

Natural and experimental tests of trophic cascades: gray wolves and white-tailed deer in a Great Lakes forest

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Abstract Herbivores can be major drivers of environmental change, altering plant community structure and changing biodiversity through the amount and species of plants consumed. If natural predators can reduce herbivore numbers and/or alter herbivore foraging behavior, then predators may reduce herbivory on sensitive plants, and a trophic cascade will emerge. We have investigated whether gray wolves (*Canis lupus*) generate such trophic cascades by reducing white-tailed deer (*Odocoileus virginianus*) herbivory on saplings and rare forbs in a northern mesic forest (Land O' Lakes, WI). Our investigation used an experimental system of deer exclosures in areas of high and low wolf use that allowed us to examine the role that wolf predation may play in reducing deer herbivory

through direct reduction in deer numbers or indirectly through changing deer behavior. We found that in areas of high wolf use, deer were 62 % less dense, visit duration was reduced by 82 %, and percentage of time spent foraging was reduced by 43 %; in addition, the proportion of saplings browsed was nearly sevenfold less. Average maple (*Acer* spp.) sapling height and forb species richness increased 137 and 117 % in areas of high versus low wolf use, respectively. The results of the exclosure experiments revealed that the negative impacts of deer on sapling growth and forb species richness became negligible in high wolf use areas. We conclude that wolves are likely generating trophic cascades which benefit maples and rare forbs through trait-mediated effects on deer herbivory, not through direct predation kills.

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Introduction

Trophic cascades occur when the regulation of a consumer by a predator, either through killing the consumer or changing its behavior, benefits the resources of that consumer (Hairston et al. 1960; Paine 1980). Traditionally defined by the green world hypothesis, this terminology normally refers to the indirect effects of carnivores on plants through regulation of herbivores (Hairston et al. 1960; Estes et al. 2011). Trophic cascades have been detected in a diverse array of ecological systems and are especially well documented in aquatic ecosystems and systems involving insects (Shurin et al. 2002; Borer et al. 2005; Estes et al. 2011). However, manipulative experimental evaluation of top-down impacts generated by large mammals is sparse,

and this methodological bias has impeded our ability to predict when and where strong trophic cascades will occur in terrestrial systems (Schmitz et al. 2000; Shurin et al. 2002; Borer et al. 2005). A lack of focus on the mechanisms through which predators are generating cascades has also impeded these predictions (Schmitz et al. 2004).

The best described trophic cascades involving large mammalian carnivores and herbivores in terrestrial systems come from correlative natural experiments in Rocky Mountain national parks (Estes et al. 2011). Restored gray wolves (*Canis lupus*) are thought to be generating measurable benefits to aspen (*Populus tremuloides*) at these locations through a combination of lethal and behavioral top-down impacts on elk (*Cervus canadensis*), a large herbivore which inhibits the growth and recruitment of this tree species (Ripple et al. 2001; Hebblewhite et al. 2005; Painter et al. 2014). Earlier research at another national park colonized by wolves, Isle Royale, also found evidence suggesting a trophic cascade. Here, wolf-induced declines in moose (*Alces alces*) populations led to an increase in balsam fir (*Abies balsamea*) growth (McLaren and Peterson 1994), although it should be noted that the effect varied considerably with winter severity and other exogenous random events (Peterson et al. 2014). There is also a long history of exclosure experiments documenting negative ungulate impacts on plant growth in African savannas, as well as of predator removals which led to increases in many African ungulate species (Sinclair et al. 2010). However, to our knowledge, this latter cascade has not been directly tested.

It is also important to note that predators can produce trophic cascades in two different ways. A density-mediated trophic cascade occurs when predators benefit plants via direct regulation of herbivore numbers (i.e., kills) (Hairston et al. 1960; Polis and Strong 1996; Werner and Peacor 2003). Numerous studies have documented density-mediated cascades in various ecosystems (Estes and Palmisan 1974; Paine 1980; Carpenter et al. 2001; Hebblewhite et al. 2005). A trait-mediated cascade can develop when predators induce anti-predator (fear) responses in their prey, including spatial and temporal avoidance, increased movement, and increased vigilance (Abrams 1995; Lima and Dill 1990; Werner and Peacor 2003; Schmitz 2008). While these responses reduce individual predation risk, they come at the cost of foraging opportunities, which indirectly benefits plants (Abrams 1995; Werner and Peacor 2003). Importantly, recent reviews suggest that trait-mediated effects should produce stronger trophic cascades than density-mediated effects, with the rationale being that trait-mediated effects reduce herbivory by the entire group, whereas density-mediated effects only reduce herbivory by killed individuals (Schmitz et al. 2004; Schmitz 2005; Preisser et al. 2005, 2007).

With respect to cascades generated by large mammalian predators, the evidence appears to support density-mediation as the primary driver, not trait-mediation (McLaren and Peterson 1994; Hebblewhite et al. 2005; Hebblewhite and Smith 2010; Kauffman et al. 2010; Sinclair et al. 2010; Painter et al. 2015). For example, Rocky Mountain wolves have substantially reduced elk numbers (Hebblewhite and Smith 2010) and altered elk movements and foraging behavior (Laundré et al. 2001; Childress and Lung 2003; Fortin et al. 2005), but research suggests the trait-mediated effects on movement and foraging are too weak to drive the observed trophic cascades (Creel et al. 2008; Hebblewhite and Smith 2010; Kauffman et al. 2010).

This is not to say that large mammalian predators, such as wolves, cannot produce trait-mediated trophic cascades elsewhere. The strength of trait-mediated trophic cascades is inherently dependent on ecosystem-specific characteristics, such as plant composition and structure (Trussell et al. 2006) as well as species behavior (Schmitz 2005; Preisser et al. 2007). Ungulates in North American and African systems have been shown to increase vigilance in areas of low visibility (e.g., dense forest) or, alternatively, avoid them in favor of areas of high visibility (e.g., open rangeland) (Underwood 1982; Kunkel and Pletscher 2001; Valeix et al. 2009). Wolves also switch behavior based on habitat visibility and prey size (Peterson and Cucci 2003). Wolves in relatively high-visibility Rocky Mountain systems with large elk as prey act as roaming chase predators (Creel et al. 2008), whereas wolves in low-visibility forest systems with smaller deer species as prey act as ambush predators (Kunkel and Pletscher 2001; Peterson and Cucci 2003). Similar to low visibility, the ambush strategy reduces the ability of prey to detect the predator from a safe distance and likewise produces stronger trait-mediated effects (Preisser et al. 2007; Schmitz 2008). Tests of trophic cascades in other ecosystems using similar measures are thus necessary to assess the generality of the Rocky Mountain findings (Pace et al. 1999; Creel et al. 2008).

Great Lakes forests represent a good experimental system for performing such an assessment. White-tailed deer (*Odocoileus virginianus*) numbers in this region dramatically increased in the absence of gray wolf predation, and the subsequent increased deer herbivory has had significant negative impacts on forest sapling growth and forb biodiversity (Anderson and Loucks 1979; Alverson et al. 1988; Augustine and Frelich 1998; Rooney and Waller 2003; Côte et al. 2004; White 2012). Density-mediated effects following wolf recolonization also appear to be weak or non-existent in these mainland forests (DeGiudice et al. 2009; Rooney and Anderson 2009), marking a stark contrast with the Rocky Mountain, Isle Royale, and African savanna systems.

Based on (1) documented negative impacts of deer on forest plants, (2) observed changes in deer distributions in relation to wolf territories (Mech 1977), and (3) the lack of a substantial decline in Great Lakes deer numbers (DeGiudice et al. 2009), we hypothesized that recolonizing wolves are generating trait-mediated cascades in Great Lakes forests (Rooney and Anderson 2009; Callan et al. 2013). Also, given that trait-mediated effects should be stronger in low-visibility systems with ambush predators (Underwood 1982; Kunkel and Pletscher 2001; Preisser et al. 2007; Schmitz 2008) and that trait-mediated effects are expected to produce stronger trophic cascades than density-mediated effects (Schmitz et al. 2004; Schmitz 2005; Preisser et al. 2005, 2007), we also hypothesized that Great Lakes cascades will be stronger than Rocky Mountain cascades in order to assess any differences between these systems.

The aims of this study were to quantify deer herbivory impacts and determine if these impacts differ in relation to wolf use. We first surveyed and compared sapling growth and forb richness in relation to wolf use, then used a network of deer exclosures in areas of high and low wolf use, respectively, to experimentally isolate and quantify deer impacts. This manipulative experiment is crucial because experimental support for wolf-generated trophic cascades is lacking, leaving previous study conclusions open to question (Kauffman et al. 2010). We also monitored the density and behavior of deer in both areas of high and low wolf use to determine if there is evidence for wolf density-mediated and/or trait-mediated effects at the scale where species interactions occur. Finally, we quantified the size of the effects and compared them with Rocky Mountain cascades.

Study area and methods

Study area

Our study took place at the University of Notre Dame Environmental Research Center (UNDERC), which is an approximately 3200-ha property located along the Wisconsin/Michigan border (46°13'N, 89°31'W). The terrestrial habitat is a complex mosaic of northern mesic forest patches scattered among bogs and conifer swamps. A mix of two deciduous species, sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*), dominates the forest canopy and understory. Balsam fir, a species which deer avoid consuming, is the dominant conifer. Maples represent the overwhelming majority of available saplings preferred for consumption by deer, while balsam fir represents the vast majority of non-preferred saplings (>90 and >70 %, respectively, based on unpublished plot data). Forb communities are largely dominated by Canada mayflower

(*Maianthemum canadense*) or Canadian bunchberry (*Cornus canadensis*), with scattered dense layers of ferns and graminoids. Deer in this region often remove rarer forbs, such as bluebead lily (*Clintonia borealis*) and Solomon's seal (*Polygonatum* spp.) (Rooney and Anderson 2009).

White-tailed deer are effectively the only ungulate in the study area. Current local deer management unit densities are 7–12 km⁻² (B.J. Dhuey, unpublished data of the Wisconsin Department of Natural Resources). This is substantially higher than pre-European settlement densities of ≤ 4 km⁻², which were maintained by natural predation, unfavorable dense forest habitat, and hunting by Native Americans. Starting in the 1850s, the creation of favorable deer habitat (opening of forests by logging), removal of predators, and protective hunting laws led to sharp rises in the deer population in this region (Alverson et al. 1988; Ripple et al. 2010). Gray wolves are the natural top predator of Great Lakes deer (Mech and Karns 1977), but targeted hunting activities by humans resulted in their complete disappearance from the UNDERC area by the late 1950s (Thiel 1993), and they remained extinct locally for 40–50 years. Michigan Department of Natural Resources wolf monitoring data and local observations indicate that a new pack established a territory which bisects UNDERC around 2002–2006. Additional packs use surrounding areas, but not UNDERC (B. Roell, unpublished Michigan Department of Natural Resources data; Wydeven et al. 2009; Callan et al. 2013). Recent numbers suggest there are about three to five wolves per 1000 deer in this region (Wydeven et al. 2009).

Isle Royale is less than 200 km from UNDERC, but it is a much different system (i.e., island, wolf–moose–fir) and has been subject to very complex temporal variation over several decades of study, making it difficult to draw direct comparisons to other systems (Peterson et al. 2014).

Wolf use

It should be noted this is not a study of wolf behavior; due to reasons beyond our control, we had only one pack to study at UNDERC. However, we employed the variable use of the area by the pack (high vs. low visitation) as a treatment effect on the deer (risk of predation). We defined the risk of predation to be high in a high wolf use area and to be low in a low wolf use area. High wolf use areas are largely within wolf territories, and low wolf use areas are outside of territories or within avoided buffer zones (Mech 1977). In collaboration with the Michigan Department of Natural Resources, we equipped three members of the pack with GPS/ARGOS collars (Lotek Wireless, Newmarket, ON) in 2010 to examine use of the UNDERC property by wolves. We estimated high wolf use areas to be within a boundary line containing 95 % of GPS collar fixes located

on or within 600 m of UNDERC property (excluding outliers). We used this approach instead of a minimum convex polygon because polygons overestimate areas (Powell 2012).

We also carried out scat surveys along all accessible UNDERC gravel roads (>37 km, usually once per week) from May through October 2008 and 2010–2013 (including accumulated overwinter scats preserved by cold) in order to obtain additional evidence in support of these collar-based area designations. Any other evidence of wolf use (scrapes, tracks, sightings, etc.) was collected and pooled these with scats, with each observation treated as a single wolf sign point (Elbroch 2003; Gese 2004). Because we did not remove wolf scats, GPS locations were recorded for individual points and were used (along with sign age/condition) to avoid re-counting. We mapped GPS collar and wolf sign locations manually in Google Earth v. 7.1.1.1888 (Google Inc., Mountain View, CA). All of the wolf work was conducted following the conditions established in University of Notre Dame Institutional Animal Care and Use Committee protocols 12-009, 15-015, and 15-022 and followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Site selection and enclosure construction

We selected ten northern mesic forest patches for enclosure construction in 2009 and included two additional patches as study sites in 2011. These sites (average distance to nearest neighbor >1 km) were distributed evenly among high and low wolf use areas throughout UNDERC and consisted of 10 × 10-m paired control (open) and experimental (enclosed to prevent deer feeding) plots. At each site, the paired enclosure and control plot were adjacent (<10 m apart) so that forest conditions were as similar as possible. We constructed 12 × 12-m enclosures around the experimental plots out of 2.4-m high polypropylene mesh fencing (Deerbusters, Frederick, MD). This allowed for a 1-m buffer around the plot to prevent unwanted fence effects and provide a walkway for researchers. To exclude only deer, we cut 0.2 × 0.2-m holes into the bottom of the fencing to allow entry by smaller herbivores and predators.

Deer responses

We monitored deer activity on five high and five low wolf use plots (controls) using ten motion-activated, infrared-flash camera traps (Bushnell, Overland Park, KS). Cameras were deployed for 3 weeks, spanning June–August 2012, which is an adequate period of time for a seasonal white-tailed deer survey (Jacobson et al. 1997). Cameras had an effective capture and trigger range of 12–15 m, which allowed for clear, differentiable photography of deer

behavior within the plots at all hours of the day (color) and night (infrared). Three time-stamped images per trigger (10-s delays between triggers) were taken. We used images of single deer visits as an index of deer density (Augustine and Frelich 1998; Altendorf et al. 2001). As an index of movement we used the duration of individual visits (time elapsed between first and last image of an individual). We considered a deer to be foraging when images showed the head in a down position. The proportion of images indicating foraging (head down) was used as an index of foraging time within the deer activity budget (Altendorf et al. 2001). Images per site were lumped as one summer of data.

Plant responses

We recorded the height of all saplings in each plot annually in August (2009–2012) in order to track changes in growth. A sapling was classified as an individual with a height of 25–240 cm. Those individuals with a height of <25 cm were either new seedlings or unavailable to deer during the previous winter (snow cover), and young trees which exceeded a height of >240 cm (enclosure height) have grown beyond the reach of deer and are part of the subcanopy. We also recorded woody browse damage on all saplings. Damage by deer (rough cuts) was differentiated from that by snowshoe hare (*Lepus americanus*; angular cuts). We also established 20 random 1 × 1-m subplots in each of the deer experimental and control plots in 2010 to monitor forb community characteristics. We surveyed these subplots each August, and the number of forb species present (pooled per plot) was used to estimate species richness.

Statistical analyses

To confirm that wolf use was statistically different between high and low wolf use areas, we compared the number of collar fixes within 600 m of enclosure sites using a Mann–Whitney *U* test. As an additional test, we also compared the distribution of all wolf sign data (scat and other use data pooled) between high and low wolf use areas using a chi-square test. The chi-square test was corrected for differences in road area between high (approx. 14.6 km) and low (approx. 22.7 km) wolf use areas. Differences in average frequency of deer use, visit duration (square-root transformed), percentage of activity spent foraging, and the percentage of browsed saplings (logit transformed) between high and low wolf use areas were examined using Student's *t* tests.

We quantified deer herbivory impacts on sapling growth and forb species richness using log response ratios [$\text{Log}(\text{Exc}_x/\text{Con}_x)$], where Exc_x represents the plant value for an enclosure plot x , and Con_x represents the value for its

adjacent control plot] and then analyzed whether wolf use significantly affected these impacts using a multi-way repeated measures analysis of variance (ANOVA), with wolf use and year as factors. In the case of a significant interaction, we used one-way repeated measures ANOVAs to see if there were significant changes over time in each wolf use category separately. The log response ratio is commonly used in enclosure/cascade studies as a measure of effect size because it reflects the proportional change resulting from the experimental manipulation (Hedges et al. 1999; Schmitz et al. 2000; Hebblewhite et al. 2005; Preisser et al. 2005; Rooney 2009). It is also preferred over the normal response ratio because the log ratio is affected equally by changes in the denominator or numerator, while the normal ratio is affected more by changes in the denominator (Hedges et al. 1999). Positive values indicate higher enclosure values than matched controls, while negative values indicate lower enclosure values.

We also wanted to compare our study results to those of previous wolf trophic cascade studies performed in the much different Rocky Mountain systems. Unfortunately, there were no comparable studies which used a dichotomous high versus low wolf use comparison and enclosures. Most Rocky Mountain studies have used either gradients of wolf use or pre-wolf reintroduction versus post-wolf reintroduction comparisons (Kauffman et al. 2010; Hebblewhite and Smith 2010). Therefore, our selection was limited to two studies which used the comparison of high and low wolf use areas and measures of similar plant characteristics. The first was the study by Ripple et al. (2001) which looked at a wolf–elk–aspen system in Yellowstone National Park (Wyoming, USA), and the second was the study by Hebblewhite et al. (2005) which looked at a wolf–elk–aspen system in Banff National Park (Alberta, Canada). In order to compare our system with the systems of these studies, we performed additional tests to compare average sapling height and the number of 100-cm size class saplings in 2012 between high and low wolf use control plots. Saplings in the 100-cm size class were limited to individuals established during wolf recolonization (diameter at breast height <2.5 cm based on Lessard et al. 2001 and unpublished data). We used Student's *t* tests for these comparisons, or Mann–Whitney *U* tests if residuals were non-normal. We also calculated effect sizes (log response ratios) for these as well as deer density, visit duration, foraging allotment, and percentage saplings browsed for non-statistical side-by-side comparison. Foraging allotment was compared with high versus low wolf use results from a wolf–elk study in Yellowstone National Park (Childress and Lung 2003).

We also compared 2012 maple sapling density (square-root transformed), maple relative abundance, and forb species richness on control plots using Student's *t* tests

in order to see whether there were substantial differences between high and low wolf use areas. The comparison of forb species richness allowed us to assess whether our data would support the results of a previous study by Callan et al. (2013) which found significant increases in forb species richness upon the re-occupation of sites in Great Lakes forests by wolves for 8–10 years.

Results

Wolf use

Analysis of GPS telemetry and wolf sign data verified that experimental sites differed in terms of wolf use. Based on GPS collar telemetry points, wolves were in the vicinity (600 m) of high wolf sites 24-fold more frequently than in the vicinity of low wolf sites [$\bar{x} \pm$ standard error: 4 ± 1.21 vs. 0.17 ± 0.17 fixes, respectively; $U = 3.5$, $df = 10$, $P = 0.013$] [Electronic Supplementary Material (ESM) 1]. The distribution of 130 wolf sign observations also corroborated the GPS collar location distribution, with 95 % of wolf sign observations ($df = 1$, $\chi^2 = 169.020$, $P < 0.001$; annual range of 92–98 %) being within high wolf use areas.

Deer responses

Deer exhibited very different behavior in areas of high and low wolf use, respectively. Deer visited high wolf use plots less frequently than they did low wolf use plots (1.00 ± 0.47 vs. 2.60 ± 0.60 visits per week; $t = -2.096$, $df = 8$, $P = 0.035$) (Fig. 1a), and the duration of the visits to high wolf use areas was shorter (36.0 ± 23.0 vs. 197 ± 85.0 s; $t = -2.228$, $df = 8$, $P = 0.028$) (Fig. 1b). Deer also spent a lesser proportion of their time foraging in high wolf use areas (32.7 ± 11.4 vs. 57.0 ± 3.7 %; $t = -2.5065$, $df = 6$, $P = 0.023$) (Fig. 1c).

Sapling characteristics and responses

In this study, we selected the most common deer-preferred sapling species (maple, *Acer* spp.; >90 % of preferred saplings) to perform our analyses in order to avoid comparing plant species with different inherent growth rates and deer palatability. Maple sapling density was not significantly different between the areas of high and low wolf use (3.31 ± 1.34 vs. 1.68 ± 1.27 m⁻², respectively, square-root transformed; $t = 1.1164$, $df = 10$, $P = 0.290$) (ESM 2a); relative abundance of maple saplings (ESM 2b) was also not significantly different (62.2 ± 13.5 vs. 66.2 ± 15.8 %, respectively; $t = -0.1891$, $df = 10$, $P = 0.854$). Per plot, deer browsed a substantially higher proportion of all maple saplings in low wolf use areas (49.7 ± 12.1 vs.

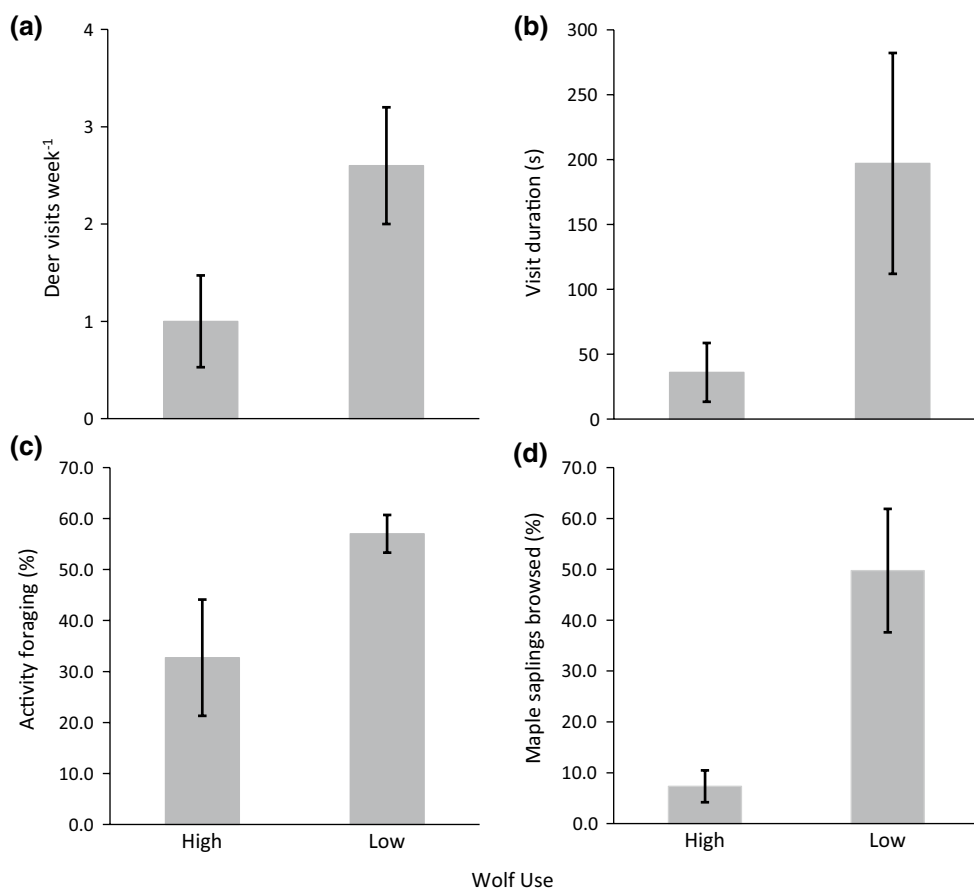


Fig. 1 Impacts of wolf (*Canis lupus*) activity on white-tailed deer (*Odocoileus virginianus*) on visit frequency (a), visit duration (b), foraging activity budget (c), and browse damage to maple (*Acer* spp.) (d). Data were collected from University of Notre Dame Envi-

ronmental Research Center (UNDERC) control plots in 2012 using camera trap images (a–c) or sapling surveys (d) of these plots. Bars: mean \pm standard error (SE). $n = 10$ (a), 10 (b), 8 (c), 12 (d)

7.3 ± 3.1 %, logit transformed; $t = -2.9075$, $df = 10$, $P = 0.008$) (Fig. 1d).

We limited analyses of maple sapling growth and forb diversity (see subsection “**Forb responses**”) using enclosure plot data for enclosures built in 2009 to maintain a constant exclusion time among plots. The impact of deer herbivory on average maple sapling height differed significantly between areas of high and low wolf use ($F_{1,8} = 13.32$, $P = 0.006$) and years ($F_{3,24} = 5.48$, $P = 0.005$). The interaction of these two factors was also significant ($F_{3,24} = 6.18$, $P = 0.003$) (Fig. 2a). In the low wolf use plots, the response ratio increased by twofold from 2009 to 2012, indicating that maple saplings grew substantially taller when protected from deer browse by deer enclosures (one-way ANOVA $F_{3,12} = 4.08$, $P = 0.033$). However, enclosures did not provide any significant benefit to maple sapling growth in high wolf use areas, where the response ratio remained statistically unchanged (total decline of <3.6 %) from 2009 to 2012 (one-way ANOVA $F_{3,12} = 1.62$, $P = 0.236$). However, this pattern was not observed for the

sapling species that deer do not prefer to consume (balsam fir, *Prunus serotina*, *Picea* spp., etc.). Log response ratios for non-preferred saplings were not significantly different based on wolf use ($F_{1,8} = 0.001$, $P = 0.976$), year ($F_{3,24} = 0.914$, $P = 0.449$), or the wolf \times year interaction ($F_{3,24} = 0.210$, $P = 0.888$) (Fig. 2b).

Post-hoc comparisons showed significant differences in maple sapling growth between high and low wolf use areas. Average maple sapling height (Fig. 2c) was approximately 70.6 ± 10.0 cm in high wolf use areas and approximately $30.1 \text{ cm} \pm 1.5$ cm in low wolf use areas ($t = 6.051$, $df = 10$, $P < 0.001$). In addition, significantly more saplings were recruited to the 100-cm size class in high wolf use areas than in low wolf use areas (38.2 ± 17.8 vs. 1.3 ± 0.80 , respectively; $U = 1.5$, $df = 10$, $P = 0.005$) (Fig. 2d).

Forb responses

The impact of deer herbivory on forb species richness was also significantly affected by wolf use ($F_{1,8} = 6.636$,

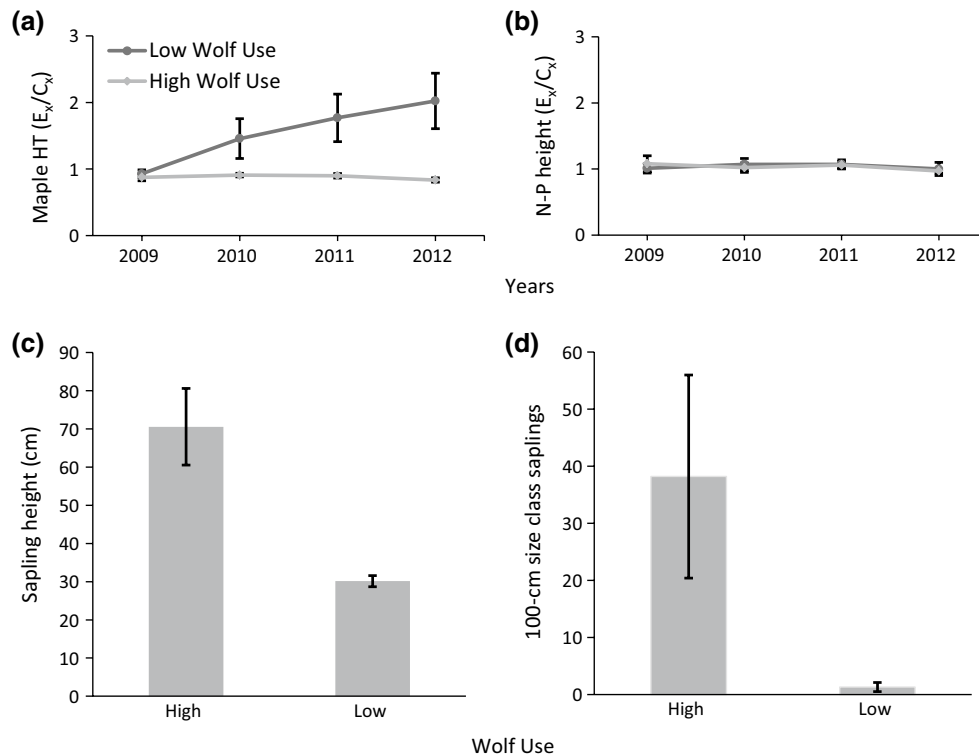


Fig. 2 Results of experiments comparing deer impacts on areas of high and low wolf use on maple sapling height (a), non-preferred (N-P) sapling height (b), and natural survey design tests (c, d) comparing maple sapling height (2012) (c) and 100-cm size class maple

sapling abundance (d). The response ratios (E_x/C_x ; see section “Statistical analyses” for explanation of E_x/C_x and Con_x ratio) and non-transformed data are shown. Values are the mean \pm SE ($n = 10$)

$P = 0.033$), but not year ($F_{2,16} = 1.418$, $P = 0.271$). There was no significant interaction between these two variables ($F_{2,16} = 0.800$, $P = 0.466$) (Fig. 3a). Average forb species richness increased by 38–110 % in exclosures in low wolf use sites while it was equivalent (SE within a ratio of 1) between exclosures and controls in high wolf use areas. Post-hoc comparisons between high and low wolf use control plots showed that forb species richness (Fig. 3b) was significantly greater in high wolf use areas than low wolf use areas (7.2 ± 0.83 vs. 4.0 ± 0.68 ; $t = 2.939$, $df = 10$, $P = 0.007$).

Discussion

The density and behavior of UNDERC deer in high wolf use areas were significantly different from those of UNDERC deer in low wolf use areas. Deer density, visit duration, and foraging time allocation were lower by 62 %, 82 %, and 43 % on high wolf use plots compared to low wolf use plots. These differences in deer density and behavior result in different impacts on plants. The proportion of saplings browsed in high wolf use areas was also lower—by 85 %. In addition, in high wolf use areas average maple

sapling height more than doubled, forb species richness nearly doubled, and recruitment of maples was 24-fold higher. Comparisons of paired experimental and control plots suggested that the presence of deer in low wolf use areas had negative impacts on maple sapling growth and forb biodiversity. Conversely, in high wolf use areas, deer impacts on maple sapling growth and forb diversity were negligible. Taken together, these results suggest that wolves have substantial effects on white-tailed deer and also positively impact maple sapling growth and forb biodiversity as a result.

Our results support previous research which suggested that wolves have density- and/or trait-mediated effects on white-tailed deer (Mech 1977; Mech and Karns 1977). They also provide manipulative experimental support for previous natural experiments which suggest wolves can generate trophic cascades affecting sapling recruitment in various regions (McLaren and Peterson 1994; Ripple et al. 2001; Hebblewhite et al. 2005) and forb species richness in the Great Lakes forests (Callan et al. 2013).

However, there are other possible factors, such as differences in abiotic characteristics, which could lead to similar plant results regardless of top-down interactions (Hebblewhite and Smith 2010; Kauffman et al. 2010).

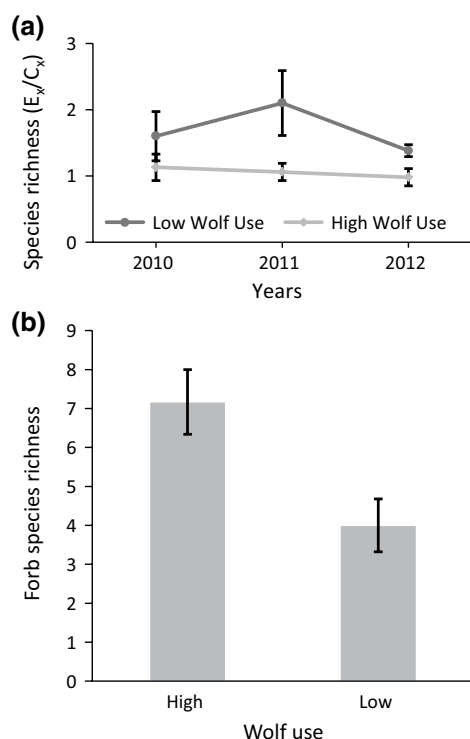


Fig. 3 Comparison of forb species richness between high- and low-wolf use areas using Exc_x/Con_x response ratios (E_x/C_x ; **a**) and control plot values (2012) (**b**). Values are the mean \pm SE ($n = 10$)

Table 1 Comparison of effect sizes among Yellowstone National Park (Wyoming, USA), Banff National Park (Alberta, Canada), and UNDERC (Wisconsin/Michigan, USA)

Wolf Impact	Yellowstone NP	Banff NP	UNDERC
Ungulates			
Density/use	-0.75*** ^a	-2.28*** ^c	-0.96*
Visit duration (s)	NA	NA	-1.70*
Foraging allotment	-0.08 ^b *	NA	-0.56*
Saplings			
Percentage saplings browsed	-0.04 ^a	-0.17 ^c	-1.92**
Height (cm)	0.14 ^a	NA	0.85***
100-cm size class	NA	0.96 ^c	3.38**

Effect sizes are presented as the log response ratio (LRR): $[\ln(\text{High Wolf}_x/\text{Low Wolf}_x)]$. Values for Yellowstone and Banff were taken from published studies with similar designs to the research reported here

NA not available

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

^a Data source: Ripple et al. (2001)

^b Data source: Childress and Lung (2003)

^c Data source: Hebblewhite et al. (2005)

We attempted to address some of these concerns by also analyzing sapling species which deer do not readily consume (i.e., non-preferred). Non-preferred plant species should not be strongly affected by changes in deer herbivory (White 2012), but they should react to confounding factors. Our observed lack of a significant difference in non-preferred sapling growth does not support the alternative hypothesis that factors other than wolf–deer interactions are responsible for the observed differences in maple and thus further supports the wolf–deer trophic cascade hypothesis. Meanwhile, given the short duration of both our experiment and wolf occupancy at UNDERC, the lack of significant differences in maple sapling density and relative abundance should be expected as maple saplings can survive repeated damage due to deer browsing over several years (albeit as short, stunted individuals) (Anderson and Loucks 1979).

Differing escape impediment levels, visibilities, and slopes could also explain our behavioral results (Underwood 1982; Kunkel and Pletscher 2001; Ripple and Beschta 2007; Valeix et al. 2009; Ripple et al. 2010). However, there was little difference in visibility as all of our UNDERC sites are densely forested, escape impediments (i.e., downed logs) were also relatively equivalent at all sites, and the terrain lacks the sharp contrasts in elevation seen in the Rocky Mountain elk behavior studies. Furthermore, a recent study using camera traps to record red deer (*Cervus elaphus*) behavior in control and experimental areas (where researchers placed fresh wolf scats) suggests that the olfactory cues of wolves are sufficiently strong to greatly increase deer vigilance (Kuijper et al. 2014). These results are in line with our scat distribution and deer behavior observations.

Great Lakes population patterns also suggest that any recent wolf cascade would have to be trait-mediated, not density-mediated (Rooney and Anderson 2009). Based on an average density of 28–36 wolves per 1000 km² (Beyer et al. 2009; Wydeven et al. 2009) and 7000–12,000 deer per 1000 km² (B.J. Dhuey, Wisconsin Department of Natural Resources data), as well as a wolf kill rate of 15–19 deer per wolf per year (Mech and Peterson 2003), wolves should be directly killing <10 % of available deer per year in this region. However, our observed reductions of deer use and sapling browse damage in high wolf use areas were multiple fold greater than 10 %, further supporting the potential importance of trait-mediated effects at UNDERC. Furthermore, regional deer numbers have been fairly stable since 1989 (DelGiudice et al. 2009), at which time the combined Michigan and Wisconsin population of wolves was <40 animals (Beyer et al. 2009; Wydeven et al. 2009).

In our study, the combined density-mediated and trait-mediated effects of the carnivore on the herbivore appear to be stronger than the effect of the carnivore on plant biomass (i.e., growth), which is consistent with the results of previous trophic cascade studies (Schmitz et al. 2000; Shurin et al. 2002, Table 1). Effect sizes of the carnivore on herbivore density, plant damage, and plant biomass are also within the respective ranges for terrestrial systems based on literature reviews. However, the effect size on biomass at UNDERC is higher than that found in most terrestrial studies conducted to date (Schmitz et al. 2000; Shurin et al. 2002; Hebblewhite and Smith 2010).

The differences in response strengths between wolf–ungulate studies also further highlight the variability of these direct and indirect effects. The effect sizes of wolves on saplings in our study system appear to be much stronger than those reported in comparable Rocky Mountain wolf–ungulate studies (see Table 1). We suspect that this difference is due, at least in part, to differing strengths of density- and trait-mediated effects in each system. Strong trait-mediated effects are expected to generate much stronger cascades than strong density-mediated effects. Trait-mediated effects reduce herbivory by all prey at risk, whereas density-mediated effects only eliminate herbivory by killed individuals (Schmitz et al. 2004; Preisser et al. 2005). Recent evidence suggests that density-mediated effects are quite strong in the Rockies (Kauffman et al. 2010; Hebblewhite and Smith 2010), while trait-mediated effects are weak (Creel et al. 2008; Kauffman et al. 2010) and may only explain plant growth variation within the same areas (Painter et al. 2014, 2015). Conversely, the declines in deer numbers due to wolf predation in the Great Lakes region are not nearly as large as those found for elk in the Rocky Mountain region (DelGiudice et al. 2009). However, our study suggests that wolves generate strong trait-mediated effects on UNDERC deer, and these trait-mediated effects appear to be stronger than those in the Rockies (see Table 1).

We suggest the strengths of the trait-mediated effects may be greater at UNDERC due to differences in behavior. Trait-mediated effect strength varies by predator hunting strategy (Preisser et al. 2007), and wolves switch hunting strategies based on prey size and habitat (Peterson and Cucci 2003). Active (search and chase) predators are expected to produce much weaker responses than ambush predators because active predators are more easily detected from a safe distance (Preisser et al. 2007; Creel et al. 2008; Schmitz 2008). Herding also helps prey detect predators (Dehn 1990). Wolves roam and chase herds of large elk through open ranges and pick out susceptible animals, whereas wolves hunting smaller deer in dense forests sneak up and ambush individuals (Kunkel and Pletscher 2001; Peterson and Cucci 2003). Thus, wolves should be

expected to generate stronger trait-mediated effects when hunting deer than when hunting elk.

An alternative hypothesis is that differences in time since wolf recovery could explain stronger cascading effects (Callan et al. 2013). The length of time after wolf recovery was indeed shorter in the Yellowstone studies (4 years in Ripple et al. 2001, 3–6 years in Childress and Lung 2003) than in our study (6–10 years). However, we also saw stronger effects at UNDERC than those observed at Banff National Park, where the recovery of wolves was longer (11–13 years). Comparison with more recent studies conducted at Yellowstone (Painter et al. 2014, 2015; 17 years post-wolf recovery) still show fivefold greater browse intensities by a sharply reduced elk population than that observed in UNDERC deer in high wolf use areas. Therefore, we propose that differences in wolf exposure time cannot fully explain observed differences in effect size between the Rockies and UNDERC.

Researchers have questioned some conclusions of past wolf–ungulate–plant studies in other systems because the use of natural experimental designs makes it difficult to eliminate confounding factors as alternative explanations. With respect to Yellowstone National Park, droughts, increased winter severity, and human harvest could be more important factors affecting elk declines, and varying inherent abiotic conditions (e.g., elevation, water table, etc.) among the sites there could be responsible for differences in aspen growth (Hebblewhite and Smith 2010; Kauffman et al. 2010; Peterson et al. 2014). We did our best to avoid or minimize the influence of these confounding factors. Instead of only comparing plant community characteristics between high and low wolf use areas, we designed a manipulative experimental set-up (deer exclosures) which allowed us to isolate and compare the impact of the ungulate on plants. By using a high versus low wolf use area comparison, we also avoided the confounding factors of winter severity or drought which affect pre-wolf versus post-wolf designs, as both wolf use areas should have been affected equally. Moreover, there were no obvious contrasts in abiotic conditions between high and low wolf use areas. Deer harvest in Great Lakes wolf range has also remained relatively constant since 1989 (DelGiudice et al. 2009), and our documented changes in deer foraging behavior provide evidence for the hypothesized cascade mechanism, further supporting our conclusions.

Our understanding of trophic cascades involving large terrestrial carnivores requires additional research (Shurin et al. 2002; Schmitz et al. 2004), and this work represents an important early step in addressing these hypotheses. Our study provides one of the first manipulative tests to support the presence of trophic cascades in forest ecosystems involving large mammalian carnivores and herbivores. Ideally, future studies will test these hypotheses

over a wider region than UNDERC. Our study was limited by the presence of only one wolf territory occupying UNDERC (although there were others just beyond our borders; unpublished data). This inherently limits our ability to generalize our results. However, given the strength and the straightforward nature of our findings, as well as our use of comparisons over time, we do not expect that there would be major qualitative differences in the results of our own work and future replications of this study (Oksanen 2001). This is even further supported by our forb richness results, which are in line with the results of another Great Lakes forest study (Callan et al. 2013).

The ability of predator-free ungulates to become drivers of environmental change in temperate and boreal forests is becoming increasingly recognized as a major conservation issue (Ripple et al. 2010). There is also a rising awareness that predator removal and reintroduction can have dramatic impacts on ecosystems (Estes et al. 2011). The question then is whether restoring these ungulate predators will halt these environmental changes (Rooney and Anderson 2009; Licht et al. 2010). If maples continue to grow towards the canopy in our high wolf use sites and if these results are transferable to other Great Lakes forests, then we propose that the natural regeneration of maples in Great Lakes forests will be restored in areas with wolves in similar fashion to what has occurred with aspen in Yellowstone (Painter et al. 2014, 2015) and Banff National Park (Hebblewhite and Smith 2010). This re-establishment of maple regeneration would allow maples to continue to be the dominant canopy species and possibly allow other preferred tree species to regenerate. We also propose that forb diversity in high wolf use areas at UNDERC will increase further over time as new species colonize from other locations and become established (Callan et al. 2013). We thus suggest that wolves and other large mammalian predators have the potential to be useful tools for forest ecosystem restoration, promoting the regeneration of ungulate-preferred species and/or increased forb diversity through the generation of density-mediated and/or trait-mediated trophic cascades.

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Author contribution statement DGF came up with the idea for the study, and the experimental design and further concept extrapolation were developed with GEB and DEB. DGF conducted the majority of fieldwork. DGF and DEB collaborated on telemetry-related work. DGF and GEB analyzed the data and interpreted results, with input from DEB. DGF and GEB wrote the manuscript, with editorial input from DEB.

References

- Abrams PA (1995) Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. *Am Nat* 146:112–134
- Altendorf KB, Laundré JW, López González CA, Brown JS (2001) Assessing effects of predation risk on foraging behavior of mule deer. *J Mammal* 82:430–439. doi:10.1644/1545-1542(2001)082<0430:AEOPRO>2.0.CO;2
- Alverson WS, Waller DM, Solheim SL (1988) Forests too deer: edge effects in northern Wisconsin. *Conserv Biol* 2:348–358. doi:10.1111/j.1523-1739.1988.tb00199.x
- Anderson RC, Loucks OL (1979) White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *J Appl Ecol* 16:855–861
- Augustine DJ, Frelich LE (1998) Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conserv Biol* 12:995–1004. doi:10.1046/j.1523-1739.1998.97248.x
- Beyer DE Jr, Peterson RO, Vucetich JA, Hammill JH (2009) Wolf population changes in Michigan. In: Wydeven AP, Van Deelen TR, Heske EJ (eds) Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story. Springer, New York, pp 205–216
- Borer ET, Seabloom EW, Shurin JB, Anderson KE, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2005) What determines the strength of a trophic cascade? *Ecology* 86:528–537. doi:10.1890/03-0816
- Callan R, Nibbelink NP, Rooney TP, Wiedenhoeft JE, Wydeven AP (2013) Recolonizing wolves trigger a trophic cascade in Wisconsin (USA). *J Ecol* 101:837–845. doi:10.1111/1365-2745.12095
- Carpenter SR, Cole JJ, Hodgson JR, Kitchell JF, Pace ML, Bade D, Cottingham KL, Essington TE, Houser JN, Schindler DE (2001) Trophic cascades, nutrients, and lake productivity whole-lake experiments. *Ecol Monogr* 71:163–186. doi:10.1890/0012-9615(2001)071[0163:TCNALP]2.0.CO;2
- Childress MJ, Lung MA (2003) Predation risk, gender and the groups size effect: does elk vigilance depend upon the behavior of conspecifics? *Anim Behav* 66:389–398. doi:10.1006/anbe.2003.2217
- Côte SD, Rooney TP, Tremblay JP, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Annu Rev Ecol Evol Syst* 35:113–147. doi:10.1146/annurev.ecolsys.35.021103.105725
- Creel S, Winnie JA Jr, Christianson D, Liley S (2008) Time and space in general models of antipredator response: tests with wolves and elk. *Anim Behav* 76:1139–1146. doi:10.1016/j.anbehav.2008.07.006
- Dehn MM (1990) Vigilance for predators: detection and dilution effects. *Behav Ecol Sociobiol* 26:337–342. doi:10.1007/BF00171099
- DelGiudice GD, McCaffery KR, Beyer DE Jr, Nelson ME (2009) Prey of wolves in the Great Lakes region. In: Wydeven AP, Van Deelen TR, Heske EJ (eds) Recovery of gray wolves in the Great Lakes region of the United States: An endangered species success story. Springer, New York, pp 155–174

- Elbroch M (2003) Mammal tracks and sign: a guide to North American species. Stackpole Books, Mechanicsburg
- Estes JA, Palmisan JF (1974) Sea otters: their role in structuring nearshore communities. *Science* 185:1058–1060
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pickett EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet Earth. *Science* 333:301–306. doi:10.1126/science.1205106
- Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330. doi:10.1890/04-0953
- Gese EM (2004) Survey and census techniques for canids. In: Silero-Zubiri C, Hoffman M, Macdonald DW (eds) Canids: foxes, wolves, jackals, and dogs. International Union for Conservation of Nature and Natural Resources, Gland, pp 273–279
- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421–425
- Hebblewhite M, Smith DW (2010) Wolf community ecology: Ecosystem effects of recovering wolves in Banff and Yellowstone National Parks. In: Musiani M, Boitani L, Paquet PC (eds) The world of wolves: new perspectives on ecology, behaviour, and management. University of Calgary Press, Calgary, pp 69–120
- 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. doi:10.1890/04-1269
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156. doi:10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2
- Jacobson HA, Kroll JC, Browning RW, Koerth BH, Conway MH (1997) Infrared-triggered cameras for censusing white-tailed deer. *Wildl Soc Bull* 25:547–556
- Kauffman MJ, Brodie JF, Jules ES (2010) Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742–2755. doi:10.1890/09-1949.1
- Kuijper DPJ, Verwijmeren M, Churski M, Zbyryt A, Schmidt K, Jędrzejewska B, Smit C (2014) What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE* 9:1–12. doi:10.1371/journal.pone.0084607
- Kunkel KE, Pletscher DH (2001) Winter hunting patterns of wolves in and near Glacier National Park, Montana. *J Wildl Manag* 65:520–530
- Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Can J Zool* 79:1401–1409. doi:10.1139/z01-094
- Lessard VC, McRoberts RE, Holdaway MR (2001) Diameter growth models using Minnesota Forest Inventory and Analysis data. *For Sci* 47:301–310
- Licht DS, Millsbaugh JJ, Kunkel KE, Kochanny CO, Peterson RO (2010) Using small populations of wolves for ecosystem restoration and stewardship. *BioSci* 60:147–153. doi:10.1525/bio.2010.60.2.9
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640. doi:10.1139/z90-092
- McLaren BE, Peterson RO (1994) Wolves, moose, and tree rings on Isle Royale. *Science* 266:1555–1558. doi:10.1126/science.266.5190.1555
- Mech LD (1977) Wolf-pack buffer zones as prey reservoirs. *Science* 198:320–321. doi:10.1126/science.198.4314.320
- Mech LD, Karns PD (1977) Role of the wolf in a deer decline in the Superior National Forest. U.S. Forest Service Research Paper NC-148. North Central Forest Experiment Station, St. Paul
- Mech LD, Peterson RO (2003) Wolf-prey relations. In: Mech LD, Boitani L (eds) Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, pp 131–160
- Oksanen L (2001) Logic of experiments in ecology: is pseudoreplication a pseudo-issue? *Oikos* 94:27–38. doi:10.1034/j.1600-0706.2001.11311.x
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. *Trends Ecol Evol* 14:483–488. doi:10.1016/S0169-5347(99)01723-1
- Paine RT (1980) Food webs: linkage, interaction strength, and community infrastructure. *J Anim Ecol* 49:667–685
- Painter LE, Beschta RL, Larsen EJ, Ripple WJ (2014) After long-term decline, are aspen recovering in northern Yellowstone? *For Ecol Manag* 329:108–117. doi:10.1016/j.foreco.2014.05.055
- Painter LE, Beschta RL, Larsen EJ, Ripple WJ (2015) Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? *Ecology* 96:252–263. doi:10.1890/14-0712.1
- Peterson RO, Cucci P (2003) The wolf as a carnivore. In: Mech LD, Boitani L (eds) Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, pp 104–130
- Peterson RO, Vucetich JA, Bump JM, Smith DW (2014) Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annu Rev Ecol Syst* 45:325–345. doi:10.1146/annurev-ecolsys-120213-091634
- Polis GA, Strong DR (1996) Food web complexity and community dynamics. *Am Nat* 147:813–846
- Powell RA (2012) Movements, home ranges, activity, and dispersal. In: Boitani L, Powell RA (eds) Carnivore ecology and conservation. Oxford University Press, New York, pp 188–217
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509. doi:10.1890/04-0719
- Preisser EL, Orrock JL, Schmitz OJ (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology* 88:2744–2751. doi:10.1890/07-0260.1
- Ripple WJ, Beschta RL (2007) Restoring Yellowstone's aspen with wolves. *Biol Conserv* 138:514–519. doi:10.1016/j.biocon.2007.05.006
- Ripple WJ, Larsen EJ, Renkin RA, Smith DW (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biol Conserv* 102:227–234. doi:10.1016/S0006-3207(01)00107-0
- Ripple WJ, Rooney TP, Beschta RL (2010) Large predators, deer, and trophic cascades in boreal and temperate ecosystems. In: Terborgh J, Estes JA (eds) Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington DC, pp 141–162
- Rooney TP (2009) High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecol* 202:103–111. doi:10.1007/211258-008-9489-8
- Rooney TP, Anderson DP (2009) Are wolf-mediated trophic cascades boosting biodiversity in the Great Lakes region? In: Wydeven AP, Van Deelen TR, Heske EJ (eds) Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story. Springer, New York, pp 205–216
- Rooney TP, Waller DM (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *For Ecol Manag* 181:165–176. doi:10.1016/S0378-1127(03)00130-0
- Schmitz OJ (2005) Behaviors of predators and prey and links with population level processes. In: Barbosa P, Castellanos I (eds) Ecology of predator–prey interactions. Oxford University Press, Oxford, pp 256–278

- Schmitz OJ (2008) Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952–954. doi:[10.1126/science.1152355](https://doi.org/10.1126/science.1152355)
- Schmitz OJ, Hamback PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am Nat* 155:141–153
- Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol Lett* 7:153–163. doi:[10.1111/j.1461-0248.2003.00560.x](https://doi.org/10.1111/j.1461-0248.2003.00560.x)
- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecol Lett* 5:785–791. doi:[10.1046/j.1461-0248.2002.00381.x](https://doi.org/10.1046/j.1461-0248.2002.00381.x)
- Sikes RS, Gannon WL, Animal Care and Use Committee of the American Society of Mammalogists (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mamm* 92:235–253. doi:[10.1644/10-MAMM-F-355.1](https://doi.org/10.1644/10-MAMM-F-355.1)
- Sinclair ARE, Metzger K, Brashares JS, Nkwabi A, Sharam G, Fryxell JM (2010) Trophic cascades in African savanna: serengeti as a case study. In: Terborgh J, Estes JA (eds) *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington DC, pp 255–274
- Thiel RP (1993) *The timber wolf in Wisconsin: the death and life of a majestic predator*. University of Wisconsin Press, Madison
- Trussell GC, Ewanchuk PJ, Matassa CM (2006) Habitat effects on the relative importance of trait- and density-mediated indirect interactions. *Ecol Lett* 9:1245–1252. doi:[10.1111/j.1461-0248.2006.00981.x](https://doi.org/10.1111/j.1461-0248.2006.00981.x)
- Underwood R (1982) Vigilance behavior in grazing African antelopes. *Behaviour* 79:82–107
- Valeix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F, Fritz H, MacDonald DW (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *For Ecol Manag* 230:96–106. doi:[10.1890/08-0606.1](https://doi.org/10.1890/08-0606.1)
- Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100. doi:[10.1890/0012-9658\(2003\)084\[1083:AROTII\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2)
- White MA (2012) Long-term effects of deer browsing: composition, structure and productivity in a northeastern Minnesota old-growth forest. *For Ecol Manag* 269:222–228. doi:[10.1016/j.foreco.2011.12.043](https://doi.org/10.1016/j.foreco.2011.12.043)
- Wydeven AP, Wiedenhoeft JE, Schultz RN, Thiel RP, Jurewicz RL, Kohn BE, Van Deelen TR (2009) History, population growth, and management of wolves in Wisconsin. In: Wydeven AP, Van Deelen TR, Heske EJ (eds) *Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story*. Springer, New York, pp 87–106