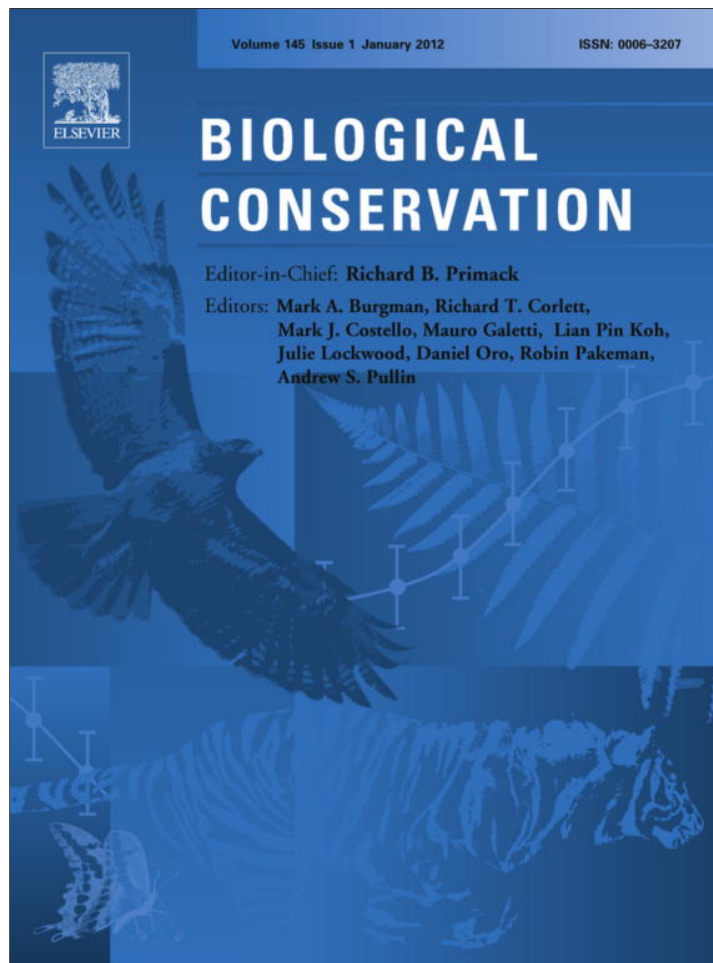


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Is science in danger of sanctifying the wolf?

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ABSTRACT

Historically the wolf (*Canis lupus*) was hated and extirpated from most of the contiguous United States. The federal Endangered Species Act fostered wolf protection and reintroduction which improved the species' image. Wolf populations reached biological recovery in the Northern Rocky Mountains and upper Midwest, and the animal has been delisted from the Endangered Species List in those areas. Numerous studies in National Parks suggest that wolves, through trophic cascades, have caused ecosystems to change in ways many people consider positive. Several studies have been conducted in Yellowstone National Park where wolf interactions with their prey, primarily elk (*Cervus elaphus*), are thought to have caused reduction of numbers or changes in movements and behavior. Some workers consider the latter changes to have led to a behaviorally-mediated trophic cascade. Either the elk reduction or the behavioral changes are hypothesized to have fostered growth in browse, primarily willows (*Salix* spp.) and aspen (*Populus* spp.), and that growth has resulted in increased beavers (*Castor Canadensis*), songbirds, and hydrologic changes. The wolf's image thus has gained an iconic cachet. However, later research challenges several earlier studies' findings such that earlier conclusions are now controversial, especially those related to causes of browse regrowth. In any case, any such cascading effects of wolves found in National Parks would have little relevance to most of the wolf range because of overriding anthropogenic influences there on wolves, prey, vegetation, and other parts of the food web. The wolf is neither a saint nor a sinner except to those who want to make it so.

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1. Introduction

"The only good wolf is a dead wolf." This and many similar slogans typified public attitudes toward wolves (*Canis lupus*) in the United States before the late 1960s. Leaders, too, agreed with this attitude. Teddy Roosevelt, for example called the wolf, "The beast of waste and desolation."

Even some of the pioneering environmentalists, naturalists, and wildlife biologists vilified wolves. Naturalist Ernest Thompson Seton poisoned them. William Hornaday stated "of all the wild creatures of North America, none are more despicable than wolves. There is no depth of meanness, treachery or cruelty to which they do not cheerfully descend." In the first comprehensive book about wolves, Young and Goldman (1944, p. 1), senior biologists of the US Fish and Wildlife Service on page 1 called the wolf "a menace to human life." Even Aldo Leopold, well-known for his conclusions that the removal of large carnivores fostered increased herbivores and overbrowsing, shot wolves and in 1946, long after he experienced the famous "fierce green fire," he recommended wolves be bountied to increase abundance of big game populations (Mech, 2002).

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Now the tables have turned. The Satan wolf has become a saint in the minds of most of the general public. Ever since the wolf was placed on the federal Endangered Species List in 1967, it became one of the main symbols of endangered species, featured in posters, tee shirts, documentaries, and magazines. Numerous books have since been written about wolves. (I count over 30 on my bookshelf.) Some 27 non-governmental organizations have been formed to promote wolf preservation. Except for some local areas where wolves have recovered and anti-wolf sentiment is increasing again, wolves are now considered by the general public primarily in a positive light (Williams et al., 2002).

The legal protection that the Endangered Species Act of 1973 afforded the wolf, as well as the reintroduction of wolves into Yellowstone National Park and Idaho, allowed wolf populations to thrive in the Upper Midwest and Northern Rocky Mountains to the point where years ago they reached official biological recovery levels (USFWS, 2011a,b). Along with their recovery came numerous studies of wolf ecology and reported effects of wolves on ecosystems, not only in Yellowstone but in other parks as well, where wolves had also been recovering. Wolves have now been credited by both the scientific literature, and especially the popular media, with everything from increasing populations of beetles and birds to replenishing ground water (Table 1). These diverse reported effects of wolves are attributed to trophic cascades, which

Table 1

Claims made by popular media and websites about ecological effects of wolves.

The basis for these claims in the scientific literature are discussed in the text.
Reducing prey numbers and changing their movements ^{a,b,c,d,e,f}
Regenerating aspen, willows ^{a,b,c,f,h,j,k}
Improving habitat for beavers, songbirds, fish, small mammals, moose, amphibians, insects and waterfowl ^{a,c-g,i,k}
Promoting streambank recovery ^{a,c,d,e,k}
Reducing coyote density ^{a,d,e,k}
Providing food for scavengers ^{a,c,k}
Selecting old, weak, sick prey and maintaining healthy herd ^a
Reducing disease transmission ^a
Increasing bison ^d
Increasing raptors ^{e,k}
Improving water quality ^a
Replenishing ground water ^a
Cooling water ^{a,c,e,k}
Increasing pronghorns ^e

^a Jackson Hole Conservation Alliance (www.jhalliance.org/).^b Pickrell, 2003. Wolves' leftovers are Yellowstone's gain, study says. National Geographic News, December 4, 2003.^c Robbins, 2005. Hunting habits of wolves change ecological balance in Yellowstone. New York Times, October 18, 2005.^d Chadwick, 2010. Wolf wars. National Geographic Magazine, March, 2010.^e Living with wolves (www.livingwithwolves.org).^f Powell, 2011. Florida panthers and Yellowstone wolves in the backyard. BBC News, 7 March 2011.^g Bass, 2005. Wolf Palette. Orion Magazine, July/August 2005.^h Anonymous, 2007. Presence of wolves allows aspen recovery in Yellowstone, Science Daily, July 31, 2007.ⁱ Holdon, 2009. Wolves to the rescue in Scotland. Science Now, July 2009.^j Smith, 2010. Destination Science: Yellowstone National Park, USA Discover Magazine, April 2010.^k Robbins, 2004. Lessons from the wolf. Scientific American 29(6):84–91.

have long been postulated for various systems (Hairston et al., 1960; Carpenter et al., 1985; Estes et al., 2011) resulting from either large carnivore reduction of prey numbers (direct effects) or from causing prey to change their movements and/or behavior (indirect effects). These changes are then hypothesized to reduce or better scatter the prey's effects on vegetation such as willow (*Salix* spp.) and aspen (*Populus* spp.). Increased willow and aspen growth in turn fosters other species such as songbirds and beavers (*Castor canadensis*) that rely on the vegetation. Those species, especially beavers, are then said to cause another cascade of effects on waterways, leading to such effects as raising the water table and the consequent effects of that (Table 1). That trophic cascades exist is well documented (Beschta and Ripple, 2009; Terborgh and Estes, 2010). Whether recently restored wolves have already wrought the cascading effects attributed to them is the question here.

As was the case with the historical anti-wolf reports of devastating effects on prey, the new reports of wolf benefits by both lay people and scientists also may be exaggerated compared to the scientific evidence. As one reviewer of this article put it, "ecologists (and particularly conservation biologists) do seem obsessed to the point of blindness with predator-induced trophic cascades." This article examines some key reported wolf benefits, mostly based on studies in Northern Yellowstone because that area has been a strong focus of recent research. It attempts to place these findings in the perspective of what we really know about the ecosystem impacts of wolves. True, some of the more extreme claims are found more in the popular media, but most of them have at least some basis in scientific articles summarized by Hebblewhite and Smith (2010) and Eisenberg (2010). With wolf recovery has come an increased polarization between those laypeople who revere the animal and those who revile it. Establishing a more-accurate public and scientific image of the wolf is important so that authorities can better manage the species and promote accurate public understanding about the rationale for various kinds of wolf management.

It is not that scientists failed early on to warn about overstating or overgeneralizing wolf effects on ecosystems. After reviewing several such reported effects, Mech and Boitani (2003, p. 160)

concluded "we do not claim to know whether the wolf's effects are positive or negative, what its net effect is, or whether the effects are of any great consequence ecologically." Smith et al. (2003, p. 339) warned that "the danger we perceive is that all changes to the [Yellowstone] system, now and in the future, will be attributed solely to the restoration of the wolf." Similarly Garrott et al. (2005) cautioned about generalizing wolf effects, and Ray et al. (2005, p. 426) warned that "... scientists will likely never be able to reliably predict cascading impacts on elements of biodiversity other than prey."

Hebblewhite and Smith (2010) explored the various complexities of trying to determine possible cascading effects of wolves on ecosystems. They concluded that across three systems, Banff, Isle Royale, and Yellowstone National Parks, trophic effects of wolves were quite variable and depended on time since wolf recolonization, ecological complexity of the community, and unknown factors that regulated the top-down strength of predation (Melis et al., 2009; Vucetich et al., 2011). Unfortunately the review by Hebblewhite and Smith (2010) was completed before some of the more recent findings discussed below were available.

2. Reports about wolf effects

The reports about wolf effects on the ecosystem fall into three main categories: (1) direct effects on coyotes (*Canis latrans*), (2) benefits to scavengers, and (3) cascading effects of wolf interactions with prey to other species in the wolf food chain.

2.1. Reduction of coyotes

Much has been made of the initial report that reintroduced wolves have reduced coyote numbers in Yellowstone National Park (Crabtree and Sheldon, 1999), a finding in accord with earlier work (Mech, 1966), and several other studies confirm that wolves kill coyotes and tend to reduce their numbers (summarized by Ballard et al. (2003)). What has grabbed the imagination of researchers and the public about a reduction in coyotes in Yellowstone is the

possibility that it might lead to both increased coyote prey (Buskirk, 1999) that then fosters a “mesopredator release,” that is, an increase in smaller predators such as raptors, foxes (*Vulpes vulpes*), and badgers (*Taxidea taxus*) (Terborgh and Winter, 1980). Such a release has not been documented in Yellowstone, however. Furthermore the number of coyote packs in the part of Yellowstone where they were at first reduced has returned to pre-wolf levels although the packs may be smaller (Crabtree and Sheldon, unpublished, in Hebblewhite and Smith, 2010). Thus any wolf release of mesopredators in Yellowstone is yet to be demonstrated.

2.2. Benefits to scavengers

Effects upon a second value reported for wolves is that they benefit scavengers, every creature from bears to beetles, and ravens (*Corvus corax*) to eagles (Wilmers et al., 2003; Sikes, 1994). In Banff National Park some 20 species were recorded feeding on wolf kills (Hebblewhite and Smith, 2010). Furthermore, some researchers have suggested that wolf predation might reduce global warming effects on scavengers by providing a more regular carrion supply (Wilmers and Getz, 2005). Certainly many species do feed on wolf kills, as they do on any carrion. However wolf kills are temporally and spatially distributed more evenly than starvation die-offs, for example. Nevertheless whether wolf predation increases scavenger reproduction and survival more than other types of mortality has not been measured. Hebblewhite and Smith (2010) recognized one offsetting factor when stating that if wolves do reduce prey numbers, they also reduce total prey biomass, which would then be detrimental to scavengers.

Another important factor that neither Hebblewhite and Smith (2010) nor the authors of scavenger studies have recognized is that in most areas wolves reduce the available biomass of individual prey carcasses by 75–100% (Peterson and Ciucci, 2003), although not yet as much in Yellowstone. That is, when wolves kill a prey animal, they almost always eat most of it; the scavengers take the leftovers. However, if wolves had not killed the animal, and it had died on its own, scavengers would have had 7–10 times the amount of food as on a wolf-eaten carcass.

It is true that generally when ungulates perish without predation, that mortality tends to occur more in seasonal bursts, whereas predation tends to distribute carrion more uniformly through the year (Mech, 1970; Wilmers et al., 2003). Nevertheless many scavengers cache surplus food they obtain during bursts of ungulate mortality so as to compensate for temporal fluctuations in food (Smith and Reichman, 1984). Furthermore, much carrion from seasonal bursts of mortality lingers for many months. Whether the more-uniform distribution of much-less biomass is more beneficial to scavengers (increases reproduction and survival) than the much-greater biomass available in total without predation is a fair question that is not yet answered.

2.3. Cascading effects of wolves

Although the above topics have garnered considerable interest, it is the possible cascading effects of wolf interactions with prey that have drawn most of the attention from scientists and the public alike (Table 1). Cascading effects have been attributed to both wolf reductions of prey numbers and to changes in prey behavior due to fear of wolves, or to “the landscape of fear” (Brown et al., 1999). Within only a few years of wolf reintroduction to Yellowstone National Park, Ripple et al. (2001) and the National Research Council (2002) suggested that wolf predation might reduce elk (*Cervus elaphus*) browsing and release vegetational growth. Yellowstone wolves do prey primarily on elk, and science has long known that elk had been controlling aspen recruitment (Singer,

1996; Kay, 2001). Furthermore, elk numbers have declined drastically since wolf reintroduction (Eberhardt et al., 2007).

2.3.1. Effects of wolf predation

What has not been clear, however, is the extent to which wolves have contributed to the decline of the main Yellowstone elk herd, that is, the Northern Range herd. Various studies have reached various conclusions about the extent to which wolves have contributed to a recent decline in the main Yellowstone elk herd (Vucetich et al., 2005; White and Garrott, 2005; Varley and Boyce, 2006), and there still is no consensus about that. The YNP elk population is affected by drought, winter severity, and human hunting as well as being preyed upon by cougars (*Felis concolor*), coyotes (Singer et al., 1997), black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos horribilis*) (Barber-Meyer et al., 2008). In many areas bears are important contributors to limiting ungulate numbers (NRC, 1997). Ferreting out the role of each of these factors in the YNP elk decline is a complex task that has yet to be accomplished.

Certainly under some conditions wolves can seriously reduce prey herds (Mech and Peterson, 2003). However, such a wolf effect occurs primarily when other conditions, usually adverse weather, is also affecting the prey (Mech et al., 1971; Peterson and Allen, 1974; Mech and Karns, 1977; Hebblewhite et al., 2005; Hebblewhite, 2005) or when populations are small and isolated (Peterson et al., 1998; Klein, 1995; Garrott et al., 2009).

2.3.2. Indirect effects of wolves

However, even if wolf predation contributed little to the elk decline, the “landscape of fear” looms large in the scientific literature about indirect cascading wolf effects. And there is some evidence that since wolf reintroduction to Yellowstone, elk have changed their foraging behavior (Laundre et al., 2001; Lung and Childress, 2007; Liley and Creel, 2007) and movements (Creel et al., 2005; Fortin et al., 2005; Gude et al., 2006). Thus several researchers have reported that wolves have benefitted aspen via a behaviorally-mediated trophic cascade (Abrams, 1984), in which aspen are recovering where risk of wolf predation on elk is high (Ripple et al., 2001; Ripple and Beschta, 2004, 2007; Beschta, 2007; Fortin et al., 2005). Similarly other researchers have produced evidence of increases in willow (Ripple and Beschta, 2004; Beyer et al., 2007) and cottonwood (Beschta, 2003) which they attribute to behaviorally-mediated-trophic cascades. That elk avoid aspen in risky sites because of their fear of wolves has been given considerable notice by scientists (Soule et al., 2003; Soule et al., 2005; Donlan et al., 2006; Morrell, 2007), as well as in the popular press (Table 1).

3. Accuracy of wolf-effect reports

The only trouble is it may well be that not all of this is correct. Science is self-correcting, and researchers who follow up on others', or even their own, work have the distinct advantage of scrutinizing the data and methods of their predecessors and thus improving on them (Ripple and Beschta, 2012). This process has now brought sharper focus on much of the early Yellowstone behaviorally-mediated-trophic-cascade research. The result is that, at the very least, scientists now disagree about whether wolf-related behaviorally-mediated-trophic cascades in Yellowstone are really occurring or at least whether that hypothesis has been rigorously tested (Kauffman et al., 2010).

At most, that well-publicized claim may not be correct at all. For example, the whole question of possible willow increase in Yellowstone after wolf restoration is rife with controversy. After Ripple and Beschta (2004) published photographs purporting to document willow increase on the only stream potentially influenced

by beavers that anyone had studied, Bilyeu et al. (2008) published photos purporting to refute the increase. Creel and Christianson (2009, p. 2465), also found that “because the presence of wolves is associated with an increase [emphasis mine] in willow consumption, our data tend not to support the narrow hypothesis of willow release through a behaviorally mediated trophic cascade.”

Similarly, with aspen, Kauffman et al. (2010, p. 2742) stated that “our estimates of relative survivorship of young browsable aspen indicate that aspen are not currently recovering in Yellowstone, even in the presence of a large wolf population. Finally, in an experimental test of the BMTC [behaviorally-mediated-trophic-cascade] hypothesis we found that the impacts of elk browsing on aspen demography are not diminished in sites where elk are at higher risk of predation by wolves.” Further, contrary to reports by Ripple and Beschta (2004, 2006) about behaviorally-mediated-trophic cascades explaining increased willow height, Johnston et al. (2011) explained the same increased height more parsimoniously by the greater access to groundwater that taller willows have.

But what about the earlier studies that seemed to evince that wolf effect on elk behavior must be causing trophic cascades? When those studies are examined closely and critically, some understanding can be reached of how study conclusions can mislead. Many of the Yellowstone studies (e.g. Ripple and Beschta, 2004; Beyer et al., 2007) compared pre- and post-wolf reintroduction vegetation with the assumption that changes measured after wolf reintroduction were related to wolf restoration, contrary to the admonition by Smith et al. (2003, p. 339) cited earlier. However, other changes that could have affected the amount of elk browsing on willows during the post-wolf period of the Beyer et al. (2007) study were worse winter conditions, drought, human harvest of elk (Vucetich et al., 2005), increased grizzly bear numbers (Schwartz et al., 2006), and long-term reduction in moose (*Alces alces*) numbers since widespread fire in 1988 (Tyers, 2006). Furthermore, the highly relevant fact was overlooked that the growing season in Yellowstone has increased by about 27 days coincident with wolf restoration, and that could account for increased willow growth (Despain, 2005 and Renkin and Despain, Yellowstone Center for Resources, pers. comm.).

4. Issues related to wolf-effects

It still could be true that the actual reduction of Yellowstone National Park elk numbers is causing a trophic cascade. In Banff National Park, for example, Hebblewhite et al. (2005) thoroughly documented such a cascade. In fact that study stands out as the only one that has provided seemingly irrefutable evidence of a true trophic cascade from wolves through prey, vegetation and song birds.

There are three concerns with the claim of a wolf-predation-based explanation for trophic cascades in Yellowstone. First, elk numbers were still three to four times higher around 1998 when willow release reportedly occurred than in the 1950s when willow remained suppressed (Hebblewhite and Smith, 2010). Second, as mentioned above, there is not scientific agreement on whether wolves are actually the primary agent of the recent Yellowstone-elk-population decline. For that matter, even if they are, then presumably where other agents are more causative of elk declines, for example, human hunting, there is no reason to think a similar trophic cascade would not result there. In other words, trophic cascades caused by wolf predation would be no more unusual than those caused by other mortality agents. Third, it would be difficult to sort out the reported effects of wolves on vegetation from that of increased growing season mentioned above.

The role of beavers in the reported trophic cascade also bears further discussion. Beavers occupy a special place in the wolf-mediated

trophic cascade in Yellowstone because of the many local ecological changes beaver ponds can bring (Naiman et al., 1986). Beavers depend primarily on willows in Yellowstone, and at the time of wolf reintroduction (1995) there were no actual beavers on the Northern Range (Smith et al. 2003). Willow regrowth in some areas during the past several years reportedly has increased, because of wolf effects on elk, which feed on willows. Beaver repopulation of Yellowstone, including its Northern Range has also begun (Smith et al., 2003), often attributed indirectly to wolves (Robbins, 2004; Ripple and Beschta, 2004; Chadwick, 2010). What has had little publicity, however, was that “the rapid re-occupation of the Northern Range with persistent beaver colonies, especially along Slough Creek, occurred because Tyers of the Gallatin National Forest released 129 beavers in drainages north of the park” (Smith and Tyers, 2008, p. 11). In any case, the assumption that beaver increase in Yellowstone and all the subsequent effects is a result of wolf restoration overlooks the possibility that the willow increase resulted from the raising of the water table by beavers and/or an increased growing season (Despain, 2005).

It should be clear from the above examples that sweeping, definitive claims about wolf effects on ecosystems are premature whether made by the public or by scientists. Some of the claims made to date might eventually be proven valid. More likely, some might be valid for specific times or places (e.g. Hebblewhite et al., 2005). Meanwhile it would be wise for all who are interested in wolves to remember the admonition of Ray et al. (2005, p. 426) cited earlier that “... scientists will likely never be able to reliably predict cascading impacts on bio-diversity other than prey.” These authors reached this conclusion after synthesizing 19 chapters of reviews relating to the ecological role of large carnivores.

5. Well-documented wolf effects

With some of the more obvious aspects of wolf interactions with their environment it is becoming increasingly clear what the nature of that interaction generally is. For example, under certain circumstances, usually adverse weather or in company with other large carnivores, wolves can definitely contribute to prey reductions (summarized by Mech and Peterson 2003). To the extent that wolves do reduce prey numbers, that would help release the vegetation those prey feed on, an effect known for decades (Leopold et al., 1947). Furthermore, it is well documented that wolves tend to cull out older, debilitated members of their prey (Mech and Peterson, 2003). How beneficial this culling is to prey herds, however, is still open to debate and conjecture.

6. Reasons for wolf-effect reports

But what explains the rash of recent research purporting to show beneficial effects of wolves beyond releasing vegetation? With wolf lay advocates it is just natural to want to promote their favorite animal and to try to counter the known negative effects of wolves and the claims fostered by people who vilify wolves, an increasing lot as wolves recover and proliferate. Thus wolf advocates eagerly seize on any study they consider favorable to wolves. The media become complicit by immediately publicizing such studies (Table 1) because of the controversial nature of the wolf. And all this publicity reverberates on the internet. Seldom, however, do studies contradicting the sensational early results receive similar publicity. The public is then left with a new image of the wolf that may be just as erroneous of the animal's public image a century ago.

Yet science is not totally blameless in all this. Not long before wolves were reintroduced into Yellowstone and wolf populations in many other areas were recovering, ecologists began uncovering

cascading effects in aquatic systems (Carpenter et al., 1985; Estes and Duggins, 1995). This discovery led researchers dealing with terrestrial systems to seek similar effects in those systems. Along came the recovering wolf populations, and soon researchers began to find what they considered to be evidence of trophic cascades in wolf-dominated systems (Hebblewhite et al., 2005). Only 3 years after wolf reintroduction into Yellowstone such findings turned up there (Ripple et al., 2001). McLaren and Peterson (1994, p. 1556) had already asserted a trophic cascade on Isle Royale; “The Isle Royale food chain [wolf/moose/vegetation] appears to be a tightly linked, three-trophic-level system dominated by top-down control,” although new evidence later indicated “... that top-down processes are not the primary influences of inter annual variation in moose dynamics” in this same system (Vucetich and Peterson, 2004). Once findings claiming wolf-caused trophic cascades were published, scientists competed to find more. Teams from several universities and agencies swarmed National Parks and churned out masses of papers, most of them drawing conclusions that wolf advocates considered positive toward the wolf (Table 1).

Aided by the popular media and the internet, a strong pro-wolf sentiment began to develop. Some of the sentiment might even have influenced scientists. Although most biologists try to resist making value judgments, not all have managed. For example, two scientists highly active in conservation biology wrote that wolves “may also have had top-down positive effects on the abundance of certain prey, such as pronghorn antelope.” But who is to say whether more or less pronghorns are “positive?” If more pronghorns are a positive development, what about more elk or bison? Are more or fewer coyotes positive? Fewer coyotes might release more mesocarnivores (see above), but the mesocarnivores might kill more birds. Is this positive or negative?

Most scientists do refrain from making value judgments. However, subtle biases could creep into their science, for example, simply by the choice of study they do. Since wolf reintroduction into Yellowstone and central Idaho, more than 20 articles have produced findings attempting to link wolves to greater vegetational growth as above, including one where <50 wolves have lived for <10 years (Beschta and Ripple, 2010). On the other hand, few recent studies have been published and popularized about what the public might consider negative about wolves. The only such study that comes to mind is that of Oakleaf et al. (2003) who found that in central Idaho, ranchers discovered only one of eight calves that were killed by wolves. That study gained little popular press.

7. Wolf effects outside of National Parks

One of the most important considerations that has been overlooked by wolf advocates when it comes to publicizing all of the putative cascading effects of wolves is that most of the studies have been conducted in National Parks. Thus to whatever extent the findings are valid, they apply to National Parks and not necessarily elsewhere (Muhly, 2010; Muhly et al., unpublished data). National Parks comprise almost all of the remaining reasonably natural environments that exist in the 48 contiguous states, and wolf-mediated trophic cascades to whatever extent they exist there would certainly add to the natural character of the parks.

However, National Parks comprise less than 10% of current wolf range in the contiguous US. Thus assuming wolves cause all of the ecological effects attributed to them, from helping increase beetle populations to cooling waters, these effects would pale in relation to the overwhelming anthropogenic effects that humans have already wrought over most of the wolf range. National Parks are protected from most hunting and trapping, logging, grazing, agriculture, irrigation, predator control, pest management, human habitation, and mining, all of which wreak pervasive, long-term

effects on ecosystems (Vitousek et al., 1997a; Vitousek et al., 1997b; Foley et al., 2005; Dambrine et al., 2007). How significant a beneficial effect can wolves have on songbirds compared with the negative effects of logging, grazing, clearing, or farming? How important would wolf effect on trout be where trout are stocked and harvested, streams are polluted, and river banks grazed? To the extent that wolves in National Parks do influence lower trophic levels, for them to do so outside of parks, their population would have to reach natural densities for long periods. Because wolf populations will almost always be managed outside of National Parks (Mech, 1995; Fritts et al., 2003; Boitani, 2003), their densities will probably never consistently reach the densities of wolves in National Parks, however.

Wolf restoration has generated a fine assortment of interesting ecological studies and has generally improved our understanding of wolves and associated species and their interactions with each other and the environment. However, we as scientists and conservationists who deal with such a controversial species as the wolf have a special obligation to qualify our conclusions and minimize our rhetoric, knowing full well that the popular media and the internet eagerly await a chance to hype our findings. An inaccurate public image of the wolf will only do a disservice to the animal and to those charged with managing it.

The wolf, while at the top of a food chain and a restored member of the world's most famous National Park and a prominent member of others, remains as one more species in a vast complex of creatures interacting the way they always have. It is neither saint nor sinner except to those who want to make it so.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.03.003>.

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