



Carnivore conservation: shifting the paradigm from control to coexistence

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For 90 years, the American Society of Mammalogists (ASM) has made science-based challenges to widespread lethal control of native mammals, particularly by the United States federal government targeting carnivores in the western states. A consensus is emerging among ecologists that extirpated, depleted, and destabilized populations of large predators are negatively affecting the biodiversity and resilience of ecosystems. This Special Feature developed from a thematic session on predator control at ASM's 2013 annual meeting, and in it we present data and arguments from the perspectives of ecology, wildlife biology and management, social science, ethics, and law and policy showing that nonlethal methods of preventing depredation of livestock by large carnivores may be more effective, more defensible on ecological, legal, and wildlife-policy grounds, and more tolerated by society than lethal methods, and that total mortality rates for a large carnivore may be driven higher than previously assumed by human causes that are often underestimated.

Key words: carnivores, depredation, nonlethal control methods, predator control

“...this is why the caribou and the wolf are one; for the caribou feeds the wolf, but it is the wolf who keeps the caribou strong.”

Eskimo legend as told to Farley Mowat ([Mowat 1973:85](#))

This Special Feature developed from a special thematic session on mammalian predator control at the 94th annual meeting of the American Society of Mammalogists (ASM) held in June 2013 in Philadelphia. Sponsored by the ASM Conservation Committee, the thematic session explored a range of perspectives—from wildlife managers, carnivore biologists, and sociologists—on issues of managing human conflicts involving native large carnivores. For 90 years, ASM has presented science-based critiques of lethal control of native wildlife—particularly large carnivores—by the United States federal government, starting with its 1st published Society resolution ([Jackson 1924](#)) and continuing to the present ([ASM 2012](#); others reviewed in [Bergstrom et al. 2014](#)). Additionally, prominent early ASM members, including Aldo Leopold, C. Hart Merriam, and E. Raymond Hall, individually published letters stating that lethal control of large carnivores, particularly in the western United States, was driven by politics rather than science and was excessive in its direct effects on targeted as well as nontargeted species of native mammals ([Bergstrom et al. 2014](#)).

These concerns by early 20th century mammalogists were well founded, given that, first, grizzly bears (*Ursus arctos horribilis*), and then, by the 1930s, gray wolves (*Canis lupus*) were extirpated from the western contiguous states by private and government agents ([Robinson 2005](#)).

The 1973 Endangered Species Act (16 U.S.C. 1531–1544, 87 Stat. 884, as amended—Public Law 93–205) alleviated concerns of American mammalogists that their government would allow or directly cause extinction or wide-scale extirpations of native mammals. However, in the United States as well as globally, most large carnivores have experienced substantial range contractions and population reductions; in fact, the American black bear (*Ursus americanus*) is the world's only large terrestrial carnivore species that has a global population of more than 200,000 and is one of the very few whose population trend is not “decreasing” ([Ripple et al. 2014](#)). Even in areas still occupied by large carnivores, predator removal locally in less-developed landscapes causes concern about nontarget mortality of certain rare species and indirect effects on biodiversity and ecosystem function from disruption of “top-down forcing” (sensu [Estes et al. 2011](#); [Bergstrom et al. 2014](#)). In the United States, legal public harvest takes 2.5 million native carnivores annually ([Association of Fish and Wildlife Agencies 2014](#)). Additional human-caused mortality of carnivores due to

poaching and road-kill is hard to quantify but may be higher than commonly assumed. Vehicles on roads, for example, have killed 13% of the gray wolf (*C. lupus*) population annually in Wisconsin (Treves et al., this issue). Lethal control of large carnivores in the United States by professional federal, state, and private agents constitutes a fraction of the total human-caused mortalities nationwide, but they are done primarily to benefit livestock producers in western states, often intensely at a very local scale (e.g., 884 coyotes [*Canis latrans*] killed on a single ranch in Nevada in a 2-year period by aerial gunning—Knudson 2015), and they can result in removal of 1 or more carnivore species from local ecosystems (Bergstrom et al. 2014).

Wildlife Services, a division of the United States Department of Agriculture's Animal Plant Health Inspection Services, is tasked by law "to provide Federal leadership and expertise to resolve wildlife conflicts to allow people and wildlife to coexist" (Wildlife Services 2015). Wildlife Services' research scientists do important studies on nonlethal methods of reducing carnivore–livestock conflict (e.g., Stone et al., this issue), but its field operations in the western United States have been criticized for their over-reliance on lethal means of resolving wildlife conflicts with livestock (Government Accountability Office [GAO] 1995; Niemeyer 2010; ASM 2012; Bergstrom et al. 2014). In Fiscal Year 2013, Wildlife Services killed > 75,000 coyotes (not counting 366 dens destroyed), 320 gray wolves, 345 cougars (*Puma concolor*), 3,546 red and gray foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*, respectively), and 372 badgers (*Taxidea taxus*—Wildlife Services 2015). The annual number of control kills of coyotes has remained remarkably constant since 1939, varying between 50,000 and 110,000 and has exceeded 70,000 annually since 1985 (Berger 2006; Bergstrom et al. 2014). Also typical, Wildlife Services in Fiscal Year 2013 unintentionally killed 397 river otters (*Lontra canadensis*), 14 kit foxes (*Vulpes macrotis*), and 41 swift foxes (*V. velox*—Wildlife Services 2015). Wildlife Services does not monitor populations of species it targets for control nor those unintentionally killed, but one of the few published estimates of an overall mortality rate is that Wildlife Services, along with state managers, removed 23.2% of the estimated coyote population of Wyoming in 1994–1995 (Taylor et al. 2009). This level of human-caused mortality of mammalian predators may have negative unintended consequences for native ecosystems and biodiversity. Lethal control of carnivores may also be unnecessary and counterproductive to its ostensible goals (see Treves et al. 2016 for a recent review). We will explore these consequences in this Special Feature. We invited individual research scientists from the National Wildlife Research Center (the research arm of Wildlife Services) to contribute a science-based defense of lethal control of native carnivores to this Special Feature, but they each, as well as the center, collectively via their director, declined the offer (L. Clark, in litt., 13 November 2013).

There are 5 categories of reasons why mammalogists and conservation biologists should be interested in guiding governments—and society at large—toward replacing localized predator removal or population reduction (lethal control) with

nonlethal means of wildlife conflict resolution: 1) potential disruption of top-down forcing and consequent loss of ecosystem resilience and biodiversity; 2) "bycatch" or unnecessary killing of nontarget species of mammals and other wildlife that occurs with nonselective methods of lethal control; 3) population reduction of certain species of native wildlife valued by many parts of society for the benefit of a few favored interest groups; 4) ineffectiveness of lethal control of predators at either reducing livestock depredation or, secondarily, enhancing game populations, over the long term; and 5) ethical considerations about both the intrinsic value of carnivores and humane methods of killing them. Some of these deserve brief attention in this overview, and others will be dealt with in more detail in the 5 other papers in this Special Feature, including new empirical evidence for the efficacy of nonlethal methods as alternatives to lethal predator control.

THE IMPORTANT ROLE OF BOTH APEX PREDATORS AND MESOPREDATORS IN MAINTAINING ECOSYSTEM FUNCTION

With this topic currently under considerable empirical and theoretical scrutiny, the evidence assembled as of 2011 led 23 prominent ecologists to conclude that loss of apex predators was a major driver of destabilization and collapse of their native ecosystems, leading to pandemics, irruptions of invasive species, and lost ecosystem services (Estes et al. 2011). Aldo Leopold was one of the 1st biologists to argue that mammalian predators played an indispensable role in controlling ungulate prey, thus preventing depletion of their resources, citing the irruption of the early 20th century herd of Kaibab deer (*Odocoileus hemionus*) after widespread predator removal (Leopold 1943). A recent review of several lines of evidence concluded that Leopold was right (Binkley et al. 2006). The poor condition of rangelands in much of the western United States can be attributed partly to native ungulates whose predators have been depleted (Beschta et al. 2013). Hebblewhite et al. (2005) documented that top-down forcing exerted by wolves on browsing prey had indirect positive effects on songbird communities in the Canadian Rockies. Restoration of a putative wolf-driven trophic cascade has restored certain riparian plant and animal communities in Yellowstone National Park (e.g., Ripple and Beschta 2012; though see Mech 2012). Top-down forcing (also known as a trophic cascade, i.e., the many indirect effects predation has on lower trophic levels and the ecosystem as a whole) by wolves may be enhanced by facilitative interactions with sympatric large carnivores (e.g., cougar—Atwood et al. 2007), or it may be dampened in more human-dominated landscapes (Muhly et al. 2013). A possible indirect effect of wolf predation is to reduce abundance of songbirds and rodents in a 4-species interaction chain, by releasing the lowest of the 3 trophic levels of carnivores (Levi and Wilmers 2012). In some systems, an apex large carnivore causing mesocarnivore suppression and, indirectly, small-carnivore release may be the more natural state. Removal of the apex carnivore, conversely,

causes mesocarnivore release and small-carnivore suppression, which allows an irruption of rodent populations. Such an altered trophic cascade is exemplified by the recent colonization of eastern North America by coyotes following extirpation of wolves and may explain the rapid increase in the incidence of Lyme disease (Levi et al. 2012). Lethal control of the Australian apex predator the dingo (*Canis dingo*) has caused similar state shifts, resulting in dominance of introduced mesopredators and herbivores, which then cause damage to native plant and animal communities (Wallach et al. 2010).

INEFFECTIVENESS AND UNINTENDED CONSEQUENCES OF PREDATOR REMOVAL

The consistent annual efforts by Wildlife Services at lethal control of coyotes in the western United States, described above, did not succeed in ameliorating the long decline of the nation's sheep industry, which began in the post-war years (Berger 2006). And, local-scale removal of coyotes has been found to cause population irruptions and reduced diversity in rodent communities (Henke and Bryant 1999). Use of public harvest of cougars in Washington state to remediate livestock depredation was found to be ineffective (Peebles et al. 2013). Similarly, recreational hunting of Eurasian lynx (*Lynx lynx*) was found to have little effect on sheep depredation unless of a magnitude to cause lynx population decline (Herfindal et al. 2005). Lethal control of gray wolves in the western United States could have such unintended consequences as shifting depredation from cattle to sheep (by mesopredator release of coyotes) and increasing mortality of pronghorn (*Antilocapra americana*) fawns (Berger et al. 2008; Bergstrom et al. 2014). Lethal control of gray wolves in the northern Rocky Mountains, causing total mortality of up to 25% of the estimated population, was found actually to increase depredation on livestock (Wielgus and Peebles 2014; but see Bradley et al. 2015). There are 3 reasons that predator removal is likely to have no long-term effect—or even adverse effects—on depredation of livestock: vacant territories are quickly recolonized (Knowlton et al. 1999; Treves and Naughton-Treves 2005); immigration rate of breeding pairs into the area experiencing lethal control can increase (Sacks et al. 1999); and immigrants are more likely to be subadults, which have a greater propensity for livestock depredation than older adults (Peebles et al. 2013). Simulation results suggest that even moderate nonselective predator control can potentially increase densities of the targeted carnivore species, because nontarget deaths of co-occurring carnivore species decrease competition for the targeted species (Casanovas et al. 2012). Use of nonselective, lethal predator-control methods (e.g., trapping and poison baits) by Wildlife Services has resulted unintentionally in the deaths of individuals of 150 species of vertebrates since 2000 (Knudson 2012) and at least 12 taxa of mammals protected (or candidates for protection) under the Endangered Species Act since 1990 (Bergstrom et al. 2014). Selective local removal of carnivores such as coyotes may eliminate the bycatch problem, but it can still trigger mesopredator release with unintended negative consequences (Mezquida et al. 2006).

The ASM has supported lethal control of large carnivores in certain cases where preservation of critically endangered wildlife species demands it (such as cougar predation on isolated populations of peninsula bighorn sheep, *Ovis canadensis nelsoni*—ASM 2012; Stephenson et al. 2012), but culling apex predators to enhance common game species may be unnecessary at best and harmful at worst. To the latter point, it is well known that wolves preferentially prey on older and diseased individuals (Mech and Peterson 2003; Wright et al. 2006), so natural predation is an important selective agent for the prey. To the former point, recent studies have concluded that gray wolf populations are intrinsically density dependent. That is, rather than being prey-limited, wolf densities are regulated through social interactions, with increasing interpack aggression and mortality at higher densities (Cariappa et al. 2011; Cubaynes et al. 2014). Large mammalian carnivores have been found to limit prey populations, broadly and in specific predator–prey interactions (Binkley et al. 2006; Ripple and Van Valkenburg 2010; Christianson and Creel 2014), but the effect of reduction or removal of predators on densities and dynamics of prey populations in any specific case can be hard to predict. Experiments removing coyotes and cougars in Idaho showed winter weather to be much more important than predation in predicting population trends of mule deer (*O. hemionus*—Hurley et al. 2011). A 7-year effort to remove all mammalian nest predators of ground-nesting birds (coyotes being the largest) from study sites in the southeastern United States concluded that removal of mammalian predators had no net effect on nest predation, primarily because of compensatory increases in predation by snakes (Ellis-Felege et al. 2012). A meta-analysis of 113 predator removal experiments (which was a taxonomically broad sample of animal predators) found that the intended beneficiary prey populations declined in 54 of them (Sih et al. 1985). This illustrates the multiple indirect pathways of potential top-down forcing that may be altered by removal of an apex predator from a complex food web, producing many possible outcomes for prey dynamics. For a mammalian carnivore example, 1 such pathway is through “apparent competition” with an alternate ungulate prey species, mediated through a different predator that increases compensatorily (Serrouya et al. 2015). Another pathway involves release of a mesopredator that preys preferentially on neonates of the same ungulate prey species (Prugh and Arthur 2015).

EFFECTIVENESS OF NONLETHAL CONTROL OF DEPREDATION

Use of nonlethal methods (such as guardian animals and livestock protection collars) to prevent livestock depredation by leopards (*Panthera pardus*), caracals (*Caracal caracal*), and jackals (*Canis mesomelas*) in South Africa was found to be less expensive and more effective than lethal predator control (McManus et al. 2014). In this Special Feature, Stone et al. (this issue) document that, over a 7-year pilot project in prime wolf habitat in Idaho, the adaptive use of a suite of nonlethal deterrent strategies reduced sheep depredation by more than

3-fold compared to sheep allotments in Idaho that used lethal controls over the same time period. Presenting results from a large cattle station in Australia, where full implementation of such nonlethal strategies may be prohibitive, Wallach et al. (this issue) argue that simply ending lethal control of dingoes reduced depredation by allowing the social structure of the predator to stabilize, and additionally that cattle mortality can be reduced most effectively by improving husbandry practices. These 2 studies do not meet the “gold standard” of replicated, randomized experimental design (which few predator-control studies do—Treves et al. 2016), because the latter would have been impossible without intentional further killing of important apex predators of great conservation value (in the case of Idaho gray wolves still legally protected for most of the study). Nonetheless, their results are valuable in providing insights into workable alternatives to lethal control for solving wildlife–livestock conflicts. Both of these studies suggest that stable, naturally regulated populations of social carnivores not significantly exploited by humans are the preferred option for both reducing livestock depredation and restoring the functional role of apex predators to ecosystems. These findings for large canids mirror those for cougars, in which excessive harvest replaces adult males with immigrating adolescent males, which are more prone to depredate (Peebles et al. 2013).

MEMBERS OF ASM ARE ACUTELY AWARE OF GUIDELINES ON HUMANE TREATMENT

There has been much discussion in recent years within the Society about the ethical constraints and obligations pertaining to working with live mammals. While we have striven to ensure that Animal Care and Use regulations imposed on us by extrinsic bodies are not overly onerous and do not prevent us from vigorous pursuit of our science, we nonetheless all feel the obligation to abide by a set of rules for humane treatment of our mammalian study subjects. Not a paper is published in this journal presenting original results from live animal subjects that does not state that the study adhered to these ASM-adopted guidelines (Sikes et al. 2016). Ironically, ASM’s guidelines were developed in large part in response to oversight by United States Department of Agriculture-monitored institutional Animal Care and Use committees at universities where many of us work, yet the agencies in the United States Department of Agriculture, including Wildlife Services, are not obligated to abide by the guidelines that their agency helped produce. Although they follow guidelines of the American Veterinary Medical Association on euthanasia, Wildlife Services claims their “management and operational programs are exempt from Animal Welfare Act (1966, 7 U.S.C. 2131, 9CFR) compliance” (Clay 2012:8).

In this Special Feature, Slagle et al. (this issue) show that, while the United States public accepts that predators may need to be controlled, there is low and declining acceptance of lethal predator-control methods, which are regarded as inhumane. Governments at the federal, state, and local levels are tasked with serving broad constituencies, and in the case of native

wildlife, which are a public trust asset (Bruskotter et al. 2011; Treves et al. 2015), they should be responsive to these public attitudes. In practice, some government resource agencies or the appointed government boards that rule them, or both, have traditionally favored narrower constituencies within the public. State wildlife or game agencies have elected to provide hunting opportunities for certain species, including large carnivores, even if citizens opposed to hunting a particular species of large carnivore greatly outnumber those wishing to hunt it. A case in point is the state of Michigan recently approving a wolf hunt following removal of federal protection by the Endangered Species Act, and in this Special Feature, Vucetich et al. (this issue) argue that the North American Model of wildlife management, to which the profession is supposedly bound, does not support the hunt. In a society in which lethal control of predators is viewed increasingly negatively and scientific consensus is emerging that social carnivores occupying apex-predator trophic levels function best and depredate least when not lethally exploited, killing native large carnivores is an issue that will become increasingly controversial and should receive increasing scientific scrutiny.

Finally, insofar as most states, probably for the foreseeable future, will continue to include large carnivore hunting among their wildlife management tools, it is important that decision-makers in wildlife agencies have valid data on mortality rates from all mortality sources and on the further effects of anthropogenic mortality on recruitment (which may be negative), so that harvest quotas may not push total mortality beyond a sustainable level (see Creel et al. 2015). To that end, Treves et al. (this issue) show that well over a third of mortality of wolves over the past 3 decades in Wisconsin was due to poaching and another 13% was due to vehicle collision, suggesting that total mortality of the population, which was subsequently exposed to harvest, is higher than the management agency assumes. Setting wildlife management goals at reducing carnivore mortality to at most sustainable levels, and eliminating human-caused mortality wherever possible, is in line with the best current ecological, social, and ethical scholarship, as papers in this Special Feature attest.

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