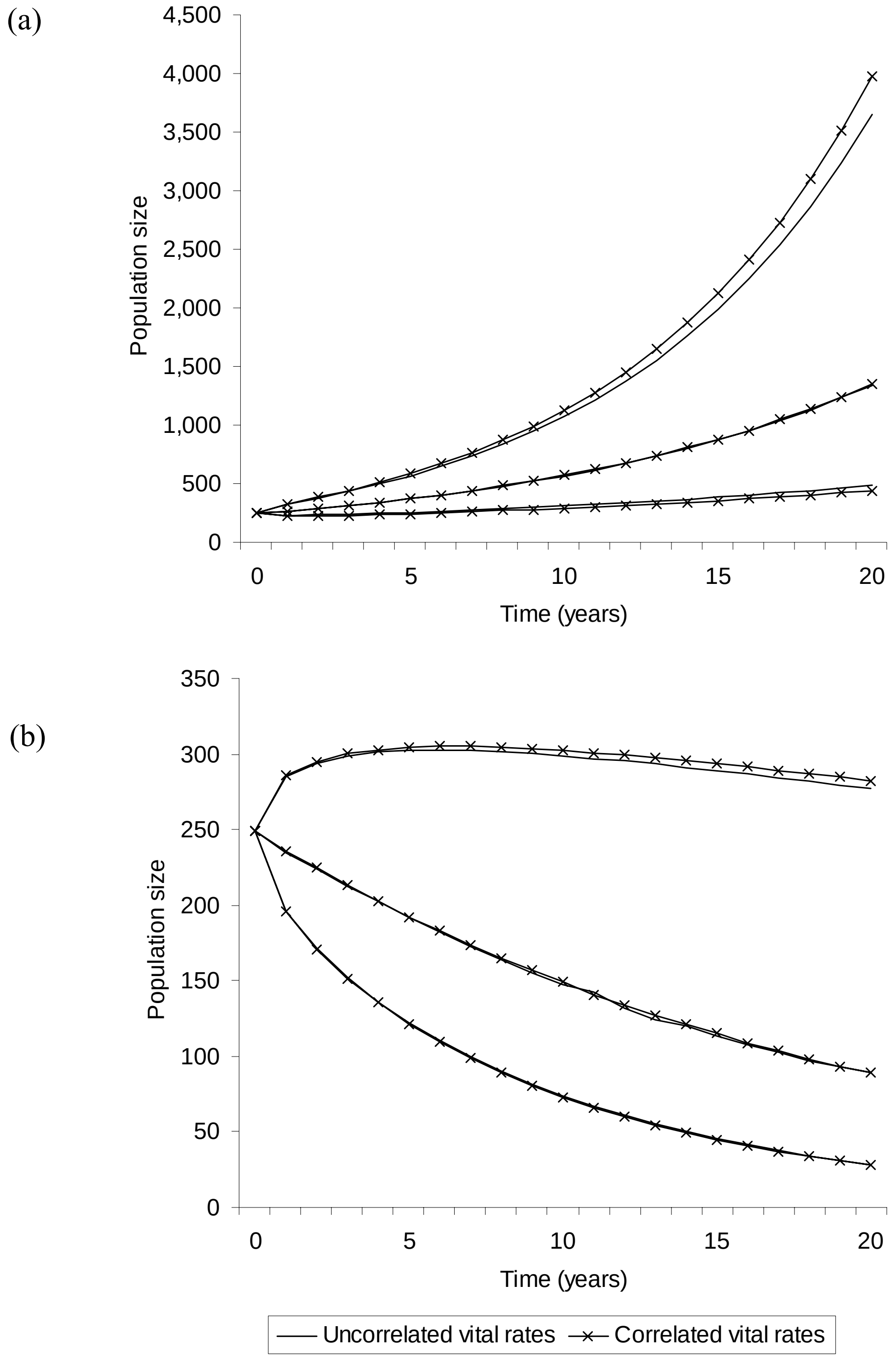


FIG. F-1. Effects of correlation in overwinter survival rates on changes in pronghorn population size over a 20-year period at (a) wolf-abundant and (b) wolf-free sites in Grand Teton National Park, Wyoming.

Appendix G.

Permission-to-Use Letters

December 3, 2007

Dr. Joel Berger
Wildlife Conservation Society
P.O. Box 985
Victor, ID 83455

Dear Dr. Berger:

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I hope to complete in the Spring of 2007.

As you are a coauthor on Chapter 3, I am requesting your permission to include the attached material as shown. I will include acknowledgements and/or appropriate citations to your work as shown. Please advise me of any changes you require.

Please indicate your approval of this request by signing in the space provided.

Thank you for your cooperation,

Kim Murray Berger

I hereby give permission to Kim Murray Berger to print the following material in her dissertation:

Chapter 3, pages 45 – 83.

Signed ____

CURRICULUM VITAE

Kim Murray Berger
(March 2007)

EDUCATION

2007	Ph.D. Wildlife Biology, Utah State University. Dissertation Title: Conservation Implications of Foods Webs Involving Wolves, Coyotes, and Pronghorn. Degree expected Spring 2007.
2001	M.S. Environmental and Natural Resource Sciences, University of Nevada, Reno. Thesis Title: Carnivores and the Fleecing of American Taxpayers: Predator Control Subsidies and the Decline of the Western Sheep Industry.
1991	B.S. Economics (*Magna Cum Laude*), Weber State University.

CURRENT POSITION

2006 -	Associate Conservation Scientist, North America Program, Wildlife Conservation Society, Bronx, NY.

CONSULTANT POSITIONS

2003 - 2006	Research Ecologist, North America Program, Wildlife Conservation Society, Bronx, NY.

PREVIOUS POSITIONS

2001 - 2002	Research Associate, Department of Environmental & Resource Sciences, University of Nevada, Reno.
1999-2001	Senior Budget Analyst, Office of Planning, Budget & Analysis, University of Nevada, Reno.
1998-1999	Budget Analyst, Office of Planning, Budget & Analysis, University of Nevada, Reno.
1995-1998	Departmental Administrator, Department of Environmental & Resource Sciences, University of Nevada, Reno.
1994-1995	Laboratory Administrator, Environmental Analysis Facility, Desert Research Institute, Reno.
1994	Program Specialist, Environmental Analysis Facility, Desert Research Institute, Reno.
1992-1993	Adjunct Faculty, Department of Economics, Weber State University, Ogden, Utah.

FIELD EXPERIENCE AND PROJECTS

2005-present	Assessment of pronghorn movements and migratory patterns in relation to energy development and human disturbance in the Upper Green River Basin, Wyoming.
2005-present	Survey of saiga and their habitat in the Sharga-Mankhan Nature Reserve and Khar Us Nuur National Park, Mongolia.
2002-2004	Evaluation of a trophic cascade involving wolves, coyotes, and pronghorn in the southern Greater Yellowstone Ecosystem.
2003	Surveys for Andean Mountain Cats, San Guillermo Biosphere Reserve, Argentina.
2003	Ungulate surveys in the northern Namib Desert.
2001	Caribou foraging and anti-predator dynamics on the Svalbard Archipelago, Norway.
2001	Effects of carnivores on ungulate foraging and antipredator tactics in Alaska.
2000	Pregnancy assessment and movements of moose in relation to population density and colonizing carnivores in Jackson Hole, Wyoming.
1999	Effects of carnivores on ungulate foraging and antipredator behavior in Alaska.
1999	Habitat Conservation Planning. In conjunction with Drs. Dennis Murphy and Peter Brussard, prepared conservation assessments (current status, habitat availability in Placer County, California, potential take at buildout, impact of take, mitigation measures, and monitoring plan) for two target species as part of the Placer County Natural Communities Conservation Plan.

TEACHING

Guest lecture in Conservation Biology (Utah State University, 2004).

Teaching Assistant, Program Mark Workshop (Utah State University, 2004).

Lead instructor for *Introductory Economics* (Weber State University, 1992).

EDITORIAL ACTIVITIES

Review of manuscripts for *Conservation Biology* and *Western North American Naturalist*.

FORMAL PRESENTATIONS

International

- Ministry of Environment and Tourism (Windhoek, Namibia) “Migration, Population Viability, and Conservation” 2003 (INVITED).
- Centro de Ecología Aplicada del Neuquén (Patagonia, Argentina) “Migration, Population Viability, and Conservation” 2003 (INVITED).

National and Regional

- Society of Conservation Biology (San Jose, California) “Simulations Comparing the Performance of Techniques Used to Assess Variable Importance: Implications for the Analysis of Noisy Ecological Data.” 2006.
- Biennial Pronghorn Workshop (Idaho Falls, Idaho) “Effects of a Species-Level Trophic Cascade on Pronghorn Fawn Survival in Grand Teton National Park.” 2006.
- The Wildlife Society (University of Wisconsin) “Predation and Pronghorn Fawn Survival in Grand Teton National Park: Management and Conservation Implications” 2005.
- National Park Service-WCS Workshop “Where Have All the Rabbits Gone?” (Grand Teton National Park, Wyoming) “Ecological Dynamics – Why Care?” 2005.
- The Wildlife Conservation Society (Bronx, New York) “Predators, Petroleum Development & Pronghorn Persistence: Piecing the Conservation Puzzle Together” 2005.
- Society of Conservation Biology (Columbia University) “Carnivore-Livestock Conflicts: Making Economic Sense of Subsidized Predator Control” 2004.
- Jackson Hole Chamber of Commerce (Jackson, Wyoming) “Is Migration Relevant to Jackson Hole?” 2004 (INVITED).
- Wyoming Wildlife Congress (Pinedale, Wyoming) “Pronghorn Persistence in Grand Teton National Park” 2003 (INVITED).

GRANTS

National Geographic Society (Washington, DC). In the footsteps of Saiga: The world's most northern antelope. 2006-07, $ 50,000. PI’s: J. Berger and K.M. Berger

Shell Exploration and Production Company (Houston, TX). Pronghorn Biology and Gas Field Development: Effects of Winter Drilling on Habitat Use, Behavior, and Body Condition. 2005-2009. $1.8 million. PI’s: J. Berger, K.M. Berger, and J. Beckmann.

Liz Claiborne/Art Ortenberg Foundation (New York, NY). An Initiative to Protect Long Distance Migration. 2004-2006. $131,000. PI’s: J Berger and K.M. Berger.

PUBLICATIONS

Berger, K.M., and E.M. Gese. 2007. Does Interference Competition with Wolves Limit the Distribution and Abundance of Coyotes? *Journal of Animal Ecology*, provisionally accpeted.

Berger, K.M., and M.M. Conner. 2007. Recolonizing Wolves and Mesopredator Suppression of Coyotes: Impacts on Pronghorn Population Dynamics. *Ecological Applications*, submitted.

Berger, K.M., E.M. Gese, and J. Berger. 2007. Evidence of a Species-Level Trophic Cascade in a Terrestrial Food Web Involving Wolves, Coyotes, and Pronghorn. *Ecology*, submitted.

Berger, J., S.L. Cain, and K.M. Berger. 2006. Connecting the Dots: an Invariant Migration Corridor Links the Holocene to the present. *Biology Letters* **2**:528-531.

Berger, K.M. 2006. Carnivore-Livestock Conflicts: Effects of Subsidized Predator Control and Economic Correlates on the Sheep Industry. *Conservation Biology* **20**:751-761.

Berger, K.M. 2005. Defense of Pronghorn Fawns by Adult Male Pronghorn Against Coyotes. *Western North American Naturalist* **65**:267-268.

Berger, J., and K.M. Berger. 2001. Endangered Species and the Decline of America's Western Legacy: What Do Changes in Funding Reflect? *Bioscience* **51**:591-593.

POPULAR PRESS

Berger, K.M. 2003. Pronghorn in Peril. *Wildlife Conservation* **August**:38-41.

REPORTS

Berger, J., K.M. Berger, and J. Beckmann. 2006. Wildlife and Energy Development : Pronghorn of the Upper Green River Basin – Year 1 Summary. Wildlife Conservation Society, Bronx, NY.

Berger, J., K.M. Berger, P.F. Brussard, R. Gibson, J. Rachlow, and A. Smith. 2006. Where Have All The Rabbits Gone? Summary and Recommendations from a Workshop Held in Grand Teton National Park – September 23-24, 2005. Wildlife Conservation Society, Bronx, NY.