



Commentary

Missing Lynx and Trophic Cascades in Food Webs: A Reply to Ripple et al.

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ABSTRACT Ripple et al. (2011) proposed a hypothesis that the recovery of gray wolves (*Canis lupus*) may positively affect the viability of threatened Canada lynx (*Lynx canadensis*) populations in the contiguous United States through indirect species interactions. Ripple et al. (2011) proposed 2 key trophic linkages connecting wolf restoration with lynx recovery. First, recovering wolf populations may benefit lynx through reduced interference and exploitative competition with coyotes (*C. latrans*). Second, recovering wolf populations may benefit lynx through reduced exploitative competition among ungulates and snowshoe hares (*Lepus americanus*), the primary prey of lynx. Both proposed linkages have weak or contradictory empirical support in the available literature on lynx–hare ecology, casting doubt on the utility of Ripple et al.’s (2011) hypothesis. Debate over Ripple et al.’s (2011) hypothesis demonstrates the importance of experimental or comparative documentation when proposing trophic cascades in complex food webs. In this case, publishing unsupported opinions as hypotheses that concern complex trophic interactions is a potential disservice to lynx conservation through misallocated research, conservation funding, and misplaced public perception. © 2012 The Wildlife Society.

KEY WORDS Canada lynx, coyote, elk, gray wolf, scientific evidence, snowshoe hare, trophic cascade, Yellowstone National Park.

Ripple et al. (2011) proposed a hypothesis that the recovery of gray wolves (*Canis lupus*) may positively affect the viability of threatened Canada lynx (*Lynx canadensis*) populations as mediated by indirect species interactions. We recognize (perhaps more than most) that large carnivores, such as gray wolves, exert top-down effects that cause major shifts in ecosystem states and services (Hebblewhite et al. 2005, Estes et al. 2011) and complement conservation planning by revealing regional-scale population processes (Carroll et al. 2001). Ripple et al. (2011) presented their hypothesis in the journal’s “opinion” section, in recognition that proposed trophic interactions were speculative. However, a careful review of available lynx–hare (*Lepus americanus*) literature rejects several of the key assumptions made by Ripple et al. (2011), firmly rejecting their hypothesis. We believe their paper, and the media attention it received, provides a strong case that scientists need to be particularly careful when speculating about trophic cascades in the literature, especially when contrary to existing results. Scientists must distinguish carefully between informed “speculation” that is central to

the scientific process and speculative hypotheses that lack necessary empirical support, even when published as “opinion.”

In our rebuttal, we illustrate the lines of evidence necessary for speculating about trophic cascades, using Ripple et al.’s (2011) hypothesis as a case study. We review the strength of scientific evidence that supports or refutes the key trophic linkages in Ripple et al.’s (2011) hypothesized trophic cascades connecting wolves and lynx (see Ripple et al. 2011; fig. 1). We use this example to illustrate the information needed to support trophic-cascade hypotheses that advance ecological understanding and species management. We evaluate the cost to conservation of sensitive carnivores associated with proposing untested hypotheses of trophic cascades that lack necessary empirical support.

TROPHIC INTERACTIONS

Realistic food webs are nuanced and complex. For example, in a simple 6-species food web with 2 predators, herbivores, and plants, there are approximately 30 direct interactions, but nearly 2,000 potential indirect interactions (Hebblewhite and Smith 2010). Thus, the study of trophic cascades requires experimental or comparative testing of both direct and indirect food-web interactions and their relative strengths (Hebblewhite and Smith 2010), as measured by

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population-level demographic response (Polis et al. 2000). We acknowledge that documenting trophic cascades with empirical field data are difficult and expensive, yet such data are needed to separate those species interactions important for management from the nearly infinite number of putative cascades. For example, the general premise that intra-guild competition and mesopredator release (Crooks and Soulé 1999, Prugh et al. 2009) structure carnivore communities may generally support Ripple et al.'s (2011) hypothesis, but the nuances of wolf-coyote (*C. latrans*)-lynx-hare food webs may offer alternative predictions that are better supported by empirical field data and available literature.

Ripple et al. (2011) propose 2 key trophic paths connecting wolf restoration with lynx recovery. First, recovering wolf populations may benefit lynx through reduced interference and exploitative competition with coyotes. Second, recovering wolf populations may benefit lynx through reduced exploitative competition among ungulates and snowshoe hares, the primary prey of lynx. Below we evaluate the empirical evidence supporting each pathway linking wolves to lynx, and we suggest alternative trophic linkages that we feel best relate to lynx.

Trophic Pathway Number1: Wolf-Coyote-Hare-Lynx

Do wolves reduce coyotes?—Ripple et al. (2011:515) state, "With wolves present, we hypothesize that coyotes would be maintained at low densities. . ." The restoration of apex predators can positively affect biodiversity conservation through regulation of mesocarnivores (Ritchie and Johnson 2009). Ripple et al. (2011) correctly state that wolves can affect coyotes, both behaviorally and ecologically, in the Yellowstone ecosystem (GYE; Berger and Gese 2007), and that such regulation can have cascading effects (Berger et al. 2008). However, despite the well-publicized initial declines in coyote abundance in the GYE following wolf recovery (Berger and Gese 2007), coyotes may now be adapting to wolves and coyote pack numbers may have rebounded (Merkle et al. 2009, Hebblewhite and Smith 2010). The trophic strength of wolf effects on coyotes may also differ geographically with variation in climate, primary productivity, carnivore and prey communities, and the degree of human persecution (Borer et al. 2005, Mech 2012). The inverse relationship between wolves and coyotes in Yellowstone is not supported outside the 2 national parks (Yellowstone and Grand Teton) included in the analyses by Berger and Gese (2007). In other systems where wolves, coyotes, and lynx coexist, research shows a positive relationship between wolves and coyotes (Paquet 1991, 1992), whereby coyotes benefit from scavenging on wolf-killed ungulate carcasses. The generally low mortality rates of radiocollared coyotes killed by wolves outside of Yellowstone in Northwest Montana is 3 times less than those killed by cougars (*Puma concolor*; Arjo 1998). Thus, this quick review of the literature suggests that the strongest generality of Ripple et al.'s (2011) hypothesis that wolves have a direct negative effect on coyotes is, at best, inconsistent, both within the GYE and across wolf-coyote range in North America.

Do coyotes compete with lynx?—Buskirk et al. (2000) hypothesized that coyotes compete with lynx through both interference competition (direct killing or displacement) and indirect exploitative competition for shared food resources. Ripple et al. (2011) speculated that these interactions are, in part, responsible for the imperiled status of southern lynx. Unfortunately, evidence for interference competition is essentially limited to anecdotal observations. An observation of a single juvenile lynx killed by a coyote in the Yukon is not *prima facie* evidence for a trophic-level interaction (O'Donoghue et al. 1995). Further, in this northern population, more predation mortality of radiocollared lynx was attributed to wolves, wolverines (*Gulo gulo*), and other lynx than to coyotes (O'Donoghue et al. 1995). Direct interactions between coyotes and lynx were rare (O'Donoghue et al. 2001).

If wolf-caused trophic cascades are important, then southern "wolf-free" populations of lynx should have high coyote-caused mortality rates, which is not the case. Cause-specific mortality data for several well-studied southern lynx populations show that human-caused mortality poses a far greater threat than does predation, particularly predation by coyotes. In a wolf-free, southern lynx population in Colorado, predation accounted for only 9% known-cause mortality (Devineau et al. 2010). In western Montana, with 55 documented lynx mortalities, we observed no instances of predation on lynx by coyotes in 10 years of study in an area that, at the time, had few wolves (J. Squires, unpublished data). Whereas, human-caused mortality accounted for 79% and 49% of known-cause mortality events in Minnesota (Moen 2009) and Colorado (Devineau et al. 2010), respectively, with considerably higher potential for population-level impacts. Thus, the low rate of observed coyote-caused mortality to lynx in southern populations, regardless of the presence of wolves, is inconsistent with Ripple et al. (2011)'s hypothesis, which casts doubt on this trophic pathway.

Ripple et al. (2011) correctly observed that hare densities in the western United States are low compared with northern populations (Hodges 2000a, b). Thus, decreases in hare abundance due to coyote predation could significantly impact southern lynx populations. However, this proposed trophic link in Ripple et al.'s (2011) hypothesis is again, weakly supported by available literature. Hodges (2000a) reviewed studies that indicate >90% of hare mortality is a result of predation. In their southern range, hares are killed by a dizzying array of avian and mammalian predators (see Hodges 2000a, b, Ellsworth and Reynolds, 2006). Even red squirrels (*Tamiasciurus hudsonicus*) are a major source of mortality on hare juveniles in northern hare populations (Boonstra et al. 2001). Although Ripple et al. (2011) correctly acknowledged that many predators consume hares, their hypothesis nonetheless focused narrowly on a single trophic link (that of coyotes reducing hares in southern population), despite a complex food web.

Starvation mortality of lynx typically occurs in late winter-early spring (Mowat et al. 2000). Thus, Ripple et al.'s (2011) hypothesis might better focus on food competition, or

bottom-up drivers, during winter. Coyotes in winter can forage in the same high-elevation boreal forests that are used by lynx (despite high foot-loading of coyotes, which causes them to sink in deep snow; Murray and Boutin 1991, Crête and Larivière 2003), regardless of low hare densities (Bekoff and Gese 2003, Kolbe et al. 2007, Burghardt-Dowd 2010). Despite spatial overlap, the winter diet of coyotes in sympatry with southern lynx is composed primarily of carrion, and there is little evidence of exploitative competition for snowshoe hares. In Montana, Kolbe et al. (2007) backtracked 12 adult coyotes for a total of 322 km in home ranges that overlapped those of lynx. Kolbe et al. (2007) located 88 feed sites on coyote backtracks and found that 88% of feed sites were carrion; only 3% of the 88 feed sites were actual snowshoe hare kills. Similarly, coyotes from northern populations scavenged carrion as a primary winter food when hare densities dropped to levels similar to those found in western Montana (Hodges 2000b). In Wyoming, Burghardt-Dowd (2010) found the percentage of coyote scats containing snowshoe hare dropped from 24% ($N = 50$) in the autumn to 4% ($N = 224$) during winter. Therefore, the most central linkage (coyote-lynx exploitative competition) in Ripple et al.'s (2011) hypothesized ecological cascade is poorly supported by empirical study.

Trophic Pathway Number 2: Wolf-Ungulate-Hare-Lynx

Ripple et al. (2011) suggested that wolf predation on ungulates may facilitate lynx recovery by decreasing exploitative competition among ungulates and snowshoe hares. Some evidence exists for diet overlap between hares and both moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) under fairly specific conditions in boreal ecosystems (Dodds 1960, Telfer 1972, Belovsky 1984). However, little evidence exists for population-level effects of ungulates upon hare dynamics, particularly relative to those ungulate species that comprise the majority of wolf diets in southern latitudes, such as elk (*Cervus elaphus*; Smith et al. 2004) and deer (*Odocoileus* spp.; Fuller et al. 2003). This proposed linkage is particularly implausible due to substantial separation between high-elevation boreal forests used by lynx and hares during winter and deer or elk winter range (Hodges 2000a, b, Squires et al. 2010), where trophic impacts of high ungulate densities on browse species have been widely documented. The winter diet of snowshoe hares in boreal forests is restricted to smaller diameter twigs and some bark of shrubs and trees (Hodges 2000a, b). In summer, snowshoe hares generally eat forbs, grasses, leaves of shrubs, and some woody browse, with no evidence of food limitation (Hodges 2000a, b). However, there is substantial evidence that population dynamics of hares are primarily a function of predation (Hodges 2000a, b, Wirsing et al. 2002). Given the basic natural history of ungulate species, ecologically meaningful impacts of exploitative competition on hares is exceedingly unlikely in either space-use or diet, particularly during winter (Hodges 2012).

THE COST OF POORLY SUPPORTED OPINION?

The *Bulletin* offers scientists a valuable outlet for open discussion and opinion in addition to true "scientific" work (Ballard 2005). Ripple et al.'s (2011) interesting hypothesis that examined possible trophic interactions between wolf and lynx did stimulate conversation in the public and scientific press. However, as we reviewed, central key trophic linkages presented in this hypothesis lack empirical or literature-based support, or are actually easily rejected by the existing literature. Their paper serves as a good case-study for considering a broader question of the value in publishing highly speculative trophic cascades in the literature that require rigorous scientific methods to disentangle, given complex species interactions (Wootton 1994). We suggest that untested hypotheses are of particularly limited value in the arenas of trophic cascade research and endangered species conservation, where the infinite number of putative indirect interactions are in stark contrast to scarce conservation attention and resources.

In their final paragraph, Ripple et al. (2011:517) describe trophic monitoring required to document ecological restoration, "Where wolf restoration is the objective..." This focus was echoed in the popular press, where the public has a difficult time distinguishing between hypotheses defined as opinion versus those tested through empirical research, especially when published in a peer-reviewed journal (Mech 2012). We believe that Ripple et al.'s (2011) focus on wolf restoration missed the mark. Instead, we prefer to conclude this discussion by considering lynx restoration as the objective. Gray wolves are no longer federally endangered under the Endangered Species Act across much of their range (Federal Register vol. 76, no. 87 [5 May 2011]) based on genetic and demographic grounds, with minimum estimates of likely >1,700 wolves roaming the Northern Rockies (e.g., Hebblewhite et al. 2010). In stark contrast, Canada lynx face an uncertain and imperiled future in the lower 48 states, with looming effects of climate change and the challenges of implementing recovery under the Endangered Species Act. Ripple et al.'s (2011) hypothesis that focuses on wolf restoration as a tool for lynx conservation will, in our professional opinion, potentially weaken much needed recovery efforts for lynx through misdirected resources and misguided public attention. The most obvious illustration of this is the exceedingly high human-caused mortality of lynx in Colorado and Minnesota (49–79% of known-caused mortality; Moen 2009, Devineau et al. 2010), respectively. Wolf restoration will not recover lynx populations to the same extent as will careful reductions in human-caused mortality and appropriate habitat management. In a recent review of research findings and needs for southern lynx conservation, Murray et al. (2008) found a similar dearth of evidence for negative impacts of mesocarnivore competition in southern populations. We echo Murray et al.'s (2008) recommendations to focus on 3 goals for southern lynx conservation: 1) further understanding of lynx population and habitat ecology, 2) conservation of lynx and hare habitat within

forest management frameworks, and 3) maintenance of connectivity with northern populations. We reiterate these goals and highlight the well-documented importance of human impacts on lynx mortality, habitat alteration, and patch connectivity, as the main threats to and the most cost-effective solution for the conservation of southern lynx populations.

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