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# Trophic cascades linking wolves (*Canis lupus*), coyotes (*Canis latrans*), and small mammals

Brian J. Miller, Henry J. Harlow, Tyler S. Harlow, Dean Biggins, and William J. Ripple

**Abstract:** When large carnivores are extirpated from ecosystems that evolved with apex predators, these systems can change at the herbivore and plant trophic levels. Such changes across trophic levels are called cascading effects and they are very important to conservation. Studies on the effects of reintroduced wolves in Yellowstone National Park have examined the interaction pathway of wolves (*Canis lupus* L., 1758) to ungulates to plants. This study examines the interaction effects of wolves to coyotes to rodents (reversing mesopredator release in the absence of wolves). Coyotes (*Canis latrans* Say, 1823) generally avoided areas near a wolf den. However, when in the proximity of a den, they used woody habitats (pine or sage) compared with herbaceous habitats (grass or forb or sedge)—when they were away from the wolf den. Our data suggested a significant increase in rodent numbers, particularly voles (genus *Microtus* Schrank, 1798), during the 3-year study on plots that were within 3 km of the wolf den, but we did not detect a significant change in rodent numbers over time for more distant plots. Predation by coyotes may have depressed numbers of small mammals in areas away from the wolf den. These factors indicate a top-down effect by wolves on coyotes and subsequently on the rodents of the area. Restoration of wolves could be a powerful tool for regulating predation at lower trophic levels.

**Résumé :** Lorsque les grands carnivores sont éliminés d'un écosystème qui a évolué avec la présence de prédateurs de sommet du réseau trophique, ce système peut changer aux niveaux trophiques des herbivores et des plantes. Ces changements qui se produisent dans les divers niveaux trophiques sont connus comme des effets en cascade et sont de grande importance pour la conservation. Les études sur les effets de la réintroduction des loups dans le parc national de Yellowstone ont examiné la voie de transmission des interactions des loups (*Canis lupus* L., 1758) aux ongulés et aux plantes. Notre travail recherche les effets des interactions des loups sur les coyotes et les rongeurs (renversant la libération des mésoprédateurs produite par l'absence de loups). Les coyotes (*Canis latrans* Say, 1823) évitent généralement les endroits proches d'un terrier de loup. Cependant, s'ils se retrouvent à proximité d'un terrier, ils utilisent les habitats ligneux (pins ou armoises) plutôt que les habitats herbacés (herbes ou plantes herbacées ou laïches) qu'ils fréquentent lorsqu'ils ne sont pas près d'un terrier de loup. Nos données indiquent une augmentation significative du nombre des rongeurs, particulièrement des campagnols (genre *Microtus* Schrank, 1798), durant une étude de 3 ans sur des parcelles situées à moins de 3 km d'un terrier de loup; aucun changement significatif dans le temps n'a été observé chez les petits mammifères sur les parcelles plus éloignées. La prédation par les coyotes pourrait avoir réduit le nombre de petits mammifères dans les régions éloignées du terrier de loup. Ces facteurs indiquent un effet descendant des loups sur les coyotes et, par la suite, sur les rongeurs de la région. Le rétablissement des loups pourrait être un outil puissant pour contrôler la prédation aux niveaux trophiques inférieurs.

[Traduit par la Rédaction]

## Introduction

After the Green World Hypothesis (Hairston et al. 1960) and experiments by Paine (1966), scientists began to take more interest in how top predators affect ecosystem form and function. The removal of apex predators initiates a cascade of indirect effects that trickle downward across trophic levels, and that cascade changes the structure and function of an entire system (see reviews by Terborgh et al. 1999; Miller et al. 2001, Soulé et al. 2003, 2005; Ray et al. 2005; Ter-

borgh and Estes 2010). The cascade caused by removing a top predator has dramatic effects on the conservation of flora and fauna.

There are manifold pathways to express top-down regulation, but it basically operates through interactions across trophic levels (Paine 1980). In general, herbivores can reduce the biomass of plants, and carnivores can reduce the numbers (or biomass) of herbivores, as well as influence their behavior—which, in turn, can affect the biomass of plants (Hairston et al. 1960; Fretwell 1977, 1987; Oksanen et al.

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1981; Terborgh et al. 1999; Oksanen and Oksanen 2000). This idea implies direct and indirect interactions among at least three general trophic levels: carnivores, herbivores, and plants.

Despite difficulties of scale, there are studies that show over the long term (>10 years) that carnivores can limit herbivores, with direct and indirect effects spreading to other trophic levels. Examples include work on sea otters (*Enhydra lutris* (L., 1758)) (Estes et al. 1978, 1989, 1998); carnivore-free islands in Venezuela (Terborgh et al. 1997, 2001); cycles of snowshoe hares (*Lepus americanus* Erxleben, 1777) (Krebs et al. 1995; 2001); cougars (*Puma concolor* (L., 1771)) (Ripple and Beschta 2006a); and wolves (*Canis lupus* L., 1758) (Pastor et al. 1988; McLaren and Peterson 1994; Peterson 1999; Post et al. 1999; White and Garrott 2005; Beschta and Ripple 2009).

More germane to this study, large carnivores can directly and indirectly regulate smaller predators, in turn affecting the abundance and diversity of birds and small mammals (Terborgh and Winter 1980; Soulé et al. 1988; Smith and Quin 1996; Crooks and Soulé 1999; Henke and Bryant 1999; Berger et al. 2001, 2008; Smith et al. 2004; Moseby et al. 2006; Sergio et al. 2008; Letnic et al. 2009; Ritchie and Johnson 2009). The restoration of an apex predator can cause interference competition, where smaller predators are either killed or change their habitat selection to avoid the larger predator. This competition may give small-mammal prey a refuge from predation by the smaller predator (Letnic et al. 2009). Dynamics such as these are difficult to discern, however, without some element of change to the system; without change, densities and distributions of flora and fauna typically seem stationary at the time scale of a given research project (Estes et al. 2011). Thus, the reintroduction of wolves into northwest Wyoming and Idaho offered a unique opportunity.

Wolves had been absent from the Greater Yellowstone Ecosystem since 1926, but during 1995 and 1996, 31 wolves from Canada were released into Yellowstone National Park (Smith et al. 2003). Wolf numbers increased rapidly, and by the end of 2002, there were 18 breeding packs totaling 270 wolves in the Greater Yellowstone Ecosystem (2004; Fed. Reg. 69: 10 956–10 971). That expansion of wolves produced a breeding pack in Grand Teton National Park. The Teton wolf pack appeared in 1999 and used the same general location for its den from that year through 2004. The pack stayed at three members through 2000, then numbered around 12–20 individuals from 2001 to 2004 (S. Cain, personal communication).

In general, small mammals are important in many systems, providing an abundant source of food for small predators (mammalian, avian, and reptilian) and affecting seed dispersal, plant biomass, and plant nutrient content. Voles (genus *Microtus* Schrank, 1798) were the most important food source for coyotes (*Canis latrans* Say, 1823) in western Montana, and the relative use of habitats by coyotes was identical to the ranking of densities of vole population in those habitats (Reichel 1991). We hypothesized a similar relationship for our study site in Grand Teton National Park in Wyoming. In 1999, we began an ongoing study of coyote and small-mammal population structure in areas away from the Teton pack wolf den, with the hope of eventually testing the effects

of wolves on these factors. In 2002, the wolf pack became secure, and we began to investigate whether wolf activity around their den changed coyote behavior and thus levels of exploitation on small mammals.

Our plot selection for trapping small mammals near wolves was limited by the presence of a single den in Grand Teton National Park and the geographic location of that den. Although Yellowstone National Park had more wolf dens, our research was limited to Grand Teton National Park for reasons beyond our control. With this simple design, we cannot calculate variability among study areas and the associated level of experimental error, limiting our ability to generalize the results (Hurlbert 1984). But, we do make comparisons over time as wolf numbers increased; comparisons over time, especially when coupled with spatial comparisons in the study area, can provide evidence that the changes are due to treatment and not due to some other confounding factor. Furthermore, as a matter of principle, Oksanen (2001) argued that in many studies, replication is unnecessary. Regardless, generalizing our specific findings to other biological systems is probably not warranted without unambiguous precautions.

This case study enabled us to evaluate the following predictions at a small scale: (1) coyotes will use the areas near the wolf den less frequently than areas more distant from the wolf den, and that disparity will increase over time as wolf numbers increase and coyotes learn to avoid them; (2) coyotes will use different habitat when they are near the wolf den than when they are distant from the wolf den; and (3) small-mammal abundance will be affected by distance to the wolf den.

## Study area

Grand Teton National Park lies on an active fault line in northwestern Wyoming. The Park covers 123 998 ha between the elevations of 1 951 and 4 198 m (<http://www.nps.gov/grte>). It includes the Teton Range to the west and is bordered by the Gros Ventre Mountains to the southeast, the Washakie range to the northeast, the Yellowstone Volcanic Plateau to the north, and the Snake River drainage to the south (Love and Reed 1971). Climate is semiarid with dry summers and cold snowy winters; snow often covers the ground from November until April (<http://www.nps.gov/grte>). Soils are glacial deposits of gravel and wind-blown loess (Love and Reed 1971). Vegetation is largely coniferous forests, sagebrush grasslands, and grassy meadows (<http://www.nps.gov/grte>). Our study area covered about 150 km<sup>2</sup> on the eastern edge of the large mountain valley that runs north and south through the Park.

## Materials and methods

To assess how wolf activity affected coyote densities at various distances from the wolf den, we counted coyote scat during the summers of 2002, 2003, and 2004 (following Gompper et al. 2006). Thus, we assumed that quantities of coyote scat indicated relative coyote use in an area and searched 147 km of trails and roads each year during June and July (Table 1).

We chose a radius of 0–6 km from the den to represent the area of highest wolf activity (about 115 km<sup>2</sup>). Wolves with

**Table 1.** Coyote (*Canis latrans*) scats collected per kilometre walked by habitat type in the three categories of distance from the wolf (*Canis lupus*) den: 0–6, 6–12, and 12–18 km.

Distance by year	Habitat*			
	Sage (M6)	Pine (P1)	Grass and forb (M3)	Sedge and grass (M1)
2002				
0–6 km	0.250	0.204	0.330	0.455
6–12 km	0.226	0.372	0.303	0.233
12–18 km	0.686	0.088	0.303	0.154
2003				
0–6 km	0.357	0.408	0.220	0
6–12 km	0.226	0.186	1.111	0.698
12–18 km	0.294	0.351	1.818	0.308
2004				
0–6 km	0.357	0.612	0	0
6–12 km	0.376	0.465	0.404	0
12–18 km	0.294	0.307	1.212	1.077

**Note:** Sampling on these transects was during 2002–2004. The numbers in the table are weighted by samples sizes within each habitat, distance, and year.  
\*Describes the total habitat type covered by the trails in each of the three categories of distance from the wolf den.

pups move by radiating out from the den, then returning periodically to care for the pups (Mech and Boitani 2003). The mean territory size for 13 wolf packs in Yellowstone National Park was 223 km<sup>2</sup> when calculated by minimum convex polygon (Smith et al. 2004). Our smaller area recognizes that minimum convex polygons depend on data extremes, and they typically overestimate areas of uniform use. We created two more concentric rings that were 6–12 km from the den and 12–18 km from the den. We avoided a circular area within 1 km of the wolf den.

Canid scats are thick strands, occasionally folded, and can be recognized by a distinctive, sharp odor. We followed Halfpenny (1986) to identify red fox (*Vulpes vulpes* (L., 1758)) scats as <18 mm wide, coyote scats as between 18 and 25 mm wide, and wolf scats as being >25 mm wide. Red fox scat can be correctly identified by this technique 92% of the time, whereas coyote and wolf scat can be identified correctly 63% of the time (Halfpenny 1986). The most common error would be confusing a small wolf scat as that of a coyote, meaning we could overestimate coyote use in areas with high wolf use. We recorded the distance that trails passed through each habitat type via global positioning system (GPS), the habitat type where each scat was located, time of observation, and distance from the wolf den. Because trail lengths varied, we standardized scat encounter rates as black coyote scats counted per kilometre of trail.

To examine the relationship between wolf activity and abundance of small mammals, as potentially mediated by coyote activity, we trapped small mammals in four vegetation types within two zones categorized by distance from the wolf den, following the maps and habitat designations created by Debinski et al. (1996) (Table 2a). The habitats we sampled included mature stands of lodgepole pine (*Pinus contorta* Douglas ex Loudon) (P1), dry big sagebrush (*Artemisia tridentata* Nutt.) (M6), mixed grasses and forbs (M3), and sedge and grass damp and wet meadow (M2 and M1) (see Debinski et al. 1996). For certain analyses, we combined these habitat classes into a meadow category (dominated by

grasses, sedges, and other low herbaceous plants) and a shrub or forest category (dominated by pine or sage).

One trapping zone was 9–11 km from the wolf den (called “away” plots). At this distance, we placed 1 ha grids in each of these habitats, referred to as 1P1, 1M6, 1M3, 1M2, and 1M1 (Tables 2a). We trapped the same five grids in the “away” zone during each summer from 1999 to 2004.

From 2002 through 2004, we sampled similar habitats (2P1, 2M6, 2M3, and 2M1) in a trapping zone that was 1–3 km from the wolf den (called “near” plots). There was not a “near” sedge and grass damp plot (a 2M2) of sufficient size for a trapping grid in this zone. All plots were at about the same altitude (2090–2150 m).

We trapped each of the “away” (1P1, 1M6, 1M3, 1M2, 1M1) and “near” (2P1, 2M6, 2M3, 2M1) plots for approximately 1000 trap-nights (range 823–2100) using folding Sherman traps (22.5 cm × 7.5 cm × 7.5 cm). Traps within these 1 ha grids were spaced every 10 m (121 traps/grid) and baited with rolled oats coated with molasses. The study followed the guidelines of the Denver Zoological Foundation’s Research Committee and Institutional Animal Care and Use Committee standards.

We converted total unique capture numbers over the total number of trap-nights at a plot into unique captures per 500 trap-nights by multiplication of 500 times the ratio for captures per night. Number of trap-nights during a session was adjusted for sprung traps via the technique of Beauvais and Buskirk (1999). If a trap was sprung during a night but was found in the morning without a captured animal, it was considered to be open for one-half of the night and thus represented half of a trap-night. To assess relationships between small-mammal indices and precipitation, we used precipitation data from the Park Service weather station at Cottonwood Creek.

We used the general linear modeling (GLM) and regression routines of Systat version 12.0 (Systat, Inc., Chicago, Illinois, USA) for analysis of coyote scat data. A multivariate general linear model was reduced in a stepwise fashion in an

**Table 2.** (a) Numbers of small mammals captured/500 trap-nights and (b) rainfall amounts from 1999 to 2004.

(a) Numbers of small mammals captured.							
Plot	Species	Number of captures/500 trap-nights					
		1999	2000	2001	2002	2003	2004
1M1	Voles	22	52	24.2	0	4.7	64.5
1M2	Voles	31.1	19.3	14.8	10.2	3.6	56
1M3	Deer mice ( <i>Peromyscus maniculatus</i> )	3.1	5.9	3.2	0.5	10.1	15.1
1M3	Voles	5.9	1.3	2.3	0	0	2.7
1M6	Deer mice	4.4	4.8	6.3	4.7	4.8	12
1P1	Chipmunks ( <i>Tamias</i> spp.)	4.7	3.2	6.3	5.2	3.2	2.1
1P1	Voles	5.9	0.6	0	0	2.1	5.8
2M1	Voles				30.4	52.1	92.7
2M3	Deer mice				2.6	3.7	4.7
2M3	Chipmunks				0	5.8	3.7
2M3	Voles				0	0	10.5
2M6	Deer mice				8.8	19.8	54.3
2M6	Chipmunks				2.6	6	4.7
2P1	Deer mice				0	10	24.6
2P1	Chipmunks				0.8	2.1	7
2P1	Voles				2.1	2.6	11.2
(b) Rainfall through June of each year.							
	Year						
	1999	2000	2001	2002	2003	2004	
Rainfall (cm)	102.8	74.9	62.5	71.4	76.9	82	

**Note:** The “voles” category is a combination of *Microtus* sp. and southern red-backed vole (*Myodes gapperi*). Effect of rainfall was assessed using the balanced subset of data within the region circumscribed by the solid line. Effect of distance to wolf (*Canis lupus*) den was assessed using the balanced subset of data by the shaded cells.

attempt to find the most parsimonious submodel that accounted for meaningful variation. For encounter rates of coyote scat, our general model was scat index = constant + wolf distance + year + habitat group + (year × wolf distance) + (year × habitat group) + (wolf distance × habitat group). Retention of interactions justified separate analyses by levels of one of the interacting variables to examine the source of the disproportionate effect. A square-root transformation improved normality and homoscedasticity of residual variation. We assessed small-mammal data with a repeated measures general linear model, analyzing capture rates from 2002, 2003, and 2004 for four plots near the wolf den paired with five plots in the same habitats away from the wolf den.

Rainfall varied annually, creating a source of variation that is confounded with effects on small-mammal abundance of annually changing wolf densities, coyote densities, and changes in behaviors of these canids. To separately examine the effect of rainfall on small mammals, we looked at relationships within the largest subset of trapping data obtainable, trapping data from plots distant from the wolf den and trapped during the full 6-year period (Table 2a, 2b). Effects of rainfall were examined using simple linear regression.

Results

During the first step of assessment using the multivariate GLM, the year × habitat group interaction was not influential ( $F_{[1,29]} = 0.731$ ,  $P = 0.400$ ) and was removed from the model. In the subsequent model, there was evidence supporting the two remaining interactions, wolf distance × habitat group ( $F_{[1,30]} = 7.890$ ,  $P = 0.009$ ) and wolf distance × year

( $F_{[1,30]} = 3.931$ ,  $P = 0.057$ ), justifying separate analyses by habitat and by year.

Both parts of our prediction 1 were supported by our data (i.e., coyotes will use the areas near the wolf den less frequently than areas more distant from the wolf den and that disparity will increase over time as wolf numbers increase and coyotes learn to avoid them). Assessments of the wolf distance effect for each year (Fig. 1) suggested an increasing effect over time (2002: slope =  $-0.003$ ,  $P = 0.749$ ; 2003: slope =  $0.029$ ,  $P = 0.175$ ; 2004: slope =  $0.041$ ,  $P = 0.075$ ). By 2004, a significant disparity in proportionate use had developed, favoring higher detections of coyote scat as distance from the wolf den increased.

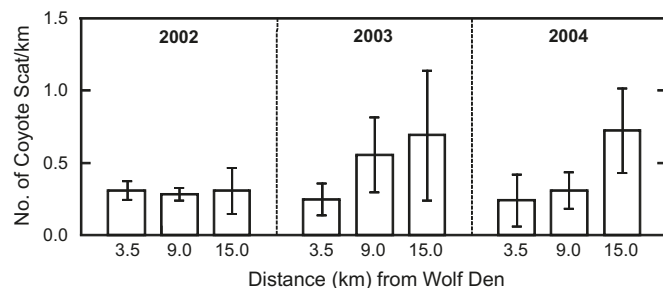
Habitat selection by coyotes was consistent with our prediction 2 (Fig. 2); pooling to create two categories of habitat (woody and herbaceous) showed differing habitat relationships in relation to distance from the wolf den. Separate analyses by habitat category showed coyote use of open habitats that were dominated by herbaceous plants (grass, sedge, forb) decreased with diminishing distance to the wolf den ( $t = 2.737$ ,  $p = 0.015$ ). In contrast, there were no detectable effects of distance from the wolf den on coyote use of habitats dominated by woody plants (pine, sage) that could provide cover ( $t = -0.465$ ,  $p = 0.648$ ) (Table 1).

Table 2a shows the number and general type of small mammals captured by habitat type. In general, the pine (P1) yielded voles (*Microtus* spp.), southern red-backed voles (*Myodes gapperi* (Vigors, 1830)), and chipmunks (*Tamias* spp.). The sage (M6) yielded deer mice (*Peromyscus maniculatus* (Wagner, 1845)). In the grass and forb meadows (M3), we trapped voles and chipmunks. By far the most productive

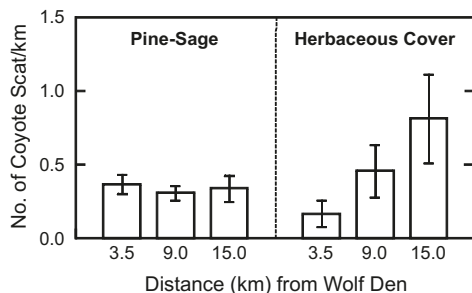
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**Fig. 1.** Influences of distance from the wolf (*Canis lupus*) den on encounter rates for coyote (*Canis latrans*) scat (mean  $\pm$  1 SE) over 3 years (2002–2004). Distances represent the midpoint of each distance category (e.g., 0–6 km is represented as 3.5 km).



**Fig. 2.** Relationship between encounters of coyote (*Canis latrans*) scat (mean  $\pm$  1 SE) and distance from the wolf (*Canis lupus*) den for two categories of habitat, woody (pine–sage) and herbaceous (grass and sedge meadows). Distances represent the midpoint of each distance category (e.g., 0–6 km is represented as 3.5 km).



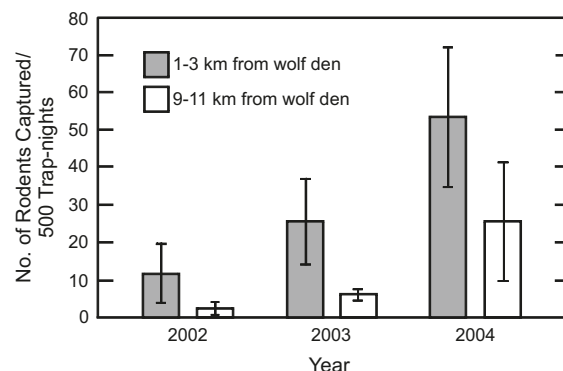
habitats were the wet meadows with sedges and grasses (M1), yielding high numbers of voles.

Although the year  $\times$  wolf distance interaction was not influential in our repeated measures model of small-mammal captures (all species combined,  $F_{[2,6]} = 1.901$ ,  $P = 0.229$ ), overall effects of year ( $F_{[2,6]} = 8.365$ ,  $P = 0.018$ ) and distance to wolf den ( $F_{[1,3]} = 6.456$ ,  $P = 0.085$ ) were supported (Fig. 3). Capture rates for plots within 3 km of the wolf den appeared to increase annually ( $F_{[2,6]} = 18.384$ ,  $P = 0.003$ ), but annual changes in capture rates were not detectable in plots 9–11 km from the den ( $F_{[2,6]} = 2.344$ ,  $P = 0.177$ ). Rainfall was not significantly associated with capture rates of all small-mammal species combined ( $F_{[1,28]} = 0.875$ ,  $P = 0.358$ ).

## Discussion

Our analysis suggested that coyotes change their activity levels as a function of distance from the wolf den. Importantly, the coyotes appeared to concentrate their activities farther from the wolves as time progressed (Fig. 1). Moreover, coyotes seemed scarcer in the pooled herbaceous category that provided little hiding cover than in the pooled woody category near the wolf den, but increased their use of more open cover types as distances from the wolf den increased (Fig. 2). Open cover types such as sedge and grass wet meadows near the wolf den showed the most dramatic differences near and away from the den (Table 1), yet those meadows were the most productive for voles (see Tables 1,

**Fig. 3.** Capture rates (mean  $\pm$  1 SE) for rodents (all species combined) on plots 1–3 km from the wolf (*Canis lupus*) den and on plots 9–11 km from the wolf (*Canis latrans*) den.



2a), the preferred food of coyotes (Reichel 1991). Because Reichel (1991) showed that the relative use of habitats by coyotes correlated with vole densities in areas where wolves were absent, predation risk to coyotes near the wolf den apparently countered the high food value of those wet meadows in our study area. Indeed, coyotes tended to use the less productive habitat (sage or pine) near the wolf den, but they seemed to favor the most productive habitats (sedge and grass wet meadows) away from the wolf den. The potential to confuse a small wolf scat as a coyote scat would, if anything, have caused us to overestimate coyote use near the wolf den, thus tending to weaken the trends noted.

We failed to detect an effect of rainfall on small-mammal capture rates; perhaps the variation in precipitation during the period 1999–2004 was insufficient to generate a trophic response in the small-mammal populations or such a response was overwhelmed by other variables. In any case, lack of detectable effect of annual precipitation during this period supports the hypothesis that annual changes in small-mammal capture rates were indeed due to cascading effects initiated by colonization of wolves.

Although we lacked replicates of wolf dens over a large geographic scale, we were able to demonstrate treatment differences at a temporal scale, supporting the hypothesis that the effect was due to treatment and not other confounding variables. Coyotes may have learned about wolves over time as wolf numbers increased during 2002–2004.

Ripple and Beschta (2006b) saw predation risk affect elk (*Cervus elaphus* L., 1758) behavior in Yellowstone National Park, and Berger et al. (2001) showed that predator-naïve ungulates in Wyoming adjusted their behavior when they came in contact with apex predators. Similarly, naïve Siberian ferrets (*Mustela eversmanii* Lesson, 1827) increased the efficiency of predator avoidance after a single aversive exposure (Miller et al. 1990).

These results fit well with other studies that have shown wolves change the distribution and abundance of coyotes (Mech 1966; Paquet 1991, 1992; Thurber et al. 1992; Berger and Gese 2007). They are also consistent with studies showing a relationship among dingoes (*Canis lupus dingo* Meyer, 1793), smaller predators, and native rodents in Australia with native rodents faring better when dingoes reduce the numbers of smaller predators (Smith and Quin 1996; Moseby et al. 2006; Letnic et al. 2009).

Elimination of wolves on the Great Plains might have led to an abundance of coyotes that now impede reintroductions of black-footed ferrets (*Mustela nigripes* (Audubon and Bachman, 1851)) (Biggins 2000). Similarly, the extirpation of wolves in the northern portions of the conterminous United States may have allowed coyotes to increase, causing high levels of predation pressure on snowshoe hares, resulting in chronically low hare densities and attenuated dynamics of hare population cycles (Ripple et al. 2011). Furthermore, marked declines in small-mammal communities were found in the Ruby Mountains of Nevada using paired historical (1927–1929) and modern (2006–2008) survey data (Rowe et al. 2011). The declines were greater for voles (preferred coyote prey) compared with little or no declines for red-toothed shrews (genus *Sorex* L., 1758; not typical coyote prey). In each of the three scenarios above, coyotes likely increased after wolf extirpation potentially causing additional top-down pressure on these traditional prey and smaller predators.

In addition to affecting coyote numbers and behavior, wolves can change the behavior and number of ungulates in an area (Crête and Manseau 1996; Boyce and Anderson 1999; Crête 1999; Peterson 1999; Post et al. 1999; Berger et al. 2001; Mech et al. 2001; White and Garrott 2005; Ripple and Beschta 2006b, 2007, 2112; Beschta and Ripple 2009). Ungulates can compete with rodents for forage, and reduced ungulate densities can also increase rodent numbers (Keesing 2000).

An important factor for future research is the temporal and spatial context of the situation. Henke and Bryant (1999) showed that 1 year after coyote removal in west Texas, while rodent and black-tailed jackrabbit (*Lepus californicus* Gray, 1837) density increased, rodent richness was reduced from 12 species to 1 species because the Ord's kangaroo rat (*Dipodomys ordii* Woodhouse, 1853) was a superior competitor. In that case, coyote removal in west Texas was the result of a 2-year aerial gunning program on fixed plots.

The context is different in Grand Teton National Park. Wolf and coyote competition is a natural event and may be temporary for several reasons. First, a long, snowy winter, such as in the Tetons, can affect predatory interactions (Oksanen and Oksanen 2000). Second, wolves can move their den sites, thus taking their top-down effects with them. And although they use the area around a den for the whole year (Trapp 2004), level of use can change with the seasons.

We also speculate that fewer coyotes and abundant prey will allow smaller mammalian carnivores and raptors to increase in number (sensu Soulé et al. 1988; Crooks and Soulé 1999). If rodent numbers increase as coyote numbers decrease, it will supply ample prey for the smaller predators. Indeed, a healthy weasel (genus *Mustela* L., 1758) population alone can play a strong role in regulating vole cycles (Andersson 1977; Fitzgerald 1977; Korpimäki and Norrdahl 1998; Gilg et al. 2003), and high vole numbers will affect the distribution and abundance of weasels (Erlinge 1974; Fitzgerald 1977).

Other factors may affect the small-carnivore community differently in the Tetons than in west Texas. The presence of wolves causes coyotes to reduce coyote group size (Crabtree and Sheldon 1999), and single coyotes are more tolerant of foxes than are large groups of coyotes (Gese et al. 1996).

Wolves also leave carrion that can be beneficial to smaller carnivores (Paquet 1991; Hayes et al. 2000). If such factors diversify a small-carnivore community in the presence of wolves, it could create a more stable system over the long term (see McCann et al. 1998; Finke and Denno 2004). Nevertheless, there is “a basic humbling message...that, with many potential routes for indirect interactions between any species pair, it may be difficult to predict the effect of 1 species upon another” (Holt and Lawton 1994, p. 509).

The temporal and spatial questions indicate that a gap in sampling time may miss the dynamics of changed interactions. We cannot predict in advance where wolves will place a den, but dynamics of interaction pathways could be monitored at both the new den site and the former den site to assess changes as wolves arrive and leave. These questions also require long-term study and commitment. Ideally, small-mammal trapping should be replicated at several wolf dens to examine on broader scales the validity of our limited experiment especially since, at the time of our project, the system might not have yet stabilized or adjusted to presence of wolves, which could have confounded our results. At broader scales, research that takes advantage of spatial and temporal differences in wolf abundance will likely produce a greater understanding of how wolves influence coyotes and their effects.

## Conclusion

Is it possible that the extirpation of wolves in the early 20th century initiated trophic and competitive adjustments across broad ecosystems in the American West as coyotes were elevated from the status of mesopredator to that of apex predator? We suggest that this scenario is plausible. After wolf extirpation, coyote densities increased and distributions generally expanded (Bekoff 1977). Because coyotes could only partially mimic the role of wolves in driving ecosystem function, ecological and evolutionary relationships were distorted over large geographic and temporal scales (Paquet et al. 2010). Finally, coyotes are effective generalist predators, and they can drive down densities of prey and smaller predators (Henke and Bryant 1999; Biggins 2000; Berger et al. 2008; Prugh et al. 2009). This adversely affects biodiversity and demography of prey, small predators, and other mesopredators (see Smith and Quin 1996; Moseby et al. 2006; Letnic et al. 2009; Ritchie and Johnson 2009).

To our knowledge, the study reported herein is the first to link wolf presence to small-mammal densities as mediated by coyotes. The findings of these linkages are consistent with the mesopredator release hypothesis in that wolves likely affect trophic interactions through both known and unknown pathways. Since being reintroduced, it appears that interference competition from wolves may be limiting coyote distribution and densities in parts of the Greater Yellowstone Area (Berger and Gese 2007). Additional research on these two sympatric predators will be needed in the future for a more complete understanding of any cascading effects owing to these interactions. Density and behaviorally mediated cascades associated with large predators appear to represent potent ecological forces potentially capable of affecting food webs through interactions of numerous species (Terborgh and Estes 2010). Repatriation of apex predators could be a powerful tool for regulating predation at lower trophic levels.

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