Using Small Populations of Wolves for Ecosystem Restoration and Stewardship

DANIEL S. LICHT, JOSHUA J. MILLSPAUGH, KYRAN E. KUNKEL, CHRISTOPHER O. KOCHANNY, AND ROLF O. PETERSON

The absence of top-level predators in many natural areas in North America has resulted in overabundant ungulate populations, cascading negative impacts on plant communities, and the loss of biodiversity and ecosystem processes. Meanwhile, distinct population segments of the gray wolf (Canis lupus) have been removed from the list of endangered and threatened species, implying an end to wolf recovery and reintroductions. We propose another paradigm for wolf conservation, one that emphasizes ecosystem recovery instead of wolf recovery. Improvements in technology, an enhanced understanding of the ecological role of wolves, lessons from other countries, and changing public attitudes provide a new context and opportunity for wolf conservation and ecosystem restoration. Under this new paradigm, small populations of wolves, even single packs, could be restored to relatively small natural areas for purposes of ecosystem restoration and stewardship. We acknowledge the complications and challenges involved in such an effort, but assert that the benefits could be substantial.

Keywords: ecosystem restoration, stewardship, Canis lupus, natural areas, parks

The gray wolf (Canis lupus) historically occupied most of North America (see Paquet and Carbyn 2003) and played an important and perhaps keystone role in most ecosystems. As an apex predator, the wolf catalyzed many components of natural systems (e.g., wolves affected ungulate populations which in turn affected plant communities), and those components adapted to and evolved with the presence of wolves. However, as a result of European settlement, the wolf was extirpated from most of the contiguous 48 US states, and was subsequently listed as endangered under the Endangered Species Act (ESA) of 1973. Protection under the ESA, and the accompanying change in societal values, was a turning point in wolf conservation.

Wolf numbers have increased in the Great Lakes and Northern Rocky Mountain regions to the point where these population segments have been delisted under the ESA, implying the existence of viable populations and an end to wolf recovery (USFWS 2009a, 2009b). However, some conservationists do not believe the species is recovered (Bergstrom et al. 2009), and have proposed additional wolf reintroduction sites based on the conventional ESA recovery model (Fascione 2006). Yet even if wolves are reintroduced to these other sites, the species will continue to be absent from many natural areas, in part because most natural areas are viewed as too small for conventional wolf recovery ("natural areas" are defined as public or private lands where the conservation of biodiversity and natural processes are a principal goal, and where hunting is not allowed or is ineffective in controlling ungulates; e.g., national parks). Consequently, many natural area ecosystems will remain degraded as a result of overabundant ungulates and the absence of top-level predators. We propose a new and complementary paradigm for wolf conservation, one that recognizes the changing status of the species, ecological needs of natural areas, advancements in science and technology, and changing societal values.

The current paradigm

Since the passage of the ESA, wolf conservation in the contiguous United States has focused on the recovery of viable wolf populations. This "recovery" paradigm focuses on the reintroduction and restoration of only large populations of wolves, necessitating vast tracts of land, preferably with sparse human populations, few roads, and minimal livestock. For example, the 1992 Great Lakes Federal Wolf Recovery Plan states that 25,600 square kilometers (km²) of contiguous habitat are needed for a viable wolf population.

Under the recovery paradigm, small wolf populations on comparatively small tracts of land have been viewed as

BioScience 60: 147–153. ISSN 0006-3568, electronic ISSN 1525-3244. © 2010 by American Institute of Biological Sciences. All rights reserved. Request permission to photocopy or reproduce article content at the University of California Press's Rights and Permissions Web site at *www.ucpressjournals.com/ reprintinfo.asp.* doi:10.1525/bio.2010.60.2.9

Forum

inconsequential, unnecessary, or second-tier populations. For example, the small, isolated population on Isle Royale in Lake Superior did not count toward recovery goals for the western Great Lakes wolf population because it did not meet sustainability criteria. Yet this population has had enormous scientific, ecological, aesthetic, recreational, and ecotourism values (McLaren and Peterson 1994, Vucetich and Peterson 2004). Similarly, the Rocky Mountain recovery plan does not view small, isolated populations as important because they do not contribute to species recovery. It is clear that the ecological and societal values of small populations of wolves mostly have been ignored under the ESA recovery paradigm (Soulé et al. 2003, Carroll et al. 2006).

Wolves strongly influence ecosystem components, structure, and processes (see Mech and Boitani 2003, Paquet and Carbyn 2003, Smith et al. 2003, Berger and Smith 2005, Fascione 2006). Most notably, wolves influence the abundance of ungulates, which in turn affects the structure and composition of plant communities. More wolves typically result in fewer ungulates, which leads to greater plant biomass and diversity; conversely, fewer wolves result in more ungulates, which in turn reduces plant biomass and diversity (figure 1). In part due to the absence of wolves, overabundant ungulates threaten vegetation health across large portions of the United States (McShea et al. 1997). Furthermore, wolves influence the distribution, behavior, and foraging of surviving ungulates, which also has an effect on plant resources. Consider that in Yellowstone National Park, reintroduced wolves have created an "ecology of fear," whereby elk (Cervus elaphus) reduce the amount of time they spend browsing on woody vegetation, allowing for recruitment of that same vegetation (Ripple and Beschta 2004). Yet wolf effects go far

beyond predator-prey-plant interactions. For example, wolf predation on ungulates influences the abundance and behavior of scavengers by providing them a source of carrion (Smith and Bangs 2009). And wolves can reduce the abundance of coyotes (*Canis latrans*) and alter their behavior, too (Smith and Bangs 2009), which directly influences other animal populations. Soulé and colleagues (2003) concluded that the absence of wolves may "result in the simplification of ecosystems" (p. 1244).

In addition to the ecological effects of wolves, their presence can have beneficial economic and recreational impacts. Wolves in Yellowstone National Park increased visitation and ecotourism spending by \$35 million in 2005 (Duffield et al. 2006). Duffield and colleagues (2006) also estimated that 325,000 park visitors saw wolves in that same year. The economic value of wolf populations is often as high as millions of dollars (see Fritts et al. 2003, Fascione 2006).

Wolves provide a variety of ecosystem and human services (see Mech and Boitani 2003, Paquet and Carbyn 2003, Smith et al. 2003, Ripple and Beschta 2004, Berger and Smith 2005); they:

- limit, and possibly regulate, the growth and abundance of prey populations;
- remove weak, injured, or otherwise less-fit prey and alter sex and age ratios;
- influence prey behavior, movement patterns, distribution, and habitat use;
- create a trophic cascade affecting the composition, structure, and functioning of plant communities, which in turn affects habitat availability for animals;
- create a trophic cascade affecting other biotic and abiotic resources, including water, soil, and geomorphology, which in turn affects habitat availability for other species;
- create carrion that provides food for other species and cycles nutrients;
- affect the abundance, distribution, and behavior of other animals (e.g., coyotes) through interspecific interactions;
- increase ecotourism and benefit local economies;
- enhance visitor experiences; and
- provide opportunities for scientific research.

We propose that these benefits be evaluated and given more consideration in the management of natural areas that are deemed too small for wolves under the current wolf recovery model.

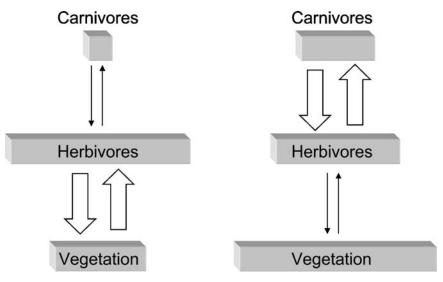


Figure 1. With carnivores reduced or absent (left), the overriding trophic interaction involves herbivores and vegetation. With intact carnivore fauna (right), however, the primary trophic interaction is between carnivores and herbivores. A trophic cascade involves correlated changes in alternating trophic layers; for example, carnivores and vegetation. Left and right diagrams indicate changes in biomass of each trophic layer as carnivores increase.

A new paradigm

We propose a new paradigm in wolf conservation, one where small and non-self-sustaining populations of wolves are reintroduced for purposes of ecosystem restoration and stewardship. Such an approach would have ecological, educational, recreational, scientific, and economic benefits. The sum of these benefits could, in some cases, outweigh the cost of managing small wolf populations on comparatively small sites. We are not naive about the biological, political, cultural, administrative, aesthetic, and ethical challenges of managing small populations of wolves for purposes of ecosystem restoration and stewardship. We acknowledge that wolves are a symbol of wilderness to many people (Wilson 1997, Montag et al. 2005), and that intensively managed populations may be viewed as inconsistent with that symbolism. Yet our proposed paradigm still allows for conventional wolf recovery, and the comparatively less-intensive management of those populations. Furthermore, we believe that our paradigm may actually enhance public understanding and appreciation of wolves. Our paradigm may also elevate the prestige of the natural areas where wolves are restored. National parks are especially well suited to the new paradigm because of their protected status, agency policies to conserve all native species and natural processes, prohibitions against hunting, potential for overabundant ungulates, and public expectations for the sites. Other public and private lands could also be used, especially where wolf protection can be assured and potential conflicts are manageable. Although the paradigm we propose is new to the United States, the reintroduction of large carnivores to small natural areas is routine in other parts of the world (Hayward et al. 2007, Licht et al. 2008).

As with conventional wolf recovery efforts, a unique set of conditions would be necessary to restore and manage wolves under the new paradigm; most important, adequate prey and manageable wolf-human conflicts. However, in contrast to current management programs, which are designed to recover large, self-sustaining wolf populations, and which therefore require immense landscapes, the new paradigm is not driven by wolf viability or ESA recovery goals, but rather by ecosystem restoration and stewardship. Therefore, sites under the new paradigm need not be vast. We do not advocate a minimum site size under the new paradigm; we simply assert that any site that has adequate prey to support a functioning wolf pack should be considered. This recommendation is made on the basis of our understanding of wolf behavior and ecology (i.e., the importance of the pack as a functioning unit), and on the positive experiences from sites such as (a) Isle Royale National Park, where only two to three packs have persisted for a half century (Vucetich and Peterson 2004); and (b) on preserves in South Africa that have successfully conserved single prides of lions (Panthera leo) or packs of African wild dogs (Lycaon pictus; Hayward et al. 2007, Funston 2008, Gusset et al. 2008, Lehmann et al. 2008).

Assuming adequate prey are available, the other primary consideration is minimizing wolf-human conflicts. Opposition to wolf reintroductions is generally on the basis of (a) wolf depredation of livestock, (b) attacks on pets, (c) concerns about human safety, (d) reduction in game populations, and (e) fear of government regulations and restrictions (see Williams et al. 2002). If these concerns can be eliminated or mitigated, then most of the ostensible resistance to wolf reintroductions will be nullified. We believe the following tools and approaches reduce or eliminate the stated concerns of wolf opponents, thereby allowing the restoration of small populations of wolves for purposes of ecosystem stewardship. We do not suggest that these management-intensive tools or approaches are applicable for conventional wolf recovery programs.

Real-time animal tracking. The development and implementation of real-time satellite tracking technology has existed since the 1970s (Rodgers 2001). This technology typically consists of a collar that transmits a signal to satellites that then relay the information to a base station, which transmits the computed location data to an end user. Recent advances integrate moreprecise (location to within approximately 15 meters) GPS (global positioning system) technology to determine the animal's location (Rodgers 2001, Fuller et al. 2005). The equipment and subscription costs are high (starting around \$125 per collar per month); however, when used to collect a large number of relatively accurate real-time locations, the technology becomes cost-efficient when compared with conventional very-highfrequency (VHF) telemetry. In some locations, cell-phone technology can be used in lieu of satellites to transmit the location data. The location data can be integrated with mapping software to create a "geofence," so once an animal approaches or crosses a predetermined boundary, an alert message is sent to a manager (see also the discussion below on virtual barriers).

These real-time systems allow managers to efficiently, relatively reliably, and accurately track an animal's whereabouts, and to quickly respond to problem animals. Such an approach is being tested in Kenya with elephants; when a collared elephant leaves the natural area, the collar sends a message to park employees who then attempt to scare the animal back to the park (www.savetheelephants.org/researchreader/items/elephant-geofencing.html). This information can also help assuage the concerns of neighbors. For example, in South Africa, the locations of certain animals are sometimes shared with local people to lessen concerns about lions in nearby protected areas (Hunter et al. 2007) and a lion project in Kenya is testing real-time collars and Google maps to share location data online (www.abycats.com/maps/catmap.html). Real-time satellite collars have been used successfully on wolves for research purposes (Walton et al. 2001), but we are not aware of any uses primarily for real-time management.

Reproductive control. Wildlife reproductive control remains contentious for several reasons, including (a) uncertainties about the efficacy of nonsurgical methods for abundant free-ranging populations, (b) the loss of potential recreational opportunities for hunters, (c) concerns about human consumption of treated animals, (d) potential changes in animal behavior, and (e) ethical concerns. However, under certain circumstances, such as for small, isolated populations of wildlife that are not hunted or consumed, reproductive control is an effective management tool. Immunocontraceptives, pharmaceuticals, and surgery could all be used to prevent or suppress growth of a small population of wolves that is reintroduced for purposes of ecosystem stewardship, as is done in South Africa for other top-level predators on small reserves. Deslorelin has been used successfully with lions, cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), and African wild dogs (Kettles and Slotow 2009) to suppress growth, and, in some cases, vasectomies are performed as well (Lehmann et al. 2008). Such tools would likely be necessary for managing small populations of wolves reintroduced for ecosystem stewardship purposes.

Barriers. The use of barriers to conserve predators is an anathema in the United States; however, barriers are widely used in other parts of the world (Hayward and Kerley 2009). For example, the "dingo fence" (Canis lupus dingo) is famously used to keep dingoes separated from livestock in Australia; in South Africa, lions and African wild dogs would likely be extirpated from most of the country if not for fenced nature preserves (Hunter et al. 2007, Funston 2008, Gusset et al. 2008). These fenced reserves-some as small as 15 km²-conserve small populations and even single social units of large predators such as lions (Hayward et al. 2007, Funston 2008, Lehmann et al. 2008). Although there are significant costs in constructing and maintaining these fences, and in the management of the small populations therein (e.g., assuring desired predatorprey ratios, genetic augmentation; see Hayward et al. 2007, Funston 2008, Hayward and Kerley 2009), the ecological and ecotourism values of having large predators on a site often outweigh the costs (Lindsey et al. 2004).

Some of the strongest objections to fences have to do with aesthetics and the public's desire that wildlife be free ranging. However, this objection is partly mitigated by scale. There are relatively few concerns in South Africa about the fence around the 20,000-km² Kruger National Park. Yet even fenced reserves as small as 100 km² are viewed as acceptable and supportive of free-ranging populations of lions and other wildlife (see Bauer and Van Der Merwe 2004). Visitors flock to these sites from around the world and report positive wildlife-viewing experiences. Likewise, at the appropriate scale, wolf observation and visitor experience within fenced protected areas can become "authentic" (Montag et al. 2005).

Fences are used in the United States to conserve herbivores such as bison (*Bison bison*) with no strong objections from the public. In fact, were it not for fenced parks, refuges, and other properties, bison would be absent from the Great Plains. Such fences could be modified to conserve wolves while still allowing egress and ingress by other species. The use of fences may have the most merit in agrarian landscapes where there is a hard boundary between natural and developed lands. Licht and colleagues (2008) stated that the consideration of fences as a wildlife management tool, such as is practiced in South Africa, may come down to a choice between managing for a handsoff "naturalness" (i.e., no fences, but also no large predators) or managing for biological diversity (i.e., with fences, but also with large predators fulfilling their ecological role).

Although fences are not used to manage predators in natural areas in the United States, the country does have a population of wolves that functions as if it were in a large, fenced reserve: the small population of wolves on Isle Royale in Lake Superior. The 550-km² island has supported a mean of 24 wolves since 1959. Were it not for the natural recolonization of the island by wolves there would likely be severe ecological degradation as a result of overabundant ungulates (McLaren and Peterson 1994), and the site would not be an International Biosphere Reserve. Wolves exist on the site with no public opposition; indeed, the public strongly supports the population there (Vucetich and Peterson 2004), demonstrating that the conservation of small populations of wolves is tenable under the right conditions.

Virtual barriers. Virtual barriers are widely used to confine the spatial movements of domestic dogs. When a collared animal approaches a buried wire (i.e., the boundary), the collar gives the animal negative stimuli, typically in the form of a mild electric shock. Many studies have shown that animals learn to avoid boundaries after just a few stimulations (see Anderson 2007). Gehring and colleagues (2006) used shock collars on wild wolves in Michigan in an attempt to condition the collared animals and their packs to avoid bait piles. The shock collars were effective in reducing pack visits to the baits, and the packs continued to avoid the baits for more than 60 days after the shock period. These results suggest that a shock collar on a single wolf could help confine a wolf pack within a natural area.

Collar systems are now being developed that integrate GPS technology with on-board algorithms (i.e., maps), thereby eliminating the need for transmitting wires in the aversion zone (Anderson 2007). Such systems are better suited for wide-ranging animals, for which construction of ground-based systems would be impractical. Perhaps the biggest remaining challenge with wolves is to develop a collar that maintains contact between electrodes and skin; however, such contact may be necessary only during the learning phase (Anderson 2007). The use of visual cues, such as fladry, may further enhance the effectiveness of negative stimuli (Gehring et al. 2006).

In Botswana, researchers are testing another form of virtual barrier by using a chemical "bioboundary" to keep African wild dogs out of undesirable areas. The method consists of depositing African wild dog scent marks at the edge of the undesired area, thereby creating a virtual neighboring pack. Like wolves, African wild dogs are very territorial and have a high level of respect for neighboring packs' territories. Initial experimental results show that the concept has enormous potential for African wild dog management (J. Weldon McNutt, PhD director, Botswana Predator Conservation Trust, personal communication, 20 January 2009). However, it is uncertain if the method could be applied to wolves because wolf territories may be defined as much by auditory signals (i.e., howling) as by olfactory markings, but the use of auditory as well as olfactory cues may keep wolves within natural areas.

Case studies

In practice, none of the tools described above are likely to be infallible; therefore, we envision the use of a combination of tools to manage small populations of wolves and to allay the concerns of wolf opponents. For example, a perimeter barrier could be used in combination with real-time telemetry. Furthermore, these technologies should be implemented in concert with community involvement and mitigation, such as is practiced in South Africa (Hunter et al. 2007). We provide three case studies; one from five decades ago, in which wolves were introduced for purposes of ecosystem restoration, but not intensively managed; and two cases in which there is a current need for ecosystem stewardship by wolves, but recent proposals were thwarted in part by the recovery paradigm (i.e., the areas were not large enough for viable wolf populations). In the latter two cases we do not claim that wolves are the best alternative to reduce overabundant ungulates and conserve these ecosystems, only that the use of wolves is feasible and should be given full consideration as one of many possible alternatives. Ultimately, site managers are in the best position to determine which tools should be used to conserve ecosystems.

Case study 1: Coronation Island, Alaska. We know of only one case where wolves were reintroduced primarily for purposes of ecosystem restoration and not for species recovery. In 1960, four wolves were introduced to the 117-km² Coronation Island in southeast Alaska for the purpose of reducing the overabundant black-tailed deer (Odocoileus hemionus sitkensis) population (Klein 1995). The wolves were extremely successful in reducing the island's deer population. However, the introduced wolves were not managed, and they soon increased to 13 animals and depleted the deer population. Eventually the wolf population crashed and deer numbers rebounded. Klein (1995) speculated that the low fecundity of the deer, a consequence of the poor quality of the habitat resulting from the long period of overbrowsing, may have contributed to the dramatic deer decline immediately following wolf introduction. More intensive management and monitoring of the predator and prey populations-as is practiced in South Africa-may have attenuated the boom-bust cycle and resulted in long-term success.

Case study 2: Rocky Mountain National Park. In 2007, Rocky Mountain National Park (NP) completed an environmental impact statement that evaluated several alternatives to reduce the elk population in the 1076-km² unfenced park, including an alternative that called for the experimental reintroduction of 14 or fewer intensively managed wolves (NPS 2007). Growth of the wolf population would have been limited by fertility control or by removing individuals. The wolves would have been intensively tracked with VHF telemetry. Animals that approached the park boundary would have been captured and relocated to a soft-release pen in the park interior or removed from the population.

Coughenour (2002) developed an ecosystem model that predicted that wolves would greatly reduce the park's elk population, thereby meeting park goals. Hobbs (2006) developed a model that suggested that the presence of 20 wolves would eradicate chronic wasting disease (a transmissible neurological disease in deer and elk that produces lesions in infected animals' brains) from elk in the park in two to three decades. Although public attitudes toward wolf reintroduction in Colorado are generally positive (Pate et al. 1996), the wolf alternative was not selected. One of the justifications for not selecting the alternative is that, at the time, wolves were an endangered species, and the use of a small number of them for ecosystem stewardship may have been incompatible with the ESA (NPS 2007).

Case study 3: Wind Cave National Park. The 114-km² Wind Cave NP is fenced to contain bison. The park also supports abundant elk, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and pronghorn antelope (*Antilocapra americana*). The ungulate biomass at the park is about 32 kilograms per hectare; a total biomass comparable to the much-larger Isle Royale NP. On the basis of known relationships between wolf abundance and prey biomass (Fuller et al. 2003), the park could support nine wolves.

Wolves are currently absent from the park. The park historically culled surplus elk through translocations to other sites, but that option is now prohibited as a result of chronic wasting disease. Consequently, the park is developing an environmental impact statement to evaluate alternatives to control the elk population. Early in the planning process the park considered developing an alternative that used intensively managed wolves as a stewardship tool. However, the alternative was not fully evaluated, in part because of the US Fish and Wildlife Service's position that the park was not large enough to sustain a viable wolf population and therefore would not contribute to wolf recovery, even though the stated purpose of the action was reducing elk overabundance and providing other ecosystem services. In other words, the ESA was used to stop the evaluation of using wolves for purposes of ecosystem stewardship.

Conclusion

The desire to restore naturally functioning ecosystems within natural areas, along with the delisting of the gray wolf from the ESA, an increased understanding of the species' ecological role, advances in technology, and changing public attitudes, provides an opportunity to reevaluate wolf conservation and natural areas management. We recommend serious consideration and full evaluation of the use of wolves as an ecosystem stewardship tool in planning efforts. There are, and will continue to be, sites in the United States that would benefit from the presence of small populations of wolves (as well as in other places such as Great Britain; see Macdonald et al. 2000). As far back as 1991, The Wildlife Society (1991) supported the restoration of small populations of wolves when it stated: "If national parks and other protected areas cannot provide large enough areas for self-perpetuating populations of wolves, systematic and periodic reintroduction of wolves from outside may ensure population survival" (p. 8).

Forum

We fully appreciate and respect the ethical and aesthetic concerns with reintroducing small populations of large mammals to natural areas and the intensive management necessary to make it work. However, active management is a prerequisite for all wolf populations in the lower 48 states, regardless of their size. Arguably, hands-on management and tools such as radio-telemetry collars are part of the reason wolves have recovered. Furthermore, intensive management of a small population of wolves for ecosystem stewardship may foster more public tolerance and appreciation of the species, and may lead to additional restoration efforts.

We are not disregarding the cost of managing a small population of wolves for ecosystem stewardship. However, we are advocating the use of small populations, and perhaps even single packs, thereby making intensive management feasible, in contrast to managing the hundreds or thousands of wolves under the current recovery paradigm. Furthermore, the cost of using wolves as an ecosystem stewardship tool should be objectively compared with other alternatives to reduce ungulates and conserve ecosystems, such as sharp shooting, roundups, fertility control, and building fences to exclude herbivores from vegetation. We believe that one of the best arguments for using wolves as an ecosystem stewardship tool is that in some cases, the other alternatives are more intrusive, unethical, and unaesthetic. If the other ecosystem services of wolves are considered, as well as the socioeconomic, visitor experience, and intangible benefits (e.g., existence values), the use of wolves becomes an even more competitive proposition. Another benefit of this new paradigm is that the research opportunities are enormous (e.g., can wolves eliminate or reduce chronic wasting disease in natural areas?). If the paradigm proposed here is implemented, it should be enacted as a series of experiments with a scientifically designed monitoring and adaptive management component.

The new paradigm is best suited to a unique set of conditions. First and foremost is that wolves are needed to restore ecosystem health. Second, sites are unlikely to be colonized by wolves from existing wolf recovery areas. Other considerations include agency missions and policies, the capability to minimize or eliminate conflicts, public expectations for a site, and ecotourism. National Park Service units are especially suitable for this new paradigm. Another example is the American Prairie Foundation effort to restore a large naturally functioning grassland ecosystem in the Northern Great Plains. Islands in the Great Lakes and elsewhere may also have potential, perhaps on a temporary basis. While the use of wolves for ecosystem restoration and stewardship on small natural areas will not be a panacea, it will move all of these areas closer to true and meaningful biodiversity conservation. In natural areas where large herbivores exist and wolf restoration is not feasible, managers will need to consider other options to prevent ungulate overabundance and ecosystem degradation.

From a biological, technological, and logistical perspective, the new paradigm appears workable; in fact, variations of it are regularly and successfully used throughout the world with large predators such as lions and African wild dogs (Hayward et al. 2007, Hunter et al. 2007, Gusset et al. 2008, Licht et al. 2008). However, wolf management in North America transcends simple precedents, technology, and science (Nie 2001, Fritts et al. 2003). The wolf is a passion-inspiring symbol to many people, but the symbolism varies and is polarizing. Restoring and managing the animal under our proposed paradigm appears doable; managing the symbolism remains the challenge.

Acknowledgments

We thank Robert Gitzen and Valerius Geist for their thoughtful and constructive reviews of an early draft of the manuscript. We also acknowledge the many others, too numerous to name, who encouraged us in this effort.

References cited

- Anderson DM. 2007. Virtual fencing—past, present, and future. Rangeland Journal 29: 65–78.
- Bauer H, Van Der Merwe S. 2004. Inventory of free-ranging lions Panthera leo in Africa. Oryx 38: 26–31.
- Berger J, Smith DW. 2005. Restoring functionality in Yellowstone with recovering carnivores: Gains and uncertainties. Pages 100–109 in Ray JC, Redford KH, Steneck RS, Berger J, eds. Large Carnivores and the Conservation of Biodiversity. Island Press.
- Bergstrom BJ, Vignieri S, Sheffield SR, Sechrest W, Carlson AA. 2009. The Northern Rocky Mountain Gray Wolf Is Not Yet Recovered. BioScience 59: 991–999.
- Carroll C, Phillips MK, Lopez-Gonzalez CA, Schumaker NH. 2006. Defining recovery goals and strategies for endangered species: The wolf as a case study. BioScience 56: 25–37.
- Coughenour MB. 2002. Elk in the Rocky Mountain National Park Ecosystem: A Model-based Assessment. Final report to the US Geological Survey Biological Resources Division and US National Park Service. Colorado State University. (20 November 2009; www.nrel.colostate.edu/ ftp/coughenour/pubs_lock/index.php?Directory=Yellowstone_Bison_Elk/ Part3_bison_elk_populations)
- Duffield JW, Patterson DA, Neher CJ. 2006. Wolves and people in Yellowstone. Paper presented to 18th Annual North American Wolf Conference; 4–6 April 2006, Pray, Montana.
- Fascione N. 2006. Places for Wolves: A Blueprint for Restoration and Recovery in the Lower 48 States. Defenders of Wildlife.
- Fritts SH, Stephenson RO, Hayes RD, Boitani L. 2003. Wolves and humans. Pages 289–316 in Mech LD, Boitani L, eds. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press.
- Fuller MR, Millspaugh JJ, Church KE, Kenward RE. 2005. Wildlife radiotelemetry. Pages 377–417 in Braun CE, ed. Techniques for Wildlife Investigations and Management. 6th ed. The Wildlife Society.
- Fuller TK, Mech LD, Cochrane JF. 2003. Wolf population dynamics. Pages 161–191 in Mech LD, Boitani L, eds. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press.
- Funston PJ. 2008. Conservation and management of lions in southern Africa: Status, threats, utilization and the restoration option. Pages 109–131 in Croes B, Buij R, de Iongh HH, Bauer H, eds. Management and Conservation of Large Carnivores in West and Central Africa. Institute of Environmental Sciences.
- Gehring TM, Hawley JE, Davidson SJ, Rossler ST, Cellar AC, Schultz RN, Wydeven AP, VerCauteren KC. 2006. Are viable non-lethal management tools available for reducing wolf-human conflict? Preliminary results from field experiments. Pages 2–6 in Timm RM, O'Brien JM, eds. Proceedings of the 22nd Vertebrate Pest Conference. University of California, Davis.
- Gusset M, et al. 2008. Efforts going to the dogs? Evaluating attempts to reintroduce endangered wild dogs in South Africa. Journal of Applied Ecology 45: 100–108.

- Hayward MW, Kerley GIH. 2009. Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? Biological Conservation 142: 1–13.
- Hayward MW, et al. 2007. The reintroduction of large carnivores to the Eastern Cape, South Africa: An assessment. Oryx 4: 205–214.
- Hobbs NT. 2006. A Model Analysis of Effects of Wolf Predation on Prevalence of Chronic Wasting Disease in Elk Populations of Rocky Mountain National Park. Report submitted to the National Park Service.
- Hunter LTB, Pretorius K, Carlisle LC, Rickelton M, Walker C, Slotow R, Skinner JD. 2007. Restoring lions *Panthera leo* to northern KwaZulu-Natal, South Africa: Short-term biological and technical success but equivocal long-term conservation. Oryx 41: 196–204.
- Kettles R, Slotow R. 2009. Management of free-ranging lions on an enclosed game reserve. South African Journal of Wildlife Management 39: 23–33.
- Klein DR. 1995. The introduction, increase, and demise of wolves on Coronation Island, Alaska. Pages 275–280 in Carbyn L, Fritts SH, Seip DR, eds. Ecology and Conservation of Wolves in a Changing World. Canadian Circumpolar Institute.
- Lehmann MB, Funston PJ, Owen CR, Slotow R. 2008. Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. African Zoology 43: 230–236.
- Licht DS, Slotow R, Millspaugh J. 2008. Out of Africa: Lessons from park management in South Africa. The George Wright Forum 25: 20–29.
- Lindsey PA, Alexander RR, du Toit JT, Mills MGL. 2004. The potential contribution of ecotourism to African wild dog *Lycaon pictus* conservation in South Africa. Biological Conservation 123: 339–348.
- Macdonald DW, Mace GM, Rushton S. 2000. British mammals: Is there a radical future? Pages 175–206 in Entwistle A, Dunstone N, eds. Priorities for Conservation of Mammalian Diversity. Cambridge University Press.
- McLaren BE, Peterson RO. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266: 1555–1558.
- McShea WJ, Underwood HB, Rappole JH. 1997. The Science of Overabundance: Deer Ecology and Management. Smithsonian.
- Mech LD, Boitani L, eds. 2003. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press.
- Montag JM, Patterson ME, Freimund WA. 2005. The wolf viewing experience in Lamar Valley of Yellowstone National Park. Human Dimensions of Wildlife 10: 273–284.
- [NPS] National Park Service. 2007. Final Environmental Impact Statement: Elk and Vegetation Management Plan. Rocky Mountain National Park.
- Nie MA. 2001. The sociopolitical dimensions of wolf management and restoration in the United States. Human Ecology Review 8: 1–12.
- Paquet PC, Carbyn LN. 2003. Gray wolf. Pages 482–510 in Feldhamer GA, Thompson BC, Chapman JA, eds. Wild Mammals of North America: Biology, Management, and Conservation. 2nd ed. John Hopkins University Press.
- Pate J, Manfredo MJ, Bright AD, Tischbein G. 1996. Coloradans' attitudes toward reintroducing the gray wolf in Colorado. Wildlife Society Bulletin 24: 421–428.

- Ripple WJ, Beschta RL. 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of southwestern Montana, USA. Forest Ecology and Management 200: 161–181.
- Rodgers AR. 2001. Recent telemetry technology. Pages 79–121 in Millspaugh JJ, Marzluff JM, eds. Radio Tracking and Animal Populations. Academic Press.
- Smith DW, Bangs EE. 2009. Reintroduction of wolves to Yellowstone National Park. Pages 92–125 in Hayward MW, Somers MJ, eds. Reintroduction of Top-order Predators. Wiley-Blackwell.
- Smith DW, Peterson RO, Houston DB. 2003. Yellowstone after wolves. Bio-Science 53: 330–340.
- Soulé ME, Estes JA, Berger J, Del Rio CM. 2003. Ecological effectiveness: Conservation goals for interactive species. Conservation Biology 17: 1238–1250.
- [USFWS] US Fish and Wildlife Service. 2009a. Final Rule to Identify the Western Great Lakes Populations of Gray Wolves as a Distinct Population Segment and to Revise the List of Endangered and Threatened Wildlife. (16 December 2009; www.fws.gov/midwest/wolf/archives/2009delisting/ fnlruleFR02april2009.pdf)
- 2009b. Final Rule To Identify the Northern Rocky Mountain Population of Gray Wolf as a Distinct Population Segment and to Revise the List of Endangered and Threatened Wildlife. (16 December 2009; www.fws.gov/mountain%2Dprairie/species/mammals/ wolf/74FR15123.pdf)
- Vucetich JA, Peterson RO. 2004. Long-term population and predation dynamics of wolves on Isle Royale. Pages 281–292 in Macdonald D, Sillero-Zubiri C, eds. Biology and Conservation of Wild Canids. Oxford University Press.
- Walton LR, Cluff HD, Paquet PC, Ramsay MA. 2001. Performance of 2 models of satellite collars for wolves. Wildlife Society Bulletin 29: 180–186.
- The Wildlife Society. 1991. Restoration of Wolves in North America. The Wildlife Society. Technical Review 9–11.
- Williams CK, Ericsson G, Heberlein TA. 2002. A quantitative summary of attitudes toward wolves and their reintroduction (1972–2000). Wildlife Society Bulletin 30: 575–584.
- Wilson MA. 1997. The wolf in Yellowstone, science, symbol, or politics? Deconstructing the conflict between environmentalism and wise use. Society and Natural Resources 10: 453–468.

Daniel S. Licht (dan_licht@nps.gov) is with the National Park Service in Rapid City, South Dakota. Joshua J. Millspaugh is with the School of Natural Resources, Department of Fisheries and Wildlife Sciences, at the University of Missouri in Columbia. Kyran E. Kunkel is with the World Wildlife Fund in Gallatin Gateway, Montana. Christopher O. Kochanny is with SirTrack in North Liberty, Iowa. Rolf O. Peterson is with the School of Forest Resources and Environmental Science at Michigan Technological University in Houghton.

