

Exhibit FF

Does interference competition with wolves limit the distribution and abundance of coyotes?

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Summary

1. 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.

2. We used spatial, seasonal and temporal 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 captured 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. 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 analysed 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.

3. 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 GTNP, and densities declined 39% in Yellowstone National Park following wolf reintroduction.

4. 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.

5. 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 captured at wolf-abundant sites were 117% higher than for transients captured in wolf-free areas.

6. 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.

Key-words: *Canis latrans*, *Canis lupus*, carnivore conservation, interference competition, intraguild predation.

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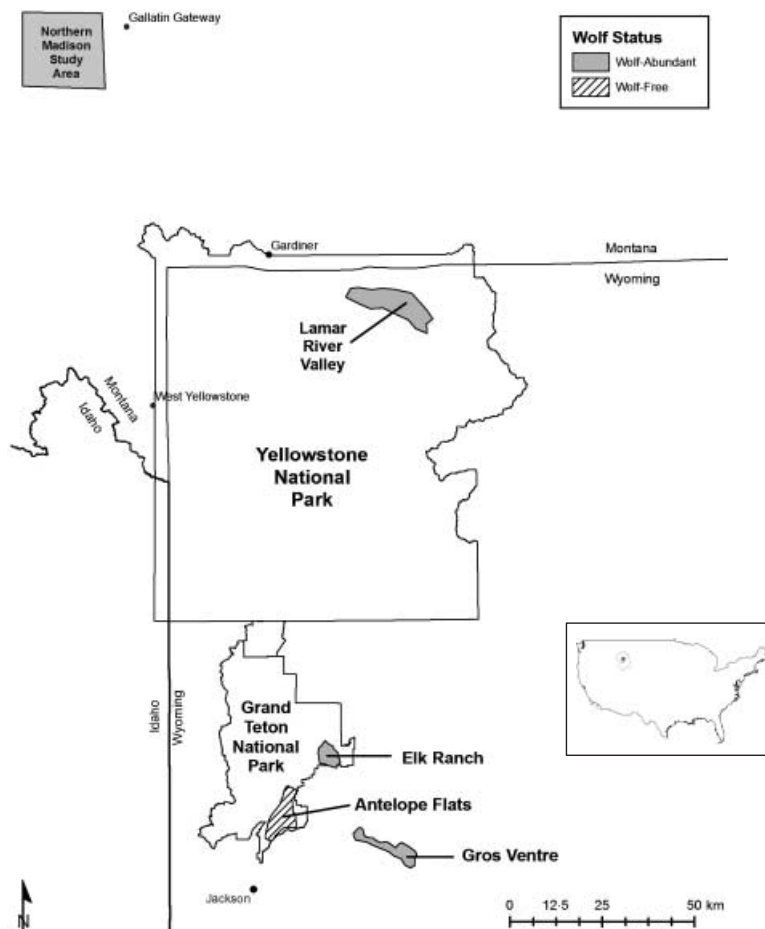


Fig. 1. Map showing the location of the Greater Yellowstone Ecosystem (GYE) in the western United States (inset), the locations of study areas, and place names referred to in the text. 'Wolf status' refers to the distribution of wolves within the GYE during the 1997–2005 period.

Introduction

Interspecific competition among large carnivores has important implications for the structure and function of carnivore communities (Palomares & Caro 1999; Caro & 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 & 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 & Holt 1992).

While numerous studies have focused on the effects of interspecific competition on the persistence of threatened carnivores (Caro 1994; Laurenson 1995; Creel & Creel 1996; Durant 1998), interference competition may also have implications for the management of abundant native species. In particular, because the loss of top carnivores may result in increases

in mesocarnivore abundance and concomitant impacts on prey populations (Crooks & Soulé 1999; Berger, Gese & Berger 2007), ecosystem restoration has been suggested as an alternative to lethal control as a means to reduce overabundant species (Goodrich & Buskirk 1995).

In much of North America, interference competition with wolves *Canis lupus* (Linnaeus) is hypothesized to be an important factor influencing the distribution and abundance of coyotes *Canis latrans* (e.g. 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 United States (Peterson 1995; Gompper 2002). 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 (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 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 captured 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 examined whether 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 captured in wolf-free and wolf-abundant areas. Finally, we analysed 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 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 (October–April; Fig. 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. 1), human harvest of coyotes was not legally permitted in either area.

CAPTURE AND MONITORING OF COYOTES

We monitored the survival and movements of coyotes captured 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, Rongstad & Mytton 1987), and were fitted with VHF radio collars with 8-h mortality sensors (Advanced Telemetry Systems Inc., Isanti, MN, 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 (Gese, Rongstad & Mytton 1988). Resident coyotes were members of packs that 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, haemorrhaging, carcass consumption and caching behaviour, as well as tracks and signs at carcass sites, were used to assign kills to specific predators (O'Gara 1978). When disease was suspected, carcasses were frozen and shipped to the Wyoming State Veterinary Laboratory (Laramie, WY, USA) for further evaluation.

Survival rates of coyotes were estimated using a known fate model in the program MARK (White & 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 25 models to assess the effects of site (wolf-free or wolf-abundant), season (summer or winter), year, sex and territorial status on coyote survival. The global model considered was $S_{\text{site} \times \text{status} \times \text{season} \times \text{sex} \times \text{year}}$, where S was the estimated monthly survival rate of coyotes. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to rank models (Burnham & Anderson 2002). Model averaging (Burnham & 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, Anderson & Rongstad 1990). Relocations were attempted at least weekly and were obtained throughout the 24-h period to reduce bias in home-range estimates (Smith, Cary & Rongstad 1981). For ground locations, ≥ 3 compass bearings with intersecting angles between 20° and 160° were used (White & Garrott 1990). Locations were estimated using the program LOCATE II (Pacer Ltd, Truro, Nova Scotia), and home ranges by the fixed-kernel (FK) density method (Worton 1989). To estimate home ranges, we used an *ad hoc* smoothing parameter ($h_{\text{ad hoc}}$) 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. $h_{\text{ad hoc}} = 0.9 * h_{\text{ref}}$, $0.8 * h_{\text{ref}}$, etc.; J.G. Kie, unpublished data). Home-range analyses were performed with the 'adehabitat' package (Calenge 2006) in program R (R Development Core Team 2006).

Overlap of coyote and wolf home ranges (95% FK) and core areas (60% FK) was evaluated using two 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. 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. 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 & Kochanny (2005):

$$\text{UDOI} = A_{i,\text{wolf}} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \hat{U}D_i(x, y) \times \hat{U}D_{\text{wolf}}(x, y) dx dy$$

where $A_{i,\text{wolf}}$ is the area of overlap between the coyote pack and wolf pack home ranges, and UD_i and 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 & 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 captured 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.

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. 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 unregulated hunting of coyotes is permitted year round.

The LRV study area (70 km²) is located in Yellowstone National Park (YNP) in north-western Wyoming (Fig. 1). Following a more than 50-year absence, wolves were translocated to YNP from western Canada in 1995–96 (Smith, Peterson & Houston 2003). Within 5 years of reintroduction, 65 wolves comprising four packs were utilizing the area surrounding the LRV (Smith, Stahler & Guernsey 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 km²) is located on a private ranch in south-western Montana, approximately 50 km north-west of YNP (Fig. 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, unpublished data).

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, Ruff & Crabtree 1996a,b; Allen, Bekoff & Crabtree 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 ($6.4\% \pm 3.9$; E.M. Gese, unpublished data) from 1991 to 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 nonlinear models. 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% and 49%, 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 favour 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 32 marked individuals in the analysis of coyote survival. Three animals were excluded from the survival analysis because they dispersed to areas beyond our study sites immediately following capture. Three additional animals were omitted because their territorial status was undetermined 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 1). The parameter estimates from the top-ranked model suggested survival of resident coyotes was higher than for transients

Table 1. Model selection results for survival of coyotes at two study sites in Grand Teton National Park, Wyoming 2001–04

Model*	K†	AIC _c	ΔAIC _c	Akaike weight	Model likelihood	Deviance
$S_{\text{status}+\text{season}}$	3	146.111	0.000	0.134	1.000	140.062
$S_{\text{trans site}+\text{status}+\text{season}}$	4	146.645	0.533	0.103	0.766	138.562
$S_{\text{trans site}+\text{status}+\text{season}+\text{year}}$	6	147.080	0.968	0.083	0.616	134.905
$S_{\text{status}+\text{season}+\text{year}}$	5	147.176	1.065	0.079	0.587	137.052
S_{season}	2	147.185	1.074	0.078	0.585	143.161
$S_{\text{site}+\text{status}+\text{season}}$	4	147.697	1.586	0.061	0.453	139.614
$S_{\text{status}+\text{season}+\text{sex}+\text{year}}$	6	148.083	1.971	0.050	0.373	135.908
$S_{\text{trans site}+\text{status}}$	3	148.515	2.403	0.040	0.301	142.465
S_{status}	2	148.582	2.470	0.039	0.291	144.557
$S_{\text{site}+\text{status}+\text{season}}$	5	148.683	2.572	0.037	0.276	138.559
$S_{\text{site}+\text{status}+\text{season}+\text{sex}}$	5	148.894	2.783	0.033	0.249	138.770
$S_{\text{season}+\text{year}}$	4	149.002	2.890	0.032	0.236	140.919
$S_{\text{status}+\text{year}}$	4	149.033	2.922	0.031	0.232	140.951
$S_{\text{site}+\text{season}}$	3	149.208	3.097	0.029	0.213	143.159
$S_{\text{site}+\text{status}+\text{season}+\text{sex}+\text{year}}$	8	149.356	3.245	0.026	0.197	133.056
S_{site}	1	149.621	3.510	0.023	0.173	147.613
$S_{\text{status}+\text{sex}}$	3	149.758	3.647	0.022	0.162	143.709
$S_{\text{site}+\text{status}+\text{season}+\text{sex}+\text{year}}$	7	149.788	3.677	0.021	0.159	135.555
$S_{\text{site}+\text{status}}$	3	150.033	3.922	0.019	0.141	143.983
$S_{\text{site}+\text{status}}$	4	150.541	4.430	0.015	0.109	142.458
$S_{\text{site}+\text{status}+\text{year}}$	5	150.593	4.482	0.014	0.106	140.469
$S_{\text{site}+\text{season}+\text{sex}}$	4	151.173	5.062	0.011	0.080	143.090
S_{sex}	2	151.579	5.467	0.009	0.065	147.554
S_{site}	2	151.633	5.521	0.008	0.063	147.608
$S_{\text{site}+\text{sex}}$	3	153.603	7.491	0.003	0.024	147.553

**status* = resident or transient; *trans site* = transient (but not resident) survival rates differ between wolf-free and wolf-abundant sites; *season* = summer [May–September] or winter [October–April]; *year* = 1st, 2nd or 3rd year of study; *site* = wolf-free or wolf-abundant; *sex* = male or female.

†Number of estimable parameters including the intercept.

($\beta = 0.882 \pm 0.498$; Wald test, $P = 0.077$), and survival rates were higher during summer than during winter ($\beta = 1.224 \pm 0.644$; Wald test, $P = 0.057$). The second- ($\Delta\text{AIC}_c = 0.533$) and third-ranked ($\Delta\text{AIC}_c = 0.968$) models suggested that survival rates of transients also differed between sites and survival rates varied among years. However, the confidence intervals on the coefficients for the year and site variables substantially overlapped zero, indicating there was no clear effect of site or year on survival rates. Model-averaged survival estimates were lowest for transient coyotes at the wolf-abundant site in 2004 ($\hat{S} = 0.255 \pm 0.118$), and highest for resident coyotes at the wolf-free site in 2002 ($\hat{S} = 0.770 \pm 0.139$), but did not differ statistically by territorial status, between sites, or among years (Fig. 2).

Cause-specific mortality of coyotes did not differ between sites (Fig. 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, 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

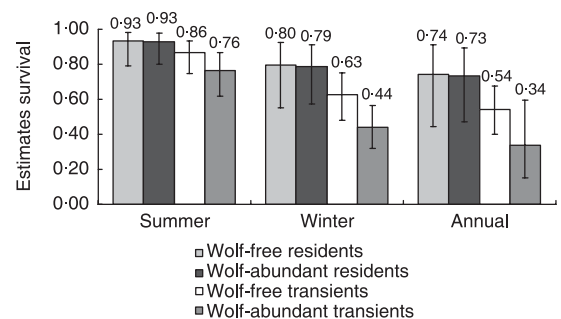


Fig. 2. Seasonal and annual model-averaged survival estimates for resident and transient coyotes in Grand Teton National Park, Wyoming 2002–04.

coyote deaths resulted from predation (Fig. 3b). Wolves accounted for 83% ($n = 5$) of predation-related mortality and mountain lions *Puma concolor* (Linnaeus) for 17% ($n = 1$).

SPATIAL SEGREGATION OF COYOTES AND WOLVES

Annual coyote home ranges averaged $13.12 \pm 1.59 \text{ km}^2$ at the wolf-free site, and $13.80 \pm 1.86 \text{ km}^2$ at the wolf-abundant site. The wolf pack's home range was 399 km^2 during summer, when wolves were concentrated in the vicinity of their den site, and 1140 km^2 during winter. Percentage overlap of coyote and wolf

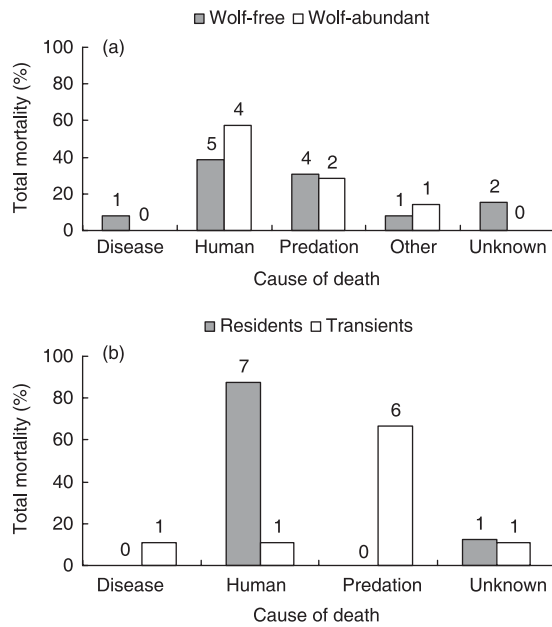


Fig. 3. Percentage of total mortality of radio-collared coyotes attributable to various causes (a) in wolf-free vs. wolf-abundant sites, and (b) by territorial status, Grand Teton National Park, Wyoming 2002–04. The numbers above each bar indicate the actual number of deaths. Note that three deaths (one human and two other) were excluded from the bottom panel because the territorial status of the animal was unknown.

home ranges was 100% (95% FK: $\bar{x} = 100\% \pm 0$, $n = 4$; Table 3), as the home ranges of all coyote 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 within 600 m 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 3), 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. Densities ranged from

a low of 0.345 coyotes per km^2 at the wolf-free site (Antelope Flats) in GTNP in 2002, to a high of 0.726 coyotes per km^2 prior to wolf reintroduction at the LRV study area in 1994 (Table 2). Based on ordinary least squares regression, a linear model ($\text{coyote density} = 0.345 - 4.102 \times \text{wolf density} + 0.192 \times \text{protected status}$, $r^2 = 0.58$, $F_{2,14} = 9.49$, $P = 0.002$, $n = 16$) fit the data slightly better than a negative exponential model ($\text{coyote density} = e^{-1.001 - 15.921 \times \text{wolf density}} + 0.170 \times \text{protected status}$, $r^2 = 0.56$, $F_{2,14} = 8.76$, $P = 0.003$, $n = 16$), 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 (Fig. 4). Both models suggested 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 when wolf densities are zero than at higher wolf densities (Fig. 4). Consequently, although the estimated regression is not affected, the standard errors and confidence intervals represent a biased estimate of the true variance (Barreto & Howland 2006).

Discussion

EFFECTS OF 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. Mean coyote densities in the LRV declined by 39% following wolf reintroduction, and densities were 33% lower at wolf-abundant sites in GTNP compared with the wolf-free site (Table 2). 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 based on the distribution of preferred prey. However, this 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 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 & 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

Table 2. Population densities of coyotes and wolves at three study areas in the Greater Yellowstone Ecosystem 1991–2005

Study area	Period	Coyotes per km ²	Wolves per km ²
Sites without wolves			
Yellowstone National Park – Lamar River Valley	1991	0.499*†	0.000
Yellowstone National Park – Lamar River Valley	1992	0.636*†	0.000
Yellowstone National Park – Lamar River Valley	1993	0.694*†	0.000
Yellowstone National Park – Lamar River Valley	1994	0.726†‡	0.000
Grand Teton National Park – Antelope Flats	2002	0.345§	0.000
Grand Teton National Park – Antelope Flats	2003	0.479§	0.000
Grand Teton National Park – Antelope Flats	2004	0.394§	0.000
Sites with wolves			
Yellowstone National Park – Lamar River Valley	1997	0.477†¶	0.032**
Yellowstone National Park – Lamar River Valley	1998	0.332†††	0.042**
Yellowstone National Park – Lamar River Valley	1999	0.477†††	0.035**
Yellowstone National Park – Lamar River Valley	2000	0.270†††	0.065**
Grand Teton National Park – Elk Ranch	2002	0.279§	0.053§
Grand Teton National Park – Elk Ranch	2003	0.308§	0.061§
Grand Teton National Park – Elk Ranch	2004	0.215§	0.053§
Grand Teton National Park – Gros Ventre	2003	0.312§	0.033§
Grand Teton National Park – Gros Ventre	2004	0.247§	0.028§
Northern Madison Study Area	2003–05	0.194†‡	0.008†‡

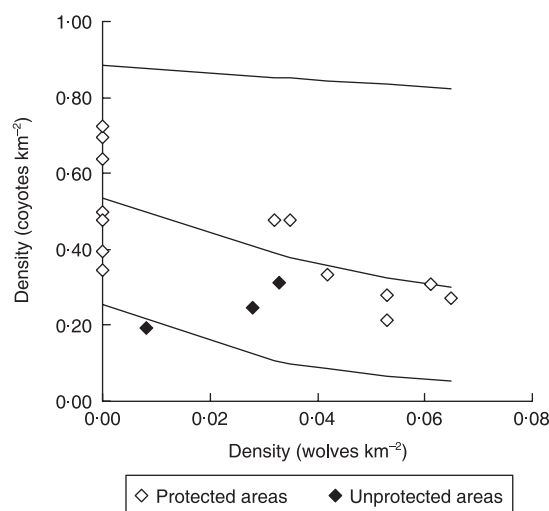
*Gese *et al.* (1996a,b).†Coyote densities adjusted to include transient coyotes ($\bar{x} = 0.064 \pm 0.039$ of total coyote numbers; E.M. Gese, unpublished data).

‡S. Grothe, unpublished data.

§Berger *et al.* (2007).¶Allen *et al.* (1999).**Smith *et al.* (2004).

††T.A. Switalski, unpublished data.

†‡T.C. Atwood, unpublished data.

**Fig. 4.** Negative exponential model 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.

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 ($\bar{x} = 0.406 \pm 0.039$) vs. 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). This is likely a result of 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 discernible 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 favour 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 autumn 2003 resulted in the deaths of 21% of all radio-collared coyotes, which contributed to the reduction in coyote densities that occurred between 2003 and 2004 (K.M. Berger, unpublished data).

wolf-free site in GTNP fluctuated by an average of 29% per year over the 3-year study (Table 2). However, while the magnitude of fluctuations in coyote densities was similar, mean coyote densities in the LRV were significantly higher prior to wolf reintroduction ($\bar{x} =$

Despite early recognition of an apparent inverse relationship between coyote and wolf densities (Fuller & 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 & 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 north-western Montana and the NMSA, respectively. In contrast, cougars killed 40% of radio-collared coyotes in north-western Montana (Arjo 1998) and 14% of coyotes at the NMSA (Atwood 2006). Note 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, Rongstad & Mytton 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. 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 ventured on to private inholdings within park boundaries ($n = 3$), 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. 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. The annual survival of transient coyotes was 37% lower than that of residents at the wolf-free site, and 117% lower at the wolf-abundant site (Fig. 2). Although

survival of transient coyotes is typically lower than that of residents independent of the presence of wolves, survival rates of transients at the wolf-abundant site 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 wolves. A similar pattern has been reported in both vervet monkeys *Cercopithecus aethiops* (Linnaeus) and white-footed mice *Peromyscus leucopus* (Rafinesque), as individuals in novel surroundings (i.e. transients) suffer higher predation rates than those of residents (Metzgar 1967; Isbell, Cheney & Seyfarth 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* (Schreber) in groups are more effective at deterring spotted hyenas *Crocuta crocuta* (Erxleben) than singletons (Caro 1994), and both dwarf mongooses *Helogale parvula* (Sundevall; Rasa 1986) and suricates *Suricata suricatta* (Schreber; 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 travelling in pairs or groups following wolf recolonization in both north-western Montana and the LRV (Arjo 1998; Crabtree & 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 WOLVES ON COYOTE DISTRIBUTION

Based on the results of an early study (Fuller & 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

Table 3. 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 2002–04

Pack	Area of overlap		UDOI	
	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

territory (Table 3). And, although mean overlap of coyote and wolf core areas was considerably lower ($48\% \pm 28$), the core areas of the two coyote packs in closest proximity to the wolf core area still overlapped by nearly 100% ($\bar{x} = 97\% \pm 0.5$).

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 $78\% \pm 5.54$ and $82\% \pm 6.69$, respectively (Atwood 2006). In north-western 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 (Fig. 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 centres (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, 67% 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-abundant 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* (Temminck) and cheetahs with lions *Panthera leo* (Meyer) and spotted hyenas (Laurenson 1995; Creel & Creel 1996; Durant 2000). As mortality rates of adult coyotes due to wolves are comparable with, or exceed, those reported for wild dogs and cheetahs due to lions and spotted hyenas (Creel & 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 & 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 with 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 grey 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 probably accounts for the considerable disparity in transient coyote densities ($0.188 \pm 0.019 \text{ km}^{-2}$ vs. $0.039 \pm 0.005 \text{ km}^{-2}$; Berger *et al.* 2007), and thus overall coyote densities ($0.406 \pm 0.039 \text{ km}^{-2}$ vs. $0.272 \pm 0.018 \text{ km}^{-2}$; Table 2), 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 interspecific 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 (Fig. 4). The failure of wolves to exclude coyotes is not surprising, as unlike Isle Royale (Krefting 1969), the GYE is not spatially closed and spatial heterogeneity in both habitat and wolf distribution creates refugia that probably 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 grey wolves from much of their former range.

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References

- Allen, J.J., Bekoff, M. & Crabtree, R.L. (1999) An observational study of coyote (*Canis latrans*) scent-marking and territoriality in Yellowstone National Park. *Ethology*, **105**, 289–302.
- Andelt (1982) *Behavioral Ecology of Coyotes in South Texas*. Wildlife Monograph, 94. The Wildlife Society, Bethesda, Maryland.
- Arjo, W.M. (1998) *The Effects of Recolonizing Wolves on Coyote Populations, Movements, Behaviors, and Food Habits*. PhD Thesis, University of Montana, Missoula.
- Atwood, T.C. (2006) *Wolves, Coyotes, Elk, and Mule Deer: Predator-Prey Behavioral Ecology in Southwest Montana*. PhD Thesis, Utah State University, Logan, UT.
- Balser, D.S. (1965) Tranquilizer tabs for capturing wild carnivores. *Journal of Wildlife Management*, **29**, 438–442.
- Barreto, H. & Howland, F.M. (2006) *Introductory Econometrics: Using Monte Carlo Simulations with Microsoft Excel*. Cambridge University Press, New York.
- Berger, K.M., Gese, E.M. & Berger, J. (2007) Indirect effects and traditional trophic cascades: a test involving wolves, coyotes and pronghorn. *Ecology*, in press.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987) *Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture*. American Fisheries Society Monograph No. 5. American Fisheries Society, Bethesda, Maryland.
- 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 and Asocial Species*. University of Chicago Press, Chicago, IL.
- Caro, T.M. & Stoner, C.J. (2003) The potential for interspecific competition among African carnivores. *Biological Conservation*, **110**, 67–75.
- Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kinsky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. (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. *Coyotes: Biology, Behavior, and Management* (ed. M. Bekoff), pp. 327–345. Academic Press, New York.
- Crabtree, R.L. & Sheldon, J.W. (1999) The ecological role of coyotes on Yellowstone's Northern Range. *Yellowstone Science*, **Spring**, 15–23.
- Creel, S. & Creel, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.
- Crooks, K.R. & Soulé, M.E. (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. & Kochanny, C.O. (2005) Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management*, **69**, 1346–1359.
- Fuller, T.K. & Keith, L.B. (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., Rongstad, O.J. & Mytton, W.R. (1987) Manual and net-gun capture of coyotes from helicopters. *Wildlife Society Bulletin*, **15**, 444–445.
- Gese, E.M., Rongstad, O.J. & Mytton, W.R. (1988) Home range and habitat use of coyotes in southeastern Colorado. *Journal of Wildlife Management*, **52**, 640–646.
- Gese, E.M., Rongstad, O.J. & Mytton, W.R. (1989) Population dynamics of coyotes in southeastern Colorado. *Journal of Wildlife Management*, **53**, 174–181.
- Gese, E.M., Andersen, D.E. & Rongstad, O.J. (1990) Determining home-range size of resident coyotes from point and sequential locations. *Journal of Wildlife Management*, **54**, 501–505.
- Gese, E.M., Ruff, R.L. & Crabtree, R.L. (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., Ruff, R.L. & Crabtree, R.L. (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. Kansas State College, Manhattan, Kansas.
- Gompper, M.E. (2002) Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of north eastern North America by coyotes. *Bioscience*, **52**, 185–190.
- Goodrich, J.M. & Buskirk, S.W. (1995) Control of abundant native vertebrates for conservation of endangered species. *Conservation Biology*, **9**, 1357–1364.
- Isbell, L.A., Cheney, D.L. & Seyfarth, R.M. (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. & Stoddart, L.C. (1992) Some observations from two coyote-prey studies. *Ecology and Management of the Eastern Coyote* (ed. H.H. Boer), pp. 101–121. 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, IL.
- Laurenson, M.K. (1995) Implications of high offspring mortality for cheetah population dynamics. *Serengeti II: Research, Conservation, and Management of an Ecosystem* (eds A. R. E. Sinclair & P. Arcese), pp. 385–399. University of Chicago Press, Chicago, IL.
- Linnell, J.D. & Strand, O. (2000) Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, **6**, 169–176.
- 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., Boutin, S., Krebs, C.J. & Hofer, E.J. (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. & Caro, T.M. (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.
- Peterson, R.O. (1995) Wolves as interspecific competitors in canid ecology. *Ecology and Conservation of Wolves* (eds L.N. Carbyn, S.H. Fritts & D.R. Seip), pp. 315–324. Circumpolar Press, Edmonton, Alberta.
- Polis, G.A. & Holt, R.D. (1992) Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution*, **7**, 151–153.
- 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.
- Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*. C. Griffin, London.
- Sih, A. (1992) Prey uncertainty and the balancing of anti-predator and feeding needs. *American Naturalist*, **139**, 1052–1069.
- Smith, G.J., Cary, J.R. & Rongstad, O.J. (1981) Sampling strategies for radio-tracking coyotes. *Wildlife Society Bulletin*, **9**, 88–93.
- Smith, D.W., Peterson, R.O. & Houston, D.B. (2003) Yellowstone after wolves. *Bioscience*, **53**, 331–340.
- Smith, D.W., Stahler, D.R. & Guernsey, D.S. (2004) *Yellowstone Wolf Project: Annual Report, 2003*. YCR-NR-2004-04. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.
- Switalski, T.A. (2002) *Coyote foraging ecology, vigilance, and behavioral cascades in response to gray wolf reintroduction in Yellowstone National Park*. MSc Thesis, Utah State University, Logan.
- Thurber, J.M., Peterson, R.O., Woolington, J.D. & Vucetich, J.A. (1992) Coyote coexistence with wolves on the Kenai Peninsula, Alaska. *Canadian Journal of Zoology*, **70**, 2494–2498.
- White, G.C. & Burnham, K.P. (1999) Program MARK. Survival Estimation from Populations of Marked Animals. *Bird Study Suppl.*, **46**, 120–138.
- White, G.C. & Garrott, R.A. (1990) *Analysis of Wildlife Radio Tracking Data*. Academic Press, London.
- Wilmers, C.C. & Getz, W.M. (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.