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. 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 méspredateurs 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 laîches) 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.

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; Terborgh 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.
stayed at three members through 2000, then numbered
location for its den from that year through 2004. The pack
Teton wolf pack appeared in 1999 and used the same general
produced a breeding pack in Grand Teton National Park. The
the end of 2002, there were 18 breeding packs totaling 270
from Canada were released into Yellowstone National Park
Ecosystem since 1926, but during 1995 and 1996, 31 wolves
community.

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 Soule 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 opportu-
nity.

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 GreaterYellowstone Ecosystem (2004; Fed.
Reg. 69: 10956 – 10971). 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, per-
sonal 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 disper-
sal, 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 Mon-
tana, and the relative use of habitats by coyotes was identical
to the ranking of densities of vole population in those habi-
tats (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. Al-
though 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 fac-
tor. Furthermore, as a matter of principle, Oksanen (2001) ar-
gued that in many studies, replication is unnecessary.
Regardless, generalizing our specific findings to other biolog-
ical systems is probably not warranted without unambiguous
precautions.

This case study enabled us to evaluate the following pre-
dictions 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 1951 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 No-
vember until April (http://www.nps.gov/grte). Soils are gla-
cial 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 km² 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 km²). Wolves with
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.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Species</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
</tr>
</thead>
<tbody>
<tr>
<td>1M1</td>
<td>Voles</td>
<td>22</td>
<td>52</td>
<td>24.2</td>
<td>0</td>
<td>4.7</td>
<td>64.5</td>
</tr>
<tr>
<td>1M2</td>
<td>Voles</td>
<td>31.1</td>
<td>19.3</td>
<td>14.8</td>
<td>10.2</td>
<td>3.6</td>
<td>56</td>
</tr>
<tr>
<td>1M3</td>
<td>Deer mice (*) (Peromyscus maniculatus)</td>
<td>3.1</td>
<td>5.9</td>
<td>3.2</td>
<td>0.5</td>
<td>10.1</td>
<td>15.1</td>
</tr>
<tr>
<td>1M3</td>
<td>Voles</td>
<td>5.9</td>
<td>1.3</td>
<td>2.3</td>
<td>0</td>
<td>0</td>
<td>2.7</td>
</tr>
<tr>
<td>1M6</td>
<td>Deer mice</td>
<td>4.4</td>
<td>4.8</td>
<td>6.3</td>
<td>4.7</td>
<td>4.8</td>
<td>12</td>
</tr>
<tr>
<td>1P1</td>
<td>Chipmunks (Tamias spp.)</td>
<td>4.7</td>
<td>3.2</td>
<td>6.3</td>
<td>5.2</td>
<td>3.2</td>
<td>2.1</td>
</tr>
<tr>
<td>1P1</td>
<td>Voles</td>
<td>5.9</td>
<td>0.6</td>
<td>0</td>
<td>0</td>
<td>2.1</td>
<td>5.8</td>
</tr>
<tr>
<td>2M1</td>
<td>Voles</td>
<td>30.4</td>
<td>52.1</td>
<td>92.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2M3</td>
<td>Deer mice</td>
<td>2.6</td>
<td>3.7</td>
<td>4.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2M3</td>
<td>Chipmunks</td>
<td>0</td>
<td>5.8</td>
<td>3.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2M3</td>
<td>Voles</td>
<td>0</td>
<td>0</td>
<td>10.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2M6</td>
<td>Deer mice</td>
<td>8.8</td>
<td>19.8</td>
<td>54.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2M6</td>
<td>Chipmunks</td>
<td>2.6</td>
<td>6</td>
<td>4.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2P1</td>
<td>Deer mice</td>
<td>0</td>
<td>10</td>
<td>24.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2P1</td>
<td>Chipmunks</td>
<td>0.8</td>
<td>2.1</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2P1</td>
<td>Voles</td>
<td>2.1</td>
<td>2.6</td>
<td>11.2</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(b) Rainfall through June of each year.

<table>
<thead>
<tr>
<th>Year</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall (cm)</td>
<td>102.8</td>
<td>74.9</td>
<td>62.5</td>
<td>71.4</td>
<td>76.9</td>
<td>82</td>
</tr>
</tbody>
</table>

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.

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...
habitats were the wet meadows with sedges and grasses (M1), yielding high numbers of voles. Although the year × 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 to 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, 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-naive 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 (Anderson 1977; Fitzgerald 1977; Korpinimaki 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.
Acknowledgements

P. Cooley, A. Degraeve, S. Hammond, K. Keffer, S. Pfister, R. Reading, and D. Stern helped with data collection over the years. Funding came from the Denver Zoological Foundation, the University of Wyoming, the Koinonia Foundation, and the Oregon State University Foundation through a L.L. Stewart Faculty Scholar award to W.J.R. The Grand Teton National Park graciously granted us permits and encouraged the study. Comments by D. Augeri, M. Boyce, J. Estes, D. Parsons, R. Reading, M. Soulé, D. Smith, and J. Terborgh greatly improved the manuscript.

References


Published by NRC Research Press


Soulé, M.E., Bolger, E.T., Alberts, A.C., Wright, J., Sorice, M., and...


