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Myths, Wishful Thinking, and Accountability in Predator Conservation and Management in the United States

Bernd Blossey[1]* *and Darragh Hare*[1,2]

[1] Department of Natural Resources and the Environment, Cornell University, Ithaca, NY, United States, [2] Wildlife Conservation Research Unit, Department of Zoology, The Recanati-Kaplan Centre, Oxford University, Tubney, UK, United Kingdom

Large predators are thought of as ecological keystone species, posterchildren of conservation campaigns, and sought-after targets of tourists and photographers. At the same time, predators kill livestock and huntable animals, and occasionally people, triggering fears and antipathy among those living alongside them. Until the 1960's government-sponsored eradication and persecution campaigns in the United States prioritized interests of livestock producers and recreational hunters, leading to eradication of wolves and bears over much of their range. Without large predators, subsidized by changes in agricultural practices and milder winters, ungulate populations erupted, triggering negative ecological impacts, economic damage, and human health crises (such as tick-borne diseases). Shifting societal preferences have ushered in more predator-friendly, but controversial wildlife policies, from passively allowing range expansion to purposeful reintroductions (such as release of wolves in Yellowstone National Park). Attempts to restore wolves or mountain lions in the U.S. and protecting coyotes appear to enjoy strong public support, but many state wildlife agencies charged with managing wildlife, and recreational hunters continue to oppose such efforts, because they perceive predators as competitors for huntable animals. There may be compelling reasons for restoring predators or allowing them to recolonize their former ranges. But if range expansion or intentional releases of large predators do not result in ecosystem recovery, reduced deer populations, or Lyme disease reductions, conservationists who have put their reputation on the line and assured decision makers and the public of the important functional role of large predators may lose public standing and trust. Exaggerated predictions by ranchers and recreational hunters of greatly reduced ungulate populations and rampant livestock killing by large carnivores may lead to poaching and illegal killing threatening recovery of predator populations. How the return of large carnivores may affect vegetation and successional change, ungulate population

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***Correspondence:**
Bernd Blossey
BB22@CORNELL.EDU

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size, other biota, livestock and human attitudes in different landscapes has not been appropriately assessed. Societal support and acceptance of living alongside predators as they expand their range and increase in abundance requires development and monitoring of social, ecological and economic indicators to assess how return of large predators affects human and animal and plant livelihoods.

Keywords: trophic cascades, conservation conflict, herbivory, ungulate, wildlife management

INTRODUCTION

Trophic cascades, specifically how large predators may regulate abundance of herbivores and structure the function of marine and terrestrial ecosystems, capture the fascination and imagination of scientists, conservationists, and naturalists alike (Terborgh and Estes, 2010). This idea of top-down regulation of ecosystem function with predation keeping herbivores in check, and the world green, was famously advanced by Hairston, Smith and Slobodkin (Hairston et al., 1960). The role of bottom-up versus top-down control of ecosystem function has been vigorously studied, analyzed and debated (Worm et al., 2002; Hatton et al., 2015; Moore and Schmitz, 2021; Renzi and Silliman, 2021). Not surprising, both are important, and the strength of trophic cascades varies widely and may be influenced by climate, ecosystem productivity and even biotic legacy effects (Borer et al., 2005; Melis et al., 2009; Wang et al., 2021). While questions about top-down vs bottom-up structuring of food webs and strength or weakness of trophic cascades will be researched and reported on for some time to come, we cannot simply assume that trophic cascades will exist or establish in all ecosystems, or under all circumstances. Regaining trophic structuring may be particularly challenging when large predators that were functionally eliminated return through range expansion or intentional introduction to fundamentally altered ecosystems, for example vastly different prey abundances or in densely settled human dominated landscapes (Estes et al., 2011).

Furthermore, allowing range expansion, facilitating introductions or maintaining large predators is challenging because they can be controversial neighbors, triggering emotional and forceful responses not only because of their impacts, but also because of different value orientations, power dynamics, or diverging ideas about appropriate land-use among different segments of society (Dickman, 2010; Redpath et al., 2015; Redpath et al., 2017). We are writing this paper about conservation and restoration of large predators at a time of shifting societal preferences regarding wildlife and biodiversity (Manfredo et al., 2021), although conflicts will certainly continue (Manfredo et al., 2017; Treves et al., 2017). Expanding ranges of large predators go along with shifting values and legal protections particularly in western Europe (Chapron et al., 2014), but also in North America (Wydeven et al., 2009; Smith et al., 2020). Neither one of us is a wildlife biologist and we come to this topic from different perspectives. BB has for decades worked on assessing impacts of invasive species and multiple stressors, development of biological control using insect herbivores, and assessment of impacts and management of white-tailed deer (*Odocoileus virginianus*) in eastern North America (Blossey, 1999; Dávalos et al., 2015; Nuzzo et al., 2017; Blossey et al., 2019). DH works on wildlife policy and governance, public perceptions of wild organisms and their conservation and the potential role of large predators in resolving persistent socio-ecological problems of large ungulate populations (Kirkland et al., 2021). We have explored how principles of public trust thinking could promote more ecologically and socially responsible wildlife decision-making (Hare and Blossey, 2014; Giacomelli et al., 2019; Pomeranz et al., 2021), and how acknowledging evolution as a structuring principle in human-human and human-wildlife interactions may help explain pro- and anti-conservation attitudes and behaviors (Hare et al., 2018; Curry et al., 2020).

We are both strong advocates of evaluating claims or hypotheses by collecting evidence using appropriate methods, whether that involves ecological networks, or socio-ecological systems (Blossey et al., 2021; Hare et al., 2021). Data can help society hold decision-makers/managers accountable, but at the same time we recognize that managers need to be required and enabled by appropriate metrics and resources to collect, archive and publish this information that guide their decisions. But decisions without data support, or not being revised with new information, can lead to negative ecological and social outcomes, for example in management of wildlife or introduced species that has led to persistent and lingering conflicts (Davis et al., 2011; Crowley et al., 2017). We recognize and acknowledge that data alone will be insufficient to resolve conflicts in wildlife management or conservation that are based on cultural differences. Data are never the only voice in the room when policy decisions are being made, and entrenched values or beliefs may override even the most sophisticated data. However, the loudest voices that tend to dominate lobbying efforts or social media campaigns are not necessarily representative majority opinions of citizens or residents. Consequently, making policy on frequently repeated claims by special interest groups that lack supporting evidence (social or ecological) does not bode well for democratic, fair, and just decision-making processes, conflict resolution, or evidence-led decisions.

We developed an interest in large predator (here defined as wolf, *Canis lupus*; bear, *Ursus spp*, and mountain lion, *Puma concolor*) conservation in the United States because these species may have an important role in managing impacts of white-tailed deer, mule deer (*O. hemionus*) or elk (*Cervus canadensis*; henceforth deer). At present abundances, deer have enormous negative impacts on species, ecosystems, local economies and

even human health over much of their range in North America (Côté et al., 2004; Rogers and McAvoy, 2018). In the U.S. state wildlife management agencies and their focus on recreational hunting have been unable to prevent or reduce deer populations to ecologically acceptable levels (Blossey et al., 2019; Reed et al., 2021; Nagy et al., 2022). Deer management itself, even without adding large predators to the mix, has led to pitched conflicts involving conservationists, residents, municipalities, farmers, ranchers, hunting advocates, animal rights and animal welfare interests with no easy resolution due to problems in the structure and governance of state wildlife agencies beholden to special interests (Frye, 2006; Cambronne, 2012; Sterba, 2012; Edelblutte et al., 2021). All sides in this conflict justify their positions by appealing to evidence regarding likely consequences (or lack thereof) in landscapes that harbor unprecedented numbers of deer and presently few but slowly increasingly numbers of large predators. Interestingly, this conflict does not include black bears, *U. americanus*, important predators of deer fawns, that are already abundant and widespread over much of North America, including in densely settled landscapes. Many of those advocating for a return of large predators claim that negative impacts of large deer populations would be greatly reduced. In contrast, those opposed to the return of large predators claim that deer hunting opportunities would be substantially reduced, and livestock producers would face large economic losses. While the importance of returning predators in reducing large herbivore populations appears to be seen as inevitable, the crux of the conflict is about whether deer herd reduction would benefit biodiversity or disrupt recreational hunting and profitability of livestock enterprises.

We were surprised to discover a paucity of conclusive evidence to back up any of the widespread claims - on both sides. We argue that, at present, the discourse surrounding large predator threats or benefits in the U.S. relies less upon evidence than it does on myths and wishful thinking. Based on the currently available evidence (not just from the United States) large predators, despite their ability to kill ungulates and livestock, will not eliminate deer, threaten people or lead to intolerable losses of livestock - the myths. On the other hand, large predators are unlikely to right all wrongs humans have inflicted on ecosystems - the wishful thinking.

Any return of large predators will require people to adjust and learn to live alongside predators, as predators learn to live alongside people (Carter and Linnell, 2016). How this may play out over time as predators increasingly settle in more human dominated landscapes is difficult to predict as it will equally depend on predator behavior and how residents accept or adjust to these species. This coexistence will inevitably involve conflicts among different stakeholders, and such tensions can be productive (Hill, 2021). Conflicts can be managed and may represent win-win situations, if realized costs, but also information about benefits ecosystems and humans derive from the presence of large predators are appropriately documented and disseminated. Range expansion of other large species, including black bears and coyotes (*Canis latrans*) into urbanized areas in North America, or how wolves behave and function in peri-urban areas in Europe can offer helpful lessons in how to deal with potential problem animals, such as those becoming conditioned to human presence because of human supplemental feeding. But we would argue that wildlife agencies should be pro-active in their efforts to prepare human residents for the new neighbors, instead of engaging after conflicts have occurred. This will likely require development of new research methods to monitor populations of large predators and new accounting metrics that capture direct and indirect impacts of deer and large predators on ecosystems and people.

At the core of conflicts over acceptance and tolerance of large predators are differences in how people interpret the role of humans in and relationship to nature. For example, when white Europeans colonized North America, they found a continent populated by people, and with unimaginable numbers of large predators and their prey (Nicholls, 2009). Yet it took Europeans only a few centuries to entirely transform the continent's social-ecological systems, wipe out some of the most abundant species and reduce many others to a fraction of their former abundance (Nicholls, 2009). Unchecked exploitation, grounded in the Judeo-Christian belief that people have dominion over all other organisms (White, 1967) and European ideas about rights and responsibilities of land ownership (Linklater, 2013), obliterated existing Native American systems of land and wildlife management, and associated interpretations of intricate and interdependent relationships among people, species and ecosystems (Kimmerer, 2013), and paved the way for current major socio-ecological crises.

Instead of valuable parts of ecological communities, European colonists predominantly saw large predators as competitors, negatively affecting livestock or huntable species, and deserving of no respect. Eliminating them with all means possible was government and individual landowner policy in the U.S., until very recently (Wise, 2016; Treves et al., 2017). While this eradication campaign, particularly for wolves, was successful except for a small remnant population in northern Minnesota, what was not anticipated were revenge effects: long-term negative consequences of short-sighted extirpation (Flader, 1974; Tenner, 1996). Without large predators, and with associated changes in agricultural practices and less severe winters, native and introduced ungulate populations irrupted, triggering enormous negative ecological impacts, economic damage, and human health crises - such as tick-borne diseases (Côté et al., 2004; Telford, 2017). Values associated with "domination" – that humans are exceptional, ecosystems and species are there for our exploitation, and that people are not members of the ecological community – remain in certain segments of the U.S. public. These values are proportionately higher among state wildlife agency employees, who are responsible for designing, implementing, and evaluating wildlife policies (Sullivan et al., 2022). Increasingly, evidence suggests that public values are shifting towards more "mutualistic" conceptions of relationships between people and ecosystems (Manfredo et al., 2021), consistent with the possibility that environmental norms become less exploitative as a function of human residence time.

THE MYTH: PREDATORS AS MAJOR THREATS TO LIVESTOCK AND UNGULATES

After decades of persecution, legal protection of grizzly or brown bears (*Ursus arctos*) and wolves in Europe and in North America ushered in a slow but persistent increase in numbers and return to some of the previously occupied ranges on both continents (Chapron et al., 2014; Treves et al., 2017). In the United States, range expansion was facilitated by purposeful reintroduction of wolves from Canada into Yellowstone National Park in 1995 (Smith et al., 2020), although these wolves remain disconnected from the expanding Great Lakes wolf population in Minnesota, Wisconsin and Michigan (Wydeven et al., 2009). Dispersal of wolves from Yellowstone and from Canada has resulted in establishment of new packs outside of the Greater Yellowstone Area in Wyoming, Idaho, Montana, Washington State, Oregon, and California. Expanding wolf populations and recolonization were not only a celebrated conservation success story, but also a charged political issue. When the US federal government delisted the wolf from the endangered species list, almost immediately hunters and livestock producers together with some state governments issued a "call to arms" due to a perceived need to safeguard wildlife and livestock reminiscent of attitudes a century ago (Robbins, 2021). "Pendulum swings" between federal protection and state-level policies illustrate a crucible of social conflict (Einhorn, 2022), with legal and illegal wolf killing impacting population size and range expansion (Olson et al., 2015).

We do not use the word "perceived" lightly in the context of safeguarding wildlife and livestock. Wolves and bears kill livestock as well as large herbivores such as elk and white-tailed and mule deer sought after by recreational hunters. However, the magnitude or importance of livestock mortality caused by large predators is difficult to accurately evaluate. Lightning strikes, cold or hot weather, parasites and diseases, poor husbandry or poor forage conditions annually kill unknown numbers of livestock. Producers typically insure their animals against weather or health-related mortality to prevent potentially devastating economic losses, but it is impossible at present to put losses due to predation into appropriate perspective because poor transparency and insufficient record keeping prevents independent and accurate data discovery to assess single or cumulative effects of other livestock mortality factors. The data that does exist suggest that economic impacts of predation are real, but minimal, in the order of 1% of annual gross income, although impacts are not evenly distributed and can be more severe locally (Muhly and Musiani, 2009).

Some may find it difficult to comprehend why some people express such vehemence and disdain and others express such admiration towards large predators, particularly wolves (Solomon, 2018). Understanding why positions are so strong and so polarized becomes clearer when we recognize that the debate is often not so much about wolves but about culture, ways of life, social identities, power, and competing visions for future land use (Nie, 2001; Lute et al., 2014; Bruskotter et al., 2019). Not surprisingly then, financial compensation for losses attributed to predators do not always increase tolerance of wolves (Naughton-Treves et al., 2003). We recognize that this debate about cultural and increasingly political identity cannot solely be resolved by data. But it is also clear that the majority of citizens and residents does not subscribe to the extreme and most loudly articulated views of hunters and ranchers on one side or animal rights activists on the opposite side (Teel and Manfredo, 2010; Manfredo et al., 2021; Sullivan et al., 2022). Evidence-based decision making should be the gold standard, regardless of the vision individuals have about the future of land-use or conservation, which also differ regionally. Having high quality information on impacts of large herbivores and their large predators needs to go hand in hand with developing a deep evidence-based understanding of the cultural significance and symbolic nature of large predators, and human attitudes and interpretation of their role in the local landscapes they share beyond opinions articulated by special interest groups. We consider high quality data pillars of responsible governance and decision-making in a democratic society, and believe that management agencies should be responsible for collecting or commissioning robust ecological and social evidence, and incorporating it into decisions. An often silent but increasing majority of residents favors co-existence with predators and a less human control centered engagement with the environments and species around us (Naughton-Treves et al., 2003; Treves et al., 2009; Manfredo et al., 2021). As the struggle between different paradigms of traditional land management versus environmental stewardship plays out, common assumptions that urban and rural people have categorically different values about wildlife conservation, or management actions, may turn out to be unfounded (Hare et al., 2021).

Recognizing the gulf between perspectives of different stakeholders, as well as the lack of detailed information on impacts of herbivores and their predators, we consider it enormously useful to collect robust evidence on whether and under what circumstances (1) lethal predator control attenuates livestock predation and (2) wild ungulate populations benefit from predator reductions. Data suggest that, unless 25% of a predator population is killed annually, predator removal may have no effect on prey populations or actually increase depredation rates (Peebles et al., 2013; Wielgus and Peebles, 2014; Kompaniyets and Evans, 2017). The mechanisms for these results are debated, but probably involve changes in social structure of predators. Furthermore, dispersing sub-adults quickly replace removed individuals, but have less local experience, potentially making livestock easier targets than wary wild ungulates. Removing nearly a third of a wolf population annually will be unacceptable for the majority of citizens; and it will result in rapid endangerment and renewed federal protection (Einhorn, 2022). However, there are claims of success in limiting wolf predation on sheep in France by creating a landscape of fear for predators through legalized lethal removal of individuals attacking livestock (Meuret et al., 2020). Despite the high-profile nature of predator attacks on livestock worldwide, a recent review came to the rather damning

conclusions, that most studies lack scientifically rigorous evaluations and hence there remains great uncertainty about the presumed effectiveness of certain interventions, (Eklund et al., 2017).

The future of coexistence of people and their livestock in landscapes that are also home to large predators will require evidence-based predator impact management practices. Particularly in North America, other predators, such as coyotes, are also often blamed for livestock losses. To achieve a goal of coexistence without livestock producers suffering large economic losses, it appears paramount for agencies, livestock producers, and researchers to collaborate and implement appropriate monitoring or experiments to assess intervention effectiveness (Eklund et al., 2017). Achieving sophisticated protection of livelihoods for those living in proximity to large predators is essential to curb mortality due to legal or illegal killings (Mech, 2017). This will require the willingness to collaborate, and substantial resources, but also clear and open accounting of all mortality factors and potential adjustments (e.g. *via* subsidies) of husbandry practices where necessary if indicated by data.

At present, we conclude there is a large literature but it provides limited evidence to suggest that (lethal) predator removal alone achieves livestock protection - but we recognize the enormous uncertainties due to data limitations (Eklund et al., 2017). Because losses are not equally distributed, limited lethal control of "problem" individuals might be the only viable solution in particular locations (Swan et al., 2017). The German Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer protection asserts that "attacks by wolves on livestock are mainly caused by migrating animals and where wolves establish themselves in new territories and the grazers have not yet adjusted to their presence. The damage in these areas usually decreases once the keepers have learned to deal with the presence of wolves", which involves changes in husbandry practices such as fencing (translation from German to English provided by source: https://www.bmuv.de/themen/naturschutz-artenvielfalt/artenschutz/nationaler-artenschutz/der-wolf-in-deutschland). Fewer than 10 individual problem wolves have been killed, typically those habituated to human presence caused by supplemental feeding, suggesting that coexistence can be learned and conflicts can be managed, although poaching will remain a large concern in North America and Europe (Mech, 2017).

One of the revenge effects of apex predator removal from large swaths of their range in the U.S. has been the build-up of unprecedentedly large native and introduced ungulate populations. This build-up was further facilitated by changes in hunting regulations, changes in land uses that favor ungulates and generally milder winters (Halls, 1984). This was initially a welcome sight for many recreational hunters and considered a success for state wildlife agencies established specifically to increase numbers of huntable animals. However, unabated browsing and grazing by enormous deer or elk populations became agricultural, forestry, biodiversity and human health nightmares (Leopold et al., 1947; Côté et al., 2004; Frye, 2006; Kilpatrick et al., 2014; Kilpatrick et al., 2017; Rogers and McAvoy, 2018; Miller and McGill, 2019). Initially, large ungulate populations persisted due their broad diets and food subsidies provided by woodland canopies, agriculture, or gardening. As coyotes expanded their range eastwards, and wolves dispersed from the Greater Yellowstone and in the Great Lakes states, hunters and many state wildlife agencies quickly claimed predation as a threat to the future of deer populations (Robinson et al., 2014; Chitwood et al., 2015). As large predators expanded their range or increased in abundance, hunters often argued that they thought local deer herds began to decline. But it is unresolved whether predators contributed to these declines, or whether slow plant community changes after decades of overbrowsing and overgrazing finally had a negative impact on ungulate population size and this coincided with (but was not caused by) larger predator populations (Le Saout et al., 2014). Food limitations (quality and quantity) could be the more important drivers - but this is insufficiently addressed in the scientific literature or in hunting publications (magazines, videos, etc.), as could be behavior adjustment by ungulates and increased vigilance that decrease their visibility (Palmer et al., 2021). There is substantial evidence in eastern North America that coyote range expansions do not affect white-tailed deer demography or recruitment (Bragina et al., 2019). There is also abundant evidence for widespread devastation of forests due to deer herbivory (Kelly, 2019; Miller and McGill, 2019). Similarly, limitations in food quality and quantity drive reduced fecundity of many elk herds in western North America and presence or absence of bears or wolves does not affect this pattern (Lukacs et al., 2018). Removal of large predators will not affect this bottom-up effect of resource limitation (Hurley et al., 2011) nor improve success of recreational deer hunters (DelGuidice, 1998).

The uncertainty about drivers of ungulate demography and effects of large predators reinforces our contention that we are in dire need of better and more comprehensive data. This should include data on tri-trophic interactions between large carnivores, their prey, and primary producers, as well as feedback loops on herbivores in the context of other potential stressors, such as invasive species or climate change (Gorchov et al., 2021). Particularly useful would be demographic data that clearly specify impacts of basal resources and large predators on ungulate population dynamics and their impacts on ecological, human health and economic interests in the context of other interacting factors and indirect effects. Without such data, emotionally charged debates will continue unabated, preventing a fair assessment of how people, predators, and ungulates may find new strategies for co-existence (Carter and Linnell, 2016).

WISHFUL THINKING -WOLVES AND OTHER PREDATORS CAN CONTROL LARGE UNGULATE POPULATIONS

We have just summarized the (missing) evidence for the threat recolonizing or reintroduced predators play in greatly reducing

wild deer populations. We recognize that this is not universally accepted by hunters, and in fact it does not eliminate the hopes, or even trust, that many conservationists have in the widespread existence of trophic cascades. Allowing large predators to return or expand their populations is often advanced as the single best opportunity to help restore degraded ecosystems, specifically through reduction of large ungulate herds (Estes et al., 2011; Ripple et al., 2014; Zimmer, 2020). But for this trophic structuring to manifest where large ungulate populations exist or are building, predators would need to depress ungulate populations well below an ecosystem's carrying capacity, with predation the major cause of mortality influencing changes in ungulate populations.

Changes in plant communities and reduction in elk herds after wolves were reintroduced to Yellowstone National Park in 1995 after a 70-year absence are often celebrated as a textbook example of a trophic cascade (Ripple and Beschta, 2004; Beschta and Ripple, 2019) and offered as ecological evidence for beneficial effects of predators. The purported transformative powers of wolves, which, through their impact on elk abundance and behavior, are thought to have facilitated aspen and willow growth and recruitment, with effects rippling through food webs benefitting many different species, has been celebrated in scientific and popular media alike. For example, the video "How wolves change rivers" (https://www.youtube.com/watch?v=ysa5OBhXz-Q) alone has been viewed over 43 million times (as of February 2022). Yellowstone's ecosystems now have thriving populations of plants, beavers (*Castor canadensis*), songbirds and many other organisms, but it is uncertain whether wolves are causal agents triggering cascading impacts (Smith et al., 2020). Claims suggesting wolves as the main change agent may be based on problems associated with selective evidence collection (Ford and Goheen, 2015; Fleming et al., 2019; Brice et al., 2022). Wolves may play a role, but so might human hunters, grizzly bears, mountain lions, bison (*Bison bison*), other ungulates, beaver, rainfall patterns, climate, quality and quantity of vegetation and time. We are unable, at present, to clearly determine how various species that make up and influence the Greater Yellowstone Ecosystem shape complex ecological and trophic relationships. And while elk numbers are significantly reduced, bison numbers have substantially increased to a point where their grazing impacts are cause for major concern, even in the presence of wolves (Beschta et al., 2020).

Available evidence seems to suggest that while large predators kill big herbivores, particularly the very young and the very old, numerically their collective impact on mortality outside of national parks appears insignificant compared to mortality due to hunting (Darimont et al., 2015). For example, collectively large predators kill only about 2% of female elk in the western US (Brodie et al., 2013), which has negligible impacts on elk population dynamics. In Wisconsin, a clash between those advocating for drastically reducing the state's wolf population to protect livestock and white-tailed deer, and those arguing for their continued protection is currently playing out in the courts (https://dnr.wisconsin.gov/newsroom/release/50751). Wisconsin's deer population, after hunting seasons have closed, is about 1-1.5 million (https://dnr.wi.gov/wideermetrics/DeerStats.aspx?R=2). The 10-15 year trend shows a substantial increase in the deer population and this coincides with an increase in the state's wolf population to slightly above an estimated 1,000 individuals in late 2020 (Widenhoeft et al., 2020). Estimated post-hunt deer densities in the presence of wolves range from 9 to >20/km^2 in different northern management units, well above desired deer densities (4 - 6/km^2) that are expected to allow forest regeneration. Each adult wolf may kill 20 deer/year, mostly fawns (Fuller, 1989), thus 1000 wolves may potentially remove 20,000 deer, about the same number killed annually by cars in the state (Raynor et al., 2021). This is an order of magnitude lower than the 10-year annual average of 300,000 deer that hunters kill (https://dnr.wi.gov/wideermetrics/DeerStats.aspx). It seems implausible to imagine that wolf predation, even in concert with other large predators such as black bears, mountain lions or bobcats (*Lynx rufus*), could control (i.e. reduce) deer populations in the state, even in the absence of human food subsidies (agriculture, forestry, gardening). Meaningfully reducing deer populations in Wisconsin alone would require tens of thousands of wolves, at least temporarily until deer populations decline - an ecologically and socially impossible scenario.

These are not novel insights. Half a century ago, Pimlott (1967) argued that based on consumption data and territoriality, wolves would be unable to control (i.e. reduce) deer densities where they exceed 7 - 8/km^2. In the vast majority of the white-tailed deer range in the U.S. deer densities exceed this density (Williams et al., 2013). While evidence from long-term studies in Canada and Minnesota suggest that wolf abundance is itself a function of ungulate biomass; i.e. a bottom-up effect (Pimlott, 1967; Fuller, 1989; Neufeld et al., 2021), these studies were done where human structures and food subsidies were minimal, and herbivore populations may not have irrupted or eliminated much of their resource base. Whether wolf or other deer predator densities can (or are allowed to) increase to a point where they become food limited by deer or other prey availability in human-dominated landscapes, including suburbia, is an important topic to explore. This is most pertinent in Europe where wolves now thrive in landscapes typically thought of as outside their ability to occupy, including close to large cities. Although wolves have an amazing ability to adjust their life-styles and may thrive where sufficient prey exists and humans allow them to thrive (Mech, 2017). The ability of wolves to reduce or assist in deer or other ungulate densities reductions may be limited by their territory size, internal conflict over territories, habitat suitability, human subsidies, the mortality inflicted on wolves and their prey by hunters, and on the existence of safe places for wolves and deer (such as residential or suburban areas where wolves or other large carnivores either may not go or will not be tolerated), deer age structure or whether predation is negatively or positively density dependent (Hoy et al., 2021).

The hope for those advocating for large predators as saviors of devastated ecosystems then rests not on a numerical reduction of

ungulate densities, but on predators creating landscapes of fear (Laundre et al., 2001; Gaynor et al., 2019). Behaviorally mediated cascading impacts are thought to affect many ecosystem components, including benefitting primary producers. Experimental studies have documented changes in herbivore behavior in the presence of predator cues such as urine or vocalizations (Calkoen et al., 2021), but predator presence does not necessarily result in significant behaviorally mediated cascades that benefit primary producers eaten by deer (Palmer et al., 2021), moose (*Alces alces*) or African ungulates (Ford et al., 2015; Ausilio et al., 2021; Sand et al., 2021). Instead, large herbivores, in response to presence of large predators, change their activity patterns and graze in risky areas of high nutritional value when predation risk is low, for example when wolves rest (Kohl et al., 2018). Not surprising then is the result of a large meta-analysis of predator recolonization or introduction events that shows across taxa very limited effects of either density or behaviorally mediated trophic cascades (Alston et al., 2019). The evidence we have at present appears to suggest that large predators alone will be unable to generate the ecological, economic, ecosystem and human health benefits people wish for, and some carnivore advocates promise.

THE FUTURE OF LARGE PREDATOR CONSERVATION AND MANAGEMENT

We are not the first to question the basis of the fears and hopes regarding predators and their importance in structuring ecosystems and people's livelihoods. To be clear, large predators kill livestock and occasionally people - these are tragic losses, and it is up to livestock producers, wildlife agencies and scientists to devise means to reduce and minimize these losses as much as possible. Protection of domestic livestock in the presence of large predators may require different forms of animal husbandry and may include physical or lethal removal of problematic individual predators. But as societal attitudes in the U.S. shift towards an increasing tolerance of predators, much work, including offering financial support during periods of transitioning to different husbandry practices may be required to find better and less costly ways to learn to live with large predators (Eklund et al., 2017).

Extirpating large predators has had widespread unintended negative consequences on ecosystems and has reduced benefits humans and other species derive from them. We recognize that legal protection and allowing return of large predator represents a shift from principles of domination and valuing ecosystem only for their utility for human use and exploitation. It represents a shift towards a more holistic and participatory ecosystem management paradigm, where different and diverse stakeholders can participate and be equal partners in decision making processes without capture by special interest groups (Hare and Blossey, 2014). Wildlife management agencies need to make sophisticated efforts to assess and incorporate the diverse attitudes and opinions of citizens and residents in their decision and rule-making processes. While some may interpret this as a dramatic break from the traditional western resource management paradigm, it does not necessarily threaten customs, cultures, and rural communities - but re-organizes decision making processes, agency responsibilities and accountabilities to all members of society, present and future (Darimont et al., 2018).

It is long overdue to recognize that public spaces and the species that should thrive in them are not just there to be grazed by livestock or for hunters and their preferred prey. We do not advocate excluding these currently dominant interests from wildlife decision-making, but argue that they should take their place alongside all other legitimate interests. When asked, a majority of people in New York and Colorado favor a return of wolves, despite substantial opposition from some segments of society (Enck and Brown, 2002; McGovern and Kretser, 2015; Niemiec et al., 2021) and apparent widespread illegal poaching (Mech, 2017). Elk, deer, moose and other species favored by hunters will thrive in the presence of predators. Hunters will be able to continue to pursue large herbivores, as long as primary producers can thrive. But the long-term well-being of habitats, ecosystems and healthy environments also requires that ungulate populations be curtailed, where such efforts are needed. This need should be assessed regularly by wildlife management agencies using sophisticated and validated metrics (Blossey et al., 2019) and data should be made openly available to inform decision-makers and the public.

Nutritional limitations, and not predation, appear to be increasingly recognized as factors limiting ungulate populations, their vital rates and thus population dynamics, not predation. This has been demonstrated for woodland caribou (Schaefer et al., 2016), moose (Jesmerr et al., 2021; Oates et al., 2021), mule deer (Bishop et al., 2009), white-tailed deer (Bragina et al., 2019) and elk (Coughenour and Singer, 1996; Lukacs et al., 2018). Some even argue that predators typically do not control their prey populations (White, 2013), but this generalization is refuted by examples from biological control, (Van Driesche et al., 2008) or benefits of eradication of introduced predators on islands (Croll et al., 2005; Aguirre-Muñoz et al., 2008).

We are concerned about the hyperbole on both sides claiming that large predators either seriously threaten livestock and wildlife populations, or do miracles to restore degraded ecosystems. None of this hyperbole is borne out by the currently available evidence. The abiotic and biotic forces that structure ecosystems and species dynamics have been fundamentally altered by human activities - regime shifts have occurred, creating alternative (stable)? states involving extinctions, biotic invasions and climate change (Folke et al., 2004; Suding et al., 2004). Historically, large predators may have prevented deer population irruptions (Leopold et al., 1947; Pimlott, 1967). But reintroduced or range expanding predators encounter unprecedented ungulate abundances, and direct consumption or indirect effects on herbivore behavior appears limited and may not result in demographic impacts on prey populations, or cascade down to benefit primary producers (Estes et al., 2011; Ford and Goheen, 2015; Alston et al., 2019). Rather than claim that wolves and other predators are either a threat to

deer, or are essential for healthy and well-functioning ecosystems, we should acknowledge that the evidence does not currently exist and the conservation importance of large predators could be distinct from their potential cascading impacts.

In the U.S. wolves and other large predators can repopulate their ancestral, and potentially new, ranges on their own, and do not require intentional releases by wildlife agencies. However, this also requires dispersal corridors and that potential source populations are not managed to curtail regional spread. We cannot envision how regional spread may occur without extended legal protection since poaching or hunting is the single largest mortality factor for wolves (Fuller, 1989; Mech, 2017; Barber-Meyer et al., 2021). This protection will need to include coyotes as hunters often claim to have mistaken wolves for coyotes when individuals explore new territory (https://www.outdoorlife.com/blogs/newshound/2013/08/dna-tests-confirm-hunter-killed-gray-wolf-kentucky/; https://www.reformer.com/local-news/rare-gray-wolf-shot-in-western-mass/article_c20e7b41-a3cf-55fa-904a-e272452c0c49.html). This will require a new appreciation for potentially important contribution large predators may make to the health of the environments around us beyond limiting deer populations. That does not mean we can glorify them as ecological miracles, and potential conflicts need to be managed proactively and sensitively.

However, many questions concerning the ecology and impacts of large carnivores remain unanswered - in no small part due to limitations in how conservation scientists have studied and interpreted trophic cascades in ecology, conservation, and wildlife management (Ford and Goheen, 2015; Fleming et al., 2019; Gaynor et al., 2019). How potential trophic cascades, resource-driven dynamics or indirect predator effects may materialize across different landscapes with different climates, different resource availabilities, different suites of alternative prey, and different human population densities with different values and cultural traditions is impossible to predict. How do these dynamics play out over years, or decades? What is the role of human subsidies? How do we return degraded landscapes to some form of productivity - what type of interventions are required? The recolonization of western Europe by large predators is a clear indication that wolves and bears can be creatures of densely inhabited and human modified environments as well as the deep woods (Chapron et al., 2014). Large predator colonization of areas densely populated by humans is quite similar to expansion of ungulate populations into suburbia, followed by their predators, including foxes, coyotes and mountain lions. As long as people learn to live with and tolerate the new (old) neighbors, a careful but not fully conflict free coexistence appears possible. Any such coexistence will require full accounting of the many ways in which large predators may positively and negatively affect people and ecosystems, and decisions based on honest collection and interpretation of evidence rather than myths and wishful thinking.

AUTHOR CONTRIBUTIONS

BB led the writing. Both authors contributed ideas and background and approved the MS.

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