Species Status Assessment for the Gray Wolf (*Canis lupus*) in the Eastern United States

Photo by: International Wolf Center

Prepared by the U.S. Fish and Wildlife Service

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Writers and Contributors
This document was prepared by U.S. Fish and Wildlife Service biologists from the Species Assessment Team, including biologists from the Midwest Region, the Northeast Region, the Southwest Region, the Mountain-Prairie Region, the Pacific Southwest Region, and the Headquarters Office.

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- 1854 Treaty Authority
- Bay Mills Indian Community
- Keweenaw Bay Indian Community
- Little River Band of Ottawa Indians
- Mille Lacs Band of Ojibwe
- Red Lake Band of Chippewa
- Sault Ste Marie Tribe of Chippewa Indians
- White Earth Nation
- Michigan Department of Natural Resources
- North Dakota Game and Fish Department
- South Dakota Game, Fish, and Parks
- Wisconsin Department of Natural Resources
- Isle Royale National Park
- United States Department of Agriculture Animal and Plant Health Inspection Service
- United States Fish and Wildlife Service Mexican Wolf Recovery Program
- United States Geological Survey Northern Prairie Wildlife Research Center
- Timber Wolf Alliance, Sigurd Olson Environmental Institute

Version Note:
We provided Draft Version 1.0 of this Species Status Assessment Report to peer reviewers and technical reviewers for review. This final Version 1.1 includes revisions in response to the peer and technical reviewer feedback and any necessary updates based on newly available information.

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Executive Summary

The purpose of this document is to provide an assessment of the status of the gray wolf (*Canis lupus*) in its current range in the Eastern United States. In the lower-48 United States, gray wolves currently exist primarily in two large metapopulations[1]—one in the Western United States and one in the Western Great Lakes region in the upper Midwestern United States. A Species Status Assessment (SSA) Report for gray wolves in the Western United States has already been completed (Service 2023, entire). Therefore, this SSA Report addresses gray wolves where they occur in the remainder of the lower-48 United States (i.e., areas not already addressed in the SSA Report for the gray wolf in the Western United States). Together these SSA Reports provide an assessment of the status of the gray wolf in the lower-48 United States We describe our analysis area in greater detail under *Analysis Area* in Chapter 1 below.

This SSA uses the conservation biology principles of **resiliency**, **redundancy**, and **representation**, collectively known as the "3Rs," as a lens to evaluate the viability of the species (U.S. Fish and Wildlife Service (Service) 2016, p. 6). **Resiliency** is the ability to sustain populations through the natural range of favorable and unfavorable conditions. **Redundancy** spreads risk among multiple populations or areas to increase the ability of a species to withstand catastrophes. Catastrophes are stochastic events that cause substantial decreases in population size and can increase extinction risk, even in large populations (Mangel and Tier 1993, p. 1083). **Representation** is a species ability to adapt to changes in the environment and it is associated with its diversity, whether ecological, genetic, behavioral, or morphological. Our SSA Framework focuses on assessing an individual species' viability as the analysis is intended to inform policy decisions under the Act (Smith et al. 2018, entire). As such, this SSA does not assess the gray wolf in the Eastern United States' cultural or ecological significance, nor does it discuss ethical dimensions of wolf management.

Biology, Life History, and Ecology

Gray wolves are the largest wild members of *Canidae* or dog family (Mech 1974, pp. 11–12). Gray wolves have a circumpolar range including North America, Europe, and Asia. In North America, wolves are primarily predators of medium and large mammals. Also, they are efficient at using available food resources (Newsome et al. 2016, pp. 260–261; Janeiro-Otero et al. 2020, p. 2).

Gray wolves are highly territorial, social animals and group hunters, normally living in packs of 7 or fewer, but sometimes depending on prey species and availability can attain pack sizes of 20 or more wolves (Mech 1970, pp. 38–43; Erb and Carlos 2009, p. 59; Wydeven et al. 2009, p. 97; Mech and Boitani 2003, p. 8; Stahler et al. 2020, p. 46; MI DNR 2022a, p. 12; WI DNR 2023a,

[1] A metapopulation is a concept whereby the spatial distribution of a population has a major influence on its viability. In nature, many populations exist as partially isolated sets of subpopulations, collectively termed "metapopulations." A metapopulation is widely recognized as being more secure over the long term than are several isolated populations that contain the same total number of packs and individuals (Service 1994, Appendix 9). This is because adverse effects experienced by one of its subpopulations resulting from genetic drift, demographic shifts, and local environmental fluctuations can be countered by occasional influxes of individuals and their genetic diversity from the other components of the metapopulation.

p.16). In wolf populations, pack social structure is very adaptable. Oftentimes, breeding members can be quickly replaced from either within or outside the wolf pack, and pups can be reared by another pack member should their parents die (Packard 2003, pp. 58–60; Brainerd et al. 2008, entire; Borg et al. 2015, pp. 184–185; Stahler et al. 2020, p. 49). Consequently, gray wolf population sustainability is a function of the productivity of the population and its proximity to other populations (Fuller et al. 2003, pp. 185–186). Where productivity is average to high and source populations are near, gray wolf populations can sustain higher rates of mortality than those with lower productivity. Wolf populations can also quickly expand and recolonize vacant, suitable habitats (e.g., Mech 1995, entire; Boyd and Pletscher 1999, entire; Treves et al. 2009, entire; Mech 2017, entire; Hendricks et al. 2019, entire).

Gray wolves are habitat generalists, meaning they can thrive in a variety of habitats (Mech and Boitani 2003, p. 163); they once occupied or transited most of the United States, except the Southeast. We consider suitable wolf habitat to be areas containing adequate wild ungulate populations (e.g., elk and deer) with a low risk of conflict with humans and livestock (conflict generally increases the likelihood of human-caused wolf mortality) to allow populations to persist (see Mech 2017, pp. 312–315).

Canid taxonomy and evolutionary history in North America are complex and controversial. Synthesizing findings from paleontological, morphological, ecological, and genetic research, large-bodied wolf-like canids inhabited the Eastern United States at the time of European colonization. In the Southeastern United States, the best available science indicates these canids were red wolves, a distinct species derived from an endemic North American canid lineage, as opposed to some form of gray wolf (Nowak 1995, entire; Nowak 2002, entire; Nowak and Federoff 1998, entire; vonHoldt et al. 2011, p. 1297; Waples et al. 2018, entire; National Academies of Sciences Engineering and Medicine 2019, pp. 45–60). Currently, the Western Great Lakes region is occupied by canids that are phenotypically and genetically recognized as gray wolves, despite their legacy of introgression. A distinct canid, commonly referred to as the eastern wolf, still occurs in southeastern Canada. The science is inconclusive as to which of these canids historically occupied the Northeastern United States: this area could have conceivably been a convergence zone of multiple types of canids. The same can also be said for Texas. The Great Plains were historically occupied by some form of gray wolf, which morphologically aligned with those in the Western Great Lakes, but it is unknown whether those animals were admixed as well. Importantly, it is implausible to assume that any purported boundaries between the ranges of species and/or subspecies were hard transition points between these entities. In other words, these various canids likely overlapped in distribution near the edges of their ranges, perhaps even forming hybrid zones. The key for this SSA Report is that we cannot confidently eliminate the possibility that gray wolves historically occupied much of the Eastern United States, with the exception of the Southeastern United States (i.e., where the red wolf historically occurred). *Taxonomy and Historical Range* is covered in detail, including relevant citations, in Chapter 1 of this SSA Report.

As explained above, the purpose of this SSA Report is to provide an assessment of the gray wolf's status in the Eastern United States. However, because the best available science indicates that gray wolves did not historically occupy the Southeastern United States, which was instead occupied by red wolves (see *Taxonomy and Historical Range* in Chapter 1), we do not include the Southeastern United States in our analysis area. We relied on the historical range map for the red wolf (Wildlife Management Institute 2016, p. 23) to determine which areas to exclude from our analysis area for the gray wolf in the Eastern United States. We assumed that gray wolves and red wolves did not co-occur within the core of red wolf's historical range (see *Interpreting Historical Range* in Chapter 1). Therefore, states entirely within red wolf historical range (Alabama, Arkansas, Delaware, Florida, Georgia, Kentucky, Louisiana, Mississippi, Maryland, North Carolina, South Carolina, Tennessee, West Virginia, and Virginia) are not included in our analysis area. If only a portion of a state is included in the red wolf historical range (Illinois, Indiana, Kansas, Missouri, New Jersey, New York, Ohio, Oklahoma, Pennsylvania, and Texas), we include the entire state in the analysis area for the gray wolf in the Eastern United States because it is likely that gray wolves and red wolves co-occurred in these areas (see *Interpreting Historical Range* in Chapter 1). Due to the uncertainty regarding the taxonomic assignment of the canids that historically occupied the Northeastern United States and the likelihood that Texas was historically a convergence point for several different canids, including different subspecies of gray wolf (see *Interpreting Historical Range* in Chapter 1), we include these states in our analysis area for this SSA Report. Based on this approach, the geographic scope of our analysis includes: Connecticut, Illinois, Indiana, Iowa, Kansas, Maine, Massachusetts, Michigan, Minnesota, Missouri, Nebraska, New Hampshire, New Jersey, New York, North Dakota, Ohio, Oklahoma, Pennsylvania, Rhode Island, South Dakota, Texas, Vermont, and Wisconsin (Figure ES 1). These 23 states encompass the potential historical range for the gray wolf in the Eastern United States, including areas of potential overlap with other canid taxa (see *Taxonomy and Historical Range* in Chapter 1). The Mexican wolf, a subspecies of gray wolf, and the red wolf, a separate species of canid, are each separately listed as endangered under the Act and are not the subject of this SSA Report.

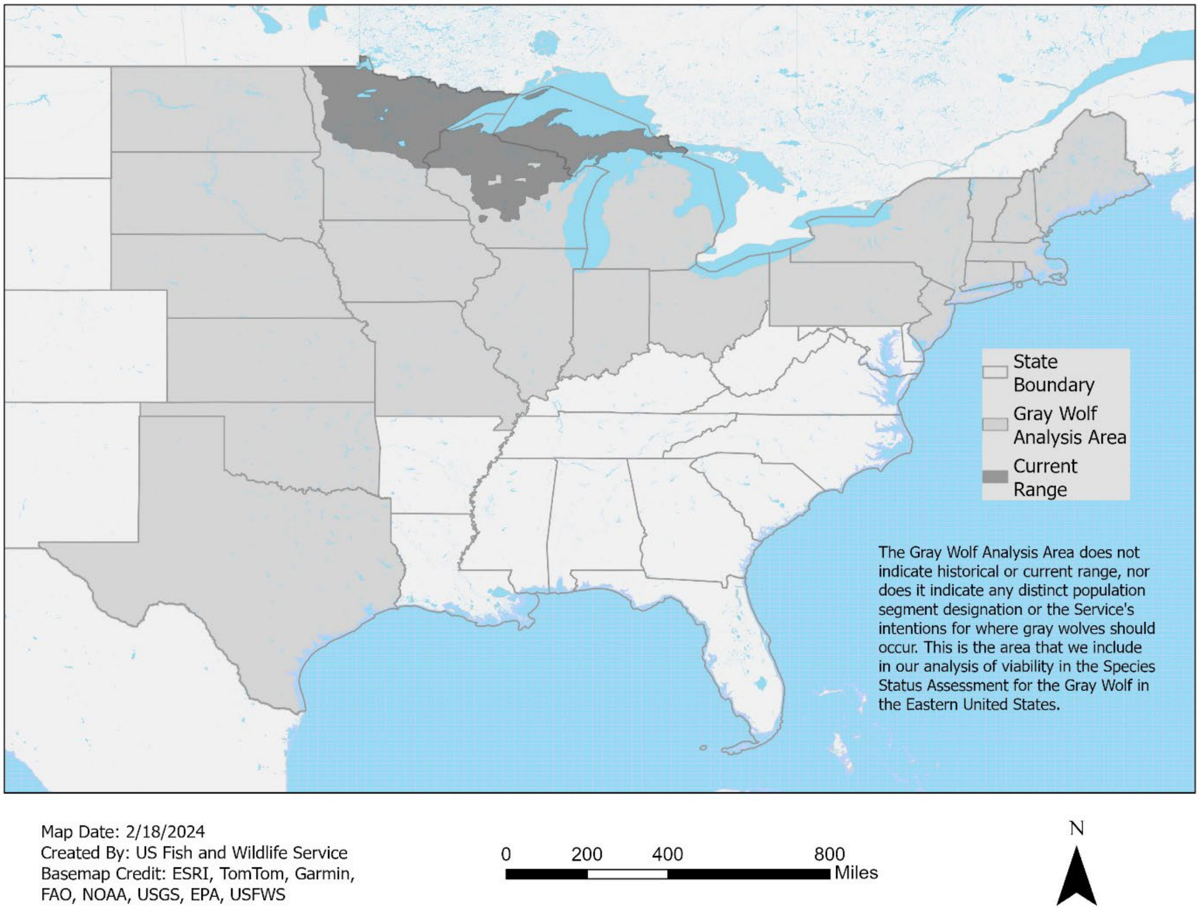

Figure ES 1. Analysis area for SSA Report for the gray wolf in the Eastern United States. Analysis area includes 23 states (gray). Note that the gray shading of this analysis area on this map does not indicate historical or current range, nor does it indicate a Distinct Population Segment (DPS) or the Service's intentions for where gray wolves should occur; rather, this map only illustrates the states we are considering in our SSA Report. The dark gray polygon in the Western Great Lakes area indicates gray wolf current range as of year-end 2023. The gaps in wolf distribution in this map include areas of large lakes, urban areas, or areas of intense agriculture where wolves are not known to exist.

In general, to maintain populations in the wild over time, gray wolves in the Eastern United States need well-connected and genetically diverse subpopulations that function as a metapopulation distributed across enough of their range to be able to withstand stochastic events, rebound after catastrophes (e.g., severe disease outbreaks), and adapt to changing environmental conditions.

Conservation Efforts and Stressors

A stressor is something that causes a change in a habitat or demographic resource that can lead to an adverse individual response. The stressors that we evaluate for gray wolves in the Eastern United States include: human-caused mortality, disease and parasites, inbreeding depression, hybridization, climate change, disease in prey species, and other sources of habitat modification. We also discuss the state, tribal, and Federal management that provide for the conservation of gray wolves in the Eastern United States by reducing the influence of a stressor, improving the condition of gray wolf habitat, or improving gray wolf demographic factors.

In the Eastern United States, the primary stressor influencing wolf populations is human-caused mortality (see *Stressors: Human-Caused Mortality* in Chapter 3). Currently, while the species is listed under the Act, the main sources of human-caused mortality are lethal removal of depredating gray wolves (in Minnesota) and illegal or accidental mortalities (see *Human-Caused Morality in Minnesota* in Chapter 3). Should gray wolves be delisted, lethal control of depredating wolves would likely occur throughout the species' current range, and regulated harvest may also occur in some or all states. All states and some Tribal Nations within the current range of gray wolves have statutes, regulations, and management plans that govern conservation and take of gray wolves (see *Management and Conservation Efforts* in Chapter 3). Federal agencies also have rules and regulations in place to minimize disturbance to gray wolves, when necessary. To date, the best available science indicates that current levels of human-caused mortality have not caused significant reductions in gray wolf abundance throughout the Western Great Lakes, the only extant wolf population in the Eastern United States. Additionally, the best available science indicates that disease in gray wolves has caused episodic, yet localized and short-term, population decreases. In this SSA, we present information on modeled future scenarios that examine the potential future effects of human-caused mortality and disease; we also note the potential for future climate-related changes in disease. Finally, we discuss the current and future status of inbreeding, inbreeding depression, connectivity, and genetic diversity in our analysis of current and future conditions. We also considered the potential effects of hybridization, diseases in prey species, climate change, or other sources of habitat modification on gray wolves in the Western Great Lakes, but we do not further analyze their future effect on gray wolf viability because, based on our review of the best available scientific information, these stressors have not negatively influenced gray wolf viability nor are they anticipated to do so in the future. *Management and Conservation Efforts* of states, Tribal Nations, and Federal land management agencies and the *Stressors* we evaluated, including relevant citations, is covered in detail in Chapter 3 of this SSA Report.

Current Condition

In the Eastern United States, gray wolves occur in one large metapopulation in the Western Great Lakes, distributed across the states of Michigan, Minnesota, and Wisconsin. As of the year-end 2022, there were over 4,550 gray wolves distributed between more than 1,050 packs in the Western Great Lakes states. Despite past harvest seasons, ongoing lethal depredation control, and periodic disease outbreaks, the population in the Western Great Lakes has maintained a large population size and broad distribution. Essentially, at current levels, human-caused mortality and other stressors have had minimal impact on wolf abundance or distribution in the Western Great Lakes; however, for much of the past 50 years, the protections of the Act have tempered the levels of human-caused mortality to which the species has been exposed in Wisconsin and Michigan and, to a lesser degree, in Minnesota (where lethal depredation control is authorized under section 4(d) when the species is listed). Dispersals of wolves from the Western Great Lakes metapopulation have been documented in at least eleven states (Colorado, Illinois, Iowa, Indiana, Kansas, Kentucky, Missouri, Nebraska, New York, North Dakota, and South Dakota), and three Canadian Provinces (Manitoba, Ontario, and Saskatchewan). The wolves in the

Western Great Lakes states occupy areas of high-quality habitat with abundant prey (DelGuidice et al. 2009, entire; Mladenoff et al. 2009, pp. 128–136; van den Bosh et al. 2022, entire). The maintenance and expansion of the Minnesota wolf population has allowed for the preservation of the genetic diversity that remained in the Western Great Lakes region when its wolves were first protected in 1974; the current population retains high levels of genetic diversity (Koblmüller 2009, p. 2322; Fain et al. 2010, p. 1758; Gómez-Sánchez et al. 2018, p. 3602). The Western Great Lakes' metapopulation's large size, the metapopulation's broad pack distribution, the metapopulation's high levels of genetic diversity and connectivity, gray wolves' high reproductive potential, and gray wolves' innate behavior to disperse into vacant suitable habitats contribute to the species' current ability to withstand stochastic and catastrophic events within the Western Great Lakes. Finally, based on multiple contributing factors to adaptive capacity, including dispersal and colonization ability, wolves in the Western Great Lakes currently retain the ability to adapt to changes in their environment (see *Current Representation* in Chapter 4 and Appendix 3). In sum, while the gray wolf currently occupies only a portion of its historical range in the Eastern United States, within its current range (i.e., within the Western Great Lakes region), the gray wolf currently retains the ability to withstand stochastic and catastrophic events and adapt to changes in its environment. *Current Condition* of the gray wolf in the Eastern United States, including relevant citations, is covered in detail in Chapter 4 of this SSA Report.

Future Condition

We developed a density-dependent population model to (1) project the future population size of gray wolves in the Western Great Lakes states of Michigan, Minnesota, and Wisconsin, under a range of future scenarios 100 years into the future and (2) conduct a PVA by evaluating the likelihood of falling below thresholds related to extinction risk and genetic health. Our model structure and thresholds were chosen to specifically evaluate the ability of gray wolves to persist in multiple areas under various mortality (i.e., harvest and lethal depredation control) scenarios and disease rates, and to evaluate the ability of gray wolves to maintain effective population sizes above those needed to prevent inbreeding depression. We qualitatively discuss expectations regarding expansion of gray wolf populations outside of the three states in which gray wolves currently occur in the Eastern United States, potential changes in suitable habitat and prey availability, and potential changes in genetic diversity.

We quantitatively projected the total future population size of gray wolves in the combined area of Michigan, Minnesota, and Wisconsin (i.e., the Western Great Lakes) under multiple future scenarios. Future scenarios allow us to explore a range of possible future conditions for wolves in the Eastern United States, given the uncertainty in the stressors they may face; uncertainty in the potential response to those stressors; and the potential for possible conservation efforts to improve future conditions (Smith et al. 2018, p. 306). We developed scenarios to evaluate the potential effects of disease, harvest, and lethal depredation control, the three primary stressors that could influence future gray wolf populations in the Western Great Lakes. Our scenarios are meant to encompass the potential range of future conditions the species may experience, given uncertainties in the true magnitude of these stressors in the future; however, the likelihoods of each of these scenarios may differ.

In our future scenarios, we simulated two levels of disease frequency and severity to explore the potential effects of disease and other catastrophic events on gray wolf population dynamics. First, we applied the frequency and severity of disease that we have recently observed in a gray wolf population in the Western United States. This first level of disease (i.e., "observed YNP disease rates") was estimated from data on gray wolves in Yellowstone National Park (YNP), where three instances of canine distemper virus resulting in 20 to 30 percent reductions in the population were observed over 25 years (Brandell et al. 2020, p. 126). Although it is highly suspected that canine parvovirus contributed to wolf declines on Isle Royale between 1980–1982 (Brand et al. 1995, p. 421) and had an effect on the Wisconsin wolf population in 1984–1985 (Wydeven et al. 1995, pp. 155–156; Wydeven et al. 2009a, p. 96), the best available science currently does not provide information regarding the frequency and severity of disease events in gray wolves in the Western Great Lakes. Wydeven et al. 1995 (pp. 155–156) conclude that increases in the wolf population occurred when the prevalence of canine parvovirus was less than 50 percent in the population. However, wolf populations are not routinely screened for parvovirus and therefore we do not know the current or future expectation regarding current or future prevalence of parvovirus in wolf populations. The data provided from Wisconsin span a range of years from 1985–2023 and likely encompasses the expected rate of growth with current frequency and severity of canine parvovirus effects. Therefore, applying a level of disease from YNP in all our future scenarios for the Western Great Lakes, potentially overestimates the effects of disease on the Western Great Lakes population. In half of our future scenarios, we applied a second level of disease (i.e., "added vertebrate black swan events"), which included the effects of high severity, but low probability, disease outbreaks on top of these past observed rates of disease.

In addition to varying the level of disease that gray wolves in the Western Great Lakes may experience in the future, we also varied the levels of human-caused mortality in the populations (i.e., regulated harvest and lethal depredation control) to examine a range of potential future effects of this stressor in the future. Due to many factors that affect hunter/trapper effort and success and future state-level management practices, uncertainty remains as to how states in the Western Great Lakes will manage wolf mortality into the future (i.e., uncertainty remains as to the exact harvest and lethal depredation control rates that will occur in each state in the future). Therefore, we projected future population sizes for Michigan, Minnesota, and Wisconsin under multiple different mortality scenarios intended to capture the range of mortality that may occur in the future based on past rates of harvest and lethal depredation control and current state management plans. Under Mortality Scenario 1, we used minimum past observed harvest and lethal depredation control rates in Michigan (during years when regulated harvest and lethal depredation control occurred) combined with population levels for Minnesota (between 2,200 and 3,000 gray wolves) and Wisconsin (between 800 and 1,200 gray wolves) intended to mimic year-to-year changes in population size in these states due adaptive regulated human caused mortality as outlined in their state plans. Under Mortality Scenario 2, rates of human-caused mortality reflected the maximum past observed harvest and lethal depredation control rates (during years when regulated harvest and lethal depredation control occurred) in Michigan, Minnesota, and Wisconsin.

Therefore, in our projections, we estimated the future number of gray wolves in each state under four total combinations of disease and mortality scenarios, spanning two disease scenarios and two mortality scenarios.

For each scenario, in addition to projecting the median future population size (and a credible interval around this projection), we also calculated the proportion of simulations that fell below an effective population size of 50. An effective population size of 50 represents a key reduction in viability or potential risk of inbreeding depression. We use two values to capture the range of possible population sizes that represent and effective population size of 50 (i.e. these values capture the uncertainty in the ratio of census population size to effective population size). In the absence of a ratio specific to the Western Great Lakes population, we estimated the average ratio of effective to census population size based on an analysis of Wildlife Genetics International genetic data (WGI 2021, unpublished data). We estimated the average ratio of effective to census population size for Western wolves as approximately 0.17, with a 95% confidence interval between 0.12 and 0.26 (see Appendix 1 of the SSA for this methodology and effective population size calculations); this means that an effective population size of 50, equates to a census population size of between approximately 192 and 417 wolves, based on the 95% confidence interval for the effective to census population size ratio. For each scenario we evaluate the proportion of simulations that fall below either of these values across the simulated timeframe of 100 years.

Future Resiliency and Redundancy

Our model projections demonstrate that even with disease, maximum past observed harvest and lethal depredation control rates occurring together every year for the next 100 years in Michigan, Minnesota and Wisconsin, the gray wolf population in the Western Great Lakes maintains its ability to withstand stochastic events (resiliency)—albeit at reduced population sizes—given the assumptions in our model. There were no simulations in which the population in the Western Great Lakes dropped below our lower threshold of an effective population size of 50 (192 wolves) or quasi-extinction (5 wolves), even considering this sustained harvest and lethal depredation control. Additionally, there was a maximum of 0.02 percent probability of falling below our upper threshold for an effective population size of 50 (i.e., 417 wolves) in 100 years, demonstrating a negligible risk of future inbreeding (see Figure ES 2). Our model projections indicate that the gray wolf in the Western Great Lakes will likely maintain its current distribution of hundreds of packs and multiple subpopulations across three states over the course of the next 100 years. This broad distribution among multiple packs and subpopulations will continue to enhance the species' ability to withstand catastrophic events (redundancy). Moreover, none of the simulations of the future population size in the Western Great Lakes resulted in quasi-extinction, even with the introduction of catastrophic levels of disease (black swan events), further illustrating the species' ability to withstand catastrophic events into the future.

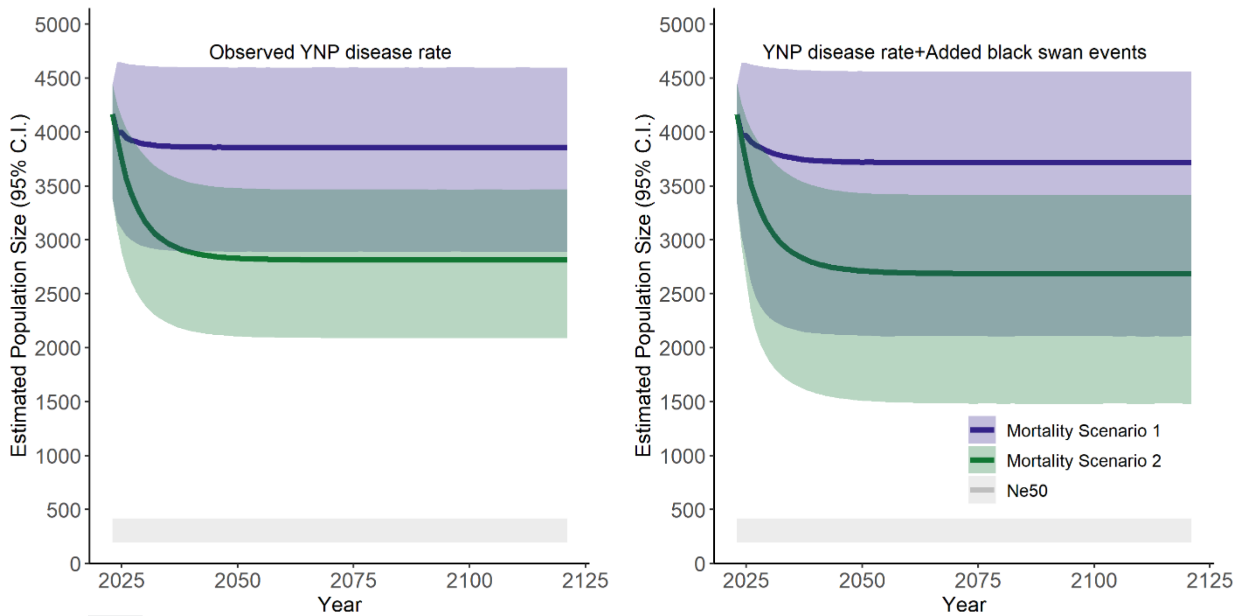

Figure ES 2. Simulated median gray wolf population size (solid line) and 95 percent credible interval (shaded area) in the Western Great Lakes population (Michigan, Minnesota, and Wisconsin, combined) with Mortality Scenario 1 in purple and Mortality Scenario 2 in green. The panel on the left includes the results for the two mortality scenarios combined with Observed YNP disease rates. The panel on the right includes the results for the two mortality scenarios combined with Observed YNP disease rates plus added black swan events. The gray bar represents the estimated census population size that is equivalent to an effective population size of 50 (N_e50 -the threshold for avoiding inbreeding depression, 192-417 wolves).

We did not quantitatively project the future number of gray wolves in any of the states in our analysis area outside of the three Western Great Lakes states because these areas are not currently occupied and modeling the expansion of the wolf population would require assumption regarding how newly occupied states would manage gray wolves, and whether gray wolf populations could persist on the landscape. We also did not include the Lower Peninsula of Michigan in our model projections, given that the current population in Michigan does not extend to the Lower Peninsula. Although we have confirmed records of dispersing gray wolves in all but a few states in our analysis area, we currently have no information indicating that gray wolves occupy or have formed breeding pairs anywhere in the Eastern United States outside of the Western Great Lakes (see *Northeastern United States* and *Confirmed Wolf Reports Elsewhere in the Eastern United States*). Further, despite the presence of large source populations of gray wolves in both the Western Great Lakes and Canada, as well as sufficient suitable habitat (see *Current Habitat Availability* and Table 6 (a-b) in the SSA), we do not expect that gray wolves will recolonize other areas of the Eastern United States and establish populations outside of Michigan, Minnesota, and Wisconsin in the future. Gray wolves dispersing into these unoccupied states have a high risk of human-caused mortality (e.g., higher human density, existing state regulations, higher livestock production and agriculture) which reduces the likelihood that gray wolves will successfully recolonize these areas in the future (see *Future Expectations of Populations in Areas Not Analyzed in the Model* in Chapter 6 of the SSA Report for more details). Therefore, because we do not expect additional populations of gray wolves to occur in the Eastern United States, outside of the Western Great Lakes region, in the future, gray wolf resiliency and redundancy in the Eastern United States is unlikely to increase in the future relative to current condition.

Our expectations for habitat and prey availability and genetic health further support the maintained resiliency of wolves in the Western Great Lakes 100 years into the future. Although some changes in habitat and prey are expected over the next century, we do not anticipate these changes will substantially alter the wolf's risk of extinction in the Western Great Lakes in the future. Given our expectation of continued connectivity in the Western Great Lakes and given wolves' life history, we do not expect any decreases in genetic diversity significant enough such that inbreeding depression will be a concern under any of our future scenarios.

Future Representation

Given the adaptable nature of gray wolves and the projections for changes in population sizes in the future scenarios we model, it is likely that gray wolves in the Western Great Lakes will remain capable of adapting to environmental change, even without further expansion into the Eastern United States. Such capability will be supported, as it is currently, by: (1) a strong ability to disperse and colonize suitable habitat; (2) tolerance to a range of environmental conditions, including behavioral and phenotypic plasticity; and (3) the ability to respond genetically through natural selection acting on the available pool of genetic diversity, maintained by connectivity throughout the metapopulation. Although human-caused mortality (the primary stressor) is one for which sufficient adaptation is unlikely, we expect gray wolves in the Western Great Lakes to otherwise be well suited to adapt to a variety of environmental change in the future, as long as human-caused mortality is kept within the bounds analyzed in our model, bounds we find are most likely should the species be delisted in the future.

Summary of Future Condition

Our model projections of the future gray wolf population in the Western Great Lakes indicate that the median population size will be between approximately 2,600 and 3,800 gray wolves over the course of the next 100 years, if mortality rates from lethal depredation control, harvest, and disease occur within the bounds we consider in our future scenarios. While these projected population sizes represent a decrease relative to the metapopulation's current size, we would expect such a change with the introduction of harvest (which does not currently occur in the population while the species is listed) and disease (which has never been detected to occur at the rates and geographic scales we model in our future scenarios in the Western Great Lakes region). Further these projections assume that background rates of illegal take, which are built-in to the intrinsic rate of growth and not explicitly included in the models will continue into the future (i.e. rates will neither increase or decrease). After this initial decline due to these stressors, the population stabilizes around a large equilibrium population size and does not fall to a level that indicates risk of quasi-extinction or inbreeding, demonstrating the population's ability to withstand the sustained human-caused mortality and disease rates we model (both stochastic events (resiliency) and catastrophic events (redundancy)). Major uncertainties include the effects of additive versus compensatory harvest (though for higher harvest rates we assume additive harvest effects), and the accuracy of monitoring programs. We explored the effects of uncertainty on these parameters in our uncertainty analyses (Appendix A) and determined the conclusions of our SSA were robust to these uncertainties. The continued availability of (or perhaps increase in) suitable habitat and prey further support the Western Great Lakes metapopulation's resiliency into the future. Moreover, the metapopulation's currently high levels of genetic diversity are unlikely to decrease in the future, given maintained connectivity within the metapopulation and with the larger, expansive, and secure gray wolf population in Canada (Canadian Endangered Species Conservation Council 2022, unpaginated). This sustained genetic diversity and connectivity also contribute to the species' continued ability to withstand stochastic events (resiliency) into the future within the Western Great Lakes metapopulation (the extant metapopulation in the Eastern United States). Finally, given this maintained genetic diversity, and gray wolves' innate characteristics that contribute to the species' ability to live in and disperse to multiple different habitat types, the adaptive capacity of the species (representation) within the Western Great Lakes is unlikely to decrease relative to current condition in the future. Due to the risk of human-caused mortality, gray wolves are unlikely to recolonize areas outside of the Western Great Lakes within the Eastern United States in the future, which means redundancy and representation is unlikely to increase in the future. However, based on our analysis, the gray wolf in the Western Great Lakes area will likely retain sufficient resiliency, redundancy, and representation to avoid extirpation for the next 100 years, meaning that, even without this recolonization, the gray wolf will successfully maintain populations in the wild in the Eastern United States into the future, despite the continued occurrence or introduction of various stressors. *Future Condition* of the gray wolf in the Eastern United States, including relevant citations, is covered in detail in Chapter 6 of this SSA Report.

Introduction

Purpose

The purpose of this document is to provide an assessment of the status of the gray wolf (*Canis lupus*) in its current range in the Eastern United States. In the lower-48 United States, gray wolves currently exist primarily in two large metapopulations[2]—one in the Western United States and one in the Western Great Lakes region in the upper Midwestern United States. A Species Status Assessment (SSA) Report for gray wolves in the Western United States has already been completed (Service 2023, entire). Therefore, this SSA Report addresses gray wolves where they occur in the remainder of the lower-48 United States (i.e., areas not already addressed in the SSA Report for the gray wolf in the Western United States). Together these SSA Reports provide an assessment of the status of the gray wolf in the lower-48 United States. We describe our analysis area in greater detail under *Analysis Area* in Chapter 1 below.

Currently, gray wolves in the Eastern United States are listed as endangered under the Act, except in Minnesota where they are listed as threatened. The legal status of wolves at the Federal level has changed several times over the past two decades. In 2003, the Service published a rule revising the 1978 listing for gray wolves (43 FR 9607, March 9, 1978), which included designating an Eastern Distinct Population Segment (DPS[3]) that was focused primarily on the occupied areas of the Eastern United States, and included classifying this DPS as threatened (68 FR 15804, April 1, 2003). In 2004, the Service proposed to remove wolves in the Eastern DPS from the Federal List of Endangered and Threatened Wildlife (List) due to recovery (69 FR 43664, July 21, 2004). However, before this rulemaking could be finalized, the 2003 rule that established the Eastern DPS was vacated by two separate Federal court rulings, returning the gray wolf to its 1978 status under the Act. Between 2007 and 2011, the Service delisted gray wolves in a Western Great Lakes DPS (an area smaller than the aforementioned Eastern DPS) on three separate occasions (72 FR 6052, February 8, 2007; 73 FR 10514, February 27, 2008; 74 FR 15070; April 2, 2009), but the wolves were relisted due to adverse Federal court decisions and, in one instance, a settlement agreement. Most recently, in 2020, the Service finalized a rule removing gray wolves in much of the lower-48 United States, including the Eastern United States, from the List (85 FR 69778, November 2, 2020). The 2020 delisting rule was vacated by a Federal court in early 2022 and gray wolves were again protected under the Act. For more details on the regulatory history of the gray wolf, see the 2020 rule (85 FR 69778, November 2, 2020).

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[2] A metapopulation is a concept whereby the spatial distribution of a population has a major influence on its viability. In nature, many populations exist as partially isolated sets of subpopulations, collectively termed "metapopulations." A metapopulation is widely recognized as being more secure over the long term than are several isolated populations that contain the same total number of packs and individuals (Service 1994, Appendix 9). This is because adverse effects experienced by one of its subpopulations resulting from genetic drift, demographic shifts, and local environmental fluctuations can be countered by occasional influxes of individuals and their genetic diversity from the other components of the metapopulation.

[3] Under the Endangered Species Act, a distinct populations segment is a vertebrate population or group of vertebrate populations that is discrete from other populations of the species and significant in relation to the entire species.

Throughout this SSA Report, when we present information specific to the current distribution of gray wolves in the Eastern United States (i.e., the gray wolves in Michigan, Minnesota, and Wisconsin), we use the term "Western Great Lakes." When we discuss information relevant to both the current and historical range of the gray wolf in the Eastern United States or to the entirety of our analysis area, we use the term "Eastern United States." Furthermore, throughout this SSA Report, we often refer to the extant gray wolves in each state (Michigan, Minnesota, and Wisconsin) as a "population" and frequently discuss each state's population separately, as gray wolves are managed at this state scale in the Eastern United States. However, the gray wolves in each of these three states are connected to populations in other states in the Western Great Lakes metapopulation; in using the term "population" as shorthand to refer to the gray wolves in each state, we are not concluding each state represents a biologically separate population nor are we making any claims about whether any individual state, or the entire analysis area, qualifies as a DPS of gray wolf.

Analytical Framework

In this document, we use the conservation biology principles of resiliency, redundancy, and representation to evaluate the current and future condition of gray wolves in the Eastern United States. We recognize there are other aspects of gray wolf conservation and management that are of interest to a diverse set of collaborators, including—but not limited to—ethical questions surrounding harvest methods or the killing of wolves in general (e.g., Haber 1996, p. 1076; Fox and Bekoff 2011, pp. 135–136), the ecological benefit of wolves as an apex predator (e.g., Ripple et al. 2001, pp. 232–233), and the cultural value of wolves (Fritts et al. 2003, pp. 291–292). However, understanding a species' (inclusive of subspecies and DPSs) biological risk of extinction is necessary to determine if the species should be listed as a threatened species or endangered species under the Act, and, therefore, our analysis is focused on assessing viability. Our assessment is divided into three parts:

1. **Species Ecology.** First, we summarize the best available information on gray wolf ecology (taxonomy, life history, habitat, and prey) in the Eastern United States and evaluate the resources and demographic factors gray wolves need to sustain populations over time *(Chapters 1 and 2)*.

2. **Current Species Condition.** Next, we describe the current condition of the gray wolf's habitat and demographics and the probable explanations for past and ongoing changes in abundance and distribution in the Eastern United States *(Chapters 3 and 4)*.

3. **Future Species Condition.** Lastly, we use a quantitative model to forecast the estimated abundance of gray wolves under plausible future scenarios that vary stressors and management. We combine the outputs of this model (estimated population sizes) with a qualitative evaluation of the gray wolf's adaptive capacity to assess the species' viability in the Eastern United States *(Chapters 5 and 6)*.

Viability is the ability of a species to maintain populations in the wild over time. To assess viability, we use the conservation biology principles of resiliency, redundancy, and representation (Shaffer and Stein 2000, pp. 308–311). These principles are rooted in ecological theory and empirical studies showing that, all else being equal, larger range, more populations, larger populations, larger habitat areas, sufficient gene flow, and distribution across a variety of ecosystems all lower extinction risk (Wolf et al. 2015, p. 204). We use definitions of resiliency, redundancy, and representation based on Smith et al. (2018, pp. 306–307), which were derived specifically for SSAs. Our definitions are somewhat different than those presented in Shaffer and Stein (2000, pp. 308–311) because our focus is on assessing the viability of a particular species rather than their broader focus on ecosystem function and biodiversity. A species with a high degree of resiliency, redundancy, and representation is better able to rebound from environmental stochasticity (resiliency), withstand catastrophes (redundancy) and adapt to changes in its biological and physical environment (representation). In general, species viability increases with increases in resiliency, redundancy, and representation (Smith et al. 2018, p. 306).

Resiliency is the ability of a species to withstand environmental stochasticity (normal, year-to-year variations in environmental conditions such as temperature and rainfall), periodic disturbances within the normal range of variation (fire, floods, and storms), and demographic stochasticity (normal variation in demographic rates such as mortality and fecundity) (Redford et al. 2011, p. 40). Simply stated, resiliency is the ability to sustain populations through the natural range of favorable and unfavorable conditions.

We can best gauge resiliency by evaluating population-level characteristics such as: demography (abundance and the components of population growth rate—survival, reproduction, and migration); genetic health (effective population size and heterozygosity); connectivity (gene flow and population rescue); and habitat quantity, quality, configuration, and heterogeneity. For species prone to spatial synchrony (regionally correlated fluctuations among populations), distance between populations and degree of spatial heterogeneity (diversity of habitat types or microclimates) are also important considerations.

Redundancy spreads risk among multiple populations or areas to increase the ability of a species to withstand catastrophes. Catastrophes are stochastic events that cause substantial decreases in population size and can increase extinction risk, even in large populations (Mangel and Tier 1993, p. 1083).

We can best gauge redundancy by analyzing the number and distribution of populations relative to the scale of anticipated species-relevant catastrophic events. The analysis entails assessing the cumulative risk of catastrophes occurring over time. Redundancy can be analyzed at a population or regional scale, or, for narrow-ranged species, at the species level.

Representation was originally conceived as the conservation of species within an array of different environments or ecological settings as part of conserving functioning ecosystems (Shaffer and Stein 2000, pp. 307–308). However, in the context of assessing species viability, representation in different ecological settings is a proxy for adaptive capacity (Smith et al. 2018, p. 306), which is the ability of a species to adapt to both near-term and long-term changes in its physical (climate conditions, habitat conditions, habitat structure, etc.) and biological (pathogens, competitors, predators, etc.) environments. Therefore, we define representation as the ability to adapt to new environments.

Although representation across the range of ecosystems in which a species occurs is one measure of how a species may be able to withstand or adapt to environmental change, we also use more direct measures of adaptive capacity to assess representation. Species can adapt to novel changes in their environment by either (1) moving to new, suitable environments or (2) altering their physical or behavioral traits (phenotypes) to match the new environmental conditions through either plasticity or genetic change (Nicotra et al. 2015, p. 1270; Beever et al. 2016, p. 132). The latter (evolution) occurs via the evolutionary processes of natural selection, gene flow, mutations, and genetic drift (Crandall et al. 2000, pp. 290–291; Zackay 2007, p. 1; Sgrò et al. 2011, p. 327).

We can best gauge representation by examining the breadth of genetic, phenotypic, and ecological diversity found within a species and its ability to disperse to and colonize new areas. In assessing the breadth of variation, it is important to consider both larger-scale variation (such as morphological, behavioral, or life history differences, which might exist across the range, and environmental or ecological variation across the range) and smaller-scale variation (which might include measures of interpopulation genetic diversity). In assessing the dispersal ability, it is important to evaluate the ability and likelihood of the species to track suitable habitat and climate over time. Lastly, to evaluate the evolutionary processes that contribute to and maintain adaptive capacity, it is important to assess: (1) natural levels and patterns of gene flow, (2) degree of ecological diversity occupied, and (3) effective population size. In our SSA Report, we assessed all three facets to the best of our ability based on available data.

Chapter 1: Biology, Life History, and Ecology

The biology and ecology of the gray wolf have been widely described in the scientific literature (e.g., Mech 1970, entire; Mech and Boitani 2003, entire), Service recovery plans (e.g., Northern Rocky Mountains Recovery Plan (Service 1987, entire); Recovery Plan for the Eastern Timber Wolf (Service 1992, entire)), and previous proposed and final rules (e.g., 68 FR 15804, April 1, 2003; 71 FR 15266, March 27, 2006; 74 FR 15123, April 2, 2009; 75 FR 46894, August 4, 2010; 76 FR 81666, December 28, 2011; 85 FR 69778, November 3, 2020). We also recognize the profound contributions of Tribal Nations and state agencies, which adds to our current understanding of the biology and ecology of the gray wolf. We include a summary of the biology and ecology of the gray wolf below.

Species Description

Gray wolves are the largest wild members of *Canidae*, or dog family, with adults ranging from 40 to 175 pounds (18 to 80 kilograms), depending on sex and geographic locale (Mech 1974, pp. 11–12; Boyd et al. 2023, p. 3). Gray wolves have a circumpolar range including North America, Europe, and Asia. In North America, gray wolves are primarily predators of medium and large mammals, such as: moose (*Alces alces*), elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*), bison (*Bison bison*), and beaver (*Castor canadensis*), and they are efficient at using available food resources (Newsome et al. 2016, pp. 260–261; Janeiro-Otero et al. 2020, p. 2). Gray wolves have long legs that are well adapted to running, allowing them to move fast and travel far in search of food, and large skulls and jaws that are well suited to catching and feeding on large mammals (Mech 1970, pp. 11–15). While mostly cursorial predators, gray wolves also use ambush behavior, especially for smaller prey such as beaver (Gable et al. 2021, p. 340). Gray wolves also have keen senses of smell, hearing, and vision, which they use to detect prey and one another (Mech 1970, pp. 15–16); they also use such sensory information to avoid detection by potential prey in ambush attempts (Gable et al. 2021, pp. 343–344). Pelt color varies in gray wolves more than in almost any other species, from white to grizzled gray to brown to coal black (Mech 1970, pp. 16–18; Schweizer et al. 2020, pp. 108–110).

Taxonomy and Historical Range

Taxonomic Overview of *Canis*

The gray wolf is a member of the canid family (Canidae), assigned to a genus (*Canis*) that includes the domestic dog (*C. familiaris*), coyote (*C. latrans*), red wolf (*C. rufus*), golden jackal (*C. aureus*), Ethiopian wolf (*C. simensis*), and African golden wolf (*C. lupaster*). Gray wolves share an evolutionary history with other mammalian carnivores (Order Carnivora), which are distinguished by their long, pointed canine teeth, sharp sheering fourth upper premolars and first lower molars (carnassial teeth), simple digestive system, sharp claws, and highly developed brains (Mech 1970, pp. 20–22). Divergence among the ancestral mammalian carnivores began 40 to 50 million years ago (Mech 1970, p. 20), and, at some point during the late Miocene Epoch (between 4.5 to 9 million years ago), the first species of the genus *Canis* arose; this species was the common ancestor of all modern wolves, coyotes, and domestic dogs (Nowak 2003, p. 241). Fossil and genetic evidence indicate different timelines for the divergence of the lineages that gave rise to the gray wolf and coyote; fossil evidence indicates they likely diverged between 1.8 and 2.5 million years ago (Nowak 2003, p. 241), while genetic evidence indicates this divergence occurred between 800,000 and 1.0 million years ago (vonHoldt et al. 2011, p. 1294; vonHoldt and Aardema 2020, p. 249; Vilaça et al. 2023, pp. 5, 8). Domestication of wolves led to all modern domestic dog breeds, which probably occurred between 15,000 and 40,000 years ago (Botigué et al. 2017, p. 2). However, the precise geographic and temporal origins of dogs remain uncertain (Frantz et al. 2016, p. 1231).

Although taxonomic relationships among *Canis* species found in North America have been studied extensively, there is a notable lack of consensus, even on issues such as the phylogenetic history of dogs, wolves, and coyotes (e.g., Chambers et al. 2012, entire; Cronin et al. 2015, entire and references therein; Freedman and Wayne 2017, entire; Fitak et al. 2018, pp. 380–381; National Academies of Sciences Engineering and Medicine 2019, pp. 68–69; Sacks et al. 2021, entire). Despite ongoing debate about canid taxonomy, there is wide recognition that gene flow among different lineages of canids has played a significant role in shaping the genus, both globally (Gopalakrishnan et al. 2018, entire; Pilot et al. 2019, entire; Krofel et al. 2022, pp. 157–159) and within North America (Hailer and Leonard 2008, entire; Koblmüller et al. 2009, pp. 2321–2323; vonHoldt and Aardema 2020, entire; Sacks et al. 2021, p. 4301; Wilson and Rutledge 2021, entire; Vilaça et al. 2023, entire). Such interspecific admixture may have, at times, conferred selective advantages, allowing for adaptation to environmental change or different habitats (Kays et al. 2010, entire; Pilot et al. 2019, p. 8).

Gray Wolf Evolutionary History and Intraspecific Variation

There is uncertainty regarding the evolutionary origins of the gray wolf. The most supported hypothesis, based on fossil records, is that the ancestor of the gray wolf originated in North America and colonized Eurasia, leading to evolution of what is recognized as the gray wolf (Nowak 2003, pp. 241–243; Wang et al. 2004, p. 46). Based on the fossil record, the oldest specimen recognized as *C. lupus* was found in Alaska and dated to around 1 million years ago (Tedford et al. 2009, pp. 148–150). The species subsequently colonized Eurasia and diversified (Nowak 2003, pp. 245, 247; reviewed in Loog et al. 2020, Appendix S1). As glacial cycles created land bridges between Asia and North America over the past 300,000 years, gray wolves colonized North America several different times (Nowak 2003, pp. 245–249), with the most recent colonization dating to around 15,000 years ago (Loog et al. 2020, pp. 1605–1606). Notably, when gray wolves colonized North America, there were already other canids present on the continent. Thus, all canids in North America fall into one of two primary phylogenetic lineages. The first is a "Eurasian" lineage, which colonized North America during the aforementioned interglacial cycles; this Eurasian lineage includes the gray wolf (Nowak 2003, pp. 241–250; Loog et al. 2020, entire). The second is an endemic "North American" lineage, which evolved solely within the North American continent (Wilson et al. 2000, pp. 2164–2165; Sacks et al. 2021, entire; Vilaça et al. 2023, entire). This North American lineage includes the coyote and potentially the red wolf. These two lineages (Eurasian and North American) have their own evolutionary histories and contain substantial phenotypic and genetic diversity (Wilson et al. 2000, entire; Nowak 2003, pp. 241–250; vonHoldt et al. 2011, entire; Chambers et al. 2012, entire; Sacks et al. 2021, entire; Khidas 2023, entire).

The gray wolf has a wide range across multiple continents and inhabits a diverse array of environmental conditions. As a result, the species displays considerable intraspecific variation that manifests itself phenotypically (e.g., physical, behavioral, ecological traits) and genotypically (i.e., genetic variation). Gray wolves show considerable variation in traits such as body size, cranial dimensions, and pelage. Genetic research confirms that gray wolves in North America are not panmictic (randomly breeding throughout the range with no differentiation), but instead display distinct genetic structure. These subdivisions are consistent with isolation by distance to some extent on a continental scale, but appear to be driven more strongly by climate and ecological factors, with the resulting groups sometimes referred to as "ecotypes" (Geffen et al. 2004, entire; Carmichael et al. 2007, entire; vonHoldt et al. 2011, p. 1298; Schweizer et al. 2016, entire; Hendricks et al. 2019, p. 31; Stronen et al. 2022, p. 188) or bioclimatic groups (González-Bernal et al. 2022, pp. 5–8). Factors such as habitat type and prey specialization have been shown to influence this genetic structuring, leading to measurable differentiation even between areas with no physical barriers to dispersal (Carmichael et al. 2001, entire; Pilot et al. 2006, entire; Musiani et al. 2007, entire). Several authors have hypothesized that such population structure arises because dispersing juveniles will seek out familiar habitat with a prey base similar to the area in which they were raised (Carmichael et al. 2001, entire; Carmichael et al. 2007, entire; Muñoz-Fuentes et al. 2009, pp. 1525–1526; Schweizer et al. 2016, p. 398; Hendricks et al. 2019, pp. 37–40). Ecological factors also have been shown to influence phenotypic factors such as cranial morphology (O'Keefe et al. 2013, entire; Khidas 2023, p. 570) and have been linked to putative functional genes that determine morphology, coat color, and metabolism (Schweizer et al. 2016, pp. 396–397).

These aspects of gray wolf biology and evolutionary history have long challenged attempts to delineate taxonomic relationships both within the species itself (i.e., subspecies) and between the gray wolf and other canid species. Although gray wolves display considerable phenotypic variation, this variation does not typically fit into neatly defined groupings. Boundaries between phenotypically and/or genetically distinct groups are porous, resulting in clinal variation rather than sharp discontinuities (Goldman 1944, pp. 389–390; Jolicoeur 1959, p. 297; Leonard et al. 2005, entire; Schweizer et al. 2016, pp. 395–396). Different characters (e.g., cranial morphology, body size, genes) may vary across different geographic scales, resulting in different groupings depending on which traits are used to define the grouping (Jolicoeur 1959, entire). Another complicating factor is that the gray wolf is not the only canid inhabiting the North American continent. When gray wolves colonized North America, there was already a diverse assortment of North American-evolved canids (Nowak 1979, entire; Nowak 2003, pp. 239–250; Tedford et al. 2009, pp. 104–149). Some of these canids were superficially similar to gray wolves (e.g., larger body size, pack social structure) and it became common to denote any large-bodied canid as a "wolf." However, we now understand that some of these larger-bodied canids were endemic to North America (Wilson et al. 2000, entire; Sacks et al. 2021, entire), or represent different gray wolf colonization events (Wilson and Rutledge 2021, entire; Vilaça et al. 2023, entire). Thus, it is difficult to sort out which historical and contemporary canids were derived from the Eurasian lineage versus the North American lineage. Also, historical and contemporary hybridization both within and between these lineages obscures patterns of divergence (vonHoldt et al. 2016a, entire; Gopalakrishnan et al. 2018, entire; Sinding et al. 2018, entire; Wilson and Rutledge 2021, entire). In summary, the gray wolf's complex evolutionary history, phenotypic and genotypic diversity, propensity to hybridize, and co-occurrence with other canids in North America challenges efforts to develop clear taxonomic designations.

History of Gray Wolf Subspecies Taxonomy

There is agreement among taxonomists that the gray wolf and coyote represent valid, distinct species in North America. While there are indications that coyotes display relatively little population structure across a wide range (vonHoldt et al. 2011, p. 1301; Koblmüller et al. 2012, entire), gray wolves in North America have consistently been divided and arranged into different taxonomic groupings. Early taxonomic work, based on phenotypic differences, led to the designation of numerous wolf subspecies across the continent (reviewed in Chambers et al. 2012, pp. 10–13). Goldman (1937, entire; 1944, pp. 411–475) attempted to reconcile early taxonomic designations and identified 24 distinct subspecies of gray wolf (Figure 1). These designations were based on a qualitative assessment of phenotypic characters, including cranial measurements. Nowak (1995, entire) later revised gray wolf taxonomy following quantitative, rather than qualitative, analysis of cranial morphology, resulting in consolidation of the number of subspecies (Figure 2) (Chambers et al. 2012, pp. 10–13). These revisions resulted in the designation of five gray wolf subspecies on the North American continent, four of which were believed to historically occur in the lower-48 United States. Of these, *Canis lupus baileyi*, the Mexican wolf, remains the most widely accepted as a distinct subspecies, based on both morphology and genetics (Nowak 1995, p. 384; vonHoldt et al. 2011, p. 1300; Fredrickson et al. 2015, entire; Fan et al. 2016, p. 169; National Academies of Science, Engineering, and Medicine 2019, pp. 35–44; though see Cronin et al. 2015, p. 34). Other subspecies identified by Nowak (1995, entire) in the United States included *C. lupus nubilus*, which historically ranged from Eastern Canada down through the Great Plains and up the West Coast, and *C. lupus occidentalis*, whose range stretched from interior Alaska south into the Rocky Mountains (Nowak 1995, p. 396; Chambers et al. 2012, pp. 34–41). Researchers hypothesized that these three subspecies represent three distinct migration events from Eurasia, with *C. lupus baileyi* being the oldest, followed by *C. lupus nubilus* and then *C. lupus occidentalis* (Chambers et al. 2012, p. 42).

The fourth of Nowak's (1995, pp. 387–390) subspecies in the lower-48 United States is the eastern wolf, *C. lupus lycaon*, which had a range covering southeastern Canada. Originally classified as a distinct species (*C. lycaon*) (Schreber (1775, as cited in Goldman 1937, pp. 37, 40), Goldman (1944, pp. 437–441) subsumed it into *C. lupus*, meaning that the subspecies *C. lupus lycaon* became the accepted taxonomy for wolves in the broader region stretching from the Western Great Lakes region into southeastern Canada and the Northeastern United States (Figure 1) (see Chambers et al. 2012, pp. 8, 11–12 for review). Nowak (1995, pp. 387–388, 395) continued to recognize *C. lupus lycaon* as a distinct subspecies, but dramatically adjusted its range based on an evaluation of morphological data, restricting the historical range of the subspecies to the Northeastern United States (east of Lake Michigan) and southeastern Canada (Figures 2 and 3). Nowak (1995, pp. 387–390) also reassigned wolves in the Western Great Lakes region (e.g., Michigan, Minnesota, and Wisconsin) to the subspecies *C. lupus nubilus,* as opposed to *C. lupus lycaon*, which was the designation proposed by Goldman (1944, pp. 437–441) (Figure 2).

Figure 14. Distribution of subspecies of *Canis lupus*

1. *Canis lupus tundrarum*
2. *C. l. pambasileus*
3. *C. l. alces*
4. *C. l. occidentalis*
5. *C. l. hudsonicus*
6. *C. l. arctos*
7. *C. l. orion*
8. *C. l. labradorius*
9. *C. l. beothucus*
10. *C. l. lycaon*
11. *C. l. nubilus*
12. *C. l. irremotus*
13. *C. l. columbianus*
14. *C. l. ligoni*
15. *C. l. fuscus*
16. *C. l. crassodon*
17. *C. l. youngi*
18. *C. l. mogollonensis*
19. *C. l. monstrabilis*
20. *C. l. baileyi*
21. *C. l. bernardi*
22. *C. l. mackenzii*
23. *C. l. manningi*

Figure 1. Historical range map the subspecies of C. lupus designated by Goldman (1944, p. 414)

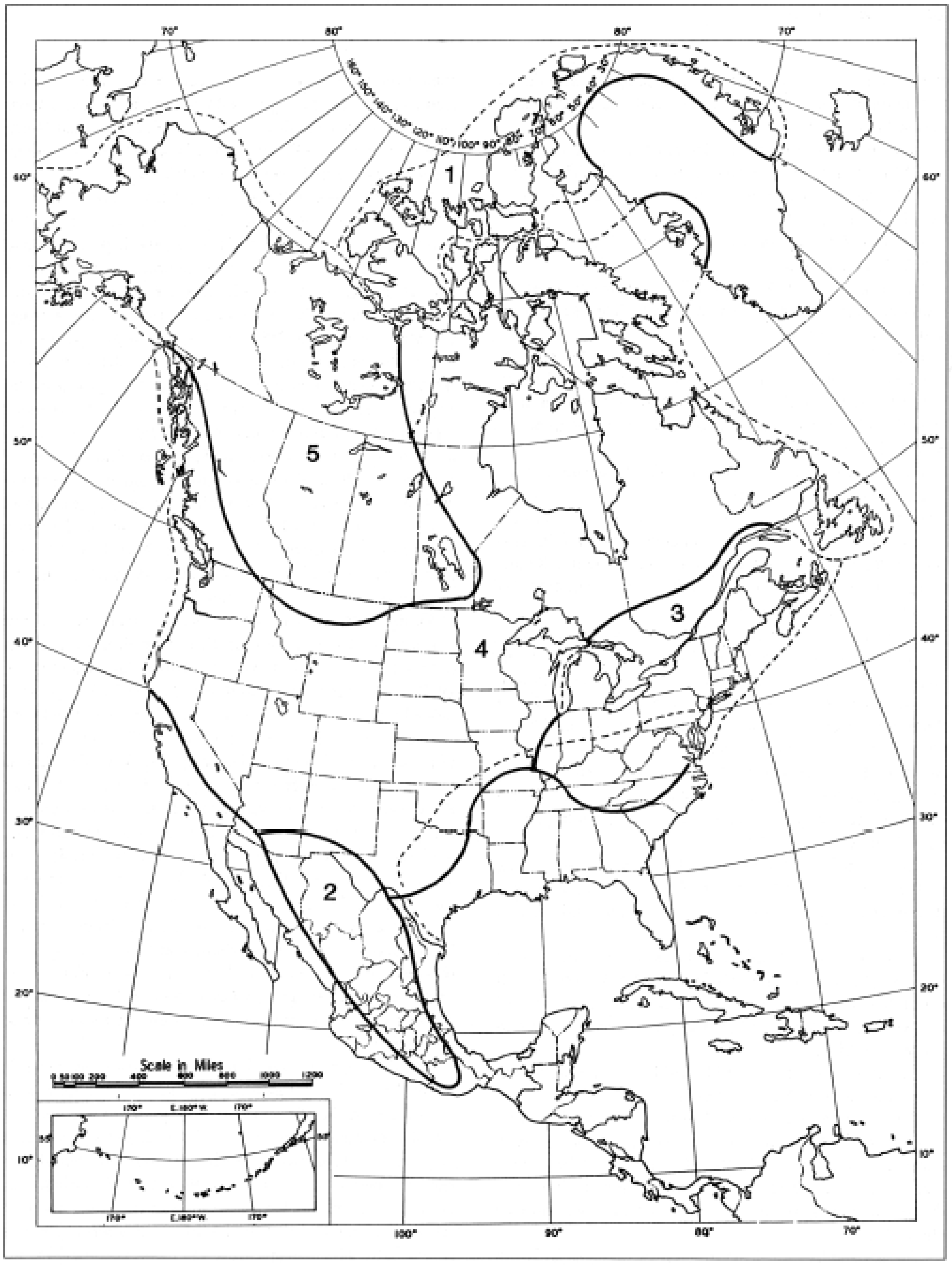

Figure 2. Historical range map of the subspecies of C. lupus designated by Nowak (1995, p. 395). The numbers correspond to the following subspecies: 1. C. lupus arctos, 2. C. lupus baileyi, 3. C. lupus lycaon, 4. C. lupus nubilus, 5. C. lupus occidentalis. The dashed line denotes the historical range of the red wolf (C. rufus), as identified by Nowak (1995).

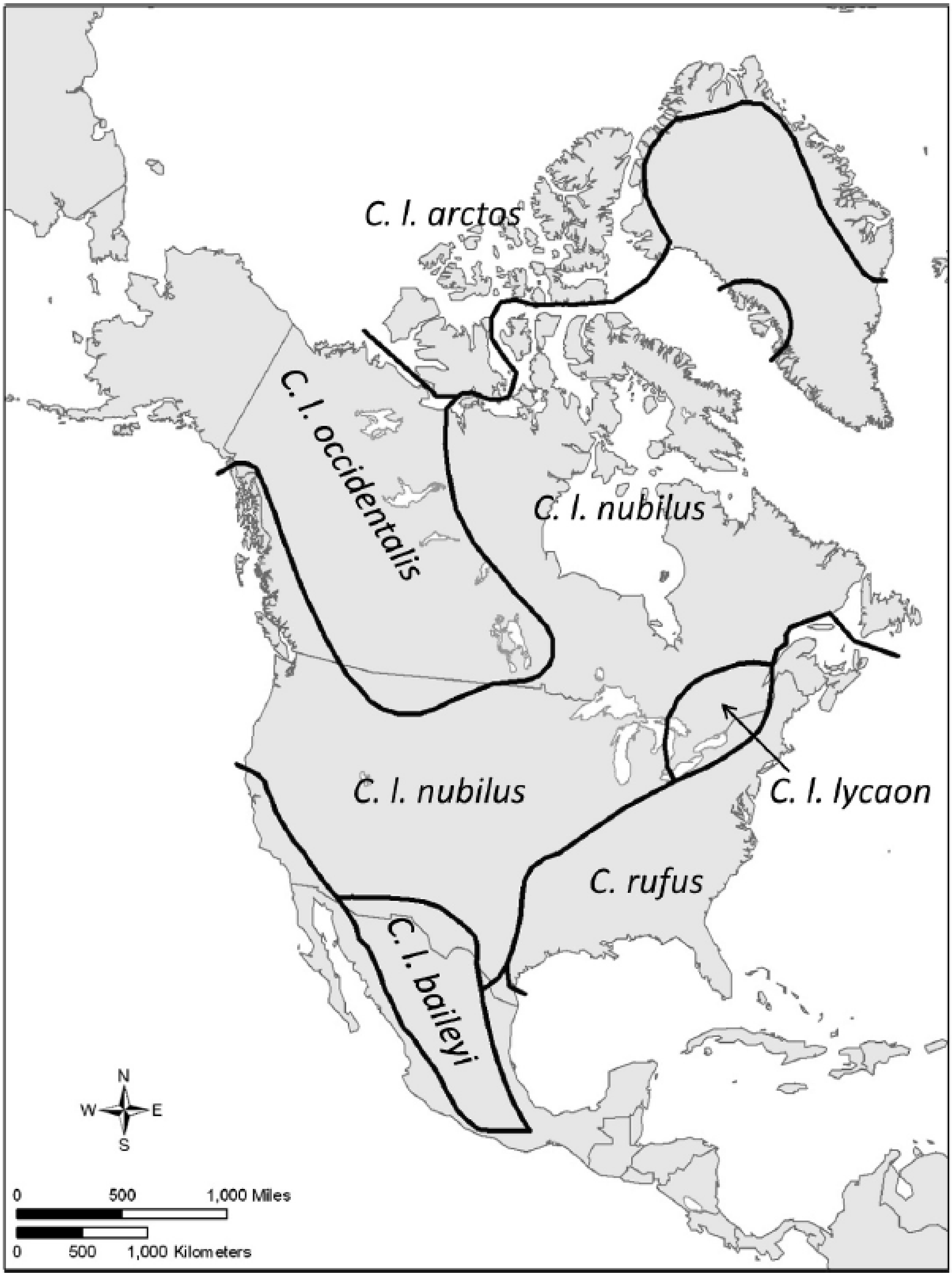

Figure 3. Historical range map of the five subspecies of C. lupus and C. rufus identified by Nowak (2002, entire).

The Red Wolf

Also relevant to this discussion is the taxonomic history of the red wolf. First described as a species in 1791, subsequent taxonomists continued to recognize the morphological distinctiveness of the red wolf compared to other North American canids (Goldman 1944, pp. 478–489; Nowak 2002, entire; Nowak 2003, pp. 250–256). However, the red wolf has also been the subject of considerable taxonomic debate (National Academies of Sciences Engineering and Medicine 2019, pp. 45–60). Although genetic introgression from coyotes has affected the red wolf, contemporary and historical red wolves are morphologically and genetically distinct from other North American canids (Nowak 1995, entire; Nowak 2002, entire; Nowak and Federoff 1998, entire; vonHoldt et al. 2011, p. 1297; Waples et al. 2018, entire; National Academies of Sciences Engineering and Medicine 2019, pp. 45–60). Furthermore, despite having the moniker "wolf" in its common name, the red wolf appears to be derived from the same endemic North American canid lineage as the coyote (Wilson et al. 2000, pp. 2160–2165; Sinding et al. 2018, pp. 4, 12; Sacks et al. 2021, entire; Vilaça et al. 2023, pp. 10–11).

The recognition of a third species of canid in North America, the red wolf, along with the coyote and gray wolf, has implications for our understanding of gray wolf taxonomy. First, researchers have noted that some canids previously recognized as members of *C. lupus* show greater phenotypic and genetic affinity towards the red wolf, specifically *C. lupus lycaon*. This has led some to posit that some canid populations currently recognized as gray wolves should be reclassified as red wolves, or even vice versa. Also, as with gray wolf subspecies, the interpretation of the historical range of the red wolf has changed over time. Originally thought to inhabit the Gulf Coast and lower Mississippi Valley (Goldman 1944, p. 479), the historical range of the red wolf has been reinterpreted to extend further north into the Ohio River Valley and mid-Atlantic region (Nowak 1995, p. 395), perhaps even as far north as Maine and southeastern Canada (Figure 3) (Nowak 2002, entire; Nowak 2003, p. 251).

Evolutionary Origins and Taxonomic Status of Contemporary Canids Inhabiting Eastern North America

There has long been recognition that several morphologically and genetically distinct groups of canids occupy the Eastern United States and southeastern Canada. The fact that wolf-like canids were eliminated from much of the Eastern United States hampers the interpretation of contemporary patterns of diversity as a means of understanding the origins and historical distribution of these groups. Also, the eastward expansion of the coyote (see Hody and Kays 2018, entire) resulted in hybridization and introgression that obscures historical relationships among eastern canids (Nowak 2003, pp. 248–256; vonHoldt et al. 2011, entire; vonHoldt et al. 2016a, b, entire; Sinding et al. 2018, entire; Vilaça et al. 2023, entire).

Based on phenotypic and genetic data, there is general recognition that there are three distinct groups of canids that currently occupy the broader region that stretches from the Western Great Lakes region into southeastern Canada: gray wolves, eastern wolves, and coyotes. Although these three entities have and continue to experience genetic introgression with each other, they have maintained their phenotypic and genetic distinctiveness (Figure 4) (Nowak 1995, pp. 387–

388, 395; Wilson et al. 2009, entire; Rutledge et al. 2010a, entire; Wheeldon et al. 2010, entire; Heppenheimer et al. 2018, entire). Gray wolves currently occupy the Western Great Lakes region and form a genetically contiguous population from Michigan, Minnesota, and Wisconsin into Central Ontario. The only extant population of the eastern wolf currently occurs in a portion of southeastern Ontario and Northern Quebec, Canada, centered around Algonquin Provincial Park, which is considered its stronghold (Figure 5) (Grewal et al. 2004, p. 630; Rutledge et al. 2010a, entire; Rutledge et al. 2010b, entire; Benson et al. 2012, entire; Heppenheimer et al. 2018, entire). The coyote is distributed throughout the entire Eastern United States and Eastern Canada.

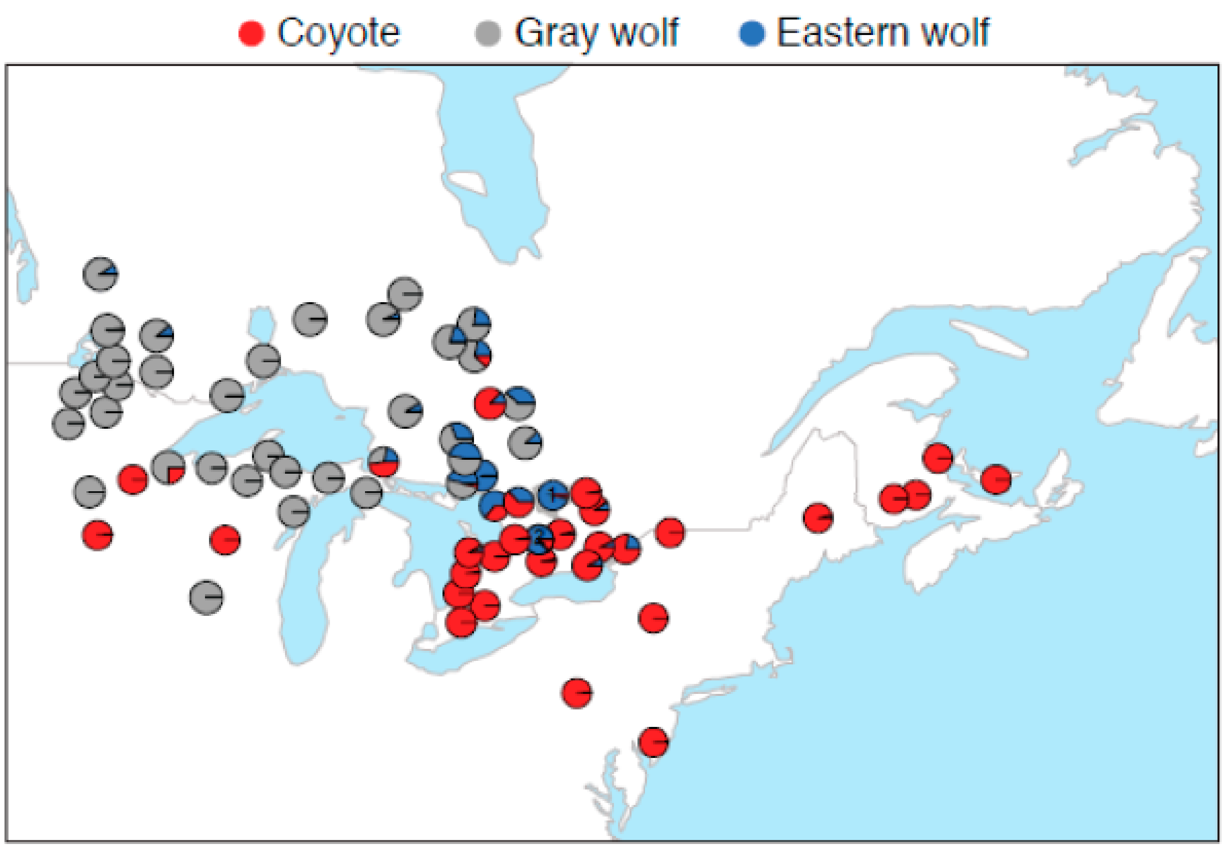

Figure 4. Distribution of gray wolves, eastern wolves, and coyotes in the Great Lakes region based on analysis of genome-wide markers. Each point represents a location where one or more canid samples were collected. The colors represent the average proportion of genetic ancestry assigned to the canids collected at those locations. From Heppenheimer et al. (2018, p. 8).

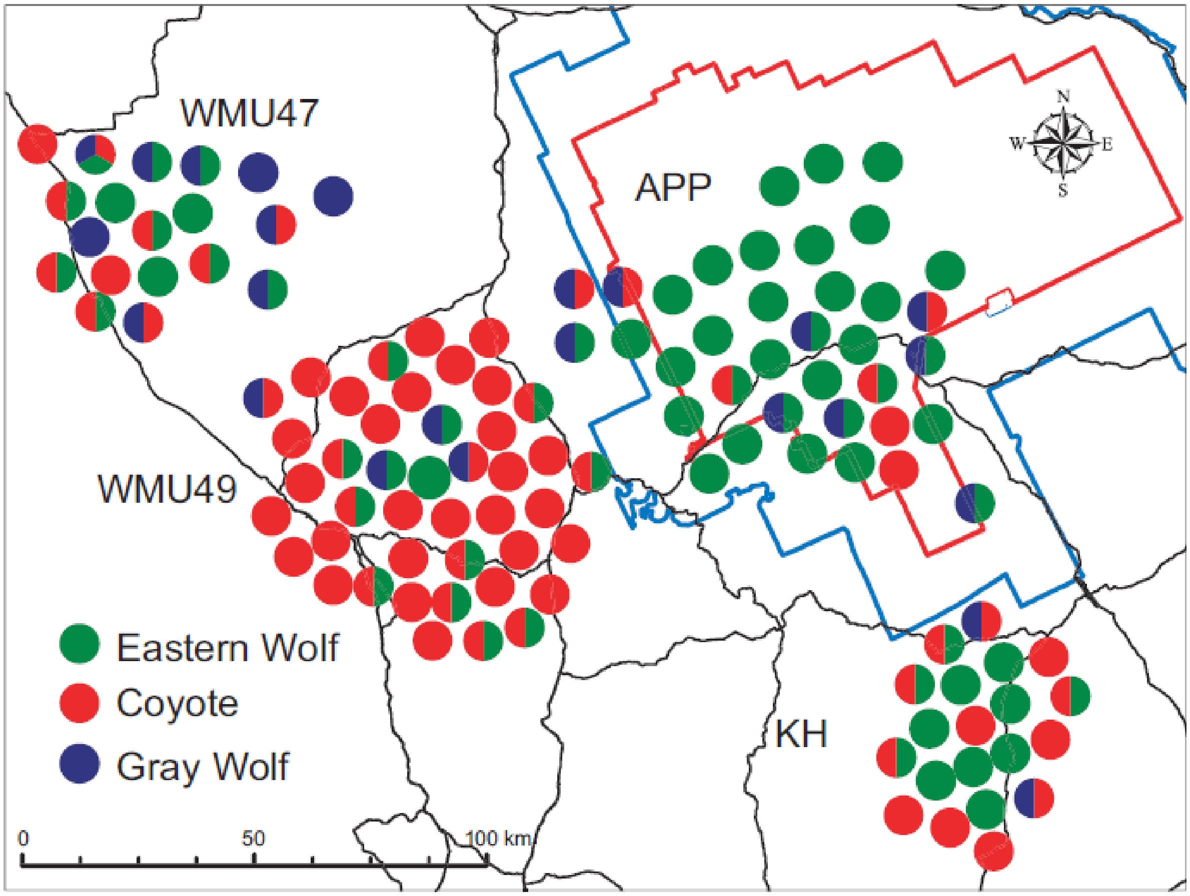

Figure 5. Distribution of canids around Algonquin Provincial Park (APP) in southeastern Ontario, Canada. Each point represents an individual canid that was sampled. The colors reflect three genetic groups (gray wolf, eastern wolf, and coyote) and each individual's ancestry assignment to those three groups. APP is denoted by the red boundary line. The blue line is the extent of a buffer around APP in which wolf harvest is banned. Other initials refer to management areas and/or sampling locations in southeastern Ontario, From Benson et al. (2012, p. 5945).

Hybridization has played, and continues to play, an important role among eastern canids (Leonard and Wayne 2008, entire; Fain et al. 2010, entire; Koblmüller et al. 2009, entire; Wheeldon and White 2009, entire; Mech 2010b, entire; Mech 2011, entire; vonHoldt et al. 2011, entire; Benson et al. 2012, entire; Rutledge et al. 2015, entire; vonHoldt et al. 2016a, entire; vonHoldt et al. 2016b, entire; Heppenheimer et al. 2018, entire; Sinding et al. 2018, entire; Vilaça et al. 2023, entire). Although this is an ever-evolving field of research, we can draw several general conclusions. Eastern wolves have admixed genomes composed of ancestry from the Eurasian and North American canid lineages. Research is mixed as to whether this admixed genome is the product of ancient introgression (Vilaça et al. 2023, entire) or reflects recent introgression between gray wolves and coyotes (vonHoldt et al. 2011, pp. 1297–1302; vonHoldt et al. 2016a, pp. 7–9; Sinding et al. 2018, pp. 3–14). Despite this legacy of hybridization, contemporary eastern wolves (i.e., wolves in southeastern Canada centered around Algonquin Provincial Park) continue to maintain their genetic distinctiveness and form a broad hybrid zone with gray wolves to the north and coyotes to the south (Figures 4 and 5) (Rutledge et al. 2010a, entire; Benson et al. 2012, entire; Heppenheimer et al. 2018, entire). In fact, coyotes in the

Northeastern United States possess the genomic signature of introgression from eastern wolves, explaining their larger size and phenotypic differences compared to western coyotes (Kays et al. 2010, entire; Monzón et al. 2014, pp. 187–194; vonHoldt et al. 2016b, entire).

Gray wolves and coyotes do not readily hybridize in the Western Great Lakes region, even when they are sympatric (overlapping in distribution) or when gray wolf numbers were drastically reduced (Wheeldon et al. 2010, entire; Mech 2011, p. 524) (see *Hybridization* in Chapter 3 below). However, these gray wolves bear the genomic signature of past introgression. Numerous studies have noted that these gray wolves derive most of their ancestry from the Eurasian lineage but have introgression from other populations, though studies differ on the source of this introgression. Some studies indicate this introgression originated from coyotes. For example, early studies of Western Great Lakes gray wolves found introgression of mitochondrial haplotypes observed in modern coyotes, indicating hybridization between the two species had occurred in the recent past (Lehman et al. 1991, entire; Koblmüller et al. 2009, pp. 2322–2323). Analyses of nuclear microsatellite data also revealed that Western Great Lakes gray wolves were intermediate between "non-hybridizing" gray wolf populations (i.e., those in Western and Northern Canada) and coyotes (Roy et al. 1996, entire) and some contemporary individuals showed signatures of recent interbreeding between the two species (Koblmüller et al. 2009, p. 2322). Recent studies using genomic-level analyses have further revealed that Western Great Lakes gray wolves, although predominantly gray wolf in ancestry, also possess admixture from coyotes (vonHoldt et al. 2016a, entire; Sinding et al. 2018, pp. 7, 12).

However, an alternative hypothesis is that the introgression observed in Western Great Lakes gray wolves originated from eastern wolves, not coyotes. Some studies have concluded that the eastern wolf is part of the same endemic North American lineage as the coyote and red wolf (Wilson et al. 2000, entire; Rutledge et al. 2012b, entire; Sacks et al. 2021, p. 4302). When analyzed under this model, Western Great Lakes gray wolves are shown to possess introgression from eastern wolves as opposed to coyotes (Wilson et al. 2000, p. 2159; Wheeldon and White 2009, entire; Rutledge et al. 2015, entire; Sinding et al. 2018, p. 4). Morphological studies also indicated such a scenario was plausible (Nowak 1995, pp. 387–390; Mech and Paul 2008, entire; Mech 2011, entire; Chambers et al. 2012, p. 14). Recently, Vilaça et al. (2023, entire) used whole genomic data and demographic modeling to test hypotheses regarding the origin of the eastern wolf and its relationship to other canids. They similarly found that eastern wolves were distinct from other canids in North America and that Western Great Lakes gray wolves were the product of introgression between eastern wolves and other gray wolves that occurred around 8,000 years ago. They also found that eastern wolves have evidence of ancient introgression from coyotes, which may explain how "coyote" mitochondrial haplotypes introgressed into Western Great Lakes gray wolves.

The complexity of canid evolution and the interpretation of conflicting genetic and morphological studies has challenged efforts to resolve taxonomy among these populations. There is consensus that the large, wolf-like canids inhabiting the Western Great Lakes region should be classified as gray wolves (*C. lupus*), even considering their, albeit low, levels of introgression from other canids (Chambers et al. 2012, p. 42). Disagreement remains as to whether these gray wolves should be recognized as a distinct subspecies of gray wolf (*C. lupus nubilus*) (Nowak 1995, pp. 381–388) or considered an ecotype (Koblmüller et al. 2009, p. 2323).

Some have even indicated that traditional taxonomic categorizations may be inappropriate for gray wolves and that those occupying the Western Great Lakes region should be viewed simply as a geographic population (Cronin and Mech 2009, p. 4992; Khidas 2023, entire).

There is also consensus that the eastern wolf is a distinct entity compared to other sympatric canid populations. However, given the differing information from studies of eastern wolf morphology and genetics, there is a lack of consensus regarding the origin of the eastern wolf and its taxonomic relationship to other canids. One hypothesis is that the eastern wolf is a product of contemporary hybridization (i.e., within the last 200 years) between gray wolves and coyotes (Lehman et al. 1991, p. 115; vonHoldt et al. 2016a, p. 8; Sinding et al. 2018, p. 12). Another is that the contemporary eastern wolf represents an ancient Eurasian-origin lineage that has experienced periodic introgression from other canids over the past 70,000 years (Vilaça et al. 2023, pp. 9–10). A third hypothesis is that eastern wolves are derived from the endemic North American canid lineage and are not gray wolves at all, but rather represent a distinct species (i.e., *C. lycaon*) (Wilson et al. 2000, entire; Kyle et al. 2006, entire; Chambers et al. 2012, p. 42; Rutledge et al. 2012b, entire; Rutledge et al. 2015, entire). Some have taken this further to propose that the eastern wolf and red wolf are conspecific (i.e., members of the same species) (Wilson et al. 2000, p. 2164; Kyle et al. 2008, entire; Sacks et al. 2021, p. 4302). Again, these different hypotheses have implications for the currently extant eastern wolf's taxonomic designation. The eastern wolf could be classified as either a population of gray wolves with no formal taxonomic rank, a subspecies of gray wolf (*C. lupus lycaon*) (Nowak 1995, pp. 381–388), or a distinct species (*C. lycaon*) (Kyle et al. 2006, entire; Fain et al. 2010, entire; Chambers et al. 2012, p. 42).

Interpreting Historical Range

The debate regarding the taxonomy and origins of these various canids also extends to corresponding uncertainties regarding their historical range. Prior to European settlement, the range of the gray wolf included most of North America except for the Southeastern United States (Young and Goldman 1944, pp. 9–10; Mech 1974, pp. 1–2; Hall 1981, pp. 928–934; Schmidt 1991, entire; Nowak 1995, p. 395; Nowak 2002, pp. 96–97). In a revision of gray wolf subspecies, Nowak (1995, p. 395) identified the historical range of the eastern wolf (*C. lupus lycaon*) to extend from southeastern Ontario and Quebec south to Appalachia and westward to the Lower Peninsula of Michigan (Figure 2). The historical range of *C. lupus nubilus* was interpreted to extend from Hudson Bay southward into the Central United States, then west to the Pacific Coast stretching as far north as Southeastern Alaska. Later, the historical range of the *C. lupus lycaon* was further adjusted to cover southeastern Ontario and Quebec, extending only into the western portion of what is now the Northeastern United States (Figure 3) (Nowak 2002, entire; Chambers et al. 2012, p. 9). In doing so, the historical range of *C. lupus nubilus* was extended eastward to include the Lower Peninsula of Michigan and the historical range of the red wolf was extended to include most of the Northeastern United States.

Historical canid specimens from the Southeastern United States align either morphologically or genetically with red wolves (Nowak 1995, entire; Nowak 2002, entire; Roy et al. 1996, p. 1419; Sacks et al. 2021, pp. 4299–4230), supporting the hypothesis that the southeastern portion of the North American continent was historically occupied by the red wolf (Wildlife Management

Institute 2016, p. 23). Due to the paucity of historical canid samples from the Eastern United States, however, genetic analyses to identify the historical range of the red wolf, eastern wolf, and gray wolf have been limited. The research that has been performed has been based primarily on mitochondrial DNA. Several studies of historical canid samples from the Eastern United States have found that those animals possess mitochondrial haplotypes that fall within the North American canid lineage (Wilson et al. 2003, entire; Brzeski et al. 2016, entire; Sacks et al. 2021, entire). This has led to the hypothesis that historical canids of the Northeastern United States were similar to, if not the same as, the contemporary eastern wolf and/or red wolf, as opposed to being gray wolves.

There has also been controversy over whether the extant wolves in the Western Great Lakes region are representative of the population that existed historically. Leonard and Wayne (2008, entire) concluded based on mitochondrial DNA that the historical genetic makeup is no longer reflected in contemporary populations, indicating the replacement of the historical population with gray wolves dispersing from Canada. However, Mech (2009, entire) and Wheeldon and White (2009, entire) drew the opposite conclusion, that the historical population was also admixed and that the extant gray wolves are similar genetically to the historical population. The findings of Vilaça et al. (2023, entire) also provide genomic support for the hypothesis that Western Great Lakes gray wolves were historically admixed.

Much less attention has been given to the taxonomic status and genetic ancestry of gray wolves that formerly inhabited the central portion of the United States. There is consensus that gray wolves historically occupied the Great Plains region. Goldman (1944, pp. 414, 441–445) classified wolves occupying the Great Plains from southern Saskatchewan and Manitoba to the northern panhandle of Texas as *C. lupus nubilus*. Gray wolves that occupied Central Texas and northeastern Mexico were designated as *C. lupus monstrabilis* (Goldman 1944, pp. 414, 466–468). Both were collapsed into the revised *C. lupus nubilus* recognized by Nowak (1995, p. 396), meaning that, based on morphological data, historical gray wolves occupying the Great Plains were similar to contemporary gray wolves in the Western Great Lakes region. No genetic analyses of historical gray wolf specimens from this region have yet been conducted.

Both Goldman (1944, pp. 414, 469–471) and Nowak (1995, pp. 395–396) considered West Texas to be part of the historical range of the Mexican wolf (*C. lupus baileyi*). It is likely that Texas was historically a convergence point for four distinct canids: two subspecies of gray wolf, *C. lupus nubilus* and *C. lupus baileyi* (Mexican wolf), the red wolf, and the coyote. Genetic analysis provides evidence of historical intermixing between the Mexican wolf, red wolf, and coyote (Hailer and Leonard 2008, entire). However, there is no evidence that contemporary canid populations in Texas have gray wolf ancestry or that any remnant gray wolf populations have persisted in the state (vonHoldt et al. 2022, pp. 5442, 5445).

Synthesis

In summary, canid taxonomy and evolutionary history in North America are complex and controversial. The science around gray wolf subspecies, unique evolutionary lineages, ecotypes, and admixture of formerly isolated populations continues to develop. With ongoing debates and continuing scientific efforts aimed at clarifying the taxonomic relationships among various canid groups, we have an imperfect understanding of their evolutionary history in North America. Furthermore, even with complete knowledge of those evolutionary histories, some uncertainty over taxonomic categorizations would remain given the application of different species concepts and the fact that evolution is a dynamic process in which evolutionary units often occur on a continuum rather than fitting into discrete categories. Nonetheless, the best available scientific information indicates that gray wolves are subdivided, to some degree, based on ecological and climatic factors.

Synthesizing findings from paleontological, morphological, ecological, and genetic research, wolf-like canids inhabited the Eastern United States at the time of European colonization. In the Southeastern United States, the best available science indicates these canids were red wolves, a distinct species derived from an endemic North American canid lineage, as opposed to some form of gray wolf. Currently, the Western Great Lakes region is occupied by canids that are phenotypically and genetically recognized as gray wolves, despite their legacy of introgression. A distinct canid, commonly referred to as the eastern wolf, still occurs in southeastern Canada. The science is inconclusive as to which of these canids historically occupied the Northeastern United States: this area could have conceivably been a convergence zone of multiple types of canids. The same can also be said for Texas. The Great Plains were historically occupied by some form of gray wolf, which morphologically aligned with those in the Western Great Lakes region, but it is unknown whether those animals were admixed as well. Importantly, it is implausible to assume that any purported boundaries between the ranges of species and/or subspecies were hard transition points between these entities. In other words, these various canids likely overlapped in distribution near the edges of their ranges, perhaps even forming hybrid zones. The key for this SSA Report is that we cannot confidently eliminate the possibility that gray wolves historically occupied much of the Eastern United States, with the exception of the Southeastern United States (i.e., where the red wolf historically occurred).

Given the uncertainty in canid taxonomy and historical range, we will use certain common names to refer to specific populations. When discussing the population that occupies the Western Great Lakes region, we will refer to them as gray wolves. We will also use the term gray wolf when referencing any populations that are unambiguously classified as *Canis lupus*, such as populations in Western North America, Northern Canada, and Eurasia. Although the eastern wolf is considered a distinct entity, its taxonomic designation is uncertain. Also, it co-occurs and interbreeds with gray wolves in southeastern Canada. Thus, when we use the term "eastern wolf," we are referring specifically to the population of canids in and around Algonquin Provincial Park in Canada. When we are referencing either gray wolves, eastern wolves, or potentially their hybrids, such as when discussing potential recolonization of the Northeastern United States, we will use the generic term "wolf." Similarly, when discussing genetic introgression, particularly within coyotes, we may use the generic term "wolf" given the uncertainty as to the origin of that ancestry. Also, we will use the generic term "wolf" when referencing biological characteristics of wolf-like animals in general (e.g., gray wolf, eastern wolf, red wolf, etc.).

Analysis Area

The purpose of this SSA Report is to provide an assessment of the gray wolf's status in the Eastern United States (see *Purpose* above). However, because the best available science indicates that gray wolves did not historically occupy the Southeastern United States, which was instead occupied by red wolves (see *Taxonomy and Historical Range* above), we do not include the Southeastern United States in our analysis area. We relied on the historical range map for the red wolf (Wildlife Management Institute 2016, p. 23) to determine which areas to exclude from our analysis area for the gray wolf in the Eastern United States. We assumed that gray wolves and red wolves did not co-occur within the core of red wolf's historical range (see *Interpreting Historical Range*). Therefore, states entirely within red wolf historical range (Alabama, Arkansas, Delaware, Florida, Georgia, Kentucky, Louisiana, Mississippi, Maryland, North Carolina, South Carolina, Tennessee, West Virginia, and Virginia) are not included in our analysis area. If only a portion of a state is included in the red wolf historical range (Illinois, Indiana, Kansas, Missouri, New Jersey, New York, Ohio, Oklahoma, Pennsylvania, and Texas), we include the entire state in the analysis area for the gray wolf in the Eastern United States because it is likely that gray wolves and red wolves co-occurred in these areas (see *Interpreting Historical Range*). Due to the uncertainty regarding the taxonomic assignment of the canids that historically occupied the Northeastern United States and the likelihood that Texas was historically a convergence point for several different canids, including different subspecies of gray wolf (see *Interpreting Historical Range*), we include these states in our analysis area for this SSA Report. Based on this approach, the geographic scope of our analysis includes: Connecticut, Illinois, Indiana, Iowa, Kansas, Maine, Massachusetts, Michigan, Minnesota, Missouri, Nebraska, New Hampshire, New Jersey, New York, North Dakota, Ohio, Oklahoma, Pennsylvania, Rhode Island, South Dakota, Texas, Vermont, and Wisconsin (Figure 6). These 23 states encompass the potential historical range for the gray wolf in the Eastern United States, including areas of potential overlap with other canid taxa (see *Taxonomy and Historical Range* above). The Mexican wolf, a subspecies of gray wolf, and the red wolf, a separate species of canid, are each separately listed as endangered under the Act and are not the subject of this SSA Report.

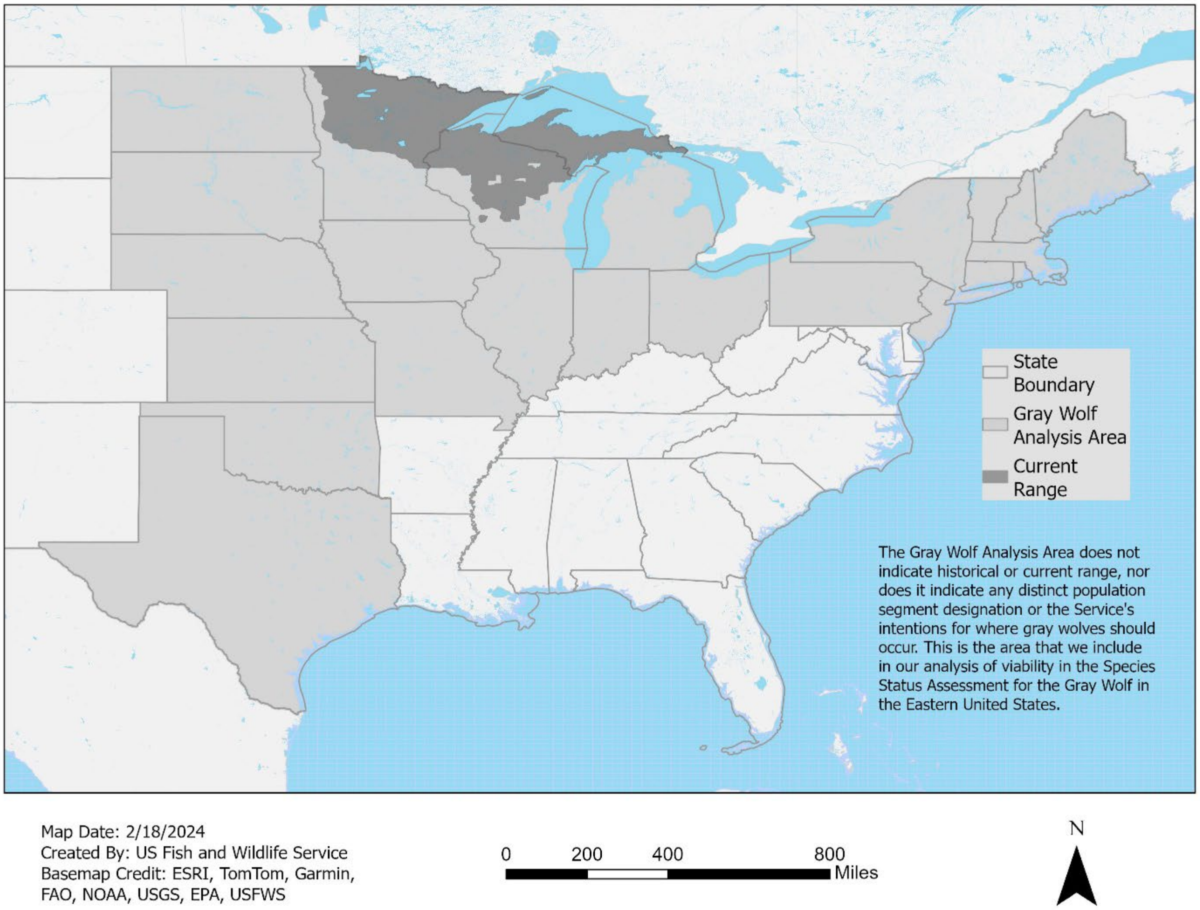

Figure 6. Analysis area for SSA Report for the gray wolf in the Eastern United States. Analysis area includes 23 states (gray). Note that the gray shading of this analysis area on this map does not indicate historical or current range, nor does it indicate a Distinct Population Segment (DPS) or the Service's intentions for where gray wolves should occur; rather, this map only illustrates the states we are considering in our SSA Report. The dark gray polygon in the Western Great Lakes area indicates gray wolf current range as of year-end 2023. The gaps in wolf distribution in this map include areas of large lakes, urban areas, or areas of intense agriculture where wolves are not known to exist.

Species Life History

Gray wolves are highly territorial, social animals and group hunters, normally living in packs of 7 or fewer but sometimes depending on prey species and availability can attain pack sizes of 20 or more individuals (Mech 1970, pp. 38–43; Erb and DonCarlos 2009, p. 59; Wydeven et al. 2009a, p. 97; Mech and Boitani 2003, p. 8; Stahler et al. 2020, p. 46; MI DNR 2022a, p. 12; WI DNR 2023a, p.16). Though gray wolf pack composition can vary, packs are typically family groups consisting of a breeding pair, their pups from the current year, offspring from previous years that have not yet dispersed, and, occasionally, an unrelated individual (Mech 1970, p. 40; Mech and Boitani 2003, pp. 1–2; Stahler et al. 2020, p. 43). Normally, only the top-ranking male and female in each gray wolf pack breed and produce pups, although sometimes unrelated or maturing wolves within a pack will also breed with unrelated members of the pack or through liaisons with members of other packs (Mech and Nelson 1989, entire; Mech and Boitani 2003, pp. 2–3).

Generation time for gray wolves—the average time between two consecutive generations—is estimated to be 4.2 to 4.7 years (vonHoldt et al. 2010, p. 4422; Mech et al. 2016, pp. 9–10; Mech and Barber-Meyer 2017, entire). Gray wolves of both sexes typically reach sexual maturity at 2 or 3 years of age, but, on rare occasions, can breed as early as 1 year of age (Fuller et al. 2003, p. 175; Mech et al. 2016, pp. 1–2). Once paired with a mate, gray wolves may produce young annually until they are over 10 years old (Fuller et al. 2003, p. 175). Litters are born from early April into May and can range from 1 to 11 pups, but generally include 5 to 6 pups (Mech 1970, pp. 118–119; Fuller et al. 2003, p. 164). Normally a gray wolf pack has a single litter annually, but two litters from different females in a single pack have been reported and, in one instance, three litters in a single pack were documented (Fuller et al. 2003, pp. 175–176; Stahler et al. 2020, p. 49; California Department of Fish and Wildlife (CDFW) 2021, p. 1). Offspring usually remain with their parents for 10 to 54 months before dispersing (Mech and Boitani 2003, pp. 11–12; Jimenez et al. 2017, p. 585).

Gray wolves rarely disperse before 10 months of age, and most commonly disperse between 1 and 3 years of age (Gese and Mech 1991, pp. 2947–2948; Treves et al. 2009, p. 193; Jimenez et al. 2017, p. 589). When pups less than 1 year of age disperse, they generally do so in late winter as they approach their first birthday. Generally, by the age of 3 years, most gray wolves will have dispersed from their natal pack to locate social openings in existing packs or to find a mate and form a new pack (Mech and Boitani 2003, pp. 11–17; Jimenez et al. 2017, p. 590). Dispersers may become nomadic and cover large areas as lone animals, or they may establish their own territorial pack upon locating unoccupied habitats and members of the opposite sex (Mech and Boitani 2003, pp. 11–17). Dispersal distances in North America typically range from 40 to 96 miles (mi) (65 to 154 kilometers (km)) (Boyd and Pletscher 1999, p. 1102; Jimenez et al. 2017, p. 585), although dispersal distances of several hundred miles are occasionally reported (Wydeven et al. 1998, p. 777; Boyd and Pletscher 1999, pp. 1102–1103; Mech and Boitani 2003, pp. 14–15; Thiel et al. 2009, p. 112; Oregon Department of Fish and Wildlife (ODFW) 2011, pp. 5–6; ODFW 2016, p. 10; Jimenez et al. 2017, p. 585; Washington Department of Fish and Wildlife et al. 2018, p. 10; CDFW 2021, p. 2). Gray wolves have also been documented to travel great distances – one wolf that was collared in Michigan in 2021 traveled at least 4,200 miles (6,760 km) to Manitoba in 18 months (Roell 2025a, in litt.). The innate ability of gray wolves to disperse long distances (Smith et al. 2020, p. 88) allows populations to quickly expand and recolonize vacant suitable habitats, but dispersers are subject to varied levels of human-caused mortality (e.g., Mech 1995, entire; Boyd and Pletscher 1999, entire; Treves et al. 2009, entire; Mech 2017, entire; Hendricks et al. 2019, entire) (see *Human-Caused Mortality* in Chapter 3 below for more detail). The extent of intervening unoccupied habitat between the source population and a newly colonized area can also affect the rate of recolonization, as mate-finding Allee effects[4] (i.e., reduced probability of finding a mate at low densities) are stronger at greater

[4] Allee effects are generally described "as a positive relationship between any component of individual fitness and either numbers or densities of conspecifics" (Stephens et al. 1999, p. 186). Others describe demographic and component Allee effects as those that may be experienced by small populations in the form of reduced population growth, elevated extinction risk, and potential bias in estimation of population parameters (Stenglein and Van

distances from source populations (Hurford et al. 2006, pp. 249–250; Stenglein and Van Deelen 2016, entire).

Gray wolf packs typically occupy and defend a territory of 13 to more than 1,016 square miles (mi^2; 33 to more than 2,600 square kilometers (km^2)), with territories tending to be smaller at lower latitudes (Fuller et al. 2003, pp. 172–175; Mech and Boitani 2003, p. 22; (Minnesota Department of Natural Resources (MN DNR) 2020, p. 6; Michigan Department of Natural Resources (MI DNR) 2022a, p. 12; WI DNR 2023c, p. 4). The large variability in territory size is likely due to the costs and benefits of differences in gray wolf pack size; differences in prey size, distribution, and availability; seasonal response to changes in prey abundance and distribution; and variation in prey vulnerability (e.g., seasonal age structure in ungulates) (Mech and Boitani 2003, pp. 20–27). Variability in estimated territory sizes is also likely related to improvements in technology over time (e.g., GPS collars vs. VHF collars or no collars) and calculation methodology (e.g., MN DNR 2022, p. 66; Erb et al. 2018, entire; Boyd et al. 2023, pp. 28–31).

In gray wolf populations, pack social structure is very adaptable. In many instances, breeding members can be quickly replaced from either within or outside the pack, and pups can be reared by another pack member should their parents die (Packard 2003, pp. 58–60; Brainerd et al. 2008, entire; Borg et al. 2015, pp. 184–185; Stahler et al. 2020, p. 49). This pack social structure, and the resulting gray wolf breeding strategies, leads to high potential fecundity and the ability for packs to act as "dispersal pumps" (see discussion of dispersal above) (Mech 1970, pp. 41–42; Fuller et al. 2003, p. 181; Mech and Boitani 2003, pp. 2–6, 11; Paquet and Carbyn 2003, pp. 485–486). Consequently, gray wolf populations can rapidly overcome severe disruptions, such as intensive human-caused mortality or disease. The likelihood a pack will maintain its territory declines if both breeders are killed; however, if one member of the breeding pair is killed, the pack may hold its territory until a new, unrelated individual arrives to replace the lost breeder (Schultz and Wilson 2002, entire; Mech and Boitani 2003, p. 28; Brainerd et al. 2008, p. 96). If both members of the breeding pair are killed, the remaining members of the pack may die, disperse, or remain in the territory until an unrelated dispersing individual arrives and mates with one of the remaining pack members (Mech and Boitani 2003, pp. 28–29; Brainerd et al. 2008, p. 96). The death of one or both breeders in a pack may increase breeder turnover and negatively affect pack persistence because, in most instances, only the dominant male and female in a pack breed (Cassidy et al. 2023, pp. 3–4). In Alaska, although packs remained intact in 67 percent of cases when one or both breeders were lost, breeder loss preceded pack dissolution 77 percent of the time (Borg et al. 2015, pp. 183–185). Factors affecting the degree of pack destabilization and any subsequent demographic effects included the cause of breeder loss, whether it was male or female breeder loss, the size of the pack in which the loss occurred, and season (Borg et al. 2015, pp. 183–185).

Gray wolf populations have been shown to increase rapidly if the source of mortality is reduced after significant declines (e.g., Fuller et al. 2003, p. 172; Service et al. 2012, entire). However, pack and population response to mortality is also influenced by many factors including habitat quality, prey abundance, gray wolf density, pack size, reproductive rates, and levels of isolation

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Deelen 2016, p. 2). Demographic or component Allee effects are described as density dependent whereby population growth or fitness change as population densities change (Kramer et al. 2018, p. 7).

(e.g., Peterson et al. 1998, entire; Sastre et al. 2011, entire; Almberg et al. 2012, entire; Borg et al. 2015, pp. 183–185; Brandell et al. 2020, pp. 129–132; Cassidy et al. 2023, entire; and see *Effects of Human-Caused Mortality* and *Disease and Parasites in Wolves*). In gray wolf populations, the density of gray wolves on the landscape can impact specific vital rates such as adult survival, natality rates[5] and recruitment, and dispersal. These vital rates can directly influence population growth and the ability for a population to recolonize vacant habitats or respond to population declines. In general, when suitable habitat is available (see *Suitable Habitat*), these vital rates are positively influenced by low gray wolf densities, which ultimately results in relatively rapid population growth and expansion. As gray wolf abundance and distribution increases and they begin to occupy most of the available suitable habitat in an area, the population growth rate declines. Examples of this density dependent relationship with population growth can be seen in the Northern Rocky Mountains (NRM) and the Western Great Lakes gray wolf populations (Service et al. 2016, Figure 7a; Service 2020, pp. 15–24). High gray wolf densities have negative effects on adult survival (Murray et al. 2010, entire; Gude et al. 2012, pp. 112–115; Cubaynes et al. 2014, pp. 5–11; O'Neil et al. 2017, pp. 9524–9528); natality rates and recruitment (Gude et al. 2012, pp. 112–115; Stahler et al. 2013, pp. 222, 232; Schmidt et al. 2017, pp. 18, 25); and dispersal distance, rate of dispersal, and age of dispersal (Jimenez et al. 2017, pp. 5–12; Sells et al. 2022a, pp. 7–12). Conversely, when gray wolf densities decline and suitable habitat remains available, any or all of the above vital rates may be positively affected (Stahler et al. 2013, pp. 226–231; Cubaynes et al. 2014, pp. 5–11; Jimenez et al. 2017, pp. 5–12; Schmidt et al. 2017, p. 25; Smith et al. 2020, pp. 77–92), thus, providing opportunity for increased population growth.

Suitable Habitat

Gray wolves are habitat generalists (Fuller et al. 2003, p. 163; MacNulty et al. 2020, p. 31; Boyd et al. 2023, pp. 14–16). They once occupied or transited most of the lower-48 United States, except the Southeast (Nowak 2002, pp. 103–121; Nowak 2009, pp. 242–244; Hohenlohe et al. 2017, pp. 1–2). Gray wolves can successfully occupy a wide range of habitats, provided adequate prey exists. However, there are areas where sufficient prey exists, but human-caused mortality prevents gray wolves from recolonizing and persisting (Mech 2017, p. 315).

To identify areas of suitable gray wolf habitat in the lower-48 United States, researchers have used data-driven and expert-elicited models to relate the distribution of gray wolves to characteristics of the landscape. These models have shown the presence of gray wolves is positively correlated with prey density and natural and forest cover; and is negatively correlated with high road density, high human density, presence of agricultural land or ranching activities, and other human disturbances on the landscape, such as land conversion and percent impervious surface (Mech 1995, entire; Mladenoff et al. 1995, pp. 289–292; Mladenoff et al. 1999, pp. 41–43; Carroll et al. 2003, entire; Carroll et al. 2006, entire; Oakleaf et al. 2006, pp. 560–561; Mladenoff et al. 2009, pp. 128–132; Mech 2017, pp. 312–315; Hanley et al. 2018a, pp. 8–11; van den Bosch et al. 2022, entire; van den Bosch et al. 2024, entire). At finer spatial scales (i.e., within their home range or territory), gray wolves appear to select simple topography where ungulate prey may be more susceptible to predation (Peterson et al. 2021, pp. 9–19; Sells et al.

[5] A natality rate is the number of pups produced.

2021, pp. 5–8; Sells et al. 2022b, p. 4). When selecting den sites, gray wolves select for areas close to water and for soils with higher-than-average sand content (Stricker et al. 2019, p. 91; Boyd et al. 2023, p. 13). Gray wolves in the Western Great Lakes region are known to locate their den sites in areas of higher elevation and lowland shrub cover (Unger et al. 2009, p. 184). Although the territory of individual packs can be relatively small, packs are not likely to establish territories in areas of small, isolated patches of suitable habitat.

To a large extent, road density has been adopted as the best predictor of habitat suitability in the Western Great Lakes region due to the connection between roads and human-caused gray wolf mortality. Several studies demonstrated that gray wolves generally did not maintain breeding packs in areas with a road density greater than about 0.9 to 1.1 linear mi per mi^2 (0.6 to 0.7 km per km^2) (Thiel 1985, pp. 404–406; Jensen et al. 1986, pp. 364–366; Mech et al. 1988, pp. 85–87; Fuller et al. 1992, pp. 48–51). Colonizing gray wolves in Wisconsin preferred areas where road densities were less than 0.7 mi per mi^2 (0.45 km per km^2) (Mladenoff et al. 1995, p. 289). Later work showed that, during early recolonization, gray wolves selected some of the lowest road density areas, but, as the population grew and expanded, gray wolves tolerated areas with higher road densities (Mladenoff et al. 2009, pp. 129–136). Recently, Van den Bosch et al. (2024) provided further evidence that as populations have continued to expand in the 2010s, wolves have begun to use areas of higher road density, specifically where road densities are 3.73 mi per mi^2 (1.44 km per km^2).

Road density is a useful parameter because it is easily measured and mapped, and it correlates directly and indirectly with various forms of other human-caused gray wolf mortality. An area with high road density generally has a greater human density, more vehicular traffic, greater access by hunters and trappers, more farms and residences, and more domestic animals. As a result, there is a greater likelihood that gray wolves in such an area will encounter humans, domestic animals, and various human activities. These encounters may result in gray wolves being hit by motor vehicles, being subjected to government control actions after becoming involved in depredations on domestic animals (i.e., killing or injuring domestic animals), being illegally killed, being trapped or shot accidentally, or contracting diseases from domestic dogs (Mech et al. 1988, pp. 86–87; Mech and Goyal 1993, p. 332; Mladenoff et al. 1995, pp. 282, 291).

Aside from prey density, prey susceptibility to predation, and characteristics associated with den sites, the environmental variables correlated with gray wolf presence are proxies for the likelihood of gray wolf-human conflict and the ability of gray wolves to escape human-caused mortality. Therefore, predictions of suitable habitat generally depict areas with sufficient prey where human-caused mortality is likely to be relatively low due to high amounts of escape cover, limited human access, or relatively low human density. Thus, in this SSA Report, we consider suitable habitat to be areas containing adequate wild ungulate populations (e.g., elk and deer) and a low risk of conflict with humans (e.g., low road density, low human density, adequate natural cover without agricultural land or domestic animal ranching) (see Mech 2017, pp. 312–315).

Chapter 2: Needed Resources and Demographic Factors that Support Viability of the Gray Wolf in the Eastern United States

As described in greater detail under *Analytical Framework* above, a species' resiliency, redundancy, and representation together contribute to its viability. In this chapter, we characterize the factors the gray wolf requires to support its resiliency, redundancy, and representation in the Eastern United States. First, we describe the resource needs of gray wolves. Second, we describe the demographic factors wolf packs and populations require to withstand stochastic variation. Both these resource and demographic needs support the species' resiliency. Third, we discuss elements that contribute to the representation and redundancy that gray wolves in the Eastern United States require to withstand catastrophic events and adapt to future environmental change. Finally, we discuss the previously established recovery criteria for the gray wolf in the Eastern United States, and provide a summary of past population viability analyses (PVA) on gray wolves; both the recovery criteria and these analyses further inform the factors the gray wolf in the Eastern United States may need to withstand stochastic and catastrophic events and adapt to future change.

Resiliency

Resource Needs

Gray wolves in the Eastern United States need suitable habitat, including sufficient quantity of prey to complete their life cycle. We consider suitable habitat for gray wolves to be areas containing adequate wild ungulate populations (e.g., elk and deer) and a low risk of conflict with humans (e.g., low road density, low human density, adequate natural cover without agricultural land), which generally allows for increased pack persistence (see Mech 2017, pp. 312–315); see *Suitable Habitat* and *Species Description* in Chapter 1 above for more detail on suitable habitat and prey resources.

Demographic Needs

The combination of reproduction, mortality, immigration, and emigration determines the distribution, size, and demographic health of gray wolf populations at any given time. Due to their high reproductive capacity and their ability to disperse long distances, gray wolf populations are remarkably resilient as long as food supply (a function of both prey density and prey vulnerability) is adequate and human-caused mortality is not too high (Fuller et al. 2003, pp. 170–171, 181, 187, 189; Adams et al. 2008, pp. 18–22; Creel and Rotella 2010, pp. 5–6; Gude et al. 2012, pp. 112–113). There is a long history of debate whether gray wolf populations are regulated by extrinsic or intrinsic factors (Mech 2024, pp. 2-3; Smith and Cassidy 2024, pp. 1-5). Where human-caused mortality is low or nonexistent, gray wolf densities may be regulated by the distribution and abundance of prey on the landscape (i.e., extrinsic factors) (Fuller et al. 2003, p. 189; McRoberts and Mech 2014, p. 966; Mech and Barber-Meyer 2015, p. 501; Mech 2024, entire). However, there is some evidence to indicate that densities of gray wolves may be regulated by density-dependent, intrinsic mechanisms when ungulate densities are high and human-caused mortality is low (Van Deelen 2009, pp. 146–149; Cariappa et al. 2011, p. 729;

Cubaynes et al. 2014, pp. 1351–1354; Stenglein et al. 2015a, p. 374; O'Neil et al. 2017, p. 9525; Stenglein et al. 2018, pp. 11–12; Smith et al. 2020, pp. 90-92). More recently, it has been suggested that wolf populations could be regulated by a combination of both extrinsic and intrinsic factors rather than just one or the other (Smith and Cassidy 2024, pp. 5-6).

Wolf populations are organized into wolf packs (Mech and Boitani 2003, p. 1). Impacts to packs or their social organization can scale-up to impact populations through at least three important natural regulating mechanisms: (1) territoriality and intraspecific strife, (2) the number of breeding females within packs, and (3) interaction between intrinsic (e.g., gray wolf density) and extrinsic (e.g., nutritional) factors (Packard and Mech 1980, entire). In general, gray wolf populations need a sufficient number of packs to support reproduction and connectivity. Impacts to connectivity between packs can scale-up to affect overall genetic diversity, which can affect viability.

Territoriality and Intraspecific Strife

Territoriality is a natural population limiting factor in many species, including gray wolves. Territoriality in gray wolves may have evolved to protect pups from infanticide by competing packs and, secondarily, to secure food (Smith et al. 2015, p. 1181). In wolf populations, each pack occupies and secures a discrete area with access to a finite amount of food resources, which influences population size (Packard and Mech 1980, pp. 146–147). Additionally, territoriality can reduce gray wolf numbers through mortality of individuals when packs defend their territories (Cassidy et al. 2020, p. 66). The loss of adult gray wolf members may reduce the competitive strength of the pack and failure to defend against intruding gray wolves may result in loss of resources, territory, and the lives of pack members (Cassidy et al. 2015, pp. 1352, 1354–1358; Cassidy et al. 2017, p. 70; Cassidy et al. 2020, entire). In areas where territories have saturated the available habitat, it is nearly impossible for new breeding units to become established without major disturbances to existing territories (Packard and Mech 1980, p. 141). In low-density populations or in areas where gray wolves are recolonizing, new breeding pairs are more easily able to establish territories (Packard and Mech 1980, pp. 141–142).

Number of Breeding Females within Wolf Packs

Gray wolf populations are also regulated by the number of breeders within each pack. Within a pack there is a dominance hierarchy and often only one female produces young each year, limiting population growth (Packard and Mech 1980, p. 142). However, in areas of higher gray wolf densities and abundant prey (Fuller et al. 2003, pp.175–176), multiple breeding females within a pack are more common, leading to a higher potential reproductive rate than packs with a single breeding female (see *Species Life History*).

Interaction between Intrinsic and Extrinsic Regulating Factors

In the absence of high-levels of human-caused mortality (the primary population regulating mechanism in many areas), gray wolf demographic rates (dispersal, reproduction, and survival) are shaped by the availability of food resources (extrinsic factors) in combination with wolf density, pack size, and pack composition (intrinsic factors) (Van Deelen 2009, pp. 146–151; Stahler et al. 2013, pp. 226–231; McRoberts and Mech 2014, pp. 966–967; Stenglein et al. 2018, pp. 7–13; Smith et al. 2020, p. 91). Adult gray wolf survival rates typically decrease as densities increase (density-dependent intrinsic population regulation), whereas recruitment appears to be more dependent on food availability (extrinsic regulation) (Stenglein et al. 2018, p. 13; Smith et al. 2020, p. 91). Pack size and composition can also play a role in population regulation because smaller packs have fewer individuals to assist with food provisioning for pups, to compete with adjacent packs for food, and to support the minimum pack size necessary for recruitment (Stahler et al. 2013, pp. 226-231). Therefore, smaller packs tend to have lower reproductive rates, especially when situated in areas of higher gray wolf densities (Stahler et al. 2013, pp. 226–231; Ausband et al. 2017a, pp. 4–7; Ausband and Mitchell 2021, pp. 996–998). At larger pack sizes, intra-pack competition for food and socially-induced stress from competitors during the breeding season can impact maternal condition, resulting in smaller litter sizes; however, larger packs generally have higher pup survival, as additional pack members help with food provisioning and inter-pack competition (Packard and Mech 1980, pp. 146–147; Ausband et al. 2017a, pp. 4–7).

Connectivity and Genetic Diversity

A key component in assessing population viability is the retention of genetic diversity. Genetic diversity within any population is a balance between opposing forces: mutation and gene flow add new alleles, while genetic drift, or the random loss of alleles, can remove them from the population, as can natural selection. A sufficiently large population or metapopulation promotes a balance between these forces and precludes diversity loss. More accurately, the rate of loss of genetic diversity is inversely related to the effective population size. Effective population size refers to the size of an idealized population that experiences the loss of genetic diversity due to genetic drift at the same rate as the population in question; it essentially reflects the number of breeders in a population. In determining how to adequately retain genetic diversity, conservation practitioners often point to the "50/500 rule," which states an effective population size of at least 50 is needed for an isolated population to avoid inbreeding depression in the short term while an effective population size of 500 is needed for an isolated population to retain sufficient evolutionary genetic potential in the long term (Franklin 1980, entire). Other authors have recommended effective population sizes of at least 100/1000 as more appropriate general targets, but advise that, when data are available, a species-specific analysis of population viability is preferrable to these generalized targets (Frankham et al. 2014, p. 61). While there are not generally-accepted species-specific effective size guidelines for gray wolves, Laikre et al. (2016, p. 284) proposed 500 as a target effective size to maintain long-term (i.e., greater than 20 generations) genetic diversity for an isolated metapopulation of gray wolves in Fennoscandia. Thus, for this SSA, our assessment of genetic viability is informed by the 50/500 rule given its acceptance in the literature and relevance to other, albeit isolated, gray wolf populations.

Since only breeding individuals pass on genes to subsequent generations, the effective population size is usually smaller than census population size. When empirical estimates of effective size are not available, the ratio between the two measures can be important for providing a generalized assessment of a given species' genetic health. For gray wolves in Yellowstone National Park (YNP), the ratio of effective to census population size has been estimated as approximately 0.3 during the decade following reintroduction (i.e., the effective size was 30 percent of the actual census size) (vonHoldt et al. 2008, pp. 265–267). However, using more recent data from the NRM (Wildlife Genetics International (WGI) 2021, unpublished data), we estimated the average ratio of effective to census population size as 0.17, with a 95% confidence interval between 0.12 and 0.26 (see Appendix 1). Given this range of ratios is from a more recent set of population data than the vonHoldt et al. (2008) analysis, and because these ratios present a more conservative range of effective to census population size ratios, we use a ratio between 0.12 and 0.26 (the 95% confidence interval from our analysis of effective population size) to infer effective population size based on the reported census population size throughout this SSA.[6] This range of ratio values means that—assuming the population is isolated (which it is not)—an effective population size of 50 wolves, the rule of thumb for avoiding inbreeding depression in the short term, equates to a census population size between approximately 192 and 417 wolves, based on the 95% confidence interval for the effective to census population size ratio. Also, an effective population size of 500, the rule of thumb for retaining sufficient evolutionary genetic potential, equates to a census population size between approximately 1,923 and 4,167 wolves. The assumption of isolated populations in these general rules of thumb is critical, however, and creates the need to specifically examine the role and importance of connectivity. Gray wolves in the Western Great Lakes metapopulation are well connected[7] to each other and also linked to populations in Canada (MI DNR 2022a, pp. 14, 23, 42; WI DNR 2023a, pp. iv, 147; MN DNR 2022, pp. 13, 28–29; van den Bosch et al. 2022, p. 6). This connectivity, as noted in a number of PVAs we discuss below, allows for adequate retention of genetic diversity at lower population sizes than theoretical estimates or general guidelines would recommend (e.g., than the 50/500 rule discussed above).

Generally speaking, connectivity or effective dispersal between populations or subpopulations is a critical component in the maintenance of genetic diversity in gray wolf populations (Wayne and Hedrick 2011, entire; Räikkönen et al. 2013, entire; Carroll et al. 2014, pp. 81–82). A study of the Scandinavian gray wolf population noted that connectivity was, in fact, more important to the retention of genetic diversity within a population than the population's size (Liberg and Sand 2012, p. 12). Such connectivity facilitates the retention of genetic diversity within subpopulations and in the larger metapopulation.

To address the specific issues related to genetic diversity of the Western Great Lakes gray wolf metapopulation, we discuss *Inbreeding Depression* in Chapter 3, *Current Genetic Diversity and Connectivity* in Chapter 4, and methods for evaluating adaptive capacity of gray wolves under *Representation* below and also in Chapter 4.

Representation

Representation refers to the ability of a species to adapt to changing environmental conditions (Nicotra et al. 2015, entire; Thurman et al. 2020, entire; Forester et al. 2022, entire). Also known as adaptive capacity, representation may be assessed by analyzing the breadth of genetic, ecological, behavioral, morphological, and physiological diversity within and among populations (Smith et al. 2018, pp. 306–307). In general, a species' adaptive capacity is often considered to have three contributing factors: (1) dispersal and colonization ability, (2) phenotypic plasticity, and (3) evolutionary genetic potential (Beever et al. 2016, p. 132; Foden et al. 2019, p. 11). These three factors taken together provide the capacity for a species to persist through

[6] We also note a recent attempt to estimate a contemporary effective to census size ratio for the Western Great Lakes gray wolf population (vonHoldt et al. 2024b, pp. 8–9); however, this analysis violated major assumption of the methodological approach and thus is unreliable (Kardos and Waples 2024, entire).
[7] Connectivity, for the purposes of this SSA report, refers to effective dispersal (dispersers that become breeders) among areas with resident wolf packs, and not to habitat permeability or other possible connotations.

environmental change by either withstanding the change within the same habitat or by shifting to more suitable habitat (Dawson et al. 2011, pp. 55–56; Nicotra et al. 2015, pp. 1269–1270; Thurman et al. 2020, p. 521).

In our analysis area, gray wolves only occur in the Western Great Lakes area, which represents a fraction of the historical range of the species. However, given that this is the only extant population, our discussion of adaptive capacity will only focus on attributes of this population, as only an existing population can contribute to the species' ability to adapt. Many attributes of gray wolves in the Western Great Lakes area, including a wide distribution, high capacity for dispersal and colonization, high genetic diversity, and a generalist life history, are all positively correlated with adaptive capacity (Thurman et al. 2020, pp. 521–522). Connectivity between subpopulations, each with unique genetic characteristics and each potentially experiencing different selective pressures, also increases adaptive capacity (Carroll et al. 2021, p. 74).

Because the full range of environmental changes that a species will encounter over time is impossible to fully predict, an assessment of needs for representation involves inherent uncertainty. Nevertheless, factors such as the effects of climate change and novel diseases are relatively certain to occur, with gray wolves' ability to respond to these factors through dispersal, behavioral plasticity, or selection from available genetic diversity likely to be critical to their long-term viability. The attributes we assessed to evaluate the representation of gray wolves in the Western Great Lakes area all related to one or more aspects of that overall ability and included the species': extent of occurrence, dispersal distance, physiological tolerance, diet breadth, population size, genetic diversity, and fecundity, among other attributes (see *Current Representation* in Chapter 4 below, Appendix 3, or Thurman et al. (2020, entire) for a complete list of the 36 attributes we analyzed to assess representation). We examined these attributes in relation to standardized categories (as presented in Thurman et al. 2020, entire) to characterize the likelihood that gray wolves in the Western Great Lakes area will be able to adapt to a range of environmental changes.

The extent of the gray wolf's distribution across different ecoregional provinces can also inform representation. First, it may indicate adaptive differences that already exist within the species, as subpopulations may be experiencing and responding to different selective pressures in different ecoregional provinces. Second, exposure to those different selective pressures and connectivity between those areas allows for the retention of the evolutionary processes that maintain and increase adaptive capacity (Crandall et al. 2000, p. 294). Our assessment of representation in this SSA Report will focus on these factors that are impacting, or are likely to impact, adaptive capacity in the future.

Redundancy

Species with redundant populations or large geographic ranges are better able to withstand catastrophic events (Carroll et al. 2010, pp. 5–6; Redford et al. 2011, pp. 40–42; Smith et al. 2018, pp. 306–307). This is because a single catastrophe (e.g., a disease outbreak) is less likely to impact all populations at the same time when there are multiple populations spread across a larger area. In addition, populations with multiple core areas are better able to rebound from catastrophes because dispersers from nearby core areas can serve as a natural source for recolonization or population augmentation. Long-term gray wolf population viability in the Eastern United States is dependent on maintaining a minimum number of gray wolves in multiple core areas. Additionally, greater numbers of packs and breeding pairs spread across the range in the Eastern United States further enhances redundancy. For example, our recovery criteria for the gray wolf in the Eastern United States includes ensuring the survival of the existing population in Minnesota and reestablishing at least one viable population outside of Minnesota (see the *Recovery Criteria for the Eastern Timber Wolf* section below). In general, gray wolves in the Eastern United States need multiple, resilient subpopulations with multiple packs distributed across a broad enough area of the Eastern United States to reduce the potential impact of catastrophic events on the species' extinction risk.

Recovery Criteria and Other Analyses on Wolf Population Viability

Recovery Criteria for the Eastern Timber Wolf

History of Developing and Validating Recovery Criteria for the Eastern Timber Wolf

The 1978 Recovery Plan (hereafter Recovery Plan) and the 1992 Revised Recovery Plan for the Eastern Timber Wolf (hereafter Revised Recovery Plan) were developed to guide recovery of the gray wolf in the Eastern United States. Those recovery plans contain the same two recovery criteria, which are meant to indicate when recovery of the gray wolf throughout its historical range in the Eastern United States has been achieved. These criteria are: (1) the survival of the gray wolf in Minnesota is assured, and (2) at least one viable population of gray wolves is reestablished outside Minnesota and Isle Royale in the lower-48 United States.

The first recovery criterion, assuring the survival of the gray wolf in Minnesota, addresses a need for reasonable assurances that future state, tribal, and Federal wolf management and protection will maintain a viable recovered population of gray wolves within the borders of Minnesota for the foreseeable future. The Recovery Team concluded that the remnant Minnesota gray wolf population must be maintained and protected to achieve recovery in the Eastern United States. Although the Revised Recovery Plan did not establish a specific numerical criterion for the Minnesota gray wolf population, it did identify, for planning purposes, a population goal of 1,251–1,400 animals for the Minnesota population (Service 1992, p. 28). A population of this size not only increases the likelihood of maintaining its genetic diversity over the long term, but also reduces the adverse impacts of unpredictable demographic and environmental events. Furthermore, the Revised Recovery Plan recommends a gray wolf population that is spread across about 40 percent of Minnesota (the majority of gray wolf range in Minnesota) (Service 1992, pp. 28, 72–73), adding a geographic component to the maintenance of the Minnesota population.

The second recovery criterion states that at least one viable gray wolf population should be reestablished within the historical range in the Eastern United States outside of Minnesota and Isle Royale, Michigan (Service 1992, pp. 24–26). That reestablished population must meet one of two conditions to be considered "viable" per the Revised Recovery Plan (Service 1992, pp. 25–26). If it is located within 100 mi (160 km) of a self-sustaining gray wolf population (e.g., the Minnesota population), it should be maintained at a minimum of 100 individuals distributed in a contiguous area of at least 5,000 mi^2 (12,800 km^2) for at least 5 years, based on late-winter population estimates. Late-winter estimates are made at a time when most winter mortality has already occurred and before the birth of pups; thus, a late-winter population estimate is made at the annual low point of the population. A second population within 100 mi (160 km) of the Minnesota population would be considered "viable" at a smaller size because it would be closely tied with the Minnesota population and, given the occasional immigration of Minnesota gray wolves, would retain sufficient genetic diversity to cope with environmental fluctuations. Alternatively, if the second population is located more than 100 mi (160 km) from the Minnesota population, it should consist of at least 200 gray wolves distributed in a contiguous area of at least 10,000 mi^2 (25,600 km^2) for at least 5 years, based upon late-winter population estimates.

The Revised Recovery Plan identified potential areas for reestablishment of this second gray wolf population; these potential areas included northern Wisconsin, the Upper Peninsula of Michigan, the Adirondack Forest Preserve of New York, a small area in Eastern Maine, and a larger area of northwestern Maine and adjacent northern New Hampshire (Service 1992, pp. 56–58). Neither the 1978 nor the 1992 recovery criteria indicate that the establishment of the gray wolf throughout all or most of what was thought to be its historical range in the Eastern United States, or within all of the identified potential reestablishment areas, is necessary to achieve recovery under the Act.

Comparison of Recovery Criteria with Other Wolf Models

One approach to assessing wolf viability is to conduct a PVA using simulation models to project future population sizes and extinction risk under various scenarios (although see Wolf et al. 2015, entire). PVAs can be a valuable tool for estimating risk among competing management scenarios, identifying knowledge gaps and population sensitivities to those uncertainties, and transparently presenting assumptions and parameter estimates—even when there is considerable uncertainty (Boyce 1992, entire; National Research Council 1995, entire; Brook et al. 2002, entire). However, there are some important caveats, especially when uncertainty is large, populations are small, or when the distributions of population vital rates are not stationary (Ludwig 1999, entire; Coulson et al. 2001, entire; Ellner et al. 2002, entire; Flather et al. 2011, entire). Importantly, when simulated populations in PVAs become small, models can overestimate population growth, underestimate population fluctuations, and seriously underestimate probabilities of extinction (Lacy 2000, p. 47). Despite their shortcomings, PVAs remain a valuable tool for predicting the risk of extinction over time in a way that is transparent and repeatable (Brook et al. 2002, entire).

Population viability analyses for wolves can provide further context for the needs and conservation targets of gray wolf populations in the Eastern United States. For example, a PVA for gray wolves in Wisconsin found a completely isolated population of 300 to 500 individuals would have a high probability of persisting for 100 years under all scenarios evaluated (Rolley et al. 1999, p. 43; WI DNR 2006a, pp. 7–8). Managing at a hypothetical "cultural carrying capacity"[8] of 300 gray wolves instead of allowing the population to reach the "biological

[8] Cultural carrying capacity is the maximum population size tolerated by a given community's social and cultural norms.

carrying capacity"[9] of 500 gray wolves had little effect on the estimated risk of extinction in Wisconsin (Rolley et al. 1999, pp. 42–43; WI DNR 2006a, pp. 7–8). A PVA on red wolves indicated that increasing the population size to between 330 and 400 wolves would greatly reduce extinction risk relative to the risk under current conditions (a population of approximately 200 wolves) (Faust et al. 2016, pp. 3–4). The PVA for Mexican wolves found that a population average of greater than or equal to 320 wolves would have a 90 percent likelihood of persistence over 100 years; it also found that 22 captive-raised Mexican wolves released into the wild that survive to breeding age would ensure 90 percent of the gene diversity in captivity is represented in the wild population (Miller 2017, pp. 41–44).

Petracca et al. (2025a, entire) conducted a PVA to estimate the probability of Washington State achieving its recovery goals for gray wolves over a 50-year projection period with a starting population of 172 gray wolves in 2020, based on a spatially explicit model from Petracca et al. (2024a and 2024b, entire). They also evaluated the risk of quasi-extinction, defined as falling below the state's management goal of 92 adult gray wolves in the state and 24 adult gray wolves in each of three recovery regions (Wiles et al. 2011, p. 279; Petracca et al. 2025a, p. 5). Petracca et al. (2025a, entire) evaluated gray wolf recovery in Washington State under twelve different management strategies. Recovery was defined as four breeding pairs in each of three recovery regions and three additional breeding pairs anywhere in the state (Petracca et al. 2025a, 1). Under ten of the management scenarios, the gray wolf population in Washington either achieved stability or increased, depending on the scenario (Petracca et al. 2025a, p. 10). Further, the median probability of recovery by 2070 was greater than 50 percent for seven of the scenarios, with three showing probabilities of more than 90 percent (Petracca et al. 2025a, pp. 7–8). Five scenarios had less than a 50 percent probability of reaching recovery by 2070, with the scenarios involving removal of 5 percent of the population every 6 months through harvest, removal of 8.53 percent of the population every year through lethal control, or immigration into the state ceasing entirely showing probabilities of less than 20 percent by 2070 (Petracca et al. 2025a, p. 8). Finally, given a starting population size of 172 gray wolves in 2020, the median probability of quasi-extinction by 2070 was less than 30 percent across all management scenarios, with seven of these having a zero percent probability of extinction. (Petracca et al. 2025, p. 8). Petracca et al. 2025a (entire) expanded on the models of Petracca et al. (2024a and 2024b, entire). Note however, Santiago-Avila et al. 2024 (entire) critique this model and suggest that estimates of extinction risk were potentially underestimates due to a lack of scientific justification regarding parameter selection and interaction, a failure to adequately address uncertainty, the omission of potential scenarios, and a failure to disclose competing interests. However, these statements were refuted in a response that outlined the process used to select parameters, including the extensive assessment of uncertainty in Petracca et al. (2024a and 2024b, entire), and refuted the claim that including a state agency biologist as a co-author constituted a competing interest (Petracca et al. 2025b, entire).

Researchers have also conducted multiple PVAs on the Scandinavian gray wolf population, which can further inform the demographic needs of gray wolves in the Eastern United States. PVAs conducted in the late 1990s to early 2000s for gray wolves in Sweden concluded approximately 200 individuals would be sufficiently viable (Swedish Environmental Protection

[9] Biological carrying capacity is the maximum population size supported by available abiotic and biotic resources (e.g., food, habitat).

Agency 2015, unpaginated). However, another PVA for gray wolves in Scandinavia that incorporated the effects of hunting, catastrophes, and inbreeding found that at least 400 individuals would be needed for a minimum viable population (Nilsson 2003, p. 236). That analysis also found that increasing hunting pressure at small population sizes (e.g., 100 or 150 gray wolves) caused an "alarming" increase in long-term extinction risk (Nilsson 2003, p. 236). In 2005, a panel of wolf experts and geneticists determined that an effective population size of 200 (600 to 800 total gray wolves) would be necessary to maintain 95 percent of genetic variation in the Scandinavian population over the next 100 years if no further immigration into the population occurred (Liberg 2005, p. 6). Chapron et al. (2012, pp. 37–41) found that gray wolf populations of 100 individuals in Scandinavia have over a 90 percent chance of persistence for 100 years, if current genetic issues (e.g., small population size, inbreeding) are ignored; they found that only extremely small gray wolf populations (fewer than 40 wolves) would have an extinction risk greater than 10 percent within 100 years. Liberg and Sand (2012, pp. 5–12) found that a population of 200 to 400 wolves, with an immigration rate of 2 to 3 gray wolves per generation, would retain 90 to 95 percent of the population's heterozygosity. With a single effective migrant per generation, a minimum of 370 individuals would maintain at least 90 percent of current genetic diversity and current inbreeding coefficients in the Scandinavian gray wolf population (Bruford 2015, pp. 10, 25–26). However, the metapopulation to which the Scandinavian gray wolf belongs (which includes Finland and Karelia) needs an effective population size of 500 for long-term survival (Bruford 2015, p. 10). In their review of wolf population models, Chapron et al. (2012, pp. 41–42) concluded that, except for the specific case of Isle Royale (see *Federal Management* below), the scientific consensus is that (1) wolves have high potential growth rates and (2) small wolf populations (i.e., populations with fewer than 100 wolves) can be demographically viable; however, they also caution against ignoring potential genetic issues (e.g., small population size, inbreeding) in small populations and using a single minimum viable population value over monitoring populations and implementing adaptive management.

Population connectivity, or lack thereof, can substantially affect PVA projections and estimates of genetic diversity over time. Populations that lack connectivity to other wolf populations require more wolves to increase their ability to withstand stochastic and catastrophic events and to ensure genetic health. However, populations that are connected to other populations (e.g., the population in the Western Great Lakes area and its connection to Canada) need fewer wolves to ensure viability. For example, in a PVA conducted on the Oregon population of gray wolves, which allowed for emigration and immigration, the modeled population never fell below a biological extinction threshold (fewer than five gray wolves) or a conservation failure threshold (fewer than or equal to four breeding pairs) in 50 years, even with a starting population of only 85 wolves (ODFW 2015, pp. 17–19). Washington also conducted a PVA to simulate when recovery might be achieved in the state and to estimate the probability of extinction (Wiles et al. 2011, p. 9). When they assumed an open population (i.e., allowed for immigration and emigration from other populations), there was no risk of the population ever declining to extinction. However, when the model assumed an isolated population, the extinction risk increased slightly. The estimated probability of extinction fell to zero once the state recovery criterion of 15 breeding pairs for 3 years was achieved.

Reed et al. (2003b, p. 109) define catastrophes as "extreme bouts of environmental variation that severely decrease the size of wildlife populations over a relatively short time" (e.g., disease outbreaks, release of environmental contaminants, or extreme weather events). The importance of incorporating catastrophes in PVAs is well recognized, as these events can sometimes limit population viability over genetic or other demographic factors (Lande 1993, pp. 921–923). However, the frequency, distribution, and consequences of catastrophes are rarely known, which can render population projections unreliable (Coulson et al. 2001, pp. 220–221). Researchers in Scandinavia used sensitivity analyses, in which parameters related to catastrophes were varied, to circumvent this challenge for gray wolves (Chapron et al. 2012, pp. 23–24). Chapron et al. (2012, pp. 23–24) computed the frequency and intensity of a catastrophe that would be needed to crash the Swedish gray wolf population to the extent that the population no longer met their definition of viability (i.e., more than 90 percent probability of persistence over 100 years). They found that a population limited to only 30 gray wolves would retain viability, even if (1) a catastrophe that caused a 40 percent decrease in population size occurred once every decade or (2) a catastrophe that caused a 70 percent population decline occurred once every century. For a population of 100 gray wolves to have less than 90 percent probability of persistence over 100 years, a catastrophe causing a 60 percent population reduction would need to occur once per decade; or a catastrophe that results in mortality of almost all individuals would need to occur at least once during the 100-year modeling timeframe.

Overall, the majority of the PVAs we summarize above indicate that several hundred individuals likely provide for a gray wolf population with a low risk of extinction, though each study differs in the specific necessary population size given the unique demographics of each population, levels of immigration, amount of human-caused mortality, distinct model structures and parameters, and variation in the amount of acceptable risk over time.

Summary of Resource and Demographic Needs

Gray wolves in the Eastern United States need suitable habitat, which includes sufficient prey resources, to withstand stochastic events. Gray wolf populations also need a sufficient number of packs to sustain reproduction, survivorship, and connectivity. In general, to maintain populations in the wild over time, gray wolves in the Eastern United States need well-connected and genetically diverse subpopulations that function as a metapopulation distributed across enough of their range to be able to withstand stochastic events, rebound after catastrophes (e.g., severe disease outbreaks), and adapt to changing environmental conditions. While viability is context-specific, recovery criteria for gray wolves in the Eastern United States and results of PVAs on other wolf populations, such as those described above, can provide further insight into the viability of gray wolf populations in our analysis area.

Chapter 3: Conservation Efforts and Stressors

Before we evaluate the current and future condition of gray wolves in the Eastern United States, we explore the stressors, whether natural or anthropogenic, that may have occurred to produce the species' current condition and that may influence the species' viability into the future (Service 2016, p. 14). A stressor is something that causes a change in a habitat or demographic resource that can lead to an adverse individual response. Some stressors may directly influence the demographics of a population through mortality of individuals resulting from actions or activities, such as harvest (which involves the direct removal of individuals). Other stressors, such as climate change, may indirectly affect the species' demographics via the alteration of their habitat. Still other stressors may directly affect individuals and habitat factors at the same time. The stressors that we evaluated for gray wolves in the Eastern United States include:

- human-caused mortality;
- disease and parasites in wolves;
- inbreeding depression;
- hybridization;
- climate change;
- disease in prey species; and
- other sources of habitat modification

In the sections below, we also summarize the state, tribal, and Federal management that have provided for the conservation of gray wolves in the Eastern United States. These conservation efforts reduce the influence of a stressor, improve the condition of wolf habitat, and/or improve gray wolf demographic factors.

Figure 7 below illustrates the relationships between relevant conservation efforts, stressors, and the species' habitat and demographic needs.

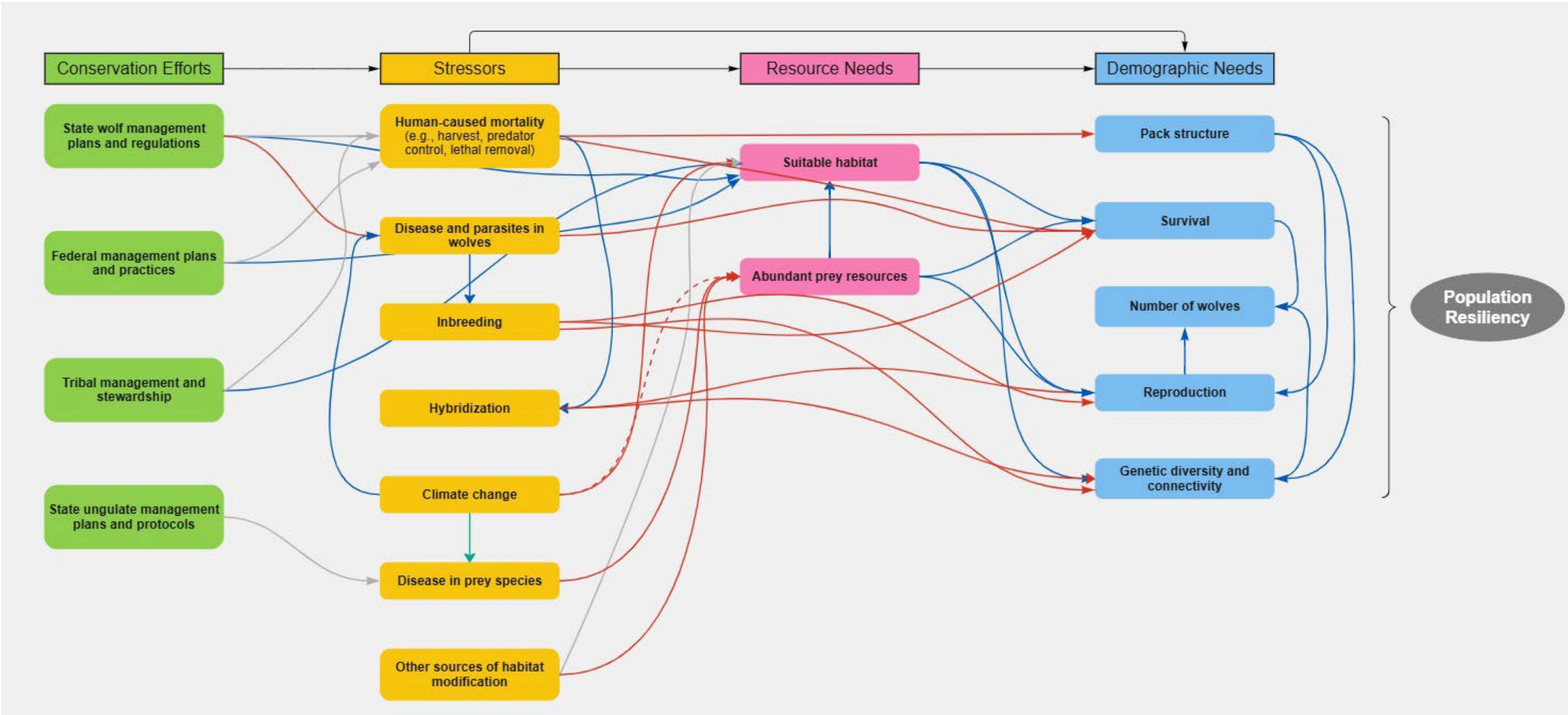

Figure 7. A conceptual model for the primary stressors that may affect individuals or cumulatively influence the resiliency of the gray wolf in the Eastern United States. Blue arrows represent positive relationships between nodes and red arrows represent negative relationships between nodes. Grey lines indicate the relationship between nodes could be either positive or negative. The dotted line indicates there is uncertainty or debate in current research regarding the relationship between the stressor and resource need.

Management and Conservation Efforts

State Management

Currently, gray wolves in the Eastern United States are listed as endangered under the Act, except in Minnesota where they are listed as threatened. There is a 4(d) rule for Minnesota that currently allows for lethal removal of gray wolves by designated government employees when the wolves have attacked livestock or other domestic animals (see *State Management: Minnesota* section below). State management agencies in Michigan, Minnesota, and Wisconsin have each developed gray wolf management plans (MI DNR 2022a, entire; MN DNR 2022, entire; WI DNR 2023a, entire). These management plans provide guidance from the state management agencies on how to manage gray wolf populations in each respective state, and the states have the authority to implement these plans. Some aspects of the gray wolf management plans apply while the species is listed (e.g., monitoring) and other aspects apply only when delisted (e.g., regulated harvest). Below, we describe each states' management plans, regulations, and laws in greater detail. We describe how these management plans are implemented when the species is listed and further clarify when application would only apply when delisted.

Michigan

Michigan removed gray wolves from the state's threatened and endangered species list and gave them Protected Animal status under the State's Wildlife Conservation Order in 2009. Since then, gray wolves were classified as a game animal in Michigan on several separate occasions (2012, 2013, 2014) and have maintained that classification since 2016 (MI DNR 2022a, pp. 2–3). Game-animal status prohibits harming or killing the species except under a permit, license, or specific conditions and allows but does not require the establishment of a regulated harvest season, if the species were to be federally delisted. With gray wolves classified as game animals, the Michigan Natural Resources Commission has the exclusive authority to enact regulations pertaining to the methods and manner of harvest. Although any decisions regarding establishment of a harvest season for gray wolves would be made by the Natural Resources Commission, the Michigan DNR would be called upon to make recommendations regarding socially and biologically responsible harvest of gray wolves.

The first Michigan Wolf Recovery and Management Plan was completed in 1997 (MI DNR 1997, entire). That plan focused on recovering a small gray wolf population and addressing the conflicts expected to result as a consequence of successful gray wolf restoration. Since then, gray wolf management in Michigan has evolved, and the Michigan DNR updated its management plan in 2008 (MI DNR 2008, entire), 2015 (MI DNR 2015, entire), and 2022 (MI DNR 2022a, entire) to reflect the biological and social issues associated with the increased population size and distribution of gray wolves in the state. The 2022 updated Michigan Wolf Management Plan (hereafter, Michigan Plan) is described below.

The Michigan Plan outlines gray wolf management goals and strategies for the state. The four principal goals of the Michigan Plan are to (1) maintain a viable gray wolf population in Michigan (above a level that would warrant its classification as threatened or endangered at either the state or Federal level); (2) facilitate gray wolf-related benefits; (3) minimize gray wolf-related conflicts; and (4) conduct science-based gray wolf management with socially responsible methods (MI DNR 2022a, pp. 21–29). The Michigan Plan does not address gray wolf management within Isle Royale National Park, where the population is fully protected by the National Park Service (NPS). The Michigan Plan will be reviewed and updated at 10-year intervals, with Tribal Nations and involvement of other interested parties, to account for changes in management context (MI DNR 2022a, p. 72).

The first goal of the Michigan Plan is to maintain a viable gray wolf population in Michigan. The Michigan DNR has chosen to manage the state's gray wolves as though they are an isolated population that receives no genetic or demographic benefits from immigrating gray wolves, even though the population currently is connected with populations in Minnesota, Wisconsin, and Canada. Therefore, the statewide winter population must exceed 200 gray wolves to achieve the Michigan Plan's first goal of maintaining a viable population in the state (MI DNR 2022a, pp. 22–23). This number is consistent with the Federal Revised Recovery Plan's definition of a viable, isolated gray wolf population (Service 1992, p. 25). The Michigan Plan, however, clearly states that 200 gray wolves is not the target population size, and that a larger population may be necessary to meet the other goals of the plan. Per the Michigan Plan, the gray wolf population in the state should be "self-sustaining and genetically diverse with an abundance greater than 200 individuals, that maintains connectivity with gray wolf populations in neighboring states and Canada while fulfilling its ecological role" (MI DNR 2022a, p. 23). The state also recognizes that its residents benefit from positive gray wolf-related interactions and opportunities for those interactions would be reduced if gray wolf numbers fall "below a viable level" (MI DNR 2022a, p. 24). The Michigan DNR acknowledges that maintaining a viable population of gray wolves in the state allows for the most effective means to address gray wolf-related conflicts, because Federal protection under the Act reduces the options available to address those conflicts. Therefore, the state will maintain a population above this minimum threshold of 200 gray wolves while minimizing and resolving conflicts where they occur (MI DNR 2022a, p. 24).

The second goal of the Michigan Plan is to facilitate gray wolf-related benefits valued by Michigan residents (MI DNR 2022a, pp. 24–26). Those benefits include ecological, cultural, and religious values; interactions with nature; personal appreciation; and tourism and recreation. The Plan identifies measures to promote positive interactions with wolves by maintaining a viable population and providing opportunities for the public to experience and appreciate gray wolves.

The third goal of the Michigan Plan is to minimize gray wolf-related conflicts that can cultivate negative public attitudes (MI DNR 2022a, pp. 26–28). Because the effects of gray wolf-related conflicts are not evenly dispersed throughout the species' range in the state, the Michigan Plan recognizes that those conflicts can best be addressed on an individual, case-by-case basis. Therefore, the Michigan Plan does not establish numerical abundance targets for gray wolves in the state (aside from the minimum threshold to maintain a population of at least 200 gray wolves), but rather guides management on a local scale. A key component of the Michigan Plan are strategies and actions to manage gray wolf depredation of domestic animals (MI DNR 2022a, pp. 58–67). The frequency of gray wolf depredation on livestock and domestic animals in Michigan is lower than in other Western Great Lakes states, however, it does occur and is an important management issue. Thus, the Michigan DNR is committed to providing timely responses to reports of suspected gray wolf depredation, implementing measures to minimize the risk of depredations, eliminating or minimizing ongoing depredation (with a priority on developing and applying nonlethal management methods), and facilitating financial compensation for livestock losses caused by gray wolves. While gray wolves are federally listed as endangered, preventative and nonlethal methods are the primary tools to minimize conflict risk and mitigate ongoing conflict. If gray wolves are federally delisted, lethal depredation control would become an additional management option. The state would also develop a regulated program to allow livestock producers to control depredating gray wolves on their property, allowing both nonlethal and lethal methods. Monitoring, reporting, and enforcement would be conducted by Michigan DNR to ensure compliance with program requirements.

The fourth goal of the Michigan Plan is to conduct science-based and socially responsible management to achieve the other goals. To do so, the approaches for managing wolves outlined in the Michigan Plan were developed based on scientific evaluation as well as considerations of the benefits, conflicts, and diverse interests associated with wolves in Michigan (MI DNR 2022a, pp. 28–29).

The Michigan Plan identifies gray wolf population monitoring as a priority activity and specifically states that the Michigan DNR will monitor abundance every other year for at least 5 years (i.e., 2-3 monitoring periods in 5 years), should gray wolves be federally delisted (MI DNR 2022a, p. 34). If wolves remained federally delisted for more than 5 years, the Michigan DNR would assess the frequency and intensity of wolf monitoring to determine appropriate levels to support the wolf management program in the State (MI DNR 2022a, p. 34). Another component of population monitoring is monitoring gray wolf health. The Michigan DNR monitors the effects of parasites and disease through necropsies of dead gray wolves and through analyzing biological samples from captured live gray wolves. Prior to 2004, Michigan DNR vaccinated all captured gray wolves for canine distemper virus (CDV) and canine parvovirus (CPV) and treated them for mange. These inoculations were discontinued to provide more natural biotic conditions and to provide biologists with an unbiased estimate of disease-caused mortality rates in the population (Roell 2005, in litt.). Because diseases and parasites are not currently a significant threat to the Michigan gray wolf population, the Michigan DNR does not actively manage disease (MI DNR 2022a, p. 45). If monitoring indicates that diseases or parasites may pose a threat to the gray wolf population, the Michigan DNR would again consider more active management similar to that conducted prior to 2004 (MI DNR 2022a, p. 45).

According to Federal and state law, for a harvest to occur in Michigan, gray wolves must be federally delisted and classified as a game animal in the state (gray wolves have been classified as a game animal in Michigan since 2016). The Michigan DNR plans to develop socially and biologically responsible management recommendations regarding regulated harvest of gray wolves in the state (MI DNR 2022a, pp. 69–73). Those recommendations would be developed to address both regulated harvest for the purpose of managing gray wolf-related conflicts as well as other purposes (e.g., potential recreational benefits). The Michigan Plan does not specify those recommendations or the details for a harvest, were one to take place, but focuses on the need to gather and evaluate biological and social information regarding a gray wolf harvest. Michigan DNR would engage all federally recognized Tribal Nations and consider input of interested parties prior to any potential gray wolf harvest. If gray wolves are federally delisted and the state deems a regulated harvest to be appropriate, it would be managed and evaluated to ensure the long-term viability of the Michigan gray wolf population is maintained (MI DNR 2022a, p. 72).

To minimize illegal take, the Michigan Plan calls for enacting and enforcing regulations to ensure adequate legal protection for gray wolves in the state with the following possible actions: (1) reclassify gray wolves as endangered or threatened under state regulations if population size declines to 200 or fewer individuals; (2) review, modify, recommend, and/or enact regulations, as necessary, to ensure appropriate levels of protection for the gray wolf population (e.g., game species regulations); and (3) designate gray wolves as a protected animal (as opposed to a game species or listed species) if necessary to avoid a lapse in legal protection until other necessary regulatory mechanisms are in place (MI DNR 2022a, p. 37). Given that the species is currently classified as a game animal in Michigan, there would be no lapse in legal protection should gray wolves be delisted in the state. Additionally, the Michigan DNR will investigate and penalize violations of regulations to deter gray wolf-related crimes. That includes increasing the public's awareness of how to report gray wolf-related violations and recommending modifications to state laws to make penalties for illegally killing a gray wolf commensurate with other similarly situated species, depending on current legal status (MI DNR 2022a, pp. 37–38).

The Michigan Plan includes maintaining habitat and prey necessary to sustain a viable gray wolf population in the state as a management component. This includes maintaining prey populations required for a viable gray wolf population while providing for sustainable human uses, maintaining habitat linkages to allow for dispersal, and minimizing disturbance at known active dens (MI DNR 2022a, pp. 38–43). The Michigan Plan emphasizes the need for public information and education efforts that focus on living with a recovered gray wolf population and ways to manage gray wolves and their interactions with humans (both positive and negative) (MI DNR 2022a, pp. 29–32). The Michigan Plan also recommends conducting important research efforts, facilitating positive gray wolf-human interactions, managing actual and perceived threats to human safety, and minimizing the impacts of captive wolves and wolf-dog hybrids on the wild gray wolf population (MI DNR 2022a, pp. 32, 50, 53, 58, 67).

In summary, the Michigan Plan identifies Michigan DNR's intentions for maintaining a viable population in the state by ensuring the population always exceeds 200 gray wolves, which is above the Federal recovery plan's criteria for a second population (Service 1992, p. 4), and ensuring the population remains connected to populations in adjacent states and Canada (MI DNR 2022a, p. 23). Michigan DNR would continue to address gray wolf-related conflicts at a local scale using nonlethal methods while gray wolves are federally listed and includes the option for lethal depredation control if delisted. The Michigan Plan highlights the need to gather and evaluate biological and social information regarding a gray wolf harvest. If gray wolves are federally delisted and the state implements a regulated harvest, it would be managed and evaluated to ensure the long-term viability of the Michigan population is maintained (MI DNR 2022a, p. 72).

Minnesota

Gray wolves in the Eastern United States are listed as endangered under the Act, except in Minnesota where they are listed as threatened. In Minnesota, a 4(d) rule is in place to provide for the conservation of the species and to allow for more effective management of wolves that depredate livestock. Specifically, under the authority of the Act's 4(d) rule that regulates take of gray wolf in Minnesota, gray wolves in Minnesota that have attacked domestic animals within specified areas of the state (i.e., in some Federal Wolf Regulatory Zones) may be lethally removed by designated government employees while the species is federally listed (88 FR 75506, November 3, 2023). The state of Minnesota is divided into five Federal Wolf Regulatory Zones and no control of depredating gray wolves is allowed in Regulatory Zone 1, comprising approximately 4,488 mi^2 (11,624 km^2) in northeastern Minnesota. In Federal Wolf Regulatory Zones 2 through 5, employees or agents of the Service (including United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services (Wildlife Services)) or the Minnesota DNR may take gray wolves in response to depredations of lawfully present domestic animals within 0.5 mi (0.8 km) of the depredation site. Young-of-the-year (young produced in one reproductive year) captured on or before August 1 must be released. The regulations that allow for this take (50 CFR 17.40(d)(2)(i)(C)) do not specify a maximum duration for depredation control, but, per state rules, a site may be worked for no more than 60 days after a verified depredation event.

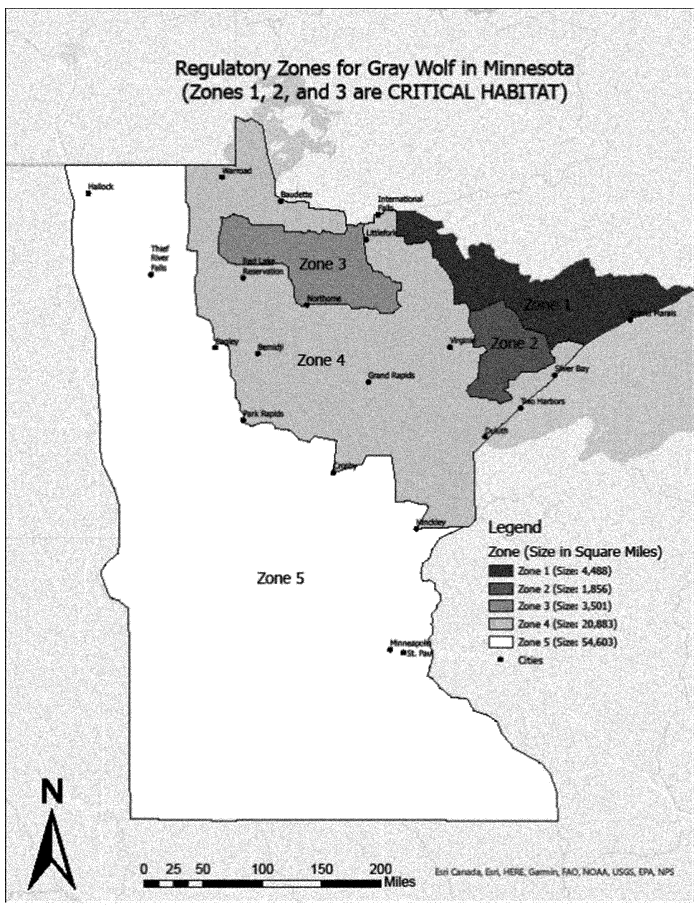

Figure 8. Map of Federal Wolf Regulatory Zones in Minnesota (88 FR 75511).

In 2000, the Minnesota Legislature passed the Wolf Management Act (Minnesota Statutes 97B.645-648, entire), which specifically requires the Minnesota DNR to adopt a gray wolf management plan that includes, among other factors, the goal of ensuring the "long-term survival of the wolf in Minnesota." It requires preparation of a management plan, describes gray wolf depredation zones (also see MN DNR 2001, Appendix 3), prohibits the taking of gray wolves in violation of Federal law, prohibits the harassment of gray wolves, and authorizes the take of individual gray wolves threatening human life and posing imminent threats to cattle or domestic pets when gray wolves are not federally listed. Finally, the Wolf Management Act establishes a civil penalty for the unlawful take, transport, or possession of a gray wolf in violation of Minnesota's game and fish laws. In 2011, the Minnesota Legislature classified gray wolves as small game in statute and authorized the Minnesota DNR to implement a harvest season following removal from the Act's protections. The 2012 Legislature established gray wolf hunting and trapping licenses and further clarified the Minnesota DNR's authority to implement a season starting no later than the beginning of the firearms deer season (MN DNR 2022, p. 19). In summary, the Wolf Management Act and the Minnesota Game and Fish Laws constitute the basis of the state's authority to manage gray wolves when they are not federally listed.

The Minnesota DNR completed the first Minnesota Wolf Management Plan in early 2001 (MN DNR 2001, entire). In recent years, to help inform a gray wolf management plan update, the Minnesota DNR conducted a public attitude survey; held public comment periods and meetings; consulted and coordinated with Tribal Nations; and created the Wolf Technical Committee, comprised of university, tribal, state and Federal wildlife managers, and scientists, to identify research and management needs, challenges, and solutions (MN DNR 2022, p. 8). The updated management plan was completed in December 2022; hereafter, we refer to this updated management plan as the Minnesota Plan (MN DNR 2022, entire). If gray wolves were to be federally delisted in Minnesota, the Minnesota DNR would manage them in accordance with the Minnesota Plan. Minnesota DNR's management of gray wolves would differ from that which has occurred while they are listed as threatened under the Act, primarily by the potential implementation of a regulated harvest season (see *Human-Caused Mortality in Minnesota* below for more information). The management of depredating gray wolves would be similar to the management under the 4(d) rule while federally listed, except for a few additional depredation options (see *Depredation Control in Minnesota* below for more information).

The Minnesota Plan outlines gray wolf management goals, objectives, and strategies for a 10-year period (2023–2032) and will be evaluated and revised 5 years after adoption, if necessary (MN DNR 2022, p. 8). It includes performance measures to track and report publicly its progress on implementing strategies in the plan. The Minnesota Plan's stated goals are to: "1) maintain a well-connected and resilient wolf population; 2) collaborate with diverse partners to collectively support wolf plan implementation; 3) minimize and address human-wolf conflicts while recognizing diverse wolf values; 4) inform and engage the public about wolves in Minnesota and their conservation; 5) conduct research to inform wolf management; and 6) administer the wolf program to fulfill agency responsibilities and public and partner needs" (MN DNR 2022, pp. 30–35). Key considerations in the plan include diverse and changing wildlife values, tribal interests, resources to support Minnesota gray wolf management, gray wolf depredation and predation, population objectives, and monitoring and research needs (MN DNR 2022, pp. 23–29).

The Minnesota Plan recommends maintaining a population comparable in size to recent estimates (2,200–3,000 gray wolves) that is distributed across the majority of the current species' range in Minnesota. This is well above the Federal planning goal of 1,251 to 1,400 gray wolves for the state, as outlined in the Service's Revised Recovery Plan for the Eastern Timber Wolf (Service 1992, p. 28). The Minnesota DNR will coordinate with the Wolf Technical Committee to evaluate population trends and implement research and management actions if a multiyear declining statewide population trend drops the population size in Minnesota below 2,000 gray wolves (MN DNR 2022, p. 31 and Figure 5). If the population size were to decline to below 1,600 gray wolves, Minnesota DNR would implement management actions to reverse population declines and no regulated harvests would occur (MN DNR 2022, pp. 28, 51). If statewide population estimates exceed 3,000 gray wolves over multiple consecutive years, the Minnesota DNR will consider management actions, including potentially increasing harvest levels, to address public concerns and will provide an opportunity for public comment on these potential actions (MN DNR 2022, pp. 31, 51).

The 2001 Minnesota Plan divided the state into two gray wolf-management zones—Zones A and B (see map in MN DNR 2001, Appendix 3). Zone A[10] contains the vast majority of the gray wolf current range in Minnesota, including federally designated critical habitat, while Zone B[11] is more developed including higher road densities, livestock, and other domestic animals. Within Zone A, gray wolves receive strong protection by the state, unless they are involved in attacks on domestic animals. The rules governing the take of gray wolves to protect domestic animals in Zone B are less protective than in Zone A (see *Depredation Control in Minnesota*, below). The updated 2022 Minnesota Plan recommends the removal of Zone B and statewide application of the more protective gray wolf depredation management used in Zone A (MN DNR 2022, p. 33). This change would require legislative action to occur.

The Minnesota DNR would consider population-management measures, including public hunting and trapping seasons and other methods, if gray wolves were federally delisted. To determine whether the Minnesota DNR would hold a future regulated harvest season, the Minnesota Plan outlines a gray wolf hunting/trapping season decision framework (MN DNR 2022 Appendix 2, pp. 47–51). The framework includes the following guiding principles: maintain a population comparable in size to recent estimates (2,200–3,000 gray wolves) that is distributed across the majority of the current gray wolf range; involve Tribal Nations (Minnesota Statutes 10.65 requires consultation with tribal governments); incorporate the best available science; monitor populations; seek public input (Minnesota Statute 97B.645 Subdivision 9 requires public involvement); and develop a gray wolf season proposal that defines the purpose and has measurable objectives (MN DNR 2022, p. 48). If the Minnesota DNR decided to implement a regulated harvest season, the Wolf Technical Committee would recommend harvest levels to Minnesota DNR annually; the Wolf Technical Committee's review of data and harvest scenarios, consideration of all other human-related mortality, and coordination with tribal biologists would influence these harvest level recommendations (MN DNR 2022, p. 51). To further inform regulated harvest levels, the Minnesota Plan includes a table (MN DNR 2022, Table A.1 on p. 51) with potential harvest rates by population size (e.g., if the population were to be between 2,000 and 3,000 gray wolves (a stable trend), the recommended harvest level would likely be 10–20 percent of the population, while if the population were to be between 1,600 and

[10] Which encompasses Federal Wolf Regulatory Zones 1-4
[11] Which encompasses Federal Wolf Regulatory Zone 5

2,000 gray wolves (a decreasing population trend), the recommended harvest level would likely be less than 5 percent).

In summary, while federally listed, all take of gray wolves in Minnesota, primarily in the form of lethal depredation control, will continue to be regulated in accordance with the existing 4(d) rule (50 CFR 17.40(d)(2)(i)(C)). If gray wolves were to be federally delisted in Minnesota, the Minnesota Wolf Management Plan would guide management of gray wolves in the state. The Minnesota Plan recommends managing for a population comparable in size to recent estimates (2,200–3,000 gray wolves) that is distributed across the majority of the current gray wolf range in the state, well above the Federal planning goal for Minnesota (Service 1992, p. 28). Decisions regarding appropriate rates of regulated harvest would be guided by a framework specified in the Minnesota Plan, which reduces the harvest rate as the population decreases (MN DNR 2022, Table A.1 on p. 51). If the population size were to decline to below 1,600 gray wolves, Minnesota DNR would implement management actions to reverse population declines and no regulated harvests would occur (MN DNR 2022, pp. 28, 51).

Wisconsin

Wisconsin removed gray wolves from the state's Protected Wild Animal status in April 2012, when Wisconsin Act 169 was passed and gray wolves were classified as a state game species (whenever they are not federally or state listed as a threatened or endangered species). When gray wolves are federally listed, they are also protected automatically under Wisconsin's threatened and endangered species law (Wisconsin Statute 29.604(3)(a) and Wisconsin Administrative Code NR 27.03(1) as cited in WI DNR 2023a, p. 67). Under Wisconsin Statute 29.014(1), the Wisconsin DNR has authority to maintain open and closed harvest seasons for state game species; however, Wisconsin Statute Section 29.185 requires the Wisconsin DNR to allow hunting and trapping when gray wolves are not listed on Federal or state threatened and endangered species lists (WI DNR 2023a, p. 75). Section 29.888 requires the Wisconsin DNR to administer a depredation control program when gray wolves are not listed (WI DNR 2023a, p. 75).

In 1989, the Wisconsin Timber Wolf Recovery Plan was completed which recommended the wolf be downlisted to state-threatened status if the mid-winter census remained above 80 animals for more than 3 years (WI DNR 1989, entire). In 1999, the Wisconsin Natural Resources Board approved the Wisconsin Wolf Management Plan (1999 Plan; WI DNR 1999, entire). In 2004 and 2005, the Wisconsin Wolf Science Advisory Committee and the Wisconsin Wolf Stakeholders group reviewed the 1999 Plan, and the Science Advisory Committee subsequently developed updates and recommended modifications to the 1999 Plan. The updates were completed and received Natural Resources Board approval in 2007 (WI DNR 2007, entire). Hereafter, we refer to this 1999 Wisconsin Wolf Management Plan, with its 2006 and 2007 addendum, as the 1999/2007 Wisconsin Plan. In August 2023, the Wisconsin DNR released an updated Wolf Management Plan (Wisconsin Plan), which was approved by the Natural Resources Board on October 25, 2023. The Wisconsin Plan has an implementation timeline of approximately 10 years but is considered valid until it is replaced (WI DNR 2023a, p. 3). The Wisconsin DNR plans to review the plan every 5 years to ensure it continues to address contemporary gray wolf management issues.

The Wisconsin Plan recommends a management framework based upon the principles of adaptive wildlife management, outlines a primary gray wolf management goal and associated objectives, and describes strategies and products to link the objectives to on-the-ground implementation (WI DNR 2023a, pp. 111–161)). The Wisconsin Plan's stated goal is to "ensure a healthy and sustainable wolf population that fulfills the numerous ecological, cultural and recreational benefits of wolves, while being responsive in addressing and preventing wolf-related conflicts and recognizing the diverse values and perspectives of all citizens in Wisconsin" (WI DNR 2023a, p. 112). The Wisconsin Plan contains six objectives: (1) ensure a healthy and sustainable wolf population to fulfill its ecological role; (2) address and reduce wolf-related conflict; (3) provide multiple benefits associated with the wolf population; (4) increase public understanding of wolves in Wisconsin; (5) conduct scientific research to inform wolf stewardship; and (6) provide leadership in collaborative and science-based wolf management (WI DNR 2023a, pp. 126–161).

The first objective outlined in the Wisconsin Plan is to ensure a healthy and sustainable gray wolf population to fulfill its ecological role. It prioritizes management actions, including whether to maintain, increase or decrease a population in a specific management zone based on biological and social factors in that zone (WI DNR 2023a, p. 111), instead of a minimum population threshold, as was included in the previous 1999/2007 Wisconsin Plan (WI DNR 2023a, p.111). The Wisconsin Plan focuses on long-term stewardship and sustainable management of the Wisconsin gray wolf population (WI DNR 2023a, p. 112).

The strategies identified under the first objective of the Wisconsin Plan (to ensure a healthy and sustainable gray wolf population) include managing the gray wolf population at sustainable levels that reflect public preferences; conducting annual population monitoring; using science-based and data-driven methods to estimate population characteristics; supporting law enforcement in enforcing laws and ensuring legal protection; monitoring and protecting gray wolf population health; maintaining sustainable prey populations; and considering gray wolves in habitat management planning and decisions (WI DNR 2023a, pp. 126–134). The first strategy for this objective provides direction for the Wisconsin DNR to manage the gray wolf population at levels that reflect public preferences, including wolf-related benefits and wolf-related conflicts. This involves ensuring gray wolf abundance remains above the Federal recovery plan's criteria for a second population outside of Minnesota (Service 1992, p. 4) and is in line with current population objectives in the Wisconsin Plan, which includes ensuring the wolf population remains above the historical state threatened listing threshold for gray wolves (i.e., late-winter count of 250 gray wolves outside of reservations). Under the Wisconsin Plan, the Wisconsin DNR intends to avoid any actions and mitigate any issues that could result in the gray wolf population approaching any of the state or Federal thresholds (WI DNR 2023a, pp. 126–127). Furthermore, the Wisconsin Plan provides a table with general guidance for likely statewide management outcomes under different population sizes (WI DNR 2023a, Table 18 on p. 127). For example, if gray wolf population abundance estimates fall below 800 gray wolves, the likely statewide population management outcome would be to grow/increase the population size, whereas if population abundance estimates exceed 1,200 gray wolves, the likely management outcome would be to decrease the population size. The thresholds identified in the Wisconsin Plan are based on the best available science (i.e., a carrying capacity estimate of approximately 1,242 gray wolves in Wisconsin from Stenglein et al. 2015b, entire) and social science findings indicating that Wisconsin citizens would prefer “about the same number” of gray wolves or more in the state; the population size was approximately 1,000 gray wolves at the time of this public attitudes survey (Bradshaw et al. 2022, pp. 41–42; WI DNR 2023a, pp. 127–129). The Wisconsin plan states that the adaptive management approach is expected to “generally maintain statewide gray wolf abundance and distribution at levels comparable to recent years (overwinter estimates of approximately 800 to 1,200 gray wolves) while explicitly allowing for fluctuations in local gray wolf densities, including population reductions as warranted” (WI DNR 2023a, p. 129).

The second objective of the Wisconsin Plan is to address and reduce gray wolf-related conflict. The strategies identified under this objective include maintaining an integrated gray wolf conflict program; implementing a gray wolf damage compensation program; maintaining a cooperative services agreement with Wildlife Services for timely and effective gray wolf conflict assistance; ensuring funding for the gray wolf conflict program; continuing research on conflict mitigation, prevention and new techniques for addressing conflicts; and increasing public awareness of the gray wolf conflict program and abatement techniques (WI DNR 2023a, pp. 135–140). Compared to earlier gray wolf management plans, the Wisconsin Plan includes similar strategies for gray wolf conflict management and builds on this further by incorporating more description and emphasis on nonlethal conflict abatement measures and active public education efforts to promote coexistence with gray wolves (WI DNR 2023a, pp. 100–105; 135–140).

The Wisconsin Plan also revises Wisconsin’s management zones, which allow for differing levels of protection and more flexible management options to ensure a healthy population while managing gray wolf-related conflicts (Figure 9 below; WI DNR 2023a, Figure 37, p. 116). Currently, the state is divided into six gray wolf harvesting zones; the Wisconsin Plan builds upon the six-zone structure and adds four additional subzones within the larger zones. Two subzones (1A and 4A) have been delineated to allow flexibility for greater harvest pressure in areas with a history of gray wolf and livestock conflict, and two subzones (1B and 2B) would minimize gray wolf harvest in areas adjacent to large tribal reservations. For example, subzones 1B and 2B would have a harvest quota of four and two gray wolves per season, respectively. The tribal reservations of Bad River, Red Cliff, Lac Courte Oreilles, Lac du Flambeau, Menominee, and the identified Stockbridge-Munsee Community Area would continue to be designated as zero quota areas for state gray wolf harvest WI DNR 2023a, pp. 116–125).

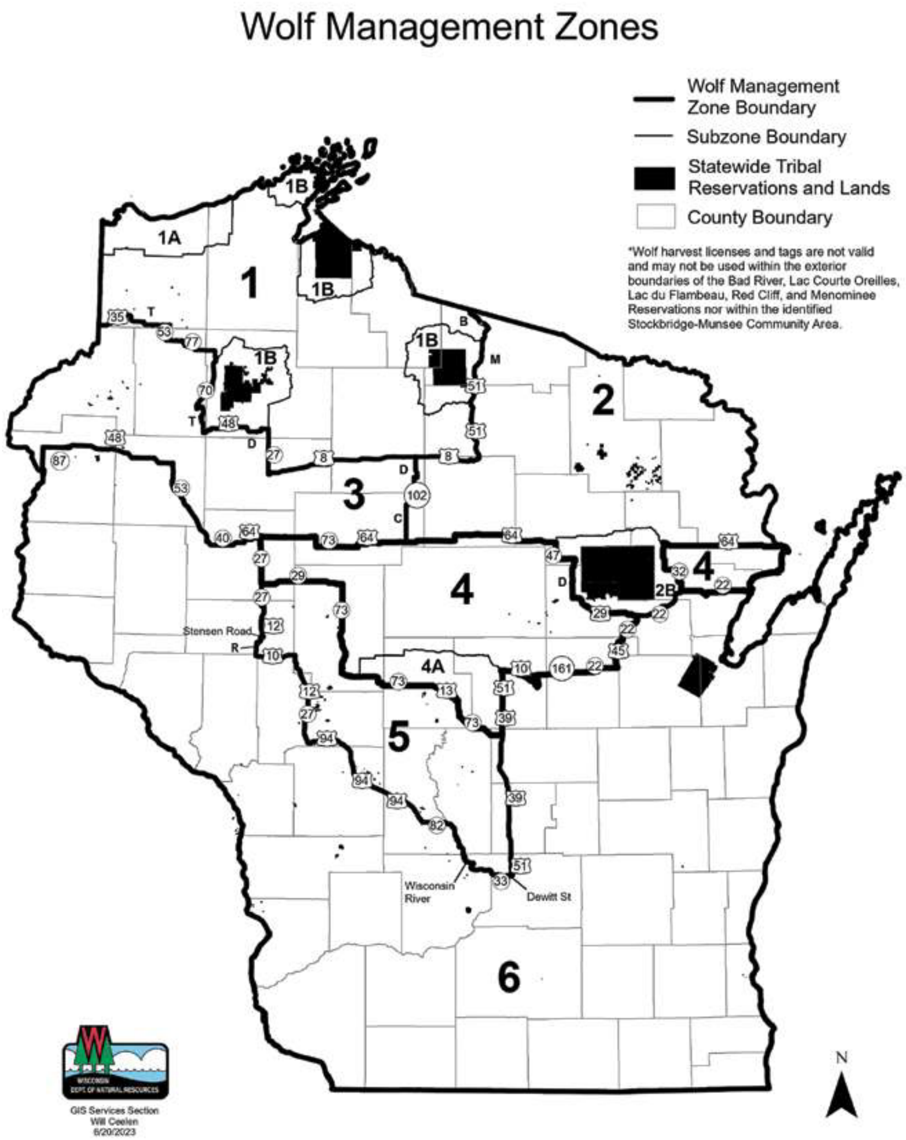

Figure 9. Map of Wolf Management Zones in Wisconsin (WI DNR 2023a, p. 116)

The third objective of the Wisconsin Plan is to provide multiple benefits associated with the gray wolf population (WI DNR 2023a, pp. 141–147). This objective is intended to "provide opportunities to appreciate and draw multiple benefits from the wolf population, including a regulated harvest of wolves consistent with state and federal law, while also safeguarding the resource for current and future generations" (WI DNR 2023a, p. 141). Strategies include implementing a regulated wolf harvest season consistent with public preferences and management plan objectives; evaluating the gray wolf public harvest season structure and implementation; and encouraging other forms of recreation and positive interactions (e.g., cultural values, gray wolf tourism) with gray wolves. Hunters and trappers are required to register a gray wolf harvest online or over the phone within 24 hours of the harvest, followed by an in-person certification process with a Wisconsin DNR conservation officer or wildlife biologist to provide demographic and biological data. As outlined in State Statute 29.185, the Wisconsin DNR must provide 24-hour public notice before zone closures. The Wisconsin Plan also includes mandatory reporting of harvested animals and recommends the Wisconsin DNR engage in rulemaking to require harvest registration time be reduced to 8 hours, instead of 24 hours, which would allow the Wisconsin DNR to better monitor harvest data and ensure timely zone closures (WI DNR 2023a, p. 144). The Wisconsin Plan also recommends issuing gray wolf harvesting licenses that are only valid in specific zones, which would allow for better regulation of season duration and harvest rates (WI DNR 2023a, p. 145). During previous regulated harvests in Wisconsin, licenses were valid in any harvest zone that remained open, which made it challenging for the Wisconsin DNR to regulate harvest pressure. The Wisconsin Plan recommends the number of licenses issued be based on zone-specific factors (WI DNR 2023a, pp. 145). This zone-specific license issuance would help Wisconsin DNR meet harvest management objectives within each zone while minimizing potential to exceed harvest quotas.

According to the Wisconsin Plan, the Wisconsin DNR would annually engage the Wolf Advisory Committee, comprised of Wisconsin DNR staff, other government agencies, non-governmental organizations, tribal representation, and conservation groups, to review data, evaluate progress towards plan objectives, and assist in the development of gray wolf harvest quotas (if the species was federally delisted). The Wisconsin DNR would decide whether to increase, decrease, or maintain gray wolf numbers in a specific management zone based on measurable criteria that encompass biological and social factors in each zone, and based on recommendations from the Wolf Advisory Committee (WI DNR 2023a, pp. 111, 145, 157–159).

When gray wolves are not federally listed, they are afforded various protections under state law in Wisconsin to regulate legal removal and prevent illegal take. To minimize illegal take, the Wisconsin Plan would support law enforcement in enforcing existing laws and ensure appropriate legal protection for gray wolves (WI DNR 2023a, pp. 131–132). This would be accomplished through review and updates to regulations, encouraging voluntary compliance with existing laws (e.g., making hunting and trapping regulations widely available, advertising the tip hotline to report illegal activity), investigating illegal activity in a timely manner, and pursuing administrative rulemaking to prohibit intentional destruction of active gray wolf dens and provide guidance to minimize den disturbance (WI DNR 2023a, pp. 131–132).

In summary, the main goal of the Wisconsin Plan is to "ensure a healthy and sustainable gray wolf population that fulfills the numerous ecological, cultural and recreational benefits of gray wolves, while being responsive in addressing and preventing wolf-related conflicts and recognizing the diverse values and perspectives of all citizens in Wisconsin" (WI DNR 2023a, p. 112). Under this plan, the Wisconsin DNR would, at a minimum, ensure the population remains above the current state threatened species level (i.e., 250 gray wolves outside of tribal reservations), which is above the Federal recovery plan's criteria for a second population (Service 1992, p. 4; WI DNR 2023a, pp. 126–127). Under the Wisconsin Plan, the Wisconsin DNR will manage gray wolves closer to current population levels (i.e., overwinter estimates of approximately 800–1,200 wolves), which takes into consideration the best estimate of sustainable carrying capacity in the state and reflects the social science findings that most Wisconsin citizens would prefer "about the same number" of wolves or more in the state (Bradshaw et al. 2022, pp. 41–42; WI DNR 2023a, pp. 127–129).

State Management of Wolves in the Remainder of the Eastern United States

Other than Michigan, Minnesota, and Wisconsin, none of the states in our analysis area have a specific management plan for gray wolf. However, several of these states list gray wolf as a protected species and/or have management recommendations or regulations focused on the species. Below, we outline the regulations and management across our analysis area outside of the Western Great Lakes states.

In Missouri, New Hampshire, and Texas, the gray wolf is state listed as endangered, but the species is considered extirpated. Given that gray wolves do not currently occupy these states, nor do they expect such occupation in the near future, these states have not developed management plans for the species (Missouri Department of Conservation (MDC) no date, entire; New Hampshire Fish and Game 2015, Appendix A Mammals-10; Texas Parks and Wildlife Department no date, entire). Gray wolf is also listed as state endangered but extirpated in New York; however, the New York Department of Environmental Conservation recently drafted a gray wolf species status assessment that outlines legal protections and provides recommendations for surveying large mammals that are considered extirpated from the state (New York State Department of Environmental Conservation (NYSDEC) 2017, entire). Specifically, as a state listed endangered species in New York, gray wolf is protected by environmental conservation laws (Section 11-0535 and New York Code of Rules and Regulations 6 Part 182), which require a permit for any proposed project that may result in take of a threatened or endangered species, including but not limited to actions that may kill or harm individual animals or result in the adverse modification, degradation, or destruction of habitat occupied by the listed species (NYSDEC 2017, p. 11). The species status assessment also provides recommendations for evaluating and managing the possible reintroduction of extirpated mammals, which include conducting surveys to gauge public opinion and implementing ecologically sound management (NYSDEC 2017, p. 12). Despite these recommendations, we are not currently aware of any intentions to reintroduce wolves to New York.

In Maine and Vermont, gray wolf is neither state listed nor are there currently any formal wolf management plans or regulations. However, these states both provide recommendations or guidance focused on the species. The Maine Department of Inland Fisheries and Wildlife (MDIFW) recommends that all wolf sightings be reported, that large blocks of forest in northern and western Maine be maintained for potential recovery, and that wolf dens or rendezvous sites be left undisturbed (MDIFW 2003, p. 2). Although the gray wolf is presumed extirpated in Vermont, the Vermont Wildlife Action Plan includes research and monitoring needs for the species (Vermont Fish and Wildlife Department 2015, p. 104). This document also outlines a species strategy aimed at better understanding public attitudes towards wolves and developing a response to possible wolf immigration (Vermont Fish and Wildlife Department 2015, p. 104). While gray wolves are protected under the Act, they may only be taken in defense of human life (Section 11(a)(3)), regardless of state rules and regulations discussed below. If gray wolves were no longer federally listed, they would be subject to state management.

The following information describes how individual states would manage the species. Illinois, Indiana, Iowa, Nebraska, North Dakota, and South Dakota have regulations permitting take of gray wolves that pose a threat to people and, in some cases, property (including livestock). In the latest iteration of the Illinois endangered species list, which was published in 2020, the gray wolf is listed as endangered to reflect the species' Federal listing status at the time (ILDNR 2020, entire). However, wolves may be lethally removed by landowners when they pose an imminent threat of physical harm or death to a human; the state also allows landowners to lethally remove wolves if they pose an imminent threat of harm to livestock, domestic animals, or structures or other property when federally delisted (Illinois General Assembly no date, entire). The status of gray wolf in Illinois will be reevaluated based on the species' Federal listing status when the Illinois endangered species list is updated in 2025 (ILDNR 2020, entire). In Indiana, state law allows resident landowners or tenants to lethally remove a gray wolf if it poses a threat to people or while it is causing damage to property owned or leased by the landowner or tenant when federally delisted. In Nebraska, the gray wolf is automatically protected by state regulation when it is federally listed, but is classified as an unprotected nongame species that may be taken year-round by any legal means when federally delisted and managed under state authority (Nebraska Game and Parks Commission no date, entire; Wilson 2023, pers. comm.). In South Dakota, when the gray wolf is not federally protected, it is managed as a predator that can be harvested by any legal means without limit across the state; when the gray wolf is federally protected, it may only be lethally removed when posing a danger to human life (South Dakota Game, Fish, and Parks, no date; Fisk 2023, pers. comm.). Iowa's regulations classify the gray wolf as a furbearer, but this is due to a historical lack of differentiation between gray wolves and coyote in early legislation (Iowa Department of Natural Resources (IADNR) 2014, p. 2; IADNR 2017, p. 2). As such, the gray wolf is protected by state furbearer laws, which allow for regulated harvest, but the harvest season for the species is indefinitely closed (IADNR 2014, p. 2; IADNR 2017, p. 2). However, a gray wolf could be lethally removed if it was causing livestock damage, if the species is not federally protected (IADNR 2014, p. 2). Similarly, gray wolves in North Dakota are classified as a furbearer with a closed season (Burgum 2022, in litt.; Tucker 2023, pers. comm.).

The remaining states in our analysis area (i.e., Connecticut, Kansas, Massachusetts, New Jersey, Ohio, Pennsylvania, and Rhode Island) lack state-level protections, management recommendations, or regulations for gray wolf.

Federal Management

Federal lands cover approximately 4 percent of our entire analysis area in the Eastern United States (Figure 10). However, not all of these Federal lands contain suitable habitat for gray wolves nor are they all large and connected enough to sustain a gray wolf population.

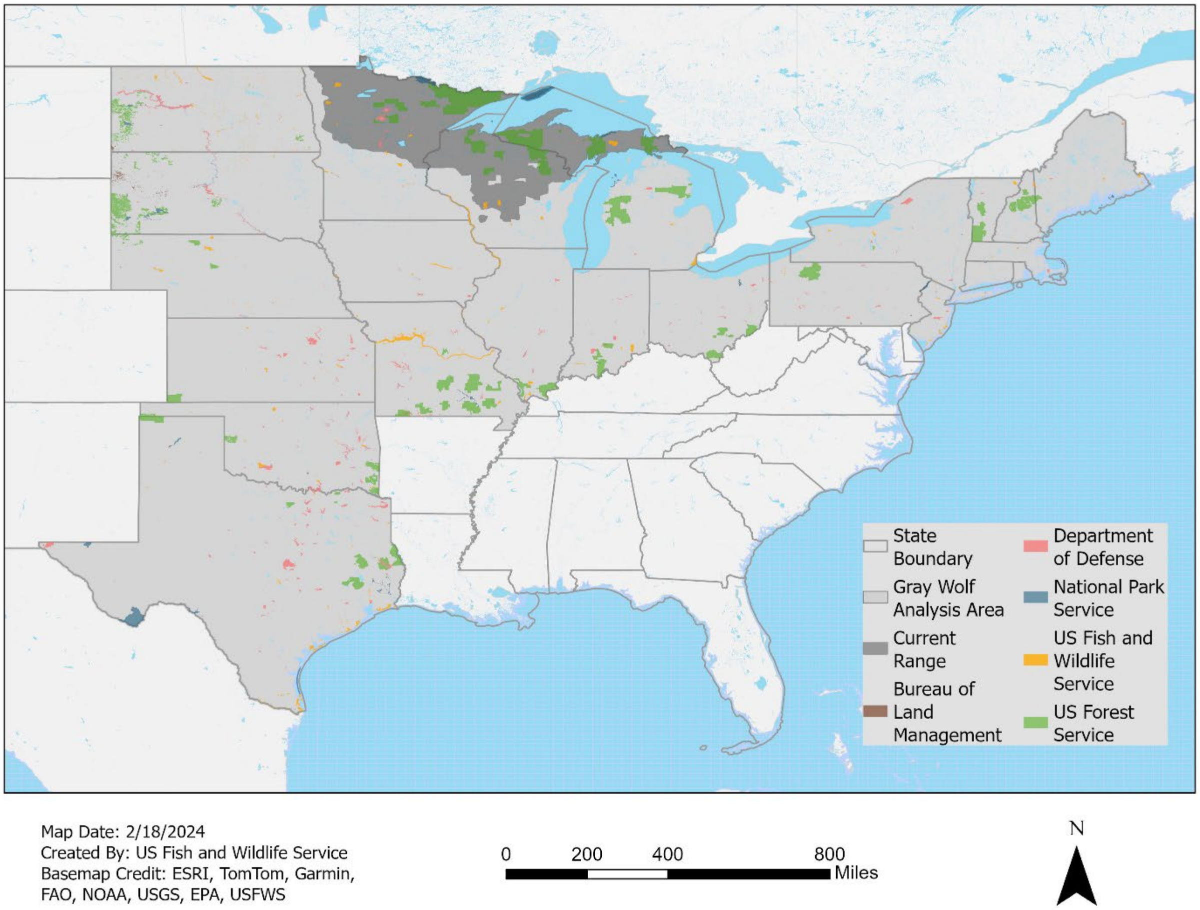

Figure 10. Primary federal land management agencies within our analysis area and the eastern United States. Federal land ownership includes Forest Service, NPS, U.S Fish and Wildlife Service, Department of Defense, and Bureau of Land Management. [Source for Federal land ownership data: BLM 2024].

Approximately 17 percent of the gray wolf's current range (i.e., Western Great Lakes area only) is Federal land managed by the U.S. Forest Service (Forest Service), NPS, U.S. Fish and Wildlife Service – National Wildlife Refuge System, and Department of Defense, with a small amount of Bureau of Land Management (BLM) lands (Figure 11). While gray wolves are federally listed, take is regulated pursuant to the Act. If gray wolves are federally delisted, the states would assume authority to regulate human-caused mortality within the states, outside of Tribal lands. Thus, while Federal land may provide safeguards for gray wolf habitat, human-caused mortality from harvest and lethal depredation control is not necessarily limited on Federal lands but is instead regulated at the state level (see *State Management* above for more details). If federally delisted, all known take of gray wolves on Federal lands would contribute to and inform the states' management objectives and thresholds. We summarize Federal land management in current gray wolf range in this section, however, to describe their conservation efforts and how they may further benefit gray wolf populations.

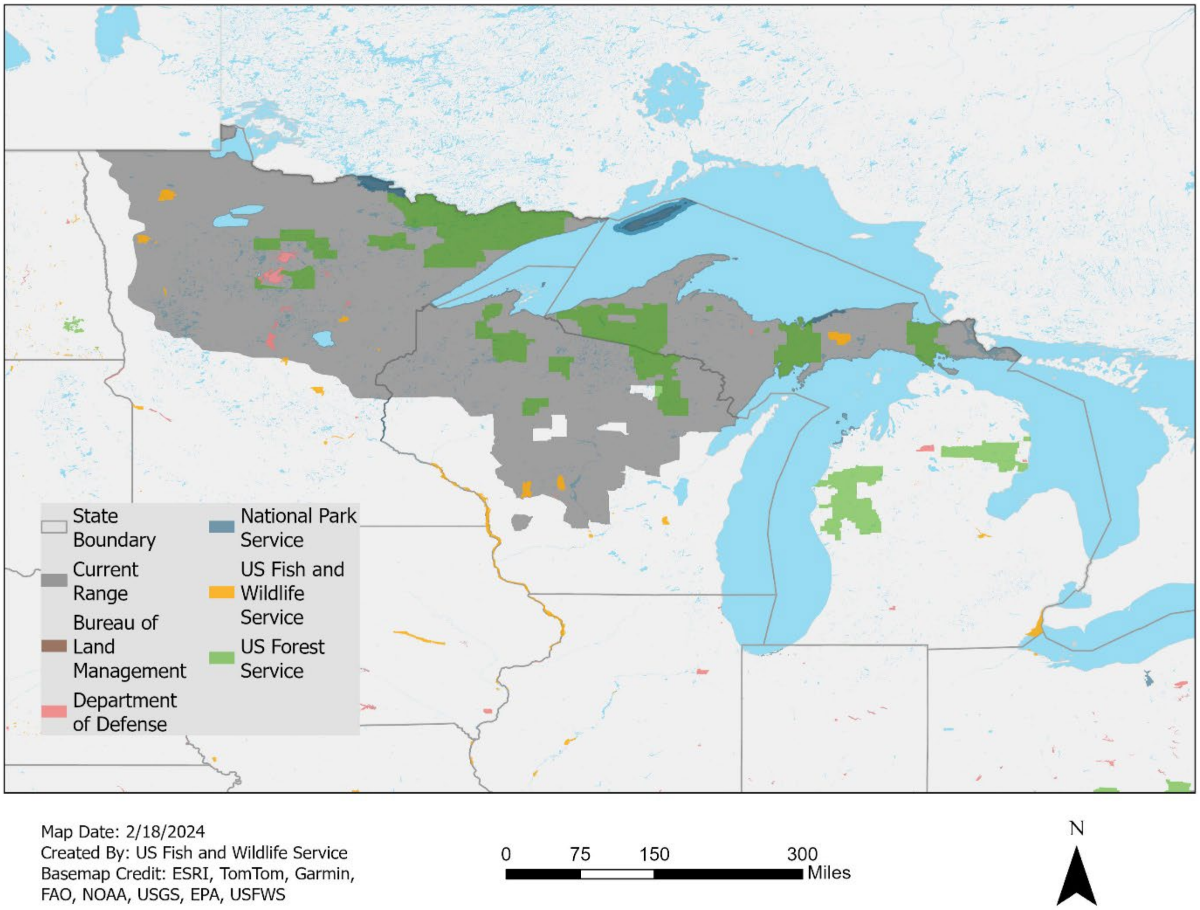

Figure 11. Primary federal land management agencies within the current range of gray wolf in the Eastern United States. Federal land ownership includes Forest Service, NPS, U.S Fish and Wildlife Service, Department of Defense, and Bureau of Land Management. [Source for Federal land ownership data: BLM 2024].

The Forest Service manages 16 percent (13,956 mi^2 (36,145 km^2)) of current gray wolf range in the Eastern United States (Figure 11). The BLM manages a small area (10 mi^2 (25 km^2)) in current gray wolf range in Minnesota and Wisconsin (Figure 11). The Forest Service and BLM manage for multiple uses, including providing habitat for fish and wildlife such as gray wolves. The other uses include, but are not limited to, providing opportunities for outdoor recreation (including hunting and trapping), livestock grazing (primarily in the Western United States), rights-of-way for energy transmission and roads, energy development, mining, and timber harvest. The Forest Service and BLM typically defer to the states on hunting and trapping decisions (16 U.S.C. 480, 528, 551, 1133; 43 U.S.C. 1732(b)). The primary exception to this deference is the Forest Service's authority to identify areas and periods when hunting or trapping is not permitted for reasons of public safety, administration, or compliance with provisions of applicable law (43 U.S.C. 1732(b)); however, even these decisions, except in the case of emergencies, must be developed in consultation with the states. In areas that are occupied by gray wolves, the Forest Service and BLM work with Federal and state partners to identify and implement management strategies consistent with state plans to minimize gray wolf conflict risk on Federal lands.

The five national forests with resident gray wolves in Michigan, Minnesota, and Wisconsin (Chequamegon-Nicolet, Chippewa, Hiawatha, Ottawa, and Superior National Forests) have operated in conformance with standards and guidelines in their management plans that follow the Federal Recovery Plan's recommendations for gray wolves in the Eastern United States (USDA Forest Service 2004a, p. 2-31; USDA Forest Service 2004b, p. 2-28; USDA Forest Service 2004c, p. 2-19; USDA Forest Service 2006a, p. 2-17; USDA Forest Service 2006b, pp. 2-28–2-29). Under these standards and guidelines, a relatively high prey base would be maintained, and road densities would either be limited to current levels or decreased. For example, on the Chequamegon-Nicolet National Forest in Wisconsin, the standards and guidelines specifically include the protection of den sites and key rendezvous sites, and management of road densities in existing and potential gray wolf habitat (USDA Forest Service 2004c, p. 2-19).

The trapping of depredating gray wolves may be allowed (currently in Minnesota and if federally delisted in Michigan and Wisconsin) on National Forest lands under the guidelines and conditions specified in the respective state management plans. However, there are relatively few livestock raised within the boundaries of National Forests in the Western Great Lakes area, so gray wolf depredation and lethal depredation control is not likely to be a frequent occurrence, or to constitute a significant mortality factor, for the gray wolves on Federal lands in the Western Great Lakes area. Similarly, in keeping with the practice for other state-managed game species, any regulated hunting or trapping season that might be opened to the public if gray wolves were federally delisted may include hunting and trapping within the National Forests. Additionally, the five National Forests occasionally collaborate with state and tribal researchers to trap and collar gray wolves in National Forests to collect health, movement, habitat, and mortality data. For example, in 2022, the Sault Ste Marie Tribe of Chippewa collared five gray wolves in the Hiawatha National Forest in coordination with Forest Service biologists.

The NPS manages 655 mi^2 (1,697 km^2) within the current gray wolf range in the Eastern United States (0.7 percent of the current range) (Figure 11). Gray wolves regularly use four units of the National Park System in the Great Lakes area and may occasionally use an additional three or four units. Although the NPS has participated in the development of some of the state gray wolf-management plans in this area, NPS is not bound by state plans. Instead, the Organic Act of 1916, which established the NPS, and the NPS Management Policies (NPS 2006, entire) generally require the agency to conserve natural and cultural resources and the wildlife present within the parks. The NPS management policies require that native species be protected against harvest, removal, destruction, harassment, or harm through human action. Should gray wolves be delisted, management emphasis in National Parks would continue to minimize the human impacts on gray wolf populations. Overall, National Parks are managed in such a way as to provide habitat for wildlife, including gray wolves and their prey. Thus, because of their responsibility to preserve all native wildlife, units of the National Park System are often the most protective of wildlife.

If gray wolves are delisted, management and protection of gray wolves in Voyageurs National Park, along Minnesota's northern border, is unlikely to change. No population targets for gray wolves would be established for the National Park (Holbeck 2005, in litt.). To reduce human disturbance, temporary closures around gray wolf denning and rendezvous sites would be enacted whenever they are discovered in the park. Hunting is already prohibited on park lands, regardless of what may be allowed beyond park boundaries (West 2004, in litt.).

The gray wolf population of Isle Royale National Park, Michigan, is small (typically varies from 18 to 27 individuals), relatively isolated, and lacks unique genetic diversity (Wayne et al. 1991, pp. 45–47; Robinson et al. 2019, entire). For these reasons, and due to constraints on expansion because of the island's small size (210 mi^2 (546 km^2)), this gray wolf population does not contribute significantly towards overall abundance in the state. However, long-term research on this gray wolf population has added a great deal to our knowledge of the species. The gray wolf population on Isle Royale was down to just two individuals (a father-daughter pair) from the winter of 2015/2016 until 2018 (Peterson et al. 2018, pp. 4–5). In 2018, the NPS announced plans to move additional gray wolves to Isle Royale in an effort to restore a viable population (83 FR 11787, March 16, 2018). Between October 2018 and September 2019, 19 gray wolves were translocated to Isle Royale National Park (Romanski et al. 2020, entire; Hoy et al. 2022, p. 9). As of January 2024, the population on Isle Royale National Park is estimated to be 30 gray wolves and has been relatively stable during the last three winter seasons (Hoy et al. 2024, pp. 7).

Gray wolves regularly use two other units (Pictured Rocks National Lakeshore and St. Croix National Scenic Riverway) and occasionally use one unit (Apostle Islands National Lakeshore) of the National Park System. Pictured Rocks National Lakeshore (Lakeshore) is a narrow strip of land along Michigan's Lake Superior shoreline. Gray wolves periodically use, and may be year-round residents of, the Lakeshore. The Lakeshore is working to secure funding to learn more about gray wolf use in the park, as there is evidence use has increased in recent years. If gray wolves were to be delisted, the Lakeshore would protect denning and rendezvous sites based on recommendations in the Michigan Plan. Harvesting gray wolves on the Lakeshore may be allowed if the Michigan DNR allows for harvest in the state, but trapping would not be allowed (Waller 2023, in litt.). The St. Croix National Scenic Riverway (Riverway), in Minnesota and Wisconsin, is also a mostly linear ownership. Should gray wolves be delisted, the Riverway would follow recommended management and protective practices outlined in the respective state gray wolf management plans. If a gray wolf season is enacted by the Minnesota or Wisconsin DNRs, then the Riverway fee-owned lands open to hunting would be open to gray wolf hunting as well, although trapping would not be allowed on NPS lands (Nagorka 2023, in litt.). At least one pack of four to five gray wolves occasionally use the shoreline areas of the Apostle Islands National Lakeshore (Burkman 2023, in litt.).

The Service manages 514 mi^2 (1,331 km^2) within current gray wolf range in the Eastern United States (0.6 percent of the current range) (Figure 11). Wolves occur on the following Refuges in the Western Great Lakes area: Agassiz National Wildlife Refuge (Minnesota), Crane Meadows National Wildlife Refuge (Minnesota), Hamden Slough National Wildlife Refuge (Minnesota), Necedah National Wildlife Refuge (Wisconsin), Rice Lake National Wildlife Refuge (Minnesota), Seney National Wildlife Refuge (Michigan), and Tamarac National Wildlife Refuge (Minnesota). National Wildlife Refuges operate under individual Comprehensive Conservation Plans, which guide their management. Harvest of gray wolves is also not allowed on National Wildlife Refuges lands in the contiguous United States except on wetland management districts, which are automatically open to hunting subject to state regulations (https://www.fws.gov/hunting/map). Overall, National Wildlife Refuge lands are managed in such a way as to provide habitat for wildlife, including gray wolves and their prey. Should gray wolves be federally delisted, trapping or hunting by government trappers for depredation control would not be authorized on National Wildlife Refuges. Because of the relatively small size of these Refuges, however, most or all gray wolf packs or individual gray wolves in these Refuges also spend significant amounts of time outside these Refuges, where such practices may be allowed.

The Department of Defense manages 167 mi^2 (432 km^2) within current gray wolf range in the Eastern United States (0.2 percent of the current range) (Figure 11). Gray wolves occupy the Fort McCoy military installation in Wisconsin and the Minnesota National Guard's Camp Ripley. The Fort McCoy military installation will continue to protect den and rendezvous sites, close hunting seasons for other species (coyote) during the gun deer season, and conduct gray wolf population surveys regardless of Federal listing status. Fort McCoy has no plans to allow harvest of gray wolves on the installation (Weichelt 2023, in litt.). Minnesota National Guard's Camp Ripley contains portions of two pack territories, which typically include 10 to 20 wolves. There have been no significant conflicts with military training nor with the permit-only public deer-hunting program at the camp (Kitzmann 2023, in litt.).

The Wilderness Act of 1964 established a system for preserving wilderness areas on Federal lands. Wilderness areas, which are managed by the Forest Service, NPS, the U.S. Fish and Wildlife Service, or BLM, afford significant protections to wildlife within their borders because, with few exceptions, development, roads, landing aircraft, and mechanical transport are prohibited. Large wilderness areas, which have more limited human access, can provide refugia (an area shielded from stressors) for gray wolves (Barber-Meyer et al. 2021, pp. 10–11), even though hunting and trapping are allowed in these areas. In a 50-year study of gray wolves in the Western Great Lakes region, survival rates were higher within wilderness areas compared to surrounding Federal land (Barber-Meyer et al. 2021, pp. 10–11). Designated wilderness areas comprise 2.5 percent of the gray wolf's current range (Figure 12), therefore the potential for large wilderness areas to provide refuge are limited, especially outside Minnesota.

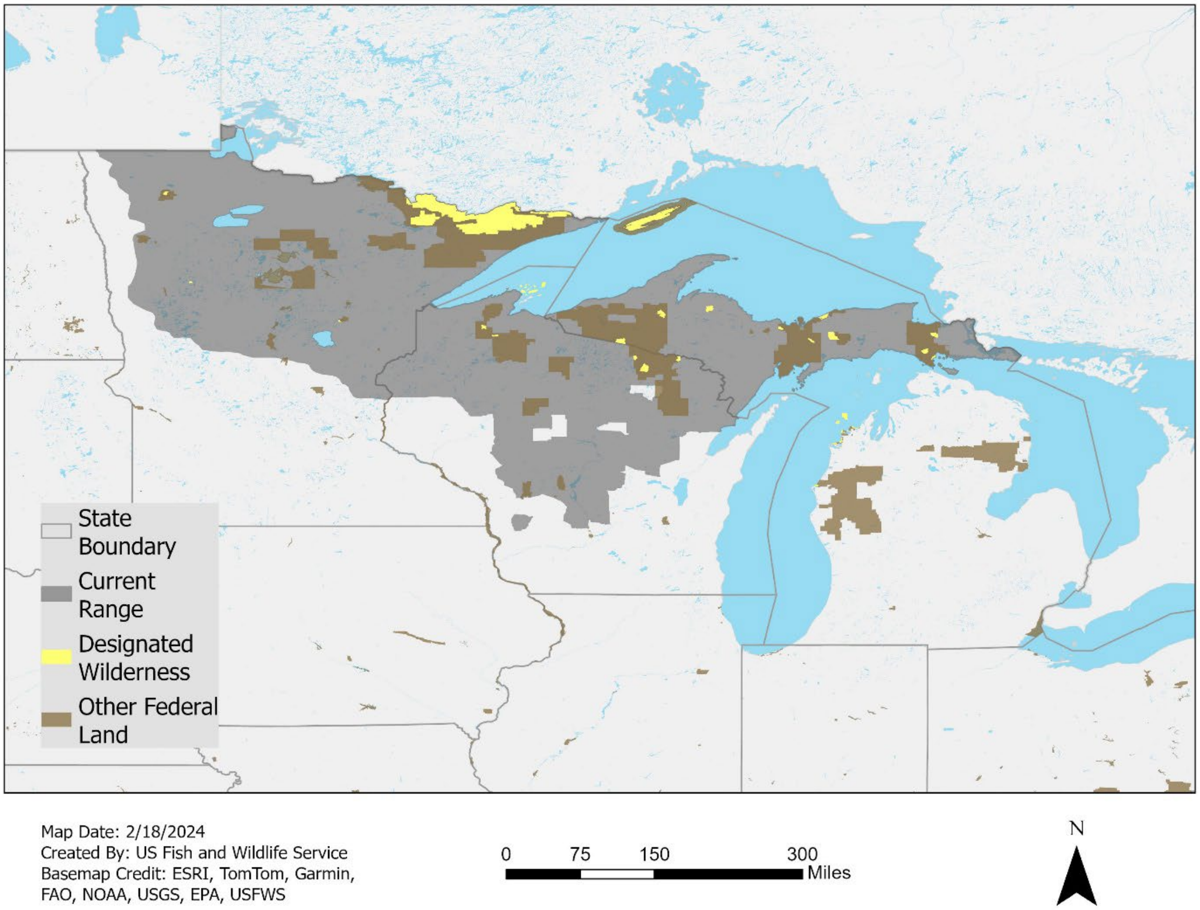

Figure 12. Federal land and wilderness areas within the current range of gray wolf in the Eastern United States. [Source for Federal land ownership: BLM 2024; Source for wilderness areas: U.S. Geological Survey (USGS) Gap Analysis Project (GAP) 2024]

Tribal Management and Stewardship in the Western Great Lakes Region

The wolf retains great cultural significance and traditional value to many Tribal Nations and their members throughout the Eastern United States and beyond. The Anishinaabe (the Chippewa/Ojibwe, the Ottawa/Odawa, and the Potawatomi/Bodewadmi) creation story shares that "Ma'iingan (wolf) was provided by the Creator to be a companion to the Original Man," and the Anishinaabe people in the Western Great Lakes region consider the wolf as their relative (Gilbert et al. 2022, p.2). This section focuses on tribal stewardship within the Western Great Lakes area where gray wolves occur. To retain and strengthen cultural connections, many Tribal Nations oppose unnecessary killing of gray wolves on reservations and on ceded lands, even if gray wolves were to be federally delisted (Dupuis 2019, in litt.; Harrington 2019, in litt.; Isham 2019, in litt.; Loonsfoot 2019, in litt.; Gilbert et al. 2022, entire; Schlender 2023b, in litt.). Many Tribal Nations aim to sustainably manage their natural resources, gray wolves among them, to ensure that they are available to their descendants. Although not all Tribal Nations with gray wolves that visit or reside on their reservations have completed stewardship plans specific to the gray wolf, several Tribal Nations have passed resolutions or otherwise informed us that they have no plans or intentions to allow commercial or recreational hunting or trapping of the species on their lands if gray wolves are no longer federally protected. It is important to note that while many tribes want to protect wolves that live on their lands, there are still challenges when it comes to managing wolves that fall under multiple jurisdictions (e.g., Ceded Territories). In these areas, harvest of wolves may be allowed by states when they are not federally listed.

As reflected by their submitted comments and communications with the Service, the Western Great Lakes Tribal Nations, their inter-tribal natural-resource-management agencies, and inter-tribal government agencies (e.g., the Great Lakes Indian Fish and Wildlife Commission and the United Tribes of Michigan), hold a predominant sentiment of strong support for the continued protection of gray wolves in a manner that will ensure occupancy by gray wolves on reservations and throughout the treaty-ceded lands[12] surrounding the reservations within the Western Great Lakes area. However, individual tribal members may harvest a small number of gray wolves for spiritual or other purposes if they are federally delisted.

The Keweenaw Bay Indian Community (Michigan), Little River Band of Ottawa Indians (Michigan), Little Traverse Bay Band of Odawa Indians (Michigan), Sault Ste. Marie Tribe of Chippewa Indians (Michigan), Grand Portage Band of the Minnesota Chippewa Tribe (Minnesota), Fond du Lac Band of the Minnesota Chippewa Tribe (Minnesota), Red Lake Band of Chippewa (Minnesota), White Earth Band of the Minnesota Chippewa Tribe (Minnesota), Bad River Band of Lake Superior Chippewa (Wisconsin), and the Red Cliff Band of Lake Superior Chippewa (Wisconsin) have developed gray wolf monitoring, management, and/or stewardship plans. Leech Lake Band of the Minnesota Chippewa Tribe (Minnesota) has passed resolutions concerning any future harvest of gray wolves and the Menominee Indian Tribe (Wisconsin) has participated in gray wolf translocations and monitoring. In addition to these plans and resolutions by individual Tribal Nations, the Great Lakes Indian Fish and Wildlife Commission developed a Ma'iingan Relationship Plan for the 1837/1842 Ceded Territory (David 2022, entire). Below, we summarize the gray wolf monitoring, management or stewardship plans for these Tribal Nations and one inter-tribal natural-resource-management agency within the Western Great Lakes area (the current range of the gray wolf in the Eastern United States) that have been shared with us or are otherwise publicly available.

Red Lake Band of Chippewa Indians

The Red Lake Band of Chippewa Indians of Minnesota completed a gray wolf management plan in 2010 (Red Lake Band of Chippewa Indians 2010, entire). A primary goal of the management plan is to maintain gray wolf numbers at a level that will ensure their long-term survival on Red Lake lands (more than 1,317 mi^2 (3,411 km^2) of reservation lands and restored ceded lands). Key components of the plan are habitat management, public education, and law enforcement. To address human–gray wolf interactions, the plan outlines the circumstances under which gray wolves may be taken on Red Lake lands while federally protected and regulated under the existing 4(d) rule. Gray wolves thought to be a threat to public safety may be harassed at any

[12] Portions of the upper and lower peninsulas of northern Michigan, northeastern Minnesota, and northern Wisconsin that were ceded by tribes of the Ojibwe to the government of the United States of America in the treaties of 1836, 1837, 1842, and 1854.

time, and if they must be lethally removed, the incident must be reported to tribal law enforcement. Livestock are not common on Red Lake lands, and gray wolf-related depredation on livestock or pets is unlikely to be a significant management issue. If such events do occur, tribal members may protect their livestock or pets by lethal means, but first "all reasonable efforts should be made to deter wolves using nonlethal means" (Red Lake Band of Chippewa Indians 2010, p. 15). If gray wolves were to be federally delisted, hunting or trapping of wolves on tribal lands would be prohibited.

Fond du Lac Band of the Minnesota Chippewa Tribe

The Fond du Lac Band (Band) of the Minnesota Chippewa Tribe believes that the "well-being of the wolf is intimately connected to the well-being of the Chippewa People" (Schrage 2003, in litt.). In 1998, the Band passed a resolution opposing Federal delisting and any other measure that would permit trapping, hunting, or poisoning of the gray wolf (Schrage 1998, in litt.; Schrage 2003, in litt.; Schrage 2009, pers. comm.). If the prohibition of trapping, hunting, or poisoning is rescinded, the Band's Resource Management Division would coordinate with state and Federal agencies to ensure that any gray wolf hunting or trapping would be "conducted in a biologically sustainable manner" (Schrage 2003, in litt.). The Band finalized a gray wolf management plan for the Fond du Lac Reservation in 2012. A primary goal of the management plan is to maintain gray wolf numbers at levels that will contribute to the long-term survival of the species. The plan expresses the Band's belief that humans and gray wolves need to coexist, in accordance with the Band's traditions and customs and, thus, also recognizes that a system must be developed to deal with concerns for human safety and instances of depredation by gray wolves on livestock and pets.

Grand Portage Band of the Minnesota Chippewa Tribe

The Grand Portage Band of the Minnesota Chippewa Tribe (Band) does not have a gray wolf stewardship or management plan; however, their general management strategies focus on ecosystem health, such as the relationship between moose and gray wolves. The Grand Portage Band has contributed to scientific research focused on gray wolf population dynamics, prey interactions (especially moose), and the impacts of climate warming on gray wolves. The Band conducts ongoing studies and monitoring of wolf populations, including tracking wolf movements and assessing pack numbers and health. This research informs land-use decisions and helps ensure the long-term survival of wolves in the region.

Leech Lake Band of the Minnesota Chippewa Tribe

The Tribal Council of the Leech Lake Band of Minnesota Ojibwe approved a resolution that describes the sport and recreational harvest of gray wolves as an inappropriate use of the animal (Googgleye 2004, in litt.). That resolution supports limited harvest of gray wolves by enrolled tribal members, if the animals are to be used for traditional or spiritual purposes, if the harvest is done in a respectful manner, and if the harvest would not negatively affect the gray wolf population (Googgleye 2004, in litt.). As of 2011, the Leech Lake Reservation was home to an estimated 60 gray wolves (Mortensen et al., no date). More recent survey data are currently not available; however, the Band's Division of Natural Resource Management recently started a wolf monitoring project, and began collaring wolves in spring 2023 (Roerick 2023, in litt.).

White Earth Band of the Minnesota Chippewa Tribe

The White Earth Band of the Minnesota Chippewa Tribe has established a comprehensive plan to protect and ensure the long-term survival of Ma'iinganeg (gray wolves) on the White Earth Reservation. The White Earth Reservation was designated as a wolf sanctuary on August 20, 2012. Hunting or trapping of wolves by both Tribal and non-Tribal members within the original 1867 boundaries of the Reservation is prohibited, as outlined in the amended White Earth Conservation Code (White Earth Tribal Council 2014, pp. 92–93). The White Earth Band have developed the Wolf (Ma'iingan) Management Plan (McArthur 2015, entire) that recognizes the cultural significance of wolves to the Anishinaabeg people. The primary objective of the Wolf Management Plan is to allow a stable and growing wolf population, permitting the taking of wolves only in cases of imminent threat to people, pets, or livestock. As described in the Wolf Management Plan, the White Earth Natural Resources Division will monitor wolf populations, implement habitat management strategies, assess wolf depredation and mitigation, enforce their Conservation Code when a wolf has been illegally taken, and provides educational resources on wolves and their management (McArthur 2015, pp. 7–8).

Red Cliff Band of Lake Superior Chippewa

The Red Cliff Band of Lake Superior Chippewa in Wisconsin implemented a Wolf Protection Plan in 2015 (Red Cliff Band of Lake Superior Chippewa 2015, entire). This plan guides management of gray wolves on the Reservation and prohibits any hunting of gray wolves during any future state managed harvests. The plan calls for increased research and monitoring of gray wolves on the Bayfield Peninsula, which may help guide the management and protection of gray wolves if federally delisted. The plan includes a 6-mile (9.7-km) buffer outside of Reservation boundaries, in which the Red Cliff Band will work cooperatively to mitigate human–gray wolf conflicts. Implementation of the plan includes: collaring and monitoring local packs, seeking Federal grants for prevention and compensation for gray wolf depredation events on the Bayfield Peninsula, education, and outreach.

Bad River Band of Lake Superior Chippewa

The Bad River Band of Lake Superior Chippewa in Wisconsin established a Ma'iingan Management Plan for the Reservation in 2013 (Hill 2013, entire). This plan was updated in 2019 and renamed as the Ma'iingan (Wolf) Relationship Plan (Fergus and Hill 2019, entire) in recognition of the wolf as a relative with whom a relationship is built, rather than managed. The Relationship Plan provides "guiding principles for the [Band] to understand and coexist with Ma'iingan and to teach others to do the same" (Fergus and Hill 2019, p. 8). The Mashkiiziibing (Bad River Reservation) Wildlife Program (MWP) does not have a specific gray wolf population goal, however they will strive for a minimum of three packs that at least partially occupy the reservation (Fergus and Hill 2019, pp. 31, 32). An emergency rule approved by the Tribal Council in 2012 prohibits the harvest of gray wolves within the boundaries of the reservation (Fergus and Hill 2019, p. 34). A goal of the Relationship Plan is to use non-lethal solutions to prevent wolf-human conflicts whenever possible; if gray wolves were to be federally delisted, lethal depredation control on the reservation would only be used in situations where non-lethal methods have not worked or are not feasible (Fergus and Hill 2019, pp. 32, 43–45). The MWP will continue to use both traditional ecological knowledge and western science to monitor the gray wolf population in and around the reservation (Fergus and Hill 2019, pp. 32–33)

Menominee Indian Tribe of Wisconsin

The Menominee Indian Tribe of Wisconsin is committed to ensuring the long-term survival of the gray wolf in Menominee, placing emphasis on the cultural significance of the gray wolf as a clan member, and resolving conflicts between gray wolves and humans. The Tribe has shown a great deal of interest in gray wolf recovery and protection. In 2002, the Tribe offered their Reservation lands as a site for translocating seven depredating gray wolves that had been trapped by Wisconsin DNR and Wildlife Services. Tribal natural resources staff participated in the soft release of the gray wolves on the Reservation and helped with the subsequent radio-tracking. Although the last of these gray wolves died on the reservation by early 2005, the tribal conservation department continued to monitor another pair that had moved onto the Reservation, as well as other gray wolves near the reservation (Wydeven 2006, in litt.). When the female of that pair was killed in 2006, Reservation biologists and staff worked diligently to raise the orphaned pups in captivity with the Wisconsin DNR and the Wildlife Science Center (Forest Lake, Minnesota) in the hope that they could later be released to the care of the adult male. However, the adult male died prior to pup release, and they were moved back to the Wildlife Science Center (Callahan 2024, pers. comm). Between 2010 and 2018, the reservation generally supported 7 to 16 gray wolves in 3 or 4 packs (Menominee Tribal Conservation Department).

Little Traverse Bay Bands of Odawa Indians

In 2009, the Little Traverse Bay Bands of Odawa Indians (LTBB) in Michigan finalized a management plan for the 1855 Reservation and portions of the 1836 Ceded Territory in the northern Lower Peninsula of Michigan (LTBB Natural Resource Department 2009). The plan provides the framework for managing gray wolves with the goal of maintaining a viable gray wolf presence on the LTBB Reservation or within the northern Lower Peninsula should a population become established by: (1) prescribing scientifically sound biological strategies for gray wolf management, research, and monitoring; (2) addressing gray wolf-related conflicts; (3) facilitating gray wolf-related benefits; and (4) developing and implementing gray wolf-related education and public information.

Keweenaw Bay Indian Community

Should gray wolves be delisted, the Keweenaw Bay Indian Community (KBIC) in Michigan would continue to list the gray wolf as a protected animal under the Tribal Code, with hunting and trapping prohibited (Loonsfoot 2019, in litt.). Furthermore, KBIC developed a gray wolf management plan in 2013 that "provides a course of action that will ensure the long-term survival of a self-sustaining, wild gray wolf (*C. lupus*) population in the 1842 Ceded Territory in the western Upper Peninsula of Michigan" (Nankervis 2013, p. 1). The plan is written to encourage cooperation among agencies, communities, private and corporate landowners, special interest groups, and Michigan residents (Loonsfoot 2019, in litt.).

Sault Ste. Marie Tribe of Chippewa Indians

The Sault Ste Marie Tribe of Chippewa Indians does not have a stewardship or management plan specifically for gray wolves; however, gray wolf conservation is integrated into broader tribal co-stewardship and adaptive management initiatives. Additionally, they actively survey for gray wolves in the eastern Upper Peninsula as part of its broader conservation and stewardship efforts.

Chippewa Ottawa Resource Authority

The five member tribes of the Chippewa-Ottawa Resource Authority are the Bay Mills Indian Community, the Grand Traverse Band of Ottawa and Chippewa Indians, the Little River Band of Ottawa Indians, the Little Traverse Bay Bands of Odawa Indians, and the Sault Ste. Marie Tribe of Chippewa Indians. These tribes collaborate with the Michigan DNR and Wildlife Services – Michigan to conduct community-based surveys in the Lower Peninsula to detect potential presence of gray wolves. Sightings, photos and other signs of wolf presence can be reported by the public to the DNR's Eyes in the Field webpage. Additionally, the Little River Band of Ottawa Indians also actively surveys for gray wolves in the eastern Upper Peninsula, in collaboration with the Sault Ste. Marie Tribe of Chippewa Indians (see *Sault Ste. Marie Tribe of Chippewa* above).

Great Lakes Indian Fish and Wildlife Commission

The Ma'iingan Relationship Plan for the 1837/1842 Ceded Territory describes the relationship between the Anishinaabeg and ma'iingang and outlines several primary goals for gray wolves (David 2022, entire). Those goals were informed by traditional Ojibwe teachings, Traditional Ecological Knowledge, and contemporary science. In its simplest form, the central goal is to have "a healthy and ecologically functional ma'iingang population occupying all areas of suitable habitat" (David 2022, p. 8). The Relationship Plan affirms that ma'iingan themselves are best at determining their range, population levels, and population demographics, and that those should not be altered by human influences, including recreational harvest, which is noted as "incompatible with the goal of a healthy wolf population" (David 2022, p. 8). The Tribal Nations represented in the Relationship Plan recognize that wolves can have negative impacts on livestock producers; therefore, they encourage preventative and non-lethal programs and that lethal control of depredating wolves should be used only when those efforts are ineffective.

Stressors

Human-Caused Mortality

Causes of gray wolf mortality can be separated into two broad categories that include natural causes (e.g., intraspecific strife, disease, starvation, and accidents) and anthropogenic causes, or "human-caused mortality" (e.g., harvest, lethal control, illegal take, vehicle strikes, and human-caused accidental mortalities). Where gray wolf populations exist with no to minimal human influence (e.g., Yellowstone and Isle Royale National Parks), mortalities from natural causes are the primary cause of death. For example, known gray wolf mortalities on Isle Royale National Park are the result of natural causes primarily from intraspecific strife (Peterson and Page 1988, p. 94; Peterson et al. 1998, pp. 832, 834–839; Peterson et al. 2014, p. 331; Hoy et al. 2020, pp. 9–13; Romanski et al. 2020, pp. 4, 15). A few records indicate an 'unknown' cause of death (death investigated with no specific cause determined), but those were not attributed to human-caused mortality (Peterson 1992, p. 4; Hoy et al. 2020, p. 13; Romanski et al. 2020, p. 15). Where human influences are greater, human-caused mortality increases and becomes the primary cause of mortality (Murray et al. 2010, pp. 2514, 2518–2519; O'Neil et al. 2017, pp. 9524–9528; Stenglein et al. 2018, p. 104; Smith et al. 2020, p. 83; Chakrabarti et al. 2022, pp. 7, 9). Such causes are estimated to account for 60–70 percent of all mortalities in Michigan (O'Neil 2017, p.

214; MI DNR 2022a, p. 13), Minnesota (Chakrabarti et al. 2022, p. 9), and Wisconsin (Treves et al. 2017a, p. 27; Stenglein et al. 2018, p. 108; WI DNR 2023a, pp. 62–65).

In the Eastern United States, the primary stressor influencing gray wolf populations is human-caused mortality. European settlers to North America brought with them negative attitudes about wolves and, primarily due to the real or perceived threats to themselves and their livestock, attempted to eliminate them entirely (Boitani 1995, pp. 3–11). Bounties were used to incentivize the killing of wolves. The earliest known wolf bounty in the New World was enacted in 1630 in the Massachusetts colony. The U.S. Congress passed a wolf bounty that covered the Northwest Territories in 1817. Bounties on wolves subsequently became the norm for states across the species' range (Hampton 1997, pp. 107–108; Beyer et al. 2009, p. 66; Erb and DonCarlos 2009, p. 50; Wydeven et al. 2009a, p. 88; Service 2020, pp. 10–13). In Michigan, an 1838 wolf bounty became the ninth law passed by the First Michigan Legislature. In Minnesota, a wolf bounty was passed in 1849, and a wolf bounty was instituted in Wisconsin in 1865. Unregulated hunting and trapping, the excessive use of poison, and the activities of government trappers eradicated gray wolves across much of their historical range in the lower-48 United States in the early 1900s (Young and Goldman 1944, pp. 286–385; Weaver 1978, p. i; Hampton 1997, entire). At the time of listing, human-caused mortality was identified as the main factor responsible for the decline of gray wolves in the lower-48 United States (43 FR 9611, March 9, 1978).

After the gray wolf was listed under the Endangered Species Act of 1973, its protections, along with state endangered-species statutes, prohibited the intentional killing except under very limited circumstances. These circumstances included defense of human life, scientific or conservation purposes, and special regulations intended to mitigate repeated gray wolf depredations on livestock or other domestic animals. The regulation of human-caused mortality has long been recognized as the most significant factor affecting the long-term conservation of wolves and the primary reason gray wolf numbers have significantly increased, and their range has expanded since the mid-to-late 1970s (Smith et al. 2010, entire; O'Neil et al. 2017, entire; Stenglein et al. 2018, entire). However, a "natural" gray wolf population free from any human-caused mortality is not required for the conservation of the species (Mech 2021, p. 27).

Effects of Human-Caused Mortality

Effects on Population Growth

Understanding the complex and interacting factors that contribute to gray wolf mortality and how this mortality plays a role as a driver of population dynamics, including survival, population growth, and persistence, is an active area of research. The risk of human-caused mortality is not uniform and tends to be highest for younger age classes of gray wolves (Ballard et al. 1987, p. 28; Adams et al. 2008, p. 14; Smith et al. 2010, p. 627; Webb et al. 2011, p. 748; Schmidt et al. 2017, p. 23), dispersing individuals (Adams et al. 2008, pp. 14–22; Smith et al. 2010, pp. 630–631; Schmidt et al. 2017, p. 23; Morales-González et al. 2022, pp. 473, 477), and individuals that occupy more fragmented habitats with less cover (which are generally found on the peripheries of occupied gray wolf range) (Murray et al. 2010, pp. 2522–2523; Smith et al. 2010, pp. 630–631; O'Neil et al. 2017, pp. 9524–9528; Stenglein et al. 2018, p. 109; Bassing et al. 2019, p. 585; Chakrabarti et al. 2022, pp. 7–9). Gray wolf survival rates are higher in protected areas, such as National Parks or wilderness areas, where human access is limited and where the potential for conflict is low (Hebblewhite and Whittington 2020, p. 6; Barber-Meyer et al. 2021, pp. 5–10).

Compiled from studies across North America and Europe, estimates of adult and overall gray wolf annual survival rates have ranged between 0.59 to 0.89, with varied levels of human-caused mortality within each study population (see Chakrabarti et al. 2022, p. 8, Table 3).

The effects of increased mortality on a population can be described as compensatory or additive and are most commonly discussed in relation to increases in human-caused mortality. Compensatory mortality involves a change in the primary type of mortality, but no change in the overall mortality rate (e.g., if these animals were not harvested, they would have died anyway through a different cause). Additive mortality causes an immediate increase in the mortality rate because these additional individuals would have otherwise survived if the cause of the additive mortality was removed (Péron 2013, p. 409). Many wildlife populations can compensate for changing levels and types of mortality up to a certain point; after this point, mortality becomes additive and survival begins to decline. Gray wolves are no exception. As described in *Species Life History* in Chapter 1, density dependence and its effect on certain life history characteristics plays a large role in the ability of gray wolves to compensate for increased human-caused mortality. Although debate continues about which is most important, the three primary mechanisms with which gray wolf populations may compensate for increased human-caused mortality include a reduction in natural mortality (Fuller et al. 2003, pp. 185–186; Murray et al. 2010, pp. 2514, 2522; Webb et al. 2011, pp. 748–749; O'Neil 2017, pp. 218–219), increased natality rates and/or recruitment (Ballard et al. 1987, p. 44; Webb et al. 2011, pp. 748–750; Schmidt et al. 2017, pp. 18, 25; Smith et al. 2020, p. 81), and dispersal or immigration into the affected area (Ballard et al. 1987, p. 44; Adams et al. 2008, pp. 20–21; Bassing et al. 2019, pp. 585–586).

Due to strong compensatory mechanisms, the additive or compensatory nature of human-caused mortality and its numerical effects on gray wolf populations remains unclear (e.g., debate remains regarding when mortality switches from compensatory to additive). Some studies have documented that gray wolf populations partially compensate for human-caused mortality (Murray et al. 2010, p. 2522; O'Neil 2017, pp. 202, 218–222). Other studies have indicated that gray wolf harvest and control are additive to natural mortalities (Schmidt et al. 2017, pp. 15, 25; Horne et al. 2019, pp. 40–41). Some researchers have even indicated that increased levels of human-caused mortality may be super-additive through the loss of dependent offspring or future reproductive output (Creel and Rotella 2010, pp. 3–6); however, other researchers have challenged this finding (Gude et al. 2012, pp. 113–116) or noted that evidence for super-additive effects was weak (Horne et al. 2019, pp. 40–41). Still others have noted that there was no clear relationship between total human-caused and harvest mortality, which indicates that harvest was neither fully additive nor compensatory (Hill et al. 2022, p. 4). In Wisconsin, human-caused mortality was found to be additive during recolonization then transitioned to compensatory as the gray wolf population grew and expanded (Stenglein et al. 2018, entire). Theory supports the findings from Wisconsin and indicates that, in general, as populations grow, expand, and approach carrying capacity, their ability to compensate for human-caused mortality increases (Péron 2013, p. 408).

Management agencies use regulated harvest (i.e., hunting or trapping by private citizens) to manipulate gray wolf populations to achieve a desired objective (Horne et al. 2019, p. 40). However, harvest mortality may not be completely additive. When harvest is not completely additive, it may be more challenging to use harvest as a management tool to achieve an objective of reducing gray wolf abundance, especially when the population is large and well-distributed. For example, although human-caused mortality increased compared to other sources of mortality, little changes in gray wolf survival and abundance were documented in Minnesota between 2012 and 2014 when harvest was authorized (Erb et al. 2016, unpaginated; Chakrabarti et al. 2022, pp. 1, 6–9). Given the partially compensatory nature of human-caused mortality, a much higher percentage of the gray wolf population must be removed annually over multiple years to significantly reduce abundance (National Research Council 1997, p. 49; Fuller et al. 2003, pp. 185–186). Efforts to intentionally reduce gray wolf populations in localized areas have been successful in the short term; however, when these efforts ceased, populations quickly rebounded to pre-control levels or exceeded pre-control levels, demonstrating resilience to reduction efforts (Ballard et al. 1987, p. 30; Boertje et al. 1996, pp. 479–480, 487; Hayes and Harestad 2000, pp. 43–45; Hayes et al. 2003, pp. 14, 25–26; Boertje et al. 2017, p. 437; B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development (B.C. Ministry) 2021, entire).

There is considerable research and continued debate surrounding the level of human-caused mortality for which gray wolf populations can compensate and maintain population stability. Dependent on the analysis, researchers estimate that human-caused mortality rates between 17 and 48 percent result in gray wolf population stability (Fuller 1989, pp. 24–25, 34; Fuller et al. 2003, pp. 182–186; Adams et al. 2008, pp. 18–21; Creel and Rotella 2010, pp. 3–6; Gude et al. 2012, pp. 112–113; Vucetich and Carroll 2012, entire; ODFW 2015, p. 31; Hebblewhite and Whittington 2020, pp. 7–8). An analysis of mortality rates and population growth, reported from studies conducted across North America over an approximate 35-year period, indicates that gray wolves are able to compensate for annual rates of human-caused mortality up to approximately 29 percent of the known or estimated population (Adams et al. 2008, pp. 18–21). However, many of the studies reviewed to estimate this rate were based on autumn/winter minimum gray wolf population counts (Adams et al. 2008, pp. 18–21). Therefore, given that minimum counts likely underestimate true population size, the actual rate of mortality that allows for population stability may be lower than 29 percent. Some have posited that because growth rates used to estimate this gray wolf population stability threshold were obtained from a relatively small sample of the larger studied population, extrapolation to the larger population is questionable (Morales-González et al. 2022, pp. 471–472). These researchers cite an earlier study that suggested a reduction in wolf population growth rates across all levels of human-caused mortality (Creel and Rotella 2010, pp. 4-6; Morales-González et al. 2022, p. 472) to support their position, but fail to consider another study that challenged those findings and demonstrated that the inclusion of recruitment and human-caused mortality data better explained variation in wolf population growth (Gude et al. 2012, pp. 112–116).

Ultimately, gray wolf population sustainability is a function of the productivity and its proximity to other populations (Fuller et al. 2003, pp. 185–186). Where productivity is average to high and source populations are near, gray wolf populations can sustain higher rates of mortality than populations with lower productivity. This indicates that moderate increases in human-caused mortality may not have a large effect on overall gray wolf survival when mortality is partially compensatory (O’Neil 2017, p. 220) and the risk of inadvertently reducing abundance to a level that compromises population resiliency through regulated harvest is low (Boertje et al. 1996, p.

479; National Research Council 1997, pp. 91–121; Mech 2001, pp. 75–76; Fuller et al. 2003, pp. 189–190; Adams et al. 2008, pp. 1, 20–22). For further information specific to gray wolf populations in Michigan, Minnesota, and Wisconsin, please see *Levels of Human-Caused Mortality in the Great Lakes* below.

Effects on Gray Wolf Dispersal

Increased human-caused mortality may either increase or decrease gray wolf dispersal rates, depending on various factors. If gray wolf harvest is significant, it may lead to an overall decline in dispersal events due to a reduction in the number of individuals available to disperse; reduced competition for resources within the pack so there is less incentive to disperse; or through direct removal of dispersing animals (Packard and Mech 1980, p. 144; Gese and Mech 1991, p. 2949; Fuller et al. 2003, p. 186; Adams et al. 2008, pp. 16–18). Trapping, in particular, may remove the age classes most likely to disperse because younger, less experienced gray wolves are often more vulnerable to this form of harvest (Adams et al. 2008, p. 18; Schmidt et al. 2017, p. 23). In a study of one heavily harvested population with a significant amount of trapping, long open seasons, and no bag limits, dispersal rates were observed to be up to 50 percent less than in unexploited populations (Webb et al. 2011, pp. 748–749). Similarly, the percentage of dispersing gray wolves decreased from 34 to 22 percent following intensive control efforts to benefit caribou populations in Alaska (Schmidt et al. 2017, pp. 14–17).

However, there appears to be considerable variability in dispersal rates from harvested populations, likely caused by a number of factors, including variation in prey availability, pack size, harvest rates, and whether or not harvest was biased toward certain age-classes (Hayes and Harestad 2000, pp. 43–44; Webb et al. 2011, pp. 748–749; Weiss et al. 2014, p. 4). Jimenez et al. (2017, p. 588) found that increased human-caused mortality (i.e., agency-directed lethal depredation control) removed individual gray wolves and entire packs and thereby provided a constant source of social openings or vacant habitat for dispersing individuals to fill or recolonize. Long-distance dispersals continue from populations with low gray wolf density, even when there is vacant habitat nearby; this dispersal contributes to recolonization of more distant vacant suitable habitats (Boyd et al. 1995, entire; Boyd and Pletscher 1999, entire; Jimenez et al. 2017, pp. 7–10; Jarausch et al. 2021, p. 102). In fact, where gray wolf densities were high, dispersal distances and rates declined (Jimenez et al. 2017, pp. 5–12) and the timing of dispersal was delayed (Sells et al. 2022a, pp. 7–12). In contrast, another study noted dispersal rates were highest at both high and low gray wolf densities and were lowest at moderate densities (Morales-González et al. 2022, pp. 469, 477). Horne et al. (2019, p. 40) found that variation in harvest rates did not translate to changes in the propensity for gray wolves to disperse, based on an integrated population model constructed from data from 197 Global Positioning System (GPS) collared individuals from 65 packs in Idaho. The authors speculated that harvest rates in their study were not high enough to cause widespread breeding vacancies and increased dispersal behavior.

Effects on Gray Wolf Social Structure

Although gray wolf populations typically have a high rate of natural turnover (Mech 2006, p. 1482), increased human-caused mortality, primarily through regulated harvest, may negatively affect the dynamics and social structure of packs (Rutledge et al. 2010b, pp. 337–338; Cassidy et al. 2023, pp. 3–4).

First, the death of one or both of breeders in a pack may increase breeder turnover and negatively affect pack persistence because, in most instances, only the dominant male and female in a pack breed (Cassidy et al. 2023, pp. 3–4). In Alaska, although packs remained intact in 67 percent of cases when one or both breeders were lost, breeder loss preceded pack dissolution 77 percent of the time (Borg et al. 2015, pp. 183–185). Mortality of breeding gray wolves was more likely to lead to pack dissolution and reduced reproductive success when mortality occurred very near to, or during, the breeding season (Borg et al. 2015, pp. 183–185; Ausband et al. 2017a, pp. 4–5) or when pack sizes were small (Brainerd et al. 2008, p. 94; Cassidy et al. 2023 pp. 3–4). Additionally, the likelihood a pack will maintain its territory declines if both breeders are killed; however, if a single breeder is killed, the pack may hold its territory until a new, unrelated gray wolf arrives to replace the lost breeder (Schultz and Wilson 2002, entire; Mech and Boitani 2003, p. 28; Brainerd et al. 2008, p. 96). Nonetheless, other studies have noted that harvest had no effect on the frequency of breeder turnover or the duration of pair bonds in Idaho (Ausband et al. 2017b, p. 1097; Ausband 2019, p. 1620) and little evidence of pack dissolution was found in a heavily harvested gray wolf population with frequent breeder loss in southwestern Alberta (Bassing et al. 2019, pp. 584–585). This indicates that factors such as the level of mortality, pack size, the availability of replacement breeders, and the timing of mortality can moderate the consequences of breeder loss at the pack level (Brainerd et al. 2008, entire; Borg et al. 2015, entire; Schmidt et al. 2017, entire; Bassing et al. 2019, entire; Cassidy et al. 2023, pp. 5–6; Zubiria et al. 2024, p. 7).

Second, through the loss of breeders or the loss of non-breeding pack members, increased human-caused mortality also may affect reproductive success and recruitment in gray wolf packs. The loss of one or both breeders may result in lower natality rates, in addition to lower pup survival and recruitment in individual packs (Ausband et al. 2015, entire; Schmidt et al. 2017, pp. 14–18; Ausband et al. 2017a, pp. 4–6). Moreover, when breeding pairs are together for shorter periods of time (e.g., because one member of the breeding pair is killed), it also may result in reduced pup survival (Ausband 2019, p. 1620). The removal of non-breeding pack members through human-caused mortality also decreases the likelihood of pack persistence and future reproduction; however, the effects on pack persistence and future reproduction from removal of non-breeding pack members are not as severe as effects from the removal of the dominant breeding pair (Cassidy et al. 2023, pp. 3–4). Harvest may have both direct and indirect effects on pup survival and recruitment, but the indirect effects on pup survival and recruitment that result from the loss of pack members and/or breeders are not well understood (Ausband et al. 2015, pp. 418–420). In some instances, gray wolves may respond to decreased population densities resulting from increased human-caused mortality by increasing reproductive output (Schmidt et al. 2017, pp. 14–18). For example, the incidence of multiple breeders within a pack increased when (1) female breeders were lost or (2) the pair bond between breeders was shorter in duration (Ausband et al. 2017b, pp. 1097–1098; Ausband 2019, p. 1620). This could partially explain the fact that mid-year recruitment of young was similar during periods of harvest versus periods without harvest in Idaho (Horne et al. 2019, pp. 37–38). However, breeding male turnover reduced recruitment of female pups, although the mechanisms for this were unknown (Ausband et al. 2017b, pp. 1097–1098).

Although increased human-caused mortality can have negative consequences on the social dynamics and reproductive success of some individual packs (as described above), the effects of breeder loss or removal of non-breeding pack members on gray wolf populations as a whole are less pronounced. In some gray wolf populations that are at or near carrying capacity, where breeder replacement and subsequent reproduction occurs relatively quickly, population growth rate and pack distribution and occupancy are largely unaffected by the loss of one or both breeders (Borg et al. 2015, pp. 182–183; Bassing et al. 2019, pp. 582–584) or by social disruption to the pack caused by the loss of any pack member (Cassidy et al. 2023, p. 5; Zubiria et al. 2024, p. 7). Breeder replacement and subsequent reproduction in colonizing populations greater than 75 gray wolves was similar to that of core populations at or near carrying capacity, whereas small recolonizing populations (less than or equal to 75 gray wolves) took about twice as long to replace breeders and subsequently reproduce (Brainerd et al. 2008, pp. 89, 93). Therefore, the effects of breeder loss may be greatest on small, recolonizing gray wolf populations. In a Scandinavian gray wolf population with little immigration from elsewhere, age of first reproduction declined as population size increased; this was hypothesized to be the result of increased turnover of breeding individuals due to increased human-caused mortality (Wikenros et al. 2021, p. 5). In some cases, where extremely high rates of human-caused mortality were intentionally used to drastically reduce gray wolf abundance, immigration from neighboring areas was found to be the most important determinant in the speed with which populations rebounded (Bergerud and Elliot 1998, pp. 1554–1559, 1562; Hayes and Harestead 2000, pp. 44–46). However, where low to moderate levels of harvest occur, immigration may not compensate for the social openings harvest creates because breeding pairs—and thus the social structure of many packs—are often retained; immigrants are less likely to join groups with intact breeding pairs (Webb et al. 2011, p. 749; Ausband et al. 2017b, p. 1097; Horne et al. 2019, p. 40; Bassing et al. 2020, pp. 6–9).

Overall, the social structure of gray wolf packs is adaptable. Breeding members can be replaced from either within or outside the pack, and pups can be reared by another pack member should their parents die (Service 2020, p. 7). These strong compensatory mechanisms of gray wolf breeding may buffer against long-term population-level impacts of breeder loss and pack dissolution (Borg et al. 2015, pp. 7–9). Consequently, gray wolf populations can overcome severe disruptions, such as intensive human-caused mortality or disease, provided immigration from either within the affected population or from adjacent populations (or both) occurs (Bergerud and Elliot 1998, pp. 1554–1559; Hayes and Harestad 2000, pp. 44–46; Bassing et al. 2019, entire). Breeder loss can and will occur in the future to some degree, regardless of the presence of human-caused mortality, and that the loss of any individual will have some effect on pack dynamics. However, the effects of this breeder loss on the metapopulation of gray wolves in the Eastern United States is likely to be minimal, as long as a sufficiently large population is maintained that is well-connected to other populations via dispersal.

Effects on Wolf Physiology

Prolonged stress in animals can affect certain life history characteristics including reproduction, immune response, and behavioral or cognitive abilities (Wingfield and Sapolsky 2003, entire; Hedges and Woon 2011, entire). All of these may have long-term implications for the affected individuals, which may also elicit individualized responses to stress (e.g., Johnstone et al. 2012, pp. 868–873). Stress comes from many sources that may include environmental conditions, availability of food resources, disease, social interactions, and human activities. As gray wolf abundance and distribution has increased, they have increasingly interacted with humans to varying degrees, which can result in a certain level of habituation as some become more comfortable living around humans (Heilhecker et al. 2007, entire). Social interactions among gray wolves surrounding breeding and the birth of pups was found to result in greater levels of glucocorticoid metabolites (byproducts of stress hormones) than other potential stressors, including human activity (Eggermann et al. 2013, pp. 172–174). Lower levels of glucocorticoid metabolites in wolves living near humans provides some evidence to support the adaptability of gray wolves that has allowed them to persist in close proximity to humans, as long as levels of human persecution are not excessive (Eggermann et al. 2013, pp. 172–173).

In areas where gray wolves seldom, if ever, interact with humans or where the interactions are relatively short in duration but of high intensity, stress may play a larger role in the physiological health of individual gray wolves. For example, high rates of human-caused mortality through hunting resulted in physiological changes to wolves that increased levels of cortisol and reproductive hormones (Bryan et al. 2015, pp. 351–354). These results are indicative of social disruptions to the pack that possibly affected the rate of female pregnancy or pseudopregnancy and the number of interactions among male gray wolves (Bryan et al. 2015, pp. 351–352). A follow-up study using the same data as the Bryan et al. (2015, entire) study used machine-learning to identify gray wolves that belonged to a heavily hunted population based on elevated stress hormone levels (Stewart et al. 2021, entire). However, it was unknown if these physiological changes affected overall fitness (i.e., reproductive and population performance) of the affected wolf population or if factors besides gray wolf harvest contributed to elevated stress levels (Bryan et al. 2015, pp. 351–354; Stewart et al. 2021, p. 5). Boonstra (2012, entire) concluded that chronic stress in wildlife was rare, but that it could benefit the affected species by allowing it to adapt to changing conditions to maintain, or improve, long-term fitness. Indeed, Bryan et al. (2015, p. 351) argued that the physiological changes observed in the stressed wolf population could be considered adaptive and beneficial to the gray wolf when dealing with the specific stressors.

Effects on Genetics

The effects of human-caused mortality on the genetic characteristics of gray wolf populations can be complex. Genetic attributes of gray wolf populations are primarily a function of population size (via effective size) and dispersal. As discussed above, human-caused mortality impacts these demographic factors, which can then result in subsequent population genetic changes over time.

At the simplest level, should mortality be additive and result in population decline, there may be a corresponding decline in genetic diversity, especially if the population falls below an effective size at which genetic drift becomes more pronounced (Wayne and Hedrick 2011, p. 16). Range contractions can also result in loss of genetic diversity if genes are not randomly distributed across the landscape (i.e., population structure and/or local adaptation are present). These phenomena have likely affected many wolf populations globally as eradication campaigns reduced population sizes and ranges, resulting in the lower levels of genetic diversity in contemporary populations compared to historical levels (Flagstad et al. 2003, entire; Leonard et al. 2005, entire; Jansson et al. 2014, entire; Salado et al. 2023, entire). Assuming human-caused mortality does not exceed those thresholds, however, populations can maintain adequate levels of genetic diversity. Several gray wolf populations subjected to human harvest continue to possess high levels of genetic diversity (Jędrzejewski et al. 2005, entire; Hindrikson et al. 2013, p. 4). Rick et al. (2017, p. 1096) in particular showed that genetic diversity and effective size in Minnesota gray wolves did not decline in the years immediately following a hunting season. Genomic diversity in the Western Great Lakes region has not declined significantly over the past 30 years despite periodic harvest and depredation management (vonHoldt et al. 2024b, p. 8). This indicates that the overall genetic diversity of a wolf population may be resilient to human-caused mortality, assuming they do not exceed thresholds that result in precipitous declines.

A population's genetic diversity is also modulated by gene flow across the landscape, which is driven by dispersing wolves (Jędrzejewski et al. 2005, p. 15). Human-caused mortality can limit opportunities for long-distance dispersal to provide influxes of genetic diversity. Therefore, human-caused mortality can create genetic subdivisions by limiting dispersal (Hindrikson et al. 2013, p. 9; Rick et al. 2017, pp. 1100-1101). These impacts of heavy harvest can be mitigated if the affected population has proximity to and dispersal from a larger population that can maintain or even increase genetic diversity (Jędrzejewski et al. 2005, p. 15; Hindrikson et al. 2013, p. 9).

In conclusion, the effects of human-caused mortality on the wolf population genetics are dependent on a variety of factors including population size and its proximity to core wolf range. Pack disruption and reductions in dispersal can alter genetics characteristics at various spatial scales, potentially homogenizing genetic diversity within localized areas while increasing subdivision at the landscape-scale. Ultimately, the overall genetic diversity of wolf population is governed by its effective size and gene flow from other populations. Thus, declines in genetic diversity are anticipated if human-caused mortality substantially affects those two attributes.

Sources of Human-Caused Mortality

Human-caused mortality includes both controllable and uncontrollable sources of mortality. Controllable sources of mortality are discretionary (i.e., they can be regulated by the managing agency) and include permitted take, legal harvest, and direct agency control. Sources of mortality that are difficult to regulate and occur regardless of population size include natural mortalities, illegal take (which we define as illegal killing of wolves, i.e., poaching), and accidental deaths (e.g., vehicle collisions, capture-related mortalities). Below, we provide a brief discussion of the forms of human-caused mortality that have been documented in the Eastern United States.

Discretionary Sources of Mortality: Regulated Harvest

Regulated harvest is a population management tool wildlife managers use to achieve a desired management outcome (i.e., objective) for a specific population or subpopulation of wildlife at a defined spatial scale, while balancing biological and social factors. The spatial scale may be large, such as the size of a state, or small, such as a hunt unit. With harvest management, the management goal may be a numerical objective (i.e., manage for a certain number of animals) or a trajectory/trend objective (e.g., manage for positive/negative growth or stability). When specific population counts or estimates are unavailable or unknown, or if species are managed based on achieving positive/negative/stable growth rather than a specific number, wildlife managers may use a trajectory/trend objective instead of a numerical objective. Wildlife managers evaluate past and present harvest and population metrics, as well as other factors that may influence harvest and population performance, to make informed decisions regarding the future harvest strategies most likely to achieve their desired objectives.

Due to uncertainties inherent in managing wildlife populations, wildlife managers often employ an adaptive management strategy that, in general, provides a structured process to implement an action, evaluate the outcome of the action based on predictions, and adapt future management decisions and actions based on what was learned (Williams 2011, entire; Organ et al. 2012, entire; Richardson et al. 2020, entire). Adaptive harvest management is one form of adaptive management that wildlife managers often use to evaluate the effects of harvest strategies and determine if they are being effectively implemented to achieve a desired management outcome (Organ et al. 2012, p. 53). This allows wildlife managers to evaluate population responses over a set period, take into account any new information about the population, and then make adjustments, if necessary, prior to implementing new harvest strategies over another set time period in order to continue working toward the desired management outcome.

A U.S. National Academy of Sciences committee recommended an adaptive management approach to guide wolf and bear harvest in Alaska (National Research Council 1997, p. 184). This framework was also used to guide the regulated wolf harvest seasons in Minnesota and Wisconsin when wolves were delisted in those states[13] (see *Regulated Harvest in Minnesota* and *Regulated Harvest in Wisconsin* below). Initially, states developed relatively conservative harvest strategies using the best population and mortality information available from their own wolf populations, as well as from other exploited wolf populations, to achieve a specific management objective while also balancing the desires of multiple interest groups with different values regarding wolves and wolf management (Mech 2010a, p. 1422). When the harvest season concluded, wildlife managers used multiple harvest and population metrics from current and past seasons to inform future harvest decisions based on management objectives.

Large carnivore harvest regulations implemented to achieve a desired management objective are often not correlated with realized harvest outcomes (Bischoff et al. 2012, pp. 828–830). This may be due to a variety of factors that work either singly or in combination to affect hunter and trapper effort and success in any given season. Some of these factors may include: changes in wolf behavior and susceptibility to harvest, environmental conditions, socioeconomic factors (e.g., gas prices, fur prices), ethical and/or biological constraints, prey availability and distribution, harvest regulations for other species that may affect the number of individuals in the field, and variability in the novelty of wolf harvest, among other influences (Fritts et al. 2003, p. 301; Adams et al. 2008, pp. 17–18; Cluff et al. 2010, entire; Mech 2010a, pp. 1422–1423; Webb et al. 2011, p. 750; Kapfer and Potts 2012, pp. 240–241; Foundation for Wildlife Management 2022, unpaginated; Mowat et al. 2022, pp. 16–17).

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[13] Michigan held only one regulated wolf harvest season, thus there was no opportunity to demonstrate an adaptive management approach for a future season. Michigan would use an adaptive management approach if they were to hold regulated harvest seasons in the future (MI DNR 2022a, pp. 69–72).

Lethal Control of Depredating Wolves

Wolf-occupied areas with a high abundance of livestock or high densities of both wolves and livestock are at higher risk for conflict (e.g., livestock depredation) (DeCesare et al. 2018, p. 7; Hanley et al. 2018a, pp. 8–10; Hanley et al. 2018b, pp. 8–11; Mayer et al. 2022, p. 8), thus reducing the probability of wolf colonization and persistence in certain areas (Oakleaf et al. 2006, pp. 558–561). Where wolves and livestock overlap, wildlife managers work with livestock owners to minimize conflict risk as much as is practical using a combination of nonlethal and lethal methods. Lethal control of wolves depredating on (killing or injuring) dogs or other pets is a rare occurrence and it is typically only allowed for pets on a landowner's property or under their owner's control. Lethal control is not typically a management response option should a wolf injure or kill hunting dogs, which represent the largest proportion of dogs killed by wolves in the Western Great Lakes region (Ruid et al. 2009, p, 285).

There are certain circumstances in which preventative and nonlethal techniques have been shown to be effective for reducing wolf depredation of livestock. These include proactive methods to prevent wolves from acquiring food rewards to curb learned behaviors (Much et al. 2018, p. 76); the inferred effectiveness of human presence at reducing recurrent depredations (Harper et al. 2008, pp. 782–783); the use of predator-proof fencing where resident wolf packs occur (Mayer et al. 2022, pp. 8–11); and the adaptive use of multiple preventative and nonlethal methods to minimize sheep (*Ovis aries*) depredations (Stone et al. 2017, entire). There are also circumstances in which lethal control has been shown to be effective at preventing future depredation events. Lethal control of depredating wolves is used reactively rather than proactively, often after other, nonlethal techniques to prevent depredations were unsuccessful (Bangs et al. 2009, p. 110), but it may improve the overall effectiveness of nonlethal methods because wolves may then associate humans with an increased risk of injury or death (Meuret et al. 2020, pp. 1, 408–411). Targeted lethal removals may be effective at resolving conflict because a relatively high proportion of depredations in any given year occur over a relatively small area and involve a relatively small number of wolves (Olson et al. 2015, entire; DeCesare et al. 2018, pp. 9–11). Although incremental removal of a few individual depredating wolves shortly after a depredation occurred (i.e., within seven days) reduced the potential for depredations to continue, full pack removal had a more immediate and longer-lasting effect on the frequency of recurrent depredations (Bradley et al. 2015 pp. 6–9). The targeted removal of at least one adult male wolf from depredating packs (Harper et al. 2008, pp. 781–783) and the targeted removal of a high number of individuals relative to pack size significantly reduced the probability of recurrent cattle (*Bos taurus*) depredations the following year (DeCesare et al. 2018, pp. 8, 10–11) in studies completed in Minnesota and Montana, respectively.

However, the use of lethal control to mitigate wolf conflicts with livestock has been criticized for lacking long-term effectiveness at reducing depredations on a large scale and for being too costly (Wielgus and Peebles 2014, entire; McManus et al. 2015, entire; Lennox et al. 2018, entire; Santiago-Avila et al. 2018, entire). Lethal control of depredating wolves is not intended to resolve long-term depredation management issues across a large spatial scale (Musiani et al. 2005, p. 885). Rather, wildlife managers have consistently used this tool as a short-term response on a relatively small scale to mitigate recurrent depredations of livestock that could not be resolved using other methods (Bangs et al. 2006, p. 13; Bangs et al. 2009, p. 110; Meuret 2020, entire). However, Wielgus and Peebles (2014, pp. 7–14) argued that lethal removal of wolves in 1 year exacerbated the conflict cycle, which resulted in an increased number of livestock killed by wolves the following year if wolf mortality did not exceed twenty-five percent of the known or estimated wolf population in the year the lethal removals occurred. Subsequent studies have refuted this assertion and found that, when the same data were reanalyzed, the use of lethal control was effective at reducing livestock depredations the following year (Poudyal et al. 2016, entire), and an increasing wolf population was the primary cause of the observed increases in the number of livestock depredations (Kompaniyets and Evans 2017, entire). Others have documented the effectiveness, or lack thereof, of certain lethal control prescriptions used to minimize depredation risk within the same year the control actions were conducted or in the year following the control actions (e.g., partial versus full pack removal, timing of removal) (Bradley et al. 2015, entire; DeCesare et al. 2018, pp. 8, 10).

Researchers disagree on whether nonlethal or lethal depredation control methods are more effective at decreasing depredations. In a review of both nonlethal and lethal methods to mitigate carnivore conflicts, researchers found that the effectiveness of nonlethal methods to minimize depredation risk was more variable than targeted, lethal control (Miller et al. 2016, pp. 3–8). In contrast, another review indicated similar effectiveness of nonlethal and lethal methods, but lethal control success was more variable at mitigating conflict (van Eeden et al. 2017, p. 29). This indicates that no single method or technique is consistently effective under all conditions to minimize conflict risk. Although continued research is needed (Treves et al. 2016, entire; Eklund et al. 2017, entire; van Eeden et al. 2018, entire; Treves et al. 2019, entire), depredation management plans that are adaptive and include a combination of nonlethal and lethal methods may improve overall effectiveness of all methods used to minimize depredation risk (Treves and Naughton-Treves 2005, p. 106; Bangs et al. 2006, p. 8; Wielgus and Peebles 2014, pp. 1, 14; Miller et al. 2016, p. 7; Stone et al. 2017, entire; DeCesare et al. 2018, p. 11; Meuret et al. 2020, pp. 1, 409–411). As long as wolves and domestic livestock share the landscape, conflict will occur, and depredation management programs that use a combination of proactive and reactive tools are often most effective at minimizing depredation risk and the number of depredations that occur.

There is some evidence that the combination of targeted lethal control of depredating wolves and regulated harvest of wolves has the potential to reduce wolf-livestock conflicts without having a significant impact on wolf abundance. For example, between 2012 and 2015, the Wisconsin wolf population decreased slightly from 815 to 746 animals (8 percent decrease) (wolves were federally delisted between 2012 and 2014). However, during that same time period, verified wolf kills on cattle declined from 48 to 28 and the number of farms with verified depredations declined by 26 percent (from 43 to 32) (Wiedenhoeft et al. 2015, pp. 4–5, 12). A similar trend was observed in the NRM when the gray wolf population, with the exception of wolves in Wyoming, was delisted in 2011. Between 2006 and 2011, when wolves were primarily federally protected in the NRM, an average of approximately 190 cattle depredations were confirmed per year; between the years of 2012 to 2015, when wolves were delisted in portions of the NRM, the number of confirmed cattle depredations decreased to an average of about 151 per year, even though wolf populations remained relatively stable to slightly increasing during that time (see Service et al. 2016, Figure 7a and Table 7b). As a result of the overall reduction in livestock depredations, the total number of wolves lethally removed to mitigate conflicts has also generally declined in Idaho, Montana, and Wyoming in recent years (Service et al. 2016, see Table 7b;

Parks et al. 2022, pp. 17–22; WGFD et al. 2022, pp. 20–21; Table 5). In Montana, the percentage of the population lethally removed to mitigate conflicts also decreased (Sells et al. 2022c, p. 12). A recent study that modeled wolf mortality across North America supported these patterns observed in the NRM; it found that the proportion of wolves lethally removed to resolve conflicts was lower in areas where wolf harvest was allowed compared to those areas where it was not authorized (Hill et al. 2022, pp. 1, 4–6).

Overall, a relative few wolf packs are implicated in livestock or pet depredations on an annual basis (Olson et al. 2015, entire; Service et al. 2016, p. 2; Wydeven et al. 2004, pp. 28–27). Furthermore, Stenglein et al. (2015b, pp. 17–21) demonstrated that regular removal of 10 percent of the wolf population for depredation controls has little impact on growth of the wolf population. For further information on the rates of lethal removal for depredation control in the Western Great Lakes states, see *Levels of Human-Caused Mortality in the Great Lakes* below.

Illegal Take (i.e., Poaching) of Wolves

Illegal take, by its very nature, can be challenging to document, regulate, and limit despite rules and regulations designed to discourage such activities. Illegal take can be a significant source of mortality in some wolf populations and tends to peak during fall and winter when increased numbers of people are afield hunting other species (Treves et al. 2017a, p. 26; Stenglein et al. 2018, p. 104; Agan et al. 2021, entire; Barber-Meyer et al. 2021, pp. 7, 9; Louchouarn et al. 2021, entire; Santiago-Ávila and Treves 2022, p. 1738) and in fragmented habitats with reduced cover (Hill et al. 2022, pp. 4, 6–7).

Although some researchers have detailed that rates of illegal take are grossly underestimated because a high proportion of this type of mortality is undocumented (Liberg et al. 2012, pp. 912–914; Treves et al. 2017a, pp. 27–29; Treves et al. 2017b, pp. 7–8), multiple other studies have supported the estimate that between 5 to 12 percent of wolves may be illegally killed annually in different areas of the lower-48 United States (e.g., one study that estimated a 9 percent rate of illegal take in Wisconsin) (Murray et al. 2010, p. 2519; Smith et al. 2010, p. 625; Ausband et al. 2017a, p. 7; O'Neil 2017, p. 214; Stenglein et al. 2018, p. 104; Barber-Meyer et al. 2021, p. 7). Most wildlife managers acknowledge that the actual number of wolves killed through illegal means is likely biased low because not every wolf is fitted with a radio collar and not every wolf that dies is recovered, so their fates are unknown. However, it is not reasonable to assume that all, or even most, wolves with unknown fates have died, particularly through illegal means, because radio-collared wolves may go missing for a variety of reasons (e.g., collar failures, end of useful battery life, wolves moving out of monitoring range) (Liberg et al. 2020, p. 5). One study estimated that a maximum of 4 percent of missing wolves in Wisconsin may have actually died from any cause (Stenglein et al. 2015a, pp. 372–374). Another demonstrated that the rate of wolves that go missing was positively related to wolf abundance (Liberg et al. 2020, pp. 4–6).

Human attitudes influence individual behaviors, such as human responses to wolf activity (Bruskotter and Fulton 2012, pp. 99–100) (see *Influence on Human-Caused Mortality: The Role of Public Attitudes* below for more information). Thus, researchers have theorized that if tolerance for a species is low or declining, individual attitudes may then be manifested through actions directed towards the species, which increases the likelihood for illegal activity to occur. In the case of wolves, if an individual feels they have limited management options to mitigate a real or perceived conflict or assist with wolf population management through legal harvest, they may be more inclined to act illegally to address their concerns (Olson et al. 2014, entire; Suutarinen and Kojola 2018, pp. 418–420).

Consistent with this theory, a growing body of evidence indicates that illegal take increases when legal take regulations become more restrictive and limit management options (Olson et al. 2014, pp. 4–8; Olson et al. 2017, entire; Pepin et al. 2017, entire; Stein 2017, entire; Suutarinen and Kojola 2018, pp. 418–420; Liberg et al. 2020, pp. 4–6); however, a more recent study that modeled wolf mortality across North America found that illegal take did not decline where wolf harvest was authorized (Hill et al. 2022, pp. 4–6). Additionally, some researchers continue to argue that less restrictive legal take regulations (e.g., regulated wolf harvest and lethal control to resolve recurrent conflicts) have resulted in increased illegal take of gray wolves (Chapron and Treves 2016, entire; Chapron and Treves 2017, entire; Santiago-Avila et al. 2020, entire; Treves et al. 2021, p. 9; Santiago-Ávila and Treves 2022, pp. 1738–1739; Oliynyk 2023, entire), although these claims have been questioned (e.g., Olson et al. 2014, pp. 4–8; Olson et al. 2017, entire; Pepin et al. 2017, entire; Stein 2017, entire; Suutarinen and Kojola 2018, pp. 418–420; Liberg et al. 2020, pp. 4–6). While competing studies on Minnesota's wolf population between 2004 to 2019 noted decreased survival rates over time with approximately two-thirds of documented mortalities caused by humans, there was no consensus on the cause of the reduced survival rates (Chakrabarti et al. 2022, pp. 6-9; Oliynyk 2023, pp. 1-5). Chakrabarti et al. (2022, pp. 8-9) suggested that a combination of human causes and density-dependent mechanisms acting on wolf populations may be responsible for the reduction in survival and population growth while Oliynyk 2023 (p. 5) suggested that reduced survival after the 2012-2014 hunting seasons may have been caused by a negative change in human attitudes due to wolves being relisted that resulted in increased illegal take of wolves in Minnesota.

In general, compared to the early twentieth century when take was unregulated, the regulation of human-caused mortality has reduced the number of wolves indiscriminately killed by humans, which has allowed wolves to recolonize areas of suitable habitat within their former range. Despite rules and regulations to discourage such activity, the illegal killing of wolves will continue in the future and although it may affect recolonization potential outside of core areas and overall distribution of gray wolves in the Eastern United States, at current levels, these mortalities have minimal impact on wolf abundance in the Western Great Lakes region.

Other Sources of Human-Caused Mortality

It is a rare occurrence for non-habituated wild wolves in North America to pose a threat to humans (McNay 2002, pp. 836–837). Nonetheless, on rare occasions, humans have killed wolves due to a real or perceived threat to their safety or the safety of others. Killing a wolf in self-defense is permissible even under the Act's protections. Other types of human-caused wolf mortalities that may occur include collisions with vehicles, incidental mortality associated with wolf monitoring programs, or wolf removal from the wild solely for educational purposes. Each of the states in the current range of gray wolves in the Eastern United States conduct scientific research and monitoring of wolf populations. Even the most intensive and disruptive of these activities (i.e., ground or aerial capture for the purpose of radio-collaring) involves a very low rate of mortality for wolves (76 FR 81666, December 28, 2011, pp. 81693–81694). The best available information does not indicate any wolves in the Eastern United States have been removed from the wild solely for educational purposes in recent years. In the Western Great Lakes area. most wolves used for educational purposes have come from euthanized depredators or wolves killed in vehicle collisions. Live wolves that are used for education are typically privately held, captive-reared offspring of wolves that were already in captivity for other reasons. States may get requests to place wolves that would otherwise be euthanized in captivity for research or educational purposes. Such requests have been and will continue to be rare, are closely regulated by either the Service or state wildlife management agencies through permitting processes (depending on the Federal status of wolves) and would not substantially increase human-caused wolf mortality rates. Overall, these types of mortality (e.g., mortality from self-defense, accidental mortality, mortality from research activities) are relatively rare (i.e., constitute a small proportion of total wolf mortalities) (e.g., Hill et al. 2022, p. 7) and they are not expected to have a significant impact on gray wolf populations in the Eastern United States now or in the future, regardless of the species' Federal protected status.

Influence on Human-Caused Mortality: The Role of Public Attitudes

While not a proximal stressor for wolves, public attitudes regarding wolves can influence the levels of human-caused mortality wolves experience. For example, negative public perceptions of wolves can lead to increased illegal take of wolves or increased motivation to legally harvest wolves. Human attitudes toward wolves vary depending on how individuals value wolves in light of real or perceived risks and benefits (Bruskotter and Wilson 2014, entire). An individual's perception of wolves may be directly influenced by an individual's proximity to wolves (Houston et al. 2010, pp. 399–401; Holsman et al. 2014, entire; Carlson et al. 2020, pp. 4–6), personal experiences with wolves (Williams et al. 2002, p. 9; Houston et al. 2010, pp. 399–401; Browne-Nunez et al. 2015, pp. 62–69; Arbieu et al. 2020, entire), or indirect factors such as social influences (e.g., news and social media, internet, friends, relatives, and political affiliation) and governmental policies (Houston et al. 2010, pp. 399–401; Olson et al. 2014, entire; Treves and Bruskotter 2014, p. 477; Browne-Nunez et al. 2015, pp. 62–69; Chapron and Treves 2016, p. 5; Lute et al. 2016, pp. 1208–1209; Carlson et al. 2020, pp. 4–6; Anderson 2021, entire; Bogezi et al. 2021, p. 5; van Eeden et al. 2021, entire; Ditmer et al. 2022, entire; Niemiec et al. 2022, entire).

Wolves often invoke deeper-rooted social conflict that stems from cultural differences related to identity, fear, knowledge, empowerment, and trust that are not directly related to the biological evaluation of gray wolves in this SSA Report (Naughton-Treves et al. 2003, pp. 1507–1508; Madden 2004, p. 250; Madden and McQuinn 2014, pp. 100–102; Browne-Nunez et al. 2015, p. 69; Carlson et al. 2020, pp. 4–6). We acknowledge that public attitudes towards wolves vary with demographics and they can change over time, which can affect human behavior toward wolves, including illegal take of wolves (see Kellert 1985; Nelson and Franson 1988; Kellert 1990; Kellert et al. 1996; Kellert 1999; Wilson 1999; Browne-Nuñez and Taylor 2002; Williams et al. 2002; Manfredo et al. 2003; Naughton-Treves et al. 2003; Madden 2004; Mertig 2004; Chavez et al. 2005; Schanning and Vazquez 2005; Beyer et al. 2006; Hammill 2007; Schanning 2009; Treves et al. 2009; Wilson and Bruskotter 2009; Shelley et al. 2011; Treves and Martin 2011; Treves et al. 2013; Madden and McQuinn 2014; Hogberg et al. 2016; Lute et al. 2016). For example, a recent survey targeting three overlapping interest groups in Minnesota (livestock producers operating in a county within wolf range, Minnesota resident firearm deer hunters, and all Minnesota residents) (Schroeder et al. 2020, entire) illustrates how different demographics, social groups, and experiences with wolves can influence one's attitudes towards wolves and their management. Most Minnesota livestock producers and deer hunters reported having a negative attitude toward wolves (62 percent and 52 percent, respectively), even though the majority of Minnesota residents reported having a positive attitude towards wolves (68 percent). Further, more survey respondents, in all categories, agreed that maintaining a wolf population in Minnesota was important (47.2 percent livestock producers, 67 percent deer hunters, 87 percent state residents) than disagreed (Schroeder et al. 2020, pp. 4, 7, 10). When asked to consider the wolf population in the fall of 2019, Minnesota livestock producers and deer hunters expressed a preference for fewer wolves and less occupied range, while Minnesota residents expressed a preference for a similar number of wolves, or more, in about the same range, or more (Schroeder et al. 2020, pp. 5, 8, 11). A strong majority of Minnesota livestock producers and deer hunters supported establishing both a regulated wolf hunting season and trapping season (Schroeder et al. 2020, pp. 6, 9). However, Minnesota residents in general were nearly evenly divided on establishing a regulated wolf hunt, with 41 percent support and 49 percent opposed. Opposition to a regulated wolf trapping season was even higher, with 58 percent expressing at least some level of opposition—including those slightly, moderately, or strongly opposed (Schroeder et al. 2020, p. 12). A public attitudes survey in Michigan found divided opinions: 49 percent of residents statewide supported a regulated wolf hunt – provided biologists and the Michigan DNR deemed the population could sustain it – while 30 percent were opposed. There was less support for a recreational trapping season, with 36 percent of residents in support and 43 percent opposed (MI DNR 2022a, p. 72; MI DNR 2022e, p. 105).

There is much debate about the role of regulated wolf harvest in changing negative attitudes about wolves and increasing tolerance for the species (Browne-Nunez et al. 2015, pp. 62–69; Hogberg et al. 2016, pp. 49–50; Lute et al. 2016, pp. 1206–1208; Lewis et al. 2018, entire; Richardson 2022, entire; Slagle et al. 2022, entire). Hogberg et al. (2016, p. 50) documented an overall decline in tolerance for wolves after regulated harvest occurred in Wisconsin, which indicates that hunting may not be the most effective policy to increase tolerance for the species (Epstein 2017, entire; Suutarinen and Kojola 2018, pp. 418–420). However, Hogberg et al. (2016, p. 50) also documented that 36 percent of respondents self-reported an increase in their tolerance toward wolves after wolf hunting began in Wisconsin. Similarly, a survey conducted in Montana (Lewis et al. 2018, entire) found that while overall tolerance remained low compared to a similar survey from 2012, it had slightly increased over time as the state has continued to manage wolves primarily through regulated harvest. Furthermore, interviewees' statements regarding hunting and trapping of wolves in Montana indicate that if those management options were no longer available to them, their tolerance and acceptance of the species would likely decline, resulting in increased polarization of opinions about wolves (Mulder 2014, p. 68; Richardson 2022, pp. 8–10). These studies indicate that two factors may slowly increase tolerance for wolves: (1) the passage of time, which may be considered equivalent to an individual getting used to having wolves on the landscape even though wolves may still be disliked, and (2) the belief that state management provides more opportunities for individual empowerment to assist with wolf population management and conflict resolution. Although general trends in overall attitudes towards wolves are most often obtained through surveys, Browne-Nunez et al. (2015, p. 69) cautioned that these surveys often do not capture the complexity of attitudes that more personal survey techniques, such as focus groups, allow. Furthermore, Decker et al. (2006, p. 431) stressed the importance of providing details about situational context when evaluating human attitudes towards specific wildlife management actions.

Generally, many forces can influence public attitudes towards wolves, and therefore, the levels of realized human-caused mortality of the species. Throughout our analysis, we examine the effects of increased human-caused mortality on the gray wolf's viability in the Eastern United States. These increases in human-caused mortality could be influenced by changes in public attitudes, in addition to a multitude of other influencing factors.

Levels of Human-Caused Mortality in the Western Great Lakes Region

Below, we summarize state law, regulations, and the management plans relevant to the management of human-caused mortality in each state where wolves occur in our analysis area.

During periods when regulated harvest and lethal control of depredating wolves have been lawful, those sources have accounted for most of the known wolf mortalities in the Eastern United States, and they are likely to be the greatest sources of human-caused mortality if wolves are federally delisted. Therefore, the discussion of human-caused mortality below focuses on the levels of these two types of mortality. All other forms of human-caused mortality, including illegal take, make up a small proportion of known human-caused wolf mortalities when compared to lethal depredation control and harvest, although much illegal take of wolves is likely undocumented (see *Illegal Take (i.e., Poaching) of Wolves and Other Sources of Mortality*). Based on wolf population estimates (Table 7) and distribution across the Western Great Lakes region, illegal take alone or in combination with all other forms of mortality has not prevented the expansion of the gray wolf population in the Western Great Lakes region.

Each state in the Western Great Lakes region conducts their population counts/estimates in mid- to late winter, when wolf populations are closest to their minimum preceding the spring breeding season. Minnesota and Wisconsin report winter counts/estimates straddling two calendar years (e.g., 2010/2011 winter count/estimate). Michigan reports its winter counts/estimates as beginning of a calendar year (e.g., early 2011). However, each state provided mortality information on a calendar year basis (i.e., number of confirmed wolf mortalities due to various causes for a single calendar year). Thus, we needed to use end-of-calendar year population estimates to calculate annual mortality rates. For the purposes of our annual mortality rate calculations (and for use in our future condition modeling), we treated the winter counts/estimates as "end-of-calendar-year" values and assigned them to the earlier of the two years or, in the case of Michigan, the end of the prior year. For example, a "2010/2011 winter count/estimate" and an "early 2011 winter count/estimate" were each assigned as "end-of-year count/estimates" for 2010 (see Appendix 2). This is an appropriate use of the data because all three of the states' counts/estimates are conducted prior to the breeding season; thus, we can be certain that a wolf counted in early February was also a member of the population in December of the prior year. Thus, all mortality rates discussed below were calculated by dividing the number of wolves that died from each type of mortality for a given year by the population count/estimate for the end of that calendar year plus the known number of wolves that died from all causes that same year (i.e., this sum in the denominator represents the minimum number of wolves known to be alive at some point during the calendar year).[14]

Currently, wolves throughout our analysis area are protected under the Act. These protections have greatly limited human-caused mortality. Several Minnesota studies provide some limited insight into the extent of human-caused wolf mortality before and after the species' listing. Examining bounty data from a period that predated wolf protection under the Act by 20 years, Stenlund (1955, p. 33) found an annual human-caused mortality rate of 41 percent. Another study by Van Ballenberghe et al. 1975 (pp. 29–31, 40) found an annual mortality rate of 20–40 percent from 1969–1972. Of the 51 documented mortalities, 37 (73 percent) were trapped or shot and 11 (22 percent) were killed by vehicles. Mech (1977, pp. 567–570) found that human-caused mortality declined after 1973, although the sample sizes were insufficient for a conclusive determination. Among the 17 deaths occurring in 1973 or earlier, eight (47 percent) were caused by humans, whereas with the seven animals that died after 1973, only two (29 percent) were human caused. Fuller (1989, pp. 23–24) evaluated data from a north-central Minnesota study area and found an annual human-caused mortality rate of 29 percent from 1980 through 1986, which includes 2 percent mortality from legal depredation-control actions. It is difficult to draw conclusions from comparisons of these studies because of differences in habitat quality, exposure to humans, prey density, time periods, and study design. Nonetheless, these figures indicate that human-caused mortality decreased significantly once the gray wolf became protected under the Act in 1973.

However, human-caused mortality has occurred while the species has been federally listed, especially in Minnesota, where the species is listed as threatened and managed under a 4(d) rule. Additionally, there have been brief periods over the past two decades during which the gray wolf was removed from the Federal List of Endangered and Threatened Wildlife in our analysis area (i.e., 2007–2008, 2009, 2011–2014, 2021–2022); during these periods, states in the Western Great Lakes area allowed lethal depredation control in all years and regulated harvest in some years. Moreover, Michigan, Minnesota, and Wisconsin would likely employ lethal control of depredating wolves and regulated harvest, within an adaptive management framework, if wolves were to be delisted again. Below, we refer to the management plans and regulations that either currently govern human-caused mortality (while wolves are federally listed) or could govern human-caused mortality (if wolves were to be federally delisted) in each state. We report the levels of regulated harvest that occurred during past periods when the species was delisted in the Western Great Lakes region. We also report the level of lethal control of depredating wolves that has occurred while gray wolves were listed in each state, and during the periods in which wolves were delisted. Our future condition projections in Chapter 6 provide quantitative illustration of the effects of potential future harvest and lethal depredation control on the wolf population in the Western Great Lakes region, should delisting occur.

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[14] For example, we calculated the harvest rate as: Harvest Rate = [Total # of Wolves Died from Harvest in 20XX]/[End-of-Year Population Count/Estimate for the State for 20XX + Total # of Wolves Died from All Known Causes in 20XX]. So, to continue the 2010 example, the lethal depredation control rate in Minnesota for 2010 would be [Total Number of Wolves Removed for Lethal Depredation Control in Minnesota in 2010]/[2010/2011 winter population estimate for Minnesota (which we call the 2010 end-of-year estimate) + Total # of Wolves Died from All Known Causes in Minnesota in 2010].

Human-Caused Mortality in Michigan

Regulated Harvest in Michigan

Regulated wolf harvest is not permitted in Michigan while wolves are listed as endangered under the Act. However, regulated harvest has occurred in Michigan when wolves were previously delisted in the state and may be considered if wolves are federally delisted in the future, given that the species is classified as a game animal. The Michigan Plan discusses the purposes of any potential regulated harvest in the future and the strategies it would use to develop harvest recommendations (see *State Management: Michigan*).

Michigan held a regulated public hunting season in 2013 that took into consideration the recommendations of the Michigan DNR, which were based on the state management plan that was in place at the time. From those recommendations, the Michigan Natural Resources Commission established three wolf harvest zones with separate quotas for each in the Upper Peninsula. These included a quota of 16 wolves in the far western part of the peninsula, a quota of 19 wolves in four central counties, and a quota of 8 wolves in the eastern part of the peninsula. The harvest season was designed to decrease the level of conflict within each zone by reducing the number of wolves in each zone and by changing the behavior of the remaining wolves, so they became increasingly wary of humans (Roell 2025a, p. 2). Twenty-two wolves were harvested during the 2013 season, representing 3.1 percent of the year-end population (or a 3.1 percent harvest rate) (Appendix 2). This was the only regulated harvest held in Michigan. While it would have been allowed, Michigan chose not to hold regulated harvests in other years when wolves were federally delisted (2012, 2014, and 2021). The Michigan DNR would consider wolf population-management measures, including regulated hunting and trapping seasons and other methods, if wolves were federally delisted again. However, its Michigan wolf management plan requires that population-management measures be implemented in such a way as to maintain a viable wolf population (above the minimum requirement of 200 wolves) in the state (MI DNR 2022a, pp. 23, 72, 73).

Depredation Control in Michigan

The frequency of depredation incidents is lower in Michigan than in the other Western Great Lakes states (Minnesota and Wisconsin); however, it is still an important issue in the state. From 1998 through 2021, a total of 319 wolf depredation events were verified on 105 farms – representing approximately 10 percent of livestock producers in the Upper Peninsula (MI DNR 2022e, p. 65; Roell 2025a, in litt.). The number of livestock producers has not changed significantly over time, with 900 estimated in 2008 (MI DNR 2008, p. 54), 900 in 2015 (MI DNR 2015, p. 47), and 1,000 in 2022 (MI DNR 2022a, p. 69). Until 2012, there was a general increase in confirmed events of wolf depredations on livestock as wolves increased in the state; specifically, an average of 2.5 depredation events occurred annually between 1998 and 2002, while an average of 25 occurred annually between 2008 and 2012 (Roell et al. 2010, p. 13; Beyer 2018, in litt.; MI DNR 2022e, p. 68). Since 2012, however, while the population has continued to increase, the number of livestock depredation incidents has declined, with an average of six incidents a year from 2018 to 2022 (Roell 2023a, in litt.). These data show a weak correlation between wolf abundance and the number livestock depredation incidents in Michigan, unlike in other states, indicating that wolf depredations in the state are driven by individual packs rather than overall wolf abundance (MI DNR 2022e, pp. 68–70). Over 80 percent of the depredation events in Michigan have been on cattle, with the rest on sheep, poultry, rabbits, goats, horses, swine, and captive deer (Roell 2023a, in litt.).

In Michigan, wolf depredation and conflict initially rose with increasing wolf numbers but have since stabilized despite population growth. This decoupling is likely attributed to improved management practices, and targeted conflict mitigation (MI DNR 2022a, pp. 26–28). The state's adaptive approach—grounded in both biological and social science—has helped maintain a relatively stable level of conflict even as wolves have expanded in range and abundance (MI DNR 2022a, pp. 26–29). While wolf numbers in Michigan have slightly increased or stabilized, depredation and conflict levels have not followed the same trend. Instead, they have remained relatively stable due to improved management, localized conflict patterns, and changes in livestock practices (MI DNR 2022a, p. 28). The 2022 plan underscores the importance of adaptive, science-based strategies to minimize conflict while maintaining a viable wolf population (MI DNR 2022a, entire).

There is also a very weak correlation between wolf depredation of dogs and wolf abundance in Michigan (Roell et al. 2010, p. 7). While wolf abundance has generally increased annually since the 1990s, yearly losses of dogs to wolf depredation varied. The number of dogs killed or injured in the state from 1996 to 2022 totaled 146 (Beyer 2018, in litt.; Roell 2023a, in litt.; Roell 2025a, in litt.). Most (78 percent) of the wolf-related dog deaths from 1996 to 2022 involved hounds used to hunt bears or rabbits/hares (Roell 2025a, in litt.).

Lethal depredation control has not been authorized in Michigan (due to the listed status of wolves as endangered) except (1) as authorized under section 4(d) when the population was reclassified to threatened (from April 13, 2003, to January 31, 2005), (2) by special permits (from April 1, 2005, to September 13, 2005, and from April 24, 2006, to August 10, 2006), and (3) when delisted (from March 12, 2007, to September 29, 2008; May 4, 2009, to July 1, 2009; January 27, 2012, to December 19, 2014; and January 4, 2021, to February 10, 2022). Outside of those times, management of depredating wolves in Michigan was limited to nonlethal methods, such as scare tactics and aversion conditioning.

Between 2003 and 2022, the Michigan DNR and Wildlife Services lethally removed a total of 53 wolves in the state in response to depredation events during the time periods when permits or special rules were in effect or while wolves were not federally protected (Roell 2023b, in litt.; Roell 2025a, in litt.). Over the same time periods, private citizens lethally removed an additional 39 wolves in response to depredation events under a depredation control permit, when those authorities allowed (Public Act 290 (for livestock), or Public Act 318 (for domestic dogs) or lethal control permits issued to livestock producers) (Roell 2023b, in litt.). Overall, during the years when lethal control was allowed, the number of wolves removed each year for depredation control (livestock and dogs) ranged from a minimum of one wolf in 2009 to a maximum of 18 wolves in 2012 (Table 1). During the years when lethal depredation control was allowed between 2003 to 2021, an average of 1.3 percent of the year-end wolf population (range 0.2–2.5 percent) was removed through lethal depredation control in Michigan (we could not calculate a lethal depredation control rate for 2014 because Michigan did not produce a population estimate that we could apply as a year-end estimate for 2014) (Table 7). The number of wolves lethally removed and the percentage of the statewide wolf population lethally removed (i.e., the annual lethal depredation control rate) for the past 20 years is presented in Table 1.

Table 1. Number of wolves lethally removed under Michigan wolf depredation control and the percentage of the statewide year-end gray wolf population (Roell 2023b, in litt.). Note that in some years lethal depredation control was only allowed for part of the year. Years in which zero gray wolves were lethally removed were years in which such removal was not authorized (i.e., the species was listed as endangered).

Calendar Year	Number of Gray Wolves Lethally Removed	Percent of Year-end Gray Wolf Population (i.e., lethal depredation control rate)[a]
2003	4	1.0
2004	5	1.1
2005	2	0.4
2006	7	1.3
2007	14	2.5
2008	8	1.3
2009	1	0.2
2010	0	0
2011	0	0
2012	18	2.5
2013	10	1.4
2014	13	NA[b]
2015	0	0
2016	0	0
2017	0	0
2018	0	0
2019	0	0
2020	0	0
2021	9	1.3
2022	0	NA[b]

[a] Each state in the Western Great Lakes conducts their population counts/estimates in mid- to late winter, when wolf populations are closest to their minimum because it precedes the spring breeding season. Minnesota and Wisconsin report winter counts/estimates straddling two calendar years (e.g., 2010/2011 winter count/estimate). Michigan reports their winter counts/estimates as beginning of a calendar year (e.g., early 2011). However, each state provided mortality information on a calendar year basis (i.e., number of confirmed wolf mortalities due to various causes for a single calendar year). Thus, we needed to use end-of-calendar year population estimates to calculate annual mortality rates. For the purposes of our annual mortality rate calculations (and for use in our future condition modeling), we treated the winter counts/estimates as "end-of-calendar-year" values and assigned them to the earlier of the two years or, in the case of Michigan, the end of the prior year. For example, a "2010/2011 winter count/estimate" and an "early 2011 winter count/estimate" were each assigned as "end-of-year count/estimates" for 2010 (see Appendix 2). This is an appropriate use of the data because all three of the states' counts/estimates are conducted prior to the breeding season; thus, we can be certain that a wolf counted in early February was also a member of the population in December of the prior year. Thus, all mortality rates discussed below were calculated by dividing the number of wolves that died from each type of mortality for a given year by the population count/estimate for the end of that calendar year plus the known number of wolves that died from all causes that same year (i.e., this sum in the denominator represents the minimum number of wolves known to be alive at some point during the calendar year).

[b] Not able to calculate the percent of the gray wolf population for this year because there is no population estimate available for the end of the calendar year (see Table 7).

Nonlethal trapping and translocating depredating wolves was used as an alternative to lethal control in the past, resulting in the translocation of 23 Upper Peninsula wolves between 1998–2003 (Beyer et al. 2006, p. 88). However, suitable relocation sites are no longer available since all suitable wolf habitat is occupied (Roell 2025a, in litt.), and there is local opposition to the release of translocated depredators. Furthermore, none of the past translocated depredators have remained near their release sites, making this a questionable method to end the depredation behaviors of these wolves (MI DNR 2005a, pp. 3–4). Therefore, reducing depredation problems by relocation is no longer recommended as a management tool in Michigan and will rarely be used (MI DNR 2022b, p. 8). Consequently, if legally allowed, lethal control of depredating wolves is likely to be the most common future response in situations when improved livestock husbandry and wolf-behavior-modification techniques (for example, flashing lights, noisemaking devices) are judged to be inadequate. Under a previous lethal take permit under section 10(a)(1)(A) of the Act that is no longer in place, Michigan DNR received authority to lethally remove up to 10 percent of the late-winter wolf population annually (MI DNR 2005b, p. 1). However, during all the years in which Michigan had the authority to use lethal means to manage depredations no more than 2.5 percent of the year-end population was removed in any year (see Table 1 above).

If wolves were federally delisted, wolf depredation control in Michigan would be carried out according to the Michigan Plan (MI DNR 2022a, entire) and any tribal wolf-management plans (existing or future) for reservation lands. The Michigan DNR has developed detailed instructions for incident investigation and response (MI DNR 2022b, entire). Michigan DNR or Wildlife Services personnel (working under a Cooperative Service Agreement or at the request of a Tribal Nation, depending on the location) trained in depredation investigation techniques first verify wolf depredation incidents. Following verification, Michigan DNR or Wildlife Services personnel (official personnel) implement appropriate control techniques for the specific situation, which may include lethal depredation control if wolves were federally delisted. The official personnel also provide advice or recommendations and materials to reduce wolf conflicts in the future. If wolves were federally delisted, the Michigan DNR guidelines for its depredation control program would also allow official personnel to conduct lethal control in response to depredations of free-ranging hunting dogs in specific areas where a wolf depredation has been verified and when nonlethal methods are determined to be ineffective (MI DNR 2022b, pp. 11–12). Lethal control of wolves (conducted by official personnel) could also be considered if wolves killed confined pets and remain in the area where more pets are being held (MI DNR 2022b, p. 12).

If wolves were federally delisted, private citizens (as opposed to official personnel) would be allowed to conduct lethal depredation control in specific situations. Livestock producers could conduct their own private lethal depredation control of gray wolves on their property to prevent additional depredations, in areas with previous depredations. That private preventative lethal depredation control would need to follow the Michigan DNR's additional requirements and guidance (MI DNR 2022c, entire). A livestock producer would be required to hold a permit to use this authority, and permits would be issued only after the use of nonlethal control measures proved ineffective; permits also would not be issued for proactive use on farms with no previous history of wolf depredation. Additionally, two laws (Public Acts 290 and 318) would become effective if wolves in Michigan were to be federally delisted. Under those laws, a livestock or dog owner (or designated agent) could use lethal control without a permit if a wolf is presently in the act of killing or injuring (not merely present near) their livestock or dog, including dogs free-roaming or hunting on public lands (MI DNR 2022d, entire). Such situations must be reported to the Michigan DNR within 12 hours.

Michigan livestock owners are compensated when they lose lawfully present livestock as a result of a confirmed wolf depredation. The Michigan Wildlife Depredations Indemnification Act (Public Act 487 of 2012) provides payment to livestock owners, but it may do so only if the Michigan DNR or its designated agent verifies the depredation was caused by wolves, coyotes, or cougars. If the investigator cannot rule out wolves as the cause for the missing animals and the farm has had "verified" wolf depredation in the past, the owner is eligible to receive indemnification payment from the Michigan Department of Agriculture and Rural Development (MI DNR 2022b, p. 10). From 1998 to 2024, a total of $213,712 was spent on compensation to Michigan farmers for livestock losses caused by wolves, which includes payments for missing animals and late payment penalties which both began after 2012 (Roell 2025b, in litt.).

Human-Caused Mortality in Michigan Summary

During the years in which regulated harvest or lethal depredation control was authorized in Michigan between May–September, when the majority of lethal depredation control activities take place (i.e., 2003, 2004, 2007, 2008, 2012, 2013, 2014, and 2021, though harvest only occurred in 2013), regulated harvest and lethal depredation control annually removed an average of 1.8 percent of the estimated year-end gray wolf population in the state (range: 0.4 percent to 4.5 percent). As expected, given the limitations on legal human-caused mortality while the species is listed, human-caused mortality increased during the periods of time in which the gray wolf was not federally protected in Michigan. Authorized human-caused mortality rarely occurs while the species is listed as endangered so any level of lethal depredation control, for example, that occurs once the species is no longer federally protected would represent an increase.

During the years in which depredation control took place, absent a regulated harvest, and in which Michigan was still providing annual population estimates (2003, 2004, 2007, and 2008), the wolf population increased, on average, 9.5 percent annually.[15] After the year-end 2010 population estimate (which Michigan calls the early 2011 population estimate), Michigan began providing population estimates less frequently (see Table 7), complicating the calculation of

[15] This value represents the average of four year-over-year population changes:
Percent population change between year-end estimates for 2002 and 2003 (Michigan's early 2003 and early 2004 estimates), representing the change in population size relative to 2002 after the lethal depredation control that occurred during 2003: 12.1 percent
Percent population change between year-end estimates for 2003 and 2004 (Michigan's early 2004 and early 2005 estimates), representing the change in population size relative to 2003 after the lethal depredation control that occurred during 2004: 12.5 percent
Percent population change between year-end estimates for 2006 and 2007 (Michigan's early 2007 and early 2008 estimates), representing the change in population size relative to 2006 after the lethal depredation control that occurred during 2007: 2.2 percent
Percent population change between year-end estimates for 2007 and 2008 (Michigan's early 2008 and early 2009 estimates), representing the change in population size relative to 2007 after the lethal depredation control that occurred during 2008: 11 percent

population trends after years with increased human-caused mortality. Nonetheless, an exponential growth model of wolf abundance estimates has shown that Michigan's wolf population has remained relatively stable between 2011 and 2024 (MI DNR 2022a, p. 19; Roell 2025a, in litt.). If the gray wolf were to be delisted again, Michigan's management plan and regulations would allow the state to conduct lethal depredation control, under certain circumstances, and would allow for consideration of a regulated harvest season (MI DNR 2022a, pp. 58–67, 69–73). However, the winter wolf population must exceed 200 wolves to achieve the Michigan Plan's goal of maintaining a viable wolf population in the Upper Peninsula (MI DNR 2022a, p. 23).

Human-Caused Mortality in Minnesota

Regulated Harvest in Minnesota

Regulated wolf harvest is not permitted in Minnesota while wolves are listed under the Act. However, it has occurred in Minnesota when wolves were previously delisted in the state and may be considered again if wolves are federally delisted in the future. The Minnesota Plan discusses the purposes of any potential regulated harvest in the future and the strategies it would use to develop harvest recommendations (see *State Management: Minnesota* above).

In 2011, the Minnesota Legislature classified wolves as small game in state statute (Minnesota Statutes 97B.645 Subdivision 9) and authorized the Minnesota DNR to implement a regulated wolf harvest season should wolves be delisted. Following Federal delisting in early 2012, the 2012 Minnesota Legislature established wolf hunting and trapping licenses, clarified the authority for the Minnesota DNR to implement a wolf season, and required the start of the season to be no later than the start of firearms deer season each year. Three regulated harvest seasons (2012, 2013, and 2014) were subsequently implemented in the state while wolves were federally delisted (Table 2). In 2012, the Minnesota DNR established a total target harvest of 400 wolves (the close of the harvest season was to be initiated when that target was met) (Stark and Erb 2013, pp. 1–2). During that first regulated season, 413 wolves were harvested (representing 14 percent of the year-end population, i.e., 14 percent harvest rate). Based on the results of the 2012 harvest season, the Minnesota DNR adjusted the target to 220 wolves for 2013; that year 238 wolves were harvested (representing 8 percent of the year-end population, i.e., 8 percent harvest rate). The 2014 target harvest was 250 wolves and 272 were harvested (representing 10 percent of the year-end population, i.e., 10 percent harvest rate). Quota exceedances are generally due to multiple wolves being harvested and/or reported on the same day the zone closes. Although Minnesota exceeded its harvest quotas in each of these three harvest seasons, the initial quotas the state set were conservative relative to the year-end population. Thus, even with the exceedances, the resulting harvest rates remained low (Table 2). Further, the responsive changes Minnesota made to the harvest quotas over the three seasons illustrate Minnesota's commitment to employ adaptive management techniques over a series of harvest seasons. When wolves were federally delisted in 2020, the Minnesota DNR decided not to hold a wolf harvest in 2021 because it was revising its wolf management plan; consideration of whether to hold a wolf harvest season, and when and how a season would be implemented, would be guided by its updated plan.

Table 2. Regulated harvest target in Minnesota, the number of wolves harvested, and the proportion of the year-end population harvested (i.e., harvest rate).

Regulated Harvest Season	Harvest Target	Total Number of Wolves Harvested	Percent of Year-end Population (i.e., harvest rate)[a]
2012	400	413	14.0
2013	220	238	8.4
2014	250	272	9.9

[a] Each state in the Western Great Lakes conducts their population counts/estimates in mid- to late winter, when wolf populations are closest to their minimum because it precedes the spring breeding season. Minnesota and Wisconsin report winter counts/estimates straddling two calendar years (e.g., 2010/2011 winter count/estimate). Michigan reports its winter counts/estimates as beginning of a calendar year (e.g., early 2011). However, each state provided mortality information on a calendar year basis (i.e., number of confirmed wolf mortalities due to various causes for a single calendar year). Thus, we needed to use end-of-calendar year population estimates to calculate annual mortality rates. For the purposes of our annual mortality rate calculations (and for use in our future condition modeling), we treated the winter counts/estimates as "end-of-calendar-year" values and assigned them to the earlier of the two years or, in the case of Michigan, the end of the prior year. For example, a "2010/2011 winter count/estimate" and an "early 2011 winter count/estimate" were each assigned as "end-of-year count/estimates" for 2010 (see Appendix 2). This is an appropriate use of the data because all three of the states' counts/estimates are conducted prior to the breeding season; thus, we can be certain that a wolf counted in early February was also a member of the population in December of the prior year. Thus, all mortality rates discussed below were calculated by dividing the number of wolves that died from each type of mortality for a given year by the population count/estimate for the end of that calendar year plus the known number of wolves that died from all causes that same year (i.e., this sum in the denominator represents the minimum number of wolves known to be alive at some point during the calendar year).

The Minnesota DNR may consider wolf population-management measures, including public hunting and trapping seasons and other methods, if wolves were federally delisted again. However, the Minnesota Plan instructs that population-management measures be implemented in a manner that maintains a population comparable in size to recent estimates (i.e., 2,200–3,000 wolves) that is distributed across the majority of the current wolf range in Minnesota (i.e., present throughout the current range) (MN DNR 2022, pp. 30–31), well above the goal of 1,251 to 1,400 wolves for the state in the Service's Revised Recovery Plan (Service 1992, p. 28).

Depredation Control in Minnesota

Under the authority of the 4(d) rule that regulates take in Minnesota, gray wolves that have attacked domestic animals may be lethally removed by designated government employees while the species is listed. We describe the details of this 4(d) rule under *State Management: Minnesota* above. During the period from 1979–2022, in years when gray wolves were federally listed, Wildlife Services and Minnesota DNR lethally removed between a minimum of 6 (in 1979) and a maximum of 216 (in 1997 and 2020) gray wolves annually under the authority of the 4(d) rule (Appendix 2). When gray wolves were federally delisted and gray wolf management was transferred to the states and Tribal Nations, Minnesota DNR also allowed certified gray wolf controllers to respond to gray wolf depredation. The highest number of gray wolves lethally removed during periods when wolves were federally delisted (2012–2014 and 2021–2022) was 295 gray wolves in 2012. The Minnesota DNR did not begin annual population estimates until 2012, so we are not able to describe annual percentages of gray wolves lethally removed before 2012, except for 2003 and 2007. Since 2003, during the years when year-end population estimates were available (i.e., 2003, 2007, 2012–2022), an average of 6.3 percent of the year-end gray wolf population (range: 3.9–10 percent) was removed through lethal depredation control in Minnesota (Table 7). The number of gray wolves lethally removed and the percentage of the statewide gray wolf population lethally removed (i.e., the annual lethal depredation control rate) is presented in Table 3.

Table 3. Number of gray wolves lethally removed under Minnesota depredation control and the percentage of the year-end statewide gray wolf population since 2003.

Calendar Year	Number of Gray Wolves Lethally Removed	Percent of Year-end Population (i.e., lethal depredation control rate)[a]
2003	125	3.9
2004	105	NA[b]
2005	134	NA[b]
2006	122	NA[b]
2007	133	4.3
2008	143	NA[b]
2009	195	NA[b]
2010	192	NA[b]
2011	203	NA[b]
2012	295	10.0
2013	140	5.0
2014	222	8.1
2015	213	8.5
2016	183	6.0
2017	190	6.7
2018	189	6.5
2019	166	5.7
2020	216	7.2
2021	162	5.6
2022	142	4.6

[a] Each state in the Western Great Lakes conducts its population counts/estimates in mid- to late winter, when wolf populations are closest to their minimum because it precedes the spring breeding season. Minnesota and Wisconsin report winter counts/estimates straddling two calendar years (e.g., 2010/2011 winter count/estimate). Michigan reports its winter counts/estimates as beginning of a calendar year (e.g., early 2011). However, each state provided mortality information on a calendar year basis (i.e., number of confirmed wolf mortalities due to various causes for a single calendar year). Thus, we needed to use end-of-calendar year population estimates to calculate annual mortality rates. For the purposes of our annual mortality rate calculations (and for use in our future condition modeling), we treated the winter counts/estimates as "end-of-calendar-year" values and assigned them to the earlier of the two years or, in the case of Michigan, the end of the prior year. For example, a "2010/2011 winter count/estimate" and an "early 2011 winter count/estimate" were each assigned as "end-of-year count/estimates" for 2010 (see Appendix 2). This is an appropriate use of the data because all three of the states' counts/estimates are conducted prior to the breeding season; thus, we can be certain that a wolf counted in early February was also a member of the population in December of the prior year. Thus, all mortality rates discussed below were calculated by dividing the number of wolves that died from each type of mortality for a given year by the population count/estimate for the end of that calendar year plus the known number of wolves that died from all causes that same year (i.e., this sum in the denominator represents the minimum number of wolves known to be alive at some point during the calendar year) (see Appendix 2).

When gray wolves were first under state management (i.e., delisted) in 2007 and 2008, the number of gray wolves lethally removed annually for depredation control remained relatively consistent with the numbers removed in the preceding years when gray wolves were federally listed and covered by the section 4(d) rule (i.e., in 2004, 2005, and 2006) (Table 3). The numbers of gray wolves lethally removed annually for depredation control were slightly higher when gray wolves were under state management for the second time (2011–2014), but were still consistent with removal numbers under the authority of the section 4(d) rule while gray wolves were federally listed in the surrounding years (i.e., in 2009, 2010, 2015, and 2016) (Table 3). The number of gray wolves lethally removed for depredation control while under state management in 2021 was similar to or lower than surrounding years when gray wolves were managed under the authority of the section 4(d) rule while gray wolves were federally listed (i.e., in 2018, 2019, 2020, and 2022) (Table 3). In summary, the effects of lethal depredation control activities have not varied substantially in Minnesota based on federal listing status.

If gray wolves in Minnesota were to be federally delisted, depredation control would be authorized under Minnesota state law and conducted in conformance with the Minnesota Plan (MN DNR 2022, entire), in addition to any tribal wolf-management plans (existing or future) for reservation lands. The management of depredating gray wolves would be similar to management under the 4(d) rule while federally listed, except with a few additional depredation control options. Under Minnesota state law, if gray wolves were to be federally delisted, an owner of livestock, domestic animals, or guard animals anywhere in the state may lethally remove gray wolves without a permit that pose "an immediate threat" (defined as "in the act of stalking, attacking or killing") to livestock, domestic animals (not including pets), or guard animals on lands that he or she owns, leases, or occupies (Minnesota Statutes, Section 97B.645, Subdivision 5). Owners of domestic pets could also lethally remove gray wolves anywhere in the state without a permit (wherever they can legally discharge a firearm) that pose an immediate threat to pets under their supervision on any land irrespective of the ownership, although such actions would be subject to local ordinances, trespass law, and other applicable restrictions (Minnesota Statutes, Section 97B.645, Subdivision 6). Private individuals would be required to report any gray wolves lethally removed without a permit to a Minnesota DNR Conservation Officer within 48 hours of the removal.

In the majority of the gray wolf current range in Minnesota (i.e., Zone A), after a recent verified depredation event, individuals would be able to request the Minnesota DNR Commissioner open a wolf control zone and the commissioner would pay a state-certified predator controller to lethally remove (including trapping as an allowable method) gray wolves within a one-mile radius of the depredation site for up to 60 days (Minnesota Statutes, Section 97B.671, Subdivision 4). There would be additional flexibility offered to private landowners in the portion of the gray wolf's current range in Minnesota that is more developed and contains higher road densities, livestock, and domestic animals (i.e., Zone B). In those areas, individuals would be able to shoot a gray wolf without a permit on land that is owned, leased, or managed by that individual to protect their livestock, domestic animals, or pets (i.e., gray wolf would not have to pose an immediate threat), or they would be able to request the Minnesota DNR Commissioner open a wolf control zone and the commissioner would pay a state-certified predator controller to trap gray wolves within 1 mile of the land that is owned, leased or managed by that individual if a verified depredation has occurred within the past 5 years (Minnesota Statutes, Section 97B.645, Subdivision 8, and Section 97B.671, Subdivision 4).

Whenever a gray wolf is lethally removed by a state-certified predator controller, the controller must surrender all salvageable remains. Additionally, under Minnesota state law, if gray wolves were to be federally delisted, private individuals statewide could harass wolves anywhere in the state within 500 yards of "people, buildings, dogs, livestock, or other domestic pets or animals" as long as it does not result in physical injury to wolves and the wolves are not purposely attracted or tracked (Minnesota Statutes, Section 97B.645, Subdivision 4). As previously described, the 2022 Minnesota Plan recommends using legislative action to standardize the provisions of Zone B to those of Zone A, thereby creating a single management zone in the state that would require wolves to present an immediate threat for an owner to lethally remove them or would require a recent depredation incident to lethally remove wolves (as is currently required in Zone A) (MN DNR 2022, p. 33).

In general, the only forms of lethal depredation control that would be allowed if wolves were to be delisted that are not currently allowed under the 4(d) rule are the provisions that allow for private citizens and state-certified predator controllers to remove wolves. Both under the 4(d) rule and under state management, Wildlife Services is allowed to remove wolves after a verified depredation (this is the only source of lethal control allowed under 4(d) rule). Thus far, this removal by Wildlife Services has made up the vast majority of removals when delisted. The removals due to private citizens and state-certified predator controllers to remove wolves are a minor addition. While wolves were under state management from 2007–2008, 2011–2014, and 2021–2022, private landowners shot 6 (2007–2008), 40 (2011–2014), and 6 wolves (2021–2022) under the authorities described above (Stark 2023a, in litt.; Stark 2023b, in litt). Fourteen additional wolves were trapped and euthanized by state-certified predator controllers (one in 2009 and 13 in 2013) (Stark 2009, in litt.; Stark 2018, in litt.; Stark 2023b, in litt.). As described earlier in this section, in general, the scale of annual lethal depredation control activities has not varied substantially in Minnesota based on whether wolves were federally listed and managed under the authority of the 4(d) rule or under state management when delisted.

The Minnesota Department of Agriculture (MDA) maintains a depredation-control program that includes compensation for verified livestock losses and maintains a grant program to help livestock owners implement strategies that help minimize wolf-livestock conflict (MN DNR 2022, pp. 18, 33, 62). In the last 10 years, MDA has paid approximately $100,000–$250,000 for between 80–140 compensation claims annually (MN DNR 2022, p. 21). For compensation to be considered, an authorized investigator must confirm that wolves were responsible for the depredation. The Minnesota statute also requires MDA to periodically update its Best Management Practices to incorporate new practices that it finds would reduce wolf depredation (Minnesota Statutes 2018, Section 3.737, Subdivision 5).

Human-Caused Mortality in Minnesota Summary

Given the threatened, rather than endangered, Federal listing status in Minnesota, and the associated section 4(d) rule that authorizes lethal depredation control under some circumstances, Minnesota has the authority to lethally remove depredating wolves even while the species is federally protected. However, regulated harvest, which occurred in 2012, 2013, and 2014 in

Minnesota, can only occur when the species is no longer federally protected. Since 2003, during the years when year-end population estimates were available, regulated harvest and lethal depredation control annually removed an average of 8.8 percent of the year-end estimated wolf population in the state (range: 3.9 percent to 24.0 percent) (see Appendix 2). As expected, given that regulated harvest can only occur when the species is delisted, authorized human-caused mortality increased during years when the species was delisted (i.e., 2012, 2013, and 2014). In contrast, generally, the effects of lethal depredation control activities have not varied substantially in Minnesota based on Federal listing status.

During the periods when wolves have been managed under the 4(d) rule in Minnesota (i.e., while the species is listed but lethal depredation control occurs), the Minnesota wolf population has continued to grow or remain stable, with occasional slight decreases between some years (the population never decreased for more than 1 year; any single-year population decrease was always followed by a population increase) (Appendix 2). During the years in which the species was delisted and regulated harvest occurred in addition to lethal depredation control (i.e., 2012, 2013, and 2014), the population grew an average of 0.65 percent annually.[16] The species also lacked Federal protection in 2021, though only lethal depredation control occurred in this year (there was no regulated harvest season). The population decreased slightly between year-end 2020 and year-end 2021, even though the lethal depredation control rate was lower in 2021 than in previous years in which the population still increased (e.g., the lethal depredation control rate in Minnesota in 2021 was 5.6 percent and the year-end 2021 population estimate decreased 2.9 percent relative to the year-end 2020 population estimate; but, in 2020, the lethal depredation control rate was 7.2 percent while the population increased 2.7 percent relative to year-end 2019). The population in Minnesota once again increased between year-end 2021 and year-end 2022 (an 8.5 percent increase). Therefore, the slight decreases and increases in the population size in Minnesota do not appear to be directly linked to the specific levels of human-caused mortality occurring in the population and may be more related to other sources of stochasticity (e.g., fluctuations in prey availability). Overall, the Minnesota population has been able to withstand the levels of lethal depredation control and regulated harvest it has experienced to date without any substantial decreases in population size. If the gray wolf were to be delisted again, Minnesota's management plan would allow the state to continue conducting lethal depredation control, under certain circumstances, and would allow for regulated harvest seasons (MN DNR 2022 Appendix 2, pp. 47–51; MN DNR 2022 Appendix 4, pp. 58–62). However, even with the continuation of lethal depredation control or the reintroduction of regulated harvest, the Minnesota Plan recommends maintaining a population comparable in size to recent year-end population estimates (2,200–3,000 wolves) that is distributed across most of the current wolf range in Minnesota.

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[16] This value represents the average of 2 year-over-year population changes (we could not calculate the percent population change between year-end estimates for 2011 and 2012, which would have represented the change in population size after the regulated harvest season in 2012, because the state did not produce a population estimate for year-end 2011 (winter 2011/2012). Thus, we averaged the:
Percent population change between year-end estimates for 2012 and 2013 (Minnesota DNR's winter 2012/2013 and winter 2013/2014 estimates), representing the change in population size relative to 2012 after the regulated harvest season that occurred during 2013: 9.6 percent
Percent population change between year-end estimates for 2013 and 2014 (Minnesota DNR's winter 2013/2014 and winter 2014/2015 estimates), representing the change in population size relative to 2013 after the regulated harvest season that occurred during 2014: -8.3 percent

Human-Caused Mortality in Wisconsin

Regulated Harvest in Wisconsin

Regulated gray wolf harvest is not permitted in Wisconsin while gray wolves are listed under the Act. However, regulated harvest has occurred in Wisconsin when gray wolves were previously delisted and will be implemented again if gray wolves are federally delisted in the future (in accordance with Wisconsin Act 169, which we describe further below). Wisconsin describes a regulated harvest strategy in the Wisconsin Plan (WI DNR 2023a, pp. 141–147). Wisconsin Act 169 was enacted in April 2012, following Federal delisting of gray wolves earlier that year. The law effectively reclassified gray wolves in Wisconsin as a game species and directed the Wisconsin DNR to administer a regulated wolf harvest season whenever gray wolves are not a Federal or state listed species. In order to establish a harvest season, the Wisconsin DNR sets harvest quotas for individual zones consistent with state laws (e.g., Emergency Rule 1210, which directs wolf harvest seasons) and Federal laws (e.g., off reservation treaty rights, and Federal listing status) and in coordination with the Ojibwe Tribes and the Wisconsin Natural Resources Board (which sets policy for the DNR and exercises its authority in accordance with state laws) (WI DNR 2023a, pp. 83–85, 141–147); harvest in each zone closes at the end of February or if the individual quotas are met, whichever occurs first. As described in the *State Management* section, hunters and trappers were required to register a gray wolf harvest online or over the phone within 24 hours of the harvest, followed by an in-person certification process with a Wisconsin DNR conservation officer or wildlife biologist to provide demographic and biological data. As outlined in State Statute 29.185, the Wisconsin DNR must provide 24-hour public notice before zone closures. In Wisconsin, the Ojibwe Tribes can request up to half of the allowable harvest within the ceded territories, which is a subset of the annual statewide harvest quota. In 2012, the Ojibwe Tribes elected not to harvest gray wolves (85 wolves were eligible for tribal harvest in the ceded territories), and the portions of allowable harvest given to the Ojibwe Tribes declined in subsequent years to 24 gray wolves in 2013 and 6 in 2014 due to a lack of demonstrated harvest (WI DNR 2013, pp. 1, 2; WI DNR 2014, p. 4; McFarland and Wiedenhoeft 2015, pp. 2, 4). In 2021, the Wisconsin DNR set a gray wolf harvest quota of 200 wolves. In accordance with their treaty rights within the ceded territories, the Ojibwe Tribes declared the full 50 percent of the allowable harvest in the ceded territories and the Wisconsin DNR honored that declaration. As a result, 119 gray wolves were allocated to the state and 81 gray wolves were allocated to the Ojibwe Tribes. The Ojibwe tribes have not harvested any of the allocated gray wolves during any of the regulated harvest seasons and it has since been clarified that the Ojibwe Tribes may use their quota share for protective purposes, rather than be required to harvest those gray wolves (Newland and Estenoz 2022, in litt.).

Table 4. Regulated harvest quotas in Wisconsin, the number of wolves harvested, and the proportion of the year-end population harvested (i.e., harvest rate).

Regulated Harvest Season[a]	State Quota	Tribal Quota	Total Quota	Total Number of Gray Wolves Harvested	Percent of Year-end Population (i.e., harvest rate)[b]
2012/2013	116	85	201	117	11.1% of year-end 2012 population
2013/2014	251	24	275	257	25.2% of year-end 2013 population
2014/2015	150	6	156	154	15.9% of year-end 2014 population
2021	119	81	200	218	17.0% of year-end 2021 population

[a] While these harvest seasons were designed to occur between October 15 and the end of February of the following year, the harvest seasons in Wisconsin always closed before the end of the calendar year, when the state reached its quota. For example, the 2012/2013 harvest season was originally opened from October 15, 2012, through February 28, 2013, but it closed December 23, 2012, when the quota was met. Therefore, all of the total number of gray wolves harvested in the table above represent the total for the first calendar year of the season (e.g., a total of 117 gray wolves were harvested in 2012).

[b] Each state in the Western Great Lakes conducts its population counts/estimates in mid- to late winter, when gray wolf populations are closest to their minimum because it precedes the spring breeding season. Minnesota and Wisconsin report winter counts/estimates straddling two calendar years (e.g., 2010/2011 winter count/estimate). Michigan reports its winter counts/estimates as beginning of a calendar year (e.g., early 2011). However, each state provided mortality information on a calendar year basis (i.e., number of confirmed gray wolf mortalities due to various causes for a single calendar year). Thus, we needed to use end-of-calendar year population estimates to calculate annual mortality rates. For the purposes of our annual mortality rate calculations (and for use in our future condition modeling), we treated the winter counts/estimates as "end-of-calendar-year" values and assigned them to the earlier of the two years or, in the case of Michigan, the end of the prior year. For example, a "2010/2011 winter count/estimate" and an "early 2011 winter count/estimate" were each assigned as "end-of-year count/estimates" for 2010 (see Appendix 2). This is an appropriate use of the data because all three of the states' counts/estimates are conducted prior to the breeding season; thus, we can be certain that a gray wolf counted in early February was also a member of the population in December of the prior year. Thus, all mortality rates discussed above were calculated by dividing the number of gray wolves that died from each type of mortality for a given year by the population count/estimate for the end of that calendar year plus the known number of gray wolves that died from all causes that same year (i.e., this sum in the denominator represents the minimum number of gray wolves known to be alive at some point during the calendar year) (see Appendix 2).

For the 2012/2013 harvest season, which included both hunting and trapping, the Wisconsin DNR established a total quota of 201 gray wolves (a state-licensed quota of 116 gray wolves and a tribal offer of 85 gray wolves). Harvest quotas for the 2012/2013 season were designed to focus higher harvest levels in areas of highest human-wolf conflict. A total of 117 gray wolves (11.1 percent of the year-end 2012 minimum population) were harvested during that first season (i.e., during 2012, given that the season closed in December of 2012, rather than February 2013, because the quota had been met), all under the state licenses (Tribal Nations did not authorize members to harvest gray wolves within reservation boundaries). Although the total harvested wolves exceeded the state-licensed quota, small quota exceedances are generally due to multiple wolves being harvested and/or reported on the same day the zone closes. After that season, the minimum count of gray wolves in the state remained relatively constant, falling slightly from 815 gray wolves at the end of 2011 to 809 gray wolves at the end of 2012 (Service 2020, p. 22). A second regulated harvest season was held in 2013/2014, with a total quota of 275 gray wolves (a state-licensed quota of 251 and a tribal offer of 24). During 2013, 257 gray wolves were harvested, which was 25.2 percent of the minimum population. Following that harvest season, the minimum population count was lower than the previous year, decreasing by 18 percent to 660 gray wolves at the end of 2013 (Wiedenhoeft et al. 2014, entire). In response to this change in the population size, the Wisconsin DNR reduced the wolf quota to 156 for the 2014/2015 hunting and trapping season (a 57 percent reduction from the 2013/2014 gray wolf quota), and 154 gray wolves (15.9 percent of the year-end population estimate) were harvested that season (a 60 percent decrease from the number of gray wolves harvested during the 2013/2014 season). With that reduced harvest, the Wisconsin gray wolf population again began to increase, to a minimum count of 746 gray wolves at the end of 2014 (a 13 percent increase over the previous year). The gray wolf was returned to the Federal List of Endangered and Threatened Wildlife in December 2014, and no additional regulated harvests were held until the gray wolf was delisted again in January 2021.

After the gray wolf was federally delisted on January 4, 2021, the Wisconsin DNR decided not to hold a regulated harvest season; however, due to litigation by Hunter Nation, a Jefferson County Circuit Court ruled the Wisconsin DNR must implement a regulated gray wolf harvest season before the end of February 2021 to comply with Wisconsin state law (Wisconsin Act 169). The total harvest quota for this February 2021 season was set at 200 gray wolves. Of the approved quota, 119 gray wolves were allocated to the state, and 81 gray wolves were allocated to the Ojibwe Tribes in the ceded territories. Harvest quotas were established for the six geographic zones. The Wisconsin DNR's approved quotas considered 2020 wolf population data, population response to previous harvest seasons, scientific literature, and population model projections. The February 2021 gray wolf harvest season opened on February 22 and all gray wolf harvest zones closed on February 24, after 5 of 6 gray wolf harvest zones (all except Zone 4) reached their quotas. A total of 218 gray wolves were registered as harvested (Johnson and Schneider 2021, pp. 2–3), representing 17 percent harvest rate. The quota allocated to the state (119 gray wolves) was surpassed (218 gray wolves harvested).

Although the state's quota allocation was exceeded in previous harvest seasons, the extent of harvest that exceeded the quota during the February 2021 season was unprecedented. The high rate of harvest combined with the 24-hour notice period that is required prior to closing a specific zone were likely at least partially responsible for the high number of gray wolves harvested during the February 2021 season. Reporting requirements for successful hunters and trappers were the same as in years past, however, due to the timing of the February 2021 hunt, the primary method of take was very different from previous harvest seasons. In past years, gray wolf harvest seasons opened on October 15 for hunters without hounds and for trapping (foothold only) and although the rate of harvest increased slightly each of the 3 years, foothold traps were the primary method of take accounting for between 52 and 81 percent of the harvest (WI DNR 2013, p. 2; WI DNR 2014, p. 2; WI DNR 2015, p. 2). The use of hounds and cable restraints to harvest gray wolves begins the Monday after the close of deer rifle season, which is generally late November to early December. As such, most gray wolf harvest zones had already met their quotas and were closed prior to these other methods of take being allowed and a total of 41 gray wolves were harvested with the use of hounds in 2013 and 2014 (WI DNR 2014, p. 2; WI DNR 2015, p. 2) (due to legal challenges, hound hunting was not permitted during the 2012 season).

During the February 2021 harvest season, the deer rifle season was already closed so hounds were permitted from the start of the season. As a result, 86 percent of the gray wolves harvested during February 2021 were harvested with the use of hounds. Moreover, due to environmental conditions that provided excellent tracking conditions, the speed of gray wolf harvest exceeded past years and prevented the Wisconsin DNR from accurately evaluating harvest in real time because its 24-hour reporting requirements, while effective at lower speeds of harvest, did not allow the state to close the season in time to limit exceeding the quotas. As described in the *State Management: Wisconsin* section above, the Wisconsin Plan incorporates several measures to minimize the potential to exceed regulated harvest quotas in the future including zone-specific license issuance, and the intent to engage in rulemaking to require harvest registration time be reduced to 8 hours, instead of 24 hours, as currently outlined in state law (State Statute 29.185). Both of these measures would allow the Wisconsin DNR to better monitor harvest data and ensure timely zone closures.

The Wisconsin DNR planned to hold a Fall 2021/2022 harvest season, for which the Wisconsin DNR recommended a quota of 130 gray wolves to the Wisconsin Natural Resources Board, but the Board approved a higher quota of 300 gray wolves; however, Wisconsin DNR instead selected the original, lower quota of 130 gray wolves for the Fall 2021/2022 harvest season. Nonetheless, that harvest never took place due to litigation (Great Lakes Wildlife Alliance et al. v. Wisconsin Natural Resources Board et al., 2021) where a Dane County judge ruled that the Wisconsin DNR proposed harvest was illegal due to not having updated regulations or an updated gray wolf management plan. At the end of the year 2021 (the estimate of the population size after this February 2021 harvest), the population estimate was lower than the previous year (i.e., the population estimate decreased from 1,126 to 972 gray wolves).

Regardless of how Wisconsin manages harvest of gray wolves in the future, the Wisconsin DNR is committed to maintaining a sustainable wolf population with the intent to maintain statewide gray wolf abundance and distribution “at levels comparable to recent years (overwinter estimates of approximately 800–1,200)” (WI DNR 2023a, p. 129). At a minimum, they would maintain a statewide gray wolf population above the threshold for state listing as threatened (250 gray wolves outside of tribal reservations) (WI DNR 2023a, pp. 126–127).

Depredation Control in Wisconsin

From 1979 through 1989, there were only five cases (an average of 0.4 per year) of verified gray wolf depredations in Wisconsin, but the number of incidents has steadily increased over the subsequent decades as gray wolf populations have expanded. During the 1990s there were an average of approximately 4 incidents per year, increasing to an average of approximately 54 per year (ranging from 14 to 92) during the 2000s and to an average of approximately 91 per year (ranging from 61 to 125) from 2010 to 2022 (WI DNR 2023a, p. 89). While wolf-livestock depredations occur across gray wolf range in Wisconsin, most occur in the northwestern part of the state where livestock production is in close proximity to gray wolf habitat (WI DNR 2023a, pp. 90–91). Although the number of incidents and impacted farms is relatively low across the state, the impacts to an individual producer can be substantial. Between 2012 and 2014, when gray wolves were delisted and lethal depredation control and regulated harvests were allowed, verified gray wolf depredations on cattle and the number of farms with verified depredations declined significantly (i.e., decreased by 26 percent from 2012 to 2013 when 43 farms were affected, and by 11 percent from 2013 to 2014 when 36 farms were affected) (Wiedenhoeft et al. 2015, pp. 4–5, 12), indicating that active management with regulated harvests and targeted lethal depredation controls can reduce conflicts.

In Wisconsin, during the early stages of gray wolf recolonization (1975–2006), there was a clear positive correlation between wolf abundance and wolf-related conflicts, such as verified complaints and livestock losses. As the wolf population grew from just a few individuals to around 500, conflict reports increased accordingly (Ruid et al. 2009, entire). However, starting in the mid-2000s, this correlation weakened. Despite the wolf population continuing to grow—now exceeding 1,000 and expanding in range—conflict levels have remained relatively stable year to year (WI DNR 2023a, pp. 89–90). This shift may be influenced by changes in farming practices, livestock distribution, or reporting behavior. For example, Wisconsin has experienced a 74.2 percent decline in dairy farms—from 24,065 in 1997 to 6,216 in 2022—accompanied by a shift toward fewer, larger, and more consolidated operations (Hadachek & Deller 2024, pp. 1–2). These structural changes in agriculture, along with the increased use of conflict mitigation techniques, may reduce the frequency or severity of wolf-livestock interactions.

A significant portion of depredation incidents in Wisconsin involve attacks on dogs. In most cases, these have been hunting dogs that were being used for, or were being trained for, hunting bears, bobcats, coyotes, and snowshoe hare (Ruid et al. 2009, pp. 285–286; WI DNR 2023a, pp. 95–97). These attacks generally occur on lands open to public hunting when hunters or trainers are not in close proximity to the dogs. It is believed that the dogs entered the territory of a gray wolf pack and may have been close to a rendezvous site or feeding location, thus triggering an attack by gray wolves defending their territory or pups. Although wolf depredation on hunting dogs is often perceived to have increased with gray wolf population growth in Wisconsin, data from 2006 to 2024 suggest a more stable pattern. Excluding two outliers in 2012 and 2016, the annual number of reported hunting dog depredations has remained relatively consistent, exhibiting natural interannual variability but no clear upward trend (Ruid 2024, USDA-Wildlife Services, unpublished data). The low incidence in 2012 coincided with ongoing legal challenges to the use of dogs in wolf hunting, likely leading to reduced hunting activity and underreporting of wolf-dog conflicts. In contrast, 2016 saw a marked increase in depredations following the removal of individual fees for bear dog training permits, potentially increasing dog exposure in wolf-occupied areas (Wydeven 2025, in litt.). While the Wisconsin DNR compensates dog owners for mortalities and injuries to their dogs, the DNR takes no action against the depredating pack unless the attack was on a dog that was leashed, confined, or under the owner's control on the owner's land (this is the case while the species is listed and would remain the case if the species were to be delisted). Instead, they send e-mail notifications to inform hunters and bear-dog trainers of the areas where depredations have occurred (Wydeven 2025, in litt.) and provide maps and education to hunters to minimize risk to hunting dogs on the Wisconsin DNR website (WI DNR 2023b, unpaginated).

Gray wolf depredation incidents are verified by trained Wildlife Services personnel. If determined to be a confirmed or probable depredation by a gray wolf or wolves, the method used to address the depredation problem depends on the Federal and state listing status. If gray wolves are federally endangered, the response is limited to nonlethal abatement (visual and auditory harassment, fencing, and alteration of husbandry practices). If gray wolves are not federally or state listed, the response could include both nonlethal and lethal control. Technical assistance, consisting of advice or recommendations to prevent or reduce further gray wolf conflicts, is provided in either case. This may also include providing the landowner with various forms of non-injurious behavior-modification materials, such as flashing lights, noise makers, temporary fencing, and fladry (a string of flags used to deter wild animals).

Lethal depredation control has not been authorized in Wisconsin (due to the federally listed status of gray wolves as endangered) except (1) as authorized under section 4(d) when the population was reclassified to threatened (from April 13, 2003, to January 31, 2005), (2) by special permits (from April 1, 2005, to September 13, 2005, and from April 24, 2006, to August 10, 2006), and (3) when delisted (from March 12, 2007, to September 29, 2008; May 4, 2009, to July 1, 2009; January 27, 2012, to December 19, 2014; and January 4, 2021, to February 10, 2022). During those times, a total of 425 gray wolves were lethally removed for depredation control under the various authorizations. The number of gray wolves removed per year ranged from a minimum of 10 (in 2009) to a maximum of 76 (in 2012) (not including 2022, because it does not include the peak depredation time period for that year) (Table 5). During the years when lethal depredation control was authorized, an average 4.8 percent of the year-end gray wolf minimum population count/estimate (range 1.3–7.2 percent) was removed through lethal depredation control in Wisconsin) (Table 5). The number of gray wolves lethally removed and the percentage of the statewide minimum wolf population count/estimate lethally removed (i.e., the annual lethal depredation control rate) since 2003 is presented in Table 5.

Table 5. Number of wolves lethally removed under Wisconsin depredation control and the percentage of the year-end statewide wolf population minimum count/estimate (see Appendix 2). Note that in some years lethal depredation control was only allowed for part of the year. Years in which zero wolves were lethally removed were years in which such removal was not authorized (i.e., the species was listed as endangered).

Calendar Year	Number of Gray Wolves Lethally Removed	Percent of Year-end Minimum Count/Estimate (i.e., lethal depredation control rate)[a]
2003	17	4.0
2004	22	4.4
2005	31	5.7
2006	18	2.9
2007	38	5.9
2008	43	5.9
2009	10	1.3
2010	0	0
2011	0	0
2012	76	7.2
2013	64	6.3
2014	35	3.6
2015	0	0
2016	0	0
2017	0	0
2018	0	0

2019	0	0
2020	0	0
2021	69	5.4
2022	2	0.19[b]

[a] Each state in the Western Great Lakes conducts its population counts/estimates in mid- to late winter, when gray wolf populations are closest to their minimum because it precedes the spring breeding season. Minnesota and Wisconsin report winter counts/estimates straddling two calendar years (e.g., 2010/2011 winter count/estimate). Michigan reports its winter counts/estimates as beginning of a calendar year (e.g., early 2011). However, each state provided mortality information on a calendar year basis (i.e., number of confirmed gray wolf mortalities due to various causes for a single calendar year). Thus, we needed to use end-of-calendar year population estimates to calculate annual mortality rates. For the purposes of our annual mortality rate calculations (and for use in our future condition modeling), we treated the winter counts/estimates as "end-of-calendar-year" values and assigned them to the earlier of the two years or, in the case of Michigan, the end of the prior year. For example, a "2010/2011 winter count/estimate" and an "early 2011 winter count/estimate" were each assigned as "end-of-year count/estimates" for 2010 (see Appendix 2). This is an appropriate use of the data because all three of the states' counts/estimates are conducted prior to the breeding season; thus, we can be certain that a gray wolf counted in early February was also a member of the population in December of the prior year. Thus, all mortality rates discussed below were calculated by dividing the number of gray wolves that died from each type of mortality for a given year by the population count/estimate for the end of that calendar year plus the known number of gray wolves that died from all causes that same year (i.e., this sum in the denominator represents the minimum number of gray wolves known to be alive at some point during the calendar year).
[b] Through the date when wolves were relisted as endangered in the state due to a court order (February 10, 2022), which does not include the peak depredation time period.

Should gray wolves be federally delisted again, gray wolf depredation control in Wisconsin would be carried out according to the Wisconsin Plan and the Guidelines for Conducting Wolf Conflict Management in Wisconsin (Guidelines) (WI DNR 2022, entire), in addition to any tribal wolf-management plans (existing or future) for reservation lands. Under the Wisconsin Plan, lethal control may be considered in response to verified livestock conflicts. The lethal control options would include trapping and removal efforts by Wildlife Services or issuing a gray wolf removal permit to the landowner. Additionally, Wisconsin Administrative Code NR 10.02(1)(b) would allow a landowner, lessee, or occupant (or any person with their permission) to shoot a gray wolf in the act of killing, wounding, or biting a domestic animal on private property. Those shootings must be reported within 24 hours and the gray wolf carcass must be turned over to the Wisconsin DNR.

In Wisconsin, owners receive monetary compensation for all verified and probable losses of domestic animals (excluding hunting dogs killed or injured while hunting wolves) (WI DNR 2023a, p. 137; WI DNR 2006b 12.54). From 1985–2020, Wisconsin DNR provided compensation for 1,250 missing calves along with verified losses of 684 verified calves, 406 hunting dogs, 262 sheep, 243 chickens, 150 turkeys, 149 cattle, 69 captive white-tailed deer, 67 pet dogs, 26 horses/donkeys, 23 goats, 4 llama and 2 pigs (WI DNR 2023a, pp. 101–102). In the past five years (2020-2024), the Wisconsin Wolf compensation program paid out approximately $200,000 for an average of about 70 claims per year (Johnson 2025, in litt.). The Wisconsin DNR also provides compensation for veterinary expenses related to pet and livestock injuries. Livestock producers do not receive compensation for non-depredation impacts caused by wolves (Wisconsin Statute 29.888). Current Wisconsin law requires the continuation of the compensation payment for gray wolf depredation regardless of Federal listing status (WI DNR 2006b 12.50).

Human-Caused Mortality in Wisconsin Summary

During the years in which regulated harvest or lethal depredation control was authorized in Wisconsin during the entire season of May through September, when the majority of lethal depredation control activities take place (i.e., 2003, 2004, 2007, 2008, 2012, 2013, 2014, and 2021, though harvest only occurred in 2012, 2013, 2014, and 2021), regulated harvest and lethal depredation control annually removed an average of 14.0 percent of the estimated gray wolf population in the state (range: 4.0 percent to 31.5 percent). As expected, given the limitations on legal human-caused mortality while the species is listed, human-caused mortality increased during the periods of time in which the gray wolf was not federally protected in Wisconsin. Authorized human-caused mortality rarely occurs while the species is listed as endangered so any level of lethal depredation control, for example, that occurs once the species is no longer federally protected would represent an increase.

During the years in which depredation control took place absent a regulated harvest (2003, 2004, 2007, and 2008), the gray wolf population in Wisconsin continued to increase; on average, the population increased 11.1 percent annually.[17] This annual rate of increase was, at times, higher than the rates at which the population grew annually prior to the introduction of lethal depredation control (e.g., the population grew 3.6 percent between year-end 1999 and year-end 2000 and 2.4 percent between year-end 2001 and year-end 2002). In 2012, 2013, 2014, and 2021, both lethal depredation control and regulated harvest occurred in Wisconsin, the population decreased 0.7 percent between year-end 2011 and year-end 2012, decreased 18 percent between year-end 2012 and year-end 2013, increased 13 percent between year-end 2013 and year-end 2014, decreased 13.7 percent between year-end 2020 and year-end 2021, and increased 3.6 percent between year-end 2021 and year-end 2022 (see Appendix 2 for data used to calculate rates). Despite some annual fluctuation due to harvest and other factors, including a transition from minimum counts and territory mapping to a modeled population estimate (see Chapter 3 *Human-Caused Mortality in Wisconsin* for more information) that resulted in an increase in wolf population size between year-end 2018 and year-end 2019, wolf abundance in Wisconsin has generally trended slightly upward then appears to have stabilized since 2011 (Appendix 2). If the gray wolf were to be delisted again, Wisconsin's management plan and regulations would allow the state to conduct lethal depredation control, under certain circumstances, and would allow for a regulated harvest season (WI DNR 2022, entire; WI DNR 2023a, pp. 135–146). However, Wisconsin DNR would, at a minimum, ensure the population remains above the current state threatened species level (i.e., 250 wolves), and, under the

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[17] This value represents the average of four year-over-year population changes:
Percent population change between year-end estimates for 2002 and 2003 (Wisconsin DNR's winter 2002/2003 and winter 2003/2004 estimates), representing the change in population size relative to 2002 after the lethal depredation control that occurred during 2003: 11.3 percent
Percent population change between year-end estimates for 2003 and 2004 (Wisconsin DNR's winter 2003/2004 and winter 2004/2005 estimates), representing the change in population size relative to 2003 after the lethal depredation control that occurred during 2004: 16.6 percent
Percent population change between year-end estimates for 2006 and 2007 (Wisconsin DNR's winter 2006/2007 and winter 2007/2008 estimates), representing the change in population size relative to 2006 after the lethal depredation control that occurred during 2007: 0.5 percent
Percent population change between year-end estimates for 2007 and 2008 (Wisconsin DNR's winter 2007/2008 and winter 2008/2009 estimates), representing the change in population size relative to 2007 after the lethal depredation control that occurred during 2008: 16.0 percent

Wisconsin Plan, the Wisconsin DNR intends to maintain the population close to the current population size (WI DNR 2023a, pp. 126-127).

Levels of Human-Caused Mortality in the Remainder of the Eastern United States

Although the only known gray wolf populations in the Eastern United States are in the Western Great Lakes region, gray wolves are occasionally encountered elsewhere in our analysis area. In the Eastern United States outside of the Western Great Lakes, human-caused gray wolf mortality is overwhelmingly the result of dispersing wolves being mistaken for coyotes and killed; such events are relatively rare but have been documented in nearly every state within our analysis area (e.g., MDIFW 2003, p. 2; Thiel and Wydeven 2011, pp. 51–54; MDC 2013, entire; IADNR 2016, entire; ILDNR no date, entire; Kansas Department of Wildlife and Parks (KDWP) no date, entire; NDGF no date, entire; NYSDEC no date, entire). In some parts of our analysis area, including the Northeastern United States, the relatively large size of coyotes and small size of potential wolves dispersing from southeastern Canada may exacerbate this source of mortality and require extra vigilance regarding target identification (Thiel and Wydeven 2011, p. 46). However, such cases of misidentification also occur in parts of our analysis area where wolves are considerably larger than coyotes (e.g., wolves misidentified as coyotes and killed by hunters in Missouri range in size from 80–104 lbs.; MDC 2013, entire).

Outside of wolves being mistakenly shot by coyote hunters, documented human-caused wolf mortality is limited. In 2007, a large canid was shot and killed by a farmer in Shelburne, Massachusetts after it had killed several sheep (Service 2020, p. 25). Following DNA analysis, the canid was confirmed to be a gray wolf (Service 2019, entire). Wolves are also occasionally struck and killed by vehicles, including three separate incidents in Illinois (ILDNR no date, entire).

Human-Caused Mortality Summary

Wolves have evolved mechanisms to compensate for relatively high rates of mortality, which makes wolf populations resilient to increased levels of human-caused mortality. Analyses have indicated that annual rates of human-caused mortality of approximately 29 percent of the known population would result in a stable to slightly increasing wolf population (Adams et al. 2008, pp. 18–20; ODFW 2015, pp. 30–33), although considerable debate continues regarding sustainable harvest rates (Creel and Rotella 2010, entire; Gude et al. 2012, entire; Vucetich and Carroll 2012, entire; Creel et al. 2015, entire; Mitchell et al. 2016, entire). Outside of national parks, human-caused mortality is estimated to account for 60 to 80 percent of all known mortalities in the lower-48 United States (Fuller 1989, p. 24; Murray et al. 2010, p. 2518; O'Neil 2017, p. 214; Treves et al. 2017a, p. 27; Stenglein et al. 2018, p. 108).

Despite human-caused wolf mortality, wolf populations in the Western Great Lakes region have generally continued to increase in both number and range since the mid-to-late 1970s, even considering that the population size has fluctuated from year-to-year (Smith et al. 2010, entire; O'Neil et al. 2017, entire; Stenglein et al. 2018, entire). The state wolf-management plans currently in place for Michigan, Minnesota, and Wisconsin each contain recommendations regarding future adaptive management of lethal depredation control and regulated harvest. Wolves are protected as game species in Michigan, Minnesota, and Wisconsin (where wolves currently occur), and lethal take is prohibited without a permit, license, or authorization, except under a few limited situations (see *State Management*). If wolves were federally delisted again, Michigan and Minnesota may consider implementing regulated harvest seasons (MI DNR 2022a, pp. 69–73; MN DNR 2022 Appendix 2, pp. 47–51); due to existing state legislation that requires the Wisconsin DNR to hold regulated harvest seasons when wolves are federally delisted (Wisconsin Act 169), regulated harvest would likely occur again in Wisconsin (WI DNR 2023a, pp. 141–147).

According to past practice in Minnesota and the state's management plan, lethal depredation control will likely continue in Minnesota under the authority of the 4(d) rule while wolves are listed under the Act, and would likely keep occurring in the state should Federal delisting occur (MN DNR 2022, Appendix 4, pp. 58–63). Based on the occurrence of lethal depredation control during past periods of delisting and the states' management plans, should Federal delisting occur again, Michigan and Wisconsin would likely implement lethal depredation control of wolves in response to conflicts (MI DNR 2022a, pp. 58–67; WI DNR 2023a, pp. 135–137). However, while each state will likely implement regulated forms of human-caused mortality should delisting occur, the state wolf management plans also contain a management goal to maintain healthy populations of wolves in each state (over 200 for Michigan, between 2,200 and 3,000 for Minnesota, and between 800 and 1,200 for Wisconsin) (MI DNR 2022a, pp. 22–24; MN DNR 2022, pp. 30–31; WI DNR 2023a, pp. 126–134). We analyze the potential future effects of harvest and lethal depredation control on the wolf population in the Western Great Lakes states in Chapters 5 and 6.

Disease and Parasites in Wolves

Disease outbreaks are the most common cause of die-offs (when a significant proportion of a population dies naturally) in carnivores (Young 1994, pp. 414–415). These outbreaks can begin in a variety of ways; factors that most influence disease transmission include the type of pathogen (e.g., directly transmitted pathogens, pathogens that require an intermediate host) and the presence and density of other species that act as disease reservoirs (i.e., a population in which a pathogen can be permanently maintained and from which infection is transmitted to the target population) (Brandell et al. 2021a, p. 2). Although disease and parasites were not identified as a threat at the time of listing, a wide range of diseases and parasites have been reported for the gray wolf during the past decades and several of them have had localized impacts (Brand et al. 1995, p. 419; WI DNR 1999, p. 61; Kreeger 2003, pp. 202–214; Stronen et al. 2011, entire; Bryan et al. 2012, pp. 785–788; Brandell et al. 2021a, entire). All three Western Great Lake states (i.e., Michigan, Minnesota, and Wisconsin) include disease surveillance in their population monitoring programs, which include direct observation of wolves to assess potential disease indicators or biological sample collection with subsequent analysis at a laboratory (MI DNR 2022a, pp. 34, 43–45; WI DNR 2023a, pp. 132–133; MN DNR 2022, pp. 20, 31).

Some diseases and parasites can increase mortality rates, but most are not known to cause long-term, population-level effects (Fuller et al. 2003, pp. 176–178; Kreeger 2003, pp. 202–214; CDFW 2016, pp. 38–41; IDFG 2023, p. 11). For example, minor diseases and parasites that have been documented in wild wolves include: plague, Lyme disease, West Nile virus, neosporosis, dog-biting lice, canine heartworm, blastomycosis, bacterial myocarditis, granulomatous pneumonia, brucellosis, leptospirosis, bovine tuberculosis, hookworm, coccidiosis, canine hepatitis, canine adenoviruses 1 and 2, canine herpesvirus, eastern equine encephalitis, anaplasmosis, ehrlichiosis, echinococcus granulosus, oral papillomatosis, hepatozoonosis, babesiosis, Rocky Mountain spotted fever, and canine bartellosis; however, impacts of these diseases on wolf population dynamics are not known to be significant (Mech et al. 1985, p. 404; Brand et al. 1995, pp. 419–429; Johnson 1995, pp. 431, 436–438; Weiler et al. 1995, entire; Thomas 1998, in litt.; Mech and Kurtz 1999, pp. 305–306; Hassett 2003, in litt.; Kreeger 2003, pp. 202–214; Zarnke et al. 2004, entire; Paul 2005, in litt.; Thomas 2006, in litt.; Almberg et al. 2009, p. 4; Foreyt et al. 2009, p. 1208; Almberg et al. 2012, pp. 2847, 2849; Bryan et al. 2012, pp. 785–788; Brzeski et al. 2015, entire; Jara et al. 2016, p. 13; CDFW 2016, pp. 38–41; Knowles et al. 2017, entire; Carstensen et al. 2017, entire; Bevins et al. 2021, entire; Greco et al. 2021, entire; Schlender 2023a, in litt.; Tolkacz et al. 2023, entire; Wymazal et al. 2024, entire). Studies and risk assessments of pathogens in gray wolves, evaluating over twenty diseases, found that only four were known to have either severe (albeit acute) or moderate (but variable) impacts on wolf population dynamics: CDV, CPV, mange, and rabies (CDFW 2016, pp. 38–41; Brandell et al. 2021a, p. 3). Therefore, we focus our analysis below on these four pathogens most likely to impact population dynamics of wolves in the Eastern United States. We also discuss the prospect of novel pathogens and the potential implications for wolves in the Eastern United States.

We caution that studying the effects of disease on wildlife population dynamics is inherently difficult and often involves evaluating blood samples of living individuals (serosurveys). Caveats of serosurveys include: (1) sampling does not capture individuals that died from the disease, (2) a sample that is positive for disease merely demonstrates that the individual has been exposed to the disease and not necessarily that the individual presented symptoms, and (3) it is often not possible to differentiate between "historic/past exposure, recent initial exposure, re-exposure, current infection, or clinical disease" (Carstensen et al. 2017, pp. 463–464). Therefore, our knowledge of the true impact of these diseases on wolf population dynamics, alone or in combination, is incomplete.

Canine Distemper Virus (CDV) is an acute disease of carnivores that infects canids worldwide, often causes significant mortality, but is highly immunizing (Kreeger 2003, p. 209; Almberg et al. 2010, p. 2058). Studies in YNP have shown that CDV outbreaks likely contribute to short-term negative population effects in gray wolves through reductions in survival rates (i.e., short-term population reductions of up to 30 percent recorded in 3 out of the 25 years of monitoring) (Almberg et al. 2010, p. 2072; Brandell et al. 2020, p. 126). Outbreaks of CDV are particularly lethal for young wolves, and can reduce pup survivorship to as low as 13 percent (Almberg et al. 2010, p. 2072). CDV has less of an impact on adult wolves, though the difference in survival rates between adult wolves exposed to CDV and those that are not exposed indicates adult wolves are still susceptible to mortality from the disease (i.e., adult wolves exposed to CDV are half as likely to survive as those that were not exposed) (Almberg et al. 2016, p. 2). However, researchers believe that a single CDV infection confers lifetime immunity to the disease, if the exposed individual is able to survive the initial infection (Almberg et al. 2016, p. 2). Given this permanent immunity, once a population experiences a CDV outbreak, it likely will not experience another for many years (i.e., when enough wolves that were not previously exposed and are, therefore, susceptible enter the population) (Almberg et al. 2016, p. 2).

There have been several documented cases of mortality from CDV among wild wolves; for example, it has been documented in two littermate pups in Manitoba (Carbyn 1982, pp. 111–112), in two Alaskan yearling wolves (Peterson et al. 1984, p. 31), in eight Wisconsin wolves (five adults and three pups) (Thomas 2006, in litt.; Wydeven and Wiedenhoeft 2003, p. 20; Thiel et al. 2009, p. 111; Wiedenhoeft et al. 2018, p. 5), and in at least two wolves in Michigan (Beyer 2019, pers. comm.). Carbyn (1982, pp. 113–116) concluded that CDV was partially responsible for a 50-percent decline in the wolf population in Riding Mountain National Park (Manitoba, Canada) in the mid-1970s. Serological evidence indicates that exposure to CDV is high among some wolf populations—29 percent in northern Wisconsin and 79 percent in central Wisconsin from 2002 to 2003 (Wydeven and Wiedenhoeft 2003, pp. 23–24, Table 7) and 2004 (Wydeven and Wiedenhoeft 2004, pp. 23–24, Table 7), and similar levels in Yellowstone National Park (Smith and Almberg 2007, p. 18). A serosurvey of free-ranging gray wolves in Minnesota using samples gathered from 2007–2013 (n=387) also documented exposure to CDV, albeit at lower levels (19 percent of adults and 5 percent of pups) (Carstensen et al. 2017, p. 459). Exposure rates for wolves in other areas of the Eastern United States have not been reported; however, CDV is present in wild carnivores and domestic dogs across the East and wolves in these areas have the potential to be infected by sympatric wild carnivores and dogs (Fitzgerald et al. 2022, p. 562). While CDV can cause localized population decreases in the short term, its effects are acute and wolf populations usually rebound shortly after disease outbreaks (e.g., recruitment remained strong in Wisconsin despite outbreaks) (Brand et al. 1995, p. 421; Almberg et al. 2009, pp. 5–9; Almberg et al. 2010, p. 2072; Almberg et al. 2012, p. 2848; Stahler et al. 2013, pp. 227–229).

Canine parvovirus (CPV) infects wolves, domestic dogs (*Canis familiaris*), foxes (*Vulpes vulpes*), coyotes, skunks (*Mephitis mephitis*), and raccoons (*Procyon lotor*). Clinical CPV is characterized by severe hemorrhagic diarrhea and vomiting, which leads to dehydration, electrolyte imbalances, debility, and shock and it may eventually lead to death. CPV has been detected in nearly every wolf population in North America including Alaska (Johnson et al. 1994, pp. 270–272; Bailey et al. 1995, p. 441; Brand et al. 1995, p. 421; Kreeger 2003, pp. 210–211; Zarnke et al. 2004, pp. 633–637; ODFW 2014, p. 7; Carstensen et al. 2017, pp. 462–468; WI DNR 2023a, p. 106), and exposure in wolves is thought to be almost universal. Nearly 100 percent of wolves handled in Montana (Atkinson 2006, pp. 3–4), YNP (Smith and Almberg 2007, p. 18; Almberg et al. 2009, p. 4), Minnesota (Mech and Goyal 1993, p. 331), Oregon (ODFW 2017, p. 8), and the Canadian Rocky Mountains (Nelson et al. 2012, p. 71) had blood antibodies indicating nonlethal exposure to CPV. The earliest evidence of CPV in a canine species was from detection of CPV antibodies in wild gray wolves sampled in northeast Minnesota in 1973 (Mech and Goyal 1995, entire). Based on 30 years of data (1973 to 2004) following detection of CPV in northeastern Minnesota, Mech et al. (2008, p. 824) showed that CPV reduced gray wolf pup survival, subsequent dispersal, and population growth rate. However, a follow-up study analyzing 35 years of data (1973 to 2007) revealed that CPV later became endemic, i.e., the population had sufficient immunity such that it could tolerate the occurrence of the disease without substantial negative effects on the population itself (Mech and Goyal 2011, pp. 28–30). Similarly, CPV apparently caused a decrease in the Wisconsin wolf population in the mid-1980s, but the population has since recovered from that decrease

(Wydeven et al. 2009a, p. 96). These observed effects are consistent with results from a study in a smaller, isolated population on Isle Royale, Michigan (Peterson et al. 1998, entire).

Mange has been detected in wolves and other mammals throughout North America (Brand et al. 1995, pp. 427–428; Kreeger 2003, pp. 207–208; Niedringhaus et al. 2019, entire). Mange mites (*Sarcoptes scabeii*) infest the skin of the host causing irritation due to feeding and burrowing activities. This causes intense itching that results in scratching and hair loss. Mortality may occur due to exposure (primarily in cold weather), emaciation, or secondary infections (Kreeger 2003, pp. 207–208; Almberg et al. 2012, pp. 2842, 2848; Knowles et al. 2017, entire). Mange mites are spread from an infected individual through direct contact with others or through the use of common areas. In a long-term study of wolves in Alberta, higher wolf densities were correlated with increased incidence of mange, and pup survival decreased as the incidence of mange increased (Brand et al. 1995, pp. 427–428). In YNP, increasing pack size has been shown to offset individual costs of infection (Almberg et al. 2015, p. 4), revealing a potentially more complex relationship between wolf densities and mange. Nevertheless, mange is known to temporarily affect wolf population growth rates in some areas (Kreeger 2003, p. 208; Paul 2005, in litt.; Wydeven et al. 2009a, pp. 96–97). In Montana and Wyoming, the percentage of wolf packs with mange annually fluctuated between 3 and 24 percent from 2003 to 2008 (Atkinson 2006, p. 5; Smith and Almberg 2007, p. 19; Jimenez et al. 2010, pp. 331–332). In packs with the most severe infestations, pup survival appeared low and some adults died, indicating that wolf populations can be affected by mange at local scales (Wydeven et al. 2009a, p. 97-98; Jimenez et al. 2010, pp. 331–332). While the effects of most outbreaks of mange are short-lived, the combined effect of an outbreak of mange in YNP in 2007 and CDV in 2008, in association with declines in prey resources, may have contributed to a decline in the wolf population to a lower long-term average of approximately 100 wolves in YNP since 2008 (DeCandia et al. 2021, p. 430). The ultimate impact of mange on wolves may partially depend on the genetic diversity of the wolf population. In a study of wolves in YNP, individual genomic diversity in gray wolves was inversely correlated with mange severity, meaning that wolf genomic variation can buffer against the risk of severe mange (DeCandia et al. 2021, p. 441); however, this implies that if a population's genomic diversity were to decrease, it could raise the incidence of severe mange in the population (DeCandia et al. 2021, p. 440).

Rabies is a fatal viral disease that infects the central nervous system (Centers for Disease Control (CDC) 2022a, unpaginated). Rabies is transmitted through direct contact and saliva (CDC 2022a, unpaginated) and is known to occur sporadically in wild wolves, where it can result in localized wolf population declines (e.g., Ballard and Krausman 1997, pp. 243–245; reviewed by Lescureux and Linnell 2014, p. 236). Although there are no recorded cases of rabies in wolves in the lower 48-United States (MI DNR 2022a, p. 55; Service 2023, p. 100), there have been infrequent detections in Canada and Alaska (Theberge et al. 1994, entire; Ballard and Krausman 1997, p. 243). In a study of wolves from northwest Alaska, an outbreak of rabies among multiple packs caused population growth rates to drop from 1.04–1.43 before the outbreak to 0.62–0.64 after the outbreak (Ballard and Krausman 1997, p. 243). However, there is no indication that wolves are a "primary host or reservoir for rabies" (Lescureux and Linnell 2014, p. 236), and rabies outbreaks in gray wolves south of the Arctic Circle appear to be extremely rare (Theberge et al. 1994, entire).

The introduction of new diseases, disease variants, and parasites into the wolf metapopulation in the Eastern United States is likely to continue (see Canuti et al. 2022, pp. 12–14), and it is difficult to predict the consequences of novel pathogens. Reed et al. (2003b, entire) attempted to estimate the frequency and impact of catastrophes in vertebrate populations using long-term population census data from the Global Population Dynamics Database. They defined catastrophes as an annual population decline of 50 percent or greater, and they documented 208 catastrophes among 88 species. The weighted mean probability of a catastrophe was 14.7 percent per generation with a standard error of 1 percent, regardless of taxa. The frequency of occurrence was negatively correlated with severity; the probability of a 33 percent, 75 percent, and 90 percent die off every 7 years was 52.5 percent, 3.2 percent, and 1.0 percent, respectively. Disease is the prevailing causal factor of high mortality events (i.e., catastrophes) in carnivore species (Chapron et al. 2012, p. 14). Given the potential of disease to affect wolf populations now and in the future, we further discuss and consider this stressor in our analysis. We use information from Reed et al. (2003b, pp. 110–114) to quantitatively assess the potential impact of known and novel disease outbreaks on wolves in the Western Great Lakes in Chapter 6.

Inbreeding Depression

There were no genetic concerns for the gray wolf identified at the time of listing because, in the late 1970s, our understanding of the link between genetic diversity and population health was in its infancy. Since the original listing, enhanced genetic techniques have vastly improved our understanding of population genetics and the potential consequences of range and population contraction and expansion. For example, research has firmly established that genetic issues, such as inbreeding depression, can be a significant concern in small populations, with potentially serious implications for population viability (Frankham 2010, entire; Hasselgren and Noren 2019, entire).

Inbreeding, or the mating of related individuals within a population, has been documented to result in negative impacts on a variety of traits linked to fitness across a wide range of taxa, with the impacts collectively referred to as inbreeding depression (Crnokrak and Roff 1999, entire; Hedrick and Kalinowski 2000, entire; Frankham 2010, entire; Liberg et al. 2005, entire). Inbreeding is generally attributed to small population size, isolation from other populations, or both. It is correlated with a decrease in metrics of genetic diversity, such as heterozygosity (Räikkönen et al. 2009, p. 6; Kardos et al. 2021, pp. 3–7). While there are numerous empirical examples of inbreeding depression, there is little evidence to show at what point inbreeding may start having negative effects on a given species or population (Hedrick and Kalinowski 2000, pp. 151–153; Räikkönen et al. 2013, pp. 5–6). Recent evidence indicates that populations that were historically large may be more susceptible to inbreeding depression if they experience dramatic population reductions, as they may have higher levels of deleterious mutations compared with populations that have always been smaller, in which such mutations may have been purged over time (Hedrick et al. 2019, p. 306; Nietlisbach et al. 2019, p. 276; Kyriazis et al. 2020, p. 34; Kardos et al. 2021, p. 4). While perhaps more common in large, genetically diverse populations, the prevalence of deleterious mutations in any specific population is hard to assess (Nietlisbach et al. 2019, pp. 267–269; Kardos et al. 2021, p. 5).

Inbreeding depression, as evidenced by physiological anomalies or other effects on fitness, has been documented in several wild wolf populations. These include the population in Isle Royale National Park, Scandinavian wolves in Norway and Sweden, Mexican wolves, wolves in the Apennine Mountains in Italy, and wolves in the Sierra Morena mountains on the Iberian Peninsula (Vilà et al. 2003, pp. 94–95; Liberg et al. 2005, entire; Räikkönen et al. 2006, entire; Fabbri et al. 2007, entire; Räikkönen et al. 2013, entire; Gómez-Sánchez et al. 2018, entire; Robinson et al. 2019, entire; Taron et al. 2021, entire). These populations have exhibited varying evidence of inbreeding depression, such as decreased pup survival in Scandinavia (Liberg et al. 2005, p. 18), bone morphology anomalies in Isle Royale and Scandinavia (Räikkönen 2021, pp. 33–46), and reduced sperm quality in Mexican wolves (Asa et al. 2007, entire).

In these populations, their demographic history has included some degree of population bottleneck along with limited or non-existent connectivity with other populations. The Isle Royale population, for example, was founded by two or three individuals who crossed an ice bridge to the island from the mainland during the winter of 1948–1949 (Adams et al. 2011, p. 3336). Since then, the population has existed largely isolated from mainland wolves. The highest recorded abundance was 50 wolves in 1980 (Peterson et al. 1998, p. 830), though, by 2016, only two wolves remained (Hedrick et al. 2019, p. 303). The seemingly imminent extirpation led the NPS to translocate 19 wolves from the surrounding mainland and another island in Lake Superior in 2018 and 2019 in an attempt to restore the population (Hervey et al. 2021, p. 914). The Scandinavian wolf population in Norway and Sweden was founded by fewer than five individuals from the larger Finnish population, though there have been small numbers of additional migrants (Vilà et al. 2003, pp. 93–94; Liberg et al. 2005, p. 18; Åkesson et al. 2016, p. 4746). The population numbered fewer than 10 wolves until 1990 and it has generally been characterized by very limited connectivity with other populations (Vilà et al. 2003, pp. 93–94). Wolves in Italy appear to have been isolated in the Apennines for several thousand generations and experienced a bottleneck of fewer than 100 individuals in the 1970s followed by population growth and expansion into the Alps (Lucchini et al. 2004, pp. 532–534; Fabbri et al. 2007, entire). The wolves in Sierra Morena have been completely isolated from other Iberian Peninsula wolves for several decades. While likely never abundant, the wolf population has declined until, as of 2018, it may be extirpated entirely, though accurate population estimates or an ultimate cause of such extirpation are unknown (Gómez-Sánchez et al. 2018, p. 3600).

Although inbreeding depression has been documented in wolves, they are adept at avoiding inbreeding, when possible, by, for example, preferentially breeding with unrelated individuals or dispersing away from natal sites to breed (vonHoldt et al. 2008, p. 262; Ausband 2022, p. 539; vonHoldt et al. 2024a, entire). Reintroduced and naturally expanding populations in the NRM have shown low levels of inbreeding even in the Greater Yellowstone Area and Idaho populations, which were begun with a limited number of translocated founders (41 and 35 founders, respectively), augmented by some natural dispersal from Canada (vonHoldt et al. 2008, p. 267; vonHoldt et al. 2010, pp. 4420–4421; Hendricks et al. 2018, p. 139; Ausband 2022, p. 539; IDFG 2023, p. 8; vonHoldt et al. 2024a, entire). Moreover, in both the Scandinavian wolf and Mexican wolf populations, many of the effects of inbreeding depression appeared to be mitigated by relatively small influxes of additional wolves (i.e., new genetic material) into the population (Vilà et al. 2003, entire; Fredrickson et al. 2007, entire; vonHoldt et al. 2008, p. 262; vonHoldt et al. 2010, p. 4421; Wayne and Hedrick 2011, entire; Åkesson et al. 2016, entire). A recent study of Mexican wolf showed that, despite relatively high measures of inbreeding, there was not significant inbreeding depression in the population as measured by recruitment and no increase in inbreeding over time despite a closed population begun from only seven founders (Clement et al. 2024, pp. 9–13). Active management of the population and purging of deleterious alleles were provided as potential explanations for the lack of inbreeding depression detected (Clement et al. 2024, pp. 12–13). Harding et al. (2016, p. 154), in an examination of recovery goals for Mexican wolves, provides a list of wolf populations that experienced notably low numbers, but later rebounded and are now increasing or stable. While increasing abundance does not necessarily indicate a complete lack of genetic concerns, it is often a positive indicator of resilience. These examples indicate that, in many cases, wolf populations may be able to avoid or overcome the effects of inbreeding if sufficient population size and connectivity among populations are maintained. As we discuss further in the section *Current Genetic Diversity and Connectivity* in Chapter 4, with the exception of the unique situation on Isle Royale, we are not aware of any instances of inbreeding or inbreeding depression within the Eastern United States. On Isle Royale, small population size and infrequent migrations to the island appear to have been too limited to reduce the effects of inbreeding depression (Hedrick et al. 2014, entire; Hedrick et al. 2019, entire). We discuss whether inbreeding depression could occur in the Western Great Lakes metapopulation in the future in Chapter 6.

Hybridization

Interspecific hybridization (i.e., interbreeding between two different species) is ubiquitous among canids and has had a central role in shaping the evolution of this family. However, under certain circumstances, hybridization can emerge as a threat to vulnerable populations. There are several ways in which hybridization can reduce long-term viability (Rhymer and Simberloff 1996, entire). One is through lost reproductive output. When members from two different species interbreed with each other rather than with members of their own species, it represents a loss of potential recruitment. This is particularly problematic if the first-generation hybrids are sterile or have lower fitness than members of the parental species (Allendorf et al. 2001, p. 616).

Hybridization can also pose a threat when the hybrid offspring are fertile and capable of interbreeding with one or both of the original parental species. In theory, when both parental species are abundant and they are segregated spatially, ecologically, and/or behaviorally, hybridization reaches an equilibrium in which the genetic nature of the parental species is maintained (Arnold 1992, pp. 248–253; Lenormand 2002, entire). However, should other stressors skew abundance or disrupt isolating mechanisms, hybridization patterns may shift (Rhymer and Simberloff 1996, pp. 85–91; Seehausen 2006, entire). As these patterns shift, there are two potential scenarios that may manifest (Allendorf et al. 2001, pp. 616, 621; Bohling 2016, p. 322). One is a hybrid swarm, in which, over time, totally random mating between members of the parental species and their hybrids results in a single hybrid population of mixed ancestry. The second scenario occurs when one of the species is more abundant than the other. This can result in genetic swamping, in which members of the less abundant species are unable to find conspecific mates and instead interbreed with the more abundant species and/or hybrids between the two species. Over time, the genotypic profile of the less abundant species disappears as it becomes absorbed into the gene pool of the more prevalent one.

Hybridization has been identified as a stressor for several canid species globally. It is most problematic for populations with low abundance in which locating conspecific mates is difficult, resulting in interbreeding with a more abundant species. It can also be exacerbated by other stressors, such as human-caused mortality, which can disrupt stable breeding pairs and packs (Rutledge et al. 2010b, entire; Rutledge et al. 2012a, entire; Bohling and Waits 2015, entire). Worldwide, the most common scenario in which hybridization between canids has been identified as a potential stressor involves interbreeding between gray wolves and free-ranging domestic dogs (Lescureux and Linnell 2014, pp. 234–235). This has been observed particularly in Europe, where most wolf populations are small and highly fragmented and feral dog populations more common, facilitating interbreeding with domestic dogs (Lescureux and Linnell 2014, pp. 234–235; Hindrikson et al. 2017, pp. 17–21). Another oft-cited example is the genetic swamping of remnant red wolf populations as coyotes expanded their range eastward in the middle of the 20th century (McCarley 1962, entire; Paradiso and Nowak 1972, pp. 3–4). Eastern wolves are also considered vulnerable to hybridization because the core population in Algonquin Provincial Park is surrounded by more abundant populations of coyotes and gray wolves (Sears et al. 2003, entire; Wilson et al. 2009, entire; Heppenheimer et al. 2018, entire). In both red wolves and eastern wolves, evidence has shown that human-caused mortality facilitates hybridization, especially if breeders are removed and packs dissolve (Rutledge et al. 2010b, entire; Rutledge et al. 2012a, entire; Benson et al. 2014, entire; Bohling and Waits 2015, entire). There are no known thresholds (e.g., abundance, population density) at which a canid population is more likely to be exposed to hybridization. The general trend is that small, declining populations that experience heavy mortality of breeders are more likely to be affected.

There has been debate regarding the role of hybridization in shaping the contemporary population of gray wolves in the Western Great Lakes. As noted in *Evolutionary Origins and Taxonomic Status of Contemporary Canids Inhabiting Eastern North America* in Chapter 1, there is uncertainty regarding the gray wolf's genetic history in this area. There is agreement among experts that the Western Great Lakes gray wolf population bears signatures of past admixture, but uncertainty remains as to when and with which canids this admixture occurred. Some have argued that the contemporary gray wolf population differs genetically from the historical population, either due to recent (i.e., within the last 200 years) introgression from coyotes (Lehmen et al. 1991, entire; Roy et al. 1996, entire; Koblmüller et al. 2009, entire; vonHoldt et al. 2016a, pp. 5–9; Sinding et al. 2018, pp. 5–6) or from genetic replacement of the original wolf population by wolves from Canada (Leonard and Wayne 2008, entire). Others contend that the historical population was also admixed, containing ancestry from the eastern wolf, and that there has been relative genetic continuity since this admixture with the eastern wolf first occurred (Wheeldon and White 2009, entire; Fain et al. 2010, entire; Mech 2010b, p. 135; Vilaça et al. 2023, entire).

Regardless of this history, contemporary hybridization between gray wolves and other canids in the Western Great Lakes appears to be minimal to non-existent. Since the gray wolf population reached its lowest level of abundance in the 1960s, there has been no documented occurrence of interbreeding in the wild between a gray wolf and a coyote in the Western Great Lakes (i.e., identification of a first-generation hybrid) (Mech 2011, p. 524). Even as small numbers of gray wolves recolonized Wisconsin and the Upper Peninsula of Michigan, there was no documented reproduction with the coyotes that already occupied this area. The contemporary gray wolf population in the Western Great Lakes is reproductively isolated from the co-occurring coyote population (Fain et al. 2010 et al. 2010, pp. 1758–1759; Wheeldon et al. 2010, entire; Heppenheimer et al. 2018, p. 8). Interbreeding with domestic dogs also appears to be rare in the Western Great Lakes population (Fain et al. 2010, p. 1759). Although the current genetic composition of wolves in the Western Great Lakes may reflect past hybridization between gray wolves and eastern wolves, this is reflective of the historical dynamics of the population and any on-going interbeeding does not pose a threat to the gray wolf population (Mech and Paul 2008, entire; Fain et al. 2010, pp. 1758–1759). Projecting into the future, we do not project that gray wolf populations in the Western Great Lakes area will reach levels (e.g., abundance, density, breeder mortality) at which hybridization will become a threat, as has been observed in other populations. Therefore, we do not further analyze the potential effects of hybridization on the gray wolf population in the Western Great Lakes because there is no evidence it is posing a risk to current or future viability.

In areas of the Eastern United States currently unoccupied by wolves, hybridization may reduce the potential for future wolf colonization, particularly in the Northeast. Coyotes in the Northeastern United States hybridized with wolves as they colonized the region a century ago and continue to possess significant wolf ancestry (Way et al. 2010, entire; Wheeldon et al. 2010, entire; Monzón et al. 2014, pp. 188–191; vonHoldt et al. 2016b, entire; Vilaça et al. 2023, entire). This introgression is believed to have resulted in the larger body sizes observed in Northeastern coyotes compared to their western counterparts (Kays et al. 2010, entire). There is continued debate whether this introgression came from eastern wolves, gray wolves, or even domestic dogs (Kays et al. 2010, entire; Wheeldon et al. 2010, entire; vonHoldt et al. 2011, p. 1300; vonHoldt et al. 2016b, entire; Vilaça et al. 2023, entire). Due to the phenotypic similarity and shared ancestry between Northeastern coyotes and wolves, it has been hypothesized that this could limit the potential for wolf recolonization (Wydeven et al. 1998 p. 780; McAlpine et al. 2015, p. 392). Essentially, the low numbers of wolves dispersing from Canada or the Western Great Lakes into the Northeastern United States are likely to be genetically swamped by the much more abundant coyote population, limiting the potential for natural recolonization and formation of a wolf population.

Wolf ancestry is notably absent in coyotes from other unoccupied portions of the Eastern United States (e.g., the Great Plains, Mississippi Valley, Texas) (Hailer and Leonard 2008, p. 7; vonHoldt et al. 2011, pp. 1297–1299; vonHoldt et al. 2022, p. 5442). Given the resulting size and ancestry differences between coyotes and wolves in these areas, hybridization is not expected to be common. Although lone wolves have been documented in some of these areas (see *Current Population Sizes and Trends*), no hybrids between wolves and coyotes have been documented.

Climate Change

The effects of climate change were not identified as threats at the time of the listing of the gray wolf. Climate change refers to the change in the mean or variability of one or more measures of climate (e.g., temperature or precipitation) that persists for an extended period, typically decades or longer, whether the change is due to natural variability, human activity, or both (Intergovernmental Panel on Climate Change (IPCC) 2023, p. 4). Human-induced changes in atmospheric chemistry, primarily from the addition of greenhouse gases caused by the combustion of fossil fuels and other activities, has driven unprecedented and significant changes in temperature and precipitation across the globe, including within the wolf's range in the United States. These changes are expected to intensify as atmospheric greenhouse gases continue to rise (IPCC 2021, entire; Rangwala et al. 2021, p. 1). There is increasing evidence that climate change is impacting species and populations in a variety of ways. The expected consequences of future changes will vary by region, species, and ecosystem type (Urban 2015, entire; Vose et al. 2018, pp. 270, 273). Climate change may have direct or indirect effects on predators, prey, and their habitats (e.g., Thomas 2010, p. 489; Boyd et al. 2023, p. 19). The impact of these changes on wolves, both direct and indirect, is difficult to quantify, but several issues have been identified as possible concerns in the Eastern United States, including: intrinsic vulnerability to changing climate and the potential for range loss; impacts to prey species and habitat; increased wildfire activity; and higher incidence of disease outbreaks and parasites.

Gray wolves are highly adaptable and efficient at exploiting available food resources and have even been called "climate generalists" (Barber-Meyer et al. 2021, pp. 1, 11; van den Bosch et al. 2023, p. 2). Because of their generalist, adaptable life history, climate change is not likely to strongly affect wolf populations directly (van den Bosch et al. 2023 entire; Mech et al. 2025, pp. 209–213). We assessed the gray wolf's intrinsic vulnerability to climate change and the potential for range loss by evaluating their physiological tolerance, global distribution, niche breadth, and dispersal capabilities (Dawson et al. 2011, p. 53). Throughout their circumpolar distribution, gray wolves persist in a variety of ecosystems with temperatures ranging from -70 °F to 120 °F (-57 °C to 49 °C) (Mech and Boitani 2003, p. xv). They live in every habitat type in the Northern Hemisphere that contains ungulates. In addition, they once ranged from central Mexico to the Arctic Ocean in North America. Historical evidence indicates that gray wolves and their prey have survived in hotter, drier environments including some near-desert conditions (Nowak 1995, pp. 382–385; 77 FR 55529, September 10, 2012, p. 55597). Range shifts (approximately 6.8 mi/year (11 km/year)) in North America for the gray wolf due to climate change are expected based on predictive models (Williams and Blois 2018, p. 8). However, over an 18-year period in Alaska and Western Canada, earlier spring growing seasons did not result in any corresponding shifts in the timing of wolf denning; but the lack of a subsequent change to the onset of denning did not negatively affect wolf reproductive success (Mahoney et al. 2020, p. 9). Moreover, recent modeling analysis indicates that wolf habitat in the Western Great Lakes will remain stable or increase during the 21st century, with limited or no change to wolf distribution or potential recolonization (van den Bosch et al. 2023, p. 1). Climate analyses examining changes in suitable habitat outside the Western Great Lakes have not been conducted.

While wolves appear to be unaffected by near-term climate change, climate change may influence prey availability for wolves over the long term (via changes in snowfall, disease dynamics, and heat stress) (Weiskopf et al. 2019, entire; Hendricks et al. 2018, unpaginated; Mahoney et al. 2020, pp. 12–13; Barber-Meyer et al. 2021, pp. 11). Changes to prey availability could arise from altered phenology of resources for ungulates and diminished foraging benefits of migration (e.g., Aikens et al. 2020, p. 4215). Between 2000 and 2017 in Alaska and Western Canada, annual weather conditions affected prey abundance, prey vulnerability, and wolf hunting success, which, in turn, possibly affected annual wolf reproductive success (e.g., high snowfall reduced overwinter survival of prey resulting in reduced prey availability in the following rearing period) (Mahoney et al. 2020, pp. 12–13). Thus, annual fluctuations in weather patterns that impact prey populations could, correspondingly, affect wolf populations (Mahoney et al. 2020, pp. 1, 13).

Therefore, if climate change ultimately affects wolf prey, this could have cascading impacts on wolf populations (e.g., changes to wolf survival, reproduction, and dispersal rates) (Barber-Meyer et al. 2021, p. 11). Overall, the extent and rate at which ungulate populations will be affected is difficult to foresee with any level of confidence (Jolles and Ezenwa 2015, pp. 9–10). In the southern portions of moose range in North America, including the Midwestern United States and southern Greater Yellowstone Area, climate change and associated changes in habitat quality may result in moose population declines (Murray et al. 2006, p. 25; Becker 2008, entire; Becker et al. 2010, p. 151; Weiskopf et al. 2019, pp. 773, 775). Moose may become heat stressed but may also face incongruous growth and loss of winter coats (Weiskopf et al. 2019, p. 773). However, despite these predictions, researchers have not yet detected any uniform responses to changing climate across moose populations (Weiskopf et al. 2019, p. 775). While these studies project that ungulate populations could decrease due to climate change, another potential consequence of climate change could be a reduction in the number of elk, deer, moose, and bison that die over the winter, thus maintaining a higher prey base for wolves (Wilmers and Getz 2005, p. 574; Wilmers and Post 2006, p. 405). Weiskopf et al. (2019, p. 773) noted an expected increase in white-tailed deer range in the Midwestern United States under changing climate conditions, where milder winters could increase forage availability. However, such conditions may not translate to more prey for wolves as reduced snow depth could also make it harder for wolves to successfully catch enough deer in winter (Gable et al. 2024, pp. 8–10).

The increase in frequency and severity of wildfires throughout the United States could also potentially change the distribution of wolf prey species across the landscape. Generally, risk of wildfire is lower for the Eastern United States than the drier Western United States, due to higher overall humidity and limited number of extreme fire weather days (Hanberry 2021, p. 13577). Hanberry (2020, entire) modeled the potential for extreme fire days across the United States; although the results are variable, there is potential for increased fire weather days in the Midwest, East, and Southeast. However, according to studies in Alaska, fire did not appear to have short-term effects on wolves because the effects to prey were within normal annual variation and unburned areas within the fire perimeter continued to attract prey (Ballard et al. 2000, p. 246).

Climate change may also increase wolf and prey exposure to disease due to shifts in the distribution or demography of disease pathogens, vectors, or hosts (e.g., Jara et al. 2016, p. 13; Allen et al. 2019, entire; Weiskopf et al. 2019, p. 773; Rocklov and Dubrow 2020, entire); or climate change may alter the interactions between pathogens, vectors, and hosts in more complex ways due to interactions with other environmental or anthropogenic variables (Gallana et al. 2013, entire; Weiskopf et al. 2019, p. 775; Rocklov and Dubrow 2020, entire). Disease vectors typically have short generation times, high effective population sizes, and strong selective pressure during disease transmission, meaning they can evolve more quickly than their hosts (Cable et al. 2017, p. 8). This indicates that climate change could increase the chances of disease infection (Cable et al. 2017, p. 8). However, given the number of pathogens affecting wolves and their prey, as well as the complexities of various lifecycles of pathogens and potential influence of other stressors, it is difficult to predict the likely effect of climate change on wolf and prey disease ecology (Cable et al. 2017, p. 8).

There is no current evidence that climate change is causing negative effects to the viability of the gray wolf in the Eastern United States. While uncertainty remains as to how climate change may affect wolf populations in the future, we do not expect that the flexible and adaptive nature of wolves will change (see Appendix 3). Therefore, we do not directly analyze the effects of climate change on the current and future condition of wolves in the Eastern metapopulation in this SSA; however, we quantitatively analyze the effects of rare but severe disease catastrophes in the future (which could manifest as a result of climate change or other causes) in our modeling (Chapters 5 and 6).

Diseases in Prey

Wolves prey on a variety of species, and those prey species are subject to an array of pathogens including chronic wasting disease (CWD) (a prion disease), bacterial diseases, viral diseases, ectoparasites, and endoparasites. Changes to prey availability through diseases in prey species have the potential to impact wolf populations because wolves depend on having sufficient prey for survival and reproduction. However, the relationship between wolf population dynamics and diseases in prey is complex because wolves can influence the prevalence of disease in their prey. For example, for certain diseases, wolves have been shown to reduce disease rates by limiting the encounter rates between prey communities, by limiting prey group size (disease transmission opportunities), by removing and consuming unhealthy individuals, and by altering prey genetics through removing individuals that are genetically predisposed to disease (Tanner et al. 2019, entire; Oliveira-Santos et al. 2021, entire; Hoy et al. 2022, entire). Our analysis below is focused on CWD, the most significant disease with the potential to affect ungulates, the primary prey species for wolves in the Eastern United States. For a discussion on other diseases in prey that may occur in our analysis area outside of the gray wolf current range (e.g., brucellosis and several viruses known to cause hemorrhagic diseases), see Service 2023 (pp. 105–108).

CWD is a contagious prion disease that affects cervids such as deer, elk, and moose, and it is neurodegenerative, rapidly progressive, and always fatal (Escobar et al. 2020, entire). Prions are "the proteinaceous infection agents responsible for human and animal prion diseases" (Escobar et al. 2020, p. 2). Prions can survive in saliva, feces, or other transmission vectors, even through efforts to disinfect, and can retain the ability to infect hosts for decades (Escobar et al. 2020, p. 8). CWD was first identified in a Colorado research facility in the 1960s and in wild deer in 1981 (CDC 2022b, unpaginated). CWD continues to spread in North America (Escobar et al. 2020, p. 24) and, as of January 2022, CWD was confirmed in 27 states in the United States (CDC 2022b, unpaginated). Within our analysis area, CWD has been confirmed in: Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, Nebraska, New York, North Dakota, Ohio, Oklahoma, Pennsylvania, South Dakota, Texas, and Wisconsin (USGS 2024, unpaginated).

While CWD has caused population declines of deer and elk in some areas (e.g., Miller et al. 2008, pp. 2–6; Edmunds et al. 2016, p. 12; DeVivo et al. 2017, entire), the prevalence of the disease across the landscape is not evenly distributed. Furthermore, there is significant uncertainty in the role of predators in facilitating or slowing CWD spread among ungulates. Experiments with captive mountain lions indicate that, if predators consume prey infected with CWD, they may be able to absorb the majority of CWD prions without getting infected themselves, effectively removing the CWD prions from the environment (Baune et al. 2021, pp. 5–6). However, a similar experiment with coyotes indicated that prions persisted in feces for up to 3 days after ingestion of infected tissue (Nichols et al. 2015, pp. 371–373). Simulation models predict that predation by wolves and other carnivores may lead to a significant reduction in the prevalence of CWD infections across the landscape (see Hobbs 2006, p. 8; Wild et al. 2011, pp. 82–88; Brandell et al. 2022, p. 1), thereby slowing its spread, partially because large carnivores may selectively prey on CWD-infected individuals (Krumm et al. 2010, p. 210). However, in areas of high disease prevalence, prion epidemics can negatively affect local prey populations even with selective predation pressure (Miller et al. 2008, p. 2). Overall, uncertainty remains as to how prey populations are altered by the emergence of CWD at larger geographic scales (Miller et al. 2008, p. 2). There is still much to learn about CWD prevalence, the spatial distribution of the disease, transmission, and the elusive properties of prions (Escobar et al. 2020, pp. 7–13), as well as the potential effects predators and scavengers may have on disease prevalence and spread.

To date, diseases in prey species have not resulted in significant, rangewide prey reductions nor have they led to wolf population declines in the Eastern metapopulation. However, wolf prey in the Eastern United States will likely continue to experience episodic outbreaks of endemic and novel diseases. State wildlife agencies—all of whom have a vested interest in maintaining robust populations of ungulates—have developed surveillance strategies and management response plans to minimize and mitigate the spread and impact of some ungulate diseases (e.g., MI DNR and MDARD 2012, entire; WI DNR 2010, entire; MN DNR 2019, entire). They also command significant regulatory authorities to adjust harvest rates seasonally or spatially if disease outbreaks emerge. State wildlife agencies coordinate on wildlife health issues through the Midwest Association of Fish & Wildlife Agencies' Wildlife Health Committee and nationally through the Association of Fish & Wildlife Agencies' Fish & Wildlife Health Committee. In addition, the USDA has a National Wildlife Disease and Emergency Response Program that manages the surveillance of wildlife diseases, provides standard processes for diagnosis and reporting, and supports collaboration (Pedersen et al. 2012, p. 74). Due to large uncertainties in the timing and impact of disease outbreaks in prey on the population dynamics of wolves, as well as uncertainties regarding the impact of management responses to these outbreaks, we did not attempt to explicitly incorporate these disease events into our quantitative projections of wolf abundance; however, our quantitative projections do include generic episodic catastrophes (e.g., disease in prey) based on observed rates of catastrophes in vertebrates (see Chapters 5 and 6).

Other Sources of Habitat Modification

As described above (see *Suitable Habitat* in Chapter 1 above), we consider habitat suitability to be influenced by a combination of areas containing adequate wild ungulate populations (e.g., elk and deer) and a low risk of conflict with humans (e.g., low road density, low human density, adequate natural cover without agricultural land) (see Mech 2017, pp. 312–315). Stressors related to prey availability and human-caused mortality are described in the preceding sections.

Thus, below, we discuss habitat modification that may occur from the "human footprint" within the range of the gray wolf in the Eastern United States. The human footprint is the collective extent of the impacts of human presence and actions on the landscape (Janzen 1998, entire; Sanderson et al. in press, p. 3). Wolves have a highly variable response to anthropogenic landscape change (Muhly et al. 2019, p. 10803). Use of areas near anthropogenic features varies with time of day, season of use, and whether the wolf is traveling fast (e.g., between patches of habitat) or slow (e.g., foraging and resting) (Whittington et al. 2022, entire). Depending on the context, wolves may avoid the human footprint (Mladenoff and Sickley 1998, p. 2; Oakleaf et al. 2006, pp. 555–560; Benson et al. 2015, pp. 229–231), select for it (Whittington et al. 2005, pp. 549–552; Bowman et al. 2010, pp. 463–465; Paquet et al. 2010, pp. 169–173; Lesmerises et al. 2012, pp. 128–130), or they may respond with indifference (Mech et al. 1988, entire).

In a large study of 176 GPS-collared wolves across the boreal forests of Canada, Muhly et al. (2019, entire) found that wolves had a functional response to timber harvest cutblocks and roads. Specifically, they showed that wolves dynamically selected for or against areas with higher densities of roads or cutblocks to maximize access to prey and minimize travel costs, while apparently avoiding areas with greater risk of mortality from humans (Muhly et al. 2019, pp. 10809–10811). Similarly, Thiel and Wydeven (2012, p. 40) indicate that logging in a sustainable manner without creating a high density of roads increases wolf access to prey like white-tailed deer. These authors also note that intense logging in the early 1800's likely facilitated movement of wolves from the Great Lakes region into Ontario and Quebec (Thiel and Wydeven 2012, pp. 40–41).

The influence of roads on wolf habitat use is well documented (e.g., Kohn et al. 2009, entire). For example, Mech et al. (1988, entire) found wolf occurrence, or lack thereof, generally corresponded to road densities with the driver of this relationship corresponding to increased potential for human-caused mortality within increasing road density. In a study of behavioral responses of wolves to roads in Scandinavia, Zimmerman et al. (2014, entire) found that roads pose a trade-off to wolves between increased risk from human-induced mortality and the reward of increased travel efficiency, efficient scent marking, and access to prey. Therefore, wolves tend to avoid areas of high road or house densities, presumably driven by avoiding risk associated with human presence (Zimmerman et al. 2014, pp. 1360–1363). Similar results were reported from a study of wolves in southwest Poland with wolves selecting areas away from high-traffic roads for resting (Bojarska et al. 2021, pp. 3–6). In YNP, wolves also did not select habitat close to road corridors when there was insufficient vegetative cover blocking their view of the roadway; however, they selected areas closer to the road at night when there was decreased human activity (Anton et al. 2020, pp. 7–13). Overall, the risk of human-caused mortality, which can be affected by human tolerance for wolves (see *Influence on Human-Caused Mortality: The Role of Public Attitudes* above), influences whether wolves associate with or avoid roads (Kohn et al. 2009, p. 229).

Development and conversion of agriculture and forest lands associated with the growth of human populations represent another form of the human footprint. These activities are occurring in the analysis area, including in the Western Great Lakes states (Hearne et al. 2003, pp. 47, 51; Wydeven et al. 2009b, p. 336; Vogler and Vukomanovic 2021, pp. 14, 18). Researchers have previously mapped the scope of the human footprint in our analysis area at a coarse scale and it coincides with development in urbanized areas (e.g., Woolmer et al. 2008, p. 48; Venter et al. 2016, p. 3; Sanderson et al., in press, pp. 31–32, 36–37).

Overall, the human footprint is not a primary stressor on wolf populations because wolves tend to avoid urbanized areas; however, the human footprint may curtail expansion of wolf populations in localized areas (e.g., due to conversion of forestlands, fragmentation, and increased risk of encounters with humans). The impacts of the human footprint are localized relative to the wide range of the species and wolves have been able to adapt to their effects (e.g., wolves are habitat generalists and are occupying areas of higher human presence in central Minnesota). Nevertheless, the human footprint, and its associated risk of human-caused mortality, in the Eastern United States likely contributes to the lack of effective dispersal of wolves from the Western Great Lakes areas to surrounding areas of unoccupied historical range. While we do not further assess the effects of habitat modification on the extant Western Great Lakes wolf population in this SSA Report given its minimal influence, we further discuss the ways in which the human footprint could affect future effective dispersal to unoccupied areas within the Eastern United States in Chapter 6 below.

Cumulative Effects

When stressors occur together, one may exacerbate the effects of another, causing effects not accounted for when stressors are analyzed individually. Many of the stressors to the gray wolf and gray wolf habitat in the Eastern United States discussed above are interrelated and could be synergistic and thus may cumulatively affect the gray wolf in the Eastern United States beyond the extent of each individual stressor. For example, a decline in available wild prey could cause wolves to prey on more livestock, resulting in a potential increase in human-caused mortality through property owner or agency-directed lethal depredation control actions. Such declines in wild prey could also increase intolerance toward wolves and exacerbate rates of illegal take. Our analyses of species' current and future condition in Chapters 4, 5, and 6 consider the potential synergistic effects of disease, catastrophes, and human-caused mortality. Because the SSA framework considers not only the presence of these stressors, but also the degree to which they collectively influence risk to the entire species, our assessment integrates the cumulative effects of these stressors into our characterization of current and future condition.

Summary of Conservation Efforts and Stressors

In the Eastern United States, the primary stressor influencing wolf populations is human-caused mortality. Currently, while the species is listed under the Act, the main sources of human-caused mortality are lethal removal of depredating gray wolves (in Minnesota) and illegal or accidental mortalities. Should gray wolves be delisted, lethal control of depredating wolves would likely occur throughout the species' current range, and regulated harvest may also occur. All states and some Tribal Nations within the current range of gray wolves have statutes, regulations, and management plans that govern conservation and take of wolves. Federal agencies also have rules and regulations in place to minimize disturbance to wolves, when necessary. To date, the best available science indicates that current levels of human-caused mortality have not caused significant reductions in wolf abundance throughout the Western Great Lakes (the only extant wolf population in the Eastern United States). However, human-caused mortality of dispersing wolves may be preventing wolf populations from establishing in areas beyond the three Western Great Lakes states. Additionally, the best available science indicates that disease in wolves has caused episodic, yet localized and short-term, population decreases. Chapters 5 and 6 present information on modeled future scenarios that examine the potential future effects of human-caused mortality and disease; we also note the potential for future climate-related changes in disease. Finally, we discuss the current and future status of inbreeding, inbreeding depression, connectivity, and genetic diversity in subsequent chapters.

While we further discuss and consider the influence of human-caused mortality, disease, and inbreeding in this SSA, we do not specifically analyze the effect of hybridization, diseases in prey species, climate change, or other sources of habitat modification on gray wolves' current and future condition. To date, based on the best available scientific information, diseases in prey species have not resulted in significant, rangewide prey reductions nor have they led to gray wolf population declines in the Eastern metapopulation. Considerable uncertainty remains as to the potential of diseases in prey species to change in the future, which makes it difficult to analyze any future effects on gray wolf populations. Moreover, each state within the current range of the gray wolf in the Eastern United States has comprehensive ungulate management plans and strategies to address disease outbreaks and manage for sustainable populations of ungulates. There is no evidence that hybridization between gray wolves and other canid species is currently on-going in the Western Great Lakes and there is no expectation for that pattern to change in the future. Climate change has the potential to influence disease rates in wolves, and we quantitatively analyze the effects of rare but severe disease catastrophes in our analysis of future condition (which could manifest as a result of climate change or other causes); however, there is no current evidence that climate change in and of itself is causing negative effects to the viability of the gray wolf in the Eastern United States, nor do we expect it to do so in the future based on the latest climate analysis. Habitat modification as a result of the human footprint is not a primary stressor on the extant gray wolf population in the Western Great Lakes; based on the best available scientific information, the impacts of these sources are localized relative to the currently wide range of the species and wolves have been able to adapt to their effects. Thus, we do not further consider these sources of habitat modification in our analysis of current and future condition of this extant gray wolf population. However, in the Eastern United States the lack of effective dispersal of gray wolves from the Western Great Lakes areas to surrounding areas of unoccupied historical range is likely a factor of the human footprint, and its associated risk of human-caused mortality; we further discuss the ways in which the human footprint could affect future effective dispersal to unoccupied areas within the Eastern United States in Chapter 6 below.

Chapter 4: Current Condition

Current Resiliency

The current resiliency of wolves in the Eastern United States is characterized by the current availability of the wolf's individual and population needs (i.e., current availability of suitable habitat, current availability of prey, current population size and trends, and current levels of genetic diversity and connectivity). In Chapter 3, we summarized our evaluation of potential stressors and conservation efforts that influence the condition of wolves in the Eastern United States. Human-caused mortality is the primary stressor that currently influences the resiliency of wolves in the Eastern United States. According to the best available science, disease also causes episodic, yet localized and short-term, population decreases. Below, we discuss the current condition of the resource and demographic factors that wolves in the Eastern United States require and examine how these stressors are affecting the wolf's current viability in our analysis area.

Current Habitat Availability

Various researchers have investigated the extent of habitat suitability for wolves in the Central and Eastern portions of the United States. Most of these efforts have focused on using a combination of human density, agricultural land density, prey density or biomass, natural or forest cover, and road density to quantify the extent of suitable habitat, or have used road density alone to identify areas where wolf populations are likely to persist or become established (Mladenoff et al. 1995, pp. 284–285; 1997, pp. 23–27; 1999, pp. 39–43; Harrison and Chapin 1997, p. 3; 1998, pp. 769–770; Mladenoff and Sickley 1998, pp. 1–8; Wydeven et al. 2001, pp. 110–113; Erb and Benson 2004, p. 2; Potvin et al. 2005, pp. 1661–1668; Mladenoff et al. 2009, pp. 132–135; Smith et al. 2016, pp. 559–562). As described in Chapter 1 (see *Suitable Habitat*), we consider suitable habitat to be areas containing adequate wild ungulate populations (e.g., elk and deer) and a low risk of conflict with humans (e.g., low road density, low human density, adequate natural cover without agricultural land or ranching activities) (see Mech 2017, pp. 312–315). Table 6 (a-b) provides an overview of the estimated suitable habitat for all states within our analysis area based on multiple different analyses in the literature; we summarize these analyses below. It is essential to recognize that the values presented in the table might not be directly comparable, as they do not completely consider the methodologies employed in the different studies or the particular habitats examined. Variations in focus and parameters across studies can have a substantial impact on the reported figures. Consequently, readers should examine this data within the framework of each study's unique parameters and limitations. Additionally, for certain studies the estimation of suitable habitat by state was determined by obtaining data from the authors and subsequently analyzed using a GIS program.

Various studies from the Upper Peninsula of Michigan indicate that there is anywhere from 7,263 mi^2 (18,812 km^2; Gantchoff et al. 2022, p. 4) to 15,992 mi^2 (41,419 km^2; Mladenoff et al. 2009, p. 134) of suitable habitat. Belongie (2008, p. 12) conducted a habitat suitability study only within the western portion of the Upper Peninsula and estimated that approximately 1,871 mi^2 (4,846 km^2) of suitable habitat exists for the gray wolf. Gantchoff et al. (2022, p. 4) and van den Bosch et al. (2022, entire), using data-driven species distribution models[18], estimated that approximately 7,263 mi^2 (18,812 km^2) and 13,892 mi^2 (35,979km^2) of suitable habitat exist in the Upper Peninsula, respectively. Using a model based on road density, Mladenoff et al. (2009, p. 134) estimated 15,992 mi^2 (41,419 km^2) of suitable habitat in the Upper Peninsula. Potvin et al. (2005, p. 1666) used deer pellet density, a measure of prey density, and road density to estimate 10,695 mi^2 (27,700 km^2) of habitat for gray wolves in the Upper Peninsula. Smith et al. (2016, Supplementary Material 2) created an expert-elicited threshold model[19], which estimated 15,824 mi^2 (40,985 km^2) of habitat. Finally, Stricker et al. (2019, p. 87) estimated that the Upper Peninsula supports around 10,200 mi^2 (26,417 km^2) of den habitat.

Research indicates that the only large, unoccupied areas of suitable habitat for gray wolves in the Western Great Lakes region are in the Lower Peninsula of Michigan (Mladenoff et al. 1997, p. 23; Mladenoff et al. 1999, p. 39; Potvin 2003, pp. 44–45; Gehring and Potter 2005, p. 1239). However, these northern Lower Peninsula patches of potentially suitable habitat contain a great deal of private land, are small in comparison to currently occupied habitat in the Western Great Lakes and are intermixed with agricultural areas and areas of higher road density (Gehring and Potter 2005, p. 1240). Gehring and Potter (2005, p. 1239) predicted 850 mi^2 (2,198 km^2) of suitable habitat (areas with greater than a 50 percent probability of wolf occupancy, according to their methods) in the northern Lower Peninsula. Potvin (2003, p. 21), using deer density in addition to road density, estimated 3,090 mi^2 (8,000 km^2) of suitable habitat exists in the northern Lower Peninsula. Gehring and Potter (2005, p. 1239) exclude from their calculations those northern Lower Peninsula low-road-density patches that are less than 19 mi^2 (50 km^2), while Potvin (2003, pp. 10–15) does not limit habitat patch size in his calculations. The updated Mladenoff et al. (2009, p. 134) road density model estimated 10,913 mi^2 (28,265 km^2), and Smith et al. (2016, Supplementary Material 2) estimated 5,456 mi^2 (14,130 km^2) of suitable habitat in the Lower Peninsula. Two separate data-driven species distribution modeling efforts have estimated 4,561 mi^2 (11,813 km^2) and 8,299 mi^2 (21,495 km^2) of suitable habitat in the Lower Peninsula (Gantchoff et al. 2022, p. 4; van den Bosch et al. 2022, entire). Finally, a recent study that assessed potential den habitat and dispersal corridors in the northern Lower Peninsula determined that 736 mi^2 (1,906 km^2) of high-quality den habitat existed in the region (Stricker et al. 2019, pp. 87–88).

The amount of estimated suitable habitat in Minnesota has varied depending on the type of modeling approach and data used. An early study by Stenlund (1955, p. 14) estimated that 12,000 mi^2 (31,080 km^2) of habitat were available in northern Minnesota. Expert-elicited models have estimated 23,128 mi^2 (59,900 km^2; Mech et al. 1988, p. 86), 19,382 mi^2 (50,200 km^2; Mladenoff et al. 1995, p. 289), or more recently 33,964 mi^2 (87,966 km^2; Smith et al. (2016, Supplementary Material 2)) of suitable habitat. In 2009, with additional wolf occupancy data available, Mladenoff et al. (2009, p. 134) revised the estimate to 31,123 mi^2 (80,608 km^2), noting that wolves were filling secondary, less suitable habitat, because primary habitat had reached

[18] Data-driven models include species distribution and machine learning models, where the model algorithm calculates the appropriate thresholds or relationships between the covariates and dependent data used to generate a suitable habitat layer.
[19] Expert-elicited models are those where previously published literature or experts decide upon thresholds, simple rules, and/or apply spatial operations, such as intersections, unions, or summing over multiple layers to create a suitable habitat layer.

capacity. Studies using data-driven species distribution models indicate that 18,565 mi^2 (48,083 km^2; Gantchoff et al. 2022, p. 4) or 26,855 mi^2 (69,554 km^2; van den Bosch et al. 2022, entire) of suitable habitat is available in Minnesota.

Estimates of suitable habitat in Wisconsin have varied considerably, mainly driven by the type of model selected. Expert-elicited models have estimated 5,739 mi^2 (14,864 km^2; Mladenoff et al. 1995, p. 289) or 21,258 mi^2 (55,059 km^2; Smith et al. 2016, Supplementary Material 2) of suitable habitat. As wolves have expanded across the Great Lakes, some estimates have been revised to reflect the ability of wolves to inhabit additional habitats that were previously thought to be unsuitable. Specifically, Mladenoff et al. (2009, p. 134) revised their estimate upwards to 16,223 mi^2 (42,017 km^2). Data-driven species distribution models have estimated 10,717 mi^2 (27,757 km^2; Gantchoff et al. 2022, p. 4) or 17,014 mi^2 (44,067 km^2; van den Bosch et al. 2022, entire) of suitable habitat.

Though the Northeastern United States (Connecticut, Maine, Massachusetts, New Hampshire, New York, Rhode Island, and Vermont) is currently unoccupied by gray wolves, three separate efforts have estimated the amount of suitable habitat within this region (see Table 6 (a-b) for specifics). Harrison and Chapin (1997, p. 7) used an expert-elicited threshold approach to estimate 24,455 mi^2 (65,928 km^2) of core and 4,941 mi^2 (12,797 km^2) of dispersal habitats in the Northeastern United States. They defined core habitats as areas with forests and fewer than 4 humans per 0.6 mi^2 (1 km^2), and dispersal habitat as forested or mixed forest/cropland with fewer than 10 humans per 0.6 mi^2 (1 km^2) (Harrison and Chapin 1997, p. 3). Mladenoff and Sickley (1998, p. 5) applied the road density model of Mladenoff et al. (1995, entire) and estimated 27,972 mi^2 (72,447 km^2) of suitable habitat in Maine, New Hampshire, New York, and Vermont. Finally, a data-driven species distribution modeling effort estimated 46,437 mi^2 (120,271 km^2) of suitable habitat in the Northeastern United States (van den Bosch et al. 2022, entire).

The analysis area for this SSA Report includes 13 additional states from New Jersey westward to the Great Plains (Illinois, Indiana, Iowa, Kansas, Missouri, Nebraska, New Jersey, North Dakota, Ohio, Oklahoma, Pennsylvania, South Dakota, and Texas). Because of the lack of gray wolf occupancy in this region and the potential overlap with other canid species (e.g., *C. rufus*) only two studies have examined suitable habitat in this region (Smith et al. 2016, Supplementary Material 2; van den Bosch et al. 2022, entire). Smith et al. (2016, entire) created an expert-elicited weighted model that used cover type, human density, road density, distance to roads, distance to water, and slope to estimate suitable habitat. Van den Bosch et al. (2022, entire) used data-driven species distribution models and human density, elevation, and proportions and distance to natural and agricultural land to estimate habitat. We report the estimated amount of suitable habitat these two studies project in each of these 13 additional states in Table 6 (a-b).

In summary, based on our evaluation of the extent of suitable habitat in the Eastern United States (Table 6 (a-b)), sufficient suitable habitat remains to support the gray wolf's resiliency, especially within the current range of the species in the Western Great Lakes metapopulation. Outside of the current range of wolves in the Western Great Lakes, additional suitable habitat likely occurs within unoccupied areas in the northern Lower Peninsula of Michigan, parts of the Northeastern United States, and areas of the Southern and Northern Great Plains.

Although some areas in the eastern U.S. appear to provide suitable habitat for wolves (Smith et al. 2016, van den Bosch et al. 2022), they have not successfully colonized regions adjacent to Minnesota, Wisconsin, and Michigan, despite notable wolf dispersal movements (Licht and Fritts 1994, Licht and Hoffman 1996). This failure to colonize may stem from the lack of protective forest cover and the prevalence of extensive livestock grazing nearby, both of which significantly diminish habitat quality for wolves. Consequently, while suitable habitats may exist within the landscape, they often remain unoccupied due to high mortality rates among dispersing individuals. Even if these areas possess the essential resources for survival and reproduction, threats from human activities and environmental hazards can severely impact the ability of wolves to establish new territories.

Table 6 (a-b). Gray wolf suitable habitat estimates from 13 studies that covered part of or all the SSA analysis area. Estimates of suitable habitat are in square kilometers.

a)

State	Stenlund 1955	Mech et al. 1988[a]	Mladenoff et al. 1995[b]	Potvin et al. 2005	Gehring & Potter 2005	Belongie 2008[c]	Mladenoff et al. 2009[b]	Smith et al. 2016	Stricker et al. 2019[d]	Gantchoff et al. 2022	van den Bosch et al. 2022[e]
Minnesota	31,080	59,900	50,200				80,608	87,966		48,083	69,554
Wisconsin			14,864				42,017	55,059		27,757	44,067
Michigan											
Upper Peninsula				27,700		4,846	41,419	40,985	26,417	18,812	35,979
Lower Peninsula					2,198-4,231		28,265	14,130	1,906	11,813	21,495
Statewide			29,348				69,684	55,115	28,323	30,625	57,474

[a]northern Minnesota; currently occupied
[b]habitat suitability above 0.50 threshold
[c]western Upper Peninsula; high and moderately suitable habitat
[d]den habitat
[e]suitable habitat was only modeled north of the northern range limit of *Canis rufus* (Nowak 1995)

b)

State	Harrison & Chapin 1997 (Core)	Harrison & Chapin 1997 (Dispersal)	Mladenoff & Sickley 1998	Smith et al. 2016	van den Bosch et al. 2022[a]
New York	14,618	5,453	16,020		41,653
New Hampshire	4,591	1,222	5,472		10,535
Vermont	2,470	1,430	3,624		11,250
Maine	44,196	4,589	47,332		53,040
Massachusetts	51	103			3,104
Connecticut	0	0			606
Rhode Island	0	0			79
New Jersey					2,388
Pennsylvania					37,515
Illinois				20,282	2,832
Indiana				11,252	2,886
Iowa				20,842	1,754
Kansas				86,945	73,836
Missouri				64,453	4,978
Nebraska				115,390	107,325
North Dakota				78,181	65,687
Ohio				12,821	4,231
Oklahoma				85,993	74,900
South Dakota				118,040	112,372
Texas				422,109	323,703

[a]suitable habitat was only modeled north of the northern range limit of *Canis rufus* (Nowak 1995)

Current Prey Availability

Across the distribution of gray wolves, wolf population density is correlated with prey biomass, supporting the theory that, unless human-caused mortality is high, wolf populations are limited by food supply (Fuller 1989, pp. 33–34; Fuller and Murray 1998, pp. 155–156; but see Vucetich et al. 2002, pp. 3008–3011; Fuller et al. 2003, pp. 147–155; Mech and Peterson 2003, p. 148); however, some researchers contend that wolf populations may become self-regulated via territoriality and intraspecific strife before they become food limited (Cariappa et al. 2011, p. 728; Smith et al. 2020, p. 92; McRoberts and Mech 2014, entire). A meta-analysis of 41 studies from across North America, indicated that a 1,000 km^2 area with 10,000 deer equivalents could theoretically support roughly 38 wolves (Mech and Peterson 2003, p. 148). However, the numerical response of wolves to prey density is not always linear and there are real world complexities not captured in this course-scale relationship, especially in multi-prey systems (Mech and Peterson 2003, pp. 147–155; Cariappa et al. 2011, pp. 728–729; McRoberts and Mech 2014, entire; Gable et al. 2018, entire; Sovie et al. 2023, entire). The numerical response of prey to wolves is also complex and is influenced by an array of factors including: various combinations of prey species; the seasonal vulnerability of prey; the presence of other predators; the social behavior of wolves; a wide range of human effects on wolves and prey; differences in the inherent productivity of habitats and prey populations; and regional differences in the importance of winter snow conditions (Mech and Peterson 2003, p. 157; Metz et al. 2020, pp. 164–167; Smith et al. 2020, pp. 91–92). Despite these complexities, the high reproductive and dispersal potential of wolves and their ability to modify territory sizes, territory overlap, and group membership in response to prey density, means that wolf populations can readily adjust to changes in proportions of vulnerable prey through intra- and inter-pack dynamics (Mech and Peterson 2003, p. 131; Sells et al. 2022a, pp. 7–10; Sells et al. 2022b, pp. 5–9; Sovie et al. 2023, entire). To provide a basic assessment of the amount of prey available for wolves in the Eastern United States, we reviewed ungulate population estimates from state natural resource agencies. We focused on large prey items (e.g., native ungulates) because they comprise the bulk of the wolf's diet and because estimates for smaller prey items were not readily available.

Prey Availability in the Western Great Lakes

The primary prey of wolves in the Western Great Lakes area is white-tailed deer (DelGiudice et al. 2009, pp. 162–163). Prey availability is high in the Western Great Lakes area; white-tailed deer populations in the region have fluctuated (in response to natural environmental conditions) throughout the period of wolf recolonization (i.e., since the mid-1970s) but have been consistently at relatively high densities (DelGiudice et al. 2009, p. 162; Erb and DonCarlos 2009, p. 55).

Current Prey Availability in Michigan

In Michigan, white-tailed deer are more prevalent than other ungulate species; however, current population estimates of white-tailed deer are not available. Michigan DNR currently uses buck harvest information to track deer population trends and, recognizing that buck harvest trends can be impacted by other factors, is investigating other methods to estimate deer abundance (MI DNR 2021, p. 5). Previous population estimates for white-tailed deer were as high as 2.2 million in 1995, but thereafter experienced a long-term decline that continues today (MI DNR 2016, p. 5–6). This trend is more pronounced in the Upper Peninsula (current wolf range in Michigan) and is attributed to continued reductions in hemlock (winter cover), harvest of aspen (summer food), and severe winters (greater than 12 inches of snow for 90 days) (MI DNR 2016, pp. 3–6, 12–14). With reduced winter cover and summer forage, deer are at increased risk of not surviving severe winters (MI DNR 2021, p. 10). Moreover, the MI DNR has noted that "the repeated occurrences of consecutive severe winters during the last 24 years have had a pronounced impact on deer populations and their ability to recover to the levels seen in the late 1980's and mid 1990's" (MI DNR 2021, p. 16). White-tailed deer are more abundant in the Lower Peninsula where winter fluctuations are not as extreme and where summer forage is more abundant, improving deer condition going into winter months (MI DNR 2016, p. 7). Populations throughout the state are able to rebound in mild and moderate winters (MI DNR 2021, p. 21). In addition, since 1998, following the marked reduction in deer population sizes, revised harvest restrictions were implemented (MI DNR 2021, p. 9). These changes are driven by Michigan's deer management plan objectives to manage deer at the appropriate scale, considering impacts of deer on the landscape and on other species, in addition to population size (MI DNR 2016, p. 16). Similarly, the Michigan wolf management plan addresses maintaining a sustainable population of wolf prey (MI DNR 2022a, pp. 38–40). Wolf abundance in the Upper Peninsula has remained stable since 2011, despite the reductions in the white-tailed deer populations in the Upper Peninsula (MI DNR 2021, p. 16). Therefore, despite reductions in white-tailed deer abundance in the northern portion of the state, we conclude that prey populations likely remain sufficient to support a sustainable gray wolf population in Michigan.

Current Prey Availability in Minnesota

Minnesota contains three deer management zones (Forest, Farmland, and Farmland-Forest Transition zones), which are subdivided into "deer permit areas" (Michel and Giudice 2022, p. 1). In Minnesota, populations of white-tailed deer increased in most deer permit areas through 2022, the latest year in which information is available (Michel and Giudice 2022, entire). The Forest Zone in the northeast portion of Minnesota encompasses most of the current gray wolf range in the state while the Farmland Zone in the southeast portion of Minnesota represents a small portion of gray wolf current range. The combination of declining habitat, wolf predation, and multiple harsh winters between 1964 and 1972 resulted in the disappearance of overwintering white-tailed deer from a 3,000-km^2 region of the Superior National Forest (Mech and Karns 1977, entire) for at least 30 years (Nelson and Mech 2006, entire). In the Forest Zone, severe winters in 2013/2014 and 2021/2022 resulted in decreased deer densities in some deer permit areas (Michel and Giudice 2022, p. 5). In 2022, for deer permit areas with established deer density goals in the Forest Zone, 22 were at goal, 17 were below goal, and 3 were above goal (Michel and Giudice 2022, p. 5). In the Farmland Zone, modeling deer densities is a challenge with the available data; however, stable buck harvests over the last 20 years continue to indicate a stable population with available habitat cited as the limiting factor for population growth (Michel and Giudice 2022, p. 4). In the Farmland-Forest Transition Zone, deer densities are high due to milder winter conditions and favorable habitat compared to other zones. Within this zone, 19 deer permit areas were at goal, 1 was below goal, and 28 were above goal in 2022 (Michel and Giudice 2022, pp. 4–5). In cases where deer permit areas are below population goals, harvest of deer is more conservative and, similarly, more liberal for areas that are above population goals. The flexibility of this approach is consistent with the *Minnesota White-tailed*

Deer Management Plan objectives to manage for healthy and sustainable deer populations across the state (MN DNR 2018, entire).

In Minnesota's wolf range, land management activities carried out by public agencies and by private landowners, including timber harvest and prescribed fire, incidentally and significantly improve habitat for deer, the primary prey for wolves in the state. There is no indication that harvest of deer or management of their habitat are significantly depressing abundance of this prey species in Minnesota. Further, implementation of the state's deer management plan is adaptive such that harvest or other management activities conducted reflect population goals (e.g., when not at goal, harvest and/or management is adjusted to be more conservative to avoid longer term trends toward population declines). Therefore, we conclude that prey populations likely remain sufficient to support the wolf population in Minnesota, even when deer permit areas report interannual variation in achieving population goals.

Current Prey Availability in Wisconsin

In Wisconsin, the statewide post-hunt white-tailed deer population estimate for 2022 was approximately 1.48 to 1.79 million deer, similar to what was reported in the previous year (Wojcik et al. 2023, entire). In the Northern Forest Zone of the state, the post-hunt population estimate has ranged from approximately 250,000 deer to more than 400,000 deer since 2002 (above 320,000 deer since 2016), with an estimate of 337,000 deer in 2023 (Wojcik et al. 2023, p. 2). Eight consecutive mild to moderate winters and limited antlerless harvest may explain the population growth in the northern deer herd in recent years; however, the 2023 population estimate is lower than 2022, likely a factor of decreased antlered harvest in 2023 and severe winters in seven deer management units (Wojcik et al. 2023, p. 2). The Central Forest Zone post-hunt population estimates have been largely stable since 2009 at 60,000 to 80,000 deer on average, with an estimate of 79,000 deer in 2023 (Wojcik et al. 2023, p. 2). The Central Farmland Zone deer population has increased since 2008, with the 2023 estimate of 823,000 deer as the highest on record (Wojcik et al. 2023, p. 2). For a fourth year in a row, the 2023 post-hunt deer population estimate (390,000 deer, the highest recorded) in the Southern Farmland Zone exceeded 300,000 deer (Wojcik et al. 2023, p. 2). Therefore, we conclude that prey populations, particularly white-tailed deer, remain sufficient to support the wolf population in Wisconsin.

Prey Availability in the Remainder of the Eastern United States

Outside of the Western Great Lakes, white-tailed deer are found in every state within our analysis area (iNaturalist 2024, unpaginated). Moose are limited to northern latitudes, with populations in Connecticut, Maine, Massachusetts, New Hampshire, New York, North Dakota, and Vermont (iNaturalist 2024, unpaginated). Elk are patchily distributed throughout our analysis area, with a few, isolated herds found in Nebraska, North Dakota, Oklahoma, Pennsylvania, South Dakota, and Texas. Outside of these herds, elk have occasionally been documented in Illinois, Iowa, Kansas, and Missouri (iNaturalist 2024, unpaginated).

Summary of Current Prey Availability in the Eastern United States

In summary, prey availability is an important factor in maintaining wolf populations. Native ungulates, primarily white-tailed deer, are the primary prey within the range of gray wolves in the Eastern United States. Conservation of white-tailed deer in the Western Great Lakes area is a high priority for state conservation agencies. Each state within gray wolf current range manages its wild ungulate populations sustainably by balancing biological and social factors to achieve a numerical or trajectory/trend objective. States use an adaptive-management approach that adjusts hunter harvest in response to changes in big game population numbers and trends when necessary, and predation is one of many factors considered when setting seasons (e.g., MI DNR 2022a, p. 40; MN DNR 2022 p. 27; WI DNR 2023a, pp. 120–121). This adaptive management approach allows states to take conservative approaches to ungulate management in cases where populations are below stated goals, such as in some areas of Minnesota and Michigan. Based on decades of sustained wolf range expansion in the Eastern United States, as well as our evaluation of prey numbers and states' management of ungulates, there is sufficient prey (millions of deer equivalent units) to support thousands of wolves; however, in many areas, wolf abundance is likely to be regulated by human tolerance rather than prey availability (see Mech 2017, pp. 314–315).

Current Population Distribution and Demographics

Methods for Counting and Estimating Annual Population Size in Each State

Michigan, Minnesota, and Wisconsin each have established monitoring programs for the wolf populations in their states. These monitoring methods have evolved over the past few decades as the wolf populations expanded. All three states conduct surveys during winter, which provide estimates of the minimum number of wolves during a given year because these estimates come from the time of year when most winter mortality has already occurred and before the birth of pups. We provide a summary of the monitoring methods each state has used below.

Michigan

From year-end 1989 (early 1990) through year-end 2005 (early 2006), the Michigan DNR used winter track surveys to estimate the size of the wolf population in Michigan, searching the entire Upper Peninsula during each survey (MI DNR 2022a, p. 33). Roads and trails were searched intensively and extensively for wolf tracks and other signs of wolf activity using trucks and snowmobiles (Potvin et al. 2005, p. 1661). Those surveys produced an annual minimum population estimate. As the wolf population increased, however, this method became more difficult and was no longer practical. Since early 2007, the Michigan DNR has been using a sampling approach called geographically stratified sampling based on an analysis by Potvin et al. (2005, entire) to increase the efficiency of the survey (MI DNR 2022a, p. 33). The first estimate produced using this method is the year-end 2006 estimate (which Michigan calls early 2007). This approach involves categorizing sample units in the Upper Peninsula into high, medium, and low wolf density units based on a cluster analysis of past wolf abundance and territory use (Potvin et al. 2005, p. 1662). Two sample units are then selected at random from each density category (six total); these units are intensively surveyed during winter to document a minimum number of wolves within each sample unit (Potvin et al. 2005, pp. 1661-1662). The mean number of wolves per sample unit within each density category is then calculated and multiplied by the total number of units in each density category, these values are then summed to provide an estimate of Michigan's total wolf population (Potvin et al. 2005, p. 1662). Computer simulations have shown that such a geographically stratified monitoring program would produce unbiased and precise estimates of the total wolf population (Beyer 2006, in litt., see attachment by

Drummer; Lederle 2006, in litt.; Roell et al. 2010, p. 3). The population estimates are considered minimums as some wolf packs may be missed due to accessibility, weather, or time constraints (Potvin et al. 2005, p. 1661).

Michigan produced wolf estimates annually up until the year-end 2010 estimate (which Michigan DNR calls early 2011), at which time the state determined that biennial (occurring every other year) abundance estimates were adequate to meet monitoring needs (Table 7). The population estimates presented for Michigan do not include the small number of wolves on Isle Royale National Park (MI DNR 2022a, p. 19), which is an isolated population on an island in Lake Superior. Given the population's minimal number of wolves, near isolation, and lack of unique genetic diversity, plus constraints on this population's expansion because of the island's small size, this wolf population does not contribute significantly towards overall abundance or viability in the state. As a result, wolves on Isle Royale do not contribute towards any of their state-based population objectives (MI DNR 2022a, p. 22). Moreover, the 1997 Michigan Wolf Recovery and Management Plan (1997 Michigan Plan) indicates that gray wolves may not have historically occurred on Isle Royale before 1940 (MI DNR 1997, p. 10).

Minnesota

Since the late-1970s, Minnesota has monitored its statewide wolf population using a well-established combination of multiple methods that have evolved only slightly over time. Counting sizeable wolf populations across expansive forested habitats presents challenges, but the Minnesota DNR has explored a variety of survey methodologies including mark-recapture, distance sampling, and aerial sampling. While no single method has proven practical or successful on its own (Erb and DonCarlos 2009, pp. 55–56) the Minnesota's surveys consistently leverage multiple sources of information (Erb et al. 2018, pp. 2–3; MN DNR 2022, pp. 64–67). Natural resource field personnel collect detections of wolf sign during their normal winter field work. Additional data is gathered from carnivore track surveys (scent station and winter track surveys), verified depredations, and radio-collared packs. A contiguous total wolf range in the state is delineated using this data along with data on forest cover, deer density, and human and road density. The amount of occupied area within total wolf range (i.e., current range) is estimated, based on the locations of observed wolf sign from the current winter survey. This information is in turn used to estimate the number of packs and, from that, the estimated population size.

Between estimates provided for year-end 1978 (i.e., winter 1978/1979) and estimates provided for year-end 1997 (winter 1997/1998), surveys were conducted at 10-year intervals in Minnesota. Starting with year-end 1997 (i.e., winter 1997/1998), surveys were conducted at approximately 5-year intervals until the estimate for year-end 2012 (i.e., winter 2012/2013). Starting with the estimates provided for year-end 2012 (i.e., winter 2012/2013), the Minnesota DNR increased the frequency of population surveys from every 5 years to every year; however, one component of the surveys (the delineation of occupied wolf range) is still assessed at 5-year intervals (Erb et al. 2018, pp. 1–2). Thus, since the estimate for year-end 2012 (i.e., winter 2012/2013), the Minnesota DNR has annually estimated the wolf population size statewide, conducted two (fall and winter) track surveys for assessment of population trends, and documented various metrics related to verified wolf depredations (MN DNR 2022, pp. 21–22) (see Table 7 for illustration of the changing frequency of these population estimates).

Wisconsin

From year-end 1978 (i.e., winter 1978/1979) through year-end 2019 (i.e., winter 2019/2020), the Wisconsin DNR monitored wolf populations in the state annually using a combination of radio-tracking, snow-tracking, summer howl surveys, recovery of dead wolves, depredation investigations, and collection of public observation reports (Wydeven et al. 2009a, pp. 90–92; Wiedenhoeft et al. 2017, p. 2). This method relied heavily on information from radio-collared wolves; thus, the Wisconsin DNR had an intensive radio-collaring program with a goal of having at least one radio-collared wolf in approximately half of the wolf packs in Wisconsin. Data gathered from the collared wolves allowed biologists to estimate wolf pack territory size. The Wisconsin DNR used this information, in combination with data from snow track surveys conducted by trained biologists and volunteer trackers, to estimate a minimum number of wolves in the state (i.e., a minimum count with territory mapping). Because those monitoring methods focused on wolf packs and on heavily forested areas, they likely undercounted lone and dispersing wolves. As a result, the actual wolf population within the state during the late-winter period was most likely larger than the minimum count. However, it is important to emphasize that the likelihood of missing a substantial number of wolves each year is low, and the minimum population count was sufficiently accurate for most applications.

In 2018, due to the amount of effort required to conduct minimum counts as wolf abundance and distribution increased in Wisconsin, the Wisconsin DNR began work to develop an alternative method to estimate wolf abundance in the state based on a scaled occupancy model (Stauffer et al. 2021, entire; WI DNR 2023a, p. 80). During development of the scaled occupancy model between 2018 and 2020, minimum counts using territory mapping—a technique that uses telemetry locations and minimum convex polygons to define and visualize the spatial boundaries that wolves occupy for activities such as feeding, mating, and raising young—for the year-end 2017 (winter 2017/2018), year-end 2018 (winter 2018/2019), and year-end 2019 (winter 2019/2020) estimates) (WI DNR 2021, p. 2, and see figure 8) were consistently within the estimated range of values produced by the scaled occupancy model indicating that model results were a reliable alternative to minimum counts (Stauffer et al. 2021, entire; WI DNR 2023a, pp. 80–82). For those three years both a statewide minimum counts and scaled occupancy model estimates were calculated. However, because of the performance of the scaled occupancy model in providing reliable wolf abundance estimates, beginning with the year-end 2020 estimate (winter 2020/2021), the Wisconsin DNR transitioned to reporting abundance estimates based on the scaled occupancy model only rather than minimum counts using territory mapping (WI DNR 2021, p. 2).

The scaled occupancy model uses (1) information from winter track surveys to estimate occupancy of wolves in the state, (2) zone specific estimates of pack sizes based on counts of wolves reported during winter surveys, and (3) range-wide average home range size estimates from GPS collared wolves to estimate the number of wolves in the state (WI DNR 2023a, pp. 80–82). The scaled occupancy model method provides several improvements over the minimum counts because this method incorporates detection probability and captures uncertainty in the population estimates. The scaled occupancy model was designed to estimate the distribution and abundance of pack wolves in Wisconsin. Although lone and dispersing wolves that occur within known wolf pack occupied areas in Wisconsin may be included in the population estimate, the model does not technically account for lone wolves, especially those that may occur outside of occupied range in the state. The scaled occupancy model method has been criticized as potentially providing overestimates of the population size of wolves in Wisconsin (Treves and Santiago-Avila 2023, entire). Concerns that may lead to potential overestimation include the use of track surveys (lone wolf tracks could be mistakenly counted as a pack or double counting of individuals may occur), the inclusion of wolves that primarily live in adjacent jurisdictions (such as Minnesota or Michigan), the use of an occupancy model that does not account for human-caused mortality (i.e., the model may predict some areas are occupied but, in reality, these areas may be unoccupied due to human-caused mortality), the estimation of wolf pack territory sizes from small sample sizes, and the use of the average (which may be more sensitive to extreme values) versus the median pack size (Treves and Santiago-Avila 2023, pp. 4–6). Stauffer et al. (2024, entire), although not documenting error in Treves and Santiago-Avila (2023), does challenge the authors criticisms concerning potential overestimation. Currently there are no available estimates of potential bias, if any, for the population estimates reported for Wisconsin, just as there are no definitive estimates of bias for minimum counts of wolves in this state. Thus, the best available scientific information does not allow us to determine if correcting the estimates from Wisconsin above or below their current values is appropriate nor does it provide a clear correction factor. Additionally, there are no alternative estimates of wolf population size in Wisconsin produced from different methods. Therefore, the current estimates provided by Wisconsin represents the best available science, and thus we rely on these estimates in this SSA (See Appendix 6 for sensitivity analyses of starting populations in Wisconsin).

Current Population Sizes and Trends

By the time gray wolf subspecies were first listed under the Act in 1974, the gray wolf had been eliminated from most of its historical range within the lower-48 United States, except for a population of approximately 1,000 wolves in northeastern Minnesota, and a small, isolated group of about 40 wolves on Isle Royale, Michigan (Service 2020, pp. 12–14). In the Eastern United States, the gray wolf currently occurs in one large metapopulation in the Western Great Lakes. As of year-end 2022, wolves in the Western Great Lakes area number over 4,550 individuals and occupy 89,581 mi^2 (232,013 km^2) across 3 states (Table 7). Additionally, gray wolves in the Western Great Lakes area are connected to the large, expansive, and secure population of wolves in Canada (Canadian Endangered Species Conservation Council 2022, unpaginated. Manitoba and Ontario, the two Canadian Provinces that border the states of Michigan, Minnesota, and Wisconsin, have an estimated 4,000–6,000 wolves (International Wolf Center 2023a, unpaginated) and 9,600 wolves (International Wolf Center 2023b, unpaginated), respectively. Saskatchewan, the Canadian Province that borders the states of North Dakota and Montana has an estimated 3,000 wolves (International Wolf Center 2023c, unpaginated). Wolves have been documented dispersing from the Western Great Lakes area to at least these three Canadian provinces (Treves et al. 2009, p. 195), and wolves from Canada likely also immigrate into the U.S. Thus, gray wolves in the Western Great Lakes area do not function as an isolated metapopulation of around 4,550 individuals but are part of a much larger "Western Great Lakes and Eastern Canada" metapopulation that includes wolves in adjacent Eastern Canada. Below, we describe the current population size and trends in each of the three Western Great Lakes states in greater detail.

Table 7 and Figure 13 below detail the minimum winter wolf population size in each state from 1976 to year-end 2022 or from 1988 through year-end 2022, respectively (see Appendix 2 for available confidence intervals). As explained above in *Levels of Human-Caused Mortality in the Western Great Lakes*, in this SSA we treat the winter counts/estimates from all three Western Great Lakes states as "end-of-calendar-year" (i.e., year-end) estimates and assign them to the earlier of the 2 years or, in the case of Michigan, the end of the prior year. For efficiency, from this point forward when discussing a population estimate for Michigan, Minnesota, or Wisconsin we will only refer to the estimate by our "year-end" assignment, rather than present both our "year-end" assignment and the state assignment.

Table 7. Minimum counts and estimated winter wolf populations in Michigan (excluding Isle Royale), Minnesota, and Wisconsin from 1976 through year-end 2022. See Appendix 2 for available confidence intervals. (Note that there are several years between the first four estimates.)

Timing of Population Estimate			*Number of Wolves*			
Winter Season (used in Minnesota and Wisconsin)	**Early Calendar Year (used in Michigan)**	**Translation to year end estimate[a]**	**Michigan**	**Minnesota**	**Wisconsin**	**3-State Total**
1976	**NA**	**1976**	NA	1,000-2,000	2	NA
1978/1979	**NA**	**1978**	NA	1,235	7	NA
1979/1980	**NA**	**1979**	NA	NA	25	NA
1988/1989	**Early 1989**	**1988**	3	1,500-1,750	31	1,534-1,784
1989/1990	**Early 1990**	**1989**	10	NA	34	NA
1990/1991	**Early 1991**	**1990**	17	NA	39	NA
1991/1992	**Early 1992**	**1991**	21	NA	45	NA
1992/1993	**Early 1993**	**1992**	30	NA	40	NA
1993/1994	**Early 1994**	**1993**	57	NA	54	NA
1994/1995	**Early 1995**	**1994**	80	NA	83	NA
1995/1996	**Early 1996**	**1995**	116	NA	99	NA
1996/1997	**Early 1997**	**1996**	113	NA	148	NA
1997/1998	**Early 1998**	**1997**	139	2,445	178	2,762
1998/1999	**Early 1999**	**1998**	169	NA	204	NA
1999/2000	**Early 2000**	**1999**	216	NA	248	NA
2000/2001	**Early 2001**	**2000**	249	NA	257	NA
2001/2002	**Early 2002**	**2001**	278	NA	327	NA
2002/2003	**Early 2003**	**2002**	321	NA	335	NA
2003/2004	**Early 2004**	**2003**	360	3,020	373	3,753
2004/2005	**Early 2005**	**2004**	405	NA	435	NA
2005/2006	**Early 2006**	**2005**	434	NA	467	NA

Timing of Population Estimate			*Number of Wolves*			
Winter Season (used in Minnesota and Wisconsin)	**Early Calendar Year (used in Michigan)**	**Translation to year end estimate[a]**	**Michigan**	**Minnesota**	**Wisconsin**	**3-State Total**
2006/2007	**Early 2007**	**2006**	509	NA	546	NA
2007/2008	**Early 2008**	**2007**	520	2,921	549	3,830
2008/2009	**Early 2009**	**2008**	577	NA	637	NA
2009/2010	**Early 2010**	**2009**	557	NA	704	NA
2010/2011	**Early 2011**	**2010**	687	NA	782	NA
2011/2012	**Early 2012**	**2011**	NA	NA	815	NA
2012/2013	**Early 2013**	**2012**	658	2,211	809	3,678
2013/2014	**Early 2014**	**2013**	636	2,423	660	3,719
2014/2015	**Early 2015**	**2014**	NA	2,221	746	NA
2015/2016	**Early 2016**	**2015**	618	2,278	866	3,762
2016/2017	**Early 2017**	**2016**	NA	2,856	925	NA
2017/2018	**Early 2018**	**2017**	662	2,655	905	4,222
2018/2019	**Early 2019**	**2018**	NA	2,699	914	NA
2019/2020	**Early 2020**	**2019**	695	2,696	1,195[b]	4,586
2020/2021	**Early 2021**	**2020**	NA	2,770	1,126	NA
2021/2022	**Early 2022**	**2021**	631	2,691	972	4,294
2022/2023	**Early 2023**	**2022**	NA[c]	2,919	1,007	NA

[a] Each state in the Western Great Lakes conducts its population counts/estimates in mid- to late winter, when wolf populations are closest to their minimum because it precedes the spring breeding season. Minnesota and Wisconsin report winter counts/estimates straddling two 2 calendar years (e.g., 2010/2011 winter count/estimate). Michigan reports its winter counts/estimates as beginning of a calendar year (e.g., early 2011). For the purposes this SSA, we treated the winter counts/estimates as "end-of-calendar-year" values and assigned them to the earlier of the 2 years or, in the case of Michigan, the end of the prior year. For example, a "2010/2011 winter count/estimate" and an "early 2011 winter count/estimate" were each assigned as "end-of-year count/estimates" for 2010 (see Appendix 2). This is an appropriate use of the data because all three of the states' counts/estimates are conducted prior to the breeding season; thus, we can be certain that a wolf counted in early February was also a member of the population in December of the prior year.

[b] Note this estimate is from the scaled occupancy model. A statewide minimum gray wolf population count of 1,034 was also calculated for this time period. This suggests that the increase in the reported population size from the previous year may, in part, be reflective of Wisconsin's transition from estimating minimum number of wolves using territory mapping to producing a modeled population estimate. All subsequent estimates reported for Wisconsin (i.e., year-end 2019 through year-end 2022) are based on the scaled occupancy model.

[c] The state of Michigan has recently reported its year end 2023 count/estimate (e.g., early 2024) as 768 wolves (MI DNR 2024, p. 1; Roell 2025a, in litt.).

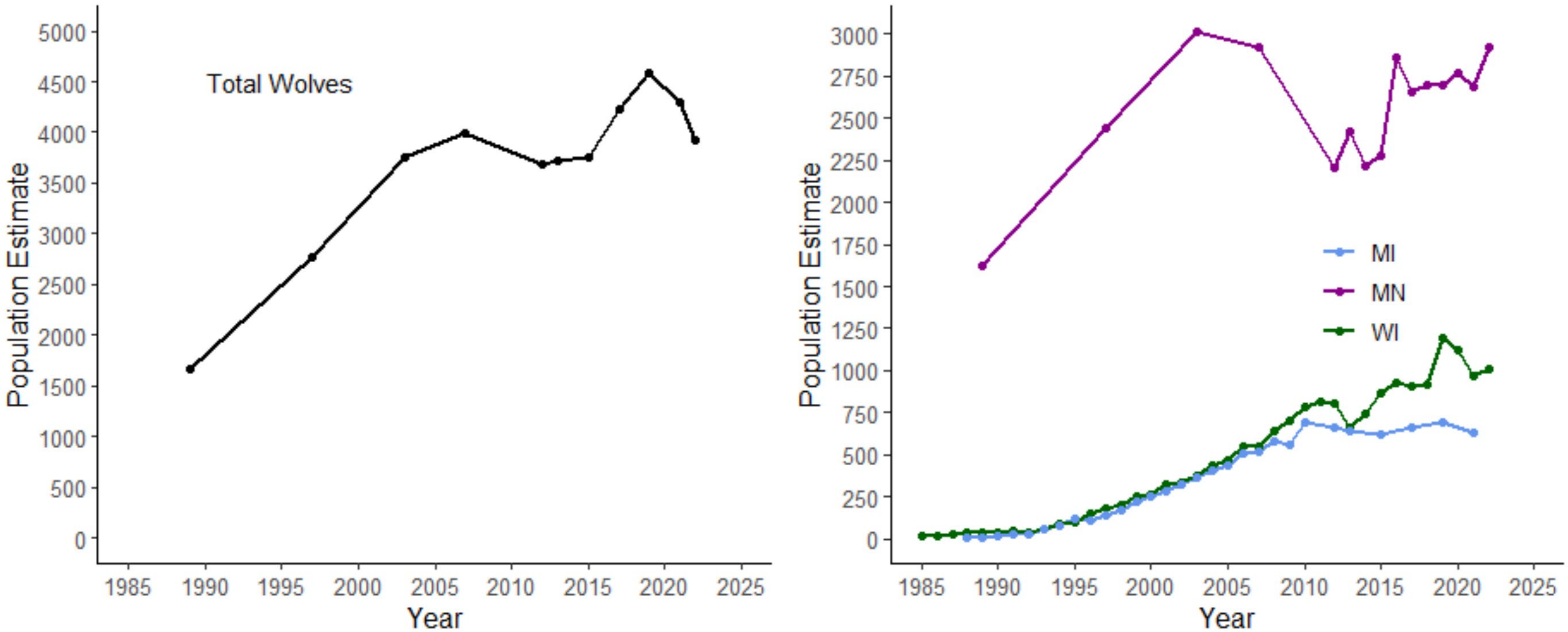

Figure 13. Number of gray wolves counted or estimated in the Western Great Lakes, 1988–2022 (excluding Isle Royale). See Appendix 2 for available confidence intervals. Each state measures the size of its wolf population at different frequencies. Total counts/estimates for all three states appear in the left panel. Points represent years when all three states in the Western Great Lakes provided counts or estimates. Total counts/estimates for each state appear in the right panel. Points represent years when individual states provided counts or estimates. Note for year-end 1988, we used the average of the range of population estimates provided for Minnesota to calculate the total number of wolves in the Western Great Lakes for that year and for year-end 2019 and beyond we used the scaled occupancy model estimate provided by the state of Wisconsin. See Table 7 footnote b for details.

Michigan

Prior to European settlement, wolves occupied both the upper and lower peninsulas of Michigan and likely occurred in every county in the state (Beyer et al. 2009, p. 65). Although no estimates of wolf abundance were recorded at that time, Beyer et al. (2009, p. 67) calculated an estimated abundance (based on maximum wolf densities from recent times) of 3,000–6,000 wolves in the state prior to European settlement. As in other areas, European settlers held a negative view of wolves, and targeted wolves in an attempt to eliminate them. A bounty was first established in Michigan in 1817 and continued in multiple forms (including a state-funded trapping program) until 1960, by which time the population in the state was believed to have dropped below 40–50 wolves (Beyer et al. 2009, pp. 69–70). Wolves were extirpated from Michigan's Lower Peninsula by 1935 and likely extirpated from the Upper Peninsula by the early 1970s (although it is possible that a few animals persisted in remote areas of the Upper Peninsula) (MI DNR 2022a, p. 18). In 1974, four gray wolves were released in Marquette County in an attempt to reintroduce gray wolves in the state. All died within 9 months, however, and never reproduced, thus they did not contribute to the wolf population that occurs in the Upper Peninsula today (Weise et al. 1975, pp. 19–21). Wolves from Wisconsin and Ontario began to recolonize the Upper Peninsula in the late 1980s and, since that time, have spread to every county in the Upper Peninsula.

Estimates of gray wolves in the Upper Peninsula increased from 10 wolves in year-end 1989 to 687 wolves at year-end 2010, the last year the Michigan DNR conducted annual surveys before switching to an every-other-year cycle (see Table 7). There appear to be two distinct phases of population growth in the state, with relatively rapid growth (25.8 percent average) from year-end 1994 through year-end 1999 and slower growth (10.1 percent average) from year-end 2000 through year-end 2009. Since year-end 2010, the population on the Upper Peninsula has remained relatively stable, varying between approximately 600 and 700 wolves, suggesting that they may be at or near their carrying capacity in the Upper Peninsula (MI DNR 2022a, p. 19). There was a minimum estimate of 631 wolves (95 percent confidence interval 582–680) in 136 packs in the Upper Peninsula at year-end 2021 (Roell 2023b, in litt.). Michigan DNR has recently reported a minimum estimate of 768 gray wolves distributed in 158 packs in the Upper Peninsula at year-end 2023 (MI DNR 2024, p. 1; Roell 2025a, in. litt.).

Wolves attempting to disperse into the Lower Peninsula of Michigan today may encounter a variety of natural and human-related challenges. The Straits of Mackinac, which span at least five miles of open water, can present a notable obstacle between the Upper Peninsula and the Lower Peninsula. Climate warming can affect the formation of ice bridges, and extended commercial shipping seasons—along with associated icebreaking—could further limit opportunities for winter crossings (Roell 2025a, in litt.). In southern Wisconsin, potential dispersal routes around Lake Michigan to reach the Lower Peninsula pass through highly developed areas, including cities such as Chicago, Illinois, and Gary, Indiana. Similarly, wolves moving from Canada into the eastern Lower Peninsula of Michigan must navigate around Lake Huron and through regions with substantial human development (Roell 2025a, in litt.). These factors collectively may influence the likelihood and success of wolf dispersal into the Lower Peninsula.

To date, despite several indications of wolf activity in the area, a breeding population has not been confirmed in the Lower Peninsula of Michigan (MI DNR 2022a, p. 20). In 2004, a coyote trapper mistakenly captured and killed a wolf in Presque Isle County in the northern Lower Peninsula of Michigan. This was the first verification of a wolf in the northern Lower Peninsula since 1910 (Roell et al. 2010, p. 4). Since 2004, Michigan has surveyed the northern Lower Peninsula to determine whether wolves have successfully colonized the area. Track surveys in 2011 and 2015 found tracks consistent with a wolf-like animal in two northern Lower Peninsula counties and, in 2014, an animal that appeared to be a wolf was seen on a trail camera. It was later confirmed as a wolf based on DNA analysis of its scat. In January 2024, a male wolf was killed by a coyote hunter in Calhoun County located in Michigan's southern Lower Peninsula (MI DNR 2024, p. 2).

There is a small, isolated population of wolves on Isle Royale in Lake Superior. The wolf population there has typically varied from 18 to 27 wolves (Peterson et al. 2018, pp. 2, 4–5) and was estimated at 30 wolves in January 2024 (Hoy et al. 2024, pp. 5). Michigan does not include the wolves on Isle Royale in its overall population estimate for the state, and we do not include the number of wolves on Isle Royale in our reports of the population size in Michigan in Table 7 or Figure 13 (see *Methods for Counting and Estimating Annual Population Size in Each State* above).

Minnesota

Gray wolves likely occurred throughout Minnesota prior to European settlement and may have numbered between 4,000 and 8,000 animals at that time (Erb and Don Carlos 2009, p. 53; MN DNR 2022, p. 11). By 1900, gray wolves were rare in the southern and western portions of the state. During the pre-1965 period of wolf bounties and legal public trapping, gray wolves persisted in the remote northeastern portion of Minnesota but were eliminated from the rest of the state. Bounties ended in Minnesota in 1965, and gray wolf hunting and trapping ended in the Superior National Forest in 1970, where most wolves lived. The elimination of the bounties and hunting/trapping seasons provided a level of protection that resulted in increases in gray wolf numbers and distribution in the mid-1970s (Erb and Don Carlos 2009, pp. 55–60). Prior to first being listed under the Act in 1974, estimated gray wolf numbers in Minnesota included 450 to 700 wolves between 1950 and 1953 (Fuller et al., 1992, p. 43), 350 to 700 wolves in 1963 (Cahalane 1964, p. 8), 750 wolves in 1970 (Leirfallom 1970, p. 11), 736 to 950 wolves in 1971/1972 (Fuller et al. 1992, p. 44), and 500 to 1,000 wolves in 1973 (Mech and Rausch 1975, p. 85). The Minnesota gray wolf population has increased from an estimated 1,000 individuals in 1976 to over 2,900 individuals today, and the estimated gray wolf current range (the overall range including unoccupied areas between pack territories) in the state has expanded from approximately 15,000 mi^2 (38,850 km^2) to approximately 43,205 mi^2 (111,901 km^2) since the 1970s (Service 2020, pp. 20–21), a nearly 300 percent increase. Occupied range, the estimate of actual area occupied by gray wolf packs, is about 70–80 percent of estimated current range and has remained between about 26,250–28,570 mi^2 (68,000–74,000 km^2) since year-end 1997 (Erb et al. 2018, p. 5; Service 2020, pp. 20–21). Over the past 15 or more years, the population size has remained relatively constant in Minnesota, fluctuating between 2,200 and 2,900 gray wolves. Because most of the suitable habitat has been occupied; these year-to-year fluctuations are expected in populations varying around a maximum population size. As of the latest estimates (year-end 2022), there were a minimum of 2,919 gray wolves distributed between 631 packs in Minnesota (Erb and Humpal 2023, p. 5).

Wisconsin

Prior to European settlement, 3,000 to 5,000 wolves were speculated to have occupied Wisconsin (Wydeven et al. 2009a, p. 88). A bounty operated in the area from 1839–1847 and again (nearly continuously) from 1865–1957, which contributed to the elimination of wolves from the state. Wolves had declined to approximately 200 individuals by the early 1920s, and only a few scattered individuals persisted by the late 1950s (Wydeven et al. 2009a, p. 89). When the bounties ended in 1957, wolves were listed as a protected species in the state, the first time the species was protected in the United States (Schanning 2009, pp. 253–254). The protections, however, began shortly before wolves were considered extirpated in Wisconsin in 1960 (Thiel 1993, p. 4; Wydeven et al. 2009a, p. 89). Wolves apparently recolonized Wisconsin in the winter of 1975/1976 and, by 1979, five wolf packs were documented in the state. The recolonizing wolves in Wisconsin most likely came from the increasing and expanding wolf population in Minnesota (Wydeven et al. 2009a, p. 89).

At the time the Wisconsin DNR began its wolf population monitoring in 1979, it estimated a year-end minimum statewide population of 25 wolves (Wydeven et al. 2009a, pp. 96, 103). This population remained relatively stable for several years but decreased to approximately 14 to 19 wolves in the mid-1980s. In the late 1980s, the Wisconsin wolf population began an increase that generally continued through year-end 2020. There were four exceptions to this population increase: year-end 2012 (the first year Wisconsin held a regulated wolf harvest, which led to a slightly lower population estimate for year-end 2012 relative to year-end 2011), year-end 2013 (when a higher wolf harvest quota during the 2013 season led to a lower population estimate for year-end 2013 relative to year-end 2012), year-end 2017 (which had a slightly lower population estimate than year-end 2016 despite no mortalities from lethal depredation control or regulated harvest), and year-end 2021 (the population estimate was lower than the previous year's estimate but larger than the population size for all years prior to 2018). The Wisconsin wolf population appeared to start to stabilize in 2017–2018, had a minor increase in 2020, decline slightly after the 2021 harvest, but again returned to a similar level as had been observed 2017–2019. The most recent estimate for year-end 2022 indicates a population size of 1,007 wolves (95% credible interval between 780 and 1,380 wolves) distributed in an estimated 283 packs (WI DNR 2023c, p. 4).

Northeastern United States

It is widely accepted that wolves became extirpated from the Northeastern United States by the year 1900 (Young and Goldman 1944, p. 437; Nowak 2002, pp. 95–96; Villemure and Jolicoeur 2004, p. 608; McAlpine et al. 2015, p. 386). The lack of reliable evidence of breeding pairs or wolves with established territories has been reaffirmed in subsequent analyses of the existing status of the wolf in the Northeastern United States, including a 2003 final reclassification rule (68 FR 15804, April 1, 2003), a 90-day finding on a petition to list a DPS of gray wolves in the Northeastern United States (75 FR 32869, June 10, 2010), a status assessment of eastern wolves conducted in 2011 (Thiel and Wydeven 2012, entire), and a finding on an October 9, 2012, petition to continue to protect all wolves in the Northeast and develop a Northeast wolf recovery plan (78 FR 35664, June 13, 2013).

Potential source populations of wolves occur north of the St. Lawrence River in Ontario and Quebec, Canada, which are within the documented dispersal distance of a wolf (Thiel and Wydeven 2012, p. 38; McAlpine et al. 2015, p. 392). Historically, it was assumed that all recently observed free-ranging wolves south of the St. Lawrence River were of wild origin; however, Kays and Feranec (2011, pp. 257–259) determined that most of these wolves in New England were of captive origin. Nevertheless, there have been several documented occurrences of wild wolves south of the St. Lawrence River, demonstrating that it is possible for individual wolves to disperse from Canada to the Northeast United States (Villemure and Jolicoeur 2004, p. 608; Service 2019, p. 2; Kays and Feranec 2011, pp. 257–259; McAlpine et al. 2015, p. 392). For example, a canid shot in Massachusetts in 2007 was confirmed to be a wolf, with genetic testing suggesting it may have been an eastern wolf (Service 2019, p. 2). A study by Kays and Faranec (2011, pp. 257–259) also indicates three wild wolves (as determined through hair and bone collagen samples) were killed in New York and Vermont between 1998 and 2006. More recently, in December 2021, a large canid was killed in upstate New York. Biological samples were collected from this individual and sent to three independent labs to determine species and possible place of origin. One analysis indicated the sample was from an eastern coyote (Chinnici 2022, entire) while two other analyses identified the sample as that of a gray wolf with Western Great Lakes ancestry (vonHoldt 2022, entire; Wilson and Harnden 2022, entire).

Although two wolves confirmed by the Maine Department of Inland Fisheries and Wildlife (MDIFW) in the 1990s were later determined to have lived at least part of their lives in captivity (Kays and Feranac 2011, pp. 258–259), MDIFW still recognizes these as the only two confirmed wolf sightings in the state in recent history (Webb 2023, pers. comm.). Contrary to recent media reports from Maine, results of a scat sample submitted for analysis in 2019 and a recent video of a canid during the spring of 2023 remain inconclusive as to species (Webb 2023, pers. comm.). However, based on additional discussions with the lab that conducted the 2019 analysis and the physical characteristics of the individual canid in the recent video, MDIFW considers these animals to more closely resemble eastern coyotes rather than gray wolves (Webb 2023, pers. comm.). Although individual wolves are capable of dispersing south across the Saint Lawrence River and may be documented on occasion in southeastern Canada and the Northeastern United States, we currently have no information indicating that wolves occupy or have formed breeding pairs in the Northeast United States (Kays and Faranec 2011, pp. 260–261; McAlpine et al. 2015, p. 392; Webb 2023, pers. comm.).

Confirmed Wolf Reports Elsewhere in the Eastern United States

There are confirmed records of a few lone gray wolves elsewhere within the Eastern United States since the early 2000s. Wolves have been documented in many states directly adjacent to, and sometimes great distances from, core populations (Licht and Fritts 1994, entire; Licht and Huffman 1996, entire; 76 FR 26100, May 5, 2011; Jimenez et al. 2017, entire). Dispersing wolves have been detected in all states within historical gray wolf range west of the Mississippi River except Oklahoma and Texas (Wydeven 2019, in litt.). For example, seven wolves have been confirmed in Missouri (Midwest Furbearer Group 2022, p. 12) and one wolf that dispersed from Wisconsin was confirmed in Indiana in 2003 (Thiel et al. 2009, p. 112; Treves et al. 2009,

p. 194). At least 11 wolves have been reported in Illinois since 2000 (ILDNR no date, unpaginated) and 9 wolves have been confirmed in Iowa since 2014 (IADNR 2022, pp. 217–220). Since 2002, five individual wolves were also confirmed in Nebraska (Wilson 2023, p. 48), and two in Kansas (Service 2020, p. 26; KDWP no date, unpaginated). A single wolf with ancestry from the Great Lakes region was confirmed in Kentucky in 2013 (Piaggio 2013, in litt.; Straughan 2023, in litt.). Since the early 2000s, there have been 16 confirmed records of individual gray wolves in South Dakota (South Dakota Game, Fish and Parks 2023, in litt.). Of the areas outside current ranges in the Western United States and Western Great Lakes, North Dakota has the most records of individual dispersing wolves, with at least 35 verified records of individual wolves in the state since 2000 (North Dakota Game and Fish Department (NDGFD) 2018, in litt.; NDGFD 2023, in litt.).

Current Genetic Diversity and Connectivity

Aside from the unique situation on Isle Royale, where infrequent migrations to the island appear to have been too limited to reduce the effects of inbreeding depression (Hedrick et al. 2014, entire; Hedrick et al. 2019, entire), we are not aware of any instances of inbreeding or inbreeding depression within the Western Great Lakes gray wolf population (the only extant gray wolf population in the Eastern United States). Across North America, the general pattern has been that that gray wolf as a species has experienced losses in genetic diversity compared to historical levels (Leonard et al. 2005, entire). However, available genetic data indicate that current gray wolf populations still retain high levels of genetic diversity in the Western Great Lakes area (Koblmüller 2009, p. 2322; Fain et al. 2010, p. 1758; Gómez-Sánchez et al. 2018, p. 3602). Over the past 30 years, the Western Great Lakes wolf population has had stable levels of genetic diversity (vonHoldt et al. 2024b, p. 8). There has been a recent attempt to estimate contemporary effective size for the Western Great Lakes gray wolf population (vonHoldt et al. 2024b, pp. 8–9); however, this analysis violated a major assumption of the methodological approach and thus is unreliable (Kardos and Waples 2024, entire). Thus, there is no reliable estimate of current effective size across the entire region. An analysis of samples just from Minnesota indicated gray wolves from that state have high heterozygosity across the genome, which is a signature of an outbred population that has maintained large effective population sizes over a long period (Robinson et al. 2019, p. 2). Microsatellite genotypes generated for just Minnesota gray wolves collected pre- and post-harvest (i.e., during 2012/2013 and 2013/2014 harvest seasons respectively) resulted in estimates of effective size between 526 to 694 (Rick et al. 2017, p. 1096). In fact, there is no evidence of a population bottleneck in Minnesota despite past range reductions (Koblmüller et al. 2009, p. 2322; Rick et al. 2017, p. 1101), likely due to sustained connectivity with gray wolves in Canada.

An important factor for maintaining genetic diversity can be connectivity or effective dispersal between populations or subpopulations (Raikonnen et al. 2013, entire; Wayne and Hedrick 2011, entire). In the Western Great Lakes area, effective dispersal and interbreeding appears to be occurring among Michigan, Minnesota, and Wisconsin as well as between these states and Canada (Fain et al. 2010, p. 1758; Wheeldon et al. 2010, p. 4438; Heppenheimer et al. 2018, pp. 8–10; vonHoldt et al. 2024b, p. 6).

Summary of Current Resiliency

Currently, sufficient prey and suitable habitat remain in the Western Great Lakes to support a healthy population that can withstand the stochastic events and stressors it has experienced to date. Despite ongoing lethal depredation control in Minnesota and occasional regulated harvest, wolves have successfully colonized most, and perhaps all, suitable habitat in Minnesota. In the past 15 years, the current range in the state has remained relatively unchanged. Wisconsin wolves now occupy most habitat areas believed to have a high probability of wolf occurrence, even though the state has reliably implemented lethal depredation control and regulated harvest during years when the species was delisted. In Michigan, the population has filled the available suitable habitat within the Upper Peninsula and has remained stable since 2011, despite occasional human-caused mortality. Vast additional areas of suitable habitat remain outside of the Western Great Lakes; however, these areas are currently unoccupied, despite multiple records of dispersing wolves in these states. To date, ongoing risk of human-caused mortality in these unoccupied areas has likely limited the gray wolf's ability to expand beyond Michigan, Minnesota, and Wisconsin in the Eastern United States.

As of year-end 2022, an estimated 4,557 wolves currently occur throughout the Western Great Lakes area[20]. While this total population estimate, and the estimate in each state, has fluctuated over the past 15 years, at times decreasing below the previous year's estimate, overall, the population size in the Western Great Lakes has steadily increased since the late 1990s, demonstrating the species' current ability to withstand previously observed stochastic events and periodic stressors. This relatively slight annual fluctuation of population size is typical of populations that have neared carrying capacity of their habitat and may also be due to annual variability in tracking conditions or variations in survey intensity. Moreover, some of the years in which we observed slight decreases in population size relative to the previous year were years in which the states conducted regulated harvests and/or increased lethal depredation control (when the species was delisted). Therefore, we would expect an immediate population response to the introduction of these new stressors of regulated harvest and lethal depredation control (sources of mortality that may not have been present in previous years). However, thus far, populations have quickly rebounded after these increases in human-caused mortality and associated single-year population decreases. In Chapter 6, we analyze the potential effects of sustained human-caused mortality rates and multi-year population reductions in the future (reductions that we have not yet observed in any states in the Western Great Lakes metapopulation).

Subpopulations within the Great Lakes metapopulation are connected, and wolves dispersing from Minnesota contributed to the expansion of the species' range in Wisconsin and Michigan (Treves et al. 2009, p. 192; MI DNR 2022a, p. 41; MN DNR 2022, p. 5). The Western Great Lakes wolf population is also connected to wolf populations in Ontario, Manitoba, and Saskachewan Canada (Treves et al. 2009, pp. 194–195; MN DNR 2022, pp. 28–29). The connectivity within the Western Great Lakes population, and to Canada, in addition to the large population size, supports high levels of genetic diversity within the population, further contributing to the species' ability to withstand stochastic events.

[20] The estimated number of wolves in Michigan contributing to this total is from year-end 2021 because they only estimate population size every other year.

Wolves in the Western Great Lakes area greatly exceed the recovery criteria (Service 1992, pp. 24–26) for (1) a secure wolf population in Minnesota, and (2) a second population outside Minnesota and Isle Royale consisting of 100 wolves within 100 mi (160 km) of Minnesota for 5 successive years. Based on the surveys conducted since 1998, the wolf population in Minnesota has exceeded 2,000 individuals over the past 25 years, and the population in Michigan and Wisconsin combined, which is less than 100 mi (160 km) from the wolf population in Minnesota, has exceeded 100 individuals every year since year-end 1993 (Table 7). Therefore, despite large areas of unoccupied suitable habitat throughout the Eastern United States, based on the criteria set by the Eastern Wolf Recovery Team in 1992 and reaffirmed in 1997 and 1998 (Peterson 1997, in litt.; Peterson 1998, in litt.; Peterson 1999a, in litt.; Peterson 1999b, in litt.) and the latest information regarding wolf abundance and resilience to stressors, the Western Great Lakes region contains sufficient wolf numbers and distribution to support the current population's ability to withstand stochastic events.

Current Representation

We used the Thurman et al. (2020, entire) standardized method to assess representation (i.e., adaptive capacity) of the gray wolf in the Western Great Lakes by examining 36 attributes related to their distribution, movement, evolutionary potential, ecological role, abiotic niche, life history, and demography. Taken together, these attributes provide a holistic picture of how well a species, in this case the gray wolf, may be able to adapt to environmental changes (e.g., climate change). We assessed each of these attributes for the gray wolf relative to standardized definitions of high, moderate, and low (see Appendix 3 for our scoring). Thurman et al. (2020, pp. 521–522) developed the category definitions to be broadly applicable across taxa and accommodate a range of data availability. For a given attribute, a "high" score indicates that the characteristic of the species may confer increased adaptive capacity, whereas a "low" score indicates the opposite. Among the 36 species attributes identified by Thurman et al. (2020, p. 522), the authors recognized 12 "core" attributes as representative of the key traits and essential components of adaptive capacity; therefore, while we scored all 36 attributes (see Appendix 3 for this evaluation), we focus our assessment on these 12 core attributes, grouped as: (1) those that affect dispersal and colonization, (2) those that relate to phenotypic and behavioral plasticity, and (3) those that impact evolutionary genetic capacity (see Table 8). This categorization should be considered with the recognition that a specific attribute can contribute to more than one component of adaptive capacity. Physiological tolerance, for example, is linked to phenotypic and behavioral plasticity, but it also contributes to the ability to disperse and colonize new and different habitats. Therefore, we use the three components to organize, not limit, the variety of attributes.

Dispersal and colonization ability provide the basis by which a species can exploit new habitats or shift their range to follow changes in current habitat. The gray wolf's dispersal and colonization ability is positively impacted by their ability to disperse long distances through a variety of habitats and by their ability to colonize habitat types that are common and broadly distributed throughout their range (score for *dispersal distance* is "high;" score for *habitat specialization* is "high") (Table 8). Colonization ability is also tied to fecundity, a trait in which wolves (five to six pups per litter) compare favorably with other carnivores (Stahler et al. 2013,

p. 223), but which scored "moderate" on the standardized scale we used (Table 8). While not considered a "core" attribute, early sexual maturity of wolves (2 or 3 years old) scored as "high" and helps facilitate rapid population growth after dispersal. Conversely, a "low" score for *commensalism with humans* indicates that dispersal and colonization are restricted in human-dominated environments and wolves are generally unable to persist in landscapes that have been altered for human use (Table 8). This restriction is largely due to conflict with humans, however, not necessarily an inability to use such habitats effectively (Mech 2017, entire). Despite that, wolves' dispersal and colonization ability has allowed them to expand successfully into vast suitable habitat throughout the Western Great Lakes states (Koblmüller et al. 2009, pp. 2318–2319; Fain et al. 2010, pp. 1756–1758; Heppenheimer et al. 2018, pp. 8–10). However, thus far, while wolves have been observed outside of the Western Great Lakes, they have not established populations in any areas outside of the Western Great Lakes in the Eastern United States, likely due to conflict with humans. Because of the factors discussed above, we do not find wolves' dispersal and colonization ability to be limiting current adaptive capacity in the Western Great Lakes; however, negative association with humans may limit effective dispersal and successful colonization in the remainder of the Eastern United States, thereby limiting the potential breadth of the species' range in the Eastern United States.

Phenotypic and behavioral plasticity facilitate persistence in place during times of environmental change. For wolves, these characteristics are positively impacted by their range covering a large area (*extent of occurrence* is "high"), adaptation to a relatively wide range of abiotic conditions (*climatic niche breadth* is "high"), and physiological tolerance to changes in those conditions (*physiological tolerance* is "high") (Table 8). In addition, wolves display some flexibility in both their reproductive phenology and diet (*reproductive phenology* is "moderate" and *diet breadth* is "moderate"). Although climatic factors are strongly correlated with wolf population structure on a continental scale, that link may be due to dispersing individuals seeking out familiar habitat and prey rather than evidence of strict physiological or life history limitations of those populations or ecotypes (Carmichael et al. 2007, pp. 3478–3479; Muñoz-Fuentes et al. 2009, pp. 1525–1526; Schweizer et al. 2016, p. 398). Because they are dispersed across a relatively wide area of suitable habitat and display a generalist life history, wolves are currently well suited to respond to environmental change within their range in the Western Great Lakes (McKelvey and Buotte 2018, p. 360). We do not find wolves' phenotypic and behavioral plasticity to be limiting current adaptive capacity in the Western Great Lakes.

Evolutionary genetic capacity provides the basis on which natural selection can act over time and is influenced by genetic diversity, population size, and life span (which can influence how rapidly natural selection may act) (Funk et al. 2019, p. 120). Studies have shown sufficient genetic diversity in the Western Great Lakes (*genetic diversity* is "high") (Koblmüller et al. 2009, pp. 2318–2319; Fain et al. 2010, pp. 1756–1758; vonHoldt et al. 2024b, p. 8) and their *life span* is "moderate," according to the generalized scale in Thurman et al. (2020, WebTable 2) (Table 8). The *population size*—not accounting for connectivity to much larger populations in Canada—is also considered "moderate," according to the Thurman et al.'s (2020, WebTable 2) generalized standards (Table 8). The importance of population size is two-fold: smaller populations have increased risk of losing genetic diversity due to drift, and smaller populations may not respond as readily to selective pressures due to a smaller pool of available variation (Stockwell et al. 2003, p. 97). For the gray wolf in the Eastern United States, these concerns are mitigated to some degree due to the population being a part of, and connected to, a larger metapopulation that includes large numbers of wolves in Canada (Koblmüller et al. 2009, pp. 2318–2319; Wheeldon et al. 2010, p. 4432; Heppenheimer et al. 2018, pp. 8–10). That connectivity has, thus far, precluded the loss of genetic diversity and any concerns about inbreeding throughout the extant metapopulation (see *Current Genetic Diversity and Connectivity* above). Additionally, the legacy of introgression (i.e., historical gene flow) in the genomes of wolves in the Western Great Lakes likely provides additional adaptive capacity for these populations (Wheeldon and White 2009, p. 10; Vilaça et al. 2023, entire; vonHoldt et al. 2024b, p. 9–10). As such, the evolutionary genetic capacity of wolves in the Western Great Lakes appears to at least be stable, with no current indications of a decline. We do not find wolves' evolutionary genetic capacity to be limiting current adaptive capacity in the Western Great Lakes.

Overall, our assessment of wolves in the Western Great Lakes using the framework established by Thurman et al. (2020, entire) resulted in only 2 of the 36 attributes in the "low" category. One was *parental investment* (relating to parental energetic costs*)*, which scores as "low" because wolves require parental investment and care for survival (as opposed to young being born already able to feed themselves, for example). Parental investment is not one of the 12 "core" attributes of adaptive capacity in Thurman et al. (2020, entire). While we acknowledge the increased energy expenditure required of wolves to care for pups, we do not find this characteristic to be a significant factor impacting adaptive capacity for wolves. The other attribute for which wolves scored "low" was *commensalism with humans*, a core attribute discussed above. Due to conflicts that arise when living near humans, wolves are unlikely to colonize human-dominated habitat in a significant way (Mech 2017, p. 312), and therefore will be restricted to other habitat areas. Our assessment of suitable habitat above, however, combined with our assessment of the remaining attributes shows that wolves in the Western Great Lakes have sufficient habitat to maintain the other components of adaptive capacity in "moderate" or "high" categories. As such, impacts on adaptive capacity from their lack of commensalism with humans can likely be overcome by other factors that contribute positively to their dispersal and colonization abilities, plasticity, and evolutionary genetic capacity, particularly if the threat of human-caused mortality is adequately managed.

Table 8. Our assessment of 12 "core" adaptive capacity attributes for the gray wolf in the Western Great Lakes. As applied here, a "high" adaptive capacity assessment means that the attribute contributes positively to overall adaptive capacity/representation for the gray wolf in the Eastern United States, whereas a "low" assessment means that attribute does not contribute or could detract from adaptive capacity/representation (see Thurman et al. 2020 for definitions of high, moderate, and low for each core attribute).

Core Attribute	Category	Adaptive Capacity Rating for Gray Wolf in the Western Great Lakes
Extent of occurrence	Dispersal and colonization	High
Habitat specialization	Dispersal and colonization	High
Commensalism with humans	Dispersal and colonization	Low
Dispersal distance	Dispersal and colonization	High
Fecundity	Dispersal and colonization	Moderate
Diet breadth	Plasticity	Moderate

Core Attribute	Category	Adaptive Capacity Rating for Gray Wolf in the Western Great Lakes
Climate niche breadth	Plasticity	High
Reproductive phenology	Plasticity	Moderate
Physiological tolerances	Plasticity	High
Genetic diversity	Evolutionary genetic capacity	High
Population size	Evolutionary genetic capacity	Moderate
Life span	Evolutionary genetic capacity	Moderate

In addition to the attributes from Thurman et al. (2020, p. 522), we also analyzed current distribution on the landscape throughout different ecoregional provinces as an additional proxy for representation. A metapopulation structure, with subpopulations connected by some level of gene flow, can facilitate increased adaptive capacity because selective pressures may vary among subpopulations (Razgour et al. 2019, p. 10421; Carroll et al. 2021, p. 74); different environmental conditions or ecological factors can create these varied selective pressures. Within a subpopulation, adaptive variants that might be masked in the larger population can be expressed and selected for, increasing their prevalence in the overall metapopulation and contributing to adaptive capacity (Funk et al. 2019, p. 120; Razgour et al. 2019, p. 10421; Carroll et al. 2021, p. 74). To assess this potential, we examined wolves' current distribution across different ecoregional provinces, which incorporate temperature, precipitation, and vegetation data, as defined by Bailey (2016, map). Given that in the Eastern United States gray wolves are only found in the Western Great Lakes region, they primarily occur in one ecoregional province (the Laurentian Mixed Forest). The population has expanded to occur in small portions of two additional ecoregional provinces (the Eastern Broadleaf Forest (Continental) and the Prairie Parkland (Temperate)). Without expanding beyond Michigan, Minnesota, and Wisconsin, the species would not occupy additional ecoregional provinces beyond these three. While currently the gray wolf in the Eastern United States may not be experiencing the different selection regimes that can result from occupying multiple different ecoregional provinces, given the vast majority of its range is in one ecoregional province, there are other, more direct measures of adaptive capacity that we discuss above, indicating that the species likely retains its ability to adapt to changing environments.

Considering these components of adaptive capacity, wolves in the Western Great Lakes appear well suited to adapt to environmental change in their current condition. Of the 36 overall attributes we assessed, inclusive of the 12 "core" attributes, 22 attributes score as "high," 12 as "moderate," and just 2 are "low," indicating a breadth of factors that contribute positively to adaptive capacity of wolves with none that are uniquely critical or otherwise impossible to overcome. Therefore, consistent with conventional wisdom about wide-ranging, habitat generalist species, the gray wolf in the Western Great Lakes has the ability to adapt to environmental changes with a range of behavioral, physiological, or evolutionary responses.

Current Redundancy

Gray wolves in the Western Great Lakes currently occur in one metapopulation, structured in a constellation of subpopulations spread across three states; this metapopulation is also connected demographically to a larger secure population of wolves in Canada (Canadian Endangered

Species Conservation Council 2022, unpaginated). Based on survey information in each state, there were at least 1,050 packs distributed between Michigan, Minnesota, and Wisconsin at the end of 2022, further contributing to redundancy of the species. Disease is the prevailing causal factor of high mortality events in carnivore species (Chapron et al. 2012, p. 14). Therefore, to assess catastrophic risk, we evaluate the frequency and impact of disease on wolf populations, and the current and future ability of wolf populations to rebound from high mortality disease events (see Chapters 5 and 6). While outbreaks of several diseases have occurred in the wolf population in the Western Great Lakes in the recent past, population decreases have been localized to specific regions, with the overall metapopulation continuing to grow and expand to new areas (see *Disease and Parasites in Wolves* in Chapter 3). Although it is possible a novel disease may arise, the gray wolf's current spatial distribution in the Western Great Lakes and its abundance throughout that distribution combined with our understanding of current gray wolf disease ecology make it unlikely that a disease outbreak would impact all subpopulations of the gray wolf metapopulation in the entire Western Great Lakes at the same time. Further, even if one subpopulation was impacted, with the gray wolf's high dispersal ability, the surrounding subpopulations can serve as a natural source for recolonization or population augmentation.

Summary of Current Condition

In the Eastern United States, gray wolves occur in one large metapopulation in the Western Great Lakes, distributed across the states of Michigan, Minnesota, and Wisconsin. As of the year-end 2022, there were over 4,550 gray wolves distributed between more than 1,050 packs in the Western Great Lakes. Despite past harvest seasons, ongoing lethal depredation control, and periodic disease outbreaks, the population in the Western Great Lakes has maintained a large population and broad distribution. Essentially, at current levels, human-caused mortality and other stressors have had minimal impact on wolf abundance or distribution in the Western Great Lakes; however, for much of the past 50 years, the protections of the Act have tempered the levels of human-caused mortality to which the species has been exposed in Wisconsin and Michigan and, to a lesser degree, in Minnesota (where lethal depredation control is authorized under section 4(d) when the species is listed). Dispersals of wolves from the Western Great Lakes metapopulation have been documented in at least eleven states (Colorado, Illinois, Iowa, Indiana, Kansas, Kentucky, Missouri, Nebraska, New York, North Dakota, and South Dakota), and three Canadian Provinces (Manitoba, Ontario, and Saskatchewan).

The wolves in the Western Great Lakes states occupy areas of high-quality habitat with abundant prey (DelGuidice et al. 2009, entire; Mladenoff et al. 2009, pp. 128–136). The maintenance and expansion of the Minnesota wolf population has allowed for the preservation of the genetic diversity that remained in the Great Lakes area when its wolves were first protected in 1974. The current population retains high levels of genetic diversity (Koblmüller 2009, p. 2322; Fain et al. 2010, p. 1758; Gómez-Sánchez et al. 2018, p. 3602). The Western Great Lakes metapopulation's large size, broad pack distribution, high levels of genetic diversity and connectivity, and gray wolves' high reproductive potential and innate behavior to disperse into vacant suitable habitats, contribute to the species' current ability to withstand stochastic and catastrophic events within the Western Great Lakes. Finally, based on multiple contributing factors to adaptive capacity, wolves in the Western Great Lakes currently retain the ability to adapt to changes in their environment. In sum, while the gray wolf currently occupies only a portion of its historical range in the Eastern United States, within its current range (i.e., within the Western Great Lakes region), the gray wolf currently retains the ability to withstand stochastic and catastrophic events and adapt to changes in its environment.

Chapter 5: Methods for Evaluating Future Condition

We developed a population model to (1) project the future population size of gray wolves in the Western Great Lakes states of Michigan, Minnesota, and Wisconsin, under a range of future scenarios (see *Future Scenarios* below) and (2) conduct a PVA by evaluating the likelihood of falling below thresholds related to extinction risk and genetic health (see *Population Thresholds* below). We developed this model to create transparency in our conclusions regarding gray wolf resiliency and redundancy, two key components of viability, and to quantify our uncertainty in these future projections. States that manage gray wolves (i.e., Montana (Messmer 2022, in litt.) and Wisconsin (Johnson and Schneider 2021, entire)) have used population-level models to estimate the effects of harvest on gray wolf populations. Our model structure and thresholds were chosen to specifically evaluate the ability of gray wolves to persist in multiple areas under various mortality (i.e., harvest and lethal depredation control) scenarios and disease rates, and to evaluate the ability of gray wolves to maintain effective population sizes above those needed to prevent inbreeding depression. We chose the type of model, scale of the model, and assumptions of the model based on the best available scientific information. In Chapter 6, we qualitatively discuss expectations regarding expansion of gray wolf populations outside of the three states in which gray wolves currently occur in the Eastern United States, potential changes in suitable habitat and prey availability, and potential changes in genetic diversity. We did not develop a quantitative model to project recolonization of these areas because these areas are not currently occupied and gray wolf demographic data specific to these areas do not exist. Undertaking such a modeling effort would have required us to make subjective assumptions about how states that are currently unoccupied would manage gray wolves in the future.

Below we describe our methods for the gray wolf population modeling and forecasting; we summarize the uncertainties and assumptions involved in our model in *Key Uncertainties* and in Table 12 below.

Analysis Units

We quantitatively projected the total future population size of gray wolves in the combined area of Michigan, Minnesota, and Wisconsin (i.e., the Western Great Lakes). For this combined area, we estimated the total number of gray wolves over time under each future scenario up to 100 years into the future. To develop these future projections for this multi-state area, we separately projected future gray wolf population size in each state (Appendix 5). We then summed the individual projections for each of these states to determine the total number of gray wolves that would occur in the three-state Western Great Lakes area in the future. Therefore, for the purposes of our model projections, each state in the Western Great Lakes area represented an analysis unit.

Models of Population Growth

Determining Density-Independent or Dependent Growth

To construct a population model for each state, we first determined whether density-dependent or density-independent growth better characterized the population dynamics in each state. Density-dependent growth describes populations in which growth rates are related to population size. Density dependence can be either positive or negative. Positive density dependence (Allee effects) involves populations in which growth rates increase as a function of population size (i.e., where small population sizes are limited by mate finding or when increasing numbers of conspecifics provide a benefit to fitness such as for herd or flocking species). Positive density dependence is generally only observed at very small population sizes and is related to other small population effects. Negative density dependence involves populations in which population growth rates decrease as a function of population size; negative density-dependent growth describes populations in which growth rates are maximal at small population sizes and decline as populations reach a maximum size, resulting in population plateaus where population size "levels-off" after an initial growth period. Models with negative density-dependent growth are most appropriate for species where habitat, prey, or other resources are limiting. In contrast to density-dependent growth, density-independent growth describes populations where growth is not related to population size, in which populations grow at a steady continuous rate indefinitely (Bacaër 2011, Chapter 6; Ricker 1954, entire; Gotelli 2001, Chapter 2, pp. 25–45).

Based on empirical estimates of current gray wolf population sizes provided by Michigan DNR, Minnesota DNR, and Wisconsin DNR (Appendix 2), we assessed both density-dependent (**Equation 1**) and density-independent (**Equation 2**) growth models for each state. We compared model results to determine which model best fit the gray wolf population data for each state. We then used the parameter estimates from the best fitting model to project future gray wolf population size under several scenarios (as we describe in further detail under *Future Scenarios* below).

Positive density-dependent growth is described by the following equation:

Equation 1: $N_{t+1}=N_t + r_{max}N_t\,(1–N_t/K)–h(m+c)$
(Bacaër 2011, Chapter 6; Ricker 1954, entire; Gotelli 2001, Chapter 2, pp. 25–45),

where N is the population size at each time step; r_{max} is the per capita intrinsic rate of growth (which captures reproduction – natural mortality + immigration – emigration); K is the estimated maximum population size for a particular state; and h is an estimate of the additive effect of harvested animals (m) + animals removed due to lethal depredation control of wolves (c) on gray wolf population dynamics (i.e., the per wolf effect of removal on the overall population growth).

We can approximate density-independent growth with the following equation:

Equation 2: $N_{t+1}=\lambda N_t–h(m+c)$
(Gotelli 2001, Chapter 2, pp. 25–45),

where λ is the ratio of the population size (N) at time (t) over the population size at the previous time step ($t - 1$), and all other variables are as defined for Equation 1 above.

Based on the analyses described below, negative density-dependent models were a better fit for the empirical data for all states (see Supplementary Material A for details of model fitting). Therefore, we used negative density-dependent models when estimating future population size in our model projections.

Understanding Maximum Population Size, Intrinsic Growth, and Harvest and Lethal Depredation Control Effects Parameters

Figure 14 provides a graphical depiction of the density-dependent growth model we used to project gray wolf population size in the future (**Equation 1** above). Below, we further describe the model parameters in this equation.

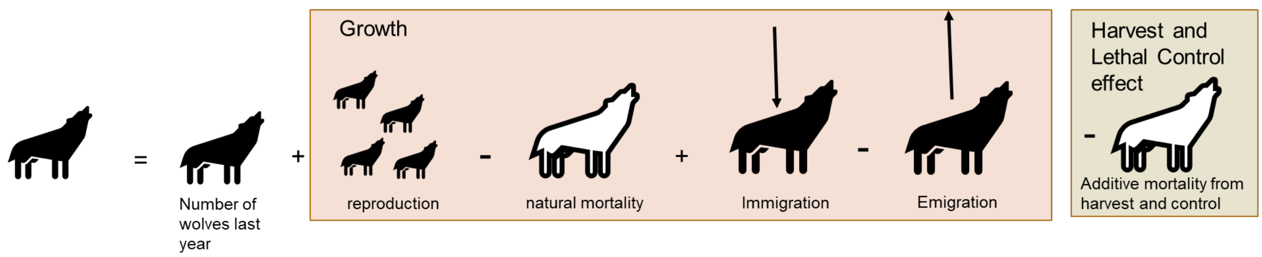

Figure 14. Schematic of density-dependent gray wolf population model. Arrows indicate direction of movement into (immigration) or out of (emigration) the population.

In negative density-dependent models, estimates of r_{max} (the per capita intrinsic rate of growth, which incorporates the effects of reproduction, natural mortality, immigration, and emigration) approach their maximum values when populations are small, and approach zero as populations reach K. In most population models, K is interpreted as a "carrying capacity" or the maximum number of animals an area can sustain due to factors such as prey density or habitat availability. Because gray wolf populations in the United States are highly managed and influenced by human activities, we chose to define K as a maximum population size (that can be limited by human social and cultural norms, in addition to biotic conditions) rather than a purely biological carrying capacity; the maximum population size is likely limited by both environmental and human societal factors.

Our density-dependent growth model also included a measure of the per-wolf additive effect of harvest and lethal depredation control (h) (Figure 14). In our models, we used reported annual harvest plus the reported number of gray wolves removed through lethal depredation control efforts to estimate this additive effect parameter from observed data. There is significant debate regarding whether gray wolf harvest and/or lethal depredation control is additive or compensatory (see *Effects on Population Growth* in the *Human-Caused Mortality* section in Chapter 3 above). In density-dependent growth models with additive effects of harvest and lethal depredation control (h) (**Equation 1**), as the estimate of h approaches zero, mortality from harvest and lethal depredation control efforts does not exceed losses that otherwise would have occurred through natural mortality and dispersal; in other words, as h approaches zero, harvest and/or lethal depredation control has no effect on the growth rate of the population either because the removed gray wolf would have died from natural causes or because recruitment or immigration rates increase in response to wolf harvest and/or lethal depredation control to compensate for losses. As the estimate of h approaches one, harvest and lethal depredation control efforts are completely additive and each gray wolf killed by harvest and/or lethal depredation control is subtracted from the population. In other words, as h approaches one, any gray wolf killed by harvest or lethal depredation control would not otherwise have died through natural causes, and increased recruitment or immigration do not compensate for this mortality. The estimate of h can also exceed one, which implies "superadditive" effects of harvest and lethal depredation control; this means that for each gray wolf removed through harvest or lethal depredation control, more than one gray wolf is lost from the population due to the effects of the removed gray wolf's loss on pack dynamics and future reproductive success and recruitment (see *Effects on Wolf Social Structure* in Chapter 3 above).

Estimating Parameters for Projections

To project the future population size of gray wolves, we first needed to estimate the input parameters in the density-dependent growth equation (**Equation 1**) above, as density-dependent growth provided the best fit to the data. To account for the unique characteristics of each state's population, we separately estimated a distribution for the initial population size (N_t) and the maximum population size (K) for each state. However, we used our density-dependent model to estimate a single distribution for r_{max} and h parameters, sharing population information from all three states. Below, we discuss in more detail how we estimated each of these parameters for our modeling.

Estimating Starting Population Sizes (N_t)

We estimated the starting population size for each state from the data provided by state agencies (either minimum counts or model estimates; see Chapter 4 for details). We sought to derive our starting population sizes in as consistent a manner as possible between states, so all states' starting population sizes contained estimates of error. Michigan DNR and Wisconsin DNR both provided estimates of population size with associated error; therefore, we used these states' estimates (along with their associated error) as the starting population size for both states. Minnesota DNR provided population estimates with 90% confidence intervals versus the 95% confidence intervals provided by the other states; therefore, we used our density-dependent models to estimate a distribution (including error) for the starting population size in Minnesota at the end of the year 2022. As such, the starting population size we used for Minnesota in our future projection modeling (which we estimated from these density-dependent models) differs slightly from the current estimated population size for year-end 2022 outlined in Table 7 in Chapter 4 (see Table 9 below for the modeled initial population sizes we used as input values in our projections).

The initial population size we used in our projections for Michigan does not include the gray wolves on Isle Royale. Therefore, our projections for Michigan exclude the potential of gray wolves on Isle Royale. Michigan DNR does not include these gray wolves in its statewide estimates or as contributing factors to the recovery of gray wolves in the state (see *Methods for Counting and Estimating Annual Population Size in Each State* in Chapter 4 above). The

Service also explicitly excluded the wolves on Isle Royale from any recovery criteria in the Revised Recovery Plan (Service 1992, p. 4), given the population's small size, limited area (210 mi^2 (546 km^2)), frequent fluctuation, and near isolation prevents it from meaningfully contributing to viability of the gray wolf in the Eastern United States. Therefore, in alignment with our past practice and Michigan's Plan, our projection of future population size and assessment of extinction risk in the Western Great Lakes area excludes consideration of any gray wolves on Isle Royale, which could result in a slight underestimate of gray wolf population size in the future.

Estimating Maximum Population Size Parameter (*K*)

We used our density-dependent model to provide individual estimates of *K* for each state (i.e., Michigan, Minnesota, and Wisconsin) from multiple years of population data. As we discuss in greater detail in Chapter 4, each state produces population estimates at different frequencies and provides population data over a slightly different time frame. Therefore, we employed a slightly different process to estimate *K* for each state, using the population data available. We estimated *K* for the gray wolf population in Michigan using all of the states' observed population data, which provided population estimates for year-end 1988 through year-end 2021, respectively; see *Levels of Human-Caused Mortality in the Great Lakes* in Chapter 3 above for explanation of our organization of population and mortality information). Michigan DNR provided estimated gray wolf population sizes annually for year-end 1988 through year-end 2010; after this year-end 2010 estimate, they produced population estimates less frequently, estimating the gray wolf population size for year-end 2012, 2013, 2015, 2017, 2019, and 2021 (see *Methods for Counting and Estimating Annual Population Size in Each State* in Chapter 4 above). Michigan DNR did not provide an estimate of gray wolf populations sizes for year-end 2022, therefore we use the year-end 2021 estimate as it was the best information available when we ran our models.

Starting in 1978, Minnesota DNR provided sporadic (approximately every 10 years) estimates of the number of wolves in the state. Beginning with the year-end 2012 estimate, Minnesota DNR began producing annual gray wolf estimates (see *Methods for Counting and Estimating Annual Population Size in Each State* in Chapter 4 above). Since Minnesota DNR began monitoring gray wolves in 1978, the methodology for estimating wolves has remained largely unchanged (with the exception of how often the state produces an estimate); therefore, we estimate the *K* values for Minnesota using all of the state's population data since 1978.

Finally, for Wisconsin, we used our density-dependent models to estimate *K* using population data Wisconsin DNR provided through year-end 2022. This population data included minimum counts through year-end 2018, and population estimates from a scaled occupancy model for year-end 2019 through year-end 2022 (Stauffer et al. 2021, entire; Johnson 2023, in litt.; (WI DNR 2023c, p. 2 and figure 8) (see *Methods for Counting and Estimating Annual Population Size in Each State* Chapter 4 for details). Comparing gray wolf abundance in Wisconsin between the two methods (minimum counts and occupancy models) would not be appropriate; therefore, we created a "piece-wise" model (McGee and Carleton 1970, entire) and estimated *K* using trends calculated between estimates for year-end 1979 through year-end 2018 and between year-end estimates for 2019 through year-end 2022. This model effectively removes the trend between the counts for year-end 2018 and the estimates for year-end 2019 (when Wisconsin

DNR's estimation methods changed from minimum counts to scaled occupancy modeling) from the overall estimate of *K*.

Estimating the Per-Wolf Effect of Harvest and Lethal Depredation Control Parameter (*h*)

While we estimated a unique starting population size (N_t) distribution and a unique maximum population size (*K*) distribution for each of the three states (i.e., three N_t values/credible intervals and three separate *K* values/credible intervals), we shared population information across all three states using a hierarchical modeling approach (See Supplementary Material A) to estimate a single distribution of the per-wolf effect of harvest and lethal depredation control (*h*), using our density-dependent model, to apply to all three states (i.e., estimating one *h* parameter instead of three separate *h* parameters). We did this to estimate a more robust distribution for *h* that accounted for sparse data from individual states. First, there is a paucity of harvest and lethal depredation control data in Michigan, which complicated the estimation of an informative *h* value specific to Michigan. In Michigan, harvest only occurred in 2013. Zero to 26 wolves have been removed from Michigan's gray wolf population through lethal depredation control between 2003 and 2021. These numbers represent a maximum of 2.5 percent of the population removed through lethal depredation control in Michigan. The rates of lethal depredation control in Michigan and the limited past harvest were not high enough to provide reliable estimates of *h* for the state. Similarly, Wisconsin has only been able to allow harvest and/or lethal depredation control on limited occasions (portions of only 8 years since 2003). Finally, Minnesota only harvested wolves in 3 years (2012 through 2014) and, though lethal depredation control was occurring annually from 2003 to 2022, observed data on effects of harvest are still relatively sparse for the state.

To estimate one distribution for *h* using the data from all three states, we fit the density-dependent model described above to the population data provided by Michigan DNR, Minnesota DNR, and Wisconsin DNR to produce three individual curves fit to the population size (one for each state). We then estimated one overall distribution for *h* that reflected the best fit to these three curves; this one parameter is approximately an average of the separate distributions of *h* from each of the three states. We did this using a hierarchical model (see code Supplemental Material A) in a Bayesian framework, which allows for sharing information. Sharing information across populations represents best practices in statistics when data are too sparse to inform a parameter, as they are in all three states individually (Kindsvater et al. 2018, p. 679). This method allowed us to estimate a more robust distribution of *h* for all three states, meaning that the estimate is more accurate in the face of assumption violations and outliers.

This method of estimating *h* also produced a distribution of *h* that accounts for the possibility of higher per capita effects of harvest should harvest seasons occur during the breeding season (i.e., February) rather than during the non-breeding season (i.e., fall/winter), in any of the three states in the future. Wisconsin harvested gray wolves during the fall and winter in the 2012/2013, 2013/2014, and 2014/2015 harvest seasons. In 2021, a Wisconsin judge ordered Wisconsin DNR to open a gray wolf harvest season, in compliance with state statute, and that harvest season occurred in February of 2021. The timing of this harvest may have had a larger effect per wolf harvested on the overall population dynamics than harvests conducted in the fall, because it occurred during the beginning of the reproductive season and, therefore, could have affected the recruitment of pups (if breeders were harvested). Thus, including population data from Wisconsin from 2021 (when harvest occurred during the breeding season) allows for the potential expansion of the distribution of h for all states to include higher values that represent these potentially higher impacts on gray wolf populations.

Estimating the Intrinsic Rate of Growth Parameter (r_{max})

Similar to the process we used for the estimate of h, we used our density-dependent model to estimate a single distribution for r_{max} using population information from all three states. Unlike Wisconsin and Michigan, gray wolves have continuously occupied Minnesota; thus, we have no past population data reflecting a "recolonization" phase for this state. Therefore, we do not have past population data on growth rates in Minnesota when populations contained fewer than 1,000 wolves (i.e., the past observed minimum population size in the available data for Minnesota); in contrast, in Michigan and Wisconsin, the population data available illustrates the rapid population growth that occurred when the first wolves recolonized these states in the 1980s (Chakrabarti et al. 2022, p. 8). This lack of information regarding population dynamics of smaller populations in Minnesota would have led to underestimates of r_{max} for the state, leading to overly conservative estimates of future growth if the population declines to a small size (i.e., the estimates would be biased towards a lower population projection). For example, if the population size were to be reduced below past observed levels through increased human mortality, disease, or catastrophic events, growth rates could theoretically exceed past observed growth rates in Minnesota, given that growth rates increase as population size decreases in density-dependent populations.

To account for this uncertainty, we chose to estimate r_{max} by sharing information across the three states (i.e., estimating one parameter instead of three separate parameters) to provide a more accurate estimate of maximum growth for the Western Great Lakes. We did this using a hierarchical model (see Supplemental Material A for code) in a Bayesian framework, which allows for sharing information. This method allows us to use information available for all three states and avoids complications associated with estimating r_{max} individually for a state with sparse data. To do this, we fit the density-dependent model described above to the population data provided by Michigan DNR, Minnesota DNR, and Wisconsin DNR to produce three individual curves fit to the population size (one for each state). However, we then estimated one overall parameter for r_{max} that reflected the best fit to these three distribution curves; this one parameter is approximately an average of the separate distributions of r_{max} from each of the three states. Sharing information across populations represents best practices in statistics when data are too sparse to inform a parameter, as it is in Minnesota for $r_{\max}$ (Kindsvater et al. 2018, p. 679). This method allowed us to estimate a more robust distribution of r_{max} for all three states, meaning that the estimate is more accurate in the face of assumption violations and outliers. Further, using a single distribution of r_{max} for the Western Great Lakes metapopulation is consistent with the observations that these wolves are part of a single metapopulation that expanded from Minnesota into Michigan and Wisconsin; in effect, the populations in Michigan and Wisconsin reflect the expanding edge of the Minnesota population (i.e., the rapid growth occurring in Michigan and Wisconsin is a reflection of the growth of the Minnesota population).

Assumptions Regarding Immigration, Emigration, Natural Mortality, and Reproduction

Immigration, emigration, natural mortality, and reproduction are all processes that contribute to estimates of r_{max}. The results of our model selection analyses indicated that these processes were related to population size (i.e., density-dependent models fit better than density-independent models) and, therefore, r_{max} is a function of population size (i.e., it increases at smaller population sizes and reaches zero as the population size approaches a maximum). In our models, the intrinsic rate of growth r_{max} is the only parameter that is directly dependent on population size. Currently, the best available science does not provide evidence for a clear relationship between harvest/lethal depredation control rates and rates of immigration, emigration, natural mortality, or reproduction (the components of the intrinsic growth rate, r_{max}) (see *Effects of Human-Caused Mortality*, Chapter 3). Overall population growth is a function of harvest/lethal depredation control through our estimates of h and the number of animals harvested or removed from the population. The estimates of h are multiplied by the number of wolves harvested or removed through lethal depredation control and subtracted from the overall expected growth of the population (**Equation 1**). However, these estimates of h are not density-dependent (i.e., they do not change as a function of population size). In addition, in our models we did not vary K across time. Uncertainty in all of our parameter estimates (h, r_{max}, and K) was included in the models by using a distribution for the parameter (i.e., 95 percent credible interval around a median) rather than a single median or mean value. See Appendix A "Uncertainty Analyses" for more details regarding the effects of uncertainty on our model results.

Estimated Parameters

In Table 9 below, we summarize the input parameters (i.e., intrinsic rate of growth, effect of harvest and lethal depredation control, maximum population size, and starting population size) we estimated for each state for our forecasting modeling. (See Supplementary Material A for additional technical details on our methods for estimating these parameters).

Table 9. Estimated input parameter values for simulations (i.e., intrinsic rate of growth, effect of harvest and lethal depredation control (the overall effect per harvested/removed gray wolf on population growth), maximum population size, and starting population size).

These parameters were estimated from observed data using a density-dependent model. Please see above for explanation of model parameters and estimation methods. The 95 percent Bayesian credible intervals (CI) reported below represent the interval in which 95 percent of the estimated values fall and within which there is a 95 percent probability that the true value lies (Gelman et al. 2020, Chapter 1).

Entity	Intrinsic Rate of Growth (r_{max}) (95 percent CI)	Per Wolf Effect of Harvest and Lethal Depredation Control (h) (95 percent CI)	Maximum Population Size (K) (95 percent CI)	Starting Population Size (95 percent CI)
Wisconsin	0.25 (0.23 – 0.27) [a]	0.11 (0.02 – 0.21) [a]	929 (901 – 989)	1007 (634– 1,379)
Minnesota			2,751 (2,630 – 2,886)	2,917[b] (2,081 – 3,755)
Michigan			683 (663 – 707)	631 (582 – 680)

[a] Note this estimate is obtained by sharing information across all three states.
[b] Note this value differs slightly from the estimated population provided by the Minnesota DNR for winter 2022/2023 (2,919 wolves). Minnesota DNR does not provide 95 percent confidence intervals (CI)) for its population estimates; therefore, to generate error on the distribution for the purposes of our population projection, we used the estimated population size for end-of-year 2022 from our density-dependent models.

Future Scenarios

We projected the future population size of gray wolves in the Western Great Lakes under multiple future scenarios. Future scenarios allow us to explore a range of possible future conditions for wolves in the Western Great Lakes, given the uncertainty in the stressors they may face, uncertainty in the potential response to those stressors, and the potential for possible conservation efforts to improve future conditions (Smith et al. 2018, p. 306). We developed scenarios to evaluate the potential effects of harvest (see *Mortality Scenarios: Harvest*, below), lethal depredation control (see *Mortality Scenarios: Lethal Depredation Control* below), and disease (see *Disease Scenarios*, below), the three primary stressors that could influence future gray wolf populations in the Western Great Lakes. Our scenarios are meant to encompass the potential range of future conditions the species may experience, given uncertainties in the true magnitude of these stressors in the future; however, the likelihoods of each of these scenarios may differ. Future scenarios are not intended to present an exact illustration of the future, but rather bookends for the range of conditions the species may experience in the future. We illustrate the future scenarios we explored in Figure 15 and explain each further below.

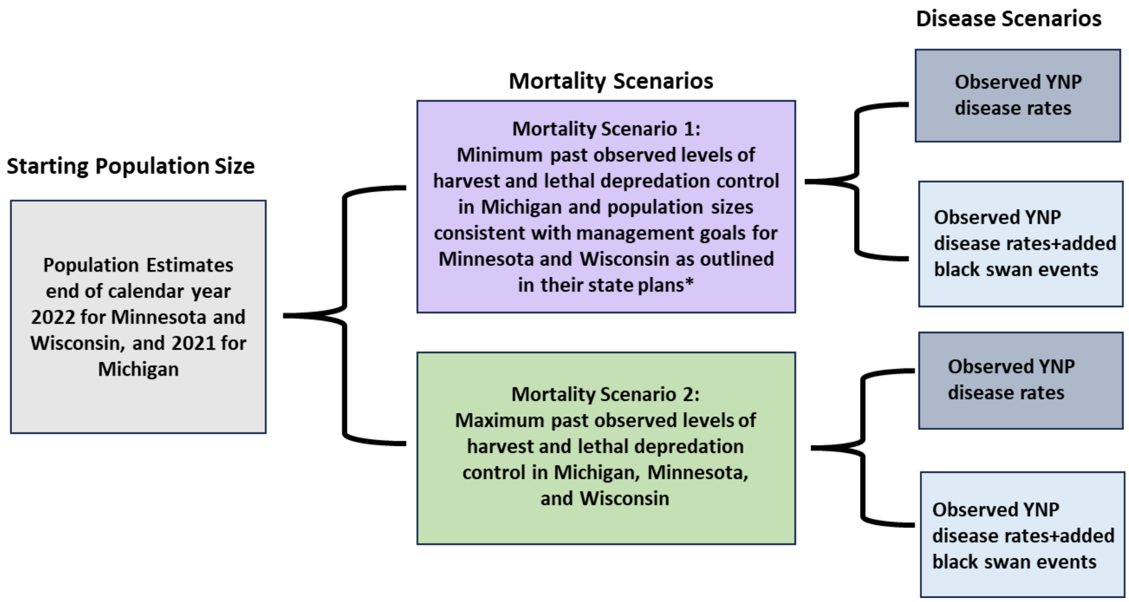

*Figure 15. Schematic of forecasting, including future scenarios for the gray wolf population in the Western Great Lakes (i.e., Michigan, Minnesota, and Wisconsin). See text for description of mortality and disease scenarios. *MN DNR 2022, p. 31; WI DNR 2023a, p. 127*

Disease Scenarios

In our future scenarios, we simulated two levels of disease frequency and severity to explore the potential effects of disease and other catastrophic events on gray wolf population dynamics. There is little data available on the spatial scale of disease events in wolves. In addition, the dynamics are complex and difficult to predict (Brandell et al. 2021b, p. 9). Due to the uncertainties in the spatial scale of disease in gray wolf populations and the fact that we modeled populations at the scale of an entire state, in our projections, these disease events occur at the state level (i.e., affect the population in an entire state). (See Table 12 for a complete list of uncertainties associated with this disease events modeling).

First, we applied the frequency and severity of disease that we have recently observed in a gray wolf population in the Western United States. This first level of disease (i.e., "observed YNP disease rates") was estimated from data on frequency and severity of CDV for wolves in YNP, where three instances of CDV resulting in 20 to 30 percent reductions in the population were observed over 25 years (Brandell et al. 2020, p. 126). Although it is highly suspected that canine parvovirus contributed to wolf declines on Isle Royale between 1980–1982 (Brand et al. 1995, p. 421) and had an effect on the Wisconsin wolf population in 1984–1985 (Wydeven et al. 1995, pp. 155–156; Wydeven et al. 2009a, p. 96), the best available science currently does not provide information regarding the frequency and severity of disease events in gray wolves in the Western Great Lakes. Wydeven et al. 1995 (pp. 155–156) conclude that increases in the wolf population occurred when the prevalence of canine parvovirus was less than 50 percent in the population. However, wolf populations are not routinely screened for parvovirus and therefore we do not know the current or future expectation regarding current or future prevalence of parvovirus in wolf populations. The data provided from Wisconsin span a range of years from 1985–2023 and likely encompasses the expected rate of growth with current frequency and severity of canine parvovirus effects. Therefore, applying a level of disease from YNP in all of our future scenarios for the Western Great Lakes, potentially overestimates the effects of disease on the Western Great Lakes population.

Disease rates and the spatial extent of disease outbreaks are difficult to estimate, and accurate estimates often require intensive monitoring programs (Ryser-Degiorgis 2013, entire). We used disease rates and estimated disease effects from a single disease (i.e., CDV) in the intensively monitored YNP wolf population in our model. However, gray wolves in YNP may have elevated disease exposure and transmission risks compared to other areas because they exist at high densities, which facilitates more pack-to-pack pathogen transmission than may occur in areas with lower wolf densities (Almberg et al. 2012, pp. 2845–2847). Furthermore, the spatial extent of disease events is difficult to predict due to various modes and rates of disease transmission within and between gray wolf packs and the concomitant impact of disease on pack dynamics (see Brandell et al. 2021b, entire). In addition, we lacked data to know the true extent of disease outbreaks beyond YNP (especially in the Western Great Lakes gray wolf population). Therefore, we simulated disease events at the statewide scale because this was the scale of our analysis units. Overall, our parameterization of YNP disease rates is likely conservative (i.e., biased towards a lower population projection) as the only instances of suspected population-level disease effects that have been documented in the Western Great Lakes occurred when wolf numbers were low, with one instance occurring on an island (Brand et al. 1995, p. 421; Wydeven et al. 1995, pp. 155-156; and Wydeven et al. 2009a, p. 96). Additionally, the effects of background disease rates in the Western Great Lakes are captured in our estimates of the intrinsic rate of growth. Thus, the frequency of these disease outbreaks would be much lower and less impactful than the YNP disease rates used in our model.

In half of our future scenarios, we applied a second level of disease (i.e., “added vertebrate black swan events”), which included the effects of high severity, but low probability, disease outbreaks on top of these past observed rates of disease (Anderson et al. 2017, p. 1). Black swan events are statistically improbable events that have potentially severe consequences. The frequency and impact of black swan events is inherently difficult to predict. However, failure to account for them in PVAs can severely underestimate the probabilities of extinction for a species (Anderson et al. 2017, p. 1). These high-severity, but low-probability, events also may become more likely with climate change, which could influence both disease frequency and severity (Munson et al. 2008, p. 5; Gallana et al. 2013, entire; Escobar et al. 2022, p. 8; see *Disease and Parasites in Wolves* and *Climate Change* sections in Chapter 3 above for more information). Therefore, we included the potential of these black swan events in our model in some scenarios to examine the possible effect of severe, but improbable, catastrophic events on the gray wolf’s probability of persistence in the future. However, specific information on the likelihood and effects of black swan disease events in gray wolves is not currently available. Therefore, we used estimates of the frequency and severity of catastrophes from Reed et al. (2003b, p. 110) as a best estimate of black swan disease events in gray wolves in the Western Great Lakes in the future. Estimates of black swan events from Reed et al. (2003b, p. 110) are not specific to the gray wolf, but they were derived from a meta-analysis of a broad range of vertebrate catastrophic events. In our models, the scenarios with “added vertebrate black swan events” included—for each state—a 1 percent chance of a catastrophe resulting in 90 percent mortality of the population and a 3.2 percent chance of a catastrophe resulting in 75 percent mortality of the population every 7 years. These rates were included in addition to the observed YNP disease rates. These rates, impacts, and geographic extent of black swan events may be an over- or underestimate of true catastrophic disease rates in the future, especially because these estimated rates were based on a meta-analysis of multiple vertebrate species and they were not specific to disease or gray wolves (Reed et al. 2003, p. 110). We have not, thus far, observed disease impacts at this catastrophic level we modeled in North American gray wolf populations.

Additionally, disease is the prevailing causal factor of high mortality events in carnivore species (Chapron et al. 2012, p. 14). Therefore, in our analysis, we characterize this "added vertebrate black swan events" scenario as a catastrophic disease event. However, this scenario simply models the effect of infrequent, but high, mortality; should another low-probability event, aside from disease, cause high mortality in the future, the results from this scenario would also demonstrate the effect of this alternative catastrophe, as long as the mortality from that catastrophe does not exceed a 1 percent chance of 90 percent mortality or a 3.2 percent chance of 75 percent mortality every 7 years.

Mortality Scenarios

In addition to varying the level of disease that gray wolves in the Western Great Lakes may experience in the future, we also varied the levels of human-caused mortality in the populations (i.e., regulated harvest and lethal depredation control) to examine a range of potential future effects of this stressor in the future. While gray wolves are currently protected under the Act in Michigan, Minnesota, and Wisconsin, we developed future scenarios that assume a lack of Federal protection. This allowed us to analyze the potential effects of the harvest and lethal depredation control the states discuss in their management plans (mortality that may not be allowed while wolves are federally listed as a threatened or endangered species). This also means our future condition projections reflect the potential future condition of wolves should delisting occur. Below, we describe how we calculated levels of harvest and lethal depredation control in our future scenarios, and then we describe the two future mortality scenarios we constructed.

Harvest

Our future scenarios included variation in harvest rates, which we define as the percent of gray wolves killed through legal hunting and trapping annually (Table 10). We calculated each year's harvest rate by dividing the number of gray wolves harvested by the population count/estimate for the end of the calendar year[21] plus the known number of gray wolves that died from all causes that same year (i.e., this sum in the denominator represents the minimum number of wolves known to be alive at some point during the calendar year) (see detailed explanation of

[21] Note that, for the purposes of our mortality rate calculations, we treated the winter counts/estimates as "end-of-calendar-year" values and assigned them to the earlier of the 2 years in the particular winter or, in the case of Michigan, the end of the prior year. For example, we considered the estimate for the winter of 2012/2013 as the end-of-calendar-year estimate for 2012 because the winter is outside of the breeding season; therefore, any wolves counted in February 2013 were also present at the end of 2012.

these mortality rate calculations in *Levels of Human-Caused Mortality in the Western Great Lakes* in Chapter 3 above).[22] As a result, our calculated harvest rates represent the number of animals harvested out of the minimum known or estimated total number of animals that were available for harvest in that calendar year in a given state.

The Minnesota Plan indicates the state would harvest a relatively consistent proportion of the population (i.e., constant harvest rate), rather than a fixed number of animals. Specifically, in the Minnesota Plan, the Minnesota DNR recommends potential harvest rates, not potential numbers of animals for harvest, that they would consider at particular population sizes in the future (MN DNR 2022, p. 51). Whether wolf harvest is opportunistic or targeted, wolf population reductions would likely result in fewer opportunities to encounter and harvest a wolf, which was demonstrated through a reduction in the number of wolves killed and the number of wolf pelts submitted for bounty payments as wolf abundance declined across the Western United States during the late 1800s and early 1900s (Wiles et al. 2011, pp. 16–18). For example, in British Columbia, Canada, as gray wolf populations began to recover and increased in abundance and distribution across the southern part of the province, the total number of gray wolves harvested increased correspondingly (Mowat et al. 2022, pp. 15–16). We assumed that a similar trend in total harvest would occur if wolf abundance was reduced. Therefore, we chose to model harvest levels as a consistent proportion of the population (i.e., a harvest rate) versus a fixed number of gray wolves removed annually; the best available science discussed above does not indicate that harvesting a fixed number of wolves consistently (especially as population sizes change) is likely.

Based on the best available scientific information in state management plans, in all scenarios, we assumed that legal harvest would cease in each state when gray wolf population sizes were reduced to a specific population size (Minnesota) or state relisting criteria (Michigan and Wisconsin), as described below. In its 1997 plan, which followed Federal recovery criterion, the Michigan DNR committed to a minimum population of 200 gray wolves, a minimum population size to which it recommitted in its updated 2022 plan (MI DNR 1997, p. 17; MI DNR 2022a, pp. 22–23). Therefore, we assumed in all scenarios that legal harvest would cease if the gray wolf population in Michigan was reduced to at or below 200 wolves. In the Minnesota Plan, the Minnesota DNR outlined population sizes where allowable harvest levels would change (MN DNR 2022, p. 51). Specifically, they note that "no harvest" would occur "if the population point estimate is fewer than 1,600 wolves, unless in specified zones as part of an approved research program" (MN DNR 2022, p. 51). In addition, in the Minnesota Plan, the Minnesota DNR commits to a population size of 1,600 gray wolves as the population size at which the state would implement management actions to reverse population declines (MN DNR 2022, pp. 28, 51). Therefore, we assumed in all scenarios that legal harvest would cease if the gray wolf population in Minnesota was reduced to at or below 1,600 wolves. Finally, in Wisconsin, gray wolves would be listed as a state-threatened species if the population size is fewer than 250 gray wolves in the state (WI DNR 2023a, pp. 126–127). Therefore, we assumed in all scenarios that if the gray wolf population size was at or below 250 in the state of Wisconsin, legal harvest would cease in that state.

[22] We calculated the harvest rate as: Harvest Rate = [Total # of Wolves Died From Harvest in 20XX]/[Year-End Population Count/Estimate for the State for 20XX + Total # of Wolves Died From All Known Causes in 20XX].

Lethal Depredation Control

Our models also included the rate of lethal control of depredating gray wolves as an influence on future population size (see **Equation 1** above); we define the rate of lethal depredation control as the percent of gray wolves removed to mitigate conflicts with livestock or pets, annually. We calculated these lethal depredation control rates by dividing the number of gray wolves removed to mitigate conflicts with livestock or pets by the population count/estimate for the end of the calendar year plus the known number of gray wolves that died from all causes that same year (i.e., this sum in the denominator represents the minimum number of wolves known to be alive at some point during the calendar year).[23] Thus, this lethal depredation control rate represents the number of animals removed out of the known, total number of animals that were available for removal in that calendar year. In our calculation of the minimum or maximum past observed lethal depredation control rates in our mortality scenarios, we chose to include only the past observed lethal depredation control rates from years when lethal depredation control was allowable in a particular state during the entire season of May through September, when most lethal depredation control activities take place. We chose to include these years (2003, 2004, 2007, 2008, 2012, 2013, 2014, and 2021) for Michigan and Wisconsin rather than all years, assuming that if wolves were delisted, these years would be representative of future management. For Minnesota, where lethal depredation control has been consistently allowed, we truncated the lethal depredation control rates we evaluated for our calculation of the maximum past lethal depredation control rates to the time period between 2003 and 2021, to match the time period we used for Michigan and Wisconsin. However, Minnesota population counts were sporadic prior to the year-end 2012 estimate (only year-end 2003 and year-end 2007 estimates were provided) and lethal depredation control rates could not be calculated for all other years prior to year-end 2012 when population counts were not provided (year-end 2004, year-end 2005, year-end 2006, year-end 2008, year-end 2009, year-end 2010, and year-end 2011).

Future Mortality Scenarios

Due to many factors that affect hunter/trapper effort and success and future state-level management practices, uncertainty remains as to how states in the Western Great Lakes will manage wolf mortality into the future (i.e., uncertainty remains as to the exact harvest and lethal depredation control rates that will occur in each state in the future). Therefore, we projected future population sizes for these three states (Michigan, Minnesota, and Wisconsin) under multiple different mortality scenarios intended to capture the range of mortality that may occur in the future based on past rates of harvest and lethal depredation control and current management plans; we describe these scenarios in detail below.

The scenarios for the Western Great Lakes were designed to reflect the levels of human-caused mortality we may expect in the future, considering each state's gray wolf management plan (current management plans are discussed in detail in Chapter 3) and past practice (see *State Management* and *Levels of Human-Caused Mortality* in Chapter 3 above). Overall, the plans

[23] We calculated the lethal depredation control rate as: Lethal Depredation Control Rate = [Total # of Wolves Died From Lethal Depredation Control in 20XX]/[Year-End Population Count/Estimate for the State for 20XX + Total # of Wolves Died From All Known Causes in 20XX].

indicate if gray wolves are federally delisted that each state intends to continue managing gray wolf populations similar to or more conservatively than in past years when gray wolves were federally delisted and state regulated harvest and lethal depredation control was allowed in all three states (MI DNR 2022a, entire; MN DNR 2022, entire; and WI DNR 2023a, entire). The Michigan Plan clarifies that the minimum population level of 200 gray wolves is not a target population size and that they plan to manage above that level (MI DNR 2022a, p. 23). The Michigan Plan, however, does not indicate a specific population size they intend to maintain. Further, the Michigan Plan focuses on harvest and lethal depredation control as a management tool to address localized gray wolf-related conflicts (MI DNR 2022a, pp. 28, 70) and only contemplates offering a harvest applied more broadly across the state if the practice is found to be biologically sustainable and socially responsible (MI DNR 2022a, p. 73), an approach that is consistent with past practice. Therefore, we reasonably assume that if gray wolves are federally delisted, the Michigan DNR will continue to manage gray wolves in the state similar to the way they have in the past when gray wolves were federally delisted and state regulated harvest and lethal depredation control was allowed and we rely on these prior mortality rates for our scenarios. The Minnesota Plan and the Wisconsin Plan both specify the number of wolves they intend to maintain in the state (between 2,200 and 3,000 wolves in Minnesota and between 800 and 1,200 wolves in Wisconsin) and they would use adaptive regulated harvest and lethal depredation control rates to maintain these population levels (MN DNR 2023a, pp. 28, 51; WI DNR 2023a, pp. 127-128). Therefore, for one scenario we use these intended population levels to mimic year-to-year changes in population size due to regulated human caused mortality or other intrinsic factors.

In addition to the scenario described above that is consistent with the updated Minnesota and Wisconsin plans, we consider a second scenario that is consistent with past practices and relies on past data from the Western Great Lakes states to inform mortality rates. This scenario reflects the observed harvest and lethal depredation control rates. We do not consider a scenario where Wisconsin, Minnesota, or Michigan increase harvest rates or lethal depredation control rates above those observed in the past (but see Appendix 4) as these states have not expressed an intention to reduce wolf populations from current population sizes. Overall, the updated plans in each state outline a conservative approach to gray wolf management with a focus on maintaining viable gray wolf populations and managing gray wolf-human conflict at a local level.

In Chapter 6 of this SSA Report, we evaluate two scenarios of future harvest and lethal depredation control that reflect the specified population sizes that states intend to maintain as detailed in the most recent wolf management plans from Michigan, Minnesota, and Wisconsin and that capture the range of previously observed rates of harvest and lethal depredation control when gray wolves were delisted in the Western Great Lakes:

- *Mortality Scenario 1*:
    - Michigan: The minimum annual harvest rate observed in Michigan[24] (during years when regulated harvest occurred) and the minimum lethal

[24] Note that for Michigan, harvest occurred in 1 year only; therefore, the maximum and minimum rates of harvest are the same value. Michigan previously chose not to open harvest seasons during years in which the gray wolf was delisted (and, therefore, such harvest would have been legal). Thus, the true minimum harvest rate in Michigan is 0

depredation control rate observed in Michigan during the years 2003, 2004, 2007, 2008, 2012, 2013, 2014, and 2021 (years when lethal depredation control was allowed during the time of year when most lethal depredation control activities occurred).

    - Minnesota: Harvest and lethal control rates are not explicitly modeled (we assume that Minnesota is adaptively managing with human caused mortality to achieve a population size in the range of 2,200–3,000). Therefore, for population sizes above 2,200, we randomly select a population size within the range of 2,200 and 3,000 for the population size the following year. This process represents population changes due to regulated human caused mortality and other intrinsic factors. The population is subject to disease events and if the population falls below 2,200 we assume the state will manage populations to promote growth as stated in its management plan. We further assume this growth occurs at the rate we would expect based on our density dependent model.
    - Wisconsin: Harvest and lethal control rates are not explicitly modeled (we assume that Wisconsin is adaptively managing with human caused mortality to achieve a population size in the range of 800–1,200). Therefore, for population sizes above 800, we randomly select a population size within the range of 800 and 1,200 for the population size the following year. This process represents population changes due to regulated human caused mortality and other intrinsic factors. The population is subject to disease events and if the population falls below 800, we assume the state will manage populations to promote growth as stated in its management plan. We further assume this growth occurs at the rate we would expect based on our density dependent model.
- *Mortality Scenario 2:* the maximum annual harvest rate observed in Michigan, Minnesota, and Wisconsin (during years when regulated harvest occurred); the maximum lethal depredation control rate observed in Michigan and Wisconsin during the years 2003, 2004, 2007, 2008, 2012, 2013, 2014, and 2021 (years when lethal depredation control was allowed during the time of year when most lethal depredation control activities occurred); and the maximum lethal depredation control rate observed in Minnesota between 2003 and 2021 (a time period for which equivalent data were available for other states).[25]

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percent. However, for the purposes of our future scenarios, we chose to assume that regulated harvest occurred in all 100 years of the model simulations, to conservatively explore extinction risk should regulated harvest occur (i.e., under Mortality Scenario 1, we assumed 3.1 percent harvest in Michigan). However, this assumption could bias population projections low.

[25] We recognize that, in past years, both Minnesota and Wisconsin have exceeded the annual harvest quotas established for the season. As we describe in further detail in Chapter 3, unique circumstances may have caused some of these exceedances (e.g., Wisconsin's exceedance of the quota in 2021). Moreover, the harvest seasons in which the states exceeded their harvest quotas did not necessarily represent the maximum harvest rates that occurred in these states (e.g., Wisconsin's harvest rate in 2021 was not the maximum harvest rate that occurred in the past). The harvest rate we used in Mortality Scenario 2 for Minnesota and Wisconsin account for this past exceedance of quotas because we used the observed harvest rates to develop this scenario. In other words, the harvest rates we analyzed to select the maximum past observed harvest rate were the harvest rates that resulted from the actual

We detail the specific harvest and lethal depredation control rates in each state under each of these two mortality scenarios in Table 10 below.

Table 10. Harvest rates (percent of gray wolves killed annually through legal hunting and trapping) and lethal depredation control rates (percent of gray wolves killed annually by the public, state, or Federal agencies in response to depredation events) in each modeled state under the two mortality scenarios we model (Scenarios 1 and 2). In our future scenarios, harvest stops once populations reach a population size of 200, 1,600, or 250 gray wolves, respectively, in Michigan, Minnesota, and Wisconsin; lethal depredation control continues in all states regardless of the population size. Note that, to date, Michigan has only held one harvest season; therefore, minimum and maximum harvest rates in Michigan were the same.

Mortality Scenario	State Harvest Rates					
	Michigan Wolf Population		Minnesota Wolf Population		Wisconsin Wolf Population	
	Fewer than 200	Greater than 200	Fewer than 1,600	Greater than 1,600	Fewer than 250	Greater than 250
Scenario 1	0	3.1	NA	NA	NA	NA
Scenario 2	0	3.1	0	14	0	25

Mortality Scenario	State Lethal Depredation Control Rate		
	Michigan	Minnesota	Wisconsin
Scenario 1	1	NA	NA
Scenario 2	2.5	10	7.2

In our projections, we estimated the future number of gray wolves in each state under four total combinations of future scenarios, spanning two disease scenarios and two mortality scenarios (as depicted in Figure 15 and Table 11, and described in more detail above).

number of wolves harvested (a number of wolves that exceeded the quota), not the rate that would have occurred if the quota was met. Therefore, as long as all states do not consistently exceed the maximum harvest rate they achieved in the past, our models account for the effects of this future harvest rate, even if this future realized harvest rate is above a future annual quota. Moreover, in its new management plan, the Wisconsin DNR recommends potential changes in harvest laws and regulations that could reduce the likelihood of exceeding quotas in the future, such as reducing the mandatory harvest registration time to 8 hours, instead of 24 hours, and issuing gray wolf harvesting licenses such that they are only valid in specific zones (WI DNR 2023a, pp. 144-147) (see *State Management: Wisconsin* above).

Table 11. Four combinations of future scenarios evaluated in future condition modeling.

	Disease Scenario	Mortality Scenario
1	***Observed YNP disease rates***	***Mortality Scenario 1:*** • Minimum past observed harvest and lethal depredation control rates in Michigan (during years when regulated harvest and lethal depredation control occurred) • Population sizes consistent with management goals for Minnesota and Wisconsin as outlined in their state plans (MN DNR 2022, p. 31; WI DNR 2023a, p. 127)
2	***Observed YNP disease rates***	***Mortality Scenario 2:*** • Maximum past observed harvest rates in Michigan, Minnesota, and Wisconsin (during years when regulated harvest occurred) • Maximum past observed lethal depredation control rates (during years when lethal depredation control occurred) in Michigan, Minnesota, and Wisconsin
3	***Observed YNP disease rates + added vertebrate black swan events***	***Mortality Scenario 1:*** • Minimum past observed harvest and lethal depredation control rates in Michigan (during years when regulated harvest occurred) • Population sizes consistent with management goals for Minnesota and Wisconsin as outlined in their state plans (MN DNR 2022, p. 31; WI DNR 2023a, p. 127)
4	***Observed YNP disease rates + added vertebrate black swan events***	***Mortality Scenario 2:*** • Maximum past observed harvest rates in Michigan, Minnesota, and Wisconsin (during years when regulated harvest occurred) • Maximum past observed lethal depredation control rates (during years when lethal depredation control occurred) in Michigan, Minnesota, and Wisconsin

The two mortality scenarios we describe above represent future scenarios that are consistent with state management plans and/or consistent with past observed levels of harvest and lethal depredation control. However, in order to capture a broader range of possible future population sizes and extinction risk, we analyzed one additional mortality scenario (Mortality Scenario X). While this additional mortality scenario is possible, Mortality Scenario X is inconsistent with both the goals of all three states' management plans and past practice in the states. Therefore, we describe Scenario X and provide details of the analysis in an appendix rather than the main body of this SSA (see Appendix 4 for further details).

As harvest and lethal depredation control rates increase, our models assume that, at some point, human-caused mortality from these two sources becomes fully additive as gray wolf populations can no longer partially compensate for these higher levels of mortality. We model the transition from partially compensatory human-caused mortality to fully additive human-caused mortality as occurring at a random value between 20 and 40 percent combined harvest and lethal depredation control each year (Fuller et al. 2003, pp. 182–186; also see Adams et al. 2008, pp. 19–20; see *Effects on Population Growth* in Chapter 3 for more information on this research regarding compensatory versus additive harvest effects). Once this value between 20 and 40 percent is chosen for a particular simulation, any combined harvest and lethal depredation control rate above this value results in wholly additive mortality (i.e., $h = 1$); any combined harvest and lethal depredation control rate below the value is partially compensatory (i.e., subject to the range of h values specified in Table 10 above).

Illegal take and gray wolves removed for health and human safety are not explicitly included in our projections. However, because our projections include estimates of population growth, r_{max}, and the effects of human-caused mortality (i.e., harvest and lethal depredation control), h, as long as future rates of illegal take and gray wolf removal for health and human safety remain consistent with past rates, the effect of those causes of mortality is captured in our estimates of these two parameters.

Timeframe

We modeled the annual size of the gray wolf population in the Western Great Lakes for 100 years into the future, with a starting point in 2022 (i.e., our graphical depictions of projected gray wolf population size illustrate the size of the population for every year between 2022 and 100 years into the future). Also, we specifically report the median population size (and 95 percent credible intervals around this median population size) at 10 years and 100 years into the future. When selecting future timeframes for future condition analysis in SSA reports, we consider the species' life history and demography. In general, longer timeframes are needed for longer-lived species to adequately capture their demographic response to stressors. We also considered the timescale of black swan events (infrequent high severity events) that might severely impact the population. Based on observed disease frequencies in gray wolves and black swan events in vertebrates, we assumed 100 years would be sufficient to capture multiple disease outbreaks; the potential for black swan events; and the impact of these events on the population. Additionally, we assumed 100 years would be sufficient to capture a broad range of variation in the population's response to known stressors over time, including changes in human-caused mortality rates. We also report the population projection results at 10 years in order to capture any near-term changes that may occur in wolf populations in the Western Great Lakes due to disease and human-caused mortality.

Population Thresholds

For each scenario, in addition to projecting the median future population size (and a credible interval around this projection), we also calculated the proportion of simulations that fell below pre-determined thresholds for at least 1 year during the 100-year timeframe. This proportion illustrates the probability that the population will fall below critical thresholds that represent key reductions in viability. In the past, gray wolf populations have rebounded from significant population reductions (e.g., the gray wolf population in the Western United States grew from fewer than 70 individuals to over 2,000 gray wolves; gray wolves recolonized Wisconsin and Michigan, growing from zero resident gray wolves to their current population sizes within 20 to 30 years; also see Harding et al. 2016, Table 2). However, we selected the thresholds below to provide an assessment of the probability the projected population size would consistently remain above estimated population sizes needed to retain genetic health or avoid an elevated risk of extirpation.

We examined the probability of the total gray wolf population in the Western Great Lakes falling below two different thresholds in our analysis of future condition.

1. **Quasi-Extinction (QE) Threshold (five wolves):** QE is defined as a situation when extinction is inevitable despite the fact that individuals may still persist in the population (Legendre et al. 2008, p. 284). PVA practitioners typically do not rely solely on estimates of absolute extinction risk (i.e., population sizes of zero) (Thomas 1990, p. 326; Reed et al. 2002, p. 15). Given that small populations can be disproportionately impacted by demographic or environmental fluctuations (i.e., catastrophic events), or demographic constraints (e.g., changes in sex-ratios) that are often not included in model parameterization, PVA practitioners often consider relative measures of "quasi-extinction" risk more useful (Reed et al. 2002, p. 15). Thus, for PVAs, biologists often select a value above zero against which to compare the projected population sizes to evaluate the risk of QE (Otway et al. 2004, p. 345; Semmens et al. 2016, pp. 2–3). We selected a QE threshold of five gray wolves based on a previous PVA for gray wolves that used five gray wolves as the definition of "biological extinction" (ODFW 2015, p. 15).[26] Also, a population of only five gray wolves has a high likelihood of going extinct due to stochastic events including, but not limited to: reproductive failure, human-caused mortality, disease, catastrophes, genetic factors, or some combination of the above. We evaluated the probability of the gray wolf population in the Western Great Lakes falling below this QE threshold of five gray wolves.

2. **Effective Population Size Threshold (192–417 wolves):** We also evaluated a range of threshold values that represent a potential risk of inbreeding depression. These threshold values are based on the 50/500 rule (Franklin 1980, pp. 138–140), which posits that an "effective" population size of 50 is needed for avoiding deleterious genetic effects (see *Connectivity and Genetic Diversity* in Chapter 2 above). Effective population sizes reflect the number of animals successfully reproducing in a population and they represent one indicator of genetic health. Currently, the best available science does not provide the data necessary to estimate this ratio specifically for Western Great Lakes gray wolves. In the absence of a ratio specific to the Western Great Lakes population, we are able to estimate the average ratio of effective to census population size based on an analysis of Wildlife Genetics International genetic data (WGI 2021, unpublished data). We estimated the average ratio of effective to census population size for Western wolves as

[26] We recognize that based on information in Washington's Wolf Conservation and Management Plan (Wiles et al. 2011, p. 278), Petracca et al. (2025a, p. 5), used a quasi-extinction threshold of up to 92 gray wolves for their analysis of wolf viability in the State of Washington. However, Wiles et al. (2011) defined quasi-extinction differently than the conventional usage of the term in PVAs; rather than the point at which extinction may be inevitable, as we use quasi-extinction above, Wiles et al. (2011), and thus Petracca et al. (2025a), define quasi-extinction as "the probability that the number of female adults and dispersers will fall below the recovery objective level at which relisting [in the state of Washington] would be warranted" (p. 279). Therefore, Petracca et al. (2025a, p. 5) and Wiles et al. (2011, p. 278) do not provide alternative quasi-extinction thresholds for our use in this analysis, given that we are evaluating the probability of dropping below a level at which extinction becomes inevitable, rather than the level that may result in the species' return to state endangered species lists.

approximately 0.17, with a 95% confidence interval between 0.12 and 0.26 (see Appendix 1 for this methodology and effective population size calculations); this means that an effective population size of 50, the rule of thumb for avoiding inbreeding depression, equates to a census population size of between approximately 192 and 417 wolves, based on the 95% confidence interval for the effective to census population size ratio. However, this general rule of thumb assumes populations are isolated. Wolves in the Western Great Lakes, similar to wolves in the Western United States, are well connected to each other and to wolf populations in Eastern Canada. Connectivity is a primary factor in retaining high levels of genetic diversity among wolf populations and in allowing wolves to recolonize suitable habitat that may become vacant due to increased levels of mortality. Even if wolf populations are reduced across much of the Western Great Lakes, sufficient levels of connectivity may allow for lower population levels in some areas than theoretical estimates or general guidelines would recommend (e.g., than the 50/500 rule discussed above; for further information, see *Connectivity and Genetic Diversity* in Chapter 2). Therefore, we consider the use of these threshold values (192 to 417 wolves) to examine the risk of losing genetic diversity and increasing inbreeding depression as a conservative approach that may underestimate viability (see Table 12). Note that for the Wisconsin-Michigan gray wolf population, Stenglein and Van Deelen (2016, p. 8) estimated that a population size of fewer than 20 gray wolves would result in an Allee effect, and decreased ability to find mates. However, our threshold for the evaluation of potential inbreeding depression (192 to 417 wolves), derived from genetic data from Wildlife Genetics International (WGI 2021, unpublished data; see Appendix 1), is considerably higher than this level at which Allee effects could occur. Therefore, if there is a low probability of gray wolves in the Western Great Lakes crossing this effective population size/inbreeding depression threshold (i.e., if there is a low probability of having fewer than 192 to 417 gray wolves), there would be an even lower probability of Allee effects occurring (i.e., of having fewer than 20 wolves).

Our effective population size threshold should not be viewed as a size for a minimum viable population (MVP). An MVP represents the population size at which society would consider the risk of extinction unacceptably high for any smaller population (Shaffer 1981, p. 132) or the smallest population size at which genetic diversity can be retained at an acceptable level to avoid inbreeding and maintain evolutionary potential (Ewens et al. 1987, pp. 60–62; Lande 1988, p. 1458; Frankham et al. 2014, pp. 60–62). The determination of an MVP requires an estimation of extinction risk at different population sizes, and an agreed upon acceptable level of extinction risk. We did not attempt to determine an MVP for the gray wolf in the Western Great Lakes or Eastern United States in this SSA, because MVPs require normative (value-based) decisions around acceptable levels of risk (Flather et al. 2011, p. 314, Frankham et al. 2014, p. 61, Wolf et al. 2015, p. 1-2). Specifically, the level of acceptable risk over a specific timeframe must be defined (i.e. a 5 percent risk of extinction over 20 years or a 10 percent risk of extinction over 30 years) in order to determine an MVP.

Key Uncertainties and Assumptions

Models can benefit decision-making by: explicitly and transparently defining assumptions; evaluating the effects of those assumptions on outcomes; providing a quantitative assessment of uncertainty; and providing an adaptable framework to incorporate new data as it becomes available (Starfield 1997, entire; Addison et al. 2013, entire; Fuller et al. 2020, pp. 37–38). We developed a model to project future population sizes and evaluate the probability of those populations falling below pre-determined thresholds. Following best practices for developing PVAs, we designed our model to evaluate a range of parameter values to explore the impact of parameter uncertainty on relative risk (Beissinger and Westphal 1998, entire). As a result, our model estimates the distribution of gray wolf population size through time, as well as the probabilities of falling below key thresholds for a given combination of parameter estimates. Decision-makers will ultimately need to weigh these estimates, confidence intervals, sensitivity analyses, assumptions, and model limitations, as well as their decision framing, when considering model results.

In our future projections, we captured the effects of three major stressors on gray wolf populations in our models (harvest, lethal depredation control of depredating gray wolves, and disease). Given our uncertainty about future disease and mortality rates, scenarios reflect our best estimates of the potential range of these stressors in the future and their effects on future population sizes. Additionally, our model assumptions were designed to avoid making quantitative predictions for situations where uncertainty was unacceptably high and to increase transparency by explicitly stating our uncertainties (and the strategies we used to address them). However, there are several factors we could not explicitly incorporate in the model that include, but are not limited to, the following:

- changes in the amount of illegal take (however, see description in Table 12 below for how we included current levels of illegal take in our models);
- changes in prey availability or suitable habitat (however, see Chapter 6 for our expectations regarding future habitat and prey availability);
- effects of climate change (however, see Chapter 3 for our discussion regarding climate change and gray wolves);
- small population effects (however, see Chapter 6 for our discussion regarding genetic diversity and connectivity); and
- effects of reduced abundance on genetic health (however, see Chapter 6 for our discussion regarding genetic diversity and connectivity).

Table 12 below further discusses additional uncertainties in our modeling and describes the implications of our assumptions for the model output. Below, we also further discuss several important considerations relevant to interpreting the model's results, given these uncertainties.

Table 12. Summary of Key Uncertainties and Assumptions in Future Condition Modeling

Area of Uncertainty or Assumption	Potential Effect on Model's Projection of Abundance
Choice of thresholds There is no widely accepted, established quasi-extinction threshold for gray wolves. Therefore, we chose five gray wolves based on the best available science because this was a threshold that researchers previously used in a PVA (ODFW 2015, p. 15).	Model projections will ***overestimate*** viability (underestimate risk of quasi-extinction) if population sizes larger than five are needed to maintain population viability. Model projections will ***underestimate*** viability (overestimate risk of quasi-extinction) if populations always rebound after falling below this threshold with no deleterious consequences.
Effects of harvest and lethal depredation control • **Additive versus compensatory:** The effect of human-caused mortality is much debated for wolves. Therefore, we estimated the additive versus compensatory effect of harvest and lethal depredation control (*h*) directly from observed data, so that this effect in our model could be specific to observed dynamics in the Western Great Lakes area. However, if harvest and/or lethal depredation control rates increase outside of the past observed range (as we model for all states under Mortality Scenario X in Appendix 4), we do not know if the value of *h* could be outside of the range estimated from past observed data. Therefore, based on the best available science regarding additive effects of wolf harvest and lethal depredation control, our model assumes that at a combined harvest and lethal depredation control rate between 20 and 40 percent, harvest and lethal depredation control become completely additive (i.e., we apply an estimate of *h* outside of the range observed in the past (a completely additive value for *h*), at combined harvest and lethal depredation control rates between 20 and 40 percent, based on the best available science regarding the effects of human-caused mortality). • **Density-independence of *h*:** Further we assumed that *h* is density independent in our models (i.e., the per wolf effect of harvest and lethal depredation control is the same at all population sizes). Best available science does not inform the relationship between *h* and population size, and this relationship is likely complex and potentially population specific. Previous researchers have modeled the per wolf effect of harvest and lethal depredation control as a constant value (ODFW 2015, p. 14, Petracca et al. 2025a, p. 7). • **Estimates of current harvest:** We estimated current harvest as a proportion of the population size available for harvest (i.e., winter population estimates plus known mortalities from that year, including mortalities from harvest and control)	If human-caused mortality from harvest and lethal depredation control becomes additive at a combined harvest and lethal depredation control rate lower than 20 percent, population projections for the Western Great Lakes may be ***overestimates***; future population projections may be ***underestimates*** if human-caused mortality from harvest and lethal depredation control becomes additive at a combined harvest and lethal depredation control rate greater than 40 percent. If the effects of harvest and lethal depredation control are density dependent (greater at small population sizes and smaller at large populations) our estimates of the harvest rates needed to reduce the population sizes to 150 would be underestimates (i.e., our estimates of the effect of harvest on large populations would be overestimates). If the effects of harvest and lethal depredation control are density dependent, our population estimates could be ***overestimates*** (for example, in Harvest Scenario 3) or ***underestimates*** (for example, in Harvest Scenario 1) depending on the strength of the density dependent effects of *h*, and the harvest scenario.

Area of Uncertainty or Assumption	Potential Effect on Model's Projection of Abundance
rather than a fixed number of animals. We estimated harvest in this way because past evidence has shown that, if wolf abundance begins to decline, harvesting a consistent number of gray wolves becomes more difficult due to access, changes in gray wolf behavior, and fewer opportunities to encounter gray wolves.	If states are able to sustain harvest as a fixed number of gray wolves over time (rather than a constant proportion), our model projections will be ***overestimates*** of abundance.
Future management of populations	
• **Future harvest and lethal depredation control rates:** Uncertainty remains regarding the exact harvest or lethal depredation control rates each state will achieve in the future. Future harvest or lethal depredation control rates could be lower than past minimum rates or higher than past maximum rates. Specifically, to date, Michigan has held one harvest season; therefore, minimum and maximum past observed harvest rates in Michigan were the same in our future scenarios. Therefore, if gray wolves were to be delisted, the best available science does not indicate the harvest rate Michigan may achieve (i.e., future minimum and maximum harvest rates could be above or below the harvest rates observed during the 2013 season). In Appendix 4, we explore the potential effect of increased rates of harvest for all three states (above past observed rates), though this scenario is inconsistent with state management plans and past practice. Moreover, we excluded any years with no harvest from our identification of minimum and maximum harvest rates for Michigan, even though there were years in which the Michigan DNR chose not to open a harvest season when it otherwise would have been legal. This means that the true minimum harvest rate in Michigan is 0 percent (from the years in which regulated harvest did not occur). There were also years in which the Minnesota DNR previously chose not to open a harvest season when the gray wolf was delisted (and, therefore, such harvest would have been legal). In our scenario 2, we chose to assume that regulated harvest occurred in all three states in all 100 years of the model simulations at the maximum rates observed in the past, to conservatively explore extinction risk should regulated harvest occur annually. However, this assumption could bias population projections low. Additionally, there will likely be spatial variation in the application of harvest rates across each state (i.e., differences in harvest rates for different harvest zones in each state) resulting in spatial dynamics that our model does not replicate.	Model projections from Mortality Scenarios 1 and 2 could be ***overestimates*** or ***underestimates*** of abundance if future harvest or lethal depredation control rates are above or below past observed minimum and maximum rates or above or below the adaptive harvest rates Minnesota DNR proposes in its management plan. However, our projections in Appendix 4 illustrate the potential effect of harvest and lethal depredation control rates above past observed rates.
• **Management of reduced populations:** We assume that Michigan, Minnesota, and Wisconsin DNRs will stop all legal harvest when 200, 1,600, or 250 gray wolves are documented in their respective state, but lethal depredation control will continue. However, Michigan, Minnesota, and Wisconsin DNRs may use its regulatory authorities to adjust	Model projections will be ***underestimates*** for Michigan, Minnesota, and Wisconsin if these states stop harvest/control when there are more than 200, 1,600, or 250 gray wolves in each state, respectively.

Area of Uncertainty or Assumption	Potential Effect on Model's Projection of Abundance
gray wolf harvest opportunities to ensure gray wolf abundance remains considerably above these levels. • **Association of lethal depredation control and harvest:** Research is inconclusive as to whether control activities increase or decrease as harvest increases (see discussion of lethal depredation control in Chapter 3). In Mortality Scenarios 1, we vary lethal depredation control, using the past observed minimum rate for Michigan, and in Mortality Scenario 2 we use the past maximum rate for all states. However, we pair the minimum past observed lethal depredation control rate with the minimum past observed harvest rate for Michigan in Scenario 1, and the maximum observed lethal depredation control, and maximum past observed harvest rate for all states in Mortality Scenario 2. In general, in all of our future scenarios, we assume there is no relationship between harvest and lethal depredation control. Nevertheless, if lethal depredation control were to increase as harvest decreases, our scenarios would still represent the potential effects to the population, as long as the actual combined mortality rate from harvest and lethal depredation control does not exceed the sum of the harvest and lethal depredation control rates we analyzed in Mortality Scenario 2 or Mortality Scenario X.	Model projections could be ***overestimates*** if the combined mortality rate from harvest and lethal depredation control in the future exceeds the sum of lethal depredation control and harvest rates we analyzed in Mortality Scenario 2 or Mortality Scenario X. On the other hand, model projections could be ***underestimates*** if the combined mortality rate from harvest and lethal depredation control in the future is lower than the sum of lethal depredation control and harvest rates we analyzed in Mortality Scenario 1.
Illegal take and wolf removals for health and human safety Current levels of illegal take and gray wolf removal for health and human safety are a component of the intrinsic rate of growth (r_{max}) and the estimated effect of harvest and lethal depredation control (h) used in the model; we are assuming that current rates of illegal take and gray wolf removal for health and human safety stay the same into the future under every scenario.	Model projections will ***overestimate*** the future size of gray wolf populations if rates of illegal take and gray wolf removal for health and human safety were to increase in the future and ***underestimate*** future population size if rates of illegal take and gray wolf removal for health and human safety were to decline.
Frequency, severity, and scope of future disease events • **Observed Disease Rate Scenarios:** We use the observed rates (frequency and impact) of canine distemper virus outbreaks in YNP (the disease with the most acute impact on the gray wolf population in YNP) as the future rate of disease in gray wolf populations in every Western Great Lakes state in our model because this is the only area within the United States where we had data on disease frequency and impact on gray wolves over an extended monitoring period. It is probable that disease incidence is higher in YNP than in other parts of the range due to relatively high gray wolf population density in YNP, which can increase disease transmission. • **Added Vertebrate Black Swan Events:** There is little data on infrequent, unlikely catastrophic events in large vertebrates. Therefore, we used Reed et al.'s (2003b, pp. 111–112) generalized estimates of the frequency and effect of catastrophes in over 100 vertebrate species as the best available estimate for the frequency and effect of these high-severity but low-probability events in wolves. We have not,	Model projections could ***underestimate*** the gray wolf population by overestimating the effects and scale of disease and catastrophes. They could ***overestimate*** the gray wolf population if a novel disease outbreak causes impacts not previously observed in wolves in the Western Great Lakes or if the actual frequency or impact of black swan events is higher than the vertebrate averages we used.

Area of Uncertainty or Assumption	Potential Effect on Model's Projection of Abundance
thus far, observed disease impacts at the catastrophic level we modeled in North American gray wolf populations. • **Scale of Disease Events:** Estimating the scale of disease events in gray wolves would have required a spatially explicit model that accounted for different modes of disease transmission, different disease transmission rates, and pack dynamics (see Brandell et al. 2021b, pp. 2–5). The best available science on gray wolf distribution did not allow us to construct a model with individual pack dynamics. Therefore, we applied the disease events at the scale of our analysis units (i.e., at the statewide scale); in other words, in a year when a disease event occurred, it affected all of the gray wolves in an entire state.	
Uncertainty in future r_{max}, h, and K values We estimated our parameters *of* r_{max}, *h*, and *K* from observed data provided by the states. Our model assumes that the future values of these parameters will be derived from the distribution of past observations. It is possible that, due to environmental changes such as climate change, shifts in human distributions, or changes to prey dynamics, the intrinsic rates of growth or carrying capacity may change in the future in an unpredictable way not aligned with past estimates.	Model projections will potentially ***overestimate*** population sizes if conditions become less favorable to growth or ***underestimate*** population sizes if conditions become more favorable to growth.
Uncertainty in estimation of model parameters To account for the sparse information on past harvest or lethal depredation control in all three states (especially Michigan), we chose to estimate one distribution of *h* for Michigan, Minnesota, and Wisconsin combined by sharing information across the three states (i.e., estimating one parameter instead of three separate parameters). This method allowed us to estimate a more robust distribution of *h* for all three states, meaning that the estimate is more accurate in the face of assumption violations and outliers.	Model projections will potentially ***underestimate*** or ***overestimate*** future population size if the *h* value differs in each state.
This method of estimating *h* also produced a distribution of *h* that accounts for the possibility of higher per capita effects of harvest should harvest seasons occur during the breeding season (i.e., February/March) rather than during the non-breeding season (i.e., fall/winter) in any of the three states in the future. Hunts that occur in February/March (e.g., Wisconsin's 2021 hunt) may have a larger effect per wolf harvested on the overall population dynamics than hunts conducted in the fall, because they occur during the beginning of the reproductive season and, therefore, could affect the recruitment of pups (if breeders are harvested). Thus, including population data from Wisconsin from year-end 2021 in our estimation of *h* allows for the potential expansion of the distribution of *h* for all states to include higher values that represent these potentially higher impacts on wolf populations. We also used our density-dependent model to estimate a single distribution for r_{max} using population information from all three states. Unlike Wisconsin and Michigan, gray wolves have continuously	Model projections will potentially ***underestimate*** future population size if no state pursues a breeding season hunt in the future, given an estimated *h* value distribution that may overestimate the effect of harvest and lethal depredation control for non-breeding season harvests (*h*).

Area of Uncertainty or Assumption	Potential Effect on Model's Projection of Abundance
occupied Minnesota; thus, we have no past population data reflecting a "recolonization" phase for this state. Therefore, we do not have past population data on growth rates in Minnesota when populations contained fewer than 1,000 wolves (i.e., the past observed minimum population size in the available data for Minnesota). This lack of information regarding population dynamics of smaller populations in Minnesota would have led to underestimates of r_{max} for the state, leading to overly conservative estimates of future growth at small population sizes. For example, if the population size were to be reduced below past observed levels through increased human mortality, disease, or catastrophic events, growth rates could theoretically exceed past observed growth rates, given that growth rates increase as population size decreases in density-dependent populations. To account for this uncertainty, we chose to estimate r_{max} by sharing information across the three states (i.e., estimating one parameter instead of three separate parameters) to provide a more accurate estimate of maximum growth for the Western Great Lakes.	Model projections will potentially ***underestimate*** or ***overestimate*** future population size if the r_{max} differs in each state.
Small population effects We do not explicitly incorporate the effects of small populations such as genetic effects (inbreeding) or loss of connectivity (decreases in immigration or emigration). We evaluate the potential of these effects when we assess the probability of crossing the threshold of 192 to 417 wolves (an effective population size of 50), a threshold we developed after conducting a thorough review of the best available science on this issue (see Appendix 1). These results, however, are specific to the Western wolf populations and the effective population size estimates may be different for the Midwestern populations. Our density dependence assumption (based on best available science) results in an increased ability of small populations to rebound. Small population dynamics are often more unpredictable due to stochastic events, loss of connectivity, and deleterious genetic effects. Therefore, our model predictions, despite using the best available science, may be overestimates at these population sizes. We further discuss these effects qualitatively in Chapter 6.	Model projections could ***overestimate*** gray wolf abundance if deleterious effects of small populations (e.g., loss of genetic diversity and inbreeding depression) occur at population sizes greater than 417 gray wolves or if our model simulations fail to capture the dynamics of small gray wolf populations. Model projections will ***underestimate*** viability if population sizes smaller than 192 wolves are adequate to avoid inbreeding depression in the Western United States, especially given the metapopulation's lack of isolation.
Changes in connectivity and genetic diversity • Connectivity of populations is an important factor in the evaluation of extinction risk, and the best available science is inconclusive regarding how changes in gray wolf population size and distribution may affect connectivity. The r_{max} values in our model include and reflect immigration and emigration (i.e., connectivity) out of and into each state in the model. Given that the best available science is inconclusive regarding the quantitative effect of increased harvest on future dispersal rates, we assume that connectivity in populations reduced by harvest will be similar to the level of connectivity in populations of the same (smaller) size during the early years of recolonization (i.e., we assume that harvest does not affect connectivity in ways dissimilar to effects of other reductions in population size). We discuss this research on dispersal and connectivity, and its implications for the	Model projections will ***overestimate*** abundance if connectivity is lower in populations reduced by harvest than in small populations.

Area of Uncertainty or Assumption	Potential Effect on Model's Projection of Abundance
future viability of wolves in the Western Great Lakes, in greater detail in Chapter 6. • We do not explicitly model genetic composition of gray wolves in the Western Great Lakes, or how this genetic composition could change in the future. Explicit modeling of genetic composition would allow us to potentially estimate a minimum population size required to avoid deleterious genetic effects of small populations. However, data is not currently available that would allow us to parameterize a model of gray wolf genetics on the landscape scale. Instead, we use a threshold value determined by a literature review to reflect the minimum population size required to avoid deleterious genetic effects of small populations.	Model projections will ***underestimate*** risk of extinction if deleterious genetic effects are experienced by gray wolf populations at sizes >417 wolves.
Monitoring and population estimate accuracy Based on current methodologies and commitments in management plans, we assumed states will continue to accurately estimate populations and evaluate trends over time so appropriate regulatory adjustments may be implemented. Specifically, we assumed that Michigan, Minnesota, and Wisconsin DNRs would close all harvest seasons when 200, 1,600, or 250 gray wolves remained in their respective states, which is contingent on accurate estimates of population size and accurate monitoring of harvested gray wolves.	Model projections of abundance will be ***overestimates*** or ***underestimates*** if states are unable to accurately estimate population sizes in the future or if current estimates are inaccurate.
Wolf population dynamics on Isle Royale In alignment with our past practice and Michigan's management plan, our projection of future population size and assessment of extinction risk in the Western Great Lakes area excludes consideration of any gray wolves on Isle Royale, given that the population's small size, limited area (210 mi^2 (546 km^2)), frequent fluctuation, and near isolation prevents it from meaningfully contributing to the viability of the Western Great Lakes metapopulation.	Model projections will ***underestimate*** total population sizes in the Western Great Lakes area, if gray wolves occur on Isle Royale in the future.

Chapter 6: Future Condition

In this chapter, we discuss the future viability of gray wolves in the Eastern United States. As described in Chapter 5, we used simulation modeling and scenario analysis to project the future population size of gray wolves in the Western Great Lakes under various rates of harvest, lethal depredation control, and disease. This approach allowed us to quantify the range of effects of these stressors on gray wolf abundance in this portion of the Eastern United States over time. Our model results characterize the ability of gray wolves to withstand stochastic variation in demographic parameters, increased human-caused mortality, and catastrophic events (resiliency and redundancy) within the portion of our analysis area that contains an extant population of gray wolves (i.e., the Western Great Lakes).

In the unoccupied portions of our analysis area, we qualitatively describe future expectations for gray wolf occupancy. We also qualitatively discuss future expectations for suitable habitat and prey availability in the Eastern United States, as these factors were not explicitly included in our models because we lacked readily available quantitative projections of these variables into the future. Finally, we discuss factors that influence future gray wolf genetic health and adaptive capacity, which contribute to resiliency and representation.

Future Resiliency and Redundancy

Interpreting Forecasting Results

We generated two million projections (based on the 200,000 iterations from the Bayesian models run 10 times) of the median future population size and 95 percent credible interval for the total gray wolf population size in the western Great Lakes (Chen and Shao 1999, entire) for each scenario (see example in Figure 16 and Supplementary Materials A and B for technical details on these projections). Median values represent the value for which 50 percent of the projected estimates are above and 50 percent of the projected estimates are below. We developed our models in a Bayesian framework and, therefore, report credible intervals rather than confidence intervals (Gelman et al. 2020, Chapter 2). A 95 percent credible interval represents the interval in which there is a 95 percent probability that the true value lies. The lower 95 percent credible interval represents the value below which 2.5 percent of the projected estimates from the model lie (and 97.5 percent of the projected estimates are above). The upper 95 percent credible interval represents the value above which 2.5 percent of the projected estimates lie (and 97.5 percent of the projections estimates are below).

We used figures to depict the projected gray wolf population size over a 100-year timeframe for the two different harvest scenarios and two different disease scenarios, as described in Chapter 5. For each figure, we included a gray box representing the range of threshold values for an effective population size of 50 (192 to 417 wolves). See Figure 16 below for an example.

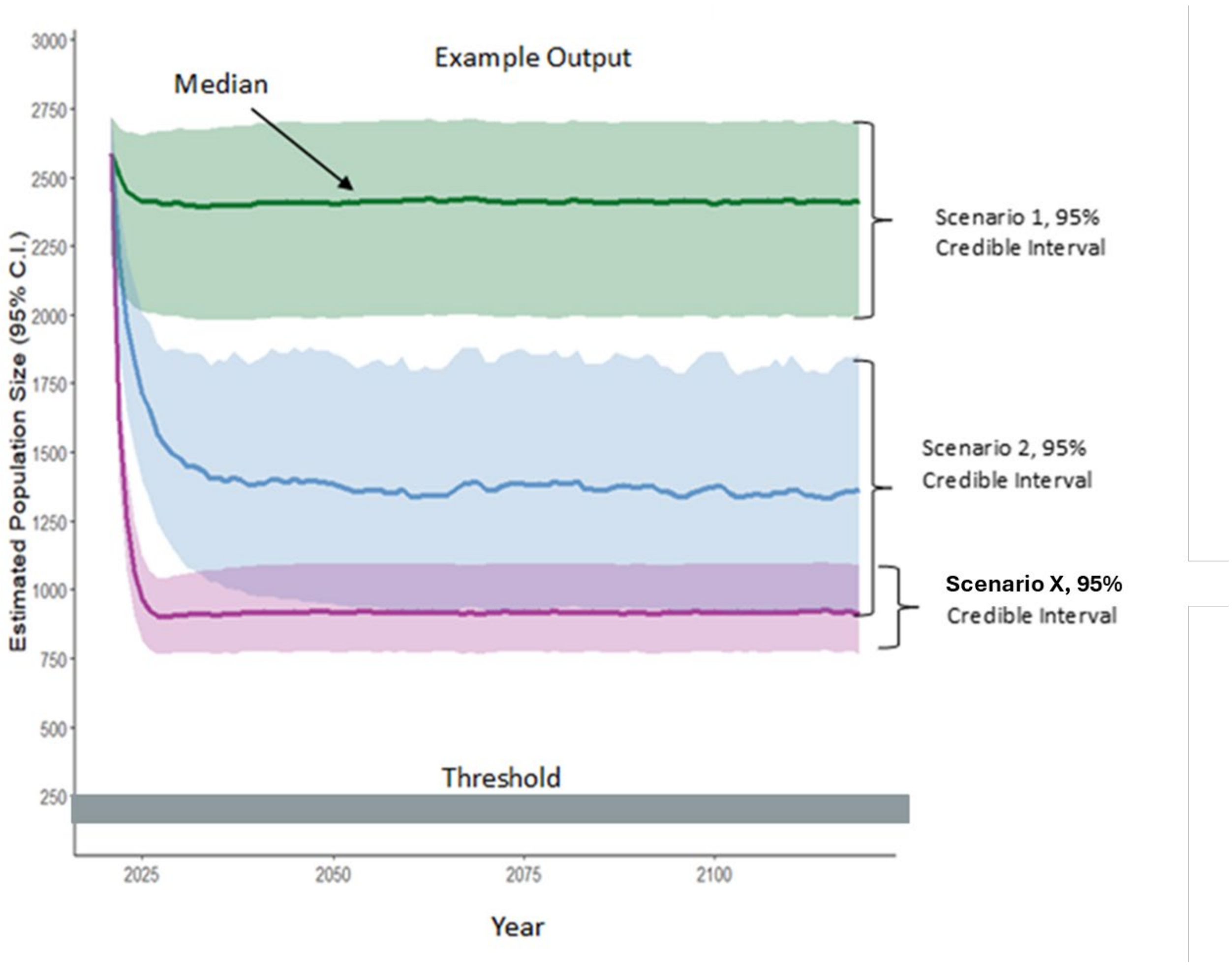

Figure 16. Example output graph depicting the median (line) and 95% credible intervals (shaded area) for three different scenarios (green, blue, and pink); gray bar represents the range of threshold values for demonstration purposes.

In the text, we report the median and upper and lower credible intervals of the estimated population size at 10 years and 100 years for only two of our four future scenario combinations we analyze in this chapter; namely, we report these values in the text for the combination of mortality scenarios and disease that results in the largest number of gray wolves (Mortality Scenario 1 combined with the observed YNP rates of disease) as well as the combination of mortality scenarios and disease that results in the smallest number of gray wolves (Mortality Scenario 2 combined with black swan levels of disease).[27] Results from the remaining two harvest and disease scenario combinations fall in between these values and they are reported in corresponding tables. Finally, we calculated the percent change between the starting population size and the projected population size at 10 years and between the starting population size and the projected population size at 100 years for each of the simulations for each scenario. We subtracted the starting population from the ending population size and divided by the starting population size for each simulation to get a distribution of percent change for all of our

[27] Note that the additional mortality scenario we analyze in Appendix 4 results in a lower population projection than Mortality Scenario 2 combined with black swan levels of disease. We report the results from this scenario, which is inconsistent with state management plans and past practice, in Appendix 4.

simulations; we report the median and the 95 percent credible interval of this distribution as the percent change from the starting population size in our tables below.

In addition to reporting median estimates and 95 percent credible intervals of projected abundance, we evaluate the number of simulations out of 2 million in which the projected population size fell below specific thresholds during a specified timeframe (i.e., below our QE threshold of 5 wolves or below our effective population size threshold of 192 to 417 gray wolves). To estimate a probability of falling below each of these thresholds, we simply divided the number of projected populations that crossed the threshold at least once during the specified timeframe by the total number of projected populations (from 2 million simulations).

Results of Forecasting Model: Resiliency and Redundancy in Michigan, Minnesota, and Wisconsin

In this section, we report the results of our model projections for the Western Great Lakes area (i.e., the total number of gray wolves in Michigan, Minnesota, and Wisconsin), though we modeled the population in each of these states separately. All reported results and our interpretation of these results are based on the assumptions we detailed in Table 12 in Chapter 5. The median estimated starting population size for this area was 4,557 gray wolves for the end-of-calendar year 2022. In Appendix 5, we detail the projected population size (median and 95 percent credible intervals) in each individual state we modeled (i.e., Michigan, Minnesota, and Wisconsin).

No individual projected Western Great Lakes area population (out of 2 million total projections for each scenario) fell below our lower threshold for an effective population size of 50 (192 wolves) or our QE threshold (5 wolves) at any time over our 100-year projection under any of the scenarios we analyzed, given the assumptions in our model (Figure 17). For Mortality Scenario 1 with added black swan events, 0.002 percent of 2 million simulations fell below our upper threshold for an effective population size of 50 (417 wolves), and for Mortality Scenario 2 with added black swan events, 0.02 percent of simulation fell below this threshold.

We report the projected median population size and 95 percent credible intervals for the Western Great Lakes area (i.e., the total population of gray wolves in Michigan, Minnesota, and Wisconsin) under each of our four future scenario combinations at 10 years and 100 years in Table 13. Overall, projections for 10 years into the future are similar to or slightly higher than projections for 100 years into the future. In Mortality Scenario 1 with observed YNP disease rates (the least impactful scenario combination we analyzed), the projected median population size for the Western Great Lakes area in 100 years was 3,858 gray wolves [95% Credible Interval 2,889–4,598] (Figure 17, Table 13b). This represented a median decline of 16 percent [95% Credible Interval 40 percent decline to 13 percent increase] in the future population size from the estimated starting population size in the Western Great Lakes area of 4,557 (95% Credible Interval 3,639–5475). In Mortality Scenario 2 with added black swan events (the most impactful scenario combination we analyzed in this chapter), the median population size in the Western Great Lakes at 100 years was 2,686 wolves [95% Credible Interval 1,479–3,415] (Figure 17, Table 13b), which was a median decline of 41 percent [95% credible interval 18–68 percent decline] from the starting population size in this area. In Mortality Scenarios 1 and 2, the vast majority of the population decline took place in the first 15-20 years of the simulation, regardless of the disease scenario (see Figure 17).

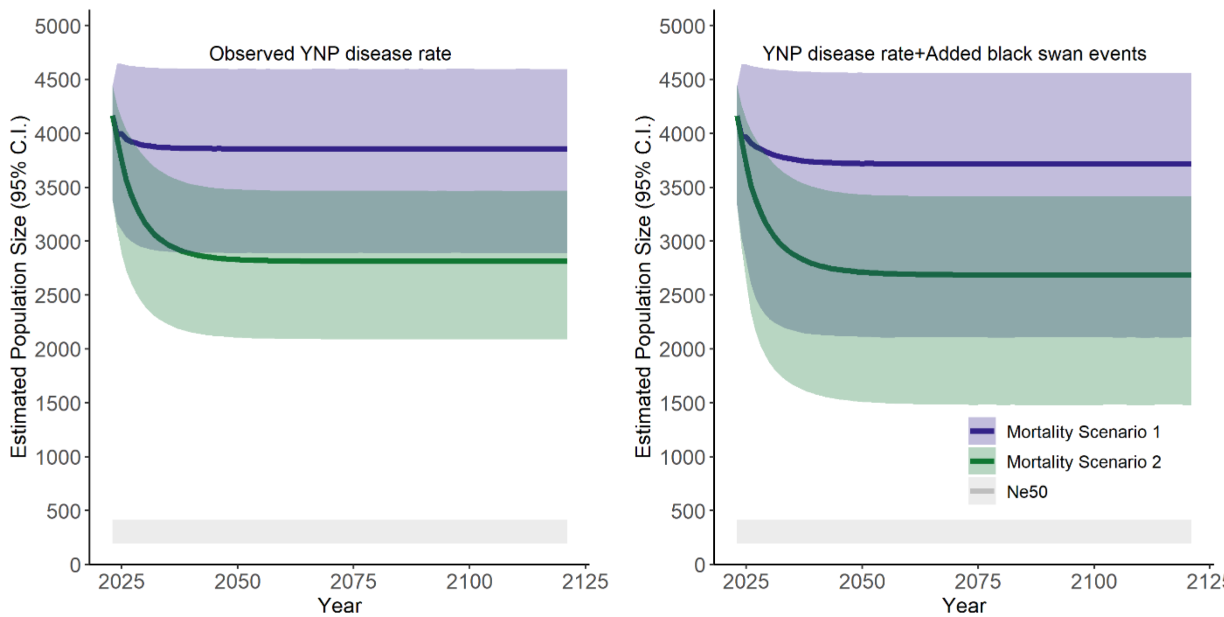

Figure 17. Simulated median gray wolf population size (solid line) and 95 percent credible interval (shaded area) in the Western Great Lakes population (Michigan, Minnesota, and Wisconsin, combined) with Mortality Scenario 1 in purple and Mortality Scenario 2 in green. The panel on the left includes the results for the two mortality scenarios combined with Observed YNP disease rates. The panel on the right includes the results for the two mortality scenarios combined with Observed YNP disease rates plus added black swan events. The gray bar represents the estimated census population size that is equivalent to N_e*50-an effective population size of 50 (the threshold for avoiding inbreeding depression, 192-417 wolves).*

Table 13. a) Median, and lower- and upper-95 percent credible interval (CI) for projected population size and the percent change in the population size relative to the starting population size in the Western Great Lakes population (Michigan, Minnesota, and Wisconsin, combined) at the end of the 10-year timeframe of our simulations in all four future harvest and disease scenario combinations. b) Median, and lower- and upper-95 percent credible interval (CI) for projected population size and the percent change in the population size relative to the starting population size in the Western Great Lakes (Michigan, Minnesota, and Wisconsin, combined) at the end of the 100-year timeframe of our simulations in all four future harvest and disease scenario combinations. Percent of simulations falling below a particular threshold represents the percent of 2 million simulations where the population size fell below 192 or 417 at least once over the 100-year timeframe.

a) Projected gray wolf population size 10 years into the future

Mortality	Disease	Median Population Size at 10 Years	Percent Change from Starting Population Size
Mortality Scenario 1	**Observed YNP Disease Rates**	3,878 (95% C.I. 2,918 – 4,609)	-15 (95% C.I. -39 – 14)
Mortality Scenario 2	**Observed YNP Disease Rates**	3,067 (95% C.I. 2,308 – 3,693)	-33 (95% C.I. -52 – -9)
Mortality Scenario 1	**YNP Disease Rates + Added Black Swan Events**	3,787 (95% C.I. 2,223 – 4,588)	-17 (95% C.I. -52 – 12)
Mortality Scenario 2	**YNP Disease Rates + Added Black Swan Events**	2,994 (95% C.I. 1,767– 3,3676)	-34 (95% C.I. -62– -10)

b) Projected gray wolf population size 100 years into the future

Mortality	Disease	Median Population Size at 100 Years	Percent Change from Starting Population Size	Percent of simulations falling below 192 wolves	Percent of simulations falling below 417 wolves
Mortality Scenario 1	**Observed YNP Disease Rates**	3,858 (95% C.I. 2,889 – 4,598)	-16 (95% C.I. -40 to 13)	0.000	0.00
Mortality Scenario 2	**Observed YNP Disease Rates**	2,815 (95% C.I. 2,088 – 3,466)	-38 (95% C.I. -56 to -16)	0.000	0.00
Mortality Scenario 1	**YNP Disease Rates + Added Black Swan Events**	3,717 (95% C.I. 2,108 – 4,562)	-19 (95% C.I. -54 to 11)	0.000	0.002
Mortality Scenario 2	**YNP Disease Rates + Added Black Swan Events**	2,686 (95% C.I. 1,479 – 3,415)	-41 (95% C.I. -68 to -18)	0.000	0.020

Models used for Scenario 1 in Michigan, and Scenario 2 in Michigan, Wisconsin and Minnesota are mathematical models of population dynamics, therefore projections eventually either reach the maximum population size (*K*) or reach an equilibrium point when growth is equal to mortality (both natural and human-caused mortality). This is because, as with all populations experiencing density-dependent growth, reproductive rates increase as population size decreases. Further, in our simulations in Mortality Scenario 1 for Michigan, and Mortality Scenario 2 for all three states, because we modeled harvest and lethal depredation control as a constant proportion of the population, as the population declines, the actual number of gray wolves removed through harvest or lethal depredation control decreases. Therefore, at some point in Mortality Scenario 1 for Michigan and Mortality Scenario 2 for all three states, as the number of gray wolves added to the population increases (due to increasing intrinsic rates of growth) and the number removed decreases (due to declining population size and/or declining harvest rates), the number of gray wolves removed from the population due to mortality will be the same as the number of gray wolves added to the population due to reproduction and immigration (i.e., the population reaches an equilibrium point).[28] If harvest was sufficiently high or if growth rates were low, this equilibrium point could be a population size of zero gray wolves. However, in the case of gray wolves in the Western Great Lakes, growth equilibrates with mortality at population sizes greater than zero under all the mortality rates we analyzed in our future scenarios. While the projections from our model do reach an equilibrium population size, our models still included stochasticity; therefore, the projected population size bounces slightly above and below this equilibrium point over time. Stochasticity is included in our models through catastrophic disease events and random selection of the combined harvest and lethal depredation control rate at which harvest and lethal depredation control become fully additive (i.e., a randomly selected value between 20 and 40 percent combined harvest and lethal depredation control).

Our model projections demonstrate that even with disease, maximum past observed harvest and lethal depredation control rates occurring together every year for the next 100 years in Michigan, Minnesota and Wisconsin, the gray wolf population in the Western Great Lakes maintains its ability to withstand stochastic events (resiliency)—albeit at reduced population sizes—given the assumptions in our model. There were no simulations in which the population size in the Western Great Lakes dropped below our lower threshold of an effective population size of 50 (192 wolves) or QE (5 wolves), even considering this sustained harvest and lethal depredation control. Additionally, there was a maximum of 0.02 percent probability of falling below our upper threshold for an effective population size of 50 (417 wolves) in 100 years, demonstrating a negligible risk of future inbreeding (Table 13b). Given that our model projects that a median of over 500 gray wolves would continue to occur in Michigan, a median of over 550 gray wolves would continue to occur in Wisconsin, and a median of over 1,600 gray wolves would continue to occur in Minnesota for the next 100 years (see Appendix 5), the gray wolf in the Western Great Lakes will likely maintain its current distribution among hundreds of packs and multiple subpopulations across three states over the course of the next 100 years. This broad distribution among multiple packs and subpopulations will continue to enhance the species' ability to withstand catastrophic events (redundancy). Moreover, none of the simulations of the future population size in the Western Great Lakes resulted in quasi-extinction, even with the introduction of catastrophic levels of disease (black swan events), further illustrating the species' ability to withstand catastrophic events into the future.

Future Expectations of Populations in Areas Not Analyzed in the Model

As we discuss in Chapter 5, we did not quantitatively project the future number of gray wolves in any of the states in our analysis area outside of the three Western Great Lakes states because

[28] Mathematically, eventually $r_{max}N_t\,(1–N_t/K)=h(m+c)$.

these areas are not currently occupied, and modeling the expansion of the wolf population would require assumption regarding how newly occupied states would manage gray wolves, and whether gray wolf populations could persist on the landscape. We also did not include the Lower Peninsula of Michigan in our model projections, despite having modeled the Upper Peninsula of Michigan, given that the current population in Michigan does not extend to the Lower Peninsula.

Gray wolves could potentially recolonize the Lower Peninsula in the future, given the proximity of the Lower Peninsula to occupied areas of the Western Great Lakes and the fact that the state of Michigan does not intend to preclude gray wolves from recolonizing the Lower Peninsula (MI DNR 2022a, p. 49). A recent study examining potential den habitat and dispersal corridors in the northern Lower Peninsula determined that 736 mi^2 (1,906 km^2) of high-quality den habitat existed in the region, but the landscape has low permeability for gray wolf movement (Stricker et al. 2019, pp. 87–88).

Wolves attempting to disperse into the Lower Peninsula of Michigan today may encounter a variety of natural and human-related challenges. The Straits of Mackinac, which span at least five miles of open water, can present a notable obstacle between the Upper Peninsula and the Lower Peninsula. Climate warming can affect the formation of ice bridges, and extended commercial shipping seasons—along with associated icebreaking—could further limit opportunities for winter crossings (Roell 2025a, in litt.). In southern Wisconsin, potential dispersal routes around Lake Michigan to reach the Lower Peninsula pass through highly developed areas, including cities such as Chicago, Illinois, and Gary, Indiana. Similarly, wolves moving from Canada into the eastern Lower Peninsula of Michigan must navigate around Lake Huron and through regions with substantial human development (Roell 2025a, in litt.).

These factors collectively may influence the likelihood and success of wolf dispersal into the Lower Peninsula. Furthermore, if gray wolves successfully recolonize the northern Lower Peninsula, the higher density of livestock farms occurring in the region are likely to result in an increase in gray wolf-human conflict and lethal depredation control (MI DNR 2022a, p. 59). Below, we provide a brief qualitative discussion of our expectations for the future number of gray wolves in the Eastern United States outside of the Western Great Lakes (i.e., outside of the states of Michigan, Minnesota, and Wisconsin).

Although we have confirmed records of dispersing gray wolves in all but a few states in our analysis area, we currently have no information indicating that gray wolves occupy or have formed breeding pairs anywhere in the Eastern United States outside of the Western Great Lakes (see *Northeastern United States* and *Confirmed Wolf Reports Elsewhere in the Eastern United States*). Further, despite the presence of large source populations of gray wolves in both the Western Great Lakes and Canada, as well as sufficient suitable habitat (see *Current Habitat Availability* and Table 6 (a-b)), for the reasons described below, we do not expect that gray wolves will recolonize other areas of the Eastern United States and establish populations outside of Michigan, Minnesota, and Wisconsin in the future.

Gray wolves are unlikely to recolonize the Northeastern United States (i.e., Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont) in the future, absent human intervention. To date, gray wolves have not recolonized any of the areas in the Northeastern United States that were identified in the Service's revised recovery plan as potential areas for reestablishment (see *Comparison of Recovery Criteria with Other Wolf Models*). Some believe natural recolonization in the Northeastern United States by gray wolves dispersing from Canada may be precluded due to high levels of mortality in Southeastern Canada (Wydeven et al. 1998, p. 777; McAlpine et al. 2015, p. 392) or physical barriers (McAlpine et al. 2015, p. 392; Woolmer et al. 2008, p. 50). In addition, most of the Northeastern United States is densely populated. Areas with higher human presence limit opportunities for gray wolves to disperse into the region undetected. Thus, gray wolves dispersing into the Northeastern United States have a greater chance of encountering humans that will either mistakenly, due to misidentification as a coyote, or intentionally, kill them (*see Levels of Human-Caused Mortality in the Remainder of the Eastern United States* in Chapter 3 above). If federally delisted, gray wolves dispersing to New Hampshire or New York would continue to receive some protections because the gray wolf is listed as a state endangered species in these two states; however, they would lack such state protections in the remainder of the Northeast.

We also do not expect gray wolves to recolonize any of the Midwestern United States outside of the Western Great Lakes (Illinois, Indiana, Iowa, Missouri, Ohio) or the eastern Great Plains states (Kansas, Nebraska, North Dakota, Oklahoma, South Dakota, Texas). The states with the highest number of confirmed gray wolf detections in the Eastern United States, outside of the Western Great Lakes, are North Dakota and South Dakota (see *Confirmed Wolf Reports Elsewhere in the Eastern United States*). However, to date, gray wolves have not recolonized either state due to human-caused mortality (see *Levels of Human-Caused Mortality in the Remainder of the Eastern United States*); under the current regulations in these and the other Great Plains and Midwestern United States, we expect interactions with humans in these states will result in continued mortality for dispersing wolves. The physical features of these states (i.e., relatively flat and open with little to no cover) and the land use practices (i.e., livestock production and agriculture) further contribute to the ongoing risk of gray wolf mortality (Mech 2017, p. 312). Gray wolves dispersing into these unoccupied states have a high risk of human-caused mortality which reduces the likelihood that gray wolves will successfully recolonize these areas in the future. Therefore, because we do not expect additional populations of gray wolves to occur in the Eastern United States, outside of the Western Great Lakes, in the future, gray wolf resiliency and redundancy in the Eastern United States is unlikely to increase in the future relative to current condition.

Future Habitat and Prey Availability

Future Suitable Habitat Availability

Few statistical models have been developed to quantify the potential future effects of climate and land cover change on the availability of suitable habitat in the Western Great Lakes. Van den Bosch et al. (2023, p. 5) examined the potential impact of climate change within the Western Great Lakes metapopulation to 2090 under four Shared Socio-economic Pathways and Representative Concentration Pathways. Each of the Shared Socio-economic Pathway/Representative Concentration Pathway pairs represent a different greenhouse gas emission and, consequently, warming scenario; they span a range of greenhouse gas emissions scenarios from reductions to a world increasingly dominated by fossil fuels. Under all scenarios, no changes in available suitable habitat occurred within the currently occupied range by 2090 (van den Bosch et al. 2023, p. 5). This same study also examined potential land cover change using projected changes from the Land Use Harmonization Project (van den Bosch et al. 2023, p. 5). Land cover changes generally resulted in increases in urban and forested areas, and a decline in open habitats, which translated into a potential 9 to 35 percent increase in suitable gray wolf habitat within the Western Great Lakes region (van den Bosch et al. 2023, p. 5). These findings support the hypothesis that the amount of suitable habitat within the currently occupied region will not significantly change and could even increase slightly by 2090.

Sufficient suitable habitat exists in the Western Great Lakes to continue to support gray wolves into the future. Current land-use practices throughout most of the species' current range in the Western Great Lakes do not appear to be affecting the viability of gray wolves. We do not anticipate overall habitat changes will occur at a magnitude that would affect gray wolves across their range in the Western Great Lakes, because gray wolves are broadly distributed in a large metapopulation, connected to an even larger metapopulation of gray wolves in Canada, and are able to withstand high levels of mortality due to their high reproductive capacity and vagility (the ability of an organism to move about freely and migrate) (Boitani 2003, pp. 328–330; Fuller et al. 2003, p. 163).

Future Prey Availability

Prey availability is one of the most important factors in determining gray wolf abundance and distribution. Native ungulates (e.g., deer) are the primary prey within the range of gray wolves in the Western Great Lakes. Each state within gray wolf current range manages its wild ungulate populations sustainably and we expect that they will continue to manage for healthy and sustainable wild ungulate populations in the future (e.g., MN DNR 2011, entire; WI DNR 2012, entire; MI DNR 2016, entire; MN DNR 2018, entire; WI DNR 2023d, entire). States use an adaptive-management approach that adjusts hunter harvest in response to changes in big game population numbers and trends when necessary, and predation is one of many factors considered when setting annual big game harvest regulations (MI DNR 2022a, p. 40; MN DNR 2022, p. 27; WI DNR 2023a, pp. 133–134).

While we are aware of emerging contagious disease threats (e.g., CWD) to ungulates, there are still significant uncertainties regarding the ultimate impact of these diseases and their prevalence across the landscape. To address the threat of diseases in prey, states and Federal agencies have developed surveillance and response plans to minimize and mitigate impacts (see *Diseases in Prey* in Chapter 4). States can also increase or decrease big game harvest in response to disease outbreaks in ungulates to reduce disease prevalence or spread, or to facilitate population growth after a disease outbreak. We expect wildlife managers will continue to respond to ungulate disease outbreaks in a way that is likely to mitigate any substantial impact to the gray wolf population in the Western Great Lakes.

Given that gray wolves are habitat generalists and have wide thermal tolerances, we expect that any effects of climate change will likely be realized through changes in the density and distribution of gray wolf prey (Barber-Meyer et al. 2021, pp. 10–11; see also *Climate Change* in Chapter 4). Climate change may also influence a prey's vulnerability to gray wolf predation (e.g., through changes in winter severity or snow depth, density, duration, or hardness (see Mech and Peterson 2003, pp. 137–139)) or facilitate the introduction of novel diseases or disease vectors in prey populations. However, the precise effect of climate change on gray wolf distribution and abundance is difficult to predict due to uncertainties in how ungulate populations will respond to climate change and how ungulate management will change as ungulate populations change. Adding to this uncertainty, climate change is expected to have a complex influence on the spatial and temporal distribution of pathogens and the emergence of disease conditions among ungulates in North America (Hoberg et al. 2008, p. 515). In turn, the precise impacts of these shifts on gray wolf populations are likely to be complex and spatially heterogeneous.

In summary, we do not anticipate prey populations will decline to the extent that they would measurably affect the gray wolf's resiliency in the Western Great Lakes. We anticipate that states will continue to be incentivized to retain relatively large populations of ungulates for a variety of interested parties, and that states will respond adaptively to mitigate any future declines in these populations. While there is uncertainty regarding the precise impacts of diseases in prey in the future, we expect that gray wolf abundance and distribution will continue to be more a function of human tolerance than prey availability in many areas of the Eastern United States, especially near the edges of human dominated landscapes where gray wolf-human conflicts are likely to be highest.

Future Genetics and Connectivity

Under all of our scenarios, we project a decrease in the gray wolf population in the Western Great Lakes over the next 100 years, which is driven primarily by human-caused mortality. This has several potential consequences for the genetic composition of the future gray wolf population. A smaller census size would result in a smaller effective size, assuming the effective to census ratio remains constant. For example, under Mortality Scenario 2 combined with added black swan events (the most impactful future scenario we analyzed above), the median projected population size in 100 years is 2,686 gray wolves, which would translate to an effective size between approximately 322 and 698 wolves. This is well within the recommended effective size threshold range to minimize risk of inbreeding (an effective population size of 50) (See Appendix 1). Thus, even without considering its connection to Canada (i.e., assuming the population is isolated), the gray wolf population in the Western Great Lakes is projected to remain at a level in which genetic processes (e.g., inbreeding, loss of heterozygosity) are unlikely to reduce future resiliency. Furthermore, especially given that management in Minnesota will be more protective in the northern portions of the state (see *State Management: Minnesota* above) and given the large wilderness areas that straddle the border between Minnesota and Canada (i.e., the Boundary Waters Wilderness Area, which connects to the Quetico Provincial Park wilderness area in Canada), there is no expectation that connectivity would be reduced with populations in Canada in the future, meaning that gene flow would continue to elevate the effective size in the future (i.e., a lack of isolation).

A key assumption, however, in this projection of future genetic diversity is that connectivity within the Western Great Lakes metapopulation will not decline to the point at which the metapopulation becomes sub-divided into discrete units that are genetically isolated. If this were to occur, we would need to analyze whether these individual isolated units themselves could maintain adequate effective population sizes. However, it is unlikely that such an extreme reduction in connectivity would occur in the future. As indicated in *Future Habitat and Prey Availability* above, we are not projecting that there would be substantial changes to the landscape that would inhibit the movement of gray wolves within the Western Great Lakes areas. However, elevated mortality, particularly through harvest, could affect connectivity if dispersing gray wolves are disproportionately removed. There is uncertainty regarding the long-term genetic consequences of harvest on gray wolf populations. Rick et al. (2017, entire) examined genetic diversity and structuring in Minnesota prior and then following a year of harvest during the period when gray wolves were delisted in the state. The results showed no difference in genetic diversity, a slight increase in large-scale genetic structuring, and some differences in the geography of effective dispersal. Because the study contained only 2 years of data, however, it is difficult to draw conclusions about long-term effects or to discern the cause or causes of the observed differences. In Idaho, harvest was found to result in no changes to genetic diversity to the gray wolf population, but did result in increased relatedness of individuals between groups (Ausband and Waits 2020, entire). This was hypothesized to be due to increases in local immigration, meaning that harvest caused pack dissolution and subsequent scattering of related individuals (i.e., family groups) into neighboring packs. These case studies, however, indicate that harvest never reached a level in which subgroups of gray wolves became totally genetically isolated. As has been shown in other gray wolf populations, even gene flow from a small number of migrants per generation (either from subpopulations within the Western Great Lakes metapopulation or from Canada) is sufficient to maintain genetic diversity (Adams et al. 2011, entire; Hedrick et al. 2014, entire; Åkesson et al. 2016, entire). Therefore, we do not project that there would be substantial changes in future genetic connectivity across the gray wolf range in the Western Great Lakes that would subsequently reduce long-term resiliency.

Future Representation

In examining the potential for representation to change over time, we first assess how the scores for each of the twelve core attributes of adaptive capacity that we evaluated in Chapter 4 might change based on our projections. Significant shifts in the core attributes that contribute to dispersal and colonization ability or behavioral and phenotypic plasticity seem highly unlikely to occur in any of our scenarios, either naturally or as influenced by management or other human interaction (see Table 8 in *Current Representation*). Many of the attributes that contribute to those abilities are consistent among gray wolf life histories globally, including high dispersal ability, high physiological tolerances to environmental variation, and early sexual maturity and fecundity that facilitate population growth and range expansion. Along with the regulation of human-caused mortality, these characteristics have allowed the gray wolf population in the Western Great Lakes to expand in number and range over the past four decades. Gray wolves' adaptable life history allowed them to exploit available prey and habitat and recolonize large areas, while maintaining high levels of genetic diversity and connectivity (Koblmüller 2009, p. 2322; Fain et al. 2010, p. 1758; Rick et al. 2017, p. 1101). As such, we expect gray wolves to continue to be able to adapt to environmental changes by dispersing to and exploiting available habitat within the Western Great Lakes area and being able to establish and reproduce in a range of climatic and habitat conditions.

The attribute of adaptive capacity that is susceptible to change is evolutionary genetic potential. This potential is in large part reflective of genetic diversity, the continued retention of which could be affected by changes in population size, particularly effective population size, and connectivity (Funk et al. 2019, p. 120; Kardos et al. 2021, p. 8). Our assessment of the attributes described by Thurman et al. (2020, pp. 521–522) noted the three attributes most linked to evolutionary genetic potential were life span, population size, and genetic diversity. While we have made no specific projections about life span, it is only reasonable to expect it to remain in the "*moderate*" category (1 to 25 years). Population size, however, is more complicated. The characteristics of Thurman et al.'s "*low*" population size category are: (1) fewer than 250 mature adults or (2) a decline of 25 percent or greater within a single generation. None of our model projections result in a population size below 250 gray wolves in the Western Great Lakes under any scenario we examined. However, depending on the combination of mortality and disease scenarios, 36 to 56 percent of simulations projected declines of at least 25 percent within the first 5 years of the modeling period (approximately one generation) (Table 14).

Table 14. Percent of simulations falling below 75 percent of the starting population size (i.e., a 25 percent decline) within 5 years.

Mortality Scenario	Disease Scenario	Percent of Simulations that Declined More than 25% from Starting Population in 5 Years
Scenario 1	**Observed YNP Disease Rates**	36
Scenario 2	**Observed YNP Disease Rates**	53
Scenario 1	**YNP Disease Rates + Added Black Swan Events**	40
Scenario 2	**YNP Disease Rates + Added Black Swan Events**	56

Thus, these projected reductions in population size in all our scenarios indicate gray wolves in the Western Great Lakes may experience some loss of evolutionary genetic potential, according to the generalized evaluation in Thurman et al. (2020, WebTable 2) (Flagstad et al. 2003, p. 878; Kardos et al. 2021, pp. 3–7; Ausband 2022, p. 539). However, there are other methods of analyzing the future of evolutionary genetic potential in the gray wolf population in the Western Great Lakes. Using the generalized threshold that an effective population size of 500 (equivalent to a census population size between approximately 1,923 and 4,167 gray wolves (according to the ratio of effective to census population size we calculate in Appendix 1) is a reasonable target to ensure retention of evolutionary genetic potential (Franklin 1980, p. 147), our projections for all four of our future scenario combinations result in median projected population sizes well within this threshold range. Although, when combined with added black swan events, Mortality Scenario 2 resulted in a lower 95 percent credible interval slightly below this threshold range (a lower 95% credible interval of 1,479 gray wolves). All model runs, however, result in population sizes more than two times higher than those that multiple gray wolf-specific PVAs have indicated would result in a high retention of genetic diversity (e.g., Liberg 2005, pp. 39–40 (600 to 800 wolves); Liberg and Sand 2012, p. 12 (200 to 400 wolves)). Perhaps most importantly, unlike the assumption of isolation involved in the generalized threshold of an effective population size of 500 for the retention of evolutionary genetic potential, our analysis area does not represent an isolated population. In fact, the connectivity with secure populations of gray wolves in Canada (Canadian Endangered Species Conservation Council 2022, unpaginated), where there are an estimated 4,000–6,000 gray wolves in Manitoba (International Wolf Center 2023a, unpaginated) and 9,600 gray wolves in Ontario (International Wolf Center 2023b, unpaginated) (see Chapter 4) will likely continue to provide dispersers that may act to buffer any potential losses of genetic diversity or evolutionary genetic potential. As such, although substantial reductions in abundance can theoretically lead to decreases in genetic diversity, such decreases in genetic diversity are unlikely to be significant or sustained under the scenarios we analyzed (see *Future Genetics and Connectivity*), thus are unlikely to negatively affect adaptive capacity in the future.

In addition to examining potential changes in the attributes of adaptive capacity described by Thurman et al. (2020, pp. 521–522), we also considered qualitatively the degree to which gray wolf occupation of different ecoregional provinces in the Eastern United States might change under our future projections. While not as direct a measure of adaptive capacity, distribution across a variety of ecoregional provinces can serve as a proxy to indicate the species' exposure to different selective pressures. In all scenarios, we expect the species' distribution to remain relatively the same as it is currently. Therefore, we expect gray wolves to remain present in the ecoregional province that currently represents the vast majority of the species range (the Laurentian Mixed Forest). While the current edges of the species range also marginally extend into the Eastern Broadleaf Forest (Continental) and the Prairie Parkland (Temperate) ecoregional provinces, should the population size decline as we project in these future scenarios, it is possible the limited distribution of gray wolves in these two ecoregional provinces could decrease. However, given the small portion of the species' range that currently overlaps these ecoregional provinces, these ecoregional provinces are not greatly influencing the selective pressures the species is currently experiencing, nor are they likely to do so in the future. We also do not expect the gray wolf population to expand beyond the main ecoregional province it occupies in the future. Even if the species were to expand into the Lower Peninsula of Michigan, this area would not introduce a new ecoregional province (the northern portions of the Lower Peninsula are primarily Laurentian Mixed Forest, the ecoregional province that already makes up the bulk of the gray wolf's current range in the Western Great Lakes). As a result, while we do not expect any projected population declines to greatly decrease the species' exposure to different selective pressures in different ecoregional provinces in the future, we do not expect any increases in representation based on this particular measure of adaptive capacity either.

Overall, given the adaptable nature of gray wolves and the projections for changes in population sizes in the future scenarios we model, it is likely that gray wolves in the Western Great Lakes will remain capable of adapting to environmental change, even without further expansion into the Eastern United States. Such capability will be supported, as it is currently, by: (1) a strong ability to disperse and colonize suitable habitat; (2) tolerance to a range of environmental conditions, including behavioral and phenotypic plasticity; and (3) the ability to respond genetically through natural selection acting on the available pool of genetic diversity, maintained by connectivity throughout the metapopulation. Although human-caused mortality (the primary stressor) is one for which sufficient adaptation is unlikely, we expect gray wolves in the Western Great Lakes to otherwise be well suited to adapt to a variety of environmental change in the future, as long as human-caused mortality is kept within the bounds analyzed in our model, bounds we find are most likely should the species be delisted in the future (see *Future Mortality Scenarios* in Chapter 5 above).

Summary of Future Condition

Our model projections of the future gray wolf population in the Western Great Lakes indicate that the median population size will be between approximately 2,600 and 3,800 gray wolves over the course of the next 100 years, if mortality rates from lethal depredation control, harvest, and disease occur within the bounds we consider in our future scenarios. While these projected population sizes represent a decrease relative to the metapopulation's current size, we would expect such a change with the introduction of harvest (which does not currently occur in the population while the species is listed) and disease (which has never occurred at the rates and geographic scales we model in our future scenarios in the Western Great Lakes). Further these projections assume that background rates of illegal take, which are built-in to the intrinsic rate of growth and not explicitly included in the models will continue into the future (i.e. rates will neither increase or decrease). After this initial decline due to these stressors, the population stabilizes around a large equilibrium population size and does not fall to a level that indicates risk of quasi-extinction or inbreeding, demonstrating the population's ability to withstand the sustained human-caused mortality and disease rates we model (both stochastic events (resiliency) and catastrophic events (redundancy)). Major uncertainties include the effects of additive versus compensatory harvest (though for higher harvest rates we assume additive harvest effects), and the accuracy of monitoring programs. We explored the effects of uncertainty on these parameters in our uncertainty analyses (Appendix A) and determined the conclusions of our SSA were robust to these uncertainties. The continued availability of (or perhaps increase in) suitable habitat and prey further support the Western Great Lakes metapopulation's resiliency into the future. Moreover, the metapopulation's currently high levels of genetic diversity are unlikely to decrease in the future, given maintained connectivity within the metapopulation and with the larger, expansive, and secure gray wolf population in Canada. This sustained genetic diversity and connectivity also contribute to the species' continued ability to withstand stochastic events (resiliency) into the future within the Western Great Lakes (the extant metapopulation in the Eastern United States). Finally, given this maintained genetic diversity, and gray wolves' innate characteristics that contribute to the species' ability to live in and disperse to multiple different habitat types, the adaptive capacity of the species (representation) within the Western Great Lakes is unlikely to decrease relative to current condition in the future. Due to the risk of human-caused mortality, gray wolves are unlikely to recolonize areas outside of the Western Great Lakes within the Eastern United States in the future, which means redundancy and representation is unlikely to increase in the future. However, based on our analysis, the gray wolf in the Western Great Lakes will likely retain sufficient resiliency, redundancy, and representation to avoid extirpation for the next 100 years, meaning that, even without this recolonization, the gray wolf will successfully maintain populations in the wild in the Eastern United States into the future, despite the continued occurrence or introduction of various stressors.

Appendix 1: Analysis of Wildlife Genetics International Data Set[29]

Brenna Forester
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October 31, 2023

Purpose

The purpose of this appendix is to report the methods and results of additional analyses of the Wildlife Genetics International (WGI) genetic data set (WGI 2021, unpublished data) delivered to the Service on May 4, 2021. Analyses conducted include assessment of genetic diversity over time in the Northern Rocky Mountains (NRM) wolf population and evaluation of contemporary effective population sizes (Ne), including calculation of an effective to census population size ratio. We added this appendix to the SSA in October 2023, after the SSA was peer reviewed, so these analyses have not yet been peer reviewed.[30]

Methods

Data

The filtered WGI data set consists of microsatellite genotyping at 24 markers for 427 individual wolves from the NRM between 1995–2018 (WGI 2021, unpublished data). See the WGI report (WGI 2021, pp. 2–8) for details on sample quality, filtering, and marker variability. The data set is highly complete, with only 0.05 percent missing data. Samples were collected so as to minimize sampling within packs (Becker 2023, pers. comm.).

Analysis of genetic diversity

All analyses of genetic diversity used R version 4.1.1 (R Core Team, 2021). We calculated the proportion of heterozygous loci in an individual (PHt = number of heterozygous loci/number of genotyped loci) using the GENHET function to evaluate individual heterozygosity (Coulon 2010, p. 168). We also calculated four other measures of individual heterozygosity, to evaluate consistency in trends in genetic diversity across metrics: standardized heterozygosity based on the mean expected heterozygosity (Hs_exp); standardized heterozygosity based on the mean observed heterozygosity (Hs_obs); internal relatedness (IR); and homozygosity by locus (HL). Coulon (2010, entire) reviews strengths and limitations of these metrics. We used Pearson correlations to evaluate change in genetic diversity metrics over time.

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[29] This October 31, 2023, analysis was included as an appendix to our SSA for the Gray Wolf in the Western United States (Service 2023, Appendix 1). Currently, the best available science does not provide the data necessary to estimate an effective to census population size ratio specifically for the Western Great Lakes region wolf population. In the absence of a ratio specific to the Western Great Lakes region wolf population, we relied on this analysis to estimate the average ratio of effective to census population size.

[30] This statement is referring to the SSA for the Gray wolf in the Western United States and the peer review of that report. Appendix 1 was subsequently peer reviewed as part of the SSA for the Gray wolf in the Eastern United States.

Analysis of effective population size

We calculated contemporary Ne for all states with a sufficient sample size (i.e., ≥ 50 individuals; Waples and Do 2010, pp. 246–249) across two years of sampling using the linkage disequilibrium (LD) method in NeEstimator version 2.01 (Do et al., 2014, entire). To reduce the downward bias associated with grouping individuals across population substructure, we grouped individuals by state for Ne calculations. We used two years of data for each group of individuals based on data availability (i.e., to attain larger sample sizes) while limiting the downward bias associated with sampling across multiple generations.

In the LD calculation, we used the monogamy mating model because wolf life history more closely matched this mating model than the random mating option (see Species Description in Chapter 1 above). To reduce upward bias while retaining precision in Ne estimates, we excluded alleles with frequencies less than a critical value of 0.02 (Waples and Do 2010, pp. 251, 254). We used the jackknife method to empirically estimate 95% confidence intervals (Waples and Do 2008, entire; Waples and Do, 2010 p. 252). There were no missing data across 24 microsatellites for any of the individuals used in LD calculations. To calculate a ratio of effective to census population size (Ne:Nc), we calculated an average of the annual census counts for the years that corresponded with genetic samples (Frankham 1995, p. 97). Due to the difficulty of distinguishing pups, yearlings, and adults during winter ground and aerial census counts, census size estimates included young-of-year, yearlings, and adults (Becker 2023, pers. comm.). We provide discussion of all potential biases related to sampling design and data availability and their potential impacts on our results below.

Results

Analysis of genetic diversity

There were no significant correlations between any metric of individual heterozygosity and time (Figure A 1, Table A 1), indicating that genetic diversity has not changed significantly over time between 1995 and 2018. We also evaluated correlations between metrics of individual heterozygosity and time for samples located in Idaho, Montana, and Wyoming only in order to ensure that the inclusion of newer sampling locations that were not part of the dataset prior to 2009 (i.e., Oregon, Washington, Grand Teton National Park, and Yellowstone National Park) were not biasing changes in heterozygosity over time. All Pearson's correlations for individual heterozygosity in Montana, Idaho, and Wyoming samples over time (1995–2018) were not significant (range of Pearson's $r = -0.02 – 0.04$, smallest p-value = 0.495) using 335 samples with 333 degrees of freedom.

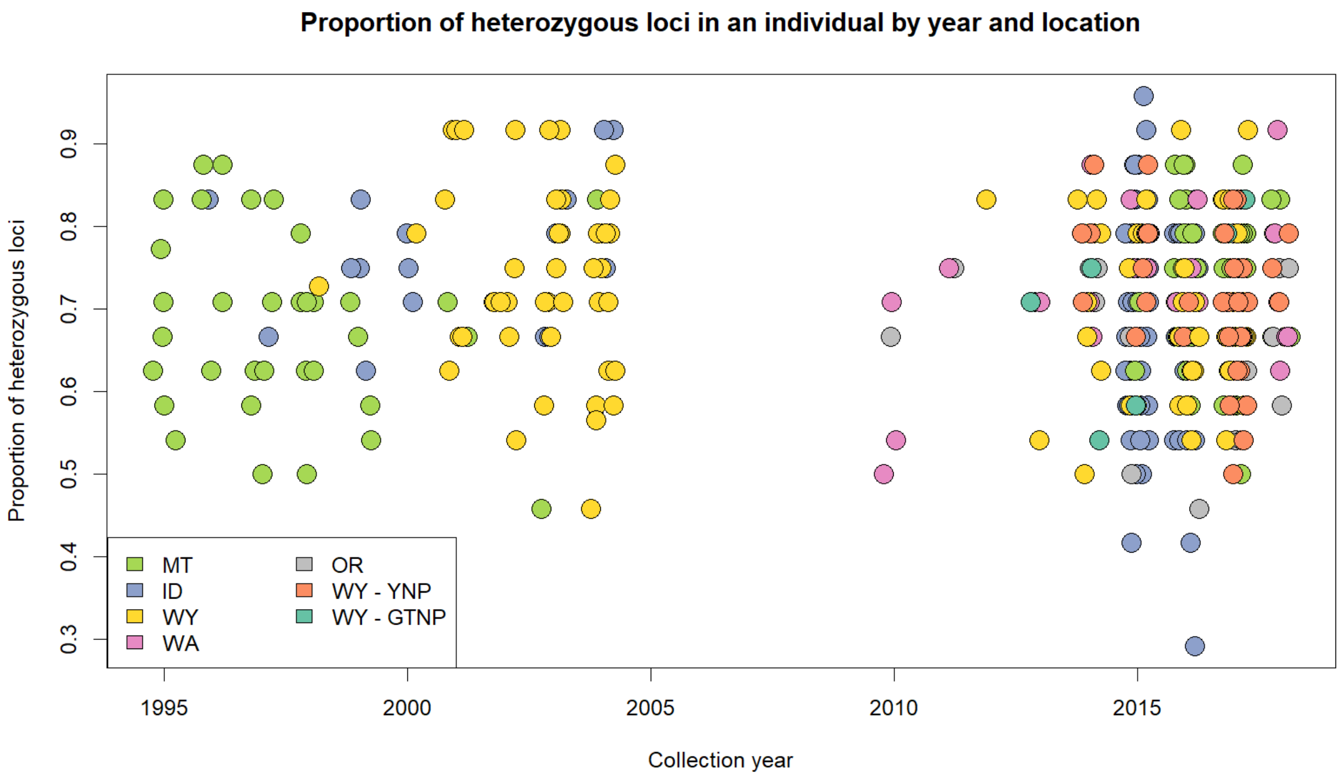

Figure A 1. Individual heterozygosity measured as the proportion of heterozygous loci in 427 individual NRM wolves (circles), color-coded by location region where the sample was collected. Individual points are jittered slightly to illustrate number and location of samples per year. YNP = Yellowstone National Park; GTNP = Grand Teton National Park.

Table A 1. Pearson's correlation between five metrics of individual heterozygosity and time (1995–2018) for 427 individual NRM wolves sampled across five states. Degrees of freedom is 424 for all tests. Individual heterozygosity abbreviations are defined in the text above.

Individual heterozygosity metric	Pearson's r	p-value
PHt	-0.032	0.507
Hs_exp	-0.033	0.498
Hs_obs	-0.033	0.499
IR	0.045	0.350
HL	0.025	0.609

Analysis of effective population size

Estimates of Ne varied by state, with point estimates ranging from 67 to 186, depending on the state (Table A 2). The relative magnitude of census population size estimates corresponded with Ne estimates, ranging from 362 to 1,113 wolves, depending on the state (Table A 3). Effective to census size ratios ranged from 0.159–0.186, depending on the state (range of lowest and highest 95% confidence intervals: 0.114–0.303; Table A 4). The average of the Ne:Nc ratios across states, including 95% confidence intervals was: 0.171 (0.121–0.264; Table A 4)[31].

Table A 2. Contemporary effective population size estimates for each state, including years included in the data set, combined sample sizes, point estimates of Ne, and jackknifed 95% lower and upper confidence intervals (CI).

	Idaho	Montana	Wyoming
Years of samples used	2015–2016	2016–2017	2016–2017
Individual sample sizes	98	77	57
Estimated effective size	125.3	185.7	67.4
95% lower CI	97.4	127.2	45.1
95% upper CI	166.7	308.9	109.8

Table A 3. Census population size estimates for each state, including years included in the data set and averaged values. Not available = count data were not available for that year; NA = no genetic data available for this year in the data set.

	Idaho	Montana	Wyoming
2015	786	NA	NA
2016	Not available	1119	377
2017	NA	1107	347
Average	***786***	***1113***	***362***

Table A 4. Effective to census population size ratio (Ne:Nc) estimated for each state, including jackknifed 95% lower and upper confidence intervals (CI).

	Idaho	Montana	Wyoming	Average
Ne:Nc ratio	0.159	0.167	0.186	0.171
Ne:Nc 95% lower CI	0.124	0.114	0.125	0.121
Ne:Nc 95% upper CI	0.212	0.278	0.303	0.264

As mentioned above, there are a number of biases associated with estimating contemporary Ne for wild populations, including NRM wolves. One potential bias is that associated with grouping individuals across population substructure; we mitigated this bias by calculating Ne estimates

[31] Applied to our model projections for the Western Great Lakes region wolf population, the effective population size would be 192–417.

separately for each state. Although NRM wolves can move long distances, they are not considered a panmictic population, instead exhibiting population substructure that reflects geographic distance and variable isolation effects (see *Current Genetic Diversity and Connectivity* in Chapter 4 above). While state lines are not a perfect proxy for this substructure, they roughly correlate with detectable substructure in the microsatellite data set (e.g., WGI 2021, p. 12). Additionally, contemporary estimates of Ne using the LD method are robust to even relatively high rates of migration (migration rate of 10% or higher; Waples 2010, p. 793), indicating that state-based estimates are unlikely to be heavily biased by substructure. Finally, the state-based Ne estimation approach allows for a direct comparison with state-provided census size estimates to calculate Ne:Nc ratios.

A bias in Ne estimation that is challenging to account for in many species, including wolves, is the impact of sampling individuals across generations. Using mixed-age samples in an LD-based Ne estimate, as we do in this analysis, produces downwardly biased estimates due to mixture LD, which is a two-locus Wahlund effect resulting from combining parents across cohorts into a single sample (Waples et al. 2014, p. 778). We can roughly estimate the impact of this bias by evaluating the ratio of adult lifespan to generation length; bias is lower when the number of cohorts included in the sample corresponds with the generation length (Waples et al. 2014, p. 778). Using definitions from Waples et al. (2013, p. 3; Appendix S1, p. 1), adult lifespan was calculated as maximum age – age at maturity + 1, where maximum age averages 13.7 years for gray wolves (Carey and Judge 2000, unpaginated, and citations within), and age at maturity averages 2.83 years for females (Fuller et al. 2003, p. 175; Mech et al. 2016, pp. 1–2), yielding an adult lifespan of approximately 11.87 years. A generation time of 4.2 to 4.7 years (vonHoldt et al. 2010, p. 4422; Mech et al. 2016, pp. 9–10; Mech and Barber-Meyer 2017, entire), yields an adult lifespan to generation length ratio estimate of 2.5 to 2.8 years. Based on simulations developed across taxonomic groups and life history parameters by Waples et al. (2014, pp. 776–777), this 2.5- to 2.8-year ratio estimate corresponds roughly with a calculated Ne that is about 75% of the true Ne value (i.e., reported value above could be ~25% lower than the true Ne value).

Counteracting the downward bias imposed by mixed-age sampling is an upward bias of unknown magnitude due to the non-random sampling design of this study that specifically avoided sampling relatives (Becker 2023, pers. comm.). Because relatedness among individuals in a population is part of the genetic signature the LD estimation method detects, non-random sampling that avoids siblings truncates family sizes and reduces disparities in reproductive success among parents, artificially increasing Ne estimates (Waples and Anderson 2017, pp. 1217–1218, 1221). Unfortunately, it is not currently possible to estimate the magnitude of this bias.

Finally, census size estimates used for Ne:Nc ratios should ideally correspond to the number of adults in the population (Frankham 1995, p. 101). However, the census size estimates we used do not allow for reliable recognition of and removal of juvenile animals, so Ne:Nc ratios may be biased downward.

Despite the biases and limitations associated with these estimates of Ne and Ne:Nc ratios, the results presented here represent the most current, transparent, and reliable estimates available for inclusion in the SSA.

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Appendix 2: Master spreadsheet with population estimates and mortality data

Michigan

Table A 5. Michigan gray wolf minimum population estimates and mortality data (Roell 2023b, in litt.; Roell 2025b, in litt.).

Timing of Population Estimate		*Number of Wolves*				*Mortality*			*Mortality Rates*		
State of Michigan Terminology	**Translation to year-end estimate**	**Wolf population estimates**	**Lower Confidence Interval**	**Upper Confidence Interval**	**Year over year population change (%)**	**Number of wolves harvested**	**Number of wolves lethally removed**	**Other known wolf mortalities**	**Harvest Rate (% of year-end estimate)**	**Lethal Control Rate (% of year-end estimate)**	**Combined Harvest and Lethal Control Rate**
Early 1989	**1988**	3	–	–	–	0	0	–	–	–	–
Early 1990	**1989**	10	–	–	233.3%	0	0	–	–	–	–
Early 1991	**1990**	17	–	–	70.0%	0	0	–	–	–	–
Early 1992	**1991**	21	–	–	23.5%	0	0	–	–	–	–
Early 1993	**1992**	30	–	–	42.9%	0	0	–	–	–	–
Early 1994	**1993**	57	–	–	90.0%	0	0	–	–	–	–
Early 1995	**1994**	80	–	–	40.4%	0	0	–	–	–	–
Early 1996	**1995**	116	–	–	45.0%	0	0	–	–	–	–
Early 1997	**1996**	113	–	–	-2.6%	0	0	–	–	–	–
Early 1998	**1997**	139	–	–	24.1%	0	0	–	–	–	–
Early 1999	**1998**	169	–	–	20.7%	0	0	–	–	–	–
Early 2000	**1999**	216	–	–	24.1%	0	0	–	–	–	–
Early 2001	**2000**	249	–	–	15.3%	0	0	–	–	–	–
Early 2002	**2001**	278	–	–	11.7%	0	0	–	–	–	–
Early 2003	**2002**	321	–	–	15.5%	0	0	–	–	–	–
Early 2004	**2003**	360	–	–	12.2%	0	4	23	0.0%	1.0%	1.0%
Early 2005	**2004**	405	–	–	12.5%	0	5	42	0.0%	1.1%	1.1%
Early 2006	**2005**	434	–	–	7.2%	0	2	40	0.0%	0.4%	0.4%

Timing of Population Estimate		*Number of Wolves*			Year over year population change (%)	*Mortality*			*Mortality Rates*		
State of Michigan Terminology	Translation to year-end estimate	Wolf population estimates	Lower Confidence Interval	Upper Confidence Interval		Number of wolves harvested	Number of wolves lethally removed	Other known wolf mortalities	Harvest Rate (% of year-end estimate)	Lethal Control Rate (% of year-end estimate)	Combined Harvest and Lethal Control Rate
Early 2007	**2006**	509	473	545	17.3%	0	7	33	0.0%	1.3%	1.3%
Early 2008	**2007**	520	374	666	2.2%	0	14	25	0.0%	2.5%	2.5%
Early 2009	**2008**	577	538	616	11.0%	0	8	26	0.0%	1.3%	1.3%
Early 2010	**2009**	557	504	610	-3.5%	0	1	32	0.0%	0.2%	0.2%
Early 2011	**2010**	687	624	750	23.3%	0	0	31	–	–	–
Early 2012	**2011**	–	–	–	–	0	0	40	–	–	–
Early 2013	**2012**	658	602	714	-4.2%	0	18	35	0.0%	2.5%	2.5%
Early 2014	**2013**	636	594	678	-3.3%	22	10	33	3.1%	1.4%	4.6%
Early 2015	**2014**	–	–	–	–	0	13	31	–	–	–
Early 2016	**2015**	618	568	668	-2.8%	0	0	36	–	–	–
Early 2017	**2016**	–	–	–	–	0	0	32	–	–	–
Early 2018	**2017**	662	593	731	7.1%	0	0	33	–	–	–
Early 2019	**2018**	–	–	–	–	0	0	16	–	–	–
Early 2020	**2019**	695	620	770	5.0%	0	0	38	–	–	–
Early 2021	**2020**	–	–	–	–	0	0	41	–	–	–
Early 2022	**2021**	631	582	680	-9.2%	0	9	27	0.0%	1.3%	1.3%
Early 2023	**2022**	–	–	–	–	0	0	25	–	–	–

Minnesota

Table A 6. Minnesota gray wolf population estimates and mortality data (Stark 2023a, in litt; Stark 2023b, in litt.; Stark 2025, in litt; Erb and Humpal, 2023).

Timing of Population Estimate		***Number of Wolves***			**Year over year population change (%)**	***Mortality***			***Mortality Rates***		
State of Minnesota Terminology	**Translation to year-end estimate**	**Wolf population estimates**	**Lower Confidence Interval**	**Upper Confidence Interval**		**Number of wolves harvested**	**Number of wolves lethally removed**	**Other known wolf mortalities**	**Harvest Rate (% of year-end estimate)**	**Lethal Control Rate (% of year-end estimate)**	**Combined Harvest and Lethal Control Rate**
1978/1979	**1978**	1,235	–	–	–	0	0	–	–	–	–
1979/1980	**1979**	–	–	–	–	0	6	–	–	–	–
1980/1981	**1980**	–	–	–	–	0	21	–	–	–	–
1981/1982	**1981**	–	–	–	–	0	29	–	–	–	–
1982/1983	**1982**	–	–	–	–	0	20	–	–	–	–
1983/1984	**1983**	–	–	–	–	0	42	–	–	–	–
1984/1985	**1984**	–	–	–	–	0	36	–	–	–	–
1985/1986	**1985**	–	–	–	–	0	31	–	–	–	–
1986/1987	**1986**	–	–	–	–	0	31	–	–	–	–
1987/1988	**1987**	–	–	–	–	0	43	–	–	–	–
1988/1989	**1988**	1,521	1,338	1,762	–	0	59	–	–	–	–
1989/1990	**1989**	–	–	–	–	0	81	–	–	–	–
1990/1991	**1990**	–	–	–	–	0	91	–	–	–	–
1991/1992	**1991**	–	–	–	–	0	54	–	–	–	–
1992/1993	**1992**	–	–	–	–	0	118	–	–	–	–
1993/1994	**1993**	–	–	–	–	0	139	–	–	–	–
1994/1995	**1994**	–	–	–	–	0	172	–	–	–	–
1995/1996	**1995**	–	–	–	–	0	78	–	–	–	–
1996/1997	**1996**	–	–	–	–	0	154	–	–	–	–
1997/1998	**1997**	2,445	1,995	2,905	–	0	216	–	–	–	–
1998/1999	**1998**	–	–	–	–	0	161	–	–	–	–

Timing of Population Estimate		*Number of Wolves*			Year over year population change (%)	*Mortality*			*Mortality Rates*		
State of Minnesota Terminology	**Translation to year-end estimate**	**Wolf population estimates**	**Lower Confidence Interval**	**Upper Confidence Interval**		**Number of wolves harvested**	**Number of wolves lethally removed**	**Other known wolf mortalities**	**Harvest Rate (% of year-end estimate)**	**Lethal Control Rate (% of year-end estimate)**	**Combined Harvest and Lethal Control Rate**
1999/2000	**1999**	–	–	–	–	0	151	–	–	–	–
2000/2001	**2000**	–	–	–	–	0	148	–	–	–	–
2001/2002	**2001**	–	–	–	–	0	109	–	–	–	–
2002/2003	**2002**	–	–	–	–	0	146	–	–	–	–
2003/2004	**2003**	3,020	2,301	3,708	–	0	125	24	0.0%	3.9%	3.9%
2004/2005	**2004**	–	–	–	–	0	105	–	–	–	–
2005/2006	**2005**	–	–	–	–	0	134	–	–	–	–
2006/2007	**2006**	–	–	–	–	0	122	–	–	–	–
2007/2008	**2007**	2,921	2,192	3,525	–	0	133	24	0.0%	4.3%	4.3%
2008/2009	**2008**	–	–	–	–	0	143	–	–	–	–
2009/2010	**2009**	–	–	–	–	0	195	–	–	–	–
2010/2011	**2010**	–	–	–	–	0	192	–	–	–	–
2011/2012	**2011**	–	–	–	–	0	203	–	–	–	–
2012/2013	**2012**	2,211	1,652	2,641	–	413	295	27	14.0%	10.0%	24.0%
2013/2014	**2013**	2,423	1,935	2,947	9.6%	238	140	23	8.4%	5.0%	13.4%
2014/2015	**2014**	2,221	1,789	2,719	-8.3%	272	222	21	9.9%	8.1%	18.1%
2015/2016	**2015**	2,278	1,865	2,784	2.6%	0	213	23	0.0%	8.5%	8.5%
2016/2017	**2016**	2,856	2,371	3,382	25.4%	0	183	9	0.0%	6.0%	6.0%
2017/2018	**2017**	2,655	1,972	3,387	-7.1%	0	190	7	0.0%	6.7%	6.7%
2018/2019	**2018**	2,699	2,046	3,430	1.7%	0	189	33	0.0%	6.5%	6.5%
2019/2020	**2019**	2,696	2,244	3,252	-0.1%	0	166	33	0.0%	5.7%	5.7%
2020/2021	**2020**	2,770	2,319	3,223	2.7%	0	216	16	0.0%	7.2%	7.2%
2021/2022	**2021**	2,691	2,173	3,240	-2.9%	0	162	30	0.0%	5.6%	5.6%
2022/2023	**2022**	2,919	2,215	3,790	8.5%	0	142	32	0.0%	4.6%	4.6%

Wisconsin

Table A 7. Wisconsin gray wolf population minimum count/estimates and mortality data (Johnson 2023, in litt.; WI DNR 2023c).

Timing of Population Estimate		*Number of Wolves*			Year over year population change (%)	*Mortality*			*Mortality Rates*		
State of Wisconsin Terminology	Translation to year-end estimate	Wolf population estimates	Lower Confidence Interval	Upper Confidence Interval		Number of wolves harvested	Number of wolves lethally removed	Other known wolf mortalities	Harvest Rate (% of year-end estimate)	Lethal Control Rate (% of year-end estimate)	Combined Harvest and Lethal Control Rate
1979/1980	**1979**	25	–	–	–	0	0	–	–	–	–
1980/1981	**1980**	20	–	–	-20.0%	0	0	–	–	–	–
1981/1982	**1981**	23	–	–	15.0%	0	0	–	–	–	–
1982/1983	**1982**	19	–	–	-17.4%	0	0	–	–	–	–
1983/1984	**1983**	18	–	–	-5.3%	0	0	–	–	–	–
1984/1985	**1984**	14	–	–	-22.2%	0	0	–	–	–	–
1985/1986	**1985**	15	–	–	7.1%	0	0	–	–	–	–
1986/1987	**1986**	18	–	–	20.0%	0	0	–	–	–	–
1987/1988	**1987**	26	–	–	44.4%	0	0	–	–	–	–
1988/1989	**1988**	31	–	–	19.2%	0	0	–	–	–	–
1989/1990	**1989**	34	–	–	9.7%	0	0	–	–	–	–
1990/1991	**1990**	39	–	–	14.7%	0	0	–	–	–	–
1991/1992	**1991**	45	–	–	15.4%	0	0	–	–	–	–
1992/1993	**1992**	40	–	–	-11.1%	0	0	–	–	–	–
1993/1994	**1993**	54	–	–	35.0%	0	0	–	–	–	–
1994/1995	**1994**	83	–	–	53.7%	0	0	–	–	–	–
1995/1996	**1995**	99	–	–	19.3%	0	0	–	–	–	–
1996/1997	**1996**	148	–	–	49.5%	0	0	–	–	–	–
1997/1998	**1997**	178	–	–	20.3%	0	0	–	–	–	–
1998/1999	**1998**	204	–	–	14.6%	0	0	–	–	–	–
1999/2000	**1999**	248	–	–	21.6%	0	1	–	–	–	–
2000/2001	**2000**	257	–	–	3.6%	0	0	–	–	–	–

Timing of Population Estimate		*Number of Wolves*			Year over year population change (%)	*Mortality*			*Mortality Rates*		
State of Wisconsin Terminology	**Translation to year-end estimate**	**Wolf population estimates**	**Lower Confidence Interval**	**Upper Confidence Interval**		**Number of wolves harvested**	**Number of wolves lethally removed**	**Other known wolf mortalities**	**Harvest Rate (% of year-end estimate)**	**Lethal Control Rate (% of year-end estimate)**	**Combined Harvest and Lethal Control Rate**
2001/2002	**2001**	327	–	–	27.2%	0	0	–	–	–	–
2002/2003	**2002**	335	–	–	2.5%	0	0	–	–	–	–
2003/2004	**2003**	373	–	–	11.3%	0	17	36	0.0%	4.0%	4.0%
2004/2005	**2004**	435	–	–	16.6%	0	22	45	0.0%	4.4%	4.4%
2005/2006	**2005**	467	–	–	7.4%	0	31	42	0.0%	5.7%	5.7%
2006/2007	**2006**	546	–	–	16.9%	0	18	58	0.0%	2.9%	2.9%
2007/2008	**2007**	549	–	–	0.6%	0	38	60	0.0%	5.9%	5.9%
2008/2009	**2008**	637	–	–	16.0%	0	43	54	0.0%	5.9%	5.9%
2009/2010	**2009**	704	–	–	10.5%	0	10	62	0.0%	1.3%	1.3%
2010/2011	**2010**	782	–	–	11.1%	0	0	76	0.0%	0.0%	0.0%
2011/2012	**2011**	815	–	–	4.2%	0	0	82	0.0%	0.0%	0.0%
2012/2013	**2012**	809	–	–	-0.7%	117	76	51	11.1%	7.2%	18.3%
2013/2014	**2013**	660	–	–	-18.4%	257	64	40	25.2%	6.3%	31.4%
2014/2015	**2014**	746	–	–	13.0%	154	35	36	15.9%	3.6%	19.5%
2015/2016	**2015**	866	–	–	16.1%	0	1	37	0.0%	0.1%	0.1%
2016/2017	**2016**	925	–	–	6.8%	0	0	40	–	–	–
2017/2018	**2017**	905	–	–	-2.2%	0	0	39	–	–	–
2018/2019	**2018**	914	–	–	1.0%	0	0	31	–	–	–
2019/2020	**2019**	1,195[a]	957	1,573	30.7%	0	0	55	–	–	–
2020/2021	**2020**	1,126	937	1,364	-5.6%	0	0	39	–	–	–
2021/2022	**2021**	972	812	1,193	-13.7%	218	69	24	17.0%	5.4%	22.4%
2022/2023	**2022**	1,007	780	1,380	3.6%	0	2	36	0.0%	0.2%	0.2%

[a] Note this estimate is from the scaled occupancy model. A statewide minimum gray wolf population count of 1,034 was also calculated for this period. This suggests that the increase in the reported population size from the previous year may, in part, be reflective of Wisconsin's transition from estimating minimum number of wolves using territory mapping to producing a modeled population estimate. All subsequent estimates reported for Wisconsin (i.e., year-end 2019 through year-end 2022) are based on the scaled occupancy model.

Appendix 3: Representation Analysis

Our characterization of current and future representation in Chapters 4 and 6 involved examining 36 attributes identified by Thurman et al. (2020, pp. 521–522) that contribute to adaptive capacity. Thurman et al. (2020, p. 522) recognized 12 of these attributes as "core" attributes; we focused our discussion in the SSA report above on these core attributes. In Table A 8, we present all 36 attributes as scored for wolves in the Eastern United States.

Table A 8. Attributes of adaptive capacity, an explanation of each attribute, the score we assessed for wolves in the Eastern United States for each attribute, and the justification for wolves fitting the score categories as defined by Thurman et al. (2020, pp. 521–522). Core attributes are highlighted with bold text and blue shading.

Attribute	Explanation	Score	Justification
Extent of Occurrence	The area that encompasses all known, inferred, or projected sites of present occurrence	High	Area is greater than 20,000 km^2
Area of Occupancy	The area of currently occupied suitable habitat	High	Area is greater than 2,000 km^2
Habitat Specialization	Habitat specificity, or the degree to which a species is able to use multiple habitats vs. being confined to specific or narrow subset of habitats	High	Has a clear preference for a particular habitat, but the habitat is among the dominant types within the species range. Described as a habitat generalist
Commensalism with Humans	Degree of tolerance of human interaction and infrastructure	Low	Intolerant of human influences, largely due to conflict and human-caused mortality
Geographic Rarity	A measure of patchiness or low local abundance	High	Broadly distributed with highly connected populations throughout its current range
Dispersal Syndrome	The degree of flexibility in either the timing or mechanism of dispersal	High	Facultative (flexible timing, or no cue dependence)
Dispersal Distance	The distance an individual can move from an existing population's location	High	Species is characterized by good to excellent dispersal or movement capability
Dispersal Phase	The phase or life-stage in which individuals disperse	High	Long period or throughout life
Site Fidelity	Natal site fidelity	Moderate	Roughly equal proportion of "stayers" and "strayers"

Attribute	Explanation	Score	Justification
Migration Frequency	Timing of migration or dispersal	High	Throughout lifetime (annually or seasonally)
Migration Demography	Stringence or flexibility in the need to migrate	High	Differential (individuals may migrate different distances or to different locations)
Migration Timing	Specificity of migration timing	High	Facultative (flexible timing, or no cue dependence)
Migration Distance	The total distance spanned during a migratory event	Moderate	Variation in distances or destinations (differential migration)
Genetic Diversity	The diversity of genotypes within a species	High	High within-population genetic variability; genetic variation reported as “average” or “high” compared to findings on related taxa
Population Size	The number of individuals in the population	Moderate	Between 250 and 10,000 mature individuals
Hybridization Potential	Existence of closely related species, subspecies, or allopatric populations for interbreeding	Moderate	Hybridization probably occurs (fitness consequences unknown)
Competitive Ability	Interaction with other species within the range	High	Competitively dominant
Diet Breadth	The ability to use a range of food resources	Moderate	More than 90 percent dependent on a few species from a restricted taxonomic group (ungulates)
Diversity of Obligate Species	The number of obligate species interactions	High	Diffuse interactions (no obligations)
Seasonal Phenology	The timing of periodic life cycle events not directly related to reproduction that are influenced by seasonal variations	High	No dependence on environmental cue that is not directly related to reproduction.
Climate Niche Breadth	Niche specialization or the range of abiotic conditions to which a species is adapted	High	Species occupies habitats that are not thought to be vulnerable to projected climate change

Attribute	Explanation	Score	Justification
Physiological Tolerances	The degree to which a species is restricted to a narrow range of abiotic conditions and the degree of tolerance of physiological stressors	High	Range of novel conditions are not likely to cause sub-lethal or lethal effects (tolerable)
Behavioral Regulation of Physiology	The ability of individuals to change their behavior to reduce exposure to climate stressors	High	High behavioral flexibility and reduction in exposure
Reproductive Phenology	The timing of reproductive events within a species' life cycle	Moderate	Moderate dependence on environmental cue, but the species is capable of adjusting the timing or duration of reproductive events
Reproductive Mode	Relationship between zygote and parents	High	Viviparity or ovoviviparity (eggs are retained within the mother's body until they are ready to hatch)
Mating System	Group structure within populations related to reproductive behaviors	Moderate	Monogamy or mixed modes of reproduction
Fecundity	Number of offspring produced on average	Moderate	Few offspring (3–10)
Parity	The number of times an organism reproduces within its lifetime	High	Iteroparous
Sex Ratio	Ratio of female to male	High	Balanced (1:1)
Sex Determination	Temperature/environmentally determined or genetic	High	Chromosomal
Parental Investment	The level of parental expenditure to benefit offspring	Low	Altricial (young are hatched or born in an undeveloped state and require care and feeding by the parent[s])
Life Span	Average period between birth and death of an individual	Moderate	1–25 years
Generation Time	The average time between two successive generations	Moderate	1–25 years
Age of Sexual Maturity	Average age of first reproduction	High	Rapid (early relative to lifespan)
Age Structure	A summary of the number of individuals in each age class	Moderate	Balanced (age classes are roughly equal)
Recruitment	Proportion of juveniles surviving to adulthood	Moderate	Approximately half

Appendix 4: Other Future Scenario Results

Given each states' management plans, the two mortality scenarios we describe in Chapters 5 and 6 represent future scenarios that are consistent with state management plans and/or consistent with past observed levels of harvest and lethal depredation control in Michigan, Minnesota, and Wisconsin. However, in order to capture a broader range of possible future population sizes and extinction risk, in this appendix, we analyze one additional mortality scenario (Mortality Scenario X). As we discuss in more detail below, while this additional mortality scenario is possible, Mortality Scenario X is inconsistent with both the goals of all three states' management plans and past practice in the states.

Description of Mortality Scenario X

In Mortality Scenario X, we calculate the harvest rate necessary to reduce the population to 200 gray wolves in Michigan, 1,600 gray wolves in Minnesota, and 250 gray wolves in Wisconsin in 5 years, assuming maximum past observed rates of lethal depredation control (as derived for Mortality Scenario 2 in Chapter 5 above) (Table A 9). These population sizes represent the level that all three states intend to manage above in order to ensure they maintain viable gray wolf populations within their respective boundaries (see *Management and Conservation Efforts* in Chapter 3 above).[32] We apply this harvest rate to the population for the first 5 years of the simulations. Once the modeled populations reach these population sizes, we assume the populations do not grow above these levels (i.e., harvest and/or lethal depredation control remove any gray wolves above 200 gray wolves in Michigan, 1,600 gray wolves in Minnesota, and 250 gray wolves in Wisconsin). As in the other scenarios, we assume that lethal depredation control (in this case, at the maximum past observed rate), disease, and black swan events continue once each state's population reaches these sizes or if the population is below these sizes.

[32] These population sizes represent larger population sizes than the Federal recovery criteria outlined in the 1992 Revised Recovery Plan for the Eastern Timber Wolf (Revised Recovery Plan). For example, in the Minnesota Plan, Minnesota DNR committed to a population size of 1,600 gray wolves as the population size at which the state would implement management actions to reverse population declines (MN DNR 2022, p. 28). Therefore, we modeled Mortality Scenario X as the harvest rate that would reduce the population size in Minnesota to 1,600 gray wolves in 5 years, assuming average past observed rates of lethal depredation control. Although the Revised Recovery Plan did not establish a specific numerical criterion for the Minnesota gray wolf population, it did identify, for planning purposes, a population goal of 1,251–1,400 gray wolves for the Minnesota population (Service 1992, p. 28). This recovery planning goal is lower than the state management plan's threshold of 1,600 gray wolves. The Revised Recovery Plan indicated that a second population outside of Minnesota should consist of at least 200 gray wolves (if more than 100 mi (160 km) from the Minnesota wolf population) or 100 gray wolves (if within 100 mi (160 km) of a self-sustaining wolf population, such as Minnesota). The Michigan and Wisconsin populations are both within 100 miles of the Minnesota population. Therefore, the recovery goals indicate that there need only be 100 gray wolves in Michigan and Wisconsin combined. However, according to their management plans, these states both intend to manage well above 100 gray wolves (Michigan DNR intends to manage above 200 gray wolves (MI DNR 2022a, pp. 23–24) and Wisconsin DNR intends to manage above 250 gray wolves, the level at which gray wolves would be relisted as a threatened species in the state (WI DNR 2023a, pp. 126–127). While these planning goals in the Revised Recovery Plan represent smaller populations than the ones we model in Mortality Scenario X, we used the details from each state's management plan (rather than from Federal planning documents that apply to listed species, like the Revised Recovery Plan) to inform this scenario because the state management plans will guide state-level management should gray wolves be delisted.

This scenario reflects a situation where legislative or management objectives result in a reduction in gray wolf population sizes to the identified thresholds where management would change to halt or reverse decline in each state (MI DNR 2022a, pp. 23, 37; MN DNR 2022, pp. 28, 30–31, 51; WI DNR 2023a, pp. 127–128). We analyze this scenario as a hypothetical to account for the possibility that gray wolf population sizes could be reduced by changes to allowable levels of harvest and/or lethal depredation control. However, this scenario is inconsistent with state management plans given that, in their management plans, none of the three states express an intent to reduce the size of their gray wolf populations to these population sizes (MI DNR 2022a, entire; WI DNR 2023a, entire; MN DNR 2022, entire; see Chapter 3 and Chapter 5 above). In fact, the new management plans in Minnesota, Michigan, and Wisconsin indicate that the states intend to manage gray wolf populations similar to or more conservatively than in the past (MI DNR 2022a, entire; MN DNR 2022, entire; and WI DNR 2023a, entire).

Minnesota DNR recently revised its gray wolf management plan (see Chapter 3 above). The Minnesota Plan recommends maintaining a population comparable to recent estimates (2,200–3,000 wolves) that is distributed across the majority of the current gray wolf range in Minnesota (MN DNR 2022, p. 31). Therefore, Minnesota's plan indicates an intent to maintain population stability, rather than an intent to use regulated harvest or lethal depredation control to reduce the size of the gray wolf population to 1,600 in the state (MN DNR 2022, p. 51). Moreover, the Minnesota Plan includes the potential harvest rates the state would consider based on the current size or trend of the population (MN DNR 2022, p. 51). The harvest rates we model in Mortality Scenario X far exceed these harvest rates the Minnesota DNR proposes in its management plan, especially as the population decreases in the future under this scenario; therefore, the harvest rates we model in this scenario are inconsistent with Minnesota DNR's intended management regime.

Similarly, the Wisconsin Plan indicates its intent to manage the gray wolf population in a manner that maintains statewide gray wolf abundance and distribution at levels comparable to recent years (overwinter estimates of approximately 800 to 1,200 gray wolves) (WI DNR 2023a, pp. 127–128). In regard to the threshold for listing as a state threatened species (i.e., 250 gray wolves (WI DNR 2023a, pp. 126–127)), the Wisconsin plan "recommends the department demonstrate dedication to long-term sustainable management of gray wolves in the state by avoiding any actions and mitigating any issues which may result in the gray wolf population approaching these thresholds" (WI DNR 2023a, pp. 127–128). Therefore, the Wisconsin Plan also provides no indication that the state plans to use regulated harvest or lethal depredation control to substantially reduce the size of its gray wolf population to 250 wolves.

Finally, the Michigan Plan includes a goal of maintaining a viable gray wolf population in the state above a level that would lead to its classification as threatened or endangered at either the state or Federal level (MI DNR 2022a, p. 21). Although having 200 gray wolves in the state would meet this criterion, the Michigan Plan clarifies that this is not a target population size and that the Michigan gray wolf population should be greater than that minimum (MI DNR 2022a, pp. 22–23). Therefore, the Michigan Plan does not indicate that the state plans to reduce its gray wolf population to 200 gray wolves. Overall, these plans illustrate that the Michigan, Minnesota, and Wisconsin DNRs do not intend to manage their populations down to 200, 1,600, or 250 gray wolves, respectively (as Mortality Scenario X models).

In addition to being inconsistent with the stated intentions in each states' management plans, this scenario is also inconsistent with the past rates of harvest each state has previously achieved (i.e., inconsistent with past practice for mortality management in the states). The harvest rates we use in our projections for this scenario (see Table A 10 below) are more than fifteen times higher than the maximum past observed harvest rate in Michigan (3.1 percent), approximately double the maximum past observed harvest rate in Minnesota (14 percent), and approximately double the maximum past observed harvest rate in Wisconsin (25.2 percent). When we consider lethal depredation control and harvest control rates together, the combined mortality rates in Mortality Scenario X still far exceed the maximum mortality from harvest and lethal depredation control that has occurred in the past in each of these three states (more than nine times the maximum past observed harvest and lethal depredation control rate in Michigan (5.6 percent), 50 percent higher than the maximum past observed harvest and lethal depredation control rate in Minnesota (24 percent), and almost double the maximum past observed harvest and lethal depredation control rate in Wisconsin (32.4 percent)).

We analyzed this additional mortality scenario in combination with the same two disease scenarios described in Chapter 5 (Observed YNP disease rates and Observed YNP disease rates + added vertebrate black swan events). Therefore, in our projections in this appendix, we estimated the future number of wolves in each state under two combinations of future scenarios, spanning two disease scenarios and one additional mortality scenario (as outlined in Table A 9).

Table A 9. Two combinations of additional future scenarios analyzed in this appendix; these scenarios include harvest rates that are inconsistent with state management plans and past observed rates of harvest.

	Disease Scenario	Mortality Scenario
1	***Observed YNP disease rates***	***Mortality Scenario X:*** • Harvest rate necessary to reduce the population size in Michigan to 200 gray wolves, in Minnesota to 1,600 gray wolves, and in Wisconsin to 250 gray wolves in 5 years (assuming maximum past observed levels of lethal depredation control in each state from years when this mortality was authorized)
2	***Observed YNP disease rates + added vertebrate black swan events***	***Mortality Scenario X:*** • Harvest rate necessary to reduce the population size in Michigan to 200 gray wolves, in Minnesota to 1,600 gray wolves, and in Wisconsin to 250 gray wolves in 5 years (assuming maximum past observed lethal depredation control rates in each state from years when this mortality was authorized)

Table A 10. Harvest rates (percent of gray wolves killed annually through legal hunting and trapping) and lethal depredation control rates (percent of gray wolves killed annually by the public, state, or Federal agencies in response to depredation events) in each modeled state under the additional scenario analyzed in this appendix (in which levels of harvest are inconsistent with state management plans and *past observations). Harvest in our future scenarios stops once populations reach a size of 200, 1,600, or 250 gray wolves, respectively, in Michigan, Minnesota, and Wisconsin. Harvest rates for Mortality Scenario X were designed to reduce the population to 200, 1,600, and 250 gray wolves, respectively, in Michigan, Minnesota, and Wisconsin within 5 years, assuming maximum past observed levels of lethal depredation control. Once populations reach these sizes in each state, we assume harvest would cease; therefore, the harvest rates in Mortality Scenario X no longer apply after the first 5 years of the modeling period (i.e., once the populations reach these sizes, we assume states no longer harvest wolves). We also assume that states would manage the population such that it does not increase above these sizes, once the populations reach these sizes (i.e., in our model, the population cannot exceed 200, 1,600, or 250 gray wolves, respectively, in Michigan, Minnesota, and Wisconsin after the first 5 years of the modeling period).*

	Michigan	Minnesota	Wisconsin
Harvest Rate	53.0	33.0	53.0
Lethal Depredation Control Rate	2.5	10.0	7.5

Considerations for the Interpretation of Results from Mortality Scenario X

In addition to being inconsistent with how states intend to manage, there are multiple factors that may make it difficult for states to achieve and sustain the population reductions projected in Mortality Scenario X. First, in our model, we assumed that harvest would occur at the same rate statewide every year for 100 years into the future. We assume a constant rate instead of a constant number of wolves will be removed from the population because as the population declines, wolves will likely become more difficult to find and therefore, overall fewer wolves will be harvested. However, gray wolves can be found over broad expanses of the Western Great Lakes (Michigan, Minnesota, and Wisconsin), and because areas within these states have varied levels of human access, harvest is not uniform. This circumstance results in areas (e.g., the Boundary Waters Wilderness Area in Minnesota, which connects to the Quetico Provincial Park wilderness area in Canada) that provide refugia where harvest is low, even when there is increased human pressure elsewhere, which may act to limit total harvest across some states. In the early 20th century, when gray wolves were extirpated from the entirety of the lower-48 United States, they were never extirpated from northeast Minnesota, an area with designated wilderness, less human access, and connectivity to source populations in Canada, further illustrating the existence of refugia for gray wolves within the Western Great Lakes. These refugia may make it difficult to achieve a consistently high harvest rate statewide. Additionally, Wisconsin manages wolf harvest by zones and its management plan indicates that harvest will vary from zone to zone depending on objectives (WI DNR 2023a, pp. 117–121). We were not able to account for this spatial heterogeneity in harvest within a state in our model because our units of analysis were entire states or large portions of a state. Second, while intense efforts to intentionally reduce gray wolf populations in relatively small, localized areas have been successful in the short term, when these efforts ceased, gray wolf populations quickly rebounded to pre-control levels or exceeded pre-control levels when the effected wolf population was well connected to other wolf populations; this demonstrates gray wolves' resilience to population reduction efforts (Ballard et al. 1987, p. 30; Boertje et al. 1996, pp. 479–480, 487; Hayes and Harestad 2000, pp. 43–45; Hayes et al. 2003, pp. 14, 25–26; Boertje et al. 2017, p. 437; B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development (B.C. Ministry) 2021, entire; Service 2023, 175–176).

While we have observed broad-scale reductions in gray wolf abundance in the historical past (i.e., when wolves were almost extirpated from the lower-48 United States in the early 20th century), these eradication programs relied on unregulated and widespread use of poisons, along with unregulated harvest incentivized through bounty programs and the use of professional trappers. Currently, the regulatory landscape in the Western Great Lakes does not allow widespread use of poison nor does it authorize bounty programs; moreover, harvest is currently regulated in the Western Great Lakes (e.g., regulatory bodies with management authority can change season regulations). At present, the use of poison in the United States is highly regulated or illegal at the Federal level (40 CFR 152.175) and there are no indications these regulations will become less restrictive in the future.

Results of Mortality Scenario X

Under Mortality Scenario X, harvest and lethal depredation control rates combined were 55.5 percent annually in Michigan, 43 percent annually in Minnesota, 60.5 percent annually in Wisconsin until populations declined to 200 gray wolves in Michigan, 1,600 gray wolves in Minnesota, and 250 gray wolves in Wisconsin in 5 years. This mortality scenario resulted in a median projected population of approximately 1,900 gray wolves under both disease scenarios in 100 years [95 percent Credible Interval 1,413–2,010 with observed YNP disease rates and 929–2,003 with added black swan events] (Figure A 2, Table A 11b). These population projections represent a median decline of 59–60 percent relative to the current population. No individual simulated population fell below our lower threshold for an effective population size of 50 (192 wolves) or our quasi-extinction threshold (5 wolves) at any time over our 100-year projection under any of the additional scenario combinations we analyzed. However, 0.003 percent of simulations fell below 417 wolves with Observed YNP Disease Rates, and 1.050 percent of simulations fell below 417 wolves with added black swan events.

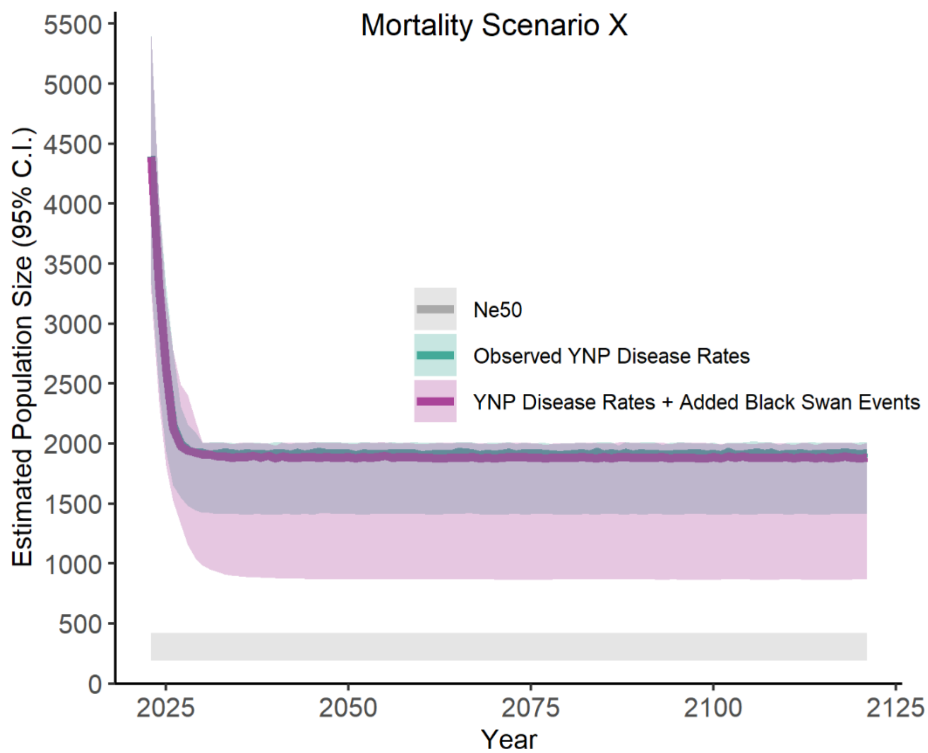

Figure A 2. Simulated median gray wolf population size (solid line) and 95 percent credible interval (shaded area) in Michigan, Minnesota, and Wisconsin with Mortality Scenario X combined with observed YNP disease rates in green and Mortality Scenario X combined with observed YNP disease rates plus added black swan events in pink. The gray bar represents the estimated census population size that is equivalent to N_e50-an effective population size of 50 (the threshold for avoiding inbreeding depression, 192-417).

Table A 11. Median, and lower- and upper-95 percent credible interval (CI) for population size and percent change in population size relative to the starting population size in the Western Great Lakes (Michigan, Minnesota, and Wisconsin) at the end of a) a 10 year and b) a 100-year timeframe of our simulations in two additional future disease and mortality scenario combinations. Percent of simulations falling below a particular threshold represents the percent of 2 million simulations where the population size fell below 192 or 417 at least once over the 100-year timeframe.

a) Projected gray wolf population size 10 years into the future

Mortality Scenario	Disease Scenario	Median Population Size at 10 Years	Percent Change from Starting Population Size
Scenario X	**Observed YNP disease rates**	1,918 (95% C.I. 1,413 – 2,010)	-59 (95% C.I. -71 to -47)
Scenario X	**Observed YNP + added black swan**	1,909 (95% C.I. 871 – 2,380)	-60 (95% C.I. -81 to -48)

b) Projected gray wolf population size 100 years into the future

Mortality Scenario	Disease Scenario	Median Population Size at 100 Years	Percent Change from Starting Population Size	Percent of simulations falling below 192	Percent of simulations falling below 417
Scenario X	**Observed YNP disease rates**	1,915 (95% C.I. 1,413 – 2,010)	-59 (95% C.I. -71 to -48)	0.000	0.003
Scenario X	**Observed YNP + added black swan**	1,894 (95% C.I. 929 – 2,003)	-60 (95% C.I. -79 to -48)	0.000	1.050

As we discuss in greater detail in Chapter 3, ultimately gray wolf population sustainability is a function of the productivity of the population, its proximity to other gray wolf populations, and the levels of human-caused mortality (Fuller et al. 2003, p. 185). Where productivity is average to high and source populations are near, gray wolf populations can sustain higher rates of mortality than populations with lower productivity. As discussed above, for Mortality Scenario X, there were no individual simulations in which the population size in the Western Great Lakes dropped below our lower threshold of an effective population size of 50 (i.e., 192 gray wolves) or quasi-extinction (5 gray wolves), even considering the projected increases in harvest. Further, 0.003 percent of simulations with observed YNP disease rates and 1.050 percent of simulations with observed YNP disease rates and added black swan events fell below our upper threshold for an effective population size of 50 (i.e., 417 wolves). This indicates that, as long as future population productivity and connectivity remain consistent with past observed data, as constructed in our model, and as long as the Michigan, Minnesota, and Wisconsin DNRs close harvest seasons when/if thereshold numbers of 200, 1,600, or 250 gray wolves are reached, respectively, increases in human-caused mortality are not projected to have a large effect on overall gray wolf resiliency in the Western Great Lakes. In short, when combined with our results for Mortality Scenarios 1 and 2 in Chapter 6, our results for this additional scenario indicate that the population of gray wolves in the Western Great Lakes would have sufficient levels of productivity to prevent extirpation across a gradient of minimal to high mortality scenarios even with catastrophic levels of disease, assuming current levels of connectivity are maintained and our other assumptions are satisfied. This demonstrates the gray wolf in the Western Great Lakes' continued ability to withstand stochastic events (resiliency) and catastrophic events such as black swan levels of disease (redundancy) into the future.

Even though the harvest and disease scenarios we analyzed are not likely to result in quasi-extinction in the Western Great Lakes, harvest at the rates applied in Mortality Scenario X would still result in population decreases. Under Mortality Scenario X, including black swan events, there could be an approximately 60 percent (95 percent Credible Interval, 48–79 percent) decline in the population size in the Western Great Lakes in 100 years. Additionally, the individual populations in Michigan, Minnesota, and Wisconsin could individually decrease by approximately 70, 52, and 78 percent, respectively, under the level of mortality in Mortality Scenario X (Appendix 5). However, this scenario is inconsistent with the management framework in each state's management plan. None of the three states indicate any intention to reduce gray wolf population sizes to the levels in this scenario. This scenario is also inconsistent with the past levels of harvest and lethal depredation control the states' have aimed to and been able to achieve. The states have not provided any information to indicate they plan to pursue less restrictive management of wolves, as compared to the levels of mortality that occurred during previous periods of delisting. Overall, the state plans in the Western Great Lakes indicate that each state intends to continue managing gray wolf populations similar to or more conservatively than in the past (MI DNR 2022a, entire; MN DNR 2022, entire; and WI DNR 2023a, entire). In addition, given the relatively large population that is projected to remain (given the assumptions of our model), and the minimal risk of quasi-extinction, this population decrease is unlike to meaningfully reduce the resiliency and redundancy of the gray wolf in the Western Great Lakes in the future.

Similar to our understanding of representation under Mortality Scenarios 1 and 2, the innate behaviors and life history traits that contribute to gray wolves' dispersal and colonization ability and behavioral and phenotypic plasticity would not change under Mortality Scenario X. The attribute of adaptive capacity that is susceptible to change is evolutionary genetic potential. Under Mortality Scenario X with the added black swan events (the highest combination of mortality we analyzed), there would be a median of 1,894 gray wolves in the Western Great Lakes in 100 years. Using the generalized threshold that an effective population size of 500 (equivalent to a census population size between approximately 1,932 and 4,167 gray wolves according to the ratio of effective to census population size we calculate in Appendix 1) is a reasonable target to ensure retention of evolutionary genetic potential (Franklin 1980, p. 147), our projections for all four of our future scenario combinations result in median projected population sizes below this threshold. In assessing the potential for significant long-term decline of genetic diversity in wolves, however, it is important to consider the species-specific information that is available and how that differs from the generalized 50/500 rule. For example, all model runs result in population sizes higher than those that multiple wolf-specific PVAs have indicated would result in a high retention of genetic diversity (e.g., Liberg 2005, pp. 39–40 (600 to 800 wolves); Liberg and Sand 2012, p. 12 (200 to 400 wolves)). Perhaps most importantly, unlike the assumption of isolation involved in the generalized threshold of an effective population size of 500 for the retention of evolutionary genetic potential (i.e., 1,932 to 4,167 gray gray wolves), the Western Great Lakes does not represent an isolated population, as connectivity with the Canadian Provinces of Manitoba and Ontario (where there are over 14,000 gray wolves; see Chapter 4) will likely continue to provide dispersers into the future that may act to buffer any potential losses of genetic diversity. As such, although reductions in abundance could theoretically lead to decreases in genetic diversity under this scenario, such decreases are unlikely to be significant or sustained, and thus are unlikely to negatively affect adaptive capacity in the future.

The size of the Western Great Lakes population is not related to the reasons why we do not expect the gray wolf population in the Western Great Lakes to expand to recolonize vacant habitat outside of Michigan, Minnesota, and Wisconsin. As such, the results for Mortality Scenario X do not change our expectations regarding lack of future recolonization outside of these three states. Therefore, while we expect the gray wolf population in the Western Great Lakes to retain its current ability to withstand stochastic and catastrophic events and adapt to future change, redundancy and representation is unlikely to increase in the future, given that gray wolf distribution is unlikely to increase greatly in the Eastern United States.

Appendix 5: State-Level Results

Michigan

Our projections for Michigan indicated that, with minimum past observed harvest (3.1 percent) and lethal depredation control (1.0 percent) rates (Mortality Scenario 1, Table A 12), the median gray wolf population size in Michigan would be 569 to 579 wolves in 10 years and 549 to 569 wolves in 100 years (depending on the disease scenario). This represents a median population decline of 8 to 9 percent in 10 years, and 10 to 20 percent decline in 100 years from the starting population size of 631 wolves (Figure A 3, Table A 13). With maximum past observed harvest (3.1 percent) and lethal depredation control (2.5 percent) rates (Mortality Scenario 2, Table A 12), median gray wolf population size in Michigan would be 531 to 540 gray wolves in 10 years and 502 to 521 gray wolves in 100 years (depending on the disease scenario). This represents a median population decline of 14 to 15 percent in 10 years, and 17 to 20 percent in 100 years from the starting population size (Figure A 3, Table A 13). Under Scenario X (Table A 12), in which a 53 percent harvest rate combined with a 2.5 percent lethal depredation control rate reduced the size of the gray wolf population in Michigan to 200 gray wolves in 5 years and maximum past observed lethal depredation control rates occurred, combined with added black swan events, the median projected gray wolf population size in 100 years was 197 gray wolves, representing a median decline of 70 percent relative to the starting population size (Figure A 3, Table A 13).

Table A 12. Harvest and Lethal Depredation Control Rates included in each mortality scenario for Michigan. Harvest rate varied based on gray wolf population size.

Mortality Scenario	Harvest Rate		Lethal Depredation Control Rate
	Fewer than 200 wolves	Greater than 200 wolves	
Scenario 1	0	3.1	1.0
Scenario 2	0	3.1	2.5
Scenario X	0	53	2.5

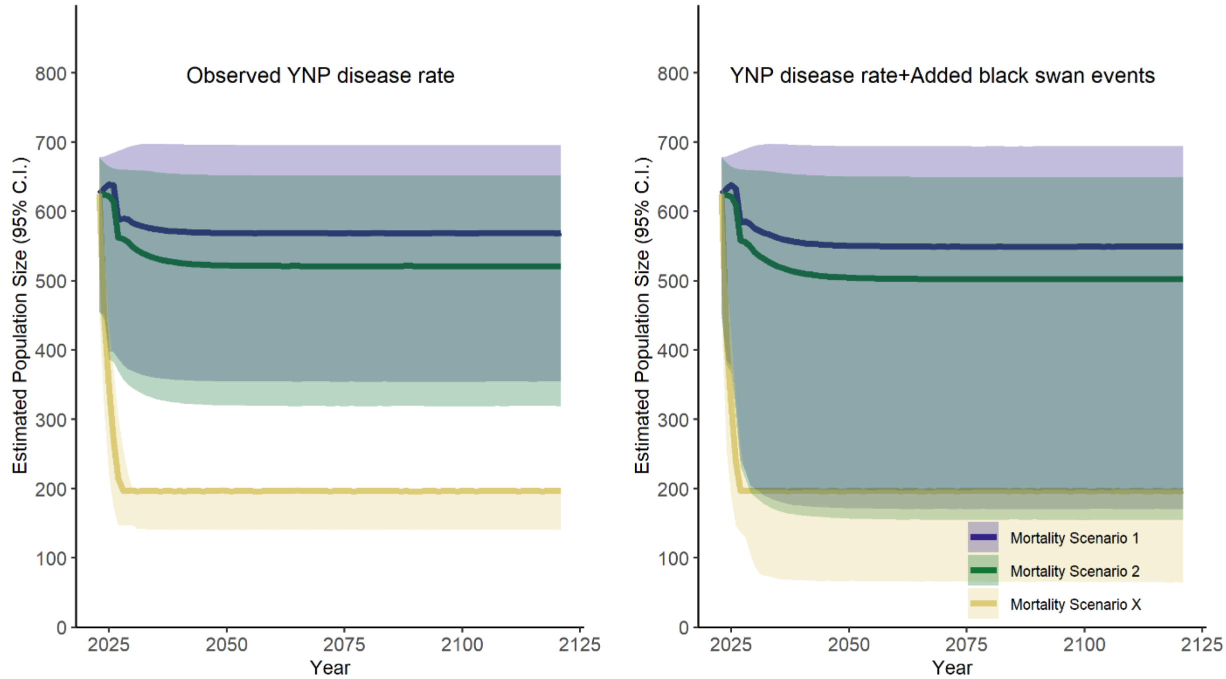

Figure A 3. Projected median gray wolf population size (solid line) and 95 percent credible interval (shaded area) in Michigan with Mortality Scenario 1 in purple, Mortality Scenario 2 in green, and Mortality Scenario X in yellow. The panel on the left includes the results for the three mortality scenarios combined with Observed YNP disease rates. The panel on the right includes the results for the three mortality scenarios combined with Observed YNP disease rates plus added black swan events.

Table A 13. Median, and lower- and upper-95 percent credible interval (CI) for population size and percent change in population size relative to the starting population size in Michigan at the end of a) a 10 year and b) a 100-year timeframe of our simulations in six future disease and mortality scenario combinations.

a) Projected gray wolf population size in Michigan 10 years into the future

Disease Scenario	Mortality Scenario	Median Population Size at Year 10	Percent Change from Starting Population Size
Observed YNP disease rates	**Scenario 1**	579 (95% C.I. 364 – 697)	-8 (95% C.I. -42 to 14)
Observed YNP disease rates	**Scenario 2**	540 (95% C.I. 337 – 659)	-14 (95% C.I. -46 to 8)
Observed YNP Disease Rates	**Scenario X**	197 (95% C.I. 141 – 198)	-69 (95% C.I. -78 to -66)
YNP + added black swan	**Scenario 1**	569 (95% C.I. 190 – 697)	-9 (95% C.I. -69 to 14)
YNP + added black swan	**Scenario 2**	531 (95% C.I. 178 – 659)	-15 (95% C.I. -71 to 8)
YNP + added black swan	**Scenario X**	197 (95% C.I. 74 – 198)	-70 (95% C.I. -88 to -66)

b) Projected gray wolf population size in Michigan 100 years into the future

Disease Scenario	Mortality Scenario	Median Population Size at Year 100	Percent Change from Starting Population Size
Observed YNP disease rates	Scenario 1	569 (95% C.I. 354 – 696)	-10 (95% C.I. -44 to 13)
Observed YNP disease rates	Scenario 2	521 (95% C.I. 319 – 652)	-17 (95% C.I. -50 to 6)
Observed YNP disease rates	Scenario X	197 (95% C.I. 141 – 198)	-69 (95% C.I. -78 to -66)
YNP + added black swan	Scenario 1	549 (95% C.I. 170 – 694)	-13 (95% C.I. -73 to 13)
YNP + added black swan	Scenario 2	502 (95% C.I. 155 – 650)	-20 (95% C.I. -75 to -5)
YNP + added black swan	Scenario X	197 (95% C.I. 64 – 198)	-70 (95% C.I. -90 to -66)

Minnesota

Our projections for Minnesota indicated that, maintaining an objective population between 2,200 and 3,000 (Mortality Scenario 1, Table A 14; MN DNR 2022, p. 51), the median gray wolf population size in Minnesota would be 2,357 to 2,395 wolves in 10 years and 2,323 to 2,387 wolves in 100 years (depending on the disease scenario). This represents a median population decline of 18 to 19 percent in 10 years, and 19 to 21 percent in 100 years from the starting population size of 2,919 wolves (depending on the disease scenario) (Figure A 4, Table A 15). With the maximum observed harvest rates (14 percent) and maximum past observed lethal depredation control rates (10.0 percent) (Mortality Scenario 2), the median gray wolf population size in Minnesota would be 1,830 to 1,861 wolves in 10 years and 1,654 to 1,709 wolves in 100 years (depending on the disease scenario). This represents a median population decline of 35 to 36 percent in 10 years, and 41 to 43 percent in 100 years from the starting population size (depending on the disease scenario) (Figure A 4, Table A 15). Under Scenario X, in which a 33 percent harvest rate combined with a 10 percent lethal depredation control rate reduced the size of the gray wolf population in Minnesota to 1,600 wolves in 5 years and maximum past observed lethal depredation control rates occurred, combined with added black swan events, the median projected gray wolf population size in 100 years was 1,509 wolves, representing a median decline of 52 percent relative to the starting population size (Figure A 4, Table A 15).

Table A 14. Harvest and lethal depredation control rates applied in each mortality scenario for Minnesota. Harvest rates varied based on gray wolf population size.

Mortality Scenario	Harvest Rate		Lethal Depredation Control Rate
	Fewer than 1600 wolves	Between 1600 and 2000 wolves	
Scenario 1	NA	NA	NA
Scenario 2	0	14	10.0
Scenario X	0	33	10.0

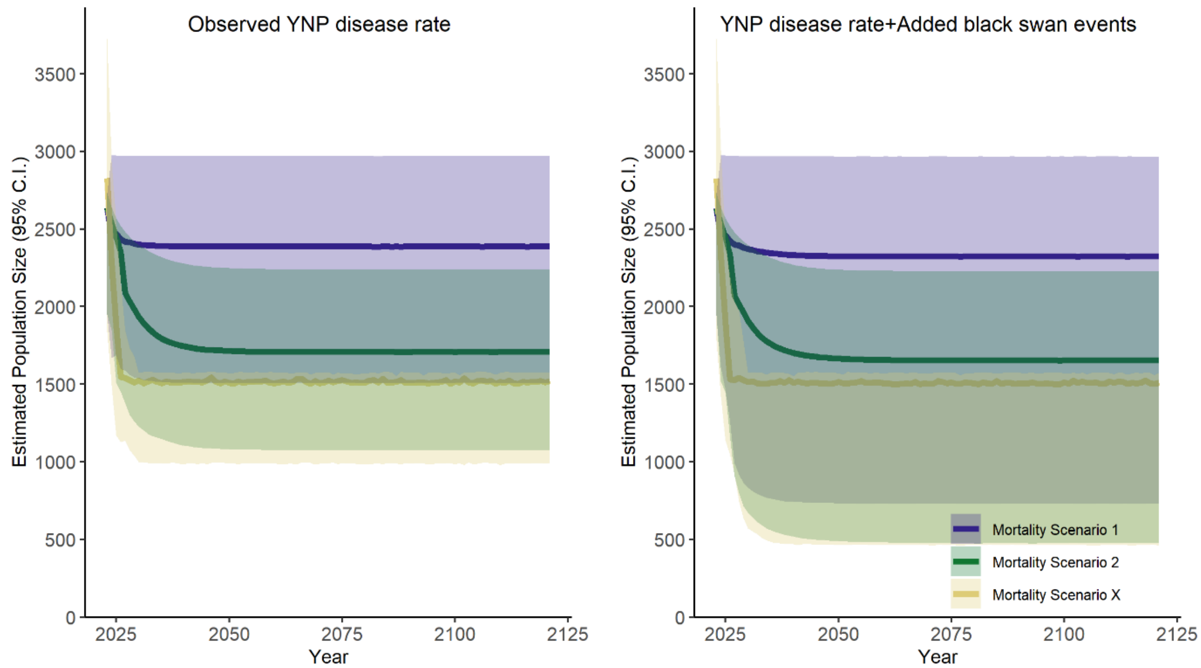

Figure A 4. Projected median gray wolf population size (solid line) and 95 percent credible interval (shaded area) in Minnesota with Mortality Scenario 1 in purple, Mortality Scenario 2 in green, and Mortality Scenario X in yellow. The panel on the left includes the results for the three mortality scenarios combined with Observed YNP disease rates. The panel on the right includes the results for the three mortality scenarios combined with Observed YNP disease rates plus added black swan events.

Table A 15. Median, and lower- and upper-95 percent credible interval (CI) for population size and percent change in population size relative to the starting population size in Minnesota, at the end of a) a 10 year and b) a 100-year timeframe of our simulations in six future disease and mortality scenario combinations.

a) *Projected gray wolf population size in Minnesota at year 10*

Disease Scenario	Mortality Scenario	Median Population Size at Year 10	Percent Change from Starting Population Size
Observed YNP disease rates	**Scenario 1**	2,395 (95% C.I. 1,524 – 2,970)	-18 (95% C.I. -51 to 25)
Observed YNP disease rates	**Scenario 2**	1,861 (95% C.I. 1,180 – 2,361)	-35 (95% C.I. -61 to 0)
Observed YNP disease rates	**Scenario X**	1,518 (95% C.I. 994 – 1,578)	-51 (95% C.I. -68 to -29)
YNP + added black swan	**Scenario 1**	2,357 (95% C.I. 794 – 2,968)	-19 (95% C.I. -72 to 24)
YNP + added black swan	**Scenario 2**	1,830 (95% C.I. 612 – 2,358)	-36 (95% C.I. -78 to -1)
YNP + added black swan	**Scenario X**	1,508 (95% C.I. 535– 1,573)	-51 (95% C.I. -81 to -29)

b) Projected gray wolf population size in Minnesota at year 100

Disease Scenario	Mortality Scenario	Median Population Size at Year 100	Percent Change from Starting Population Size
Observed YNP disease rates	**Scenario 1**	2,387 (95% C.I. 1,506 – 2,969)	-19 (95% C.I. -51 to 24)
Observed YNP disease rates	**Scenario 2**	1,709 (95% C.I. 1,075 – 2,240)	-41 (95% C.I. -65 to -9)
Observed YNP disease rates	**Scenario X**	1,521 (95% C.I. 993 – 1,577)	-51 (95% C.I. -68 to -28)
YNP + added black swan	**Scenario 1**	2,323 (95% C.I. 732 – 2,966)	-21 (95% C.I. -75 to 23)
YNP + added black swan	**Scenario 2**	1,654 (95% C.I. 477 – 2,228)	-43 (95% C.I. -84 to -10)
YNP + added black swan	**Scenario X**	1,509 (95% C.I. 462 – 1,575)	-52 (95% C.I. -84 to -40)

Wisconsin

Our projections for Wisconsin indicated that, if the state of Wisconsin maintains its wolf population size between 800 and 1,200 according to its management plan (Mortality Scenario 1, Table A 16), the median gray wolf population size in Wisconsin would be 897 to 914 wolves in 10 years and 885 to 911 wolves in 100 years (depending on the disease scenario). This represents a 9 to 10 percent decline in 10 years, and a 9 to 12 percent decline in 100 years from the starting population size of 1,007 wolves (Figure A 5, Table A 17). With maximum past observed harvest (25.2 percent) and lethal depredation control (7.2 percent) rates (Mortality Scenario 2, Table A 16), median gray wolf population size in Wisconsin would be 661 to 673 wolves in 10 years and 563 to 591 wolves in 100 years (depending on the disease scenario). This represents a median population decline of 32 to 33 percent decline in 10 years, and a 41 to 44 percent decline in 100 years from the starting population size (Figure A 5, Table A 17). Under Scenario X (Table A 16), in which a 53 percent harvest combined with a 7.5 percent lethal depredation control rate reduced the size of the gray wolf population in Wisconsin to 250 wolves in 5 years and maximum past observed lethal depredation control rates occurred, combined with added black swan events, the median projected gray wolf population size in 100 years was 237 wolves, representing a median decline of 78 percent relative to the starting population size (Table A 17).

Table A 16. Harvest and Control Rates applied in each mortality scenario for Wisconsin. Harvest rates varied based on gray wolf population size.

Mortality Scenario	Harvest Rate		Lethal Depredation Control Rate
	Fewer than 250 wolves	Greater than 250 wolves	
Scenario 1	NA	NA	NA
Scenario 2	0	25.2	7.2
Scenario X	0	53	7.5

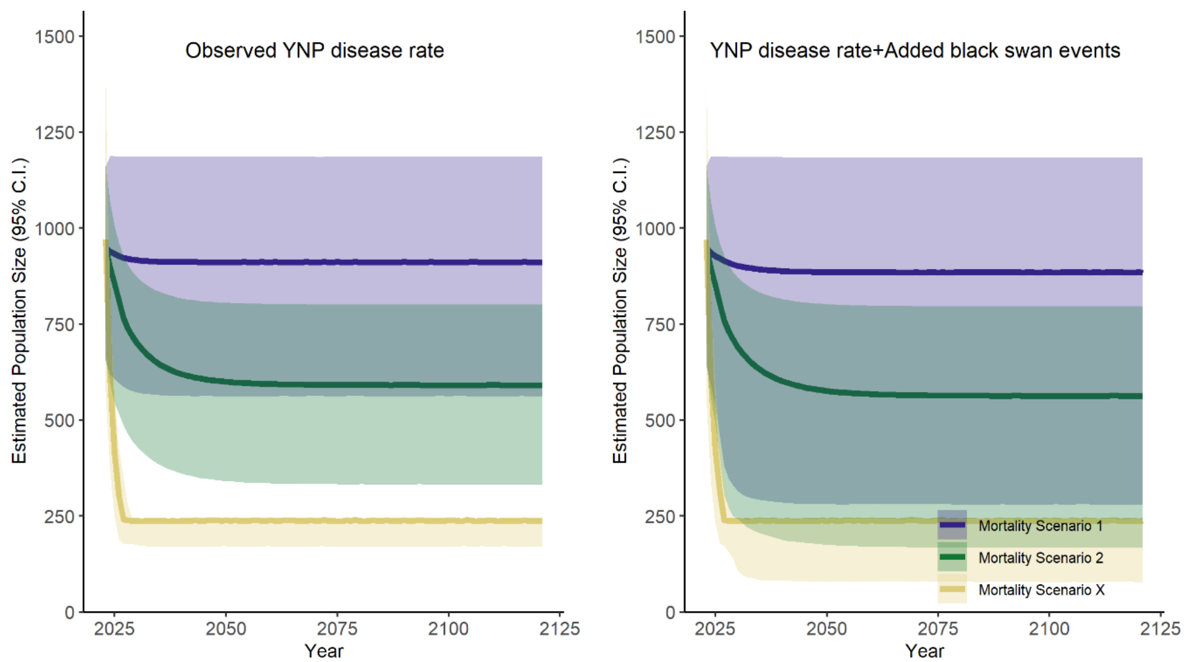

Figure A 5. Projected median gray wolf population size (solid line) and 95 percent credible interval (shaded area) in Wisconsin with Mortality Scenario 1 in purple, Mortality Scenario 2 in green, and Mortality Scenario X in yellow. The panel on the left includes the results for the three mortality scenarios combined with Observed YNP disease rates. The panel on the right includes the results for the three mortality scenarios combined with Observed YNP disease rates plus added black swan events.

Table A 17. Median, and lower- and upper-95 percent credible interval (CI) for population size and percent change in population size relative to the starting population size in Wisconsin, at the end of a) a 10 year and b) a 100-year timeframe of our simulations in six future disease and mortality scenario combinations.

a) Projected gray wolf population size in Wisconsin 10 years into the future

Disease Scenario	Mortality Scenario	Median Population Size at 10 Years	Percent Change from Starting Population Size
Observed YNP disease rates	Scenario 1	914 (95% C.I. 568 – 1186)	-9 (95% C.I. -49 to 57)
Observed YNP disease rates	Scenario 2	673 (95% C.I. 408 – 852)	-32 (95% C.I. -62 to 16)
Observed YNP Disease Rates	Scenario X	238 (95% C.I. 171– 242)	-78 (95% C.I. -86 to -64)
YNP + added black swan	Scenario 1	897 (95% C.I. 300 – 1185)	-10 (95% C.I. -69 to 56)
YNP + added black swan	Scenario 2	661 (95% C.I. 221 – 851)	-33 (95% C.I. -77 to 15)
YNP + added black swan	Scenario X	237 (95% C.I. 90 – 241)	-78 (95% C.I. -90 to -64)

b) Projected gray wolf population size in Wisconsin 100 years into the future

Disease Scenario	Mortality Scenario	Median Population Size at 100 Years	Percent Change from Starting Population Size
Observed YNP disease rates	Scenario 1	911 (95% C.I. 562 –1186)	-9 (95% C.I. -49 to 57)
Observed YNP disease rates	Scenario 2	591 (95% C.I. 332 – 801)	-41 (95% C.I. -70 to 3)
Observed YNP disease rates	Scenario X	238 (95% C.I. 171 – 243)	-77 (95% C.I. -85 to -63)
YNP + added black swan	Scenario 1	885 (95% C.I. 280 –1184)	-12 (95% C.I. -72 to 55)
YNP + added black swan	Scenario 2	563 (95% C.I. 167 – 796)	-44 (95% C.I. -84 to 1)
YNP + added black swan	Scenario X	237 (95% C.I. 77 – 242)	-78 (95% C.I. -93 to -64)

Appendix 6: Analysis of the Effects of Uncertainty in the Initial Population Size, *h*, and r_{max} Values for the Western Great Lakes Wolf Population

Summary: *We conducted a sensitivity analysis to evaluate the effects of the value of the intrinsic rate of growth (r_{max}), the per wolf effect of harvest and lethal depredation control (h) for the Western Great Lakes wolf populations, and the initial population size in Wisconsin, Minnesota, and Michigan on the results of our population projections. To achieve this, we ran 200,000 simulations of our model for all six of our future scenario combinations (two disease scenarios and three mortality scenarios) at the minimum and maximum estimated values of the r_{max}, h, and initial population size in Wisconsin, Minnesota, and Michigan (for a total of 24 projections, resulting from running each of the 6 future scenario combinations for the minimum and maximum values of r_{max}, and h (12 projections), and the minimum and maximum population sizes in Minnesota, Michigan, and Wisconsin (an additional 12 projections). Overall, results of Harvest Scenario 2 regardless of disease scenario, were most sensitive to changes in r_{max} and h in the Western Great Lakes, while results of Mortality Scenario X were least sensitive to changes in these parameters. Overall, our analysis indicates that results of Mortality Scenario X are robust to uncertainty associated with r_{max} and h, and all scenarios are robust to uncertainty associated with the initial population sizes in the Western Great Lakes states. These results are only valid across the range of values (the minimums and maximums) we included in our simulations.*

We conducted a sensitivity analysis to evaluate the effects of uncertainty in the initial population size, intrinsic rate of growth (r_{max} – the maximum intrinsic rate of growth exhibited when population sizes are small), and effect of harvest and lethal depredation control (*h* – the level of additive versus compensatory human-caused mortality where 0 is completely compensatory and 1 is completely additive) on the projected wolf population size in the Western Great Lakes wolf populations in Minnesota, Michigan, and Wisconsin. The results of our sensitivity analysis only apply over the range of values we used in the our scenarios, i.e., within the range of the minimum and maximum initial population size for Michigan, Minnesota, and Wisconsin, and the minimum and maximum r_{max}, and *h* values for the Western Great Lakes (Table A 18) estimated from fitting our density-dependent population model to observed data, which differ from the upper and lower credible intervals for these parameters reported in Chapter 5 because 95 percent credible intervals do not represent the absolute minimum and maximum values from the estimated distribution of potential parameter values. Additionally, distributions of values estimated from the density-dependent model are not normally distributed (some parameter distributions have very long tails); therefore, minimum and maximum estimated parameter values may represent values far outside the credible intervals. For example, this analysis examines the effect of the initial population size being as low as 516 or as high as 739 wolves in Michigan (the minimum and maximum initial population sizes we estimated for Michigan). Estimating the effects of using parameter values outside of the range of values estimated for use in our models would require making assumptions regarding linearity of the relationships between the parameters (Altman and Bland 1998, entire; Bartley et al. 2019, pp. 1–2). The best available science provides no basis for making these assumptions; therefore, we conducted our sensitivity analyses within these bounds following accepted methods for conducting such analyses (Altman and Bland 1998, entire; Bartley et al. 2019, pp. 1–2).

To evaluate the changes in the total projected population size that results from using the minimum and maximum values of various parameters (rather than the full distribution of the parameters estimated from the model, which is what we used in Chapters 5 and 6), we fixed the value of the initial population size, r_{max}, or h to the minimum or maximum value while allowing the other parameters to vary across the range of the distribution used to generate the results presented in Chapter 5 and 6 (Table 9). For example, to examine the effect of initial population size in Michigan, Minnesota, and Wisconsin, we first held the initial population sizes constant at the minimum values, and allowed all other parameters (i.e., r_{max}, and h, for the Western Great Lakes, and K for the individual states) to vary across the distributions reported in Chapter 5 (Table 9). We then held the initial population size in Michigan, Minnesota, and Wisconsin constant at the maximum value, and allowed all other parameters (i.e., r_{max}, and h for the Western Great Lakes, and K for the individual states) to vary across the distributions reported in Chapter 5 (Table 9). We then compared these results to determine the effect of initial population size on the population projections. We repeated this for the minimum and maximum r_{max} and h values for the Western Great Lakes.

We ran the model for each of the 24 projections once with a total of 200,000 simulations for each projection (i.e., 200,000 simulations in which one parameter is fixed and the full distribution was included for all the other parameters) (note in Chapters 5 and 6, we ran the 200,000 simulations 10 times for a total of 2 million simulations; see Supplementary Material B). Below, we report the results of this sensitivity analysis on the population projections for all Western Great Lakes states modeled (Michigan, Minnesota, and Wisconsin).

Table A 18. Minimum and maximum values evaluated in our analysis of uncertainty (i.e., minimum and maximum values estimated from fitting our density-dependent population model to observed data).

Parameter	Michigan	Minnesota	Wisconsin	Western Great Lakes
Initial Population size	Min: 516 Max: 739	Min: 1,040 Max: 4,786	Min: 170 Max: 1,895	Min: 1,726 Max: 7,420
r_{max}	NA	NA	NA	Min: 0.21 Max: 0.29
h	NA	NA	NA	Min: 0.38 Max: -0.17

Uncertainty Analysis for Initial Population Size

We examined the effect of varying the initial population size in Michigan, Minnesota, and Wisconsin on the median projected population size in all Western Great Lakes states modeled. Overall, projected population sizes were similar for a particular scenario, regardless of whether the initial population sizes in Michigan, Minnesota and Wisconsin was the maximum or minimum value from the density-dependent models described in Chapters 5 and 6 (Table A 19, Figure A 6). The largest differences between the projected population sizes estimated from the minimum initial population size versus the maximum initial population size are under Mortality Scenario 2; the difference between the projected population size with Michigan, Minnesota, and Wisconsin's maximum initial population size and minimum initial population size for Mortality

Scenario 2 is 67 wolves when combined with observed YNP disease rates and 29 wolves when combined with observed YNP disease rates and added black swan events. All other scenario combinations resulted in a less than 8-wolf difference between the projected population sizes from the minimum initial population size and the maximum initial population size. The percent of simulations falling below 192 wolves, the lower bound of our threshold for evaluating risk of inbreeding depression, at any time during our 100-year simulation period was zero, regardless of the initial population size. The percent of simulations falling below 417 wolves, the upper bound of our threshold for evaluating risk of inbreeding depression, was highest (1.08%) for Mortality Scenario X with added black swan disease events, when Michigan, Minnesota, and Wisconsin's population size was at its minimum population size; this probability is the approximately same as what results from our projections using the full distribution of the parameter values (1.05% of simulations falling below 417 wolves) in Appendix 4.

Table A 19. Results of population projections for the total wolf population in Michigan, Minnesota and Wisconsin when the initial population sizes in each state were at their maximums (population max) or minimums (population min). Projected population LCI indicates the lower 95 percent credible interval of the projected population size and projected population UCI indicates the upper 95 percent credible interval of the projected population size. The percent of simulations falling below 417 or 192 indicates the percent of 200,000 simulations that fell below 417 wolves or 192 wolves at least once over the 100-year time frame. Note that due to stochasticity inherent in the model, each model run (all 200,000 simulations) will produce slightly different results.

Disease Scenario	Mortality Scenario	Initial Population Size	Median Projected Population Size	Projected Population LCI	Projected Population UCI	Percent of simulations falling below 417	Percent of simulations falling below 192
Observed YNP disease rates	Scenario 1	population min	3,780	2,796	4,564	0.000%	0.000%
		population max	3,781	2,793	4,561	0.000%	0.000%
Observed YNP disease rates	Scenario 2	population min	2,961	2,146	3,654	0.000%	0.000%
		population max	3,028	2,200	3,741	0.000%	0.000%
Observed YNP disease rates	Scenario X	population min	1,919	1,402	1,986	0.000%	0.000%
		population max	1,926	1,425	1,998	0.000%	0.000%
Observed YNP disease rates + added black swan events	Scenario 1	population min	3,634	2,058	4,521	0.009%	0.000%
		population max	3,634	2,059	4,523	0.002%	0.000%
Observed YNP disease rates + added black swan events	Scenario 2	population min	2,860	1,532	3,628	0.014%	0.000%
		population max	2,889	1,578	3,666	0.011%	0.000%
Observed YNP disease rates + added black swan events	Scenario 3	population min	1,879	859	1,980	1.079%	0.003%
		population max	1,884	868	1,995	1.036%	0.002%

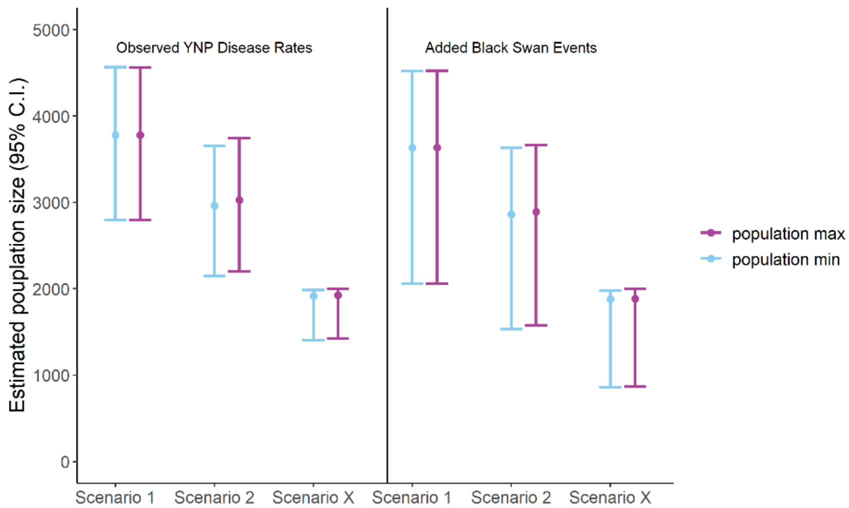

Figure A 6. Median projected wolf population size with 95 percent credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western Great Lakes states region's wolf populations modeled under three different scenarios (Mortality Scenario 1, Mortality Scenario 2 and Mortality Scenario X), when initial population size in Michigan, Minnesota, and Wisconsin was either the minimum (blue) or maximum (pink) value estimated from the density-dependent models described in Chapter 5.

The results of this analysis indicate that, when examining the range of initial population sizes within the minimum and maximum values used in the simulations for Michigan, Minnesota, and Wisconsin there is minimal effect of the initial population size in Michigan, Minnesota and Wisconsin on the median projected population size in all Western Great Lakes states modeled for all Mortality Scenarios. In other words, the total future projected population size is only slightly different (i.e., within 67 wolves) for Mortality Scenario 2 combined with either disease scenario, whether we start with 1,726 wolves in the Western Great Lakes (the minimum value we estimated from observed data) or 7,420 wolves in the Western Great Lakes states (the maximum value). For Mortality Scenarios 1 and X, the differences are negligible between the projected population size at minimum or maximum initial population size values (i.e., differences <8 wolves). However, this analysis does not provide an estimate of the potential decrease in the total projected population size in all Western Great Lakes states modeled if the initial population size in the Western Great Lakes was below 1,726 wolves or above 7,240 wolves.

Uncertainty Analysis for Intrinsic Rate of Growth (r_{max})

We examined the effect of varying the intrinsic rate of growth in all Western Great Lakes states (Michigan, Minnesota, and Wisconsin) on the median projected population size in the Western Great Lakes states included in our models. Overall, projected population sizes were similar for a particular scenario, regardless of whether the initial intrinsic rate of growth in Michigan, Minnesota and Wisconsin was the minimum or maximum value estimated from the density-dependent models described in Chapters 5 and 6 (Table A 20, Figure A 7). The largest differences between the projected population sizes estimated from the minimum intrinsic rate of growth versus the maximum intrinsic rate of growth are under Mortality Scenario 2; the difference between the projected population size with the minimum intrinsic rate of growth and the maximum intrinsic rate of growth for Mortality Scenario 2 is 423 wolves when combined with observed YNP disease rates and 544 wolves when combined with observed YNP disease rates and added black swan events. The difference between the projected population size with the maximum intrinsic growth and minimum intrinsic rate of growth for Mortality Scenario 1 is 228 wolves when combined with observed YNP disease rates and 294 wolves when combined with observed YNP disease rates and added black swan events, and finally for Mortality Scenario X the differences were smallest (67 with observed YNP disease rates and 84 when combined with observed YNP disease rates and added black swan events). The percent of simulations falling below 192 wolves, the lower bound of our threshold for evaluating risk of inbreeding depression, at any time during our 100-year simulation period was only greater than zero for Mortality Scenario X and for Scenario 2 with added black swan events and these probabilities were less than or equal to 0.01%, regardless of the initial intrinsic rate of growth. The percent of simulations falling below 417 wolves, the upper bound of our threshold for evaluating risk of inbreeding depression, was highest (1.64%) for Mortality Scenario X with added black swan disease events, when the intrinsic rate of growth is at its minimum value of 0.21. This probability is higher than what results from our projections using the full distribution of the parameter values (1.05% of simulations falling below 417 wolves) in Appendix 4.

Table A 20. Results of population projections for the total wolf population in Michigan, Minnesota and Wisconsin when intrinsic rate of growth (r_{max}) was at its maximum (maximum r_{max}) or minimum (minimum r_{max}). Projected population LCI indicates the lower 95 percent credible interval of the projected population size and projected population UCI indicates the upper 95 percent credible interval of the projected population size. The percent of simulations falling below 417 or 192 indicates the percent of 200,000 simulations that fell below 417 wolves or 192 wolves at least once over the 100-year time frame. Note that due to stochasticity inherent in the model, each model run (all 200,000 simulations) will produce slightly different results.

Disease Scenario	Mortality Scenario	Intrinsic Rate of Growth (r_{max}) Value	Median Projected Population Size	Projected Population LCI	Projected Population UCI	Percent of simulations falling below 417	Percent of simulations falling below 192
Observed YNP disease rates	Scenario 1	maximum (r_{max})	3,872	2,936	4,603	0.000%	0.000%
		minimum (r_{max})	3,644	2,621	4,506	0.000%	0.000%
Observed YNP disease rates	Scenario 2	maximum (r_{max})	3,218	2,403	3,838	0.000%	0.000%
		minimum (r_{max})	2,795	1,974	3,604	0.000%	0.000%
Observed YNP disease rates	Scenario X	maximum (r_{max})	1,945	1,445	2,002	0.000%	0.000%
		minimum (r_{max})	1,878	1,366	1,961	0.000%	0.000%
Observed YNP disease rates + added black swan events	Scenario 1	maximum (r_{max})	3,754	2,230	4,571	0.001%	0.000%
		minimum (r_{max})	3,460	1,863	4,448	0.008%	0.0000%
Observed YNP disease rates + added black swan events	Scenario 2	maximum (r_{max})	3,133	1,797	3,826	0.004%	0.000%
		minimum (r_{max})	2,589	1,336	3,423	0.048%	0.001%
Observed YNP disease rates + added black swan events	Scenario X	maximum (r_{max})	1,940	935	2,016	0.770%	0.001%
		minimum (r_{max})	1,856	801	2,018	1.643%	0.007%

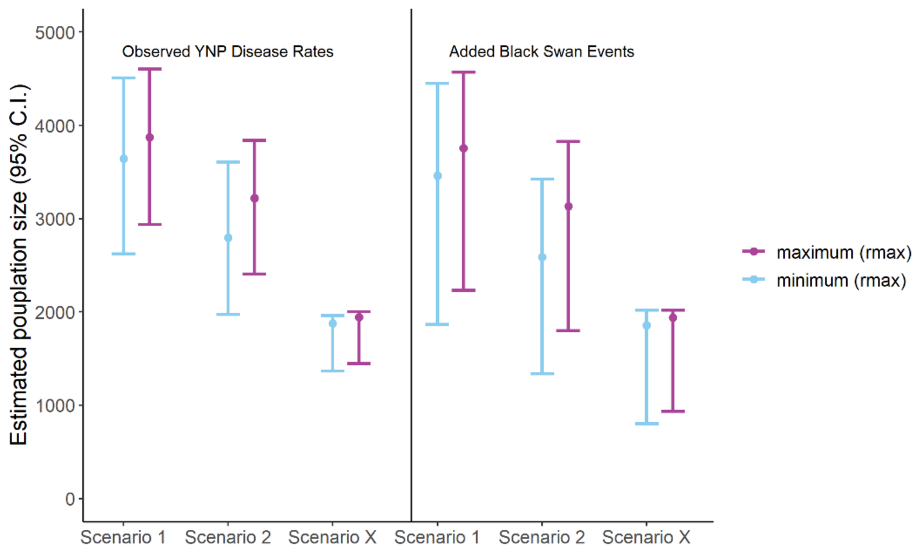

Figure A 7. Median projected wolf population size with 95% credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western Great Lakes states region's wolf populations modeled under three different scenarios (Scenario 1, Scenario 2 and Scenario X), when the intrinsic rate of growth for the Western Great Lakes was either the minimum (blue) or maximum (pink) value estimated from the density-dependent models described in Chapter 5.

The results of this analysis indicate that, when examining the range of intrinsic rates of growth within the minimum and maximum values used in the simulations for the Western Great Lakes there is an effect of the intrinsic rate of growth on the median projected population size in all Western Great Lakes states modeled for all Scenarios. However, this effect does not produce results with projected population sizes less than 192. Further, less than 0.05% of simulations fell below a population size of 417 for Mortality Scenarios 1 and 2 under both disease scenarios. Only Mortality Scenario X with minimum intrinsic rates of growth results in population sizes below 417 wolves in greater than one percent of simulations. However, this analysis does not provide an estimate of the potential decrease in the total projected population size in all Western Great Lakes states modeled if the intrinsic rate of growth in the Western Great Lakes was below 0.21 or above 0.29 wolves.

Uncertainty Analysis for Effect of Harvest and Lethal Depredation Control (*h*)

We examined the effect of varying the effect of harvest and lethal depredation control (*h*) in Michigan, Minnesota, and Wisconsin on the median projected population size in all Western Great Lakes states modeled. Overall, projected population sizes were similar for Mortality Scenarios 1 and X, regardless of whether the effect of harvest and lethal depredation control (*h*) in Michigan, Minnesota and Wisconsin was the minimum (-0.17) or maximum (0.38) estimate from the density-dependent models described in Chapters 5 and 6 (Table A 21, Figure A 8). The largest differences between the median projected population sizes occurred under Mortality Scenario 2. The difference between the median projected population size with the minimum *h* value and the maximum *h* value for Mortality Scenario 2 is 1,826 wolves when combined with observed YNP disease rates and 1,950 wolves when combined with observed YNP disease rates and added black swan events. The difference between the median projected population size with the minimum *h* value and maximum *h* value for Mortality Scenario 1 is 65 wolves when combined with observed YNP disease rates and 65 wolves when combined with observed YNP disease rates and added black swan events, and finally for Mortality Scenario X the differences between the median projected population size with the minimum *h* value and maximum *h* value were 105 wolves with observed YNP disease rates and 204 wolves when combined with observed YNP disease rates and added black swan events. The percent of simulations falling below 192 wolves, the lower bound of our threshold for evaluating risk of inbreeding depression, at any time during our 100-year simulation period was greater than zero for Mortality Scenario X and for Mortality Scenario 2 with added black swan events. These probabilities were less than or equal to 0.01%, regardless of the *h* value. The percent of simulations falling below 417 wolves, the upper bound of our threshold for evaluating risk of inbreeding depression, was highest (1.66%) for Morality Scenario X with added black swan disease events, when the effect of harvest and lethal depredation control was at its maximum (0.38); this probability is higher than the results from our projections using the full distribution of the parameter values (1.05% of simulations falling below 417 wolves) in Appendix 4.

Table A 21. Results of population projections for the total wolf population in Michigan, Minnesota and Wisconsin when the effects of harvest and lethal depredation were at the maximum (maximum h) or minimum (minimum h). Projected population LCI indicates the lower 95 percent credible interval of the projected population size and projected population UCI indicates the upper 95 percent credible interval of the projected population size. The percent of simulations falling below 417 or 192 indicates the percent of 200,000 simulations that fell below 417 wolves or 192 wolves at least once over the 100-year time frame. Note that due to stochasticity inherent in the model, each model run (all 200,000 simulations) will produce slightly different results.

Disease Scenario	Mortality Scenario	*h* value	Median Projected Population Size	Projected Population LCI	Projected Population UCI	Percent of simulations falling below 417	Percent of simulations falling below 192
Observed YNP disease rates	Scenario 1	minimum *h*	3,811	2,828	4,593	0.000%	0.000%
		maximum *h*	3,746	2,764	4,526	0.000%	0.000%
Observed YNP disease rates	Scenario 2	minimum *h*	4,018	3,021	4,641	0.000%	0.000%
		maximum *h*	2,192	1,636	2,461	0.000%	0.000%
Observed YNP disease rates	Scenario X	minimum *h*	1,963	1,465	2,024	0.000%	0.000%
		maximum *h*	1,858	1,317	1,939	0.000%	0.000%
Observed YNP disease rates + added black swan events	Scenario 1	minimum *h*	3,666	2,100	4,555	0.001%	0.000%
		maximum *h*	3,601	2,028	4,489	0.003%	0.000%
Observed YNP disease rates + added black swan events	Scenario 2	minimum *h*	4,062	2,273	4,818	0.002%	0.000%
		maximum *h*	2,112	1,095	2,451	0.139%	0.001%
Observed YNP disease rates + added black swan events	Scenario X	minimum *h*	1,986	919	2,047	0.737%	0.001%
		maximum *h*	1,782	790	1,932	1.656%	0.006%

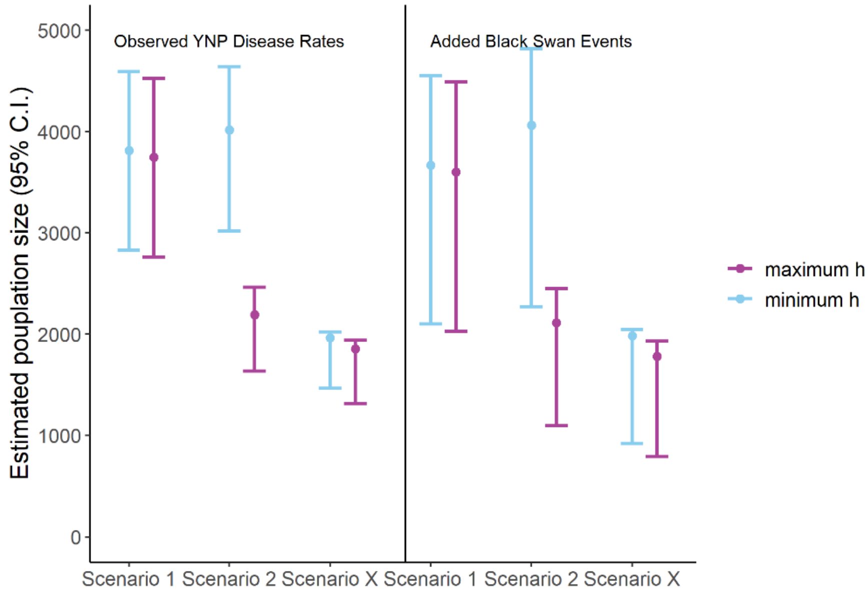

Figure A 8. Median projected wolf population size with 95% credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western Great Lakes states region's wolf populations modeled under three different Mortality Scenarios (Scenario 1, Scenario 2 and Scenario X), when the effect of harvest and lethal control (h) was either the minimum (blue) or maximum (pink) value estimated from the density-dependent models described in Chapter 5.

The results of this analysis indicate that, when examining the range of *h* values within the minimum and maximum values used in the simulations for Michigan, Minnesota, and Wisconsin (0.17–0.38) there is an effect of *h* on the median projected wolf population size in all Western Great Lakes states modeled for Mortality Scenario 2. For our scenarios, we modeled the transition from partially compensatory human-caused mortality to fully additive human-caused mortality (i.e. an *h*=1) as occurring at a random value between 20 and 40 percent combined harvest and lethal depredation control each year (Fuller et al. 2003, pp. 182–186; also see Adams et al. 2008, pp. 19–20). Therefore, for some simulations the effect of harvest and lethal control was 1, regardless of the minimum or maximum value for *h* that was selected. Overall, these results indicate that model results of Mortality Scenario 2 are sensitive to the assumptions regarding compensatory versus additive mortality of human caused wolf mortality. Mortality Scenario 1 and Mortality Scenario X are relatively robust to assumptions regarding the effect of harvest and lethal depredation control on wolves (*h*). This analysis does not provide an estimate of the potential decrease in the total projected population size in all Western Great Lakes states modeled if the effect of harvest and lethal control on wolves is greater than 0.38 at harvest rates below 20-40 percent.

Uncertainty Analyses for Initial Population Sizes (State-Level Results)

We examined the effect of varying the initial wolf population size in Michigan, Minnesota, and Wisconsin on the median projected population size in Michigan, Minnesota, and Wisconsin. Overall, projected population sizes were similar for Mortality Scenario X for all states regardless of whether the initial population sizes for the Western Great Lakes was the minimum or maximum estimate from the density-dependent models described in Chapters 5 and 6 (Table A 22, Figure A 9). The largest differences between the median projected population sizes estimated from the minimum initial population size versus the maximum initial population size are under Mortality Scenario 2. For Wisconsin the difference between the median projected population size when the initial population size in Wisconsin was at its minimum versus when the initial population size in Wisconsin was at its maximum was 74 with observed Yellowstone disease rates and 46 with combined observed Yellowstone disease rates plus added black swan events. For Michigan and Minnesota this difference was less than 15 wolves for all Scenarios. Overall, these results indicate that model results for projected population sizes are most sensitive to initial population sizes for Mortality Scenario 2 and that those differences are attributable to the differences in projected population sizes in Wisconsin.

Table A 22. Median, and lower and upper 95 perecent credible interval (CI) for projected wolf population size in Michigan, Minnesota, and Wisconsin when initial population size was the minimum or maximum value. Note that due to stochasticity inherent in the model, each model run (all 200,000 simulations) will produce slightly different results.

Disease Scenario	Mortality Scenario	Initial Population Size	Median Projected Population Size in Michigan	Median Projected Population Size in Minnesota	Median Projected Population Size in Wisconsin
Observed YNP disease rates	Scenario 1	Population minimum	561 (95% C.I. 353-680)	2,348 (95% C.I. 1,462-2,969)	871 (95% C.I. 520-1,183)
		Population maximum	562 (95% C.I. 352-680)	2,349 (95% C.I. 1,463-2,968)	871 (95% C.I. 518-1,183)
Observed YNP disease rates	Scenario 2	Population minimum	556 (95% C.I. 348-677)	2,004 (95% C.I. 1,256-2,562)	410 (95% C.I. 230-611)
		Population maximum	557 (95% C.I. 349-677)	1,999 (95% C.I. 1,252-2,556)	484 (95% C.I. 265-710)
Observed YNP disease rates	Scenario X	Population minimum	196 (95% C.I. 141-197)	1,532 (95% C.I. 973-1,551)	240 (95% C.I. 171-241)
		Population maximum	197 (95% C.I. 141-198)	1,542 (95% C.I. 1,003-1,565)	237 (95% C.I. 171-240)
Observed YNP disease rates + added black swan events	Scenario 1	Population minimum	543 (95% C.I. 175-678)	2,276 (95% C.I. 733-2,964)	837 (95% C.I. 272-1,181)
		Population maximum	543 (95% C.I. 176-679)	2,279 (95% C.I. 731-2,965)	836 (95% C.I. 270-1,181)
Observed YNP disease rates + added black swan events	Scenario 2	Population minimum	538 (95% C.I. 170-676)	1,928 (95% C.I. 606-2,539)	420 (95% C.I. 146-635)
		Population maximum	539 (95% C.I. 175-676)	1,916 (95% C.I. 614-2,520)	466 (95% C.I. 152-694)
Observed YNP disease	Scenario X	Population minimum	197 (95% C.I. 63-197)	1,527 (95% C.I. 465-1,549)	236 (95% C.I. 78-238)

rates + added black swan events		Population maximum	197 (95% C.I. 65-197)	1,536 (95% C.I. 458-1,559)	241 (95% C.I. 77-243)

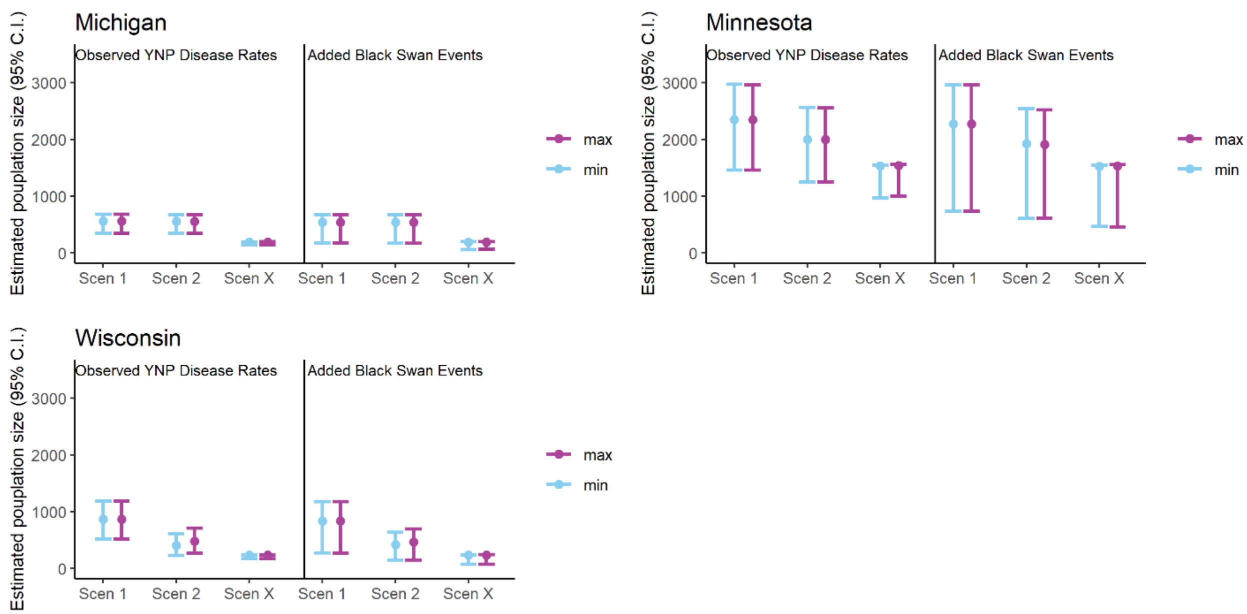

Figure A 9. Median projected wolf population size in Michigan, Minnesota, and Wisconsin with 95% credible intervals at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western Great Lakes states region's wolf populations modeled under three different scenarios (Scen 1= Mortality Scenario 1, Scen 2 = Mortality Scenario 2, and Scen X=Mortality Scenario X), when the initial population sizes in Michigan, Minnesota, and Wisconsin are at the minimum (blue) or maximum (pink) value estimated from the density-dependent models described in Chapter 5.

Uncertainty Analyses for Intrinsic Rate of Growth (r_{max}) (State-Level Results)

We examined the effect of the intrinsic rate of growth (r_{max}) value in the Western Great Lakes on the median projected wolf population size in Michigan, Minnesota, and Wisconsin. Overall, projected population sizes were similar for Mortality Scenario X for all states regardless of whether the intrinsic rate of growth (r_{max}) in the Western Great Lakes region's wolf populations was the minimum or maximum value from the density-dependent models described in Chapters 5 and 6 (Table A 11, Figure A 6). For Michigan the difference between the projected population size when the intrinsic rate of growth (r_{max}) was at the minimum value versus the maximum value for Mortality Scenarios 1 and 2 ranged from 55 (for Mortality Scenario 1 and observed Yellowstone disease rates) to 63 (for Mortality Scenario 2 and observed Yellowstone disease rates plus added black swan events). For Minnesota the difference between the projected population size when the intrinsic rate of growth (r_{max}) was at the minimum value versus the maximum value for Mortality Scenarios 1 and 2 ranged from 139 (for Mortality Scenario 1 and observed Yellowstone disease rates) to 346 (for Mortality Scenario 2 observed Yellowstone disease rates plus added black swan events). For Wisconsin the difference between the projected population size when the intrinsic rate of growth (r_{max}) in Wisconsin was at its minimum versus when the intrinsic rate of growth was at its maximum for Mortality Scenarios 1 and 2 ranged from 67 (for Mortality Scenario 1 and observed Yellowstone disease rates) to 166 (for Mortality Scenario 2 observed Yellowstone disease rates plus added black swan events). Overall, these results indicate that model results for median projected population sizes are most sensitive to intrinsic rate of growth (r_{max}) under Mortality Scenarios 1 and 2 and all state estimates contribute to this result.

Table A 23. Median, and lower- and upper-95 percent credible interval (CI) for projected wolf population size in Michigan, Minnesota and Wisconsin when intrinsic rate of growth (r_{max}) was the minimum or maximum value. Note that due to stochasticity inherent in the model, each model run (all 200,000 simulations) will produce slightly different results.

Disease Scenario	Mortality Scenario	Intrinsic Rate of Growth (r_{max}) Value	Median Projected Population Size in Michigan	Median Projected Population Size in Minnesota	Median Projected Population Size in Wisconsin
Observed YNP disease rates	Scenario 1	Minimum (r_{max})	531 (95% C.I. 320-674)	2262 (95% C.I. 1356-2963)	829 (95% C.I. 473-1181)
		Maximum (r_{max})	586 (95% C.I. 379-686)	2401 (95% C.I. 1555-2970)	896 (95% C.I. 554-1185)
Observed YNP disease rates	Scenario 2	Minimum (r_{max})	526 (95% C.I. 316-671)	1859 (95% C.I. 1131-2513)	413 (95% C.I. 227-651)
		Maximum (r_{max})	583 (95% C.I. 376-683)	2089 (95% C.I. 1345-2552)	574 (95% C.I. 334-764)
Observed YNP disease rates	Scenario X	Minimum (r_{max})	197 (95% C.I. 131-199)	1499 (95% C.I. 968-1540)	239 (95% C.I. 159-242)
		Maximum (r_{max})	196 (95% C.I. 147-197)	1544 (95% C.I. 1024-1565)	241 (95% C.I. 180-243)
Observed YNP disease rates + added black swan events	Scenario 1	Minimum (r_{max})	510 (95% C.I. 148-672)	2179 (95% C.I. 630-2958)	785 (95% C.I. 226-1177)
		Maximum (r_{max})	571 (95% C.I. 203-685)	2348 (95% C.I. 842-2967)	871 (95% C.I. 316-1183)
Observed YNP disease rates + added black swan events	Scenario 2	Minimum (r_{max})	504 (95% C.I. 146-668)	1721 (95% C.I. 502-2387)	380 (95% C.I. 116-636)
		Maximum (r_{max})	567 (95% C.I. 203-682)	2067 (95% C.I. 726-2581)	546 (95% C.I. 198-745)
Observed YNP disease	Scenario X	Minimum (r_{max})	197 (95% C.I. 59-199)	1512 (95% C.I. 402-1583)	240 (95% C.I. 69-242)

rates + added black swan events		Maximum (r_{max})	198 (95% C.I. 75-198)	1559 (95% C.I. 539-1585)	236 (95% C.I. 90-237)

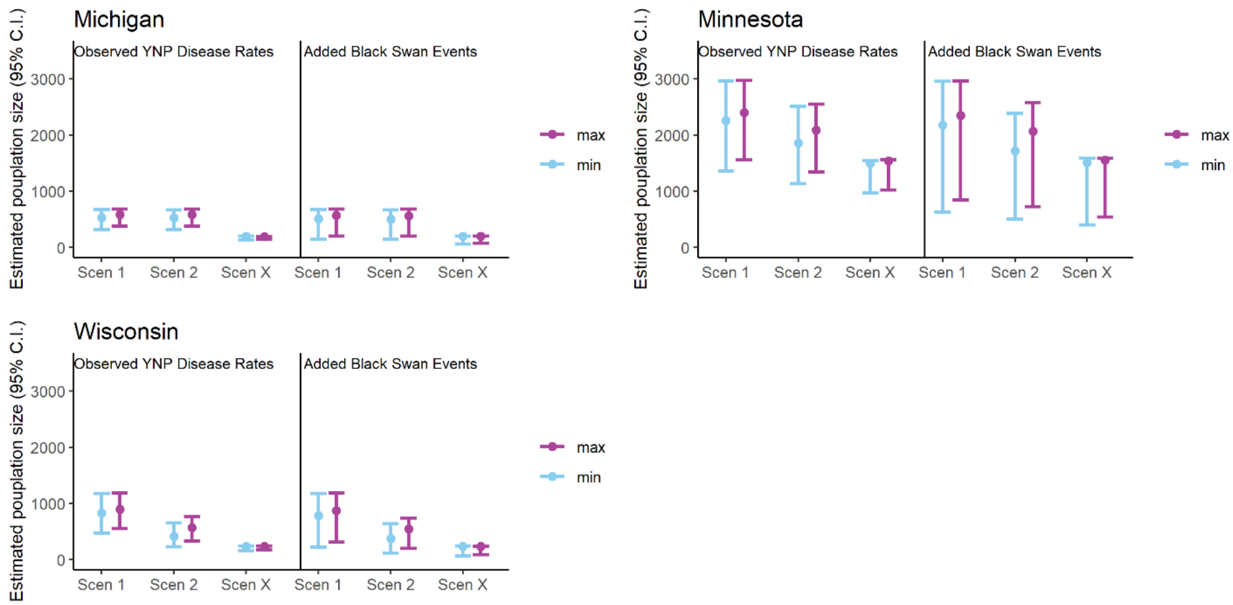

Figure A 10. Median projected wolf population size in Michigan, Minnesota, and Wisconsin with 95% credible intervals at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western Great Lakes states region's wolf populations modeled under three different scenarios (Scen 1= Mortality Scenario 1, Scen 2 = Mortality Scenario 2, and Scen X=Mortality Scenario X), when the intrinsic rate of growth for the Western Great Lakes is at the minimum (blue) or maximum (pink) value estimated from the density-dependent models described in Chapter 5.

Uncertainty Analyses for Effect of Harvest and Lethal Depredation Control (*h*) (State-Level Results)

We examined the effect of harvest and lethal depredation control (*h* value) in the Western Great Lakes on the median projected wolf population size in Michigan, Minnesota, and Wisconsin. Overall, projected population sizes were similar for Mortality Scenario X for all states regardless of whether the *h* value in the Western Great Lakes was the minimum or maximum estimate from the density-dependent models described in Chapters 5 and 6 (Table A 11, Figure A 6). For Michigan the difference between the median projected population size when the *h* value was at the minimum estimate versus the maximum estimate for Mortality Scenarios 1 and 2 ranged from 70 (for Mortality Scenarios 1 and 2 and observed Yellowstone disease rates) to 96 (for Scenarios 1 and 2 and observed Yellowstone disease rates plus added black swan events). For Minnesota and Wisconsin, the difference between the median projected population size when the *h* value was at the minimum estimate versus the maximum estimate for Mortality Scenario 1 was less than 2 wolves. For Mortality Scenario 2, the difference for

Minnesota was approximately 1,200 wolves for both Disease Scenarios, and the difference in Wisconsin was 550 for observed Yellowstone disease rates and 628 for observed Yellowstone disease rates plus added black swan events. Overall, these results indicate that model results for median projected population sizes are most sensitive to effects of the *h* value under Mortality Scenario 2, and all state estimates contribute to this result.

Table A 24. Median, and lower- and upper-95 percent credible interval (CI) for projected wolf population size in Michigan, Minnesota and Wisconsin when the effect of harvest and lethal depredation control (h) was at the minimum or maximum value. Note that due to stochasticity inherent in the model, each model run (all 200,000 simulations) will produce slightly different results.

Disease Scenario	Mortality Scenario	*h* value	Median Projected Population Size in Michigan	Median Projected Population Size in Minnesota	Median Projected Population Size in Wisconsin
Observed YNP disease rates	Scenario 1	minimum *h*	594 (95% C.I. 376-710)	2349 (95% C.I. 1,468-2,968)	871 (95% C.I. 519-1,183)
		maximum *h*	524 (95% C. I.325-643)	2348 (95% C.I. 1,467-2,967)	871 (95% C.I. 521-1,184)
Observed YNP disease rates	Scenario 2	minimum *h*	602 (95% C.I. 383-718)	2675 (95% C.I. 1,725-3,148)	785 (95% C.I. 496-954)
		maximum *h*	506 (95% C.I. 312-626)	1523 (95% C.I. 943-1,642)	239 (95% C.I. 178-290)
Observed YNP disease rates	Scenario X	Minimum *h*	198 (95% C.I. 144-198)	1567 (95% C.I. 1,047-1,597)	238 (95% C.I. 178-239)
		maximum *h*	196 (95% C.I. 137-196)	1486 (95% C.I. 927-1,507)	237 (95% C.I. 159-240)
Observed YNP disease rates + added black swan events	Scenario 1	minimum *h*	576 (95% C.I. 186-709)	2277 (95% C.I. 734-2,963)	838 (95% C.I. 269-1,181)
		maximum *h*	507 (95% C.I. 161-642)	2276 (95% C.I. 730-2,964)	837 (95% C.I. 271-1,181)
Observed YNP disease rates + added black swan events	Scenario 2	minimum *h*	584 (95% C.I. 188-716)	2686 (95% C.I. 869-3,232)	867 (95% C.I. 286-1,078)
		maximum *h*	488 (95% C.I. 153-624)	1458 (95% C.I. 400-1,645)	239 (95% C.I. 75-280)
Observed YNP disease rates + added black swan events	Scenario X	minimum *h*	199 (95% C.I. 65-199)	1608 (95% C.I. 523-1,608)	239 (95% C.I. 88-240)
		maximum *h*	196 (95% C.I. 60-196)	1425 (95% C.I. 389-1,500)	238 (95% C.I. 70-240)

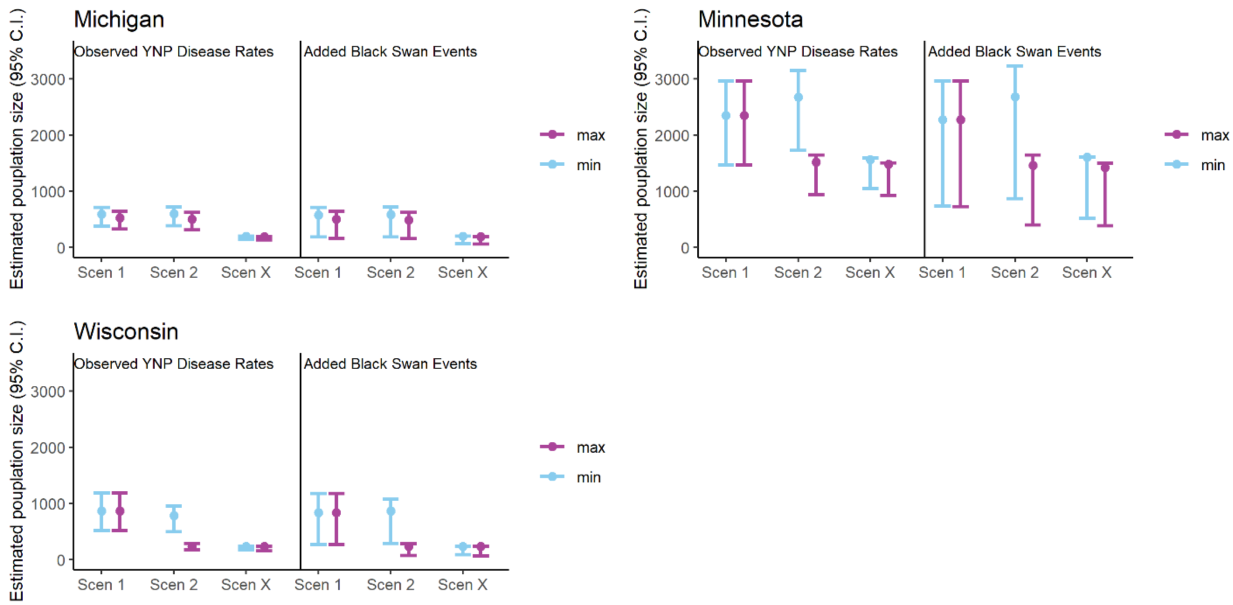

Figure A 11. Median projected wolf population size in Michigan, Minnesota, and Wisconsin with 95% credible intervals at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western Great Lakes states region's wolf populations modeled under three different scenarios (Scen 1= Mortality Scenario 1, Scen 2 = Mortality Scenario 2, and Scen X=Mortality Scenario X), when the effect of harvest and lethal depredation control for the Western Great Lakes is at the minimum (blue) or maximum (pink) value estimated from the density-dependent models described in Chapter 5.

Literature Cited in Appendix 6

Altman, D.G., and J. M. Bland. 1998. Generalisation and Exrapolation. British Medical Journal 317: 409–410.

Bartley, M.L., E.M. Hanks, E.M. Schliep, P.A. Soranno, and T. Wagner. 2019. Identifying and characterizing extrapolation in multivariate response data. PLoS ONE 14: e0225715.

Greenwell, B.M. 2017. pdp: An R Package for Constructing Partial Dependence Plots. The R Journal, 9(1): 421–436. URL https://journal.r-project.org/archive/2017/RJ-2017-016/index.html.

Lonsdorf, E.V., W.E. Thogmartin, S. Jacobi, K. Aagaard, J. Coppen, A. Davis, T. Fox, P. Heglund, R. Johnson, M.T. Jones, K. Kenow, J. E. Lyons, K. Luke, S. Still, and B. Tavernia. 2016. A generalizable energetics-based model of avian migration to facilitate continental-scale waterbird conservation. Ecological Applications, 26: 1136–1153

Appendix 7: Wisconsin Department of Natural Resources 2025 Gray Wolf Monitoring Report

In 2025, the Wisconsin Department of Natural Resources enhanced its occupancy modeling methods, resulting in smaller estimated home range sizes and, consequently, higher gray wolf population estimates (WI DNR 2025, entire). These updated methods were subsequently applied retroactively to occupancy-based population estimates from year-end 2019 onward.

Changes in Occupancy Modeling Methods (WI DNR 2025, pp. 2–3): The revised population estimates are based on improved home range analyses of GPS-telemetry data, and include the following methodological updates: (1) increased sample sizes through standardized monitoring periods and more rigorous classification of resident status; (2) use of an autocorrelated kernel density estimator to better account for the temporal structure of GPS data; and (3) implementation of a more statistically robust estimator for calculating population means.

Table A 25. Comparison of populations estimates from Appendix 2 of the SSA and the revised estimates from the 2025 Wisconsin Gray Wolf Monitoring Report (WI DNR 2025, entire).

	Translation to year-end estimate	Appendix 2 SSA	WI DNR 2025 Report	Difference
2019/2020	2019	1,195	1,340	+145
2020/2021	2020	1,126	1,175	+49
2021/2022	2021	972	985	+13
2022/2023	2022	1,007	1,283	+270
2023/2024	2023	Not in SSA	1,311	
2024/2025	2024	Not in SSA	1,226	

The estimated wolf population for year-end 2024 was 1,226 wolves (95% CI: 1,087–1,379), showing no statistically significant change from the previous year's estimates of 1,311 wolves (95% CI: 1,150–1,497) (WI DNR 2025, p. 34).

All revised population estimates from year-end 2019 onward are higher than those used in the SSA analysis (Table A 7 and A 25). Therefore, the SSA model results—based on the original, lower estimates—represent a conservative scenario. Re-running the models using the updated estimates would not be expected to produce meaningful changes in the outcome. We are providing updated information for Table A 7 in Appendix 2, below.

Table A 26. Wisconsin gray wolf population estimates and mortality data from year-end 2019 to year-end 2024 (Johnson 2023, in litt; Johnson 2025, in litt; WI DNR 2023c; WI DNR 2024; WI DNR 2025). Population estimates have been updated using data from the 2025 Wisconsin Gray Wolf Monitoring Report (WI DNR 2025, entire); revised values are shown in parentheses. New population estimates for year-end 2023 and 2024 are also included.

Timing of Population Estimate		***Number of Wolves***				***Mortality***			***Mortality Rates***		
State of Wisconsin Terminology	**Translation to year-end estimate**	**Wolf population estimates**	**Lower Con-fidence Interval**	**Upper Con-fidence Interval**	**Year over year population change (%)**	**Number of wolves harvested**	**Number of wolves lethally removed**	**Other known wolf mortalities**	**Harvest Rate (% of year-end estimate)**	**Lethal Control Rate (% of year-end estimate)**	**Combined Harvest and Lethal Control Rate**
2019/2020	**2019**	1,195 (1,340)	957 (1,113)	1,573 (1,592)	30.7 (46.6)	0	0	55	–	–	–
2020/2021	**2020**	1,126 (1,175)	937 (966)	1,364 (1,412)	-5.6 (-12.3)	0	0	39	–	–	–
2021/2022	**2021**	972 (985)	812 (849)	1,193 (1,133)	-13.7 (-16.2)	218	69	24	17.0 (16.8)	5.4 (5.3)	22.4 (22.1)
2022/2023	**2022**	1,007 (1,283)	780 (1,103)	1,380 (1,474)	3.6 (30.3)	0	2	36	0.0 (0.0)	0.2 (0.2)	0.2 (0.2)
2023/2024	**2023**	1,311	1,150	1,497	2.2	0	0	31	0.0	0.0	0.0
2024/2025	**2024**	1,226	1,087	1,379	-6.5	0	2	34	0.0	0.2	0.2

Literature Cited in Appendix 7

Johnson, R. 2023. Email dated March 9, 2023, from Randy Johnson, Wisconsin Department of Natural Resources, to Megan Kosterman, U.S. Fish and Wildlife Service, providing data on gray wolf abundance, lethal control, and regulated harvest in Wisconsin. 95 pp.

Johnson, R. 2025. Emails dated June 20, 2025 and October 30, 2025 from Randy Johnson, Wisconsin Department of Natural Resources, to Megan Kosterman, U.S. Fish and Wildlife Service, providing information on the Wisconsin compensation program, depredations/conflicts, USFWS interpretations of the Wisconsin Wolf Management Plan 2023, and clarifications on revised abundance estimates in the 2025 Wisconsin Gray Wolf Monitoring Report. 5 pp.

Wisconsin Department of Natural Resources (WI DNR). 2023c. Wisconsin Gray Wolf Monitoring Report: 15 April 2022 to 14 April 2023. Wisconsin Department of Natural Resources, Bureau of Wildlife Management. Madison, Wisconsin. 29 pp.

Wisconsin Department of Natural Resources (WI DNR). 2024. Wisconsin Gray Wolf Monitoring Report: 15 April 2024 through 14 April 2024. Wisconsin Department of Natural Resources, Bureau of Wildlife Management. Madison, Wisconsin. 23 pp.

Wisconsin Department of Natural Resources (WI DNR). 2025. Wisconsin Gray Wolf Monitoring Report: 15 April 2024 through 14 April 2025. Wisconsin Department of Natural Resources, Bureau of Wildlife Management. Madison, Wisconsin. 36 pp.

Supplementary Material A

Technical Details of Modeling to Estimate Parameters for Forecasting

We conducted our analysis in a Bayesian framework to fully capture uncertainties associated with our data (Kéry and Schaub 2011, Chapter 1; Gelman et al 2020, Chapter 2). This statistical approach combines a prior distribution and the observed data to produce a posterior distribution of parameter estimates that does not assume a statistical distribution (such as normality). It can be used in subsequent analyses with minimal assumptions. All models were run in rjags (Plummer et al. 2021, R package, code provided below in Supplement A) for 300,000 iterations with 100,000 burn-in, leaving 200,000 iterations (i.e., long enough to achieve convergence) to estimate the posterior distribution of the parameter estimates. Priors (assumptions regarding the distributions) for h and r_{max} were modeled in the standard Bayesian fashion using a diffuse (i.e., non-informative) distribution (mean = 0, precision = 0.0001) (Kéry and Schaub 2011, Chapter 1; Gelman et al 2020, Chapter 2). Model priors for K were somewhat informative to assist with convergence and based on maximum observed values (i.e., priors for K were limited to be within the maximum observed value to twice the maximum observed value). Posterior distributions were visually inspected to determine if priors were too restrictive (i.e., if values were highly skewed toward a limit of the prior distribution of K). We used modeling best practices to evaluate model diagnostics; we checked $\hat{R}$ for values greater than 1.1 and we inspected trace plots for chain convergence (Gelman et al. 2020, Chapter 2).

Table. A1. Deviance Information Criteria (DIC) for density dependent versus density independent models

Model	DIC
Density Dependent (three state model)	975.22
Density Independent (three state model)	1247.89

Model Code for Estimating Parameters

```
 sink("DD.jags")
cat("
model {
   # Priors and constraints

   # error on population estimates
for(i in 1:3){
sigma.obs[i] ~ dgamma(0.25,0.25)
   tau.obs[i]<-pow(sigma.obs[i], -2)# SD of observation process
}

  r ~ dnorm(0, 0.0001)   ### prior on intrinsic rate of growth

    h~dnorm(0, 0.0001)  ### prior on per wolf effect of harvest and lethal depredation control

     ###Initial value for starting population in Michigan and Minnesota
```

```
   N.est1[1] ~ dunif(N.min[1], N.max[1])
    N.est2[1] ~ dunif(N.min[2], N.max[2])

###Initial values for carrying capacity for all three states
   for(j in 1:3){
   K[j]~dunif(K.min[j], K.max[j])
  }
   # Likelihood
   # State process state 1
###Michigan
   for (t in 1:(nYears[1]-1)){

   N.est1[t+1]<-max(0.00001, N.est1[t]+r*N.est1[t]*(1-(N.est1[t]/K[1]))-h*m1[t])
   }

   # Observation processMichigan
   for (t in 1:nYears[1]) {
     y1[t] ~ dnorm(N.est1[t], tau.obs[1])
   }

   # State process state Minnesota
   for (t in 1:(nYears[2]-1)){

   N.est2[t+1]<-max(0.00001, N.est2[t]+r*N.est2[t]*(1-(N.est2[t]/K[2]))-h*m2[t])
   }

   # Observation processMinnesota
   for (t in 1:nYears[2]) {
     y2[t] ~ dnorm(N.est2[t], tau.obs[2])
   }

       # Initial values for starting population Wisconsin and first year with new ###estimator
    N.est3[1] ~ dunif(0, 200)  # Initial population size
  N.est3[41]~dunif(900,1200)

   for (t in 1:39){
   N.est3[t+1]<- N.est3[t]+r*N.est3[t]*(1-N.est3[t]/K[3])-h*m3[t]
   }

   for(t in 41:42){
   N.est3[t+1]<- N.est3[t]+r*N.est3[t]*(1-N.est3[t]/K[3])-h*m3[t]
   }
   # Observation process Wisconsin
   for (t in 1:43) {
     y3[t] ~ dnorm(N.est3[t], tau.obs[3])

   }




  ####for harvest as a percentage of population
   }
```

```
#######Run the code
###y is the count data, nYears is the number of years of data, add nYears2 for broken stick
###m is the harvest + lethal depredation control animals dat1 is Michigan, dat2 is Minnesota, dat3 is
####Wisconsin
 jags.data <- list(y1 = dat1$Median,y2=dat2$Median,y3=dat3$Median,
              K.min=c(500,2200,900), K.max=c(2000,4000,1500),
              N.min=c(0,100), N.max=c(50, 1400),
              nYears = nYears,
              m1=(dat1$harvest+dat1$lethal.control), m2=dat2$harvest+dat2$lethal.control,
m3=dat3$harvest+dat3$lethal.control)


####Next, set initial values.  Remember that we need to set initial values for N1 but not the remainder of
the N's.  So we will randomly generate an initial value for N[1] and then fill in NA for all other other
elements in the N vector:
inits <- function(){list(r=runif(1, 0,1),
                  K=c(runif(1,600,800),runif(1,2200,3500),runif(1,900,1500)),
                  sigma.obs = runif(3, 0, 10),
                  h=runif(1,0, 1),
                  N.est1 =c(runif(1,0,50), rep(NA, nYears[1]-1)), N.est2=c(runif(1,1000,1300), rep(NA,
nYears[2]-1)),
                  N.est3=c(runif(1,0,50),rep(NA, 39),runif(1,900,1200),NA, NA))}
####Finally, set the parameters to monitor and the MCMC settings:


# Parameters monitored
parameters <- c("r", "sigma.obs", "N.est1", "N.est2", "N.est3", "K","h")
# MCMC settings
ni <- 300000
nt <- 3
nb <- 100000
nc <- 3

# Call WinBUGS from R (BRT <1 min)
ssm.test<- jagsUI::jags(data = jags.data, inits = inits, parameters.to.save = parameters,
                model.file = "DD2state.jags", n.chains = nc, n.thin = nt,
                n.iter = ni, n.burnin = nb)
```

Supplementary Material B

This material illustrates how we projected the population forward in time using the estimates from the model. Note that due to stochasticity in individual model projections, particularly variation in the point at which harvest and lethal depredation control become additive, any individual simulation (representing one draw from the posterior distributions of r_{max}, h, and K) will not exactly replicate another simulation (even if r_{max}, h, and K are identical). Therefore, in total, we conducted simulations with each of the 200,000 iterations from the distributions of each of the parameters (r_{max}, K, starting population size, and h) that we estimated from the models 10 times for each scenario. This resulted in a total of 2 million population projections from 2 million total simulations for each scenario.

- Model inputs include: h.rate is a vector of harvest rates for each state: Michigan, Minnesota, and Wisconsin. Control.rates is a vector of control rates for each state, Michigan, Minnesota, and Wisconsin. Dis.cat=1 if using observed YNP disease rates, dis.cat=2 for black swan events. Threshold is a vector of values at which harvest stops for a particular state. Scenario is an indicator for Mortality Scenario X.

```
rharvest.model<-function(h.rate, control.rates, dis.cat, threshold, scenario){
 N.pred<-array(0, dim=c(iters, 100, 3))
 states<-c("MI","MN","WI")


 for(j in 1:3){

    r<-test.r
    K<-get(paste(states[j],".K",sep=""))
    start.pop<-get(paste(states[j],".start", sep=""))
    h<-test.h
   N.pred[,1,j]<-start.pop
   ###Check for adaptive harvest scenarios in MN
   check<-ifelse(scenario%in%c(1,4)&j==2, 1,ifelse(scenario%in%c(2,5)&j==2, 2,0))

   for(i in 2:100){

    comp.h<-runif(1,0.2,0.4)#### at what rate does harvest become additive
    ###check for background versus blackswan
    if(dis.cat==1){
    disease<-rbinom(length(r), 1, 0.15)*0.25
    cat.rate<-disease
    }else{
      disease<-rbinom(length(r), 1, 0.15)*0.25
  cat1<-rbinom(length(r), 1, 0.01/7)*0.90
  cat2<-rbinom(length(r), 1, 0.032/7)*0.75
```

```
 cat.rate<-(apply(cbind(cat1, cat2, disease),1, max))  ##take maximum disease rate
     }
     ##find control rate
     c.rate<-control.rates[j]
     ###did the population last year experience a catastrophe?
     N.pred[,i-1,j]<-N.pred[,i-1,j]*(1-cat.rate)
     ####grow the population
     N.tot<-N.pred[,i-1,j]+r*(N.pred[,i-1,j])*(1-(N.pred[,i-1,j]/K) )
     ######create harvest vector
     h.rate.j<-rep(h.rate[j], length(test.r))
     if(check==1){
      h.rate.j<-ifelse(N.tot>=2200,0.1, ifelse(N.tot<2200&N.tot>=2000,0.05,
ifelse(N.tot<2000&N.tot>1600, 0.01,0 )))
     }else if(check==2){
      h.rate.j<-ifelse(N.tot>=2200,0.2, ifelse(N.tot<2200&N.tot>=2000,0.1,
ifelse(N.tot<2000&N.tot>1600, 0.05,0 )))
     }else{
      h.rate.j<-h.rate.j
     }

     ####harvest rate is zero if the population is less than or equal to threshold[j]
     h.rate.j<-ifelse(N.tot<=threshold[j],0,h.rate.j)
     comp.rate<-ifelse((h.rate.j+c.rate)<comp.h,(h.rate.j+c.rate),comp.h)
     add.rate<-ifelse((h.rate.j+c.rate)>=comp.h,(h.rate.j+c.rate)-comp.h,0)
     comp.m<-N.tot*comp.rate
     add.m<-N.tot*add.rate
     ###proportion of mortality due to harvest and control
     harvest.tot<-(h*comp.m+add.m)*(h.rate.j/(c.rate+h.rate.j))
     control.tot<-(h*comp.m+add.m)*(c.rate/(c.rate+h.rate.j))

     #####check for floors scnearios
     check.scenario<-ifelse(scenario%in%c(3,6),1,0) ###mortality scenario X
     if(check.scenario==1){
      ###if floor scenario and population is above threshold after fall below once
      ###make it the threshold

      ###if the population has fallen below the minimum and the growth will take it above make
it the threshold

        test1<-ifelse(i>2, apply(N.pred[,1:(i-1),j], 1, function(x) min(x)), N.pred[,i-1,j])
```

```
        N.pred[,i,j]<-ifelse((N.tot>=threshold[j]&((N.tot-
harvest.tot)<threshold[j]))|(test1<threshold[j]&N.tot>=threshold[j]), threshold[j],N.tot-
harvest.tot)
        ###subtract control
        N.pred[,i,j]<-N.pred[,i,j]-control.tot
         }else{
        N.pred[,i,j]<-ifelse(N.tot>=threshold[j]&(N.tot-harvest.tot)<threshold[j], threshold[j],N.tot-
harvest.tot)
        ##subtract control
        N.pred[,i,j]<-N.pred[,i,j]-control.tot
        }
      N.pred[(which(N.pred[,i,j]<5)),i,j]<-0
    }

  }
  out<-N.pred
  return(out)
}
```

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