Received: 17 September 2020 | Revised: 10 February 2021 | Accepted: 21 February 2021

DOI: 10.1111/csp2.413

CONTRIBUTED PAPER

Conservation Science and Practice — A journal of the Society for Conservation Biology — Open Access

WILEY

Intended and unintended consequences of wolf restoration to Yellowstone and Isle Royale National Parks

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Funding information
Detroit Zoological Society; Isle Royale National Park, Grant/Award Number: P11AC90808; James L. Bigley Revocable Trust; McIntyre-Stennis Grant, Grant/Award Number: USDA-Nifa#1004363; Robbins Chair in Environmental Sustainability; Robert Bateman Endowment at the Michigan Tech Fund; U.S. National Park Service; U.S. National Science Foundation, Grant/Award Numbers: DEB-06137730, DEB-1245373, DEB-1453041; Yellowstone Forever

Abstract

Wolves (*Canis lupus*), a once widely distributed species, were systematically removed from many temperate zone ecosystems due to conflicts with humans. A change in human attitudes and cultural norms has brought about a recovery in some suitable areas, yet reintroductions are still controversial. Two notable reintroduction areas in the United States were Yellowstone and Isle Royale National Parks. Both proposals caused polarization and debate. In Yellowstone opposition focused on outside the park effects, mainly wolves killing livestock and wild game also desired by human hunters. At Isle Royale, opposition was mostly about human interventions into nature and impairment of wilderness values contrary to the spirit of 1964 Wilderness Act. Both locations had periods in the 20th century with and without wolves and the presence of wolves had a dampening effect on ungulate population fluctuations. Most outcomes of reintroduction at Yellowstone were predicted as the Environmental Impact Statement written beforehand correctly predicted 78% of the 51 outcomes that were examined. Wolves were too recently reintroduced to Isle Royale to make similar comparisons, but we conclude that intervention is not contrary to the Wilderness Act, nor author Howard Zahniser's vision, partially because wolf reintroduction was a mitigation for human actions. Also, not intervening, or inaction, often perceived as safer, would have had more damaging impacts to ecosystem functioning.

KEYWORDS

national parks, reintroduction, restoration, wilderness, wolves

1 | INTRODUCTION

Wolves are large carnivores indigenous to most of North America. Originally, they were the most widespread large carnivore over this area and had important ecosystem and food web effects (Mech, 1970; Peterson, Vucetich, Bump, & Smith, 2014). As such, they had significant ecological influences on the landscape through top-down forcing; a keystone species (Peterson et al., 2014; Ripple, Estes, Beschta, et al., 2014). With European colonization, wolf abundance and distribution were greatly reduced. Virtually, all of the contiguous U.S. lost wolves due to human killing save for a small population in northern Minnesota, and despite remoteness and low human populations, they were also reduced across much of Canada and Alaska (Mech, 1970). Although this near extirpation is widely documented, it is an underappreciated story in terms of the ecological repercussions. Wolves, the dominant carnivore across North America, were eliminated from ecosystems before scientists even knew what they did or their role in food webs. Accordingly, ecological theory developed without them (and other carnivores for that matter), and this resulted in a bias favoring influences of bottom-up forces structuring ecosystems that stubbornly persists today (Estes, 2016). In short, and importantly for this special journal issue, wolves were native to virtually every North American ecosystem and humans extirpated them. The duration of absence varied from decades to a century or more, but the systems from which they were removed were thousands of years in the making. Would such a wink of time gone make a difference if they were restored? And why was it necessary to restore them?

This elimination of wolves from large portions of North America and U.S. National Parks clearly departed from the goals and objectives for the National Park Service (NPS, Leopold, Cain, Cottam, Gabrielson, & Kimball, 1963, USNPSC, 2012) and the Wilderness Act (P.L. 88-577, 78 Stat. 890). Broadly speaking, the goals for both areas were to maintain *naturalness*, which has been hard to define and much debated, but the understanding of the term revolved around maintenance of biological diversity (Aplet & Cole, 2010) and "ecological integrity" (USNPSC, 2012). Both may require human intervention (Aplet & Cole, 2010; Leopold et al., 1963). A 2012 NPS revision of the 1963 Leopold report referred to ecological integrity as "possess complete food webs" including "naturally functioning ecological processes such as predation" (USNPSC, 2012). In another article in this special issue, Rowher and Marris (2021) question the meaning and usefulness of the term "ecological integrity," but for the purposes of this paper, we will adhere to the above definition. Regardless of ambiguity about the term, the role of large carnivores in maintaining food webs through natural predation is well known (Peterson et al., 2014; Ripple et al., 2014), creating what Rowher and Marris call "diversity and complexity" and certainly consistent with the above stated goals. Despite this policy, restoration of natural predation by wolves to two national parks was debated partly because it required human intervention, which in the tangled meaning of natural, also meant lack of human influence (Aplet & Cole, 2010). Yellowstone and Isle Royale, where human impacts led to wolf extirpation or near-extirpation, are managed as wilderness, the former not legally so but as de-facto, and the latter as legally designated, had drawn-out and controversial debates about wolf reintroduction. Ultimately, both parks reintroduced wolves. The purpose of our essay is to explain what an intervention such as this entails, what happened, and to defend it as restoring naturalness, consistent with policy statements for both areas (parks and wilderness). Importantly, this decision and its eventual outcomes were arrived at through vigorous scientific research—a cornerstone in maintaining the "ecological integrity" and biological diversity of protected areas (USNPS, 2012) and an antidote to inaction (Brister, Holbrook, & Palmer, 2021).

2 | BACKGROUND FOR WOLF RESTORATION

Yellowstone National Park (YNP), the world's first national park established in 1872, originally had wolves, but they were eradicated according to park policy by 1926 (Smith, Stahler, MacNulty, & Whittlesey, 2020). Isle Royale National Park (IRNP), established in 1941, had wolves colonize through natural dispersal in the late 1940s by crossing a Lake Superior ice bridge (Mech, 1966; Peterson, 1977). Genetic connectivity to the large mainland population of wolves was dependent on these ice bridges, which formed in eight of 10 years in the 1960s. Climate change has reduced that frequency and currently ice bridges allowing unrestricted wolf movement from the mainland to IRNP are relatively uncommon. This diminished connectivity led to genetic isolation resulting in inbreeding depression causing the island wolf population, typically 20–25 wolves with a high of 50, to collapse to just two wolves by 2016 (Hedrick, Peterson, Vucetich, Adams, & Vucetich, 2014).

One other event also led to this genetic decline. In 1980, a dog infected with canine parvovirus was brought to the island illegally by a private boater. The virus swept through the formerly unexposed wolf population, already in decline because of food limitation, and catastrophic mortality brought the population down from 50 wolves to 14 in 2 years (Peterson, Thomas, Thurber, Vucetich, & Waite, 1998). Hence, human actions contributed to a dramatic genetic bottleneck.

Both parks, founded, at least in part, on the notion of preservation (NPS, 2006; White, Garrott, & Plumb, 2013), lost a top-level carnivore critical to ecosystem functioning and food web dynamics because of human actions. In the case of YNP, human killing, both in the park and the surrounding area, extirpated the population and limited the potential for natural recolonization (Fritts, Watters, Bangs, Smith, & Phillips, 2020); in the case of IRNP, climate change reduced ice bridge connectivity to the mainland and humans contributed to a bottleneck from introduced disease which caused the wolf population to decline (Vucetich, Nelson, & Peterson, 2012). Although not prohibited by policy, U.S. National Park managers do not commonly intervene. In instances where they do, the justification is usually because of human-caused disturbance or exploitation, which for YNP was very clear (Leopold et al., 1963; Smith et al., 2020). Justification to intervene was not as clear for IRNP. The complex, diffuse, and indirect effects of climate change do not provide a clear link to taking action; some argue nothing can be done due to overwhelming effects, or there may be more ice bridges in the future (Gostkowski, 2013; Mech, 2013). Introduced disease is more justifiable, but some question that too (Mech, 2013).

Besides controversy about intervening, another problem was how it should be done; groups in favor of reintroduction disagreed on implementation. Polarization characterizes virtually all wolf issues, so none of this was unexpected, and this is essentially the history of wolves, but disagreement dissipates action (Brister et al., 2021). In YNP, the chosen reintroduction strategy was to relax some of the stringency of the Endangered Species Act (ESA) under provisions provided in the Act by section 10j—which allowed wolves to be reintroduced as "*experimental and non-essential*". This management flexibility *slightly* reduced some of the opposition to reintroduction. Alternatively, some conservation groups wanted wolves reintroduced as a fully protected endangered species, or to *not* invoke relaxations in ESA regulations (Fritts et al., 2020). In the case of IRNP, some wilderness advocates opposed reintroduction because it was contrary to the vision of the Wilderness Act of 1964 (Gostkowski, 2013) or violated the concept of naturalness (Cochrane, 2013).

The rationale behind these arguments is interesting and complex, and beyond the scope of this paper, and we are evaluating them from the perspective of ecologists, not wilderness scholars, but it is pertinent nonetheless, and important to briefly explain. Some of it directly concerns the reservations some people have for interventions into nature. For YNP (and central Idaho), reintroducing wolves as a fully protected endangered species meant they could not be killed under any circumstances, with the notable issue being even when wolves killed livestock (Smith & Bangs, 2009). Reintroduced as an experimental, non-essential population, which section 10j of the ESA provides for, allowed livestock-killing wolves to be killed. Ranchers were bitterly opposed to reintroduction, especially if wolves had fully endangered status. Hunters too were concerned, even though 10j provided for management flexibility (e.g., wolf reductions) when wolves caused declines in ungulate populations. These two very large, politically influential, and important stakeholder groups needed to be heard, or accommodated in some fashion as they would bear some of the costs of wolf recovery. Trust was fragile. "Cramming wolves down their throats" was not the way to accomplish recovery, some argued for natural recolonization which would have more social acceptance (Boyd, 2020). It was uncertain, however, if wolves could make it to YNP across a sea of humanity prone to killing (Fritts et al., 2020). This conflict is not new. The 1963 Leopold Report championed pristine nature—do not intervene unless you need to, but do so to get it back—even if it introduced artificiality. The wilderness vision was about "absence of human control" and "wildness" (Sutter, 2002). Both philosophies then share a view of "pristine" and human disruption of nature. The issue then is how to regain natural systems following damage by humans. Many on both sides view wolves as the quintessential wilderness animal, symbolic of wildness, and a top-down force keeping food webs robust. Yet, disagreement over how to reintroduce wolves in YNP almost ended the program (Fritts et al., 2020).

One solution was to do nothing, and this is often the preferred alternative for intractable debates (Brister et al., 2021). It is unknown how frequently this occurs because inaction is rarely publicized or published because nothing happens. Potentially, natural wolf dispersal could have reached both areas, but analyses and expert opinion rated this as improbable (USFWS, 1994). Nonetheless, this potential left an opportunity for debate and a hope that intervention was unnecessary (Boyd, 2020; Mech, 2013).

The heart of the debate was about the role of humans in nature. YNP was not big enough to contain all the wolves, nor was it big enough to allow for a sustainable population by itself. Wolves would spill out of the 8,991 km^2 park onto human dominated landscapes where wolves were not welcome, causing livestock damage and impacting big game populations. IRNP, smaller (544 km^2) and an island, the same argument applied. Alone it is not big enough, and connectivity to the mainland via an ice bridge was vital to the sustainability of the wolf population. The future of such ice bridges was uncertain. At IRNP, where there was no concern about wolf–human conflict, the central issue was the acceptability of human intervention in wilderness.

The 1964 Wilderness Act, authored by the deeply philosophical Howard Zahniser, who was inspired by Thoreau, is a tremendously important piece of environmental legislation. It lays out thoughtful protection of life and land separate from humanity. However, as a visionary, Zahinser, did not consider his vision of wilderness as immutable (Harvey, 2014). Speaking to the skeptical Society of American Foresters 7 years before the Act being signed into law, he said any wilderness legislation must include a provision to change—or any language must be "living," or it would not be workable in the long term (Zahniser, 1958).

Presumably, what Zahinser did not see, nor could he foresee in 1964, was the near complete takeover of the planet by humans. Nor could he anticipate the global impacts of anthropogenic climate change. To cling to a pure vision of nature preservation, in a time of desperation and overwhelming change, will not preserve—and may even degrade—biodiversity and functioning food webs (Cole & Yung, 2010). So the question is, when we have already disturbed natural processes significantly, how can we step back and "let nature take its course?" We are midstream in a rising river, how can we turn around and go back to the bank where we started? Further, the state of scientific understanding is far greater than it was in 1964. This is not an argument for human hubris or arrogance, much is still unknown, and much is still unpredictable, and most everything is best when left alone, but we did not leave it alone, and we may now understand some of the damage we have done. Novak (in press) recently researched *all* reintroductions and translocations in the United States and found that *none* of them were deleterious and *none* of the impacts were unintended. In most cases, we were restoring a missing constituent to an ecosystem and the outcomes were predictable. We refer the reader back to our "wink of time idea" from the Introduction.

We also know a lot more about the role of wolves in North American ecosystems and this knowledge further limits "unintended consequences" (Brister et al., 2021). The idea, much admired by proponents of nonintervention, was to be "guardians and not gardeners." We have *not* done a good job guarding nature, and as a result, we no longer live in a pristine world. Now we have to help (Wilson, 2016).

3 | SCIENCE AS ARBITER IN A NONSCIENTIFIC WORLD

How, then, are we to preserve nature in areas where that is the primary objective? What shall we do in a world increasingly under human pressure, to preserve what is left of pristine nature—the heart of the Wilderness Act? Should we intervene in nature and restore the wolf? The goal is to help preserve, or retain, naturally functioning food webs and preserving biodiversity, which is how we defined "natural" at the outset. The foundational question is: do we know enough to not mess it up? Or will intervention continue a pattern of destructive human domination? In the case of wolf restoration, we have several advantages. Wolves are generalists, they occurred across nearly all of North America, and they are among the most-studied of all mammals (Mech, 1970), so we have a wide berth for intervention. In this case, science provides a reliable road map.

For example, both YNP and IRNP had ample science to back up decision-making. YNP is one of the best studied parks world-wide and there had been an exhaustive 20-year process to understand the impacts of wolf reintroduction on the ecosystem and human communities. Besides the Environmental Impact Statement (EIS; 1994), four volumes of material were published, called "Wolves for Yellowstone" I, II, III, and IV (Varley & Brewster, 1992; YNP et al., 1990), a scientific monograph (Cook, 1993), and other books (Fischer, 1995). At IRNP, wolf-moose (*Alces alces*) research represented the longest predator–prey study in the world, with unbroken monitoring back to 1958 (Mech, 1966; Peterson, 1977; Peterson, 2007). Also, on IRNP, there was data going back to the 1930s on what the island looked like *with and without* wolves and how the moose population and vegetation responded to each condition, a natural experiment (Brandner, Peterson, & Risenhoover, 1990; Mech, 1966; Peterson, 2007). This body of work did not eliminate the debate about what would happen, nor alleviate the controversy about what should be done, suggesting that the road map provided by science is necessary but perhaps not sufficient.

In the YNP region, the most pressing issues were impacts on ranching and big game hunting, both issues occurring outside the park, but most of the elk (*Cervus canadensis*) using the park were migratory and not immune to wolf predation inside the park, nor human hunting outside. The most pressing issue inside the park was elk population fluctuations without a robust predator community and no human control. Since about 1923, following dramatic reductions in predators, elk were culled (e.g., killed or shipped to other locations) by the NPS inside and Montana hunters outside the park because of perceived damage to the vegetation (Houston, 1982; Wagner, 2006). How would wolves affect this situation inside the park and what would they do to game outside park boundaries was a crucial question. At IRNP, the forest had already been through several cycles of forest suppression and release due to fluctuating moose numbers, at times influenced by wolf predation, so the debate about wolf recovery centered more on the philosophical debate about human intervention in nature. The debate did generate keener interest into ecosystem functioning and predator–prey population ecology, but this hinged on a top-down perspective of wolves being absent or present. The science was rich and well worked out. Despite the science, there was, nevertheless, stark disagreement. For IRNP a frequent refrain by critics was meddling was simply wrong (e.g., conservation group *Wilderness Watch*).

Perhaps more important than the role of science as arbiter in decision-making are the scientific opportunities that were presented by wolf reintroduction in these two national parks. Ecosystem functioning and predator–prey dynamics are fundamental aspects of ecology, dealing as they do with food webs and trophic structure as well as the phenomena of top-down versus bottom-up control. The work in these areas is deep in marine and freshwater ecology, and despite the work in YNP and IRNP, nascent in terrestrial systems (Hebblewhite & Smith, 2010; Shurin, Borer, Seabloom, Anderson, & Blanchette, 2002). For IRNP, restoring wolves helped maintain one of the few areas in the world where there is no harvesting of wolves, prey, and the forest—a chance to learn about *real* natural regulation. For YNP, natural regulation in the elk population may have been the most important wildlife management controversy of the last half century (Wagner, 2006), but in fact the elk population was limited by harvest in the decades before wolf reintroduction. Something approaching natural regulation was finally achieved after natural recovery of grizzly bears (*Ursus arctos*) and cougars (*Puma concolor*), along with purposeful reintroduction of wolves.

4 | INTENDED AND UNINTENDED CONSEQUENCES

The issue with wolf recovery, and virtually all nature restoration, is that predicting nature is almost impossible. Nature is so complex, and human understanding of it still so rudimentary, that almost any position can be taken that has at least some scientific support. Yet, we have learned a great deal and some of what we have learned is from natural experiments.

The story of predator removal in YNP is well known and mostly told through the story of elk (Eberhardt, White, Garrott, & Houston, 2007). After park establishment, park policy was to kill all predators except bears, whom one administrator had a fondness for and spared (Pritchard, 1999). The result of this was a burgeoning elk population that had to be controlled by park rangers and state of Montana officials across the park line when the elk migrated to lower elevation in winter. Between 1923 and 1968 > 70,000 elk were killed or shipped to repopulate other areas where elk were reduced by market hunting (Eberhardt et al., 2007). The rationale was to protect range and vegetation (Houston, 1982; Wagner, 2006). It is debated if these elk reductions achieved their goal (Kay, 1997; Wagner, 2006), but it is widely agreed that woody vegetation was suppressed, as were beavers (*Castor canadensis*), and stream dynamics were altered (Peterson et al., 2020). Virtually all palatable deciduous woody vegetation was browsed by elk (Singer, Mark, & Cates, 1994), and in 1996, simultaneous with wolf reintroduction, an aerial survey found only one beaver colony in all of northern Yellowstone (Smith & Tyers, 2012). This is a brief description, more detailed accounts exist, primarily YNP (1997), NRC (2002), Wagner (2006), and Eberhardt et al. (2007), and many other sources cited therein. It is a large literature, subjectivity bleeds through commonly, and arguments can be personal, so the debate about wolves was just a continuation of this 100-year-old story and controversy.

Twenty-five years on, wolves have established and recovered. This recovery was dependent on the greater Yellowstone area and genetic connectivity to other populations, or as stated above, a much larger area than just the park (Fritts et al., 2020). In short, reintroduction succeeded, wolves were delisted, and although their ecological effects may be mostly confined to YNP, they roam across Idaho, Montana, and Wyoming numbering about 2,000 wolves (Fritts et al., 2020).

The ecological effects have mostly been described in the context of the woody vegetation response. Although debated as to why, most conclude willow (*Salix spp.*) and aspen (*Populus tremuloides*) have recovered in some areas of northern Yellowstone (Peterson et al., 2014). The significant change was greater heterogeneity in vegetation structure, so recovery has not been uniform (Peterson et al., 2020). Beaver colonies have increased 14-fold (Smith & Tyers, 2012) and songbirds recovered in willow stands (Baril, Hansen, Renkin, & Lawrence, 2011) with some areas seeing an influx of new species (YNP unpublished data). Most agree the woody plant recovery was due to less elk herbivory (Peterson et al., 2020), primarily fewer elk, rather than a behavioral response. The reduction in elk density was only partly attributable to carnivore recovery, as there are other significant influences such as elk reductions by the state of Montana outside the park, and possibly climate effects (Eberhardt et al., 2007; Lemke & Mack, 1998; Vucetich, Smith, & Stahler, 2005). Soil moisture played a prominent role, and retreat of the water table following historic reductions in beaver may prove intractable (Marshall, Hobbs, & Cooper, 2013). These myriad influences are functioning in a tiered or nested fashion of limiting factors for vegetation growth now that elk browsing is not overwhelming (Peterson et al., 2020).

Further, carnivore recovery attenuated elk population fluctuations (Figure 1a). Once wolves and cougars were eradicated in the early twentieth century, the NPS had to control the elk population. When they stopped, the population increased only to be controlled by hard winters and hunting outside the park regulated by the state of Montana (Eberhardt et al., 2007; Lemke & Mack, 1998).

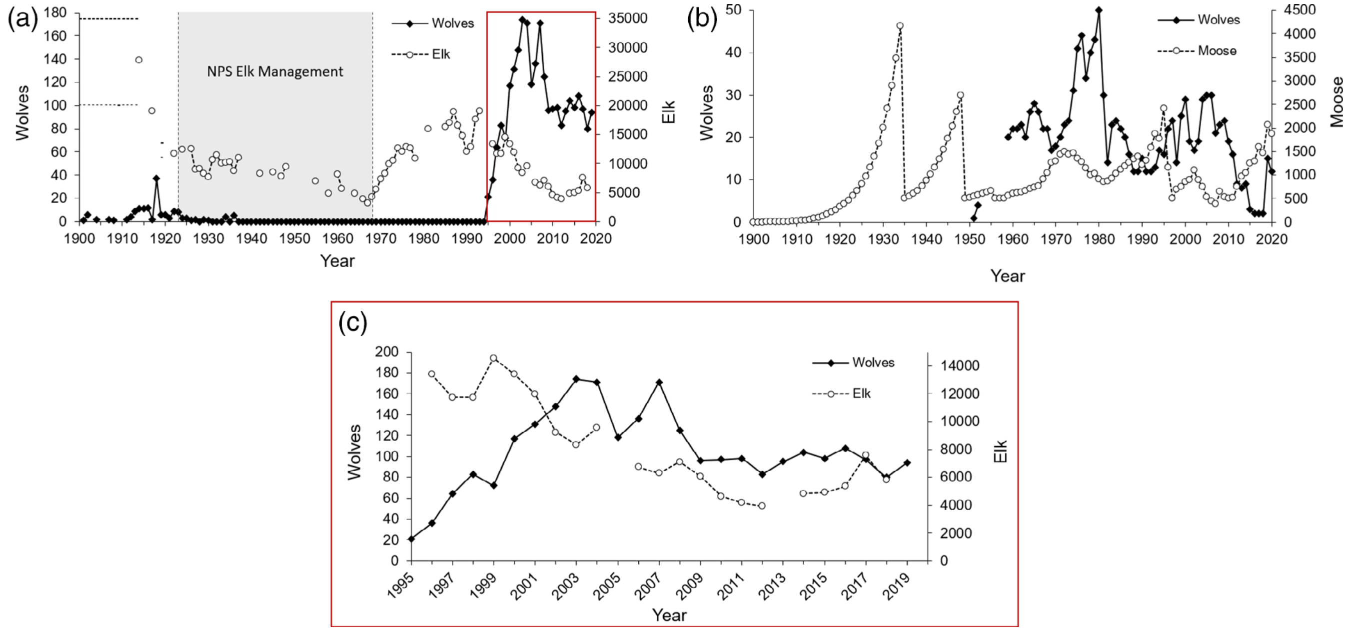

FIGURE 1 (a) Wolf–elk population fluctuations in Yellowstone National Park 1900–2020. (b) Isle Royale National Park wolf-moose population fluctuations 1900–2020. (c) Wolf–elk population fluctuations in Yellowstone National Park since wolf reintroduction 1995–2019. Population estimates derived prior to modern day surveys for Yellowstone were obtained from Houston (1982), Weaver (1978), Wagner (2006), and Whittlesey and Bone (2020); for Isle Royale sources were Mech (1966) and Peterson (1977)

Post-carnivore recovery—cougars via natural dispersal and wolves via reintroduction—the elk population declined by 60% and has been approximately stable the last decade (MacNulty et al., 2020). Some of this decline can be attributed to winter hunting of female elk in state-sponsored hunts in Montana (Eberhardt et al., 2007, Vucetich et al., 2005), but this hunt was terminated in 2008, which corresponds with a period of elk population stability at a new, lower level.

Finally, predictable late winter die-offs of elk have declined even when winter-conditions are severe (Regan, 2016; Wilmers & Getz, 2005). Catastrophic winter die-offs occurred during the hard winters of 1988–1989 and 1996–1997 when thousands of elk died (Regan, 2016, Wilmers & Getz, 2005) and the carnivore community was still colonizing. Later, when the carnivore populations were saturated (natural densities regulated by prey), severe winters (as in 2010–2011) did not produce the same large-scale die offs (Regan, 2016). One analysis predicted that the addition of wolves and cougars would buffer against future boom-bust cycles of elk which are predicted for some climate change scenarios in the absence of large carnivores (Wilmers & Getz, 2005).

Was all of this intended? Predictions about the impacts of wolf recovery to the Yellowstone region as a whole were fairly accurate. In 2005, an analysis was done of the pre-wolf EIS predictions and a 10-year assessment of what *actually happened* (White et al., 2005). Fifty-one topics in seven areas were analyzed: (a) wolf recovery, (b) impacts on ungulate populations, (c) impacts on hunter harvests, (d) impacts on domestic livestock, (e) impacts on land use, (f) impacts on visitor use, and (g) impacts on economics. Of these 51 predictions, 40 (78%) were correct, 7 (14%) were incorrect, and 4 (8%) were inconclusive or not able to be determined. In short, intended consequences far outweighed those that were unintended.

In the case of IRNP, the intervention is so recent that such an analysis is not possible, but a look back to the island's past offers some confidence in a prediction. Moose first came to the island without wolves. The population grew exponentially (Figure 1b) until the population crashed in the 1930s. After the crash, the moose population increased again, then another die-off occurred in the late 1940s. Seeing this boom-bust cycle *twice*, and in an attempt to prevent it, wolves from a zoo were unsuccessfully reintroduced by the Park Service in 1952. Unbeknownst to park officials, wolves had colonized the island—crossing on an ice bridge—on their own in the late 1940s. After wolf colonization, the moose population has fluctuated much less (Figure 1b) and impacts on vegetation were lessened as measured by browsing on balsam fir (*Abies balsamea*)—a palatable evergreen tree preferred by moose in winter (Brandner et al., 1990). After wolves were established on the island, the boom-bust cycles of moose were not so prevalent (Figure 1b),

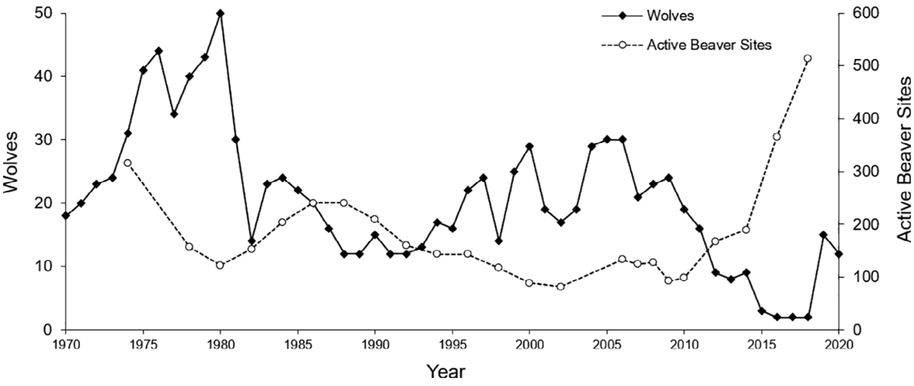

FIGURE 2 Wolf-beaver population estimates Isle Royale National Park 1970–2018

nor were the impacts on the vegetation, despite some coniferous species being reduced in abundance.

No similar studies on songbirds have been undertaken on Isle Royale, but beaver population counts have been conducted since 1964. Beavers are a key prey item for wolves in IRNP. During this time, beaver population increases occurred through periods of low wolf numbers (Figure 2). Beaver habitat in IRNP near existing ponds has been heavily used for decades, without renewal by fire. Unused forage, which is far from water, is accessible only when wolf numbers are low, allowing for distant and safe travel from a beaver pond or lake. This situation has caused beaver populations to increase and decrease with wolf abundance (Figure 2). Although not specifically studied on Isle Royale, beaver ponds are known to be biodiversity hotspots (Jenkins & Smith, 1999), so creation and maintenance of hotspots are indirectly connected to wolf presence/absence (Gable, Johnson-Bice, Homkes, Windels, & Bump, 2020). Wolf predation has likely slowed the decline of beaver habitat by allowing for vegetative recovery during periods of high wolf predation causing beaver forage to regenerate and their cycle to repeat indefinitely.

5 | HUMAN INTERVENTIONS AND NATIONAL PARKS: NATURAL OR UNNATURAL?

Wolf restoration to YNP and IRNP impacted both national parks similarly: wolves successfully reestablished and limited prey populations resulting in less herbivory allowing for other ecosystem components to emerge or take place (Smith et al., 2020, RO Peterson unpublished data). In both areas, characterized by ecosystems that evolved with wolves as the top predator, intervention through wolf restoration had predictable results. Had neither intervention taken place, each park and ecosystem would have become *less natural*. Past ungulate population fluctuations, with reduced predation, had led to system degradation or dominance of some species at the expense of others (Peterson, 2007; Wagner, 2006). Whether or not this is the desired state for these ecosystems, is a value-laden debate left to humans; it is important to not confuse the issues (Aplet & Cole, 2010).

The wish to not intervene must consider how natural systems evolved and what led to their dysfunction. In both of these examples, human effects caused reduced predation, so to stop and *not* intervene would have made these systems more *unnatural*, potentially requiring continual human intervention subject to human value judgements for decades to come. These are clear choices for us to make, but often, at least in these cases and many others (Novak, in press), the science is worked out and should not confuse the debate. When possible, given massive human transformation of the planet, and feasible with scientifically informed management action, human intervention may allow nature to restore itself rather than be subject to never-ending human debate and policy changes. Put another way, such actions are not interventions, rather they make conditions possible for nature to restore herself, leading in the end to the "hands off" approach so many find desirable (Brister et al., 2021).

Can such experiences inform other controversial wolf restoration programs? The ongoing issues about Mexican wolf (*C.l. baileyi*) restoration to the southwestern United States and Mexico do not readily compare to YNP and IRNP as it does not occur within national parks or wilderness managed in a similar fashion as IRNP; the significant difference being cattle grazing in southwest U.S. wilderness is allowed (Brown & Parsons, 2001). Hence, would wolf recovery restore a more naturally functioning ecosystem with greater "diversity and complexity" bringing back "preferred historical" ecological states (Rowher & Marris, 2021)? Likely no, the human footprint is too great. But it could help nature, and cause humans to make room for difficult to live with species inching human dominated landscapes toward these conditions. It could be the same in Colorado, another site of wolf restoration. Both required human intervention.

ACKNOWLEDGMENTS

Wolf reintroduction and wolf and elk monitoring in Yellowstone National Park was supported by the U.S. National Park Service and many donors to Yellowstone Forever. Notable among those donors were V. Gates, B. and A. Graham, and G. Orhstrom. The authors thank *Revive and Restore* for the invitation to contribute to this special issue of *Conservation Science and Practice* and to participate in the Intended Consequences Workshop in June 2020. The authors also appreciate funding support from the U.S. National Science Foundation grants (DEB-06137730 and DEB-1245373). Isle Royale Research was supported by the U.S. National Science Foundation (DEB-1453041 to J. A. V.), Isle Royale National Park (CESU Task Agreement No. P11AC90808 to J. A. V.), a McIntyre-Stennis Grant (USDA-Nifa#1004363 to J. A. V.), Robert Bateman Endowment at the Michigan Tech Fund, James L. Bigley Revocable Trust, and Detroit Zoological Society. Support for ROP came from the Robbins Chair in Environmental Sustainability. Both projects are grateful to the many individuals who contributed to the collection of field data. N. Tatton made both figures and the authors thank her for her excellent work in a timely fashion.

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REFERENCES

Aplet, G. H., & Cole, D. N. (2010). The trouble with naturalness: Rethinking park and wilderness goals. In D. N. Cole & L. Yung (Eds.), *Beyond naturalness: Rethinking park and wilderness stewardship in an era of rapid change* (pp. 12–29). Washington, DC: Island Press.

Baril, L. M., Hansen, A. J., Renkin, R., & Lawrence, R. (2011). Songbird response to increased willow (*Salix* spp.) growth in Yellowstone's northern range. *Ecological Applications*, *21*, 2283–2296.

Boyd, D. (2020). To reintroduce or not to reintroduce, that is the question. In D. W. Smith, D. R. Stahler, & D. R. MacNulty (Eds.), *Yellowstone wolves: Science and discovery in the world's first national park* (pp. 19–20). Chicago, IL: University of Chicago Press.

Brandner, T. A., Peterson, R. O., & Risenhoover, K. L. (1990). Balsam fir in Isle Royale National Park, Michigan: Effects of moose herbivory and population density. *Ecology*, *71*, 155–164.

Brister, E., Holbrook, B., & Palmer, M. J. (2021). Conservation science and the ethos of restraint. *Conservation Science and Practice*, Xx *(this issue)*, Xx. https://conbio.onlinelibrary.wiley.com/doi/full/10.1111/csp2.381.

Brown, W. M., & Parsons, D. R. (2001). Restoring the Mexican gray wolf to the desert southwest. In D. S. Maehr, R. F. Noss, & J. L. Larkin (Eds.), *Large mammal restoration: Ecological and sociological considerations in the 21st century* (pp. 169–186). Washington, DC: Island Press.

Cochrane, T. (2013). *Island complications: Should we retain wolves on Isle Royale?* (Vol. 30, pp. 313–325). George Wright Society, Hancock, MI: George Wright Forum.

Cole, D. N., & Yung, L. (2010). Park and wilderness stewardship: The dilemma of management intervention. In D. N. Cole & L. Yung (Eds.), *Beyond naturalness: Rethinking park and wilderness stewardship in an era of rapid change* (pp. 1–9). Washington, DC: Island Press.

Cook, R. S. (1993). *Ecological issues on reintroducing wolves into Yellowstone National Park*. Denver, CO: U.S. Department of Interior. National Park Service.

Eberhardt, L. L., White, P. J., Garrott, R. A., & Houston, D. B. (2007). A seventy-year history of trends in Yellowstone's northern elk herd. *The Journal of Wildlife Management*, *71*, 594–602.

Estes, J. A. (2016). *Serendipity: An ecologist's quest to understand nature*. Oakland, California: University of California Press.

Fischer, H. (1995). *Wolf wars*. Helena and Billings, Montana: Falcon Press.

Fritts, S. H., Watters, R. J., Bangs, E. E., Smith, D. W., & Phillips, M. K. (2020). How wolves returned to Yellowstone. In D. W. Smith, D. R. Stahler, & D. R. MacNulty (Eds.), *Yellowstone wolves: Science and discovery in the world's first national park* (pp. 13–25). Chicago, IL: University of Chicago Press.

Gable, T. D., Johnson-Bice, S. M., Homkes, A. T., Windels, S. K., & Bump, J. K. (2020). Outsized effect of predation; wolves alter wetland creation and recolonization by killing ecosystem engineers. *Science Advances*, *6*, eabc5439.

Gostkowski, T. (2013). *Are Isle Royale wolves too big to fail? A response to Vucetich et al* (Vol. 30, pp. 96–100). George Wright Society, Hancock, MI: George Wright Forum.

Harvey, M. (Ed.). (2014). *The wilderness writings of Howard Zahnhiser*. Seattle, WA: University of Washington Press.

Hebblewhite, M., & Smith, D. W. (2010). Wolf community ecology: Ecosystem effects of recovering wolves in Banff and Yellowstone national parks. In M. Musiani, L. Boitani, & P. Paquet (Eds.), *The world of wolves: New perspectives on ecology, behavior and management* (pp. 69–122). Calgary, Canada: University of Calgary Press.

Hedrick, P. W., Peterson, R. O., Vucetich, L. M., Adams, J. R., & Vucetich, J. A. (2014). Genetic rescue in Isle Royale wolves: Genetic analysis and the collapse of the population. *Conservation Genetics*, *15*, 1111–1121.

Houston, D. B. (1982). *The northern Yellowstone elk: Ecology and management*. New York, London: Macmillan Publishers.

Jenkins, S. H., & Smith, D. W. (1999). Family Castoridae: Beaver. In D. E. Wilson & S. Ruff (Eds.), *The Smithsonian book of North American mammals* (pp. 548–552). Washington, DC: Smithsonian Institution Press.

Kay, C. E. (1997). Viewpoint: Ungulate herbivory, willows, and political ecology in Yellowstone. *Journal of Range Management*, *50*, 139–145.

Lemke, T. O., & Mack, J. A. (1998). Winter range expansion by the northern Yellowstone elk herd. *Intermountain Journal of Sciences*, *4*, 1–8.

Leopold, A. S., Cain, S. A., Cottam, C. M., Gabrielson, I. N., & Kimball, T. L. (1963). *Wildlife management in the national parks: The Leopold report*. Washington, DC: National Park Service.

MacNulty, D. R., Stahler, D. R., Wyman, T., Ruprecht, J., Smith, L. M., Kohl, M. T., & Smith, D. W. (2020). Population dynamics of northern Yellowstone elk after wolf reintroduction. In D. W. Smith, D. R. Stahler, & D. R. MacNulty (Eds.), *Yellowstone wolves: Science and discovery in the world's first national park* (pp. 184–199). Chicago, IL: University of Chicago Press.

Marshall, K. M., Hobbs, N. T., & Cooper, D. J. (2013). Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proceedings of the Royal Society B*, *280*, 20122977.

Mech, L. D. (1966). *The wolves of Isle Royale* (p. 210). Washington, D.C.: National Park Service Fauna Series No. 7. U.S. Government Printing Office.

Mech, L. D. (1970). *The wolf* (p. 384). Garden City, New York: Natural History Press.

Mech, L. D. (2013). *The case for watchful waiting with Isle Royale's wolf population* (Vol. 30, pp. 326–332). George Wright Society, Hancock, MI: George Wright Forum.

Novak, Ben J., Phelan, Ryan, & Weber, Michele. (2021). U.S. conservation translocations: Over a century of intended consequences. *Conservation Science and Practice*, http://dx.doi.org/10.1111/csp2.394.

NPS (National Park Service). (2006). *Management policies 2006*. Washington, DC: USDOI.

NRC (National Research Council). (2002). *Ecological dynamics on Yellowstone's northern range*. Washington, DC: National Academy Press.

Peterson, R. O. (1977). *Wolf ecology and prey relationships on Isle Royale* (p. 210). Washington, D.C.: U.S. National Park Service Scientific Monograph Series No. 14. U.S. Government Printing Office.

Peterson, R. O. (2007). *The wolves of Isle Royale: A broken balance*. Ann Arbor, MI: The University of Michigan Press.

Peterson, R. O., Beschta, R. L., Cooper, D. J., Hobbs, N. T., Johnston, D. B., Larsen, E. J., ... Wolf, E. C. (2020). Indirect effects of carnivore restoration on vegetation. In D. W. Smith, D. R. Stahler, & D. R. MacNulty (Eds.), *Yellowstone wolves: Science and discovery in the world's first national park* (pp. 204–222). Chicago, IL: University of Chicago Press.

Peterson, R. O., Thomas, N. J., Thurber, J. M., Vucetich, J. A., & Waite, T. A. (1998). Population limitation and the wolves of Isle Royale. *Journal of Mammalogy*, *79*, 828–841.

Peterson, R. O., Vucetich, J. A., Bump, J. M., & Smith, D. W. (2014). Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 325–345.

Pritchard, J. A. (1999). *Preserving Yellowstone's natural conditions: Science and the perception of nature*. Lincoln & London: University of Nebraska Press.

Regan, B. S. (2016). *Carcass monitoring and grizzly bear scavenging across two management jurisdictions of the northern Yellowstone winter range (1997–2012)*. [M.S. thesis]. Montana State University, Bozeman, MT

Ripple, W. J., Estes, J. A., Schmitz, O. J., Constant, V., Kaylor, M. J., Lenz, A., ... Wolf, C. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*, 1241484.

Rowher, Y., & Marris, E. (2021). Ecosystem integrity in neither real nor valuable. *Conservation Science and Practice*, (this issue), Xx.

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., & Blanchette, C. A. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, *5*, 785–791.

Singer, F. J., Mark, L. C., & Cates, R. C. (1994). Ungulate herbivory of willows on Yellowstone's northern range. *Journal of Range Management*, *43*, 295–299.

Smith, D. W., & Bangs, E. E. (2009). Reintroduction of wolves to Yellowstone National Park: History, values, and ecosystem restoration. In M. W. Hayward & M. J. Somers (Eds.), *Reintroduction of top-order predators* (pp. 92–125). Oxford: Wiley-Blackwell.

Smith, D. W., Stahler, D. R., MacNulty, D. R., & Whittlesey, L. H. (2020). Historical and ecological context for wolf recovery. In D. W. Smith, D. R. Stahler, & D. R. MacNulty (Eds.), *Yellowstone wolves: Science and discovery in the world's first national park* (pp. 3–12). Chicago, IL: University of Chicago Press.

Smith, D. W., & Tyers, D. B. (2012). The history and current status and distribution of beavers in Yellowstone National Park. *Northwest Science*, *86*, 276–288.

Sutter, P. S. (2002). *Driven wild: How the fight against automobiles launched the modern wilderness movement*. Seattle, WA: University of Washington Press.

USFWS (United States Fish and Wildlife Service). (1994). *The reintroduction of gray wolves to Yellowstone National Park and Central Idaho. Final environmental impact statement*. Helena, MT: US Fish and Wildlife Service.

USNPSC (United States National Parks Science Committee). (2012). *Revisiting Leopold: Resource stewardship in the national parks*. Washington, DC: National Park System Advisory Board.

Varley, J. D., & Brewster, W. B. (Eds.). (1992). *Wolves for Yellowstone? A report to the United States congress* (Vol. 3 and 4). Yellowstone National Park, WY: National Park Service.

Vucetich, J. A., Nelson, M. P., & Peterson, R. O. (2012). *Should Isle Royale wolves be reintroduced? A case study on wilderness management in a changing world* (Vol. 29, pp. 126–147). George Wright Society, Hancock, MI: George Wright Forum.

Vucetich, J. A., Smith, D. W., & Stahler, D. R. (2005). Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos*, *111*, 259–270. https://doi.org/10.1111/j.0030-1299.2005.14180.x

Wagner, F. H. (2006). *Yellowstone's destabilized ecosystem*. Oxford, UK: Oxford University Press.

Weaver, J. (1978). *The wolves of Yellowstone*. Washington, DC: Natural Resources Report No. 14. U.S. National Park Service.

White, P. J., Garrott, R. A., & Plumb, G. E. (2013). *Yellowstone's wildlife in transition*. Cambridge, Massachusetts and London England: Harvard University Press.

White, P. J., Smith, D. W., Duffield, J. W., Jimenez, M., McEneaney, T., & Plumb, G. (2005). *Yellowstone after wolves: Environmental impact statement predictions and ten-year* *appraisals* (Vol. 13, pp. 34–41). Yellowstone National Park: Yellowstone Science.

Whittlesey, L. H., & Bone, S. (2020). *The history of mammals in the greater Yellowstone ecosystem, 1796–1881: A multi-disciplinary analysis of thousands of historical observations* (Vol. 2). Seattle, WA: Kindle Direct Publishing.

Wilmers, C. C., & Getz, W. M. (2005). Gray wolves as climate change buffers in Yellowstone. *PLoS Biology*, *3*, 571–576.

Wilson, E. O. (2016). *Half-earth: Our planet's fight for life* (p. 258). New York, NY: W.W. Norton and Company.

YNP (Yellowstone National Park). (1997). *Yellowstone's northern range: Complexity and change in a wildland ecosystem*. Yellowstone National Park, WY: National Park Service.

YNP (Yellowstone National Park), University of Wyoming, University of Idaho, Interagency Grizzly Bear study Team, and University of Minnesota Cooperative Park Service Studies Unit. (1990). *Wolves for Yellowstone? A report to the United States Congress* (Vol. 1 and 2). Yellowstone National Park, WY: National Park Service.

Zahniser, H. (1958). *The case for wilderness preservation legislation* (pp. 104–110). Washington, D.C.: Society of American Foresters.

How to cite this article: Smith DW, Peterson RO. Intended and unintended consequences of wolf restoration to Yellowstone and Isle Royale National Parks. *Conservation Science and Practice*. 2021;e413. https://doi.org/10.1111/csp2.413