Widespread Mesopredator Effects After Wolf Extirpation

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Abstract

Herein, we posit a link between the ecological extinction of wolves in the American West and the expansion in distribution, increased abundance, and inflated ecological influence of coyotes. We investigate the hypothesis that the release of this mesopredator from wolf suppression across much of the American West is affecting, via predation and competition, a wide range of faunal elements including mammals, birds, and reptiles. We document various cases of coyote predation on or killing of threatened and endangered species or species of conservation concern with the potential to alter community structure. The apparent long-term decline of leporids in the American West, for instance, might be linked to increased coyote predation. The coyote effects we discuss could be context dependent and may also be influenced by varying bottom-up factors in systems without wolves. We make recommendations for ecological research in light of ongoing wolf recovery in parts of the West. Strong ecological effects of wolf repatriation may not occur outside of large reserves where wolves are prevented from achieving ecologically effective densities. Finally, we advocate for more studies relating to the management of coyotes that compare exploited and unexploited populations and evaluate the influence of anthropogenic food subsidies on coyote densities.

Keywords: wolves, coyotes, mesopredator release, predation, trophic cascades

1. Introduction

Humans have a long history of altering populations of native animal species, substituting domestic forms for wild taxa, influencing food webs, and modifying interactions among species. On a worldwide basis, humans have persecuted large predators for centuries, reducing their distributions and abundances. The removal of these apex predators from much of the natural world has had diverse direct and indirect effects, oftentimes manifested through long and complex interaction chains (e.g. Estes et al., 2011). Typically, our understanding of the details of these indirect effects is still poorly known. Loss of large predators has been linked to irruptions of herbivore prey (Beschta and Ripple, 2009) and of smaller predators (Ritchie and Johnson, 2009). The irruption of smaller predators after extirpation of larger ones is known as mesopredator release (Crooks and Soulé, 1999). Mesopredators typically are efficient hunters that are buffered against population collapse by their capacity to switch among prey species (Prugh et al., 2009). Thus, released mesopredators often achieve densities that are sufficiently high and persistent to drive the decline or extinction of prey populations, and affect community structure and stability (Holt and Lawton, 1994; Prugh et al., 2009; Loehle and Eschenbach, 2012).

In North America and Eurasia, researchers have found that through additive effects wolves (*Canis lupus*) with sympatric bears (*Ursus arctos* and/or *U. americanus*) generally limit densities of cervids (Crête et al., 1999; Peterson et al., 2003; Ripple and Beschta, 2012). Across a variety of environments, wolf and bear extirpation can therefore lead to cervid irruptions and a variety of ecological cascades (Berger et al., 2001; Beschta and Ripple, 2009). These cervid irruptions have been documented to have cascading impacts on plant biomass, vertebrate and invertebrate species abundance, and stream hydromorphology (Berger et al. 2001, Hebblewhite et al. 2005, Ripple and Beschta 2006; but see Mech, 2012). Whereas much is known about irrupting herbivore prey in the American West, there is little work identifying the ecological effects of released mesopredators after wolf extirpation, specifically those of irrupting coyote (*Canis latrans*) populations (Berger et al., 2008; Miller et al., 2012). However, studies from other regions and continents demonstrate that the maintenance of interactions between top predators and mesopredators can play a pivotal role in structuring ecosystems and sustaining biodiversity (Ritchie and Johnson, 2009). For example, this cascading process has been shown for dingoes (*Canis lupus dingo*) and red foxes (*Vulpes vulpes*) in Australia (Letnic and Dworjanyn, 2011) and Eurasian lynx (*Lynx lynx*) and red foxes in Scandinavia (Elmhagen et al., 2010). Moreover, in Minnesota, increases in the gray wolf population have led to a cascade among carnivores whereby wolves suppress coyotes and indirectly release red fox populations (Levi and Wilmers, 2012).

The main objectives of this paper are to 1) develop and investigate hypotheses regarding the community-level effects of wolf extirpation in the American West, with particular focus on effects mediated by changes in the distribution and abundance of smaller coyotes, and 2) propose a research agenda to test these hypotheses. Our study area consists of the eleven most westerly states in the conterminous United States (>3 million square km). We selected this region because it is mostly comprised of federal public lands (Fig. A1) with large expanses of habitat dominated by forest, shrub, grass, and desert land covers. Livestock grazing allotments are ubiquitous on these public lands;

logging and mining are also common, but urban areas and cropland are negligible except on private lands within these states.

Below, we first review the historical relationship between coyotes and wolves. Next, we describe potential ecological effects of coyotes with special focus on leporids, which are often an important component of this carnivore's diet. We end by discussing possible interacting bottom-up factors and make recommendations for more research.

2. Historical relationship between wolves and coyotes

Interspecific competition between wolves and coyotes has been well documented, and is to be expected, based on the morphological similarity of the two species, dietary overlap, and a difference in body sizes of a factor between 2-5 (Donadio and Buskirk, 2006). This ratio of body sizes predisposes wolves and coyotes to a high likelihood of interference competition, including interspecific killing (Donadio and Buskirk, 2006), with the coyote being the consistent loser in these interactions. Although coyotes may benefit from carrion subsidies provided by wolves (Wilmers et al., 2003), multiple lines of evidence described below show that where wolves are abundant and ecologically effective, coyotes are absent, occur at low density, or alter their activity patterns to avoid wolves.

Prior to European settlement, coyotes were reportedly uncommon throughout much of the West (Parker, 1995) such as the Yellowstone area (Schullery and Whittlesey, 1992), but common in the prairies and grasslands of Midwest (Parker, 1995). The American West was settled and livestock were added to the landscape mostly during the second half of the 19th and early 20th century. During that time, large predators were the targets of widespread eradication efforts over much of the American West (Dunlap, 1988). In 1915, the U. S. Congress authorized eliminating any remaining large predators. As part of this program, the United States Biological Survey systematically killed wolves, coyotes, and other predators. Wolves were effectively extirpated from nearly all the western contiguous United States by the 1930's (Fig. 1a). This period also coincided with extensive management efforts to reintroduce ungulates to historical ranges. At least partially due to wolf extirpation, wild ungulate irruptions soon followed, with most population increases taking place in the West between 1935 and 1945 (Fig. 1b). Coyote harvest numbers increased dramatically after wolf extirpation in the West as well (Fig. 1c).

Aldo Leopold and his son A. Starker Leopold initiated wildlife studies in the 1930s in the relatively pristine Sierra Madre Mountains of Northern Mexico. Aldo Leopold (1937) reported "There are no coyotes in the [Sierra Madre] mountains". Later, Starker Leopold (1949) wrote, "One interesting sidelight on predator relationships was the *total absence of coyotes* [emphasis in original] in the wild areas occupied by wolves". Later, he documented increased coyote abundance as wolves were decreasing in the Sierra Madres (Leopold, 1959). As a result of his observations in Mexico, Aldo Leopold (1937) developed a hypothesis regarding the increasingly abundant coyote after wolf extirpation in much of the western United States. He wrote:

> "There are no coyotes in the [Sierra Madre] mountains, whereas with us there is universal complaint from Alaska to New Mexico that the coyote has invaded the high country to wreak havoc on both game and livestock. I submit for conservationists to ponder the question of whether the wolves have not kept the coyotes out? And whether the presence of a normal complement of predators is not, at least in part, accountable for the absence of [coyote] irruption?"

Scientific research – some of it experimental – supports the view that coyotes are typically suppressed by wolves, with coyotes being absent or at low densities in wolf-dominated systems (Stenlund, 1955; Pimlott and Joslin, 1969; Berg and Chesness, 1978; Fuller and Keith, 1981; Thurber et al., 1992; O'Donoghue et al., 1997; Ballard et al., 2001; Berger and Gese, 2007; Levi and Wilmers, 2012). For example, the range of the coyote expanded after gray wolf reductions/extirpations in parts of the American West, Midwest, and Northeast, and after the near elimination of the red wolf (*Canis rufus*) in the southeast (Gier, 1975; Parker, 1995).

On the Kenai Peninsula of Alaska, wolves were extirpated by 1915, coyotes colonized the area by 1926, and the latter species soon after achieved "unique abundance" prompting federal control (Thurber et al., 1992). Furthermore, coyotes were reduced in distribution and abundance after wolves recolonized the Kenai in the 1960s (Thurber et al., 1992). Likewise, Ballard et al. (2001) state, "In these systems [Alaska and British Columbia], wolves have effectively eliminated coyotes as serious predators of deer".

In northern Minnesota, fewer coyotes were bountied in the major wolf range counties compared to an adjacent region to the south with lower wolf densities (Stenlund, 1955). In central Minnesota, Berg and Chesness (1978) found few coyotes where wolves were well established and that coyotes "generally avoided the wolf-occupied range".

During 16 years of field work that started in 1979 in Wood Buffalo National Park, Alberta, numerous wolves were observed, but only one coyote was detected (Carbyn, 2003). Moreover, coyotes were reported to be common in this park during an earlier period of wolf control (Carbyn, 2003). Similarly, in Algonquin Park, Ontario, an area with high wolf densities, no coyotes were detected, but they were common in adjacent areas outside the park where there were no wolves (Pimlott and Joslin, 1969). With no opportunities for immigration, coyotes were driven to extinction on Isle Royale National Park in Lake Superior soon after the colonization of the island by wolves over the ice in 1948-49 (Peterson, 1995).

In Yellowstone National Park coyotes declined by 39% after wolf restoration, and mean densities of coyotes were 33% lower at abundant wolf sites in Grand Teton National Park (Berger and Gese, 2007). Berger and Gese (2007) suggested that interference competition with wolves has resulted in localized population reductions, but not drastic overall suppression of coyote populations, in the Greater Yellowstone Ecosystem. Their findings may in fact be conservative, however, given that most of the coyotes reported on by Berger and Gese (2007) were within < 4 km of well-traveled roads, which are used by coyotes as refuges from wolves. Indeed, on the Kenai Peninsula, Thurber et al. (1992) found that wolves caused 67 % of coyote deaths, and based on an index (coyote/wolf capture ratio), coyotes were 14 times more abundant near roads than away from them. It appears that coyotes use roaded areas as an antipredator defense (human shielding) against wolves because wolves avoid roads due to higher levels of human disturbance (Thurber et al., 1992).

Despite an extensive and decades-long control effort killing millions of coyotes, the coyote has thrived in the West (Bekoff and Gese, 2003). Indeed, after wolf extirpation, densities of coyotes varied temporally and spatially with control measures and other environmental factors (Knowlton and Gese, 1995). One of the most effective control measures involved the use of sodium monofluoroacetate (compound 1080) baiting; this approach was used in the western states between 1948 and 1972 (Cain et al. 1972). By the 1970's, Knowlton (1972) estimated that coyote densities generally ranged from 0.2-0.4 km^2 over a large portion of the western United States. Using 0.3 coyotes per km^2 for the 11 western states comprising over 3 million square km results in roughly 1 million coyotes present now in the West. This density estimate is consistent with what field studies have found including 0.4-0.5/km^2 in Oregon (Dunbar and Giordano, 2002), 0.30/km^2 in Colorado (Gese et al., 1989), and 0.27/km^2 in Montana (Pyrah, 1984).

When coyotes are food subsidized near urban areas (Gehrt and Riley, 2010), significantly higher densities have been recorded, such as 2.4-3.0/km^2 in California (Fedriani et al., 2001). Along the Baja California coast, Coyote populations were 2.4–13.7 times denser than in adjacent inland areas that did not receive marine input as food subsidies (Rose and Polis, 1998). Conversely, with coyotes co-existing with wolves in the Yukon, coyote densities were much lower and ranged from 0.014-0.090/km^2, averaging approximately 0.038/km^2 (O'Donoghue et al., 1997), nearly an order of magnitude lower in density than estimated for the American West above. Lower productivity in the Yukon might account for part of these differences in coyote densities.

An alternative explanation for coyote expansion in the American west is forest harvesting. During the same period when wolves were being exterminated, humans were also logging forests and clearing land. Coyotes attain high densities in open areas, and much of their original distribution in North America was prairie and other open habitat (Parker, 1995). Accordingly, these landscape changes were conducive to coyote populations. Yet, wolves have been reported suppressing coyotes in areas both with forest harvesting (Stenlund, 1955; Berg and Chesness, 1978; Fuller and Keith, 1981; Thurber et al., 1992; Ballard et al., 2001; Levi and Wilmers, 2012) and in parks without forest harvesting (Peterson, 1995; Berger and Gese, 2007). Thus, habitat changes associated with deforestation are unlikely to have been the sole reason for the observed coyote expansion.

3. Ecological effects of coyotes

The influence of coyotes in suppressing red foxes and other smaller mesopredators has been shown to increase waterfowl, small mammal and songbird abundance and diversity in some situations (Sovada 1993; Crooks and Soule, 1999; Henke and Bryant, 1999). In suburban and urban areas, research has indicated that coyotes perform a vital ecosystem service by suppressing feral cat populations and possibly those of other small carnivores whose densities might otherwise be higher than normal because of human food subsidies (Crooks and Soule, 1999; Ritchie and Johnson, 2009; Gehrt and Riley, 2010).Yet, in the absence of wolves and while subsisting on alternative foods of wild and domestic ungulates, plants, or human food sources, coyotes can exert intense predation pressure on their typical prey (Fig. 2, Table 1). Indeed, the coyote has been described as a major predator of a number of vertebrate taxa that are on the U. S. Fish and Wildlife Service (USFW) threatened and endangered species list and state lists for species of concern including large rodents, ungulates, carnivores, leporids, and birds (Table 1). These taxa include some preyed upon by coyotes for food (e.g. ground-nesting birds), and others that are not consumed – victims of interspecific killing [e.g. foxes, black-footed ferrets (*Mustela nigripes*)], the most extreme form of interference competition.

Table 1 provides evidence of proximate effects and not ultimate cause of threat for the listed species. We define proximate effect as a current cause of mortality for a species and ultimate cause as that which caused the species to originally decline. Of the two, ultimate causation is difficult to determine because species typically become rare before scientific investigation into their threat occurs. We note that the documentation of predation does not necessarily equate to predation impacts on the demography of prey. Therefore, the information in Table 1 does not imply that coyotes are the cause for endangerment of these declining species, and it is beyond the scope of this paper for us to speculate as to what degree coyotes contributed as a cause to their decline.

4. Where have all the rabbits gone?

Leporids (rabbits and hares), traditionally the primary prey of coyotes, have apparently declined precipitously in the West. For example, the number of jackrabbits (*Lepus spp.*) and snowshoe hares (*Lepus americanus*) harvested in Colorado have dramatically declined in recent decades (Fig. 3). We hypothesize that, in some places, this decline is at least partially linked to 1) mesopredator release of coyotes after wolf extirpation and 2) additional coyote release after the coyote poison, compound 1080, was banned in 1972 (Cain et al., 1972). Interestingly, both the decline of leporids in Colorado and the coyote effects on all the other species documented in Table 1 occurred after the 1972 ban of compound 1080, when coyote numbers likely increased in the West (Cain et al., 1972). Consistent with this scenario are data from Minnesota and evidence that a coyote population increase in the absence of wolves may have caused a decline in white-tailed jackrabbits (*Lepus townsendii*) there (Levi and Wilmers, 2012). The white-tailed jackrabbit,which also became rare after wolf extirpation in the Greater Yellowstone Area (Berger, 2008), is on species of concern lists in New Mexico, Oregon and Washington, and has recently been extirpated from western Kansas and parts of Nebraska (Armstrong et al., 2011). Meanwhile, the black-tailed jackrabbit (*Lepus californicus*) is currently on species of concern lists in Oregon, Washington, and Montana. Interestingly, black-tailed jackrabbit numbers increased following experimental coyote removal (Henke and Bryant 1999).

In Arizona, cottontail (Sylvilagus spp.) harvests have fallen precipitously over the past several decades from means of ~360,000 between 1961-1989 to ~80,000 for the 1990-2009 period (*t*-test, $p < 0.001$) (Arizona Game and Fish Department, 2001, 2009). In addition, the number of cottontails harvested per hunter day in Arizona decreased from an average of 1.4 for the period of 1961-1989 to 0.8 for the period of 1990-2009 (*t*-test, $p < 0.001$). This decline in both cottontail harvest and hunter success was apparently due to a combination of a long-term decline in the cottontail population and a decline in the total number of hunter days, the latter of which dropped by 60% between the two time periods (Arizona Game and Fish Department, 2001, 2009).

The range of the pygmy rabbit (*Brachylagus idahoensis*) is believed to have shrunk substantially relative to its historical extent in the American West (Verts and Carraway, 1998, p.p. 127-131). Recent research has linked continuing decline of the pygmy rabbit to heavy predation by coyotes, resulting in low survival in parts of Oregon where wolves are absent (Crawford et al., 2010). Finally, snowshoe hares also have likely decreased in the American West compared to historical times, and chronically low densities of snowshoe hares in this region may be at least partially the result of increased coyote predation after extirpation of the wolf (Buskirk et al., 2000). We note, however, that habitat fragmentation, fire suppression, and climate change are potential contributing factors.

Coyotes are highly effective predators of hares (Wirsing et al., 2002). Consequently, an increased density of coyotes in the absence of wolves may be causing exploitive competition with Canada lynx (*Lynx canadensis*) *via* higher predation pressure on hares and potentially contributing to the threatened status of this felid in some situations (Buskirk et al., 2000). Notably, in support of this idea on the Kenai Peninsula of Alaska, Stapes (1995) found exploitation competition for hares between coyotes and lynx. Furthermore, snowshoe hare harvests decreased in wolf-free southern Quebec soon after coyote colonization there in the 1970s (see Fig. 4 in Etcheverry et al., 2005). Likewise, in the wolf-free Elk Island National Park in central Alberta, ungulates and coyotes attained high densities (0.87-1.05 coyotes/km^2), while snowshoe hares apparently have remained at a relatively constant, low level without the population cycles that typify the region (Cairns, 1976; Keith and Windberg, 1978; Pruss, 2002).

We hypothesize that coyote predation, in combination with the effects of widespread livestock grazing causing reduced vegetative cover, may have contributed to reported leporid declines in the American West. This hypothesized cascade may not have played out in all areas and, instead, could have been context dependent due to interactions with other factors. Additional empirical evidence that directly links heavy coyote predation and/or ungulate herbivory to leporid declines is currently limited, however, and should be a focus of future research.

The purported effects of top predator removal on the abundance of leporids that we hypothesize for the American West are mirrored in the Strzelecki Desert, Australia. Here, the removal of dingoes (15-22 kg) has resulted in the irruption of red foxes (4-7 kg) and suppression of rabbits (*Oryctolagus cuniculus*). Where dingoes were common, foxes were rare and rabbits were abundant (Letnic et al. 2012). An analogous situation was discovered in Scandinavia involving a Eurasian lynx-red fox-hare (*Lepus timidus*) cascade (Elmhagen et al. 2010).

5. Interactions with other factors

Wolves appear to exert a dominant influence on coyote abundance, but bottom-up factors such as food availability and habitat structure could influence the abundance of coyotes once they are released from apex predator control (Ritchie and Johnson, 2009). The coyote is an opportunistic omnivore, with the composition of its diet determined by the availability of both plant and animal food. Coyote densities can be correlated with the densities of their primary prey (e.g. leporids) especially in systems where coyotes are not well supported by alternative prey or food subsidies (Knowlton and Gese, 1995; O'Donoghue et al., 1997). Thus, coyotes are well suited to exploit food subsidies/alternative prey and can maintain high and persistent densities if such subsidies or alternative prey are available.

The importance of food subsidies to coyote population dynamics has long been recognized; for example, Clark (1972) suggested that coyote populations may not vary with changes in the density of a single prey species when they are well supported by other prey or food types. For example, coyotes were found to exert significant predation pressure on the threatened desert tortoise (*Xerobates agassizii*), especially when they were subsidized by anthropogenic food sources (Esque et al., 2010).

Scavenging can have strong effects in structuring communities, especially when carrion subsidies are involved (Wilmers et al., 2003; Wilson and Wolkovich, 2011). High densities of domestic ungulates can help to maintain coyote abundance by providing food subsidies in the form of prey and carcasses for scavenging. In 2005, coyotes killed approximately 19,000 cattle (mostly calves) and 75,000 sheep in the 11 western states, equating to approximately 0.09% of all cattle and 2.6% of all sheep (Table A1). Furthermore, most of the nearly 1 million cattle that die annually of non-predator causes in the 11 western states are not disposed of, by rendering or other methods, and many of these become available to scavengers (Table A1). Available livestock carrion to coyotes has been widespread and is closely related to the density and spatial distribution of livestock in the American West (Fig. 4). Carrion from livestock has likely been increasing in recent years. For example, in 2005, 45% of all U.S. cattle mortalities were processed by renderers, but by 2010, only 23% of cattle mortalities were processed by rendering (Informa Economics Inc., 2010). Carrion can be a major source of food for coyotes (Sperry, 1934) and coyotes have been known to travel long distances (over 20 km) to feed on livestock carrion (Kamler et al., 2004).

In the absence of wolves, high densities of wild ungulates also can create large amounts of carrion that benefits coyotes. Weaver (1979) found that available elk carrion was a strong influence on coyote abundance in Wyoming, stating that "…coyotes were most numerous where carrion from winter-killed elk was most abundant". In addition to high domestic livestock densities (~8/km^2, Table 2, Fig. 4), elk populations (and resulting carrion) have been greatly increasing in western states in recent decades. Between 1984 and 2009, the elk population in the 11 western states grew from an estimated 710,000 to 1,010,000, a 42% increase (Rocky Mountain Elk Foundation, www.rmef.org). Thus, the ecological implications of a large carrion subsidy for coyotes are not trivial, and with more carrion from either domestic or wild ungulates, coyote pressure on native species in areas lacking wolves may be high.

Domestic and wild ungulates could also affect herbivorous coyote prey (e.g. leporids, rodents, ungulates) by decreasing cover and forage available to them. For example, high domestic and/or wild ungulate densities may have contributed to the apparent decrease in leporids shown in Fig. 3. The loss of cover has been linked to increases in avian and mammalian predation on small mammals and ground nesting birds, triggering population declines (Flowerdew and Ellwood, 2001). In Africa, likely because of reduced forage and/or cover availability, the density of small mammals was significantly higher where ungulates were absent compared to where these large herbivores were present (Keesing, 2000). In livestock-affected systems where coyotes are present, researchers have observed significantly greater success ($p < 0.001$) of coyotes capturing prey in short grass (< 10 cm high) cropped by cattle than in tall grass (10 – 100 cm high) (Bekoff and Wells,1986).

6. Suggested research agenda

The evidence we have presented thus far suggests a link between wolf decline and an expansion in the ecological influence of coyotes. Here, we propose several lines of ecological research that should help to more rigorously test this mesopredator release hypothesis. In general, the ecological consequences of species' loss and repatriation are difficult to determine without some form of perturbation. Accordingly, manipulative experiments represent potentially powerful tools with which to explore the influence of wolf extirpation or recovery on coyote effects. Such experiments could compare, for example, the consequences of coyote removals in areas where wolves are present versus where wolves have been extirpated.

Natural experiments that take advantage of spatial and temporal variation in wolf abundance are also likely to yield important insights into the degree to which the presence of this top predator depresses coyote effects. For example, with the reintroduction of wolves in the northern Rocky Mountains and the recolonization of wolves in Washington and Oregon (and potentially Utah and Colorado), we see opportunities for research to take advantage of these ongoing natural experiments.

Research could examine the extent to which wolf re-establishment 1) modifies interference and exploitative competition between coyotes and smaller mesopredators [e.g. foxes, lynx, bobcats (*Lynx rufus*)], and 2) triggers indirect effects on the abundance, survival and behavior of species preyed on by coyotes. In some situations, the return of wolves could coincide with increases in populations of smaller mesopredators formerly suppressed by coyotes, and increases in the abundance of coyote prey. We caution, however, that the strength of mesopredator cascades triggered by wolf recolonization may be context dependent. For example, cascade strength may hinge upon whether or not wolves can achieve "ecologically effective" densities and specifically on amounts of unfragmented wolf habitat, levels of wolf harvests and removals, as well as refugia (roads and built-up areas) and food subsidies available to coyotes. This research could be conducted temporally (before vs. after wolves) or spatially (areas with and without wolves). Some of this research has already been completed for pronghorn (*Antilocapra americana*) (Berger et al., 2008) and small mammals (Miller et al., 2012) with results consistent with our hypothesis.

We offer four additional types of ecological studies that should provide context for and strengthen the inferences drawn from the more direct assessments of the wolf-coyote relationship listed above. First, historical records such as time series that index predator/prey populations represent a potential source for understanding the wolf-coyote relationship (e.g., Levi and Wilmers, 2012). Second, in anticipation of continued changes to wolf abundance across the American West, there is need for systematic monitoring of the abundance of coyotes and their prey, both to establish reliable baselines and identify areas where the ecological impacts of this mesopredator are likely to be acute. Third, analyses of survival and cause-specific mortality should be applied to prey species and competitors that are allegedly suffering as a result of hyper-abundant coyotes to provide a better understanding of whether coyotes are the ultimate and/or proximate cause of declining prey over space and time. Fourth, it would be beneficial to establish studies to enumerate the abundance of mammalian mesopredators, leporids, etc. similar to or in conjunction with systematic annual bird surveys across the country using the citizen science approach. Systematic and long-term data on these mammalian taxa would provide much needed insights on predator/prey dynamics at a large scale.

Mountain lions (*Puma concolor*) are also a predator of coyotes. Several dietary studies of mountain lions throughout the West have found that they will regularly kill and eat coyotes (Logan and Sweanor, 2001). However, no study has evaluated whether mountain lions can suppress coyote populations. If so, then maintaining or increasing mountain lion densities could also reduce coyote populations or at least limit their ecological impacts to habitats not occupied by mountain lions. Additional research is also needed on the effects of multiple predators on coyotes and coyote prey. Are the effects of wolves and mountain lions on coyotes additive, or is there sufficient interference competition between these top carnivores that their respective impacts on coyotes are merely compensatory or depensatory? Answering these questions will be crucial to provide a more complete understanding of how carnivore competition could be used as a management tool to limit mesopredators, if such limitation is the goal.

Applied research is also needed to help advance coyote management in rural areas without wolves. While humans expend extraordinary resources to control coyote populations, these canids have proved incredibly adaptable (Bekoff and Wells, 1986). In spite of more than a century of persecution, coyotes have significantly increased in numbers and expanded their range. Although short-term endeavors can be effective, long-term efforts to suppress coyote populations in the American West have generally failed because they have not effectively controlled the breeding potential of coyote populations or stopped the emigration of coyotes from other areas (Knowlton et al., 1999; but for successful examples see Nunley, 2004 for Edwards Plateau in Texas and Cain et al., 1972 for compound 1080).

Indeed, control of coyote populations can actually release surviving individuals from density dependent processes such as intra-specific competition and lead to a compensatory increase in the number of breeding pairs, and an increase in litter sizes (Goodrich and Buskirk, 1995; Crabtree and Sheldon, 1999). For example, near the

Idaho/Nevada border, Davison (1980) compared coyote densities in a heavily exploited area to a lightly exploited area nearby and found no significant differences in their densities. Annual kill rates of coyotes in the heavily exploited area were 0.39 and 0.54, as compared to 0.25 and 0.12 for the lightly exploited area, for adults and juveniles respectively (Davison, 1980). Additional empirical evidence, namely that killing coyotes may not result in significantly lower coyote densities, comes from a coyote population study in south-central Washington. Coyotes in this Washington system were unexploited (not harvested), without food subsidies, and at relatively moderate densities based on scent-post-survey indices (index = 63) when compared to other areas of Washington (index = 109.5, n = 11 survey lines) and the 11 western states (index = 108.3, n = 222 survey lines) where coyotes were typically both food subsidized and exploited (Roughton, 1976; Springer, 1982). In a five-year demographic study in this same area, Crabtree (1989) estimated an average coyote density of 0.38-0.41/km^2, which is similar to exploited coyote population densities in the American West (as we describe in Section 2 above).

We suggest research on the combined effects of 1) not killing coyotes and 2) removing livestock carrion subsidies. Carrion could be sent to processors for rendering, thereby removing a critical food resource for coyotes (Sperry, 1934). These two treatments could be studied together for cumulative effects as long as they are also studied separately in order to avoid confounding results due to changing two variables at once. We hypothesize that in some cases where coyote populations are density dependent and livestock carrion is a limiting resource, coyote densities in areas without livestock carrion subsidies and without coyote killing will not be significantly higher than in areas with coyote killing and with these food subsidies. In systems without wolves, coyote social behavior (Crabtree and Sheldon, 1999) and food abundance (Knowlton and Gese, 1995) appear to set the upper limit on coyote densities. Also, unexploited coyote populations are functionally and structurally distinct from exploited ones, having very low reproductive rates and relatively low recruitment into the adult population (Knowlton and Gese, 1995).

The loss of large-bodied predators from ecological communities, or trophic downgrading, has been associated with marked changes to myriad ecosystems (Estes et al., 2011). Accordingly, we also advocate for studies on the ecological effects of potential red fox irruptions due to coyote control in areas without wolves (i.e. areas where the red fox is the largest canid predator) because in the absence of larger predators, red foxes have been shown to have increased and substantial effects on their prey (Elmhagen et al., 2010; Letnic et al., 2011). We hypothesize that removal of all or most coyotes from wolf-free areas may shift predatory impacts to other species such as waterfowl and smaller prey [i.e. prey of foxes, (see Sovada, 1993; Levi and Wilmers 2012)].

7. Conclusions

Could the loss of an apex predator, the wolf, be contributing to the decline and the potential extinction of other vertebrate species in parts of the American West? If so, is more research warranted? Our answer to both questions is “yes” based on the evidence presented above. Although generally convincing, some of the evidence we supply is hypothetical or preliminary in nature and we caution that our ideas need more testing. Indeed, we envisage our hypotheses as a catalyst for further examination of wolf-coyote-community dynamics. Notably, two such examinations in Grand Teton National Park have already shown that wolves appear to have positively affected populations of pronghorn and small mammals as mediated by coyotes (Berger et al., 2008; Miller et al., 2012). However, such wolf-coyote cascades may not occur outside of large reserves where wolves do not achieve ecologically effective densities because of a lack of habitat or they are removed due to conflicts with livestock or are hunted (Berger and Gese, 2007). These factors may also interact with any food subsidies and refugia available to coyotes to additionally dampen trophic cascades.

Our mesopredator release hypothesis is consistent with theory and observations on other continents suggesting that because apex predators often exert strong influences on smaller predators, the loss of an apex predator can trigger a cascade of secondary population changes and extinctions with far-reaching consequences for ecosystem structure and function (Holt and Lawton, 1994; Borrvall and Ebenman, 2006; Ritchie and Johnson, 2009; Letnic et al., 2012). Even if the degradation of habitat or other factors were the original primary (ultimate) causes for declines of some prey species, predation by hyper-abundant mesopredators (e.g. coyotes) could contribute to continued declines to extinction.

In terms of restoration, we suggest a research agenda focused on the ecosystem perturbations that caused the rarity or hyper-abundance of the vertebrates, thus working on the underlying causes (e.g. lost trophic interactions, food subsidies) rather than just the symptoms of the problem. Although, in cases of extreme habitat loss or fragmentation, this work will be rather challenging. Moreover, we suggest that, in areas with extensive public lands, restoring wolves to ecologically effective densities and/or reducing food subsidies to coyotes could be effective alternatives to lethal control of these mesopredators.

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Appendix A: Supplementary material

Supplementary data associated with this article can be found, in the online version, at

References

Arizona Game and Fish Department, 2001. Arizona Game Survey and Harvest Special Data Summary: Statewide Historical Data, 1919-2000. Phoenix, Arizona.

Arizona Game and Fish Department, 2009. Hunt Arizona: Survey, Harvest and Hunt Data for Big and Small Game. Phoenix, Arizona.

Armstrong, D.,M., Fitzgerald, J.P., Meaney, C.A., 2011. Mammals of Colorado, second edition. University Press of Colorado.

Atwood, J.L., Masey, B.W., 1988. Site fidelity of least terns in California. Condor 90, 389–394.

Ballard, W.B., Lutz, D., Keegan, T.W., Carpenter, L.H., deVos, J.C. Jr., 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildl. Soc. Bull. 29, 91–98.

Bekoff, M., Gese, E.M., 2003. Coyote (*Canis latrans*), in: Feldhamer, G.A., Thompson, B.C., Chapman, J.A. (Eds.), Wild Mammals of North America: Biology, Management, and Conservation, 2nd edition. Johns Hopkins University Press, Baltimore, pp. 467– 481.

Bekoff, M., Wells, M.C., 1986. Social Ecology and Behavior of Coyotes. Adv. Study Behav. 16, 251–337.

Berg, W.E., Chesness, R.A., 1978. Ecology of coyotes in northern Minnesota, In: Bekoff, M. (Ed), Coyotes: biology, behavior, and management. Academic Press, New York, New York, 384p.

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

Berger, J., Stacey, P.B., Bellis, L., Johnson, M.P., 2001. A mammalian predator–prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11, 967–980.

Berger, K.M., Gese, E.M., 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? J. Anim. Ecol. 76, 1075–1085.

Berger, K.M., Gese, E.M., Berger, J., 2008. Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. Ecology 89, 818–828.

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

Biggins, D.E., Godbey, J.L., Livieri, T.M., Matchett, M.R., Bibles, B., 2006. Post-release movements and survival of adult and young black-footed ferrets, in: Roellle, J.E., Miller, B.J., Godbey, J.L., Biggins, D.E. (Eds.), Recovery of the Black-footed Ferret--Progress and Continuing Challenges: U.S. Geological Survey Scientific Investigations Report 2005-5293. pp. 191–200.

Borrvall, C., Ebenman, B., 2006. Early onset of secondary extinctions in ecological communities following the loss of top predators. Ecol. Lett. 9, 435–442.

Bright, J.L., Hervert, J.J., 2005. Adult and fawn mortality of Sonoran pronghorn. Wildl. Soc. Bull. 33, 43–50.

Buskirk, S.W., Ruggiero, L.F., Krebs, C.J., 2000. Habitat Fragmentation and Interspecific Competition: Implications for Lynx Conservation, in: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and conservation of lynx in the United States. University Press of Colorado, pp. 83–100.

Cain, S.A., Kadlec, J.A., Allen, D.L., Cooley, R.A., Hornocker, M.G., Leopold, A.S., Wagner, F.H., 1972. Predator Control-1971. Report to the Council on Environmental Quality and the Department of the Interior, University of Michigan, Ann Arbor, Michigan.

Cairns, A.L., 1976. Distribution and food habits of moose, wapiti, deer, bison, and snowshoe hare in Elk Island National Park, Alberta. MS thesis, University of Calgary, Calgary, Canada.

Carbyn, L., 2003. The buffalo wolf: predators, prey, and the politics of nature, Smithsonian Books, Washington D.C., 248 p.

Clark, F.W., 1972. Influence of jackrabbit density on coyote population change. J. Wildl. Manage. 36, 343–356.

Crabtree, R., 1989. Sociodemography of an unexploited coyote population. PhD thesis, University of Idaho, Moscow.

Crabtree, R., Sheldon, J., 1999. Coyotes and canid coexistence in Yellowstone, in: Clark, T., Curlee, A.P., Minta, S., Kareiva, P. (Eds.), Carnivores in Ecosystems: The Yellowstone Experience. Yale University Press, New Haven, pp. 127–163.

Crawford, J.A., Anthony, R.G., Forbes, J.T., Lorton, G.A.. 2010. Survival and causes of mortality for pygmy rabbits (*Brachylagus idahoensis*) in Oregon and Nevada. J. Mammal. 91, 838–847.

Crête, M., 1999. The distribution of deer biomass supports the hypothesis of exploitation ecosystems. Ecology Letters 2, 223-227.

Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 563, 563–566.

Cypher, B.L., Spencer, K.A., 1998. Interactions between coyotes and San Joaquin kit foxes. J. Mammal. 79, 204–214.

Davidson, R.P., 1980. Effects of exploitation on some parameters of coyote populations. Ph.D. Thesis, Utah State University, Logan.

Donadio, E., Buskirk, S.W., 2006. Diet, morphology and interspecific killing in Carnivora. Am. Nat. 136, 524–536.

Drewien, R.C., Bouffard, S.H., Call, D.D., Wonacott, R.A., 1985. The Whooping Crane cross-fostering experiment: the role of animal damage control. Proceedings of the 2nd Eastern Wildlife Damage Control Conference, North Carolina State University, Raleigh, pp. 7-13

Dunbar, M.R., Giordano, M.R., 2002. Abundance and condition indices of coyotes on Hart Mountain National Antelope Refuge, Oregon. West. N. Am. Naturalist 62, 341–347.

Dunlap, T., 1988. Saving America’s Wildlife. Princeton University Press, Princeton.

Elmhagen, B., Ludwig, G., Rushton, S.P., Helle, P., Linden, H., 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. J. Anim. Ecol. 79, 785-794.

Esque, T.C., Nussear, K.E., Drake, K.K., Walde, A.D., Berry, K.H., Averill-Murray, R.C., Woodman, A.P., Boarman, W.I., Medica, P.A., Mack, J., Heaton, J.S., 2010.

Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endang. Species Res. 12, 167–177.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic Downgrading of Planet Earth. Science 333, 301–306.

Etcheverry, P., Crête, M., Ouellet, J-P., Rivest, L-P., Richer, M-C., Beaudion, C., 2005. Population dynamics of snowshoe hares in relation to furbearer harvest. J. Wildl. Manage. 69, 771–781.

Flowerdew, J.R., Ellwood, S.A., 2001. Impacts of woodland deer on small mammal ecology. Forestry 74, 277–287.

Fredriani, J.M., Fuller, T.K., Sauvajot, R.M., York, E.C., 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125, 258–270.

Fuller, T.K., Keith, L.B., 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. J. Mammal. 62, 403–405.

Gehrt, S.D., Riley, S.P.D., 2010. Coyotes (*Canis latrans*). In Gehrt, S.D., Riley, S.P.D., Cypher, B.L. (Eds.), Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, Maryland. pp. 79-95.

Gese, E.M., Rongstad, O.J., Mytton, W.R., 1989. Population dynamics of coyotes in southeastern Colorado. J. Wildl. Manage. 53, 174–181.

Goodrich, J.M., Buskirk, S.W., 1995. Control of abundant native species for conservation of endangered species. Cons. Biol. 9, 1357–1364.

Gier, H.T., 1975. Ecology and behavior of the coyote (*Canis latrans*), in: Fox, M.W. (Ed.), The Wild Canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Company, pp. 247–262.

Griffin, S.C., 2007. Demography and Ecology of a Declining Endemic: The Olympic Marmot. PhD Thesis, University of Montana, Missoula.

Hartman, C.A., Oring, L.W., 2009. Reproductive success of long-billed curlews (N*umenius americanus*) in Northeastern Nevada hay field. The Auk 126, 420–430.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86, 2135-2144.

Henke, S.E., Bryant, F.C., 1999. Effects of coyote removal on the faunal community in western Texas. J. Wildl. Manage. 63, 1066–1081.

Holt, R.D., Lawton, J.H., 1994. The ecological consequences of shared natural enemies. Ann. Rev. Ecol. Evol. Syst. 25, 495–520.

Informa Economics, Inc., 2011. A Profile of the North American Rendering Industry. National Renderers Association, Inc.

Kamler, J.F., Ballard, W.B., Gilliland, R.L., Lemons, P.R., Mote, K., 2003. Impacts of coyotes on swift foxes in northwestern Texas. J. Wildl. Manage. 67, 317–323.

Kamler, J.F., Ballard, W.B., Gilliland, R.L., Lemons, P.R., Mote, K., 2004. Coyote (*Canis latrans*) movements relative to cattle (*Bos Taurus*) carcass areas. West. N. Am. Naturalist 64, 53–58.

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

Keith, L.B, Windberg, L.A., 1978. A demographic anlaysis of the snowshoe hare cycle. Wildlife Monographs 58, 3-70.

Knowlton, F.F., 1972. Preliminary Interpretations of Coyote Population Mechanics with Some Management Implications. J. Wildl. Manage. 36, 369-382.

Knowlton, F.F., Gese, E.M., 1995. Coyote population processes revisited. Symposium Proceedings, Coyotes in the Southwest: A compendium of Our Knowledge, University of Nebraska, Lincoln, pp. 1-6.

Knowlton, F.F., Gese, E.M., Jaeger, M.M., 1999. Coyote Depredation Control: An Interface between Biology and Management. J. Range Manage. 52, 398-412.

Leopold, A., 1937. Conservationist in Mexico. Am. Forests 43, 118–120, 146.

Leopold, A.S., 1949. Adios, Gavián. Pac. Discovery 2, 4–13.

Leopold, A.S., 1959. Wildlife of Mexico: the game birds and mammals. University of California Press, Berkeley.

Letnic M, Dworjanyn SA. 2011. Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? Ecography 34, 827-835.

Letnic, M., Ritchie, E.G., Dickman, C.R., 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. Biol. Rev 87, 390–413.

Levi, T., Wilmers, C.C., 2012. Wolves-coyotes-foxes: a cascade among carnivores. Ecology 93, 921–929.

Littlefield, C.D., 1995. Demographics of a declining flock of greater sandhill cranes in Oregon. Wilson Bull.107, 667–674.

Loehle, C., Eschenbach, W., 2012. Historical bird and terrestrial mammal extinction rates and causes. Divers. Distrib. 18, 84–91.

Logan, A.L., Sweanor, L.L., 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington.

Mech, L.D., 2012. Is science in danger of sanctifying the wolf? Biological Conservation 150:143-149.

Miller, B., Harlow, H.J., Harlow, T., Biggins, D., Ripple, W.J., 2012. Trophic cascades linking wolves, coyotes, and small mammals. Can. J. Zool. 90, 70–78.

Nunley, G., 2004. Coyote in the Edwards Plateau of Texas-an update. Sheep and Goat Research Journal 19, 23-28.

O'Donoghue, M., Boutin, S., Krebs, C.J., Hofer, E.J., 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos 80, 150–162.

Parker, G. 1995. Eastern Coyote: The Story of Its Success. Nimbus Publishing, Halifax, Nova Scotia . 254 p.

Peterson R.O., 1995. The wolves of Isle Royale: a broken balance. Willow Creek Press, Minocqua, Minnesota.

Peterson, R.O., Vucetich, J.A., Page, R.E., Chouinard, A., 2003. Temporal and spatial aspects of predator-prey dynamics. Alces 39, 215–232.

Pimlott, D.H., Joslin, P.W., 1968. The status and distribution of the red wolf.

Transactions of the North American Wildlife Conference 33, 373–379.

Presnall, C.C., 1948. Applied ecology of predation on livestock ranges. J. Mammal. 29, 155–161.

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

Pruss, S.D. 2002. Ecology of coyotes (Canis latrans) in Elk Island National Park, Alberta, Canada. PhD thesis, University of Alberta, Edmonton, Alberta.

Pyrah, D., 1984. Social distribution and population estimates of coyotes in north-central Montana. J. Wildl. Manage 48, 679–690.

Ripple, W.J., Beschta, R.L., 2005. Linking Wolves to Plants: Aldo Leopold on Trophic Cascades. BioScience 55, 613–621.

Ripple, W.J., Beschta, R.L., 2006. Linking a cougar decline, trophic cascade, and a catastophic regime shift in Zion National Park. Biological Conservation 133, 397–408.

Ripple, W.J., Beschta, R.L., 2012. Large predators limit large mammal densities in northern forest ecosystems. European Journal of Wildlife Research 12, 733–742.

Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. 12, 982–998.

Rose, M.D., Polis, G.A., 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79, 998–1007.

Roughton, R.D., 1976. Indicies of predator abundance in the western United States, 1976. U.S. Department of Interior, Fish and Wildlife Service, Denver, Colorado, 124p.

Schullery, P., Whittlesey, L., 1992. The documentary record of wolves and related wildlife species in the Yellowstone National Park area prior to 1882, in: Varley, J.D., Brewster, W.G. (Eds), Wolves for Yellowstone? A report to the United States Congress, vol. 4, research and analysis. National Park Service, Yellowstone National Park, pp. 1–174.

Sovada, M.A., 1993. Differential effects of coyotes versus red foxes on duck nest success in managed uplands. Ph.D. Dissertation, North Dakota State University.

Sperry, C.C., 1934. Winter food habits of coyotes: a report of progress, 1933. J. Mammal. 15, 286–290.

Springer, J.T., 1982. Movement patterns of coyotes in south central Washington. J. Wildl. Manage. 46, 191-200.

Stenlund, M.H., 1955. A field study of the timber wolf (*Canis lupus*) on the Superior National Forest, Minnesota. Minnestota Department of Conservation, Technical Bulletin No. 4.

Stapes, W. R. III. 1995. Lynx and coyote diet and habitat relationships during a low hare population on the Kenai Peninsula. MS thesis, University of Alaska, Fairbanks, Alaska, USA.

Thurber, J.M., Peterson, R.O., Woolington, J.D., Vucetich, J.A., 1992. Coyote coexistence with wolves on the Kenai Penninsula, Alaska. Can. J. Zool. 70, 2494–2498.

USFW Service., 1983. Columbian white-tailed deer recovery plan. U. S. Fish and Wildlife Service, Portland, Oregon.

Van Vuren, D.H., 2001. Predation on Yellow-bellied Marmots (Marmota flaviventris). Am. Midl. Nat. 145, 94–100.

Verts, B.J., Carraway, L.N., 1998. Land Mammals of Oregon. University of California Press, Berkeley, pp. 359-362.

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

Wilmers, C.C., Crabtree, R.L., Smith, D., Murphy, K.M., Getz, W.M., 2003. Trophic facilitation by introduced top predators: gray wolf subsidies to scavengers in Yellowstone National Park. J. Anim. Ecol. 72, 909–916.

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: how carnivores and carrion structure communities. Trend. Ecol. Evol. 26, 129–135.

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

Table 1. Coyote predation effect size on threatened and endangered species in the American West as listed by the U.S. Fish and Wildlife Service and species of concern in the American West according to state Natural Heritage Programs. The information in this table does not imply that coyotes are the cause of the endangerment of these declining species.

Killed Species/Status	Effect Size	Reference
Black-footed ferret (*Mustela nigripes*) Endangered	Of 137 released ferrets, coyotes caused the most losses; at least 63% of 59 deaths.	Biggins et al. 2006
Pygmy rabbit (*Brachylagus idahoensis*) Endangered	Annual survival of pygmy rabbits was notably low with coyotes the most common cause of mortality.	Crawford et al. 2010
San Joaquin kit fox (*Vulpes macrotis mutica*) Endangered	Coyote predation was the main cause of kit fox mortality	Cypher and Spencer 1998
Columbian white-tailed deer (*Odocoileus virginianus leucurus*) Endangered	Coyotes took 23 of 40 radio-collared fawns during the summers of 1978, 1979, and 1980.	USFW Service 1983
Least tern (*Sterna antillarum*) Endangered	Nearly 100% of nesting attempts failed due to predation by coyotes.	Atwood and Massey 1988
Whooping crane (*Grus americana*) Endangered	Between 1975-84, 14 eggs and 23 to 58 flightless young whoopers were lost to predators, primarily coyotes	Drewien et al. 1985
Olympic marmot (*Marmota olympus*) Species of concern WA	All mortality appeared to be due to predation by coyotes and it is likely that coyotes are the primary driver of Olympic marmot declines.	Griffin 2007
Swift fox (*Vulpes velox*) Species of concern CO, MT, NM, WY	Foxes had low survival and predation by coyotes was the major cause of death.	Kamler et al. 2003
Sandhill crane (*Grus canadensis tabida*) Species of concern CO, OR, WA	Coyote predation was primarily responsible for low fledging success.	Littlefield 1995
Snowshoe hare (*Lepus americanus*) (*Lepus americanus klamathensis*) (*Lepus americanus seclusus*) (*Lepus americanus tahoensis*) Species of concern NM, CA, WY	The coyote was the number one predator of snowshoe hares. Among the known causes of predation, 44% were due to coyotes.	Wirsing et al. 2002
Long-billed curlew (*Numenius americanus*) Species of concern CO, OR	Predation, predominantly by large mammalian predators such as Coyotes, was the greatest cause of nest failure in Long-billed curlews.	Hartman and Oring 2009
Yellow-bellied marmot (*Marmota Flaviventris*) Species of concern NM	Coyotes were the most important predators on yellow-bellied marmots. Of the 97 marmots that died during the study, 47% were confirmed as caused by coyotes.	Van Vuren 2001

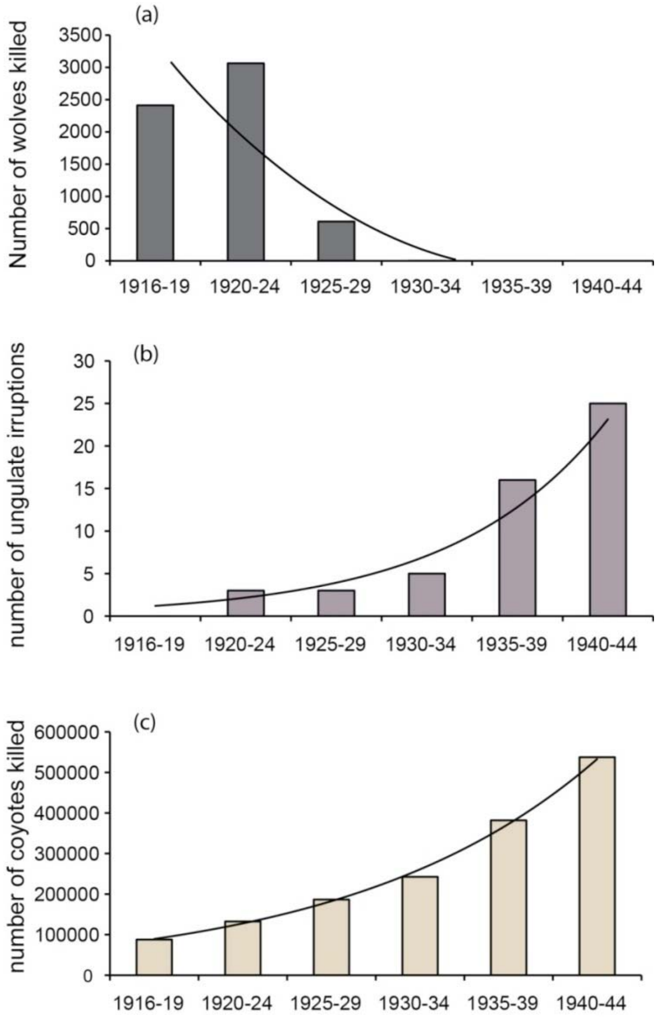

Fig. 1. (a) Number of wolves killed by the US Bureau of Biological Survey on and after 1915 in the western United States, (b) number of deer irruptions in the western United States, and (c) number of coyotes killed in the western United States by hunters supervised by the federal government. No wolf kills were reported by the US Bureau of Biological Survey after 1929. Note that this figure draws from different sources that index general population trends over time. Consequently, it cannot be used for cross-taxa comparisons of absolute abundance. Source (a) annual reports of the US Bureau of Biological Survey, (b) Ripple and Beschta 2005, and (c) Presnall (1948).

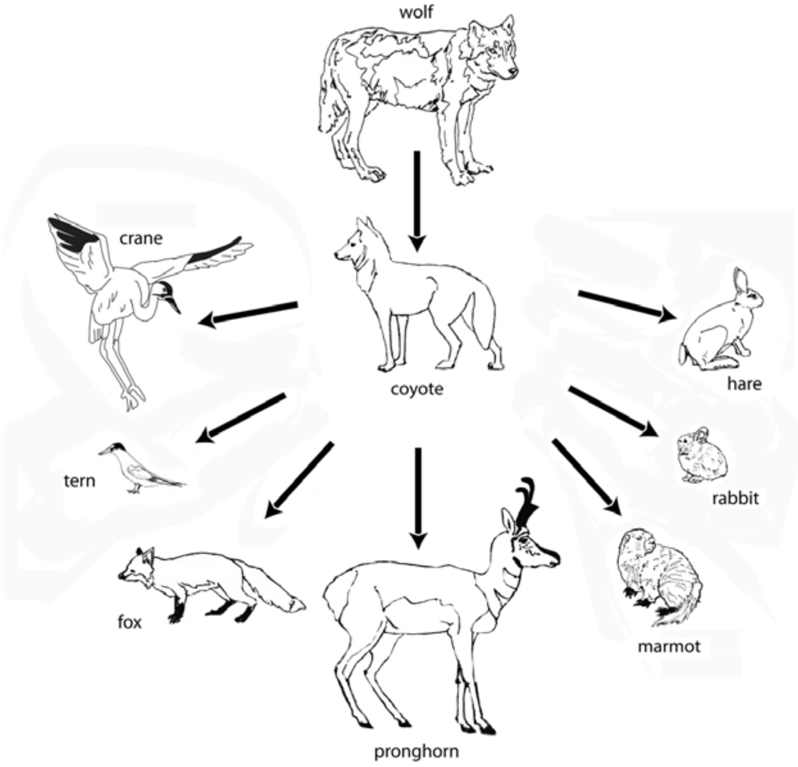

Fig. 2. Trophic linkages are shown among wolves, coyotes, and the prey of coyotes. Conceptually, the repatriation of wolves would cause decreases coyote populations and increases in coyote prey numbers, while the extirpation of wolves would cause increases in coyote populations and decreases in coyote prey numbers.

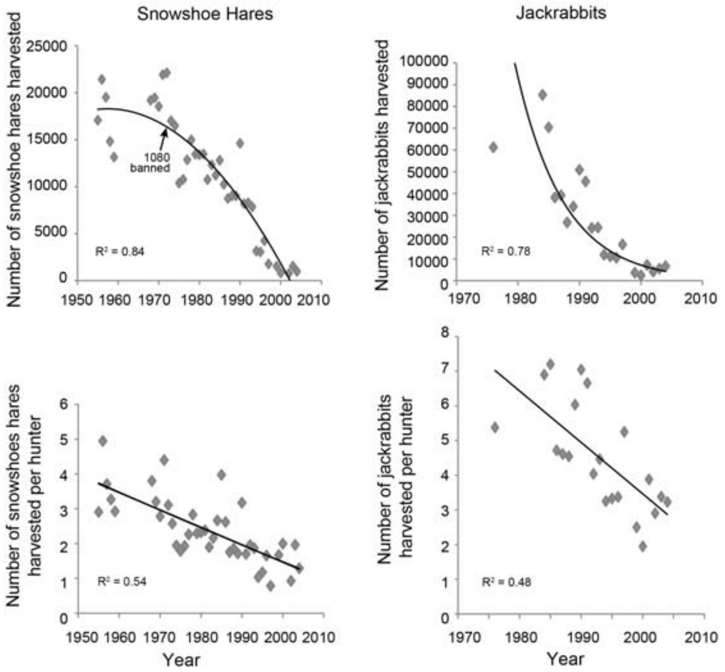

Fig. 3. Scatter diagrams showing a history of declining snowshoe hare (*Lepus americanus*) harvest (upper left) and jackrabbit (*Lepus townsendii*, *Lepus californicus*) harvest (upper right) for the state of Colorado. Hunter success (bottom set of graphs) for both snowshoe hare and jackrabbit hunters has also decreased over time. Note how hare harvest consistently declined after the highly effective coyote poison, compound 1080, was banned in 1972. Used together, the data on harvest trend and hunter success serve as an index of population trend, suggesting a long-term decline in snowshoe hares and jackrabbits. We hypothesize that the apparent decrease in snowshoe hare and jackrabbits is at least partially due to coyote predation in the absence of top-down forcing by wolves. Because other factors can contribute to harvest trend and hunter success, we suggest that the data presented here should be used with caution. For example, the number of hunters per year has significantly declined over time. Source: Colorado Division of Wildlife, unpublished data.

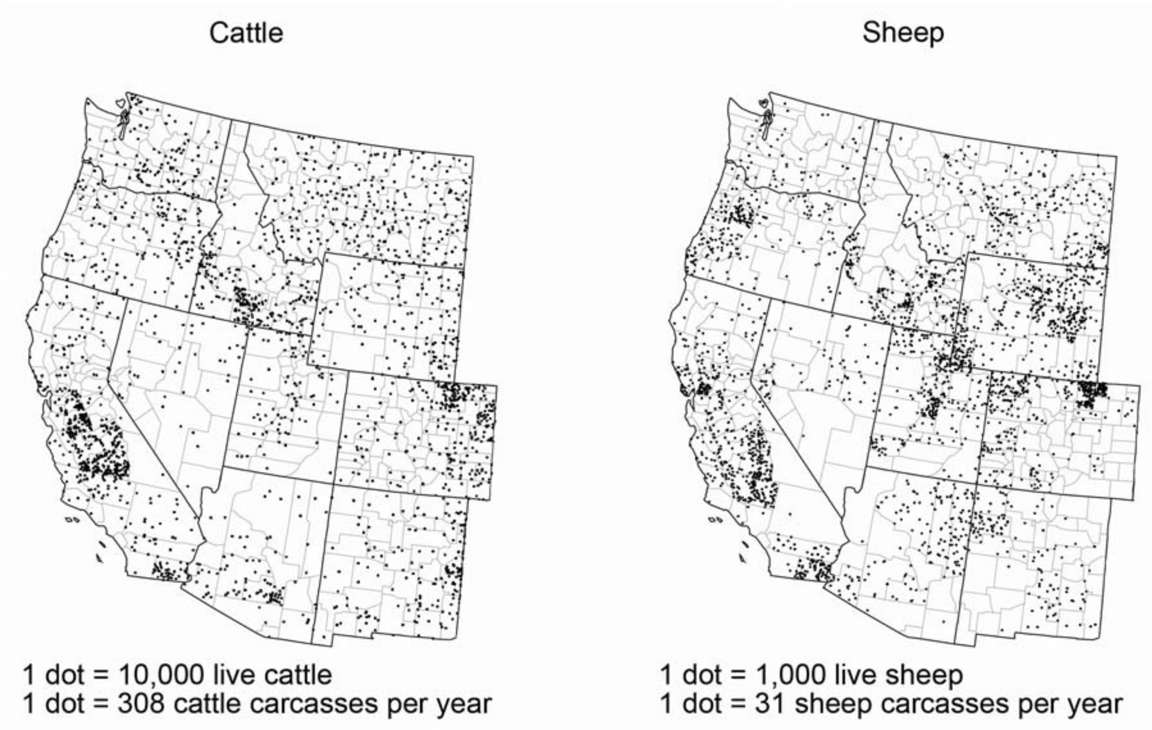

Fig. 4. Dot maps showing cattle (left) and sheep (right) live densities and estimated amounts of livestock carrion in the American West as of 2007. For cattle, one dot represents approximately 10,000 live individuals and 308 carcasses per year. For sheep, each dot represents approximately 1,000 live individuals and 31 carcasses per year. Based on the density and spatial arrangement of the dots, both livestock and livestock carrion are ubiquitous throughout most of the American West. Both of these sources provide a large and spatially distributed food subsidy to coyotes throughout the West. Carrion carcasses were estimated assuming a 4% rate of annual livestock mortality with 77% of carcasses not being rendered. Source: US Department of Agriculture, National Agricultural Statistics Service and Informa Economics Inc. (2011).

Appendix A: Supplementary material

Table A1. Livestock mortalities and livestock carrion estimates for the 11 western states[1].

	Cattle	Sheep	Total
Number of head	21,450,000	2,905,000	24,355,000
Total Deaths	859,000	213,000	1,072,000
Non-predator deaths	817,000	100,600	917,700
Predator deaths	41,900	112,400	154,300
Wolf-caused deaths	97	244	341
Coyote-caused deaths	19,000	74,500	93,500
Estimated carrion (kg/yr)	232,056,440	10,524,360	242,580,800

[1] Livestock and depredation data are from the U.S. Department of Agriculture for the years 2004 or 2005 (http://www.nass.usda.gov/). Wolf-caused deaths are from the USFW for 2005 for the northern Rockies only (http://www.fws.gov/mountain-prairie/species/mammals/wolf/). Potential carrion was determined by assigning a mass of 1,500 lbs (682 kg) for each of 338,000 adult cows that died in 2005, and by assigning a mass of 60 lbs (27 kg) for each of 91,000 adult sheep and 60 lbs (27 kg) for each of 122,000 lambs that died in 2004. Estimated carrion in kg/yr was set at 77% of the total mass of dead cattle and sheep because an estimated 23% of carcasses were rendered (Informa Economics Inc. 2011).

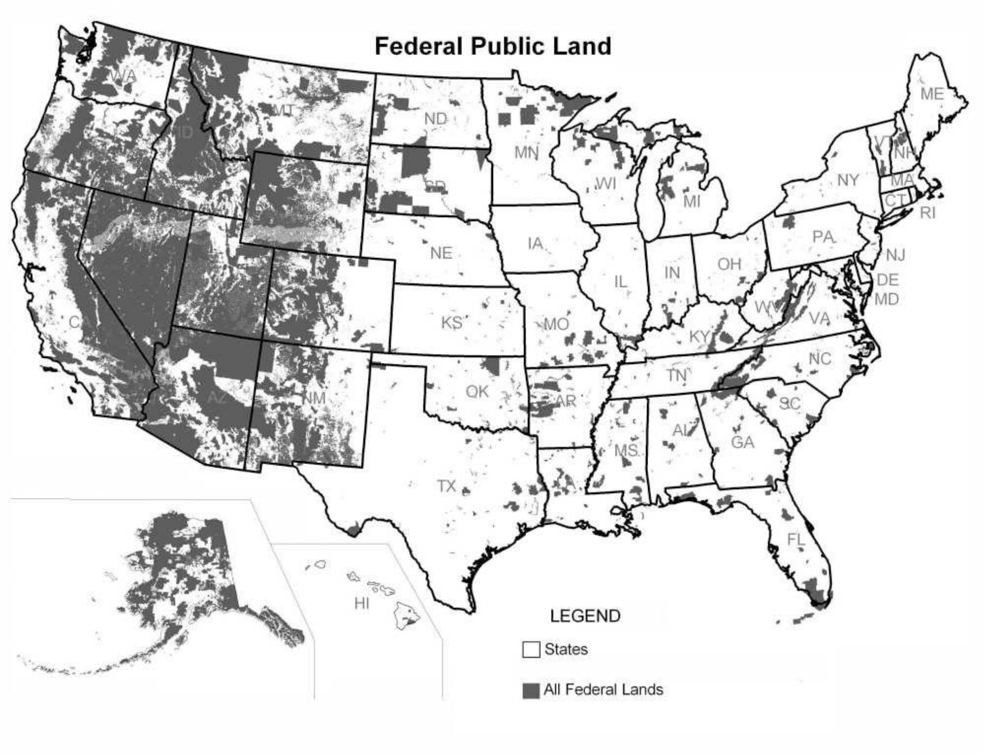

Fig. A1. Map of the United States showing all types of federal public land including Indian reservation land. The vast majority of public land in the conterminous United States is in our study area of the eleven western states of Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming. Source: USGS National Atlas. The map illustrates the vast extent of public lands in the West. These lands represent a significant amount of wildlife habitat and provide opportunities to study large predator, mesopredator, and prey interactions at large scales. Potential confounding factors such as urbanization and the cropland development are minimal on these public lands.