

Large predators limit herbivore densities in northern forest ecosystems

William J. Ripple · Robert L. Beschta

Received: 17 October 2011 / Revised: 16 February 2012 / Accepted: 20 February 2012
© Springer-Verlag 2012

Abstract There is a lack of scientific consensus about how top-down and bottom-up forces interact to structure terrestrial ecosystems. This is especially true for systems with large carnivore and herbivore species where the effects of predation versus food limitation on herbivores are controversial. Uncertainty exists whether top-down forces driven by large carnivores are common, and if so, how their influences vary with predator guild composition and primary productivity. Based on data and information in 42 published studies from over a 50-year time span, we analyzed the composition of large predator guilds and prey densities across a productivity gradient in boreal and temperate forests of North America and Eurasia. We found that predation by large mammalian carnivores, especially sympatric gray wolves (*Canis lupus*) and bears (*Ursus* spp.), apparently limits densities of large mammalian herbivores. We found that cervid densities, measured in deer equivalents, averaged nearly six times greater in areas without wolves compared to areas with wolves. In areas with wolves, herbivore density increased only slightly with increasing productivity. These predator effects are consistent with the exploitation ecosystems hypothesis and appear to occur across a broad range of net primary productivities. Results are also consistent with theory on trophic cascades, suggesting widespread and top-down forcing by large carnivores on large herbivores in forest biomes across the northern hemisphere. These findings have important conservation implications involving not

only the management of large carnivores but also that of large herbivores and plant communities.

Keywords Large carnivores · Wolves · Bears · Cervids · Productivity · Trophic cascades · Herbivory

Introduction

Over a half century ago, Hairston et al. (1960) introduced the green world hypothesis (GWH), suggesting that predators maintain global plant biomass at high levels by limiting herbivore densities. This view of “top-down” controls upon food-web interactions contradicted the prevailing bottom-up view that food-webs are nutrient-driven, as reflected in the classic food-web theory. Subsequently Fretwell (1977) and Oksanen et al. (1981) refined and extended the GWH to what is known as the exploitation ecosystems hypothesis (EEH). The EEH predicts stepwise trophic relationships among plants, herbivores, and predators along an increasing net primary productivity (NPP) gradient. The EEH also suggests that herbivore biomass increases linearly with increasing NPP in unproductive ecosystems (<0.7 kg/m²/year), but remains somewhat constant in the presence of predators in productive ecosystems (>0.7 kg/m²/year). According to the EEH, plants and carnivores in forests and other relatively productive ecosystems are resource-limited, whereas herbivores are regulated by predation. Thus, with increasing primary productivity, the EEH predicts significant increases in plant and carnivore biomass, but little increase in herbivore biomass. Conversely, where apex predators have been functionally extirpated, herbivore irruptions (sharp increases in densities) and impacts to plant communities would be likely.

Communicated by C. Gortázar

W. J. Ripple (✉) · R. L. Beschta
Department of Forest Ecosystems and Society, College of Forestry,
Oregon State University,
Corvallis, OR 97331, USA
e-mail: bill.ripple@oregonstate.edu

Since these seminal top-down theories were advanced, questions have been raised and the importance of trophic cascades in ecosystem processes and functions remains controversial (Polis 1999; Schmitz et al. 2000; Terborgh et al. 1999). Trophic cascades have been criticized as simplistic, only rarely relevant at the community level, and far less significant within terrestrial ecosystems than aquatic ecosystems (Halaj and Wise 2001). Additionally, the vast majority of studies concerning trophic cascades in terrestrial ecosystems involve invertebrate communities (Borer et al. 2005). Thus, uncertainty persists about whether terrestrial trophic cascades are common in the presence of large carnivores (Crête and Manseau 1996; Ray et al. 2005).

Large mammalian carnivore species have experienced substantial range contractions throughout the world during the last two centuries (Ceballos and Ehrlich 2002; Laliberte and Ripple 2004). Nevertheless, there have been a significant number of case studies performed in an attempt to understand the effects of wolves and other predators on prey populations in northern North America (Mech and Peterson 2003; Orians et al. 1997; citations in Appendix 1). In general, these reviews suggest that wolf predation can be a limiting factor for prey populations, especially when wolves coexist with bears, holding prey to levels well below what could be supported by the forage base. However, Mech and Peterson (2003) state that there is “still no scientific consensus on the significance of wolf predation in prey population dynamics,” because each case study has a combination of ecological factors that make it unique from the others.

Because little work has been done comparing predator/prey dynamics across productivity gradients (Crête 1999), there has been a lack of literature addressing trophic level dynamics in endotherm food webs across boreal and temperate forests of the Northern hemisphere (Aunapuu et al. 2008). Little is known, for example, about the range in cervid densities normally occurring for partial versus complete large predator guilds and how cervid densities vary with productivity (Crête and Manseau 1996).

Herein we address relationships among predator guilds and cervid densities in boreal and temperate forest biomes of the northern hemisphere. In retrospect, the extirpation of large carnivores by the 20th century in portions of the mid and northern latitudes provided a series of natural experiments (Diamond 1983). Thus, previously published studies allowed us to compare results from areas where carnivores remain and where they had been extirpated.

Consistent with the GWH (Hairston et al. 1960) and the EEH (Oksanen 1992), we hypothesize a set of trophic interactions across a gradient of primary productivity for boreal and temperate ecosystems that are productive enough to support carnivores. In systems with intact and ecologically effective large carnivore guilds (i.e., tri-trophic cascades,

left side of Fig. 1), we expect (1) carnivore densities to be resource-limited and positively correlated with primary productivity and (2) herbivores mainly predator-limited, such that herbivore density increases only slightly with increasing productivity. In this system, herbivore damage to palatable plants would be relatively low regardless of productivity. Although not rigorously tested herein, EEH predicts that when the removal of large predators occurs (i.e., truncated trophic cascades, right side of Fig. 1), herbivore density would be positively correlated with productivity and damage to palatable plants relatively high regardless of primary productivity.

Understanding the effects of large predator and herbivore populations upon native plant communities has potentially important conservation implications. If large predators reduce plant damage by altering cervid behavior and limiting

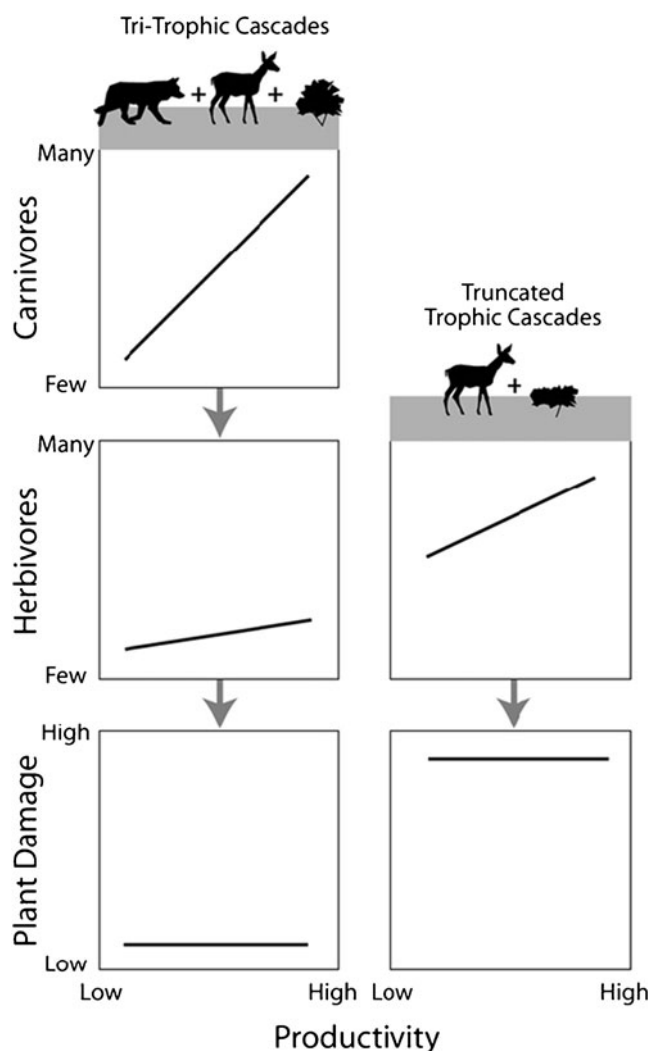


Fig. 1 Conceptual diagram of trophic cascades showing hypothesized predator densities, herbivore densities, and plant damage for populations across a productivity gradient in the presence (left column) and absence (right column) of large predators in productive ecosystems with NPP > 0.7 kg/m²/year (based on Oksanen 1992; Oksanen et al. 1981)

their densities, the maintenance of large predators across landscapes could be a crucial option for sustaining the ecological integrity of ecosystems (Estes et al. 2011; Miller et al. 2001; Soulé et al. 2003; Terborgh and Estes 2010). Furthermore, in areas where large predators have been displaced or locally extirpated, their reintroduction may represent a particularly effective approach for passively restoring those ecosystems.

Methods

Expanding on previous work by Peterson et al. (2003), we conducted a literature search to find articles that reported cervid densities [white-tail deer (*Odocoileus virginianus*), caribou (*Rangifer tarandus*), elk (*Cervus elaphus*), and moose (*Alces alces*)]. We searched the literature using electronic databases as well as reference lists from Peterson et al. (2003) and other publications. In selecting articles, we avoided using case studies with migrating cervids, non-native cervids, and islands (e.g., Isle Royale). Some cervids are hypothesized to migrate to avoid their predators, which can reduce the impacts of predation on their numbers. We did not attempt to examine migratory cervids because their densities exhibit high spatial and temporal variability and are thus difficult to characterize for comparative purposes. This criterion resulted in the exclusion of elk in the northern Rocky Mountains of North America, because elk densities in this region are highly variable as animals migrate between summer and winter ranges across an elevation gradient. We also excluded vicinities of major human impacts such as built-up areas, agriculture, or livestock. We excluded areas with high levels of large carnivore harvesting by humans. For example, wolf/cervid data from Poland's primeval forest were not included due to wolf harvesting, limited habitat, and other human disruptions there (Jędrzejewski and Jędrzejewski 1998). We inspected each study area with remote sensing imagery and all selected study areas were composed of >90% forest/grass cover. We did not exclude sites that contained forest harvesting. Finally, we examined historical range maps to determine the original range of wolves and bears to determine sites where they have been extirpated. Due to a lack of consistent information on felids, we were unable to include felid species in our analysis.

For each case study, we recorded (1) an estimate of NPP from MC1, a dynamic global vegetation model, (2) the presence or absence of predators including wolves, bears, and human hunters, and (3) the density (#/km²) of the primary cervid species present. We recorded wolf density (#/1,000 km²) when available and normalized cervid densities to deer equivalent (DE) densities (DE/km², deer=1 DE, caribou=2 DE, elk=3 DE, moose=6 DE) for comparative

purposes (Peterson et al. 2003). We also recorded if the authors described cervid impacts to plants.

T-tests (unequal variances) were used to test for significant ($p<0.05$) differences in cervid densities for areas with versus without wolves. Linear regression was used to determine if wolf densities or cervid densities were significantly related to NPP. Multiple regression was used to test for significant slope differences in cervid densities in relation to NPP between sites with wolves present versus those without wolves (i.e., extirpated or rare).

The dynamic global vegetation model (0.5° lat.×0.5° long. grid cells), MC1, includes a biogeochemical module that simulates monthly carbon (C) and nutrient dynamics for a combined tree and grass ecosystem. Furthermore, MCI is a whole ecosystem model which accounts for both overstory and understory processes in detail, including plant production, soil organic matter decomposition, and water, and nutrient cycling where NPP in kg of dry mass/m²/year is a function of a maximum potential rate of plant production constrained by the effects of soil moisture, soil temperature, soil nutrients, atmospheric CO₂ concentration, shading, and leaf area index (Bachelet et al. 2001; Daly et al. 2000). Temperature, precipitation, humidity, and soil properties are basic drivers for the biogeochemical module (see Bachelet et al. 2001 for technical documentation of the MC1 model including the biogeochemical module).

Results

We obtained estimates of cervid densities for 42 sites in North America and Eurasia meeting our criteria (Fig. 2, Appendix 1). Wolf densities were available for 19 of the 42 sites. Human hunting occurred at 24 of the 42 sites. Both wolves and bears historically existed at all 42 sites, with wolves being extirpated from 16 sites and bears extirpated from 7 of these 16 sites. We found that bears were sympatric with wolves in 26 of 42 studies, while bears occurred alone in 9 of 42 studies, all of which were areas where wolves had been extirpated. None of our 42 sites had wolves without bears.

Sites without wolves ($n=16$) had significantly higher average cervid densities relative to sites with wolves ($n=26$; 15.5 vs. 2.6 DE/km², respectively, $p<0.001$, Fig. 3a). Also at sites without wolves, 11 of 16 studies reported impacts to plants (see Appendix 1). Cervid densities without wolves ranged from 2.8 to 32.4 DE/km² and with wolves ranged from 0.03 to 8.4 DE/km². While cervid densities were significantly related to productivity when wolves were absent ($p=0.035$) and present ($p=0.036$), densities increased with productivity at a significantly greater rate in the absence of wolves compared to when wolves were present (regression slope over five times steeper, $p=0.02$, Fig. 3b).

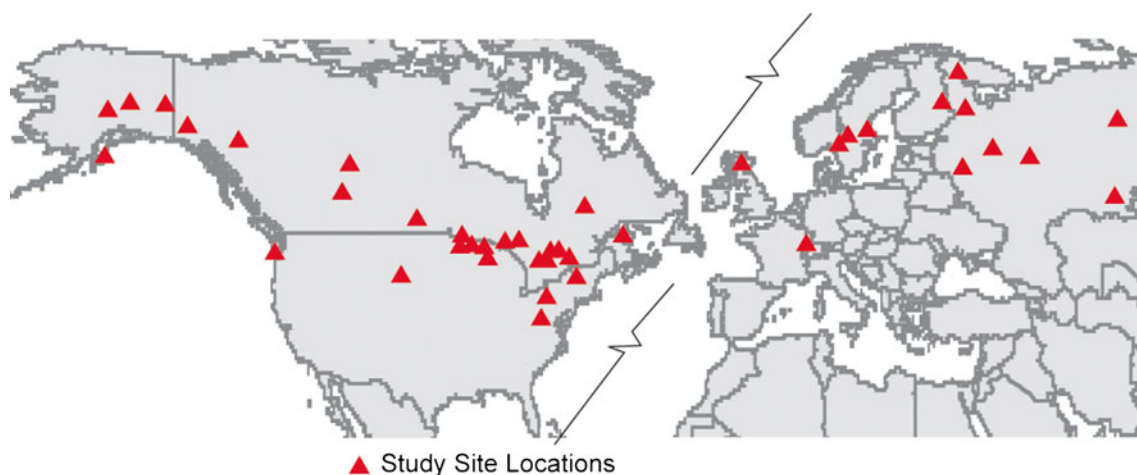


Fig. 2 Locations of study sites in North America and Eurasia

Variance of cervid density was not constant and increased with increasing *NPP*, but a natural log transformation of

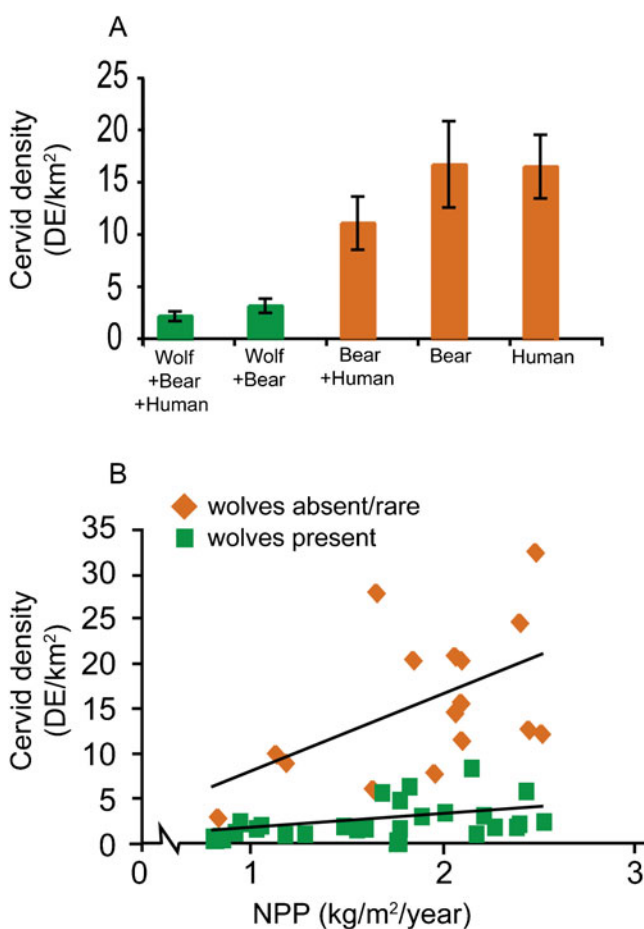


Fig. 3 **a** Mean cervid densities with standard errors by predator guild [wolf+bear+human ($n=14$), wolf+bear ($n=12$), bear+human ($n=3$), bear ($n=6$), human ($n=7$)]. **b** Cervid densities (y) as a function of net primary productivity (x) for study sites with wolves present ($y=1.54x-0.06$; $SEE=1.9$, $R^2=0.17$, $p=0.036$, $n=26$) and study sites where wolves are absent/rare ($y=8.64x-0.99$; $SEE=7.0$, $R^2=0.28$, $p=0.035$, $n=16$). *SEE* Standard error of the estimate

density resolved this issue and allowed a more direct evaluation of the effect of wolves on the relationship. The log of cervid density was significantly related to productivity ($p=0.002$), but the R^2 was low (0.22). The addition of a categorical variable for wolf presence or absence resulted in a highly significant relationship ($p<0.001$) that explained 70% of the variation in density (adjusted $R^2=0.70$). In fact, wolf presence alone, without accounting for productivity, explained 60% ($R^2=0.60$) of the variation in log of cervid density.

On average, we found wolf densities to be 17.8 / 1,000 km² (range 2.3–40.2). Wolf densities were positively related to increases in productivity ($p=0.008$, Fig. 4).

Discussion

Results from our analyses suggest that top-down forcing may be relatively strong in systems with wolves, in that cervid densities are significantly lower than in predator guilds where wolves are absent. These findings support

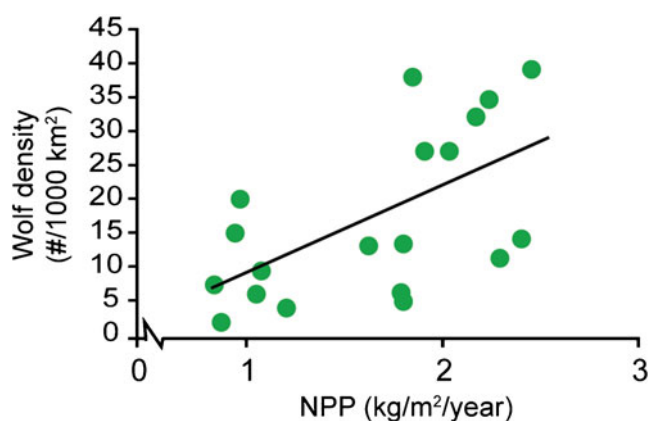


Fig. 4 Wolf densities (y) as a function of net primary productivity (x), where $y=13.08x-3.49$; $SEE=10.0$, $R^2=0.35$, $p=0.008$, and $n=19$. *SEE* Standard error of the estimate

research findings by others that the combined predation pressure from wolf and bear populations may limit cervid densities (Gasaway et al. 1992b; Mech and Peterson 2003; Messier 1994; Orians et al. 1997). Our results are also consistent with predictions made by Oksanen et al. (1981) for (1) the predator trophic level, because wolf density increased with increasing productivity and (2) the herbivore trophic level, because cervid densities in ecosystems with wolves remained relatively low regardless of productivity.

Other than humans, which occupy an ecological niche as top predator in many ecosystems, gray wolves, by virtue of their widespread geographic distribution, group-hunting, and year-round activity, represent the most significant cervid predator in the northern hemisphere (Peterson et al. 2003). Thus predation pressure from wolves, in combination with bears, can apparently maintain cervid populations at low densities. An exception, perhaps, is that some migrating cervids, such as barren ground caribou herds, may not be limited by predation and often cycle over wide ranges of abundance.

With both wolves and bears present, we found cervid densities to increase only slightly with increasing NPP, possibly because of an evolutionary response to intense predation pressure involving anti-predator adaptations and selection for more elusive prey (Oksanen 1992). Because predators may not completely counter anti-predator adaptations of their prey, increasing primary productivity should lead to slight increases in herbivore density (Oksanen 1992). Costs related to antipredator behavior could be partially offset by any positive effects of increasing productivity. In systems with high primary productivity, traits that affect prey fitness through their ability to avoid predation are prone to be under strong selection (Abrams 2000). Like Crête (1999), we found that cervid densities increased steeply with increasing productivity for ecosystems without wolves. The high variance in cervid densities associated with an absence of wolves may be due to unevenness in the effectiveness of partial predator guilds and human hunting as well as various bottom-up factors such as climate variability or forest conditions.

Our results are consistent with a relatively extensive body of literature in that bears alone appear insufficient to preclude cervid irruptions, whereas the combination of wolf and bear predation, with or without human hunting, maintains cervid densities lower than without wolves and bears (Ballard et al. 1987; Bergerud and Elliot 1985b; Bergerud et al. 1983b; Fuller 1989b; Gasaway et al. 1983b; Hayes and Harestad 2000; Messier 1994; Van Ballenberghe 1987). Because bears are opportunistic omnivores, have access to a variety of foods, and their effects appear to be secondary to wolves, an understanding of their role in trophic cascades has been elusive. Both black (*Ursus americanus*) and brown

(*Ursus arctos*) bears commonly prey on neonatal cervids, taking a large percentage of the annual offspring less than 1 month old (Zager and Beecham 2006). Their role as predator appears to vary with the density of cervids and has the greatest impact when cervid densities are low rather than high (Gasaway et al. 1992b). At low cervid densities, bear predation on neonates is mostly additive rather than compensatory, thus removing young animals before they have an opportunity to reproduce (Zager and Beecham 2006). This leads us to hypothesize that bears may provide multiple and linked positive feedback loops in their sympatric predation effects with wolves such that: (1) as wolves provide subsidies to bears through scavenging opportunities on wolf-killed carrion, higher bear densities are supported, causing more predation on neonatal cervids and lower cervid densities; and (2) when cervid densities become lower, bear predation tends to be more effective as an additive predation force further limiting cervid densities. In the case of Isle Royale National Park where wolves exist on an island, wolves alone have been unable to consistently limit cervid densities over time possibly due to inbreeding, disease, and/or a lack of bears (Peterson 2007; Peterson et al. 2003; Wilmers et al. 2006).

Hypercarnivorous felids may also have important roles in affecting cervid densities and trophic cascades. In western North America, cougars (*Puma concolor*) were found to limit mule deer (*Odocoileus hemionus*) densities releasing woody plants from browsing suppression, thus maintaining biodiversity (Ripple and Beschta 2006; Ripple and Beschta 2008). Furthermore, our two-predator results for wolves and bears in this study are similar to the findings of Melis et al. (2009) involving combined wolf and lynx (*Lynx lynx*) predation on roe deer (*Capreolus capreolus*) in Europe. They found that roe deer densities were significantly lower in areas with sympatric wolves and lynx compared to areas with wolves alone or areas without either predator (Fig. 5). Their results indicate that top-down influences were stronger than bottom-up influences because there were no significant differences in productivity as measured by the fraction of photosynthetically active radiation (FPAR) in their areas with both wolves and lynx ($\bar{x} = 0.562$, 95% C.I. 0.044), wolves without lynx ($\bar{x} = 0.544$, 95% C.I. 0.053), and neither predator present ($\bar{x} = 0.562$, 95% C.I.=0.035).

While the occurrence of human hunting and winter weather events in the presence of wolves can influence cervid populations through additive mortality (Gasaway et al. 1983b; 1992b; Mech and Peterson 2003; Orians et al. 1997), evidence from our analysis shows that in many cases, humans, using contemporary hunting laws and strategies, are ineffective in the absence of wolves in preventing hyperabundant cervid densities. Similarly, Melis et al. (2009) found that human hunting in Europe had little influence on roe deer abundance. This situation likely occurs because the

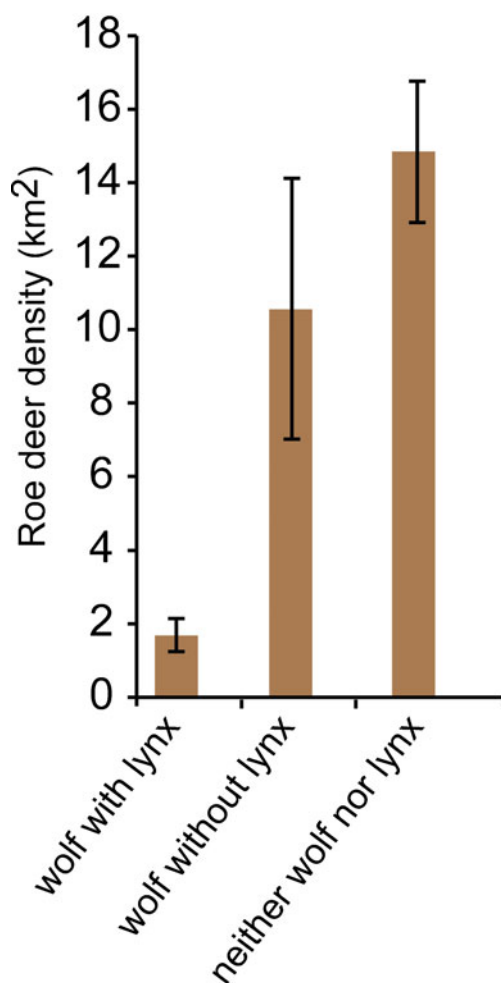


Fig. 5 Mean roe deer densities in Europe with standard errors by predator guild [wolf with lynx ($n=15$), wolf without lynx ($n=21$), neither wolf nor lynx ($n=36$)]. Adapted from Melis et al. (2009)

interest of hunting managers is to generally maximize game meat production, not to limit cervid densities. In addition, hunting by humans is often not functionally equivalent to predation by large, wide-ranging carnivores such as wolves. Differences include factors such as killing distance, seasonal and diurnal timing, age and sex of selected prey, as well as effects on mesopredators, intra-guild predation, and carrion-scavenger relationships (Berger 2005). Nonlethal effects such as predation risk and the “ecology of fear” triggered by large mammalian carnivores can also influence ecosystem structure and function, and these effects may be different than any risk effects caused by human hunters (Berger 2005; Laundré et al. 2001; Ripple and Beschta 2004).

Although we were unable to rigorously test for trophic cascades in our dataset, below we tentatively address the plant damage portion of EEH. In reviewing our case studies, at sites with wolves absent/rare ($n=16$), we found that most authors ($n=12$) reported impacts to plants. In the presence of a functional large predator guild that can exert significant

influence via lethal and nonlethal effects, cervids are normally unable to impact the general recruitment (i.e., growth of seedlings and sprouts into tall saplings and larger growth forms) of palatable woody species (Ripple et al. 2010). However, where reduced lethal/nonlethal effects of large predators and higher cervid densities occur, deforestation can develop gradually, as herbivory prevents tree recruitment over time (Beschta and Ripple 2009) as well as the closure of forest gaps. Thus, over ecological time the exclusion of large carnivores from forest landscapes may lead to simplified plant communities, alternative stable states, and altered biodiversity (Beschta and Ripple 2009; Côté et al. 2004; Estes et al. 2011; Terborgh et al. 2001). Examples from the case studies we reviewed include a lack of tree regeneration for fir (*Abies* spp.), pine (*Pinus* spp.), hemlock (*Tsuga* spp.), and deciduous species, sometimes resulting in a conversion to less palatable spruce (*Picea* spp.) forests or increases in grasses (Angelstam et al. 2000b; Heuze et al. 2005b; Palmer and Truscott 2003b). Declines in palatable understory shrub species (Schreiner et al. 1996b; Trumbull et al. 1989b), as well as changes in invertebrate communities (Suominen 1999b), were also identified.

Cervid irruptions following wolf extirpation have been documented in diverse ecosystems of western North America (Leopold et al. 1947; Ripple and Beschta 2005). Plant damage following cervid irruptions has also been found in regions with relatively low productivity as well as those with very high productivity (Beschta and Ripple 2009). Changes in forest plant communities, such as a reduction in the abundance of woody browse species after wolf extirpation, can cause accelerated streambank erosion, thus leading to changes to stream morphology and fish habitat (Beschta and Ripple 2011). Loss of large carnivores may have potential implications for climate change by reducing long-term sequestration of carbon due to a lack of recruiting woody plants as well as creating simplified and novel ecosystems that may be less resilient to a changing climate. Any reductions in intense herbivory that slow deforestation and increase forest regeneration could conserve and sequester carbon, especially in the mid and high latitudes where most of the world’s forest carbon is stored (Dixon et al. 1994; Luyssaert et al. 2008).

Our analysis of published studies may contain various biases (e.g., non-randomization of study sites, continental bias, biome bias, species bias). Our reliance on published articles resulted in the data herein being biased toward North America ($n=29$) over Eurasia ($n=13$), and for moose ($n=26$) over the other cervid ($n=16$) species. There are also more study sites in the boreal than in the temperate biomes. This is likely due to more human development and predator extirpations in temperate regions. We were also unable to assess the potential importance of bottom-up variables, other than productivity, that could affect cervid abundance in

northern latitudes (e.g., winter severity). Results may be affected by the influence of humans upon wolves, since wolf density in southern areas may be reduced due to greater abundance of people. However, southern sites also have less severe winters which may partially account for any increases in ungulate abundance, so results could be confounded. We also note that our estimates of potential *NPP* were derived from a global model with grid cells typically larger than the cervid study areas.

There are other factors that can contribute to high herbivore densities in the absence of wolves, such as the creation of early seral forests by humans, which may make it difficult for predators to serve as restorative agents (Ray et al. 2005; Ritchie et al. 2012). However, in our analysis, we consistently found relatively low cervid densities in regions that have both wolves and extensive logging including southern Canada and northern Minnesota. Moreover, due to the limits of human tolerance, it may not be possible for predators to achieve ecologically functional population sizes in many of the areas where cervids have become highly abundant (e.g. Beschta and Ripple 2010).

Conclusions

On average, we found cervid densities in systems without wolves to be approximately six times greater than that of systems with wolves (2.6 vs. 15.5 DE/km²). Cervid densities in systems with wolves and bears ranged from 0.03 to 8.4 DE/km² with density increasing slightly with *NPP*. These results could serve as benchmarks, based on the productivity of a particular region, for designing and evalu-

ating the management of non-migratory cervid populations, where the goal is to emulate the range of densities typically found when wolves and bears are present in northern forests. Additionally, the wolf densities presented herein ($\bar{x} = 17.8/1000 \text{ km}^2$, range 2.3–40.2) could also be used as benchmarks for assessing wolf management goals across a range of productivities. In general, regions with higher productivity and intact habitat have the capability to support higher wolf densities than areas with lower productivity (Fig. 4).

Recent research suggests that conservation programs based on the presence of apex predators may lead to broader biodiversity benefits (Sergio et al. 2008). Thus, sites containing intact carnivore guilds and which retain ecological processes should be considered as priority areas for both research and conservation planning (Woodroffe and Ginsberg 2005). Additionally, repatriating large carnivores to portions of their former range may still be possible and could have positive ecological effects. For example, the reintroduction or recolonization of wolves, decades after extirpation, has shown to positively affect tree and shrub recruitment at some sites on ungulate winter ranges where cervids seasonally migrate (Beschta and Ripple 2007; Ripple and Beschta 2012). More research is needed to determine to what extent large predators structure ecosystems in areas with both migrating and nonmigrating large herbivores. The preservation or recovery of large predators may thus represent an important conservation need for helping to maintain the resiliency of northern forest ecosystems, especially in the face of a rapidly changing climate.

Acknowledgements We thank J. Hollenbeck, J. Leniham, C. Melis, L. Painter, and A. Souther for providing assistance on this project.

Appendix 1

Table 1 Locations, species, densities of cervids and wolves, predator present/absent, *NPP*, and plant damage for 42 sites used in analysis

Location	Latitude	Longitude	Cervid species	Cervid density ^a	DE density ^b	Wolf density ^c	Human	Bear	<i>NPP</i> ^d	Plant damage ^e	Ref. #
Cent. Sweden	59.5 N	12.37E	Moose	2.6	15.6	A	P	A	2.10	yes	(Cederlund & Markgren 1987)
Elk Island NP ^f , Cent. Alberta	53.63 N	112.85 W	Moose	1.5	9	A	P	A	1.19	N/A	(Cairns & Telfer 1980)
Riding Mt NP, S. Manitoba	50.76 N	100.24 W	Moose	0.94	5.6	P	A	P	1.69	N/A	(Carbyn 1983)
Gaspésie Park, E. Quebec	48.9 N	66.40 W	Moose	1.9	11.4	A	A	P	2.10	No	(Crête 1989)
S.W. Yukon	61.25 N	138.67 W	Moose	0.17	1	P	P	P	1.29	N/A	(Larsen 1982)
Denali, Cent. Alaska	63.60 N	151.50 W	Moose	0.26	1.6	5.6	A	P	1.78	N/A	(Haber 1977; Singer & Dalle-Molle 1985)
E. Cent. Alaska	64 N	142 W	Moose	0.09	0.5	8	P	P	0.82	No	(Gasaway et al. 1992)
Pukaskwa NP, S. Cent. Ontario	48.25 N	85.92 W	Moose	0.3	1.8	14.9	A	P	2.39	N/A	(Bergerud et al. 1983)
S.W. Quebec (MW area)	47.1 N	76.7 W	Moose	0.27	1.6	13.8	Rare	P	1.60	N/A	(Crête & Manseau 1996)
N.E. Alberta (AOSERP area)	57.19 N	111.64 W	Moose	0.26	1.6	6.6	P	P	1.03	N/A	(Fuller & Keith 1980)
E. Alaska	64.25 N	148 W	Moose	0.2	1.2	15.6	P	P	0.93	N/A	(Gasaway et al. 1983a)
Papineau-Labelle, S. Quebec	46.17 N	75.50 W	Deer	3	3	28	A	P	1.89	N/A	(Potvin 1988)
E.Cent. Ontario	45.92 N	78.97 W	Deer	5.8	5.8	40.2	A	P	2.44	N/A	(Pimlott et al. 1969)
N.Cent. Minnesota	47.75 N	93.25 W	Deer	6.3	6.3	39	P	P	1.83	N/A	(Fuller 1989)

Table 1 (continued)

Location	Latitude	Longitude	Cervid species	Cervid density ^a	DE density ^b	Wolf density ^c	Human	Bear	NPP ^d	Plant damage ^e	Ref. #
Wind Cave NP W. South Dakota	43.6 N	103.45 W	Elk	3.3	9.9	A	P	A	1.14	No	(Detling 1998)
Olympic NP, W. Washington	47.78 N	123.93 W	Elk	6.8	20.4	A	A	P	2.10	Yes	(Schreiner et al. 1996)
Cent. Scotland	57.13 N	3.93 W	Elk	9.3	27.9	A	P	A	1.66	Yes	(Palmer & Truscott 2003)
N.W. Michigan	46.77 N	89.75 W	Deer	6	6	A	P	P	1.64	Yes	(Frelich & Lorimer 1985)
N. Pennsylvania	41.60 N	79 W	Deer	12.6	12.6	A	P	P	2.45	No/yes	(Hough 1949; Trumbull et al. 1989)
S. Cent. Sweden	60.5 N	13.60E	Moose	1.3	7.8	A	P	A	1.96	Yes	(Angelstam et al. 2000)
Karelia Russia	63.50 N	33.1E	Moose	0.25	1.5	P	P	P	1.56	No	(Angelstam et al. 2000)
N. New York	44.15 N	74.15 W	Deer	12.2	12.2	A	A	P	2.52	Yes	(Behrend et al. 1970)
Cent. Quebec (MCW area)	52.50 N	73.00 W	Moose	0.03	0.2	6.7	P	P	1.77	N/A	(Crête & Manseau 1996)
N.E. France	47.83 N	6.97E	Elk	8.2	24.6	A	P	A	2.40	Yes	(Heuze et al. 2005)
N.E. Wisconsin	45.87 N	88.70 W	Deer	14.5	14.5	Rare	P	P	2.07	Yes	(Stoeckeler et al. 1957)
E. Cent. Sweden	61.00 N	17.00E	Moose	3.4	20.4	A	P	A	1.85	Yes	(Suominen 1999)
Canaan Park, West Virginia	39.07 N	79.52 W	Deer	32.4	32.4	A	A	P	2.49	Yes	(Michael 1992)
Mauricie Park, S.E. Quebec	46.80 N	78 W	Moose	0.4	2.4	P	A	P	2.53	N/A	(Crête 1987)
Chapleau N.E. Ontario	47.90 N	83.40 W	Moose	0.35	2.1	P	A	P	2.40	N/A	(Welsh et al. 1980)
Voyageurs NP, N. Minn.	48.5 N	92.9 W	Deer	8.4	8.4	33	A	P	2.15	N/A	(Mech & Boitani 2003)
Bashkirsky, Russia	53.33 N	58.00E	Moose	0.4	2.4	20.8	A	P	0.95	N/A	(Filonov 1980)
Darvinsky, Russia	58.74 N	37.90E	Moose	0.3	1.8	12	A	P	2.27	N/A	(Filonov 1980)
Laplandsky, Russia	67.95 N	31.87E	Caribou	1.4	2.8	Rare	A	P	0.84	N/A	(Filonov 1980)
Pechoro-Ilychsky, Russia	62.46 N	58.72E	Moose	0.05	0.3	2.3	A	P	0.85	N/A	(Filonov 1980)
Tver Region, Russia	56.48 N	32.9E	Moose	0.17	1	P	P	P	2.18	N/A	(Kochetkov 2002)
Kostroma Region, Russia	58.11 N	44.E	Moose	0.15	0.9	4.4	P	P	1.19	N/A	(Baskin 1994)
E. Cent. Finland	64.50 N	29.12E	Moose	0.31	1.9	P	P	P	1.49	N/A	(Kojola et al. 2004)
E. Cent. Ontario	46 N	80.1 W	Deer	3.1	3.1	35.7	P	P	2.22	N/A	(Kolenosky 1972)
N.E. Wisconsin	45.87 N	88.70 W	Deer	20.8	20.8	Rare	A	P	2.07	Yes	(Stoeckeler et al. 1957)
N.E. Minnesota	47.67 N	91.56 W	Moose	0.56	3.4	28	P	P	2.01	N/A	(Mech & Boitani 2003)
Kenai Alaska	59.78 N	150.71 W	Moose	0.8	4.8	14.2	P	P	1.78	N/A	(Peterson et al. 1984)
N. British Columbia	59.00 N	131.67 W	Moose	0.34	2.0	10.0	P	P	1.06	N/A	(Bergerud & Elliot 1985)

NPP Net primary productivity, NP National Park, P present, A absent

^a Cervid densities are #/km²

^b Deer equivalent (DE) densities are #/km² (deer=1 DE, caribou=2 DE, elk=3 DE, moose=6 DE)

^c Wolf densities are #/1,000 km²

^d Unit: kg of dry mass/m²/year

^e Effects of herbivory on plants: yes=plant damage described in article; no=little or no plant damage described in article; N/A=herbivory effects not a subject covered in the article

References

- Abrams PA (2000) The evolution of predator–prey interactions: theory and evidence. *Annu Rev Ecol Syst* 31:79–105
- Angelstam P, Wikberg PE, Danilov P, Faber WE, Nygren K (2000) Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland, and Russian Karelia. *Alces* 36:133–145
- Aunapuu M, Dahlgren J, Oksanen T, Grellmann D, Oksanen L, Olofsson J, Rammul U, Schneider M, Johansen G, Hyden HO (2008) Spatial patterns and dynamic responses of arctic food webs corroborate the exploitation ecosystems hypothesis. *Am Nat* 171:249–262
- Bachelet D, Lenihan JM, Daly C, Neilson RP, Ojima DS, Parton WJ (2001) MC1: a dynamic vegetation model for estimating the distribution of vegetation and associated ecosystem fluxes of carbon, nutrients, and water. USDA General Technical Report PNW-GTR-508, 95 pp
- Ballard WB, Whitman JS, Gardner CL (1987) Ecology of an exploited wolf population in south central Alaska. *Wildl Monogr* 98:1–54
- Baskin LM (1994) Population ecology of the moose in the Russian Southern Taiga. *Alces* 30:51–55
- Behrend DF, Mattfeld GF, Tierson WC, Wiley JE III (1970) Deer density control for comprehensive forest management. *J For* 68:695–700
- Berger J (2005) Hunting by carnivores and humans: does functional redundancy occur and does it matter? In: Ray JC, Redford KH, Steneck RS, Berger J (eds) *Large carnivores and the conservation of biodiversity*. Island Press, Washington, DC, pp 315–341
- Bergerud AT, Elliot JP (1985) Dynamics of caribou and wolves in northern British Columbia. *Can J Zool* 64:1515–1529
- Bergerud AT, Wyatt W, Snider B (1983) The role of wolf predation in limiting moose population. *J Wildl Manage* 47:977–988

- Beschta RL, Ripple WJ (2007) Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Can J For Res* 37:1873–1885
- Beschta RL, Ripple WJ (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biol Conserv* 142:2401–2414
- Beschta RL, Ripple WJ (2010) Mexican wolves, elk, and aspen in Arizona: is there a trophic cascade? *For Ecol Manage* 260:915–922
- Beschta RL, Ripple WJ (2011) The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology*, in press. doi:10.1016/j.geomorph.2011.04.042
- Borer ET, Seabloom EW, Shurnin JB, Anderson KE, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2005) What determines the strength of a trophic cascade? *Ecology* 86:528–537
- Cairns AL, Telfer ES (1980) Habitat use by four sympatric ungulates in boreal mixedwood forest. *J Wildl Manage* 47:977–988
- Carbyn LN (1983) Wolf predation on elk in Riding Mountain National Park, Manitoba. *J Wildl Manage* 47:963–976
- Ceballos G, Ehrlich PR (2002) Mammal population losses and the extinction crisis. *Science* 296:904–907
- Cederlund G, Markgren G (1987) The development of the Swedish moose population, 1970–1983. *Swedish Wildl Res Suppl* 1:55–61
- Côté SD, Rooney TP, Tremblay J, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Annu Rev Eco Evol Syst* 35:113–147
- Crête M (1987) The impact of sport hunting on North American moose. *Swedish Wildl Res Suppl* 1:553–563
- Crête M (1989) Approximation of K carrying capacity for moose in eastern Quebec. *Can J Zool* 7:373–380
- Crête M (1999) The distribution of deer biomass supports the hypothesis of exploitation ecosystems. *Ecol Lett* 2:223
- Crête M, Manseau M (1996) Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. *Evol Ecol* 10:51–62
- Crête M, Manseau M (1996) Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. *Evol Ecol* 10:51–62
- Daly C, Bachelet D, Lenihan JM, Neilson RP, Parton W, Ojima D (2000) Dynamic simulation of tree-grass interactions for global change studies. *Ecol Appl* 10:449–469
- Detling JK (1998) Mammalian herbivores: ecosystem-level effects in two grassland national parks. *Wildl Soc Bull* 26:438–448
- Diamond JM (1983) Ecology: laboratory, field and natural experiments. *Nature* 304:586–587
- Dixon RK, Solomon AM, Brown S, Houghton RA, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science* 263:185–190
- 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, Pikitch 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
- Filonov C (1980) Predator–prey problems in nature reserves of the European part of the USSR. *J Wildl Manage* 44:389–396
- Freligh LE, Lorimer CG (1985) Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biol Conserv* 34:99–120
- Fretwell SD (1977) The regulation of plant communities by food chains exploiting them. *Perspect Biol Med* 20:169–185
- Fuller TK (1989) Population dynamics of wolves in north-central Minnesota. *Wildl Monogr* 105:1–141
- Fuller TK, Keith LB (1980) Wolf population dynamics and prey relationships in northeastern Alberta. *J Wildl Manage* 44:583–602
- Gasaway WC, Stephenson RO, Davis JL, Shepherd PEK, Burris OE (1983) Interrelationships of wolves, prey, and man in interior Alaska. *Wildl Monogr* 84:13
- Gasaway WC, Stephenson RO, Davis JL, Shepherd PEK, Burris OE (1983b) Interrelationships of wolves, prey, and man in interior Alaska. *Wildl Monogr* 84:1–50
- Gasaway WC, Boertje RD, Grangaard DV, Kelleyhouse DG, Stephenson RO, Larson DG (1992) The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl Monogr* 120:1–59
- Haber GC (1977) Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. PhD thesis, University of British Columbia
- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421–425
- Halaj J, Wise DH (2001) Terrestrial trophic cascades: how much do they trickle? *Am Nat* 157:262–281
- Hayes RD, Harestad AS (2000) Wolf functional response and regulation of moose in the Yukon. *Can J Zool* 78:60–66
- Heuze P, Schnitzler A, Klein F (2005) Is browsing the major factor of silver fir decline in the Vosges Mountains of France? *For Ecol Manage* 217:219–228
- Hough AF (1949) Deer and rabbit browsing and available winter forage in Allegheny hardwood forests. *J Wildl Manage* 13:135–141
- Jędrzejewski B, Jędrzejewski W (1998) Predation in vertebrate communities: the Białowieża primeval forest as a case study. Springer, New York
- Kochetkov VV (2002) Factors determining moose population dynamics in the Central Forest Reserve. *Alces Suppl* 2:57–51
- Kojala I, Huitu O, Toppinen K, Heikura K, Heikkinen S, Ronkainen S (2004) Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. *J Zool* 263:229–235
- Kolenosky GB (1972) Wolf predation on wintering deer in East-Central Ontario. *J Wildl Manage* 36:357–369
- Laliberte AS, Ripple WJ (2004) Range contractions of North American carnivores and ungulates. *BioScience* 54:123–138
- Larsen DG (1982) Moose inventory in the southwest Yukon. *Alces* 18:142–167
- 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
- Leopold A, Sows LK, Spencer DL (1947) A survey of over-populated deer ranges in the United States. *J Wildl Manage* 11:162–183
- Luyssaert S, Schulze ED, Börner A, Knohl A, Hessenmöller D, Law BE, Ciais P, Grace J (2008) Old growth forests as global carbon sinks. *Nature* 455:213–215
- Mech LD, Boitani L (eds) (2003) Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago
- 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
- Melis C, Jędrzejewski B, Apollonio M, Bartań KA, Jędrzejewski W, Linnell JDC, Kojala I, Kusak J, Adamic M, Ciuti S, Delehan I, Dykyy I, Krapinec K, Mattioli L, Sagaydak A, Samchuk N, Schmidt K, Shkvrya M, Sidorovich VE, Zawadzka B, Zhyla S (2009) Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Global Ecol Biogeogr* 18:724–734
- Messier F (1994) Ungulate population models with predation: a case study with the North American moose. *Ecology* 75:478–488
- Michael ED (1992) Impact of deer browsing on regeneration of balsam fir in Canaan Valley, West Virginia. *North J Appl For* 9:89–90
- Miller B, Dugelby B, Foreman D, Martinez del Rio CR, Noss M, Phillips R, Reading ME, Terborgh Soule J, Willcox L (2001) The importance of large carnivores to healthy ecosystems. *Endang Spec Update* 18:202–210
- Oksanen L (1992) Evolution of exploitation ecosystems. I. Predation, foraging ecology and population dynamics in herbivores. *Evol Ecol* 6:15–33

- Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *Am Nat* 118:240–261
- Orians GH, Cochran PA, Duffield JW, Fuller TK, Gutierrez RJ, Hanemann WM (1997) Wolves, bears, and their prey in Alaska: biological and social challenges in wildlife management. National Academy Press, Washington, DC, p 207
- Palmer SCF, Truscott AM (2003) Seasonal habitat use and browsing by deer in Caledonian pinewoods. *For Ecol Manage* 174:149–166
- Peterson RO (2007) The wolves of Isle Royale: a broken balance. University of Michigan Press, Ann Arbor, p 192
- Peterson RO, Woolington JD, Bailey TN (1984) Wolves of the Kenai Peninsula, Alaska. *Wildlife Monogr* 88
- Peterson RO, Vucetich JA, Page RE, Chouinard A (2003) Temporal and spatial aspects of predator–prey dynamics. *Alces* 39:215–232
- Pimlott DH, Shannon JA, Kolenosky GB (1969) The ecology of the timber wolf in Algonquin Provincial Park. Ontario Department of Lands and Forests Research Paper Wildlife No. 87, Toronto, Ontario, Canada
- Polis GA (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of green biomass. *Oikos* 86:3–15
- Potvin F (1988) Wolf movements and population dynamics in Papi-neau–Labelle reserve, Quebec. *Can J Zool* 66:1266–1273
- Ray JC, Redford KH, Steneck RS, Berger J (eds) (2005) Large carnivores and the conservation of biodiversity. Island Press, Washington, DC, p 526
- Ripple WJ, Beschta RL (2004) Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* 54:755–766
- Ripple WJ, Beschta RL (2005) Linking wolves to plants: Aldo Leopold on trophic cascades. *BioScience* 55:613–621
- Ripple WJ, Beschta RL (2006) Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biol Conserv* 133:397–408
- Ripple WJ, Beschta RL (2008) Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biol Conserv* 141:1249–1256
- Ripple WJ, Beschta RL (2012) Trophic cascades in yellowstone: the first 15 years after wolf reintroduction. *Biol Conserv* 145:205–213
- Ripple WJ, Rooney TP, Beschta RL (2010) Large predators, deer, and trophic cascades in the mid-latitudes. In: Terborgh J, Estes JA (eds) *Trophic cascades*. Island Press, Washington, DC, pp 141–161
- Ritchie EG, Elmhagen B, Glen AS, Letnic M, Ludwig G, McDonald RA (2012) Ecosystem restoration with teeth: what role for predators? *Trends Ecol Evol*, in press. doi:10.1016/j.tree.2012.01.001
- Schmitz OJ, Hamback PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. *Am Nat* 155:141–153
- Schreiner EG, Krueger KA, Houston DB, Happe PJ (1996) Understorey patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. *Can J For Res* 26:255–265
- Sergio F, Caro T, Brown D, Clucas B, Hunter J, Ketchum J, McHugh K, Hiraldo F (2008) Top predators as conservation tools: ecological rationale, assumptions and efficacy. *Annu Rev Ecol Syst* 39:1–19
- Singer FJ, Dalle-Molle J (1985) The Denali ungulate-predator system. *Alces* 21:339–358
- Soulé ME, Estes JE, Berger J, del Rio CM (2003) Ecological effectiveness: conservation goals for interactive species. *Conserv Biol* 17:1238–1250
- Stoekeler JH, Strothmann RO, Krefting LW (1957) Effect of deer browsing on reproduction in the northern hardwood-hemlock type in northeastern Wisconsin. *J Wildl Manage* 21:75–80
- Suominen O (1999) Impact of cervid browsing and grazing on the terrestrial gastropod fauna in the boreal forests of Fennoscandia. *Ecography* 22:651–658
- Terborgh J, Estes JA (eds) (2010) *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington, DC, p 464
- Terborgh J, Estes JA, Paquet P, Ralls K, Boyd-Heigher D, Miller BJ, Noss RF (1999) The role of top carnivores in regulating terrestrial ecosystems. In: Soulé M, Terborgh J (eds) *Continental conservation: scientific foundations of regional reserve networks*. Island Press, Washington, DC, pp 39–64
- Terborgh J, Lopez L, Nunez P, Rao M, Shahabuddin G, Riveros M, Ascanio R, Lambert TD, Adler GH, Balbas L (2001) Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926
- Trumbull VL, Zielinski EJ, Aharrah EC (1989) The impact of deer browsing on the Allegheny forest type. *North J Appl For* 6:162–165
- Van Ballenberghe V (1987) Effects of predation on moose numbers: a review of recent North American studies. *Swedish Wildl Res Suppl* 1:431–460
- Welsh DA, Morrison KP, Oswald K, Thomas ER (1980) Winter utilization of habitat by moose in relation to forest harvesting. *Proc North Am Moose Conf Workshop* 16:398–428
- Wilmers CC, Post ES, Peterson RO, Vucetich JA (2006) Disease mediated switch from top-down to bottom-up control exacerbates climatic effects on moose population dynamics. *Ecol Lett* 9:383–389
- Woodroffe R, Ginsberg JR (2005) King of beasts? Evidence for guild redundancy among large mammalian carnivores. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) *Large carnivores and the conservation of biodiversity*. Island Press, Washington, DC, pp 154–175
- Zager P, Beecham J (2006) The role of American black bears and brown bears as predators on ungulates in North America. *Ursus* 17:95–108