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Coyotes, deer, and wildflowers: diverse evidence points to a trophic cascade

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Abstract Spatial gradients in human activity, coyote activity, deer activity, and deer herbivory provide an unusual type of evidence for a trophic cascade. Activity of coyotes, which eat young mule deer (fawns), decreased with proximity to a remote biological field station, indicating that these predators avoided an area of high human activity. In contrast, activity of adult female deer (does) and intensity of herbivory on palatable plant species both increased with proximity to the station and were positively correlated with each other. The gradient in deer activity was not explained by availabilities of preferred habitats or plant species because these did not vary with distance from the station. Does spent less time feeding when they encountered coyote urine next to a feed block, indicating that increased vigilance may contribute, along with avoidance of areas with coyotes, to lower herbivory away from the station. Judging from two palatable wildflower species whose seed crop and seedling recruitment were greatly reduced near the field station, the coyote–deer–wildflower trophic cascade has the potential to influence plant community composition. Our study illustrates the value of a case-history approach, in which different forms of ecological data about a single system are used to develop conceptual models of complex ecological phenomena. Such an iterative model-building process is a common, but underappreciated, way of understanding how ecological systems work.

Keywords Herbivory · Plant communities · Predation · Rocky Mountains · Spatial distribution · Vigilance

Introduction

Predators affect prey populations by killing individuals and by eliciting antipredator responses such as vigilance, avoidance, and defense. These consumptive and nonconsumptive effects in turn can affect species at lower trophic levels (Pace et al. 1999). Recent evidence for such "trophic cascades" involving large terrestrial mammalian predators has come mainly from deliberate manipulations of predator abundance (e.g., Schmitz et al. 2000; Harrington and Conover 2007; Letnic et al. 2009; Beschta and Ripple 2009; Ripple et al. 2014). Such manipulations are relatively rare because of ethical, political, and financial considerations, and other ways of detecting trophic cascades in these terrestrial mammalian systems would be highly desirable.

Several possible alternatives to deliberate predator manipulation also present themselves, including natural predator recolonization events that involve no manipulation and temporal variation in presence or abundance of predators (e.g., Burkholder et al. 2013). An additional alternative is to capitalize on natural spatial variation in predator abundance (e.g., Hebblewhite et al. 2005; Harrington and Conover 2007). This latter approach has allowed us to explore a possible trophic cascade that involves coyotes (*Canis latrans*), mule deer (*Odocoileus hemionus*), and wildflowers. Coyotes prey on mule deer, especially young animals in their first year

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(fawns; Lingle 2000; deVos et al. 2003; Pojar and Bowden 2004), and female deer (does) choose to hide their newborn fawns in relatively safe habitats (Long et al. 2009). When coyotes are present, mule deer also tend to move from preferred feeding habitats into safer habitats, at a cost of lower feeding rate (Lingle 2002; see also Laundré et al. 2001). Coyotes might therefore indirectly benefit plant species that deer eat by reducing the number of deer and their feeding rates.

Fawns are born in June in the subalpine valley in Colorado, USA where we worked. Human activity in this valley is seasonal, peaking during summer, and is concentrated at a biological field station that is surrounded by undeveloped natural lands. Coyotes tend to avoid humans when their own predators are rare (Gese et al. 1989; George and Crooks 2006; Ripple et al. 2013), as is the case in our study area. Based on these elements of natural history, the hypothesis of a coyote–deer–wildflower trophic cascade leads to a series of predictions about local spatial gradients that can be compared to evidence from observations and experiments (Fig. 1). We made the following specific predictions. First, we predicted that coyote activity would increase with distance from humans, i.e., from the field station. Second, we predicted that activity of does would be highest near the station, whereas male deer (bucks), which are not at risk from coyotes, would exhibit no strong spatial pattern. Third, we predicted that herbivory by deer would be highest near the station and positively correlated with deer activity. Here, we evaluate these predictions based on data accumulated over multiple summers of field work, and we comment more generally on the value of such a cumulative process for understanding ecological phenomena.

Methods

Study site

We worked at the Rocky Mountain Biological Laboratory (RMBL, 38.96°N, 106.99°W, 2,900 m a.s.l.) in the Elk Mountains of western Colorado (Fig. 2). All the buildings at the station cluster within an area of≈30 ha at the junction of Copper Creek and the East River, where the mining town of Gothic stood in the 1870s. There is no development in the public- and privately-owned lands that surround the RMBL. The East River and Copper Creek valleys are typical U-shaped glacial valleys with gentle valley bottoms that rise to flanking mountains. Foot trails and unpaved roads radiate from the Gothic "townsite" along the East River valley, with branching trails into the Copper Creek valley (Fig. 2). The trails and roads traverse the relatively gentle terrain of lower valley slopes, which contain a mosaic of open dry subalpine meadows dominated by herbaceous perennials and a few woody perennials such as sagebrush (*Artemisia tridentata*); wetter meadows that support willows (*Salix* spp.), false hellebore (*Veratrum californicum*), and other herbaceous species; open forest of aspen (*Populus tremuloides*) mixed with conifers; and stands of conifers, mainly Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies bifolia*), along watercourses.

RMBL is populated during summers by approximately 160 resident humans and increasingly, over the past 25 years, by mule deer—primarily pregnant does and yearling offspring early in the summer and lactating does with fawns later in the summer. The deer overwinter at lower elevations and move up into the East River valley just after spring snowmelt to establish relatively stable summer home ranges of ca. 200–400 ha. At the RMBL, deer feed exclusively on natural browse

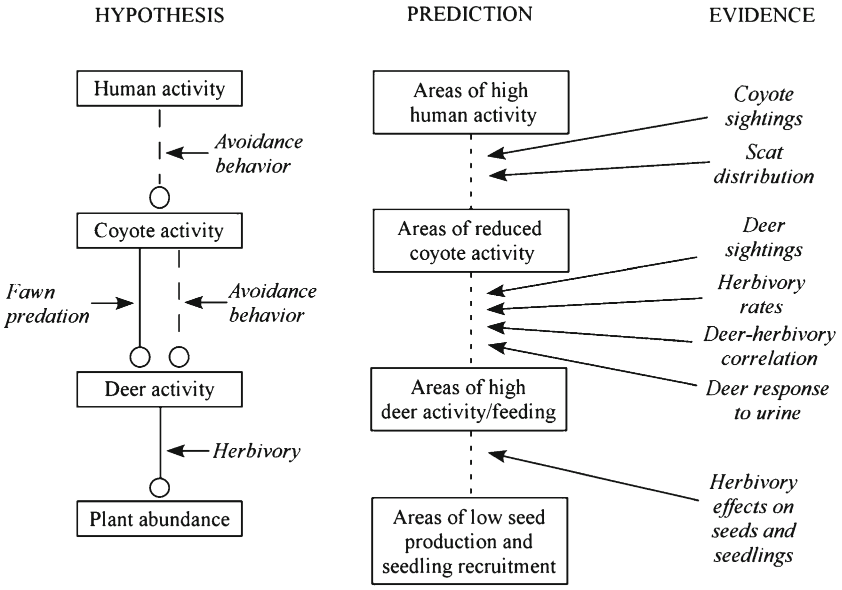

Fig. 1 Diagrammatic representation of the trophic cascade hypothesis, its predictions, and the evidence brought to bear in this study. The cascade (*left*) links adjacent trophic levels via consumptive (*solid lines*) and nonconsumptive (*dashed lines*) negative effects (*lines ending in circles*). If this cascade exists, we predict (*center*) a series of spatial relationships (*dotted lines*) between human activity and coyote activity, between coyote activity and activity of does and fawns, and between deer activity and plant reproduction. Diverse pieces of evidence (*right*) all support the predictions

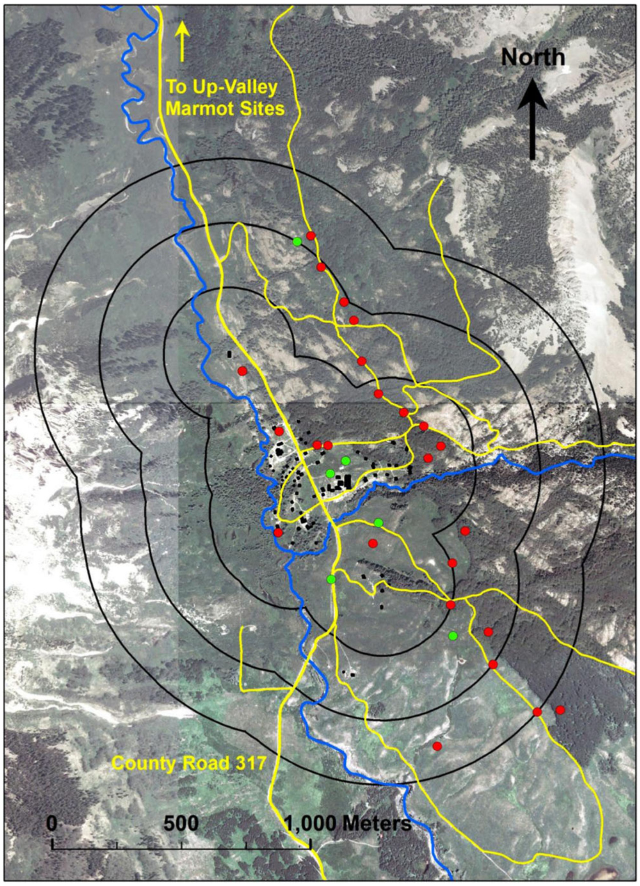

Fig. 2 The Gothic townsite and surrounding landscape. Buildings are *black polygons. Blue lines* trending north-south and east-west are rivers; *yellow lines* are main trails and roads. *Rounded black lines* are isolines 250, 500, and 750 m from the most peripheral summer-occupied cabins. *Green and red circles* are centroids of viewsheds scanned for deer in 2010 and 2011, respectively. Coyote scats were collected along trails and roads (*yellow lines*), out to the 750 m isoline. Coyote sightings were recorded at marmot colonies (not shown) more or less distant from the townsite

because the RMBL prohibits "recreational" (nonresearch) feeding of animals and requires food waste to be disposed of in containers that animals cannot access.

Human activity in the Upper East River Valley is concentrated within the townsite, which contains residential, academic, and administrative buildings. Activity decreases with distance away from the townsite in parallel with decreasing density of field research sites: one third of over 1,000 research plots in 2013 occurred within a 500-m radius of the town center, and another 13 % were within 1,000 m. The rest of the research plots were evenly scattered out to a distance of 100 km.

Spatial gradients in activity of coyotes

During morning (0700–1000 hours) and afternoon (1600–1900 hours) timed observations of yellow-bellied marmots (*Marmota flaviventris*) in the East River valley conducted over nine summers, observers recorded any marmot predators seen, thus obtaining estimates of diurnal coyote activity in the vicinity of marmot colonies. In addition, we repeatedly walked 17−19 km of trails during summers of 2010, 2011, and 2013; collected all coyote scats (feces) deposited on the trails; and mapped their locations. From this, we calculated scat density per meter of trail at different distances from the most peripheral summer-occupied RMBL building (hereafter "nearest cabin"; Fig. 2). Coyotes typically deposit scent (urine, feces, and glandular secretions) to mark their territories, often along well-traveled routes such as trails (Barrette and Messier 1980). Scat density along trails therefore provides a cumulative estimate of both diurnal and nocturnal coyote activity.

Spatial gradients in activity of deer

During summers of 2010 and 2011, we recorded activity of deer at varying distances from the RMBL. In 2010, we chose six points inside and outside of the Gothic townsite (Fig. 2) that afforded a clear view of a nearby meadow, and we mapped the perimeter of the "viewshed" visible from each point. We surveyed deer for approximately 1.5 h near dawn (0500–0700 hours) and 1.5 h near dusk (1900–2100 hours) once per week over 6 week in June and July. During each survey period, we scanned the viewshed every 10 min for 1 min and recorded the number of deer present. In 2011, we walked two standard routes along trails inside and outside of the townsite near dawn and dusk once per week over 6 week in June and July. We scanned for deer continually as we walked each route at constant speed, and also stopped at 24 specified points (Fig. 2) for 360° scans, each timed to last 1 min. Because in 2011 the routes traversed habitats that differ in visibility, we mapped the perimeter of the viewshed visible from route segments and points by walking a life-sized cardboard image of a mule deer away from an observer standing on the route until half of the image was obscured by vegetation. Defining the viewshed in this way corrected for habitat-specific variation in visibility. We alternated the start of each route so that distant points were not always sampled last. Because surveys were blocked by time of day and week, we could sum deer counts across replicate scans and divide by scan number to arrive at a single average value of deer per scan for each point or route segment. Deer were sufficiently separated in space that double counting during a census was not an issue. All observations in a given summer were made by the same person to avoid variation arising from individual differences in visual acuity. Finally, mule deer are known to seek steep topography in the presence of predators (e.g., Lingle 2002), so it is important to note that ruggedness did not vary with distance from the townsite along our survey routes.

Behavioral response of deer to coyote urine

In summer 2011, we placed a feed block (Purina Mills, St. Louis, MO, USA) at each of two locations near the townsite (there was no other feeding of deer during our study). Observations near dawn and dusk at a feed block began 2 days after deer discovered it. Thereafter, blocks were covered and unavailable to deer except during observations. At the start of each observation, we placed next to the block a 10-cm diameter Petri dish containing 10 mL of Terra-sorb hydrogel (Garden Harvest Supply, Berne, IN, USA) and 15 mL of either deionized water or coyote urine (PredatorPee.com). These treatments were alternated between successive 2-h observations at each site. Deer behaviors were spoken into a voice recorder, and JWatcher 1.0 (Blumstein and Daniel 2007) was used to calculate the time that each individual deer (identified by distinctive scars or other features) spent feeding during the first minute after it had approached within 10 m of the feed block. We focused on does because few bucks approached the feed blocks, and we focused on the first minute because some bouts lasted only that long and because behaviors during this period differed the most between treatments.

Habitat and plant species preferences, and spatial distribution of preferred habitats and species

During 2011 scan samples, we recorded whether deer were sighted in open forest, open dry meadow, or wet meadow with willows. To estimate habitat preferences, we compared habitat-specific sighting frequency to that expected if deer were observed in proportion to areas of these habitats within the viewsheds of scan points or route segments. To determine if the availability of the three habitats varied with distance from the Gothic townsite, we calculated the proportion of the viewshed visible from each point or route segment that consisted of each habitat. We then regressed those proportions on distance of the scan point or segment midpoint from the nearest cabin. Mapping of viewsheds as described above ensured that detectability of deer was equivalent across habitats.

To characterize plant palatability, we sampled 15 m of line transect in summer 2005 in each of nine meadows containing blue columbine (*Aquilegia coerulea*), a plant often browsed by deer around the RMBL (personal observations). For every nongraminoid herbaceous plant (forb) that intersected the transect line, we recorded whether any shoots had been clipped by deer, using the proportion of all individuals of a species at a site with at least one clipped shoot as a measure of the intensity of deer herbivory on that species. We augmented these measures in 2010 with 18 m of line transect near the center of each of the viewsheds scanned for deer activity during that summer. We sampled these as described for 2005 transects, except that herbivory was expressed as the proportion of all shoots of intersected plants that were clipped, rather than as the proportion of individuals that had at least one shoot clipped. Clipping by deer could be distinguished from that of small rodents, which take smaller bites than deer and clip stalks much closer to the ground. Also, no transect was within 50 m of a burrow used by marmots, whose herbivory sometimes resembles that of deer, and marmots were never observed feeding near the transects. Finally, we pooled 2005 and 2010 data, and from them derived an index of palatability for each species as the mean proportion clipped across the 14 sites sampled by transects. Graminoids (grasses and sedges) are so rarely eaten by mule deer (personal observations) that we assumed their clipping rates were zero.

To see if the abundance of palatable plants varied with distance from the townsite, we established a single 50-m line transect laid out in random compass orientation in the center of each of the 24 scan-point viewsheds observed in 2011. We lowered a stiff wire “pin” every 1 m along these transects and identified all plants touched by the pin, as well as bare ground if no plant was touched. This “point intercept” method can be used to characterize canopy cover of vegetation as a whole, or of individual plant species or groups of species (Elzinga et al. 2001). We estimated overall vegetation cover by dividing the number of plant contacts by the total number of pin drops (50 per transect), the proportion of vegetation contacts that consisted of palatable forbs by dividing total forb contacts by total vegetation contacts, and the proportion of vegetation contacts that consisted of unpalatable graminoids by dividing total graminoid contacts by total vegetation contacts. Finally, we derived an index of palatability for each site by multiplying the relative cover of each species (contacts of that species divided by total vegetation contacts) times that species’ palatability.

Spatial gradients in herbivory and correlation with deer activity

We pooled data from plant transects at the nine sites sampled in 2005 and five sampled in 2010 to ask whether intensity of herbivory showed any spatial pattern. We first eliminated species with low palatability (those with <10 % of shoots clipped on average), because including them necessarily lowers the slope of any spatial trend, making it harder to detect. We also eliminated species recorded at only one site. Then, for each transect, we subtracted each remaining species’ overall mean clipping proportion in the pooled dataset from its transect-specific value. We regressed these “residuals” on the distance of each site from the nearest cabin.

As an additional assessment of spatial gradients in herbivory, in 2013 we examined deer browsing of a single highly palatable species, aspen sunflower (*Helianthella quinquenervis*). Over a 2-day period, we located 56 patches of flowering sunflowers inside and outside of the Gothic townsite. In each patch, we counted all browsed and unbrowsed flowering stalks within a circular plot of 5-m radius and regressed the proportion of stalks browsed against distance of the center of each plot from the nearest cabin.

Finally, in 2010, we estimated deer activity in the same sites that contained the 2010 plant transects. For this year, we could ask whether residual herbivory values in the transects (described above) were positively correlated with deer activity in the surrounding viewsheds.

Effects of deer herbivory on two palatable wildflower species

We estimated the impact of deer herbivory on reproduction and seedling recruitment for two additional native species, blue columbine (*A. coerulea*) and scarlet gilia (*Ipomopsis aggregata*), whose flowering stalks are frequently clipped by deer. In summer 2005, we chose three pairs of columbine plants at each of two locations, one ca. 1 km north of the townsite and one within the townsite. Plants were paired by stature and number of flower buds, and one chosen at random was caged to exclude deer but not pollinators. At the end of summer, we counted fruits on all plants and left them intact to disperse seeds. In summer 2006, we returned to locate all seedlings within 50 cm of each 2005 study plant; these plants were sufficiently isolated from one another, and seeds fall sufficiently close to the parent, that assignment to parent was unambiguous.

In 1996 and 1997, we mapped 5,324 seedlings of scarlet gilia at three sites within the Gothic townsite and followed these individuals for the next 9 years, by which time all had flowered and died or had died without flowering (for details, see Brody et al. 2007). For a subsample of about half of those that flowered, we measured the fraction that suffered deer herbivory of the single central elongating inflorescence. In 1999 and 2000, we chose 78 plants at three additional sites near the RMBL and clipped their inflorescences in a fashion that mimics deer herbivory, leaving an additional 112 plants unclipped as controls. Most of the clipped plants subsequently produced lateral inflorescences, and we could then compare their seed production to that of the controls (for details, see Sharaf and Price 2004).

Spatial and statistical analyses

A Garmin 12 GPS unit provided map locations of coyote scat, aspen sunflower patches, and deer survey points. ArcMap 10/ArcInfo software (ESRI, Redlands, CA, USA) allowed us to overlay points and viewshed/habitat boundaries onto high-resolution aerial photographs of the East River Valley and to analyze distances, viewshed areas, and habitat distributions.

We evaluated the hypothesized spatial gradient in coyote activity (Fig. 1) in two ways. For the first measure—coyote sightings near marmot colonies—we regressed total sightings per hour of observation at a colony on viewshed area for that site and distance from the nearest cabin at RMBL. Viewshed area had no effect, perhaps because it varied little among sites, so we dropped it from the model and regressed sightings per hour on distance. For the second measure—coyote scat per meter of trail—we drew isolines at increasing distances from the nearest cabins (Fig. 2) and calculated total meters of trail walked in each distance interval for 2011, 2012, and 2013. We then pooled data across summers and regressed scat per meter of trail against the midpoint of each distance interval. A chi-squared goodness-of-fit test showed whether scat numbers were proportional to m of trail walked at each distance.

To evaluate the predicted spatial gradient in deer activity (Fig. 1), we first analyzed data from 2010 and 2011 separately and then combined probabilities across the 2 years to assess the overall statistical strength of any distance effect. For each year, we did preliminary factorial ANCOVAs with all possible effects and used backwards elimination to simplify the models. To visualize any distance effect, we then took residuals from models with distance removed, and regressed the residuals on distance from the nearest cabin. In 2010, only viewshed area and distance were important and they did not interact, so we could express activity as deer seen per scan per viewshed area. In 2011, viewshed area, distance, and their interaction all were significant, so we expressed activity as residuals from a model of deer per scan as a function of viewshed area and its interaction with distance from the nearest cabin. In no case were residuals from final models heteroscedastic or non-normal.

To analyze the relationship between deer activity and herbivory (Fig. 1), we regressed residual herbivory rate, treating species residuals as nested within sites, against the site's distance from the nearest cabin. For 2010, we also had information on deer activity from scan samples in the viewshed around plant transects, and so could ask whether residual herbivory rate varied with deer activity. Again, we examined all residuals from fitted models and found no need to transform raw variables.

Results

Spatial gradients in activity of coyotes

Two different metrics indicate that coyotes avoid the Gothic townsite, as predicted (Fig. 1). First, 148 coyotes were recorded during 7,865 h of marmot observations in the East River valley over the nine summers between 2002 and 2010. Of these, 7 were seen at marmot colonies within the townsite, 39 at a colony ca. 500 m south, and 102 at four colonies 1,300−3,500 m north. Total sightings per hour increased with distance of the viewshed centroid from the nearest cabin (Fig. 3a; $F_{1,4}$=14.98, P=0.018, R^2_{adj}=0.74). Second, of 178

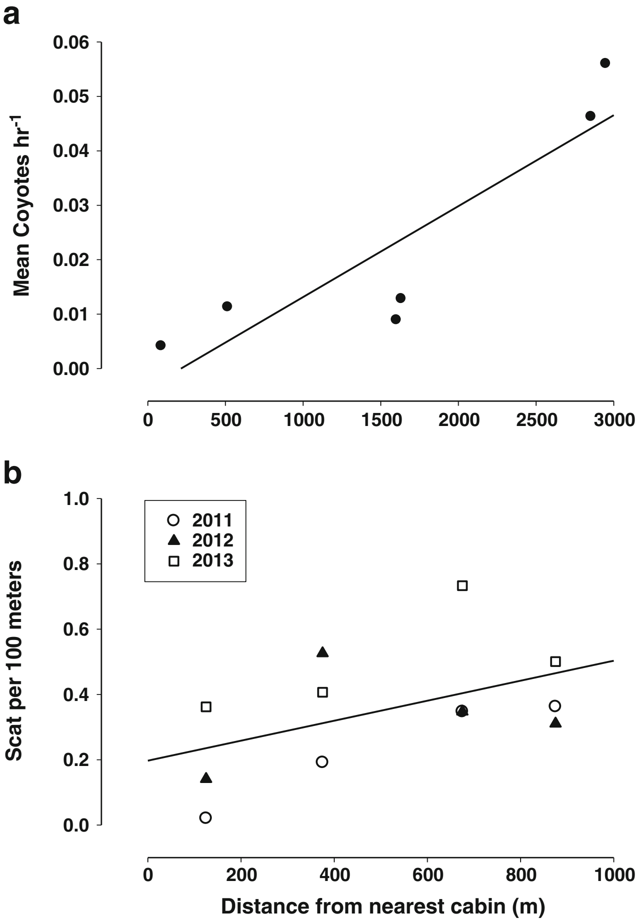

Fig. 3 Coyote activity as a function of distance from the townsite. **a** Coyote sightings at marmot colonies. **b** Distribution of coyote scats along main trails and roads in three summers. Lines are best-fit least-squares linear regressions. Predictions are for sightings and scats to increase with distance from the Gothic townsite

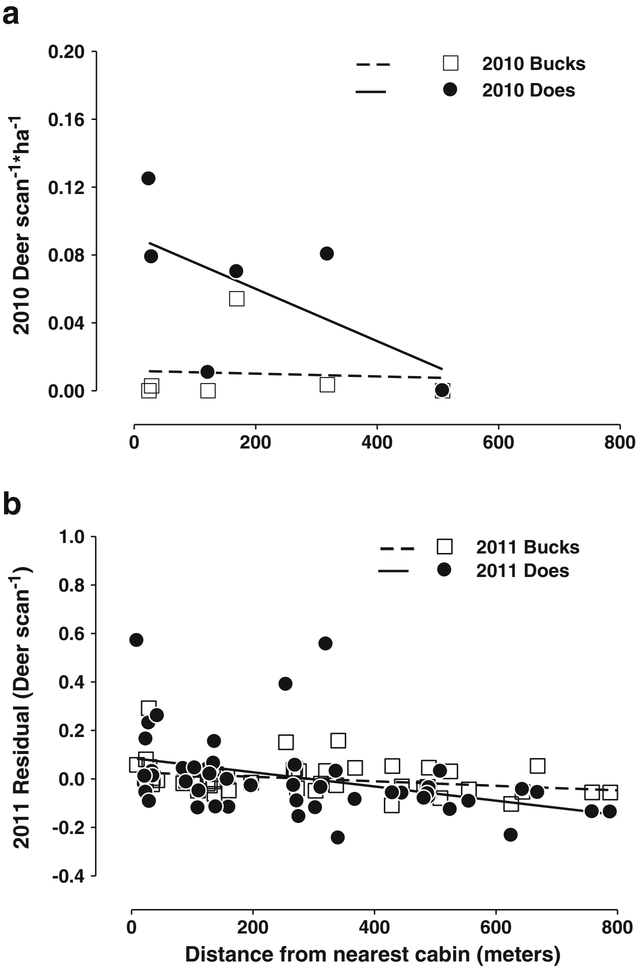

Fig. 4 Deer activity as a function of distance from the townsite. **a** 2010 surveys for does and bucks, expressed as deer seen per scan per ha of viewshed. **b** 2011 surveys, expressed as residuals from a model of deer per scan as a function of viewshed area and its interaction with distance from the nearest cabin. Predictions are for activity of does to decrease with distance from the townsite and for no strong spatial pattern in activity of bucks

coyote scats mapped in 2011, 2012, and 2013, the number per 100 m of trail increased with distance from the townsite, based on midpoints of trail segments <250, 250–500, 500–750, and >750 m from the nearest cabin (Fig. 3b; ANCOVA with year as random effect and distance as covariate, $F_{1,8}$=5.18, P=0.052 for distance effect, insignificant year × distance interaction, R^2_{adj}=0.49). There were about half as many scats <250 m from the townsite as expected from the relative lengths of trail walked at that distance vs. the others (X^2=18.13, df=3, P<0.005).

Spatial gradients in activity of deer

In contrast to coyotes, does were especially apparent in the Gothic townsite, as predicted (Fig. 1). In 2010, the number of deer observed per scan per ha of viewshed tended to decline with distance of the centroid of the viewshed from the nearest cabin ($F_{1,4}$=1.84, P=0.25, R^2_{adj}=0.14). Any trend was due entirely to does (Fig. 4a; $F_{1,4}$=2.41, P=0.20, model R^2_{adj}=0.22) rather than bucks (Fig. 4a; $F_{1,4}$=0.02, P=0.89, model R^2_{adj}=−0.24; this negative value indicates a poor model fit), as predicted. Turning to 2011, preliminary ANOVA showed that the way deer were sighted (whether during a point scan or while walking a route segment) did not influence the number seen, so we pooled point and segment sightings. Deer sightings decreased with distance of the scan point or segment midpoint to the nearest cabin and increased with viewshed area, but in contrast with 2010, the area effect was smaller at long distances ($F_{1,45}$=11.76, P<0.001 for distance; $F_{1,45}$=49.34, P<0.0001 for area; $F_{1,45}$=6.87, P<0.012 for distance × area interaction; model R^2_{adj}=0.51). Does again dominated this pattern (Fig. 4b; $F_{1,45}$=9.59, P=0.003 for distance; $F_{1,45}$=38.52, P<0.0001 for area; $F_{1,45}$=4.49, P<0.04 for distance × area interaction; model R^2_{adj}=0.45). In contrast to 2010, activity of bucks in 2011 did decline away from the townsite (Fig. 4b; $F_{1,45}$=5.15, P=0.028 for distance; $F_{1,45}$=

24.62, $P<0.0001$ for area; $F_{1,45}=5.29$, $P<0.03$ for distance× area interaction; model $R^2_{\mathrm{adj}}=0.32$). However, a difference between the sexes becomes clear when we consider results from both summers together: the overall decline in activity with distance from the townsite is highly significant for does ($X^2=16.51$, $df=4$, $P=0.002$; combined probability after (Fisher 1970, pp. 99−100)) but not for bucks ($X^2=7.38$, $df=4$, $P=0.12$).

Behavioral response of deer to coyote urine

Does were more vigilant when they encountered a stimulus that suggests coyote presence. In 58 h of observation in 2011, 22 individual does approached blocks paired with coyote urine and 9 approached blocks paired with water. Differential approach to urine ($X^2=5.45$, $df=1$, $P=0.02$) suggests investigation of a potentially important cue, and does allocated significantly less time to foraging in the first minute following their approach to blocks with urine (11.9 s on average vs. 23.5 s for deer approaching control feed blocks; $F_{1,31.02}=4.96$, $P=0.033$; linear mixed-effects model).

Habitat and plant species preferences, and spatial distribution of preferred habitats and species

Neither habitat nor food preference provides an alternative explanation for the spatial gradient in activity of does and fawns. Proportions of forest, dry meadow, and wet meadow—the three main habitats in viewsheds scanned for deer in 2011—did not vary significantly with distance from the nearest cabin (linear regressions, $P>0.75$ for each habitat type). In any case, does exhibited no strong habitat preference. Of 87 does seen in 2011, 19 (22 %) were in forest, 62 (71 %) in dry meadow, and 6 (7 %) in wet meadow. These values do not differ significantly from the representation of forest (19 %), dry meadow (68 %), and wet meadow (13 %) in 2011 viewsheds ($X^2=3.03$, $df=2$, $0.5>P>0.1$). Bucks, in contrast, preferred forest—of 29 seen in 2011, 12 (41 %) were in forest, 15 (52 %) in dry meadow, and 2 (7 %) in wet meadow ($X^2=9.65$, $df=2$, $P<0.01$).

Similarly, spatial gradients in deer activity cannot be explained by the distribution of palatable plant species. Transects taken in 2011 at each of the 24 deer survey points (Fig. 2) indicate that overall vegetation cover, proportion of vegetation hits to graminoids (grasses and sedges, which mule deer rarely eat), and proportion of vegetation hits to forbs (nongraminoid herbs, some of which they eat) did not vary significantly with distance (for total vegetation cover, graminoid proportion, and forb proportion respectively, $F_{1,22}=1.22$, $P=0.28$; model $R^2_{\mathrm{adj}}=0.01$; $F_{1,22}=1.45$, $P=0.24$; model $R^2_{\mathrm{adj}}=0.\ 019$; $F_{1,22}=1.05$, $P=0.32$; model $R^2_{\mathrm{adj}}=0.002$). The mean palatability of the forbs in each transect (species palatability values in Table 1 weighted by relative cover of each species) also did not vary with distance to the nearest cabin ($F_{1,22}=0.34$, $P=0.57$; model $R^2_{\mathrm{adj}}=-0.034$).

Table 1 Palatability of forbs (herbaceous, nongraminoid plants), indicated by overall proportions of shoots clipped for each species in pooled 2005 and 2010 transects

Species[a]	Proportion clipped
Valeriana edulis	0.75
Heuchera parvifolia	0.64
Pseudocymopteris montanus	0.50
Aquilegia coerulea	0.44
Senecio integerrimus	0.33
Agoseris sp.[b]	0.25
Helianthella quinquenervis	0.22
Valeriana occidentalis	0.19
Collomia linearis	0.14
Viola nuttallii	0.13
Epilobium angustifolium	0.12
Solidago multiradiata	0.12
Geranium richardsonii	0.10
Potentilla pulcherrima	0.07
Taraxacum officinale	0.05
Linum lewisii	0.03
Delphinium barbeyi	0.02
Lathyrus leucanthus	0.02
Pedicularus bracteosa	0.02
Ligusticum porteri	0.01

[a] Species in our samples that were never eaten were *Achillea lanulosa*, *Arnica cordifolia*, *Artemisia dranunculus*, *Aster foliaceus*, *Campanula rotundifolia*, *Castilleja sulphurea*, *Descurainea pinnata*, *Dugaldia hoopesii*, *Erigeron elatior*, *Erigeron speciosus*, *Fragaria virginiana*, *Frasera speciosa*, *Galium septentrionale*, *Geum macrophyllum*, *Heliomeris multiflora*, *Heracleum lanatum*, *Hydrophyllum fendleri*, *Lomatium dissectum*, *Lupinus argenteus*, *Mahonia repens*, *Osmorhiza occidentalis*, *Pneumonanthe parryi*, *Rosa woodsii*, *Senecio bigelovii*, *Senecio serra*, *Smilacina stellata*, *Thalictrum fendleri*, and *Vicia americana* Those that were commonly eaten but by chance were recorded only at a single one of our study sites were *Ipomopsis aggregata* and *Tragopogon pratensis*

[b] Not in flower when transects were sampled, but most likely *A. aurantiaca*

Spatial gradients in herbivory and correlation with deer activity

As predicted (Fig. 1), shoots of palatable plant species were less likely to be eaten the farther a transect was from the nearest cabin (Fig. 5a; $F_{1,78}=3.86$, $P=0.053$, $R^2_{\mathrm{adj}}=0.04$). Considerable scatter reflects the fact that we included species differing greatly in their palatability. Proportional consumption of flowering stalks of a single highly palatable species, aspen sunflower (*H. quinquenervis*), declined much more distinctly with distance from the nearest cabin in 2013 (Fig. 5b; $F_{1,55}=16.45$, $P=0.0002$, $R^2_{\mathrm{adj}}=0.22$).

We can also relate the proportion of clipped forb shoots in 2010 transects to estimates of deer activity in each transect's viewshed. As predicted, these measures are positively correlated (Fig. 6; $F_{1,26}=5.73$, $P=0.024$, $R^2_{\mathrm{adj}}=0.15$).

Effects of deer herbivory on two palatable wildflower species

Deer herbivory greatly reduced the seed production and seedling recruitment of two palatable native wildflowers. Blue columbine (*A. coerulea*) plants that were exposed to deer produced on average <30 % as many mature fruits as plants that were caged to exclude deer (least-squares means of 5.33 vs. 18.50 fruits; $F_{1,10}=10.60$, $P=0.009$). Estimating from counts of seeds per fruit vs. fruit size on plants not used in the experiment, uncaged plants produced <40 % as many seeds as caged plants (means of 990 vs. 2,563 seeds; $F_{1,10}=4.02$, $P=0.073$). These differences carried through to the next stage of the life cycle: in 2006, only 16 % as many seedlings emerged within 50 cm of columbines that were uncaged in 2005 as emerged under plants that had been caged (means of 1.0 vs. 6.1 seedlings, $F_{1,8}=12.10$, $P=0.008$, randomized-blocks ANOVA).

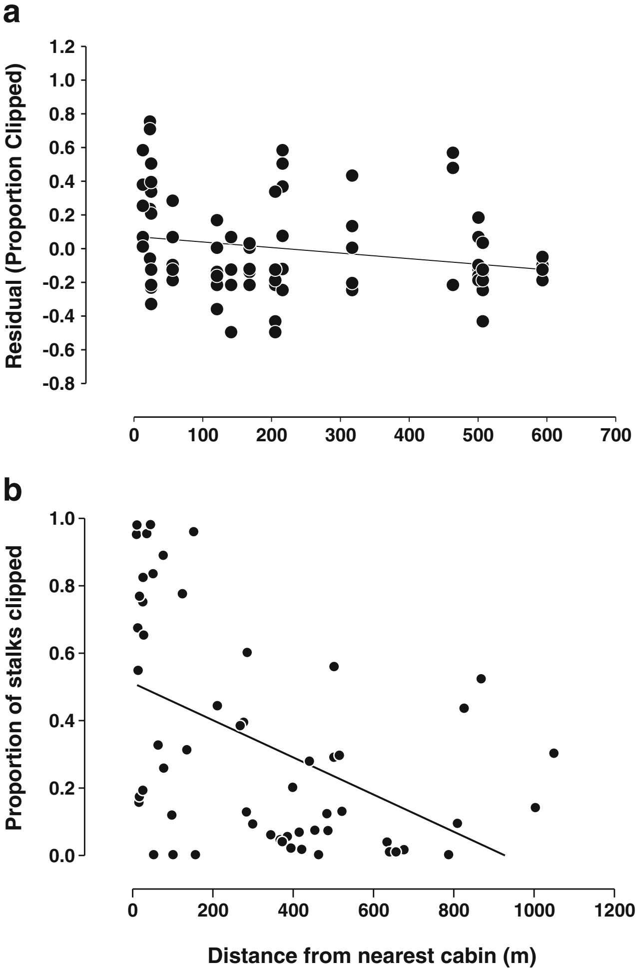

Fig. 5 Deer herbivory as a function of distance from the townsite. **a** Herbivory rate of all palatable species in 2005 and 2010, expressed as deviations (residuals) from species-specific mean clipping rates. **b** Proportion of flowering stalks clipped of the preferred species *Helianthella quinquenervis*. Predictions are for herbivory rates to decrease with distance from the townsite

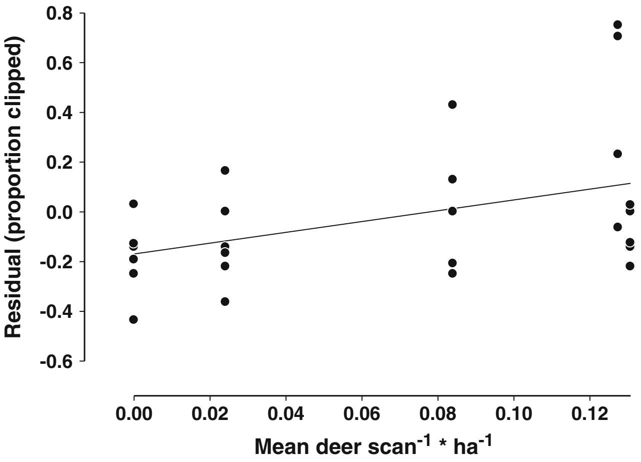

Fig. 6 Intensity of shoot clipping in 2010 plant transects as a function of deer activity in the surrounding viewshed. Herbivory is expressed as the average, over all palatable species in a transect, of residuals from a model of proportion of shoots clipped that includes species as the only independent variable (Table 1). The prediction is for a positive relationship between herbivory and deer activity

Scarlet gilia (*I. aggregata*) exhibited a similar effect (this species is not listed in Table 1 as "palatable" because by chance it occurred in only one plant transect). Our previous demographic study of two different seedling cohorts of this species in three natural populations (Brody et al. 2007) indicated that 55 % of individual plants had their inflorescences browsed by deer. We also found (Sharaf and Price 2004) that plants whose inflorescences were clipped to mimic deer damage set only 16 % as many seeds on average as unclipped plants (means of 32.9 vs. 202.6 seeds; $F_{1,182}=48.32$, $P<0.0001$). Combining these values, we estimate that deer herbivory within the townsite reduces seed set on average to only about 9 % of that in unbrowsed *I. aggregata* plants. Again, these differences should carry through into the offspring life cycle since reduced seed set in this species corresponds in a linear fashion to fewer emerging seedlings and fewer individuals surviving to reproduce (Price et al. 2008; Waser et al. 2010).

Discussion

Cascading effects of predator–prey interactions on lower trophic levels have been described less often for terrestrial ecosystems, particularly those involving large mammals, than for aquatic ecosystems (Pace et al. 1999; Schmitz et al. 2000).

This difference might derive from variation among ecosystems in attributes that affect the strength and thus detectability of cascades, such as the magnitude of compensatory food–web processes, but other explanations are possible. Many recent reviews have focused on biomass or productivity responses at the scale of whole communities, and on experimental addition or removal of top predators, as the "gold standards" of evidence for trophic cascades. Cascades can strongly affect a subset of species, however, without detectable change in overall biomass or productivity of a trophic level (Polis 1999). An emphasis on experiments, which are rarely feasible for large mammals, can unnecessarily overlook other evidence (Pace et al. 1999; Schmitz et al. 2000). We submit that alternative types of evidence often are at hand, the example here being the spatial variation in predation risk that allowed us to visualize cascade processes (see also Hebblewhite et al. 2005; Harrington and Conover 2007).

A second philosophical point is in order. We used a "case study" approach (sensu Yin 1994), gathering information on relationships among humans, coyotes, deer, and plants from a variety of studies, done at different times that explored different parts of the system and used various study designs. Because of this heterogeneity of evidence, we explored each link in the proposed trophic cascade separately (Fig. 1) and evaluated the overall hypothesis that a cascade exists by asking how consistently the results supported predicted relationships. The overall approach, as data from different sources accumulate, is to repeatedly update our assessment of the probability of the model given the totality of the data. This process is essentially "Bayesian" (Price and Billick 2010) even without a formal Bayesian statistical analysis (which was not possible in our study given the heterogeneous evidence). It is common in ecology to instead insist on a one-step approach in which a biological hypothesis such as "a coyote–deer–plant trophic cascade exists" is tested via a statistical hypothesis such as "herbivore activity and plant consumption are equal with and without carnivores," from which the resulting P value is the probability of the data given the model. But the way that humans—including infants and scientists—form an understanding of the natural world is "Bayesian" in the same sense as used above (Téglás et al. 2011), and most ecological hypotheses are in fact complex conceptual models (Price and Billick 2010) not properly evaluated by a single test. Although we did use a null hypothesis approach to explore specific parts of the cascade model, what is important is that the numerous pieces of evidence gathered over 12 summers of field work (2002–2013) consistently supported the model and did not support the alternative possibility that deer are responding to spatial gradients in preferred habitats or plant species rather than to predator distribution. In general, ecologists often accumulate diverse clues about natural phenomena, and we stress that all such information can and should be used to refine and gain confidence in our models of nature.

In exactly this spirit, several pieces of natural-history evidence suggest that antipredator behavior contributes to the gradient in doe activity away from the townsite (mortality from coyote attack may contribute as well, but we have not observed such mortality and so cannot directly assess this possibility). Of all age classes, fawns are at highest risk of mortality from coyotes (e.g., Lingle 2000; Pojar and Bowden 2004), and mule deer does choose relatively low-risk habitats in which to hide their newborn fawns (Long et al. 2009). Among these low-risk habitats are those frequented by humans or containing structures built by humans, which seemingly deter predators—an effect that Berger (2007) refers to as a "human shield." At the RMBL, the shield effect not only reduces the risk to fawns, but also may allow does to devote less time to vigilance and more to feeding in support of energetically-costly lactation. Our finding that deer investigate more and feed less when they encounter coyote urine suggests that vigilance does incur a lost opportunity cost, consistent with results from studies of other ungulates (cf. Laundré et al. 2001 and references therein; Conover 2007). Other work at the RMBL also suggests that deer are more likely to pay the cost of vigilance in high-risk areas. Carrasco and Blumstein (2012) found that deer in the townsite discriminate between neutral and risk-associated auditory stimuli, whereas those farther away immediately flee from either stimulus. Furthermore, deer alert to and flee from an approaching human sooner when the deer are farther from the townsite (Price et al. 2014), where coyotes are more abundant.

The wide variation among plant species in palatability, and the striking effect of deer herbivory on the demography of two highly palatable species, indicate that the primary effect of the trophic cascade could be to shift the species composition of the plant community toward unpalatable species (see also Rooney 2001; Suzuki et al. 2012). It would be logical to address this possibility by comparing the demography of palatable and unpalatable plants, and the species composition of plant communities, across a gradient in deer activity. Unfortunately, we cannot yet expect a pattern in community composition to be evident around the RMBL. Deer became common in the townsite only in the late 1980s, when the human population at RMBL reached its current self-imposed summer maximum of 160 persons. In contrast, any detectable changes in species composition of our subalpine plant communities are likely to take many decades, because almost all of the species are long-lived herbaceous perennials that do not accumulate a record of their growth history in above-ground woody tissues. Instead, their abundances change slowly, through often-sporadic seedling recruitment. Furthermore, cattle also graze the subalpine in the autumn, following the summer months in which we did the work described here. Addressing the effect of the trophic cascade on community composition will therefore require long-term monitoring with experimental exclusion of cattle as well as deer. These are challenging tasks for the future.

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References

Barrette C, Messier F (1980) Scent-marking in free-ranging coyotes, *Canis latrans*. Anim Behav 28:814–819

Beschta RL, Ripple WJ (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biol Conserv 142:2401–2414

Berger J (2007) Fear, human shields and the redistribution of prey and predators in protected areas. Biol Lett 3:620–623

Blumstein DT, Daniel JC (2007) Quantifying behavior the JWatcher way. Sinauer Associates, Sunderland, MA

Brody AK, Price MV, Waser NM (2007) Life–history consequences of vegetative damage in scarlet gilia, a monocarpic plant. Oikos 116: 975–985

Burkholder DA, Heithaus MR, Fourqurean JW, Wirsing A, Dill LA (2013) Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade? J Anim Ecol 82:1192–1202

Carrasco MF, Blumstein DT (2012) Mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot (*Marmota flaviventris*) alarm calls. Ethology 118:243–250

Conover MR (2007) Predator–prey dynamics: the role of olfaction. CRC Press, Boca Raton, FL

deVos JC Jr., Conover MR, Headrick NE (2003) Mule deer conservation: issues and management strategies. Berryman Institute Press, Utah State Univ., Provo, UT

Elzinga CL, Salzer DW, Willoughby JW, Gibbs JP (2001) Monitoring plant and animal populations. Blackwell Science, Malden, MA

Fisher RA (1970) Statistical methods for research workers, 14th edn. Hafner Press, New York

Gese EM, Rongstad OJ, Mytton WR (1989) Change in coyote movements due to military activity. J Wildlife Manag 53:334–339

George SL, Crooks KR (2006) Recreation and large mammal activity in an urban nature reserve. Biol Conserv 133:107–117

Harrington JL, Conover MR (2007) Does removing coyotes for livestock protection benefit free-ranging ungulates? J Wildlife Manag 71: 1555–1560

Hebblewhite M, White CA, Nietvelt CG, McKenzie JA, Hurd TE, Fryxell JM, Bayley SE, Paquet PC (2005) Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135–2144

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Can J Zoolog 79:1401–1409

Letnic M, Koch F, Cordon C, Crowther MS, Dickman CR (2009) Keystone effects of an alien top-predator stem extinctions of native mammals. Proc R Soc Lond B Biol Sci 276:3249–3256

Lingle S (2000) Seasonal variation in coyote feeding behaviour and mortality of white-tailed deer and mule deer. Can J Zoolog 78:85–99

Lingle S (2002) Coyote predation and habitat segregation of white-tailed deer and mule deer. Ecology 83:2037–2048

Long RA, Kie JG, Bowyer T, Hurley MA (2009) Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage. Wildlife Biol 15:288–298

Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483–488

Pojar TM, Bowden DC (2004) Neonatal mule deer survival in west-central Colorado. J Wildl Manag 68:550–560

Polis GA (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86:3–15

Price MV, Billick I (2010) Building an understanding of place. In: Billick I, Price MV (eds) The ecology of place: contributions of place-based research to ecological understanding. Univ. Chicago Press, Chicago, pp 177–183

Price MV, Campbell DR, Waser NM, Brody AK (2008) Bridging the generation gap in plants: from parental fecundity to offspring demography. Ecology 89:1596–1604

Price MV, Strombom EH, Blumstein DT (2014) Human activity affects the perception of risk by mule deer. Curr Zool (in press)

Ripple WJ, Wirsing AJ, Wilmers CC, Letnic M (2013) Widespread mesopredator effects after wolf extirpation. Biol Conserv 160:70–79

Ripple WT, Estes JC, Beschta RL, Wilmers CC, Ritchie EE, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith DW, Wallach AD, Wirsing AJ (2014) Status and ecological effect of the world's largest carnivores. Science 343:1241484

Rooney TP (2001) Deer impacts on forest ecosystems: a North American perspective. Forestry 74:2001–2008

Schmitz OJ, Hambäck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am Nat 155:141–153

Sharaf KE, Price MV (2004) Does pollination limit tolerance to browsing in *Ipomopsis aggregata*? Oecologia 138:396–404

Suzuki M, Miyashita T, Kabaya H, Ochiai K, Asada M, Kikvidze Z (2012) Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. Oikos 122: 04–110

Téglás E, Vul E, Girotto V, Gonzales M, Tenenbaum JB, Bonatti LK (2011) Pure reasoning in 12-month-old infants as probabilistic inference. Science 332:1054–1059

Waser NM, Campbell DR, Price MV, Brody AK (2010) Density-dependent demographic responses of a semelparous plant to natural variation in seed rain. Oikos 119:1929–2935

Yin RK (1994) Case study research: design and methods. Sage, Thousand Oaks