The challenges of success: Future wolf conservation and management in the United States

Article *in* BioScience · August 2023

DOI: 10.1093/biosci/biad053

David Ausband
USGS University of Idaho

BioScience, 2023, **0**, 1–5
https://doi.org/10.1093/biosci/biad053
Advance access publication date: 0 2023
Forum

The challenges of success: Future wolf conservation and management in the United States

David E. Ausband and L. David Mech

David E. Ausband (dausband@uidaho.edu) is affiliated with the US Geological Survey's Idaho Cooperative Fish and Wildlife Research Unit, at the University of Idaho, in Moscow, Idaho, in the United States. L. David Mech (mechx002@umn.edu) is affiliated with the US Geological Survey's Northern Prairie Wildlife Research Center, in Jamestown, North Dakota, and the University of Minnesota, St. Paul, Minnesota, in the United States

Abstract

Gray wolf (*Canis lupus*) recovery and conservation has been a remarkable success over the last 30 years in the United States. Remarkable success yields remarkable challenges, however. As populations expand, wolves will colonize more human-dominated landscapes and face numerous challenges, such as fragmented habitats, barriers to dispersal, and increased encounters with humans, pets, and livestock. In such areas, conflicts between humans and wolves will increase. We summarize several major scientific and social challenges that wolf conservation, recovery, and management will face in the coming years. In addition, we suggest actions to help address each challenge. Future wolf conservation in the United States will be affected by the ability of managers to predict colonization and dispersal dynamics, to reduce hybridization and disease transmission, to mitigate and deter wolf–livestock conflicts, to harvest wolves sustainably while satisfying diverse stakeholders, to avert a reduction in tolerance for wolves due to a disinterest in nature, and to engage diverse stakeholders in wolf conservation to avoid management by ballot initiative or legislative and judicial decrees.

Keywords: Canis lupus, gray wolf, management, tolerance

Gray wolf (*Canis lupus*) conservation in the United States has been a remarkable success over the last 30 years. In the lower 48 states, many regions that had very few wolves three decades ago now have robust wolf populations with broad distributions (Wydeven et al. 2009, USFWS et al. 2015). Some of this success is due to direct human intervention by way of reintroductions (Bangs and Fritts 1996). Captive breeding has even been used to help conserve genetic lineages, repopulate vacant habitat, and promote species conservation (USFWS 2022). Meanwhile, we have also learned a great deal about wolf ecology and population demography. Wolf conservation has changed considerably in recent decades. Fifty years ago, wolves in the contiguous United States numbered approximately 750 and were only found in northern Minnesota and on Isle Royale, Michigan; now, more than 6000 wolves occupy much of the suitable habitat in 11 different states (Mech 2017).

Remarkable wolf conservation success yields remarkable challenges (Mech 1995), however. As populations expand, wolves will continue to colonize habitats dominated by human use. In such landscapes, conflicts between humans and wolves will increase. Indeed, humans are the highest source of mortality for wolves and the dominant factor limiting wolf population expansion (Wabakken et al. 2001, Gude et al. 2012, Stenglein et al. 2018, Quevedo et al. 2019). In addition, as wolves attempt to colonize human-dominated landscapes, they will face numerous challenges, such as fragmented habitats and barriers to dispersal, as well as increased encounters with humans, pets, and livestock (Woodroffe 2000, Blanco et al. 2005, Kuijper et al. 2019).

Wolves are quite adept at overcoming various hurdles to dispersal and recolonization (e.g., highways, large rivers, poaching), as can be seen by their expansion from Idaho into parts of Washington and Oregon and, ultimately, into California. Wolf population increase in an area depends on the amount of prey (Fuller et al. 2003); therefore, wolves can live almost anywhere. Although some dispute remains about whether wolves regulate themselves at very high densities (Cariappa et al. 2011, Cubaynes et al. 2014, McRoberts and Mech 2014, Smith et al. 2020, Mech 2022), at low to moderate densities (5–50 wolves per 1000 square kilometers) their density depends on prey (Mech and Barber-Meyer 2015). Most wolf population densities are less than about 30 per 1000 square kilometers. Therefore, wolves can thrive wherever there is sufficient prey, as long as humans allow them to. Consequently, we can expect these canids to attempt expanding their range farther (Mech 2017). In some areas, such as Minnesota, wolf populations proliferate (Chakrabarti et al. 2022), whereas elsewhere, they may bypass areas with too much human activity such as in Wisconsin (Simpson et al. 2023). Wolves may even try to recolonize such areas, but they ultimately fail because of conflicts with humans (Mech et al. 2019).

Where wolves succeed in recolonizing but are not revered by local citizens, their presence leads to adverse political pressure. In Wisconsin, the legislature requires a public hunting or trapping season whenever wolves are delisted from the US Fish and Wildlife Service's (USFWS) list of Endangered species (Wydeven et al. 2021). In Idaho and Montana and parts of Washington, Oregon, and Utah, the US Congress legislatively removed wolves from the USFWS list of Endangered species (Mech 2013). This first ever legislative action to supersede the US Endangered Species Act arose in response to persistent lawsuits by wolf advocates that threatened to prevent wolf management by states and keep wolves legally protected forever. The rash of these suits also began to sully the reputation of conservation groups (Boyce 2011) and led to greater polarization of wolf constituencies. As wolf populations continue to recover and expand, these matters will come more to the fore. Several major challenges that wolf conservation,

Received: April 16, 2023. **Revised:** May 22, 2023

recovery, and management will face in the coming years fall into two categories, scientific and social.

Scientific challenges

We outline three emerging scientific challenges of future wolf conservation: predicting colonization and dispersal dynamics, reducing hybridization and disease transmission, and mitigating and deterring wolf–livestock conflicts.

Reintroduction efforts and intensive population monitoring have provided a wealth of data on wolf dispersal ecology (Jimenez et al. 2017, Morales-Gonzalez et al. 2022). In addition, analyses of habitat use have increased our knowledge of what wolves need and do not necessarily need (e.g., untouched wilderness) to thrive (Mladenoff et al. 1995, Mech 2006, Kittle et al. 2017). Despite this, we are not particularly adept at predicting wolf dispersal and colonization patterns (Mech 2020). For example, why have dispersing wolves from eastern Oregon, in the United States, colonized parts of western Oregon, bypassing what is considered by experts (Roblyn Brown, Oregon Department of Fish and Wildlife, Salem, Oregon, United States, personal communication, 28 March 2023) to be highly suitable habitat with abundant ungulate prey and few people in parts of central Oregon (figure 4 in ODFW 2022)? Similar patterns can be seen for recolonizing wolves in Montana, in the United States (e.g., Seeley–Swan Valley, western Montana, in the 2000s; figure 5 in Sime et al. 2008). With protection, wolves can be expected to fill suitable habitat (Simpson et al. 2023), and predictions from a rigorous habitat model will likely prove to be true, given enough time. Despite extensive wolf dispersals into the Great Plains (Licht and Fritts 1994), however, wolves have not been able to colonize this region, even though studies suggest potential suitable habitat exists (van den Bosch et al. 2022). Accurately predicting the wolf colonization process in short time intervals (more than 10 years) is difficult.

Although wolves are notoriously capable of dispersing long distances (Wabakken et al. 2007, Morales-Gonzalez et al. 2022), both natural and human barriers to dispersal and colonization remain (Quevedo et al. 2019). For example, an unfrozen Saint Lawrence Seaway likely reduces the probability that wolves will naturally recolonize the northeast United States from extant populations in Canada (Wydeven et al. 1998). In addition, a radio-collared Mexican wolf (*C. lupus baileyi*) dispersed south from Arizona to the United States–Mexico border only to travel along a border wall until eventually returning north to its former population (Main 2022). Predicting where barriers exist and facilitating dispersal may be particularly important for conserving local genetic diversity or repopulating vacant wolf habitat.

Hybridization with other species is already a concern in some small, isolated populations of wolves (e.g., red wolves, *Canis rufus*; Gese et al. 2015). In addition, eastern wolves (*Canis lycaon*) dispersing out of protected areas in Ontario have limited ability to recolonize the northeastern United States because of high mortality outside of protected areas and hybridization with coyotes (*Canis latrans*; Rutledge et al. 2012). We suspect this will become a bigger challenge as wolves occupy marginal habitats and human-dominated landscapes where interactions with domestic dogs (*Canis familiaris*) will be common. Hybridization, particularly with dogs, may be problematic for small wolf populations, where limited genetic diversity is a concern.

Wolves are susceptible to several diseases that can affect population growth (Kreeger 2003, Mech et al. 2008), many of which are transmissible from domestic dogs (Mech and Goyal 1995, Muller et al. 2011). More disease outbreaks in wolves can be expected as they colonize human-dominated landscapes and interact more with species that can act as disease reservoirs. Disease may be particularly troubling for small wolf populations where a disease outbreak would be catastrophic. For example, an outbreak of distemper or parvovirus in Mexican wolves would likely reduce reproductive output and genetic diversity in the population that are key Endangered Species Act recovery criteria (USFWS 2017).

Finally, wolf predation of livestock is particularly problematic and limits wolf distribution almost everywhere wolves live around the globe (Fritts et al. 2003, Heikkinen et al. 2011, Rigg et al. 2011). Although wolf predation is not a leading source of mortality for the livestock industry, it can be particularly acute for individual producers. Mitigating livestock depredations by wolves and compensating losses are crucial if rural communities are to coexist with wolves (Naughton-Treves et al. 2003). The use of livestock guarding dogs and range riders to deter wolf livestock interactions have been embraced by producers living with wolves for centuries (Fritts et al. 2003). Minimizing wolf–livestock conflicts is essential if more wolves in more areas are desired by society.

Social challenges

Similar to the aforementioned scientific challenges, we outline three emerging social challenges of future wolf conservation: harvesting wolves sustainably while satisfying diverse stakeholders, averting a reduction in tolerance for wolves due to a disinterest in nature, and engaging diverse stakeholders in wolf conservation to avoid management by ballot initiative or legislative and judicial decrees.

Wolves were delisted from the USFWS list of Endangered species several times during the past two decades and management responsibility returned to states until lawsuits overturned those decisions (Mech 2017). Once states regained wolf management, most set regulated wolf hunting and trapping seasons, allowing public harvests to control their wolf populations. Some management agencies have faced intense pressure from some constituents to harvest wolves liberally because of impacts, both real and perceived, on ungulate populations. Recently, fierce debate has arisen over wolf hunting and trapping seasons in the United States (Creel et al. 2015, Mitchell et al. 2016). Although harvests can affect wolf populations both directly (wolves are killed) and indirectly (harvests affects group composition, which can reduce individual survival; Ausband et al. 2015), wolves are generally quite resilient to harvest. Unless a harvest is more than 29% annually (Fuller et al. 2003, Adams et al. 2008, Stenglein et al. 2015) for several consecutive years, it is unlikely to lead to population extinction in large wolf populations unless the harvest is coupled with other changing conditions or catastrophes (e.g., prey population declines, disease outbreaks). The harvest of small wolf populations (fewer than 500 wolves) can be approached conservatively, particularly if the population is isolated and immigration is very low. The debate over wolf harvests is often values based. Therefore, it is unlikely that any number of population viability analyses—although they might be scientifically comforting—will assuage all those concerned with wolf hunting and trapping.

Although the adage “familiarity breeds contempt” may be extreme, proximity to wolves and interactions with them typically leads to less tolerance for them (Williams et al. 2002, Karlsson and Sjöström 2007). This is particularly true for farmers and ranchers (Carlson et al. 2020). As wolf populations expand to landscapes where conflict with humans, pets, and livestock becomes more common, tolerance for wolves will decline. Similarly, there can be stark differences between attitudes of urban and rural residents regarding wolf conservation (Bruskotter et al. 2007). With increased urbanization, this divide may grow, diminishing support for rural communities dealing with frequent wolf conflict. Furthermore, increasing urbanization could even lead to a decoupling of humans and nature, where an unfamiliarity with nature and wildlife could reduce support for wolf conservation (Heberlein and Ericsson 2005). Finally, too many wolves in too many places could result in a strong public backlash against the species, as happened in Poland years ago and as has seeped into parts of the United States (Taylor 2021).

Tensions over wolf management and conservation certainly predate the last 30 years. Recently, however, such tension and disagreements for influence over wolf management policy have led to developments antithetical to the North American Model of Wildlife Conservation, which states that wildlife is a public trust resource with management decisions rooted in science (Organ 2018). For example, Wisconsin initiated a wolf harvest in 2021 in response to a court requirement (Wydeven et al. 2021). The harvest quickly exceeded the quota, and the wildlife management agency has since been the focus of fierce criticism. In the Rocky Mountains, the Idaho and Montana legislatures passed legislation requiring their respective wildlife agencies to increase wolf harvests and even outlined methods of take (e.g., Idaho Senate Bill 1211, MT House Bill 627).

Not only has wolf recovery led to circumventions of the traditional North American Model of Wildlife Conservation, but it has also fostered extraordinary maneuvers by private citizens on behalf of wolves. Colorado voters recently passed a ballot initiative requiring their wildlife agency to reintroduce wolves to the state (CPW 2022). Although some applaud such efforts to further wolf conservation, others point out that conservation by ballot initiative, legislation, or adjudication may not be the best path forward (Mech 1996). A ballot initiative to prevent wolf reintroduction is just as feasible as one leading to reintroduction. Wolf management and conservation provisions without input from wildlife management professionals could cause wolf populations to fluctuate wildly as the management direction changes on the basis of whoever holds the most power. Interest groups will try to influence wolf management in their favor even outside the traditional processes for input.

Future paths

To summarize, future wolf conservation in the United States will be affected by the ability of managers to predict wolf colonization and dispersal dynamics, to reduce hybridization and disease transmission, to mitigate and deter wolf–livestock conflicts, to harvest wolves sustainably while satisfying diverse stakeholders, to avert a reduction in tolerance for wolves due to a disinterest in nature, and to engage diverse stakeholders in wolf conservation to avoid management by ballot initiative or legislative and judicial decrees.

Research that develops more accurate predictive models of wolf dispersal and colonization patterns would greatly benefit managers as wolves recolonize new areas. Agencies that manage small wolf populations or areas where wolves are recolonizing human-dominated landscapes would benefit from monitoring for potential hybridization. In addition, monitoring for disease exposure and developing treatments where none exist would be useful. Minimizing depredation on livestock and investigating new nonlethal methods to reduce wolf conflict are warranted and could be encouraged and funded. Finally, developing risk maps of areas likely to have wolf–livestock conflict would be a useful tool for areas where wolf recolonization is likely (Treves et al. 2011).

The social challenges we present in the present article can be met in part through outreach about wolves, their roles in ecosystems, and the value of their continued conservation. The most promising path forward is to continue outreach efforts about wolves in both rural and urban areas (Mech 1995). Promptly addressing and mitigating wolf–human conflicts is paramount as wolves colonize new areas. Fostering dialogue between parties with competing interests in wolf management will also be crucial to avoid management decisions being made by legislatures, courts, and ballot initiatives. This may mean agencies invest in formal decision-making frameworks (e.g., structured decision-making) or even conflict resolution processes when considering management or policy about wolves. Furthermore, maintaining relationships to help manage wolves across jurisdictional boundaries, sometimes with differing conservation viewpoints and policies, will become increasingly necessary (Gilbert et al. 2022). Zoning for different types of management (e.g., control, regulated taking, total protection) in areas of differing degrees of human habitation can also be useful (Mech 2017). Some have suggested that wolf sanctuaries could be instituted where wolves are not subject to harvest if addressing the concerns of a segment of society that believes wolves should not be hunted or trapped is a priority (Mech 2021). Such areas can also act as reservoirs to help recover wolf populations in the event of declines elsewhere. Finally, citizens and governments in areas likely to be recolonized by wolves could establish stakeholder groups or initiate contingent management plans to proactively plan for wolf recolonization.

Caveats

Although wolves in the contiguous United States have enjoyed remarkable conservation success in recent decades, we recognize that not all wolf populations are faring well. Red wolves continue to face the stark reality of extinction despite extensive efforts and large amounts of recovery funding from the federal government. Recent discoveries of red wolf DNA in wild canids in the southeastern United States, however, may benefit future red wolf conservation (Mech and Nowak 2010, 2023, Murphy et al. 2019). Similarly, captive breeding is ongoing for Mexican wolves, and wolves in the US population are still quite isolated from wolves in Mexico, although the US population has been increasing in recent years (USFWS 2022). Continued outreach about the importance of such populations to wolf conservation and evolution will be important as wolves expand and become more common.

Although we focused on challenges facing wolves in the contiguous United States, we expect challenges for wolves in other areas of the world where their populations are expanding. For example, wolves recolonized Scandinavia and other parts of Europe in recent decades (Valière et al. 2003, Chapron et al. 2014, Recio et al. 2018). In Europe, wolves occupy more human-dominated landscapes than they do in much of the United States (Kuijper et al. 2019). Wolf recolonization in many countries has led to increased conflict with livestock production and even reduced tolerance as wolves have become more abundant and conspicuous (Karlsson and Sjostrom 2007, Davoli et al. 2022). Wolf recolonization in many parts of Europe in particular has benefited from early engagement of stakeholder groups and citizenry, as well as adequate resources for population monitoring and conflict prevention and reimbursements. The actions we propose to address wolf conservation and management challenges in the United States may also be useful for recolonizing wolf populations elsewhere.

Acknowledgments

We thank Caitlin Jacobs for an early manuscript review and anonymous reviewers who helped strengthen the manuscript.

References cited

Adams LG, Stephenson RO, Dale BW, Ahgook RT, Demma DJ. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range. *Wildlife Monographs* 170: 1–25.

Ausband DE, Stansbury C, Stenglein JL, Struthers JL, Waits LP. 2015. Recruitment in a social carnivore before and after harvest. *Animal Conservation* 18: 415–423.

Bangs EE, Fritts SH. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin* 24: 402–413.

Blanco JC, Cortés Y, Virgós E. 2005. Wolf response to two kinds of barriers in an agricultural habitat in Spain. *Canadian Journal of Zoology* 83: 312–323.

Boyce MS. 2011. Wolf hysteria. Is the conservation community losing credibility? *Alberta Outdoorsman* 2011: 12–14.

Bruskotter JT, Schmidt RH, Teel TL. 2007. Are attitudes toward wolves changing? A case study in Utah. *Biological Conservation* 139: 211–218.

Cariappa CA, Oakleaf JK, Ballard WB, Breck SW. 2011. A reappraisal of the evidence for regulation of wolf populations. *Journal of Wildlife Management* 75: 726–730.

Carlson SC, Dietsch AM, Slagle KM, Bruskotter JT. 2020. The VIPs of wolf conservation: How values, identity, and place shape attitudes toward wolves in the United States. *Frontiers in Ecology and Evolution* 8: 6.

Chakrabarti S, O'Neil ST, Erb J, Humpal C, Bump JK. 2022. Recent trends in survival and mortality of wolves in Minnesota, United States. *Frontiers in Ecology and Evolution* 10.

Chapron G et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1517–1519.

[CPW] Colorado Parks and Wildlife. 2022. Draft Colorado wolf restoration and management plan. CPW. https://cpw.state.co.us/Documents/Wolves/DRAFT-CO-Wolf-Plan.pdf.

Creel S, et al. 2015. Questionable policy for large carnivore hunting. *Science* 350: 1473.

Cubaynes S, MacNulty DR, Stahler DR, Quimby KA, Smith DW, Coulson T. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology* 83: 1344–1356.

Davoli M, Ghoddousi A, Sabatini FM, Fabbri E, Caniglia R, Kuemmerle T. 2022. Changing patterns of conflict between humans, carnivores and crop-raiding prey as large carnivores recolonize human-dominated landscapes. *Biological Conservation* 269: 109553.

Fritts SH, Stephenson RO, Hayes RD, Boitani L. 2003. Pages 289–316 in Mech Boitani L, eds. *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Fuller TK, Mech LD, Fitts-Cochran J. 2003. Population dynamics. Pages 161–191 in Mech LD Boitani L, eds. *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Gese EM, Knowlton FF, Adams JR, Beck K, Fuller TK, Murray DL, Steury TD, Stoskopf MK, Waddell WT, Waits LP. 2015. Managing hybridization of a recovering endangered species: The red wolf Canis rufus as a case study. *Current Zoology* 61: 191–205.

Gilbert JH, David P, Price MW, Oren J. 2022. Ojibwe perspectives toward proper wolf stewardship and Wisconsin's February 2021 wolf hunting season. *Frontiers in Ecology and Evolution* 10: 782840. https://doi.org/10.3389/fevo.2022.782840.

Gude JA, Mitchell MS, Russell RE, Sime CA, Bangs EE, Mech LD, Ream RR. 2012. Wolf population dynamics in the US Northern Rocky Mountains are affected by recruitment and human-caused mortality. *Journal of Wildlife Management* 76: 108–118.

Heberlein TA, Ericsson G. 2005. Ties to the countryside: Accounting for urbanites attitudes toward hunting, wolves, and wildlife. *Human Dimensions of Wildlife* 10: 213–227.

Heikkinen HI, Moilanen O, Nuttall M, Sarkki S. 2011. Managing predators, managing reindeer: Contested conceptions of predator policies in Finland's southeast reindeer herding area. *Polar Record* 47: 218–230.

Jimenez MD, Bangs EE, Boyd DK, Smith DW, Becker SA, Ausband DE, Woodruff SP, Bradley EH, Holyan J, Laudon K. 2017. Wolf dispersal in the Rocky Mountains, western United States: 1993–2008. *Journal of Wildlife Management* 81: 581–592.

Karlsson J, Sjöström M. 2007. Human attitudes towards wolves, a matter of distance. *Biological Conservation* 137: 610–616.

Kittle AM, et al. 2017. Landscape-level wolf space use is correlated with prey abundance, ease of mobility, and the distribution of prey habitat. *Ecosphere* 8: e01783.

Kreeger TJ. 2003. The internal wolf: Physiology, pathology, and pharmacology. Pages 192–217 in Mech LD Boitani L, eds. *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Kuijper DPJ, Churski M, Trouwborst A, Heurich M, Smit C, Kerley GIH, Cromsigt JPGM. 2019. Keep the wolf from the door: How to conserve wolves in Europe's human-dominated landscapes? *Biological Conservation* 235: 102–111.

Light DS, Fritts SH. 1994. Gray wolf (*Canis lupus*) occurrences in the Dakotas. *American Midland Naturalist* 132: 74–81.

Main D. 2022. An endangered wolf went in search of a mate. The border wall blocked him. *National Geographic (21 January 2022)*. www.nationalgeographic.com/animals/article/mexican-gray-wolf-migration-stopped-by-border-wall.

McRoberts RE, Mech LD. 2014. Wolf population regulation revisited—again. *Journal of Wildlife Management* 78: 963–967.

Mech LD. 1995. The challenge and opportunity of recovering wolf populations. *Conservation Biology* 9: 270–278.

Mech LD. 1996. A new era for carnivore conservation. *Wildlife Society Bulletin* 24: 397–401.

Mech LD. 2006. Prediction failure of a wolf landscape model. *Wildlife Society Bulletin* 34: 874–877.

Mech LD. 2013. The challenge of wolf recovery: An ongoing dilemma for state managers. *The Wildlife Professional* 7: 32–37.

Mech LD. 2017. Where can wolves live and how can we live with them? *Biological Conservation* 210: 310–317.

Mech LD. 2020. Unexplained characteristics of wolf natal dispersal. *Mammal Review* 50: 314–323.

Mech LD. 2021. Should governments provide more sanctuaries for grey wolves (*Canis lupus*)? *Canadian Wildlife Biology and Management* 10: 25–32.

Mech LD. 2022. Do wolves control their own numbers? *International Wolf* 31: 4–7.

Mech LD, Barber-Meyer SM. 2015. Yellowstone wolf (*Canis lupus*) density predicted by elk (*Cervus elaphus*) biomass. *Canadian Journal of Zoology* 93: 499–502.

Mech LD, Goyal SM. 1995. Effects of canine parvovirus on gray wolves in Minnesota. *Journal of Wildlife Management* 59: 565–570.

Mech LD, Nowak RM. 2010. Systematic status of wild canis in North-central Texas. *Southeastern Naturalist* 9: 587–594.

Mech LD, Nowak RM. 2023. A plea for red wolf conservation throughout its recent distribution. *Southeastern Naturalist* 22: N23–N27.

Mech LD, Goyal SM, Paul WJ, Newton WE. 2008. Demographic effects of canine parvovirus on a free-ranging wolf population over 30 years. *Journal of Wildlife Diseases* 44: 824–836.

Mech LD, Isbell F, Krueger J, Hart J. 2019. Wolf recolonization failure: A Minnesota case study. *Canadian Field-Naturalist* 133: 60–65.

Mitchell MS, et al. 2016. Management of wolves in the US Northern Rocky Mountains is based on sound science and policy. *Science* 350: 1473–1475. www.science.org/doi/10.1126/science.aac4768.

Mladenoff DJ, Sickley TA, Haight RG, Wydeven AP. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* 9: 279–294.

Morales-González A, Fernández-Gil A, Quevedo M, Revilla E. 2022. Patterns and determinants of dispersal in grey wolves (*Canis lupus*). *Biological Reviews* 97: 466–480.

Müller A, Silva E, Santos N, Thompson G. 2011. Domestic dog origin of canine distemper virus in free-ranging wolves in Portugal as revealed by hemagglutinin gene characterization. *Journal of Wildlife Diseases* 47: 725–729.

Murphy SM, Adams JR, Cox JJ, Waits LP. 2019. Substantial red wolf genetic ancestry persists in wild canids of southwestern Louisiana. *Conservation Letters* 12: e12621.

Naughton-Treves LI, Grossberg R, Treves A. 2003. Paying for tolerance: Rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology* 17: 1500–1511.

[ODFW] Oregon Department of Fish and Wildlife. 2022. *Oregon Wolf Conservation and Management 2021 Annual Report*. Oregon Department of Fish and Wildlife.

Organ J. 2018. The North American model of wildlife conservation and the public trust doctrine. Pages 125–135 in Leopold BD et al., eds, *North American Wildlife Policy and Law*. Boone and Crockett Club.

Quevedo M, Echegaray J, FernándezGil A, Leonard JA, Javier Naves J, Ordiz A, Revilla E, Vilà C. 2019. Lethal management may hinder population recovery in Iberian wolves. *Biodiversity and Conservation* 28: 415–432.

Recio MR, Zimmermann B, Wikenros C, Zetterberg A, Wabakken P, Sand H. 2018. Integrated spatially-explicit models predict pervasive risks to recolonizing wolves in Scandinavia from human-driven mortality. *Biological Conservation* 226: 111–119.

Rigg R, Find'o S, Wechselberger M, Gorman ML, Sillero-Zubiri C, Macdonald DW. 2011. Mitigating carnivore–livestock conflict in Europe: Lessons from Slovakia. *Oryx* 45: 272–280.

Rutledge LY, White BN, Row JR, Patterson BR. 2012. Intense harvesting of eastern wolves facilitated hybridization with coyotes. *Ecology and Evolution* 2: 19–33.

Sime CA, Asher V, Bradley L, Laudon K, Ross M, Trapp J, Atkinson M, Steuber J. 2008. *Montana Gray Wolf Conservation and Management 2007 Annual Report. Montana Fish, Wildlife, and Parks*.

Simpson TL, Thiel RP, Sailer DT, Reineke DM, Thomsen M. 2023. Demographics of gray wolf (*Canis lupus*) packs recolonizing variable habitats in central Wisconsin. *Northeastern Naturalist* 30: 75–98.

Smith DW, Cassidy KA, Stahler DR, MacNulty DR, Harrison Q, Balmford B, Stahler EE, Brandell EE, Coulson T. 2020. Population dynamics and demography. Pages 77–92 in Smith DW, Stahler DR MacNulty DR, eds. *Yellowstone Wolves*. University of Chicago Press.

Stenglein JL, Gilbert JH, Wydeven AP, Van Deelen TR. 2015. An individual-based model for southern Lake Superior wolves: A tool to explore the effect of human-caused mortality on a landscape of risk. *Ecological Modelling* 302: 13–24.

Stenglein JL, Wydeven AP, Van Deelen TR. 2018. Compensatory mortality in a recovering top carnivore: Wolves in Wisconsin, USA (1979–2013). *Oecologia* 187: 99–111.

Taylor C. 2021. Wisconsin wolf hunt overshoots quota, worrying conservationists. Minnesota Public Radio News (5 March 2021). www.mprnews.org/story/2021/03/05/science-friday-wisconsin-wolf-hunt-overshoots-quota-worrying-conservationists.

Treves A, Martin KA, Wydeven AP, Wiedenhoeft JE. 2011. Forecasting environmental hazards and the application of risk maps to predator attacks on livestock. *BioScience* 61: 451–458.

[USFWS] US Fish and Wildlife Service. 2017. *Mexican Wolf Recovery Plan, First Revision*. USFWS.

[USFWS] US Fish and Wildlife Service. 2022. *Mexican Wolf Recovery Program*. USFWS. Progress report no. 24.

[USFWS] US Fish and Wildlife Service *et al.* 2015. *Northern Rocky Mountain Wolf Recovery Program 2014 Interagency Monitoring Report*. USFWS.

Valière N, Fumagalli L, Gielly L, Miquel C, Lequette B, Poulle ML, Webert JM, Arlettaz R, Taberlet P. 2003. Long-distance wolf recolonization of France and Switzerland inferred from non-invasive genetic sampling over a period of 10 years. *Animal Conservation* 6: 83–92.

van den Bosch M et al. 2022. Identifying potential gray wolf habitat and connectivity in the eastern USA. *Biological Conservation* 273: 109708.

Wabakken P, Sand H, Liberg O, Bjärvall A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula 1978–1998. *Canadian Journal of Zoology* 79: 710–725.

Wabakken P, Sand H, Kojola I, Zimmermann B, Arnemo JM, Pedersen HC, Liberg O. 2007. Multistage, long-range natal dispersal by a global positioning system-collared Scandinavian wolf. *Journal of Wildlife Management* 71: 1631–1634.

Williams CK, Ericsson G, Heberlein TA. 2002. A quantitative summary of attitudes toward wolves and their reintroduction (1972–2000). *Wildlife Society Bulletin* 2002: 575–584.

Woodroffe R. 2000. Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation* 3: 165–173.

Wydeven AP, Fuller TK, Weber W, MacDonald K. 1998. The potential for wolf recovery in the northeastern United States via dispersal from southeastern Canada. *Wildlife Society Bulletin* 1998: 776–784.

Wydeven AP, Van Deelan TR, Heske E. 2009. *Recovery of Gray Wolves in the Great Lakes Region of the United States*. Springer.

Wydeven AP, Clark F, Daulton T, David P, Hauge T, Habush-Sinykin J, Peterson S, Stricker H, Van Deelen T. 2021. The February 2021 Wisconsin Wolf Hunt: A Preliminary Assessment. Wisconsin's Greenfire. https://wigreenfire.org/2019/wp-content/uploads/2021/04/WGF-Cons-Bulletin-Feb-Wolf-Hunt-04-28-2021.pdf.

Received: April 16, 2023. **Revised:** May 22, 2023