In My Opinion

Can Restoring Wolves Aid in Lynx Recovery?

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ABSTRACT Herein, we examine the hypothesis that relatively low densities of snowshoe hares (*Lepus americanus*) and the imperiled status of lynx (*Lynx canadensis*) may be partially due to an ecological cascade caused by the extirpation of gray wolves (*Canis lupus*) in most of the conterminous United States decades ago. This hypothesis focuses on 2 plausible mechanisms, one involving "mesopredator release" of the coyote (*C. latrans*), which expanded its distribution and abundance continentally following the ecological extinction of wolves over the temperate portion of their geographic range. In the absence of wolves, coyotes may have affected lynx via increased predation on snowshoe hares, on which the lynx specializes, and/or by direct killing of lynx. The second mechanism involves increased browsing pressure by native and domestic ungulates following the declines in wolves. A recovery of long-absent wolf populations could potentially set off a chain of events triggering a long-term decrease in coyotes and ungulates, improved plant communities, and eventually an increase in hares and lynx. This prediction, and others that we make, are testable. Ecological implications for the lynx may be dependent upon whether wolves are allowed to achieve ecologically effective populations where they recolonize or are reintroduced in lynx habitat. We emphasize the importance of little-considered trophic and competitive interactions when attempting to recover an endangered carnivore such as the lynx. © 2011 The Wildlife Society.

KEY WORDS Canada lynx, *Canis lupus*, competition, coyote, endangered species, gray wolf, *Lynx canadensis*, mesopredator release, *Lepus americanus*, white-tailed jackrabbit.

Under the auspices of the Endangered Species Act of 1973, the Canada lynx (*Lynx canadensis*) was listed in 2000 as a threatened species across the conterminous United States (US; U.S. Fish and Wildlife Service 2000). This listing was in part a response to sharp declines in distribution and abundance of lynx in several states for which reliable historical trapping records were available during the latter stages of the 20th century (e.g., MN, MT, NH, and WA; Federal Register 2000). These "southern lynx" are poorly understood relative to conspecifics occupying the boreal forests of northern Canada and Alaska, USA; therefore, their conservation remains a subject of debate (Koehler et al. 2008, Murray et al. 2008). Lynx face numerous factors that could limit their distribution and abundance, including competition with other mid-sized carnivores and habitat alteration by stand-replacing fires, timber harvest, and insect outbreaks (Buskirk et al. 2000, Koehler et al. 2008, Murray et al. 2008). Even so, there is broad agreement that the fate of the lynx at lower latitudes is closely linked to the distribution and abundance of its obligate primary prey, the snowshoe hare (*Lepus americanus*; Kolbe et al. 2007, Murray et al. 2008). That is not to say that widespread abundance of snowshoe hares is the only condition for lynx recovery; however, it is a necessary one (Aubry et al. 2000, Murray et al. 2008).

Snowshoe hare populations occupying the forests of northern Canada and Alaska typically exhibit dramatic stable limit cycles with periods of 9–11 yr (Keith 1963, Krebs et al. 2001). The mechanism underlying the hare cycle across this region is debated vigorously, with 2 mechanistic pathways contending for priority. The first, a tri-trophic-level interaction among quantity of winter browse, hare population density, and densities of hare predators involves time-lagged density dependence. Under this mechanism, declining winter browse availability helps to slow the growth of hare populations during the increase phase of the cycle, but predation, especially by lynx, initiates the decline and represents the primary driver of changes in hare abundance (Wolff 1980, Hodges 2000a, Krebs et al. 2001). The second, a hare–winter–browse hypothesis, invokes plant secondary chemical responses to herbivory as the chief factor eliciting the hare cycle (Bryant et al. 2009). Decadal-scale climate fluctuation (Stenseth et al. 2002) is invoked with both mechanisms to account for broad geographic synchrony. Yet, neither primary mechanism is alleged to operate strongly in the temperate, or southern, portion of the distribution of the hare; rather, southern hare populations in the conterminous US appear to exhibit attenuated dynamics and exhibit only relatively low densities at population peaks (Murray 2000, Murray et al. 2008, but see Hodges 2000b).

Dampened dynamics in southern hare populations have been attributed to a combination of forest fragmentation and predation by prey-generalists (Wolff 1980, Wirsing et al. 2002, Griffin and Mills 2009). Specifically, both limited suitable habitat offering enough protective cover and persistent pressure from facultative predators (e.g., coyotes [*Canis latrans*]) appear to not only increase predation mortality to hares but also prevent the recruitment necessary to generate a cycle. By implication, forces that reduce forest fragmentation or suppress facultative hare predators could enhance the size of southern hare populations and perhaps promote cyclic dynamics. Increased hare abundance in this region can plausibly be expected to improve the viability of southern lynx populations.

The objective of this article is to briefly examine a hypothesis that chronically low densities of southern snowshoe hares and the imperiled status of lynx may be partially the result of an ecological cascade caused decades ago by the extirpation of the gray wolf (*Canis lupus*) over most of its conterminous US range. This hypothesis focuses on the subsequent ecological release of coyotes and of the ungulate prey of wolves and leads us to the prediction that wolf restoration could help facilitate lynx recovery in the conterminous US.

THE CONCEPTUAL MODEL

During the 1800s and early 1900s, gray wolves were extirpated throughout much of the conterminous US, and ungulate and coyote irruptions often followed the loss of wolves (Leopold et al. 1947, Presnall 1948, Prugh et al. 2009, Ripple et al. 2010). Herein, we describe a series of trophic and competitive interactions connecting wolves to lynx (Fig. 1). With wolves present, we hypothesize that coyotes would be maintained at low densities, resulting in little competition—either exploitative or interference—between coyotes and lynx. Interspecific interactions helped shape

the evolution, structure, and function of carnivore communities, with exploitative competition occurring when one species limits populations of another by using a common resource. Interference competition involves harassment, kleptoparasitism, or outright killing of one species by another (Van Valkenburgh 1991, Merkle et al. 2009).

In the absence of wolves, coyote densities and distributions generally expanded in the US—into the Midwest (Bekoff 1977), to the northeast as far as Newfoundland (Parker 1995), and as far northwest as Alaska (MacDonald and Cook 2009). And, because coyotes are known to be effective predators of hares (Wirsing et al. 2002), increased coyote populations can cause exploitative competition with lynx via higher predation pressure on hares (Buskirk et al. 2000, Bunnell et al. 2006). Further, interference competition between coyotes and lynx could limit densities of the latter, since examples of coyotes killing lynx have been reported (O'Donoghue et al. 1995). Interestingly, researchers have attributed declines in bobcat (*Lynx rufus*) populations to exploitation competition for prey caused by increasing coyote populations (Litvaitis and Harrison 1989), as well as increases in bobcats due to decreases in coyotes (Henke and Bryant 1999). Also, in the absence of wolves, population densities of wild cervids typically increase (Leopold et al. 1947), creating prey and winter-killed carrion subsidies to coyotes (Weaver 1979). These carrion subsidies have the potential to increase densities of facultative hare predators, and thereby predation on hares, during periods when lynx are ordinarily uncommon and predation on hares is low (Kolbe et al. 2007, Gompper and Vanak 2008). Note that coyotes may also benefit from the provision of wolf-killed carrion in wolf-dominated landscapes (Merkle et al. 2009), but we hold that interference competition with wolves would likely have a stronger negative effect on coyotes that any positive effects from this type of carrion subsidy. Additionally, we
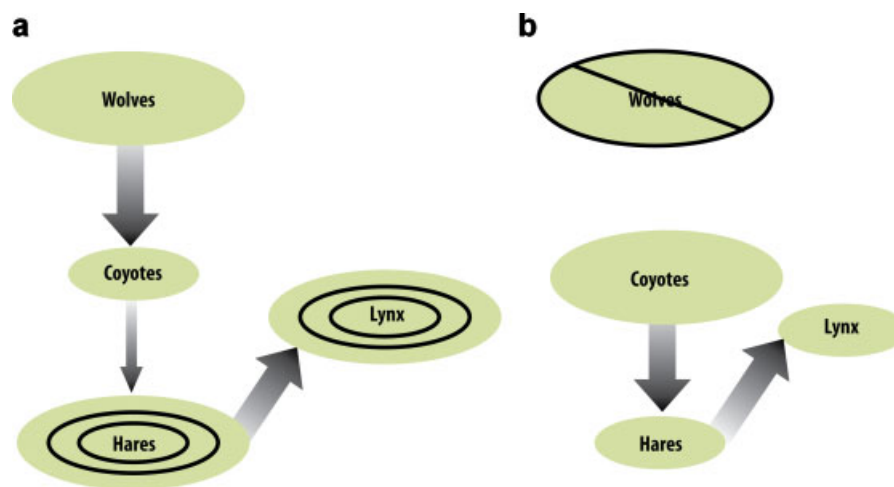

Figure 1. Conceptual diagram showing how the (a) presence or (b) absence of wolves may affect lynx across multiple trophic levels. We hypothesize (a) that in the presence of wolves, this apex predator maintains coyote populations at low densities, thus minimizing the potential influence of coyotes on hares. However, (b) in the absence of wolves, coyote densities increase, causing exploitative competition with lynx through high predation pressure on hares. Furthermore, in the absence of wolves, wild ungulates may not only provide a prey and carrion subsidy to coyotes but can also increase herbivory levels upon forest understory plants that satisfy important habitat needs for hares. Changes in ungulate herbivory and interference competition are not shown on the above diagrams. Note: Wide arrows denote strong effects; thin arrows, weak effects; large ellipses denote high densities; small ellipses, low densities; concentric lines in ellipses, variable and/or cycling densities.

hypothesize that elevated coyote predation pressure can, in addition to that from other hare predators, contribute to trait-mediated effects on hare populations via behavioral and physiological pathways. For example, in the Yukon Territory of Canada, increased stress from high levels of predation risk has been documented to cause marked deterioration in hare reproductive rates (Boonstra et al. 1998) and quality of offspring (Sheriff et al. 2009). Such trait-mediated effects could result in sustained, rather than decadal periodic, reductions in hare reproduction.

In northern latitudes (e.g., Yukon) where wolves are present and where hares are the main prey for coyotes, populations of coyotes generally occur at relatively low densities, as well as cycle up and down in concert with hares and lynx (O'Donoghue et al. 1998, Sheriff et al. 2009). This is in contrast to wolf-free southern latitudes (e.g., the conterminous US) where coyote densities are commonly an order of magnitude higher than those in the north (O'Donoghue et al. 1998, Bekoff and Gese 2003). Coyote diets are also more varied in the south. For example, in Wisconsin, coyote numbers did not decrease with declining snowshoe hare densities, because of attendant buffering from alternative food sources (Niebauer and Rongstad 1977). Thus, coyotes in the south have the potential to suppress hares through both habitat switching and prey switching, while subsisting, as opportunists, on other food resources: ungulate prey and carrion, fruits, smaller mammals, insects, birds, and human-generated garbage. Further, domestic cattle and sheep occur more broadly and at higher densities in the south than the north, which, for the southern portion of the range of the hare, could 1) increase the prey and carrion subsidy to coyotes, and 2) affect hare habitat through decreased forest understory vegetation due to herbivory. Most spatial overlap between lynx and livestock would occur at lower elevations of the lynx range because livestock are not generally distributed as high as lynx. Murie (1951) suggested that high densities of cattle in Arizona resulted in a lack of vegetative cover causing low densities of leporids.

To further explore hare dynamics in the south, we contrast hare populations in 2 unfragmented National Park settings: Isle Royale and Yellowstone. Neither park features livestock grazing. On Isle Royale, wolves colonized the park in 1949, and soon thereafter eliminated all coyotes from the island. With wolves and no coyotes, hares on Isle Royale cycled to high levels (Hodges 2000b). In Yellowstone National Park, Bailey (1930:125) described the distribution and abundance of snowshoe hares at around the time of the final eradication of wolves in this way: "Snowshoe rabbits are fairly common throughout the Canadian Zone timbered area." Similarly, Murie (1940:124) reported snowshoe hares in Yellowstone to be abundant in the early 1900s, writing that, "... at Sylvan Pass in 1903, 15 or 20 hares were frequently reported seen in a day so that hares at that time must have been quite plentiful." In contrast, a recent survey spanning the years 2002–2007 documented snowshoe hares as rare in Yellowstone (Hodges et al. 2009). This putative hare decline generally coincides with the absence of wolves and the consequent abundance of coyotes and high levels of herbivory

from elk (*cervus elaphus*; Murie 1940, Berger and Gese 2007, Beschta and Ripple 2009). Ungulates can compete with small mammals for forage and reduced ungulate densities can cause increases in small mammals (Keesing 2000). Lynx were common in Yellowstone at the turn of the 20th century but, similar to hare trends, have since declined (Buskirk 1999). Thus, we hypothesize that even with a lack of human fragmentation of landscapes or livestock grazing—as observed in Yellowstone National Park—disrupted trophic and competitive interactions alone may have been enough to chronically depress hare and lynx populations. With wolves now reestablished in Yellowstone (as of 1995), a test of this hypothesis is possible because it appears that coyote densities significantly declined in parts of the Greater Yellowstone Area following wolf reintroduction (Berger and Gese 2007). Moreover, early evidence tentatively suggests that a hare recovery may be taking place; namely, the 6 hare sampling sites for which the aforementioned Yellowstone survey had the longest time series all showed an upward trend in hare abundance in the final year (2007; Hodges et al. 2009). More hare sampling in Yellowstone in the future will be required to determine whether this initial trend continues.

An alternative explanation for the low snowshoe hare densities observed in Yellowstone invokes human-caused fire suppression in altering the spatial patterning of various successional stages important to this species. Fortunately, this mechanism can be tested by examining patterns of hare abundance in relation to changes to lodgepole pine (*Pinus contorta*) communities brought about by the wildfires of 1988, and subsequent successional changes. Under the fire suppression hypothesis, for example, we would expect increases in hare abundance to coincide primarily with the regeneration of high sapling density in stands burned in 1988 (Bryant et al. 2009, Hodges et al. 2009) rather than depression of coyote numbers caused by the presence of wolves.

We considered whether other leporids might have been affected by the processes hypothesized above for snowshoe hares. Again, early on Bailey (1930:127) described white-tailed jackrabbits (*Lepus townsendii*) as common in northern Yellowstone National Park "... and along the open valley of Lamar River." However, white-tailed jackrabbits in the Yellowstone–Grand Teton region apparently declined over the course of the mid- to late 20th century in the absence of wolves, and were recently reported as rare (Gunther et al. 2009) or completely absent (Berger 2008a, b) from the shrub–steppe-dominated Lamar Valley. Could this decline of white-tailed jackrabbits have been caused by increased coyote populations and elk herbivory following wolf extirpation? We believe that this scenario is both plausible and consistent with our hypothesis. During the 7-decade wolf-free period in Yellowstone, the Lamar Valley had both high densities of coyotes (high predation pressure on leporids) and intensive herbivory (reduced shrub and understory cover) from elk (Murie 1940, Beschta and Ripple 2009). Also, during the wolf-free period and consistent with the food-subsidy portion of our hypothesis, Gese et al. (1996) found that coyote densities and litter sizes in the Lamar Valley were

directly correlated with the amount of elk carcass biomass (carrion).

The hypothesized negative effect of wolf removal on snowshoe hares and lynx that we describe here could be exacerbated by climate change. In the high-elevation regions of the conterminous US where lynx still occur, deep winter snow provides these boreal specialists with a competitive advantage over coyotes, which have a higher foot-load (Murray and Boutin 1991, Crête and Lariviere 2003). Accordingly, while both species can overlap where snow is deep (Kolbe et al. 2007), coyotes have been shown to be more abundant during winter than lynx at lower elevations where snow is shallow and the energetic cost of movement is affected by snow (Murray and Boutin 1991). Thus, if climate change results in warmer and less severe winters, declining snow pack could allow coyotes (released by the absence of wolves) to exploit hares at higher elevations. Accordingly, additional studies, with and without wolves, that elucidate the winter sympatry among southern coyotes, lynx, and hares at high elevations are required to test for this scenario. Results of this research could be important for lynx conservation efforts in the conterminous US (Kolbe et al. 2007).

CONCLUSIONS

If the removal of wolves initiated trophic and competitive adjustments resulting in the decline of hare and lynx populations in southern latitudes, would the restoration of this apex predator help their recovery? Based on the above considerations, we hypothesize that the answer is yes, but we are unsure as to what extent and how long it might take. A recovery of long-absent wolf populations could potentially set off a chain of events triggering a long-term decrease in coyotes and ungulates, recovery of previously degraded native plant communities, and eventually an increase in hares and possibly other leporids as well. Furthermore, we think the answer is at least partially dependent upon whether wolves are allowed to achieve ecologically effective populations (Soulé et al. 2003) where they recolonize or are reintroduced. For example, aggressive wolf harvesting may have important negative effects on hares and lynx as described above, as well as on other species of concern. We encourage managers and policy makers to consider the potential for the types of ecological cascades hypothesized herein when 1) significantly altering or fragmenting habitat via intensive herbivory from high numbers of livestock or wild ungulates, as well as from other management practices (e.g., logging), and 2) designing and implementing wolf and lynx management plans. Perhaps more importantly, we encourage ecologists to test—experimentally or with observational data—our hypotheses regarding community interactions originating with wolves, but manifested in the distribution and abundance of snowshoe hares and lynx. We have proposed mechanisms that involve food of hares (via ungulate densities), predation on hares (coyote populations released from top-down control by wolves and food subsidized by ungulates and humans), and behavioral–physiological effects on hares via temporally sustained predation and harassment by facultative hare predators. We propose exacerbation of these effects by

an abiotic factor: altered patterns of snow depth and hardness in the face of climate change. All of these hypotheses are testable, at least indirectly.

Where wolf restoration is the objective, we believe that it is especially important to consider the ecological roles of these top predators in the ecosystem, rather than focusing solely on their demography (Estes et al. 2009). Accordingly, wolf recovery criteria in regions where hares and lynx occur can and should include measures of coyote densities, to index predation on hares, and the recruitment of woody browse species, which provide food and cover for hares.

LITERATURE CITED

Aubry, K. B., G. M. Koehler, and J. R. Squires. 2000. Ecology of Canada lynx in southern boreal forests. Pages 373–396 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R., Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Bailey, V. 1930. Animal life of Yellowstone National Park. Charles C. Thomas, Springfield, Illinois, USA.

Bekoff, M. 1977. *Canis latrans*. Mammalian Species 79:1–9.

Bekoff, M., and E. M. Gese. 2003. Coyote (*Canis latrans*). Pages 467–481 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Berger, J. 2008a. Undetected species losses, food webs, and ecological baselines: a cautionary tale from the Greater Yellowstone Ecosystem, USA. Oryx 42:139–142.

Berger, J. 2008b. Extant or extinct? White-tailed jack rabbits and Yellowstone's food web. Oryx 42:176.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76:1075–1085.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401–2414.

Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs 79:371–394.

Bryant, J. P., T. P. Clausen, R. K. Swihart, S. M. Landhausser, M. T. Stevens, C. D. B. Hawkins, S. Carriere, A. P. Kirilenko, A. M. Veitch, R. A. Popko, D. T. Cleland, J. H. Williams, W. J. Jakubas, M. R. Carlson, K. L. Bodony, M. Cebrian, T. F. Paragi, P. M. Picone, J. E. Moore, E. C. Packee, and T. Malone. 2009. Fire drives transcontinental variation in tree birch defense against browsing by snowshoe hares. American Naturalist 174:13–23.

Bunnell, K. D., J. T. Flinders, and M. L. Wolfe. 2006. Potential impacts of coyotes and snowmobiles on lynx conservation in the Intermountain West. Wildlife Society Bulletin 34:828–838.

Buskirk, S. W. 1999. Mesocarnivores of Yellowstone. Pages 165–187 in T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Buskirk, S. W., L. F. Ruggiero, and C. J. Krebs. 2000. Habitat fragmentation and interspecific competition: implications for lynx conservation. Pages 83–100 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Crête, M., and S. Lariviere. 2003. Estimating the costs of locomotion in snow for coyotes. Canadian Journal of Zoology 81:1808–1814.

Estes, J. A., M. T. Tinker, and J. L. Bodkin. 2009. Using ecological function to develop recovery criteria for depleted species: sea otters and kelp forests in the Aleutian Archipelago. Conservation Biology 24:852–860.

Federal Register. 2000. Endangered wildlife and plants; determination of threatened status for the contiguous U.S. distinct population segment of the Canada lynx and related rule. Federal Register 65:16052–16086.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. Canadian Journal of Zoology 74:769–783.

Gompper, M. E., and A. T. Vanak. 2008. Subsidized predators, landscapes of fear and disarticulated carnivore communities. Animal Conservation 11:13–14.

Griffin, P. C., and L. S. Mills. 2009. Sinks without borders: snowshoe hare dynamics in a complex landscape. Oikos 118:1487–1498.

Gunther, K. A., R. A. Renkin, J. C. Halfpenny, S. M. Gunther, T. Davis, P. Schullery, and L. Whittlesey. 2009. Presence and distribution of white-tailed jackrabbits in Yellowstone National Park. Yellowstone Science 17:24–32.

Henke, S. E., and F. C. Bryant. 1999. Effects of coyote removal on the faunal community in western Texas. Journal of Wildlife Management 63:1066–1081.

Hodges, K. E. 2000*a*. The ecology of snowshoe hares in northern boreal forests. Pages 117–162 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Hodges, K. E. 2000*b*. Ecology of snowshoe hares in southern boreal and montane forests. Pages 163–206 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Hodges, K. E., L. S. Mills, and K. M. Murphy. 2009. Distribution and abundance and snowshoe hares in Yellowstone National Park. Journal of Mammalogy 90:870–878.

Keesing, F. 2000. Cryptic consumers and the ecology of the African savanna. BioScience 50:205–215.

Keith, L. B. 1963. Wildlife's ten-year cycle. University of Wisconsin Press, Madison, USA.

Koehler, G. M., B. T. Maletzke, J. A. Von Kienast, K. B. Aubry, R. B. Wielgus, and R. H. Naney. 2008. Habitat fragmentation and the persistence of lynx populations in Washington State. Journal of Wildlife Management 72:1518–1524.

Kolbe, J. A., J. R. Squires, D. H. Pletscher, and L. F. Ruggiero. 2007. The effect of snowmobile trails on coyote movements within lynx home ranges. Journal of Wildlife Management 71:1409–1418.

Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair. 2001. What drives the 10-year cycle of snowshoe hares? BioScience 51:25–35.

Leopold, A., L. K. Sowls, and D. L. Spencer. 1947. A survey of over-populated deer ranges in the United States. Journal of Wildlife Management 11:162–183.

Litvaitis, J. A., and D. J. Harrison. 1989. Bobcat–coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology 67:1180–1188.

MacDonald, S. O., and J. A. Cook. 2009. Recent mammals of Alaska. University of Alaska Press, Fairbanks, USA.

Merkle, J. A., D. R. Stahler, and D. W. Smith. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology 87:56–63.

Murie, A. 1940. Ecology of the coyote in the Yellowstone. Fauna of the national parks of the United States. U.S. Government Printing Office, Washington, D.C., USA.

Murie, A. 1951. Coyote food habits on a southwestern cattle range. Journal of Mammalogy 32:191–195.

Murray, D. L. 2000. A geographic analysis of snowshoe hare population demography. Canadian Journal of Zoology 78:1207–1217.

Murray, D. L., and S. Boutin. 1991. The influence of snow on lynx and coyote movements: does morphology affect behavior? Oecologia 88:463–469.

Murray, D. L., T. D. Steury, and J. D. Roth. 2008. Assessment of Canada lynx research and conservation needs in the southern range: another kick at the cat. Journal of Wildlife Management 72:1463–1472.

Niebauer, T. J., and O. J. Rongstad. 1977. Coyote food habits in north-western Wisconsin. Pages 237–251 *in* R. L. Phillips and C. Jonkel, editors. Proceedings of the 1975 Predator Symposium. Montana Forestry and Conservation Experimental Station, Missoula, USA.

O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology 79:1193–1208.

O'Donoghue, M., E. J. Hofer, and F. I. Doyle. 1995. Predator versus predator. Natural History 104:6–9.

Parker, G. 1995. Eastern coyote. Nimbus, Halifax, Nova Scotia, Canada.

Presnall, C. C. 1948. Applied ecology of predation on livestock ranges. Journal of Mammalogy 29:155–161.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

Ripple, W. J., T. P. Rooney, and R. L. Beschta. 2010. Large predators, deer, and trophic cascades in boreal and temperate ecosystems. Pages 141–161 *in* J. Terborgh and J. Estes, editors. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, D.C., USA.

Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. Journal of Animal Ecology 78:1249–1258.

Soulé, M. E., J. A. Estes, J. Berger, and C. Martinez del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17:1238–1250.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.

U.S. Fish and Wildlife Service. 2000. Determination of threatened status for the contiguous U.S. distinct population segment of the Canada lynx and related rule; final rule. Federal Register 65:16051–16086.

Van Valkenburgh, B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: *Canivora*): evolutionary interactions among sympatric predators. Paleobiology 17:340–362.

Weaver, J. 1979. Influence of elk carrion upon coyote populations in Jackson Hole, Wyoming. Pages 152–157 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: ecology, behavior, and management. University of Wyoming Press, Laramie, USA.

Wirsing, A. J., T. D. Steury, and D. L. Murray. 2002. A demographic analysis of a southern snowshoe hare population in a fragmented habitat: evaluating the refugium model. Canadian Journal of Zoology 80:169–177.

Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecological Monographs 50:111–130.

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