

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



Photo by Oregon Department of Fish and Wildlife

**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, the Mountain-Prairie Region, the Pacific Region, and the Pacific Southwest Region. This document does not predetermine any future agency decision under the Endangered Species Act.

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- California Department of Fish and Wildlife
- Colorado Parks and Wildlife
- Idaho Department of Fish and Game
- Idaho Governor’s Office of Species Conservation
- Montana Fish, Wildlife and Parks
- Oregon Department of Fish and Wildlife
- Utah Division of Wildlife
- Washington Department of Fish and Wildlife
- Wyoming Game and Fish Department
- Bureau of Land Management
- National Park Service
- U.S. Forest Service
- Nez Perce Tribe

***Version Note:***

We provided Draft Version 1.0 of this Species Status Assessment Report to peer reviewers for review. Version 1.1 of this Species Status Assessment Report included revisions in response to peer reviewer and technical reviewer feedback and any necessary updates based on newly available information; we provided Version 1.1 of this Species Status Assessment Report to recommenders to inform our discussion at the Recommendation Team Meeting for this species. The conclusions of this final Version 1.2 did not change substantively from the version shared with recommenders prior to the Recommendation Team Meeting (i.e., Version 1.1). However, it includes relevant updates based on scientific and commercial data released after the Recommendation Team Meeting, minor corrections of erroneous content, and edits to ensure 508 compliance.

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## Table of Contents

Executive Summary .....	viii
Biology, Life History, and Ecology .....	viii
Stressors and Conservation Efforts .....	xi
Current Condition .....	xii
Future Condition .....	xiii
Future Resiliency and Redundancy .....	xiv
Future Representation .....	xvii
Summary of Future Condition .....	xvii
Introduction.....	1
Purpose and Geographic Scope .....	1
Analytical Framework .....	2
Traditional Ecological Knowledge .....	5
Chapter 1: Biology, Life History, and Ecology .....	6
Taxonomy .....	6
Species Description.....	10
Species Life History.....	10
Suitable Habitat.....	13
Historical Distribution and Abundance .....	14
Chapter 2: Needed Resources and Demographic Factors that Support Viability of the Gray Wolf in the Western United States.....	18
Resiliency.....	18
Resource Needs.....	18
Demographic Needs.....	18
Representation.....	21
Redundancy.....	22
Recovery Criteria and Other Analyses on Wolf Population Viability.....	23
Recovery Criteria for the Northern Rocky Mountains .....	23
Comparison of Recovery Criteria with Other Wolf Models.....	28
Summary of Resource and Demographic Needs .....	31
Chapter 3: Stressors and Conservation Efforts .....	32
Human-Caused Mortality.....	34
Effects of Human-Caused Mortality .....	35
Sources of Human-Caused Mortality.....	41

Influence on Human-Caused Mortality: The Role of Public Attitudes .....	48
Levels of Human-Caused Mortality in Idaho, Montana, Oregon, Washington, and Wyoming .....	49
Human-Caused Mortality in Arizona, California, Colorado, New Mexico, and Utah .....	91
Human-Caused Mortality Summary .....	97
Disease and Parasites in Wolves.....	98
Inbreeding Depression .....	101
Climate Change.....	103
Diseases in Prey .....	105
Other Sources of Habitat Modification.....	108
The Human Footprint.....	108
Wildfire .....	109
Cumulative Effects.....	110
Conservation Efforts on Federal Lands in the Western United States.....	110
Summary of Stressors and Conservation Efforts .....	113
Chapter 4: Current Condition.....	115
Current Resiliency .....	115
Current Habitat Availability .....	115
Current Prey Availability .....	120
Current Population Distribution and Demographics.....	123
Current Genetic Diversity and Connectivity.....	140
Current Representation .....	142
Current Redundancy .....	146
Summary of Current Condition .....	147
Chapter 5: Methods for Evaluating Future Condition .....	148
Analysis Units.....	148
Models of Population Growth.....	149
Determining Density-Independent or Dependent Growth.....	149
Understanding Maximum Population Size, Intrinsic Growth, and Lethal Depredation and Harvest Effects Parameters .....	151
Estimating Parameters for Projections.....	152
Estimating Starting Population Sizes.....	153
Estimating Parameters for Idaho Projections.....	153
Estimating Parameters for Montana Projections.....	154
Estimating Parameters for Wyoming Projections.....	154

Estimating Parameters for Yellowstone National Park Projections .....	155
Estimating Parameters for Oregon and Washington Projections.....	157
Assumptions Regarding Immigration, Emigration, Natural Mortality, Reproduction, and Harvest and Lethal Depredation Control Effects.....	157
Estimated Parameters.....	158
Future Scenarios.....	159
Disease .....	159
Harvest .....	160
Lethal Depredation Control .....	167
Timeframe.....	168
Population Thresholds .....	169
Key Uncertainties and Assumptions.....	171
Disease Scenarios.....	171
Harvest Scenarios.....	172
Chapter 6: Future Condition .....	183
Future Resiliency and Redundancy .....	183
Interpreting Forecasting Results .....	183
Results of Forecasting Model: Resiliency and Redundancy in Idaho, Montana, Oregon, Washington, and Wyoming .....	185
Future Expectations of Populations in States Not Analyzed in the Model (Arizona, California, Colorado, Nevada, New Mexico, and Utah).....	194
Future Habitat and Prey Availability .....	199
Future Genetics and Connectivity.....	200
Summary of Future Resiliency and Redundancy.....	204
Future Representation .....	205
Summary of Future Condition .....	207
Appendix 1: Report: Indigenous Knowledge and Cultural Significance of the Gray Wolf to Tribal Nations with Lands in Idaho, Montana, and Wyoming .....	209
Introduction.....	209
Confederated Salish and Kootenai Tribes <i>Séliš (Salish)</i> , <i>Qlispé (Pend d’Oreille)</i> , and <i>Ksanka</i> ( <i>Kootenai</i> ) .....	211
Salish and Pend d’Oreille.....	211
Kootenai.....	211
Nez Perce Tribe <i>Nimí pu</i> .....	212
Blackfeet Nation <i>Siksika, Kainai, Piikuni</i> .....	212
Crow Tribe <i>Apsáalooke</i> .....	213

Arapaho <i>Hinoni'ei</i> .....	214
Shoshone <i>Newe</i> .....	214
Chippewa Cree <i>Ne Hiyawak</i> .....	215
Discussion .....	215
Acknowledgments.....	216
References.....	217
Appendix 2: Analysis of Wildlife Genetics International Data Set.....	220
Purpose.....	220
Methods.....	220
Data .....	220
Analysis of genetic diversity.....	220
Analysis of effective population size .....	220
Results.....	221
Analysis of genetic diversity.....	221
Analysis of effective population size .....	223
Literature Cited in Appendix 2 .....	225
Appendix 3: Citations for Population Monitoring and Mortality Data.....	227
Appendix 4: Representation Analysis.....	230
Appendix 5: Sensitivity Analysis of the Effects of Uncertainty in the Initial Population Size, $h$ , and $r_{max}$ Values for Montana and Idaho.....	233
Sensitivity Analysis for Initial Population Size .....	234
Sensitivity Analysis for Intrinsic Rate of Growth ( $r_{max}$ ).....	238
Sensitivity Analysis for Effect of Harvest and Lethal Depredation Control ( $h$ ).....	241
Conclusion .....	244
Appendix 6: State-Level Modeling Results.....	245
Post-Delisting Monitoring Thresholds for Individual States .....	245
Idaho .....	245
Montana .....	247
Alternative Models of Population Dynamics in Montana .....	250
Wyoming.....	251
Oregon and Washington (statewide and within the NRM).....	252
Appendix 7: Population Monitoring and Mortality Data Used in the Population Projection Model .....	257
Idaho .....	257
Montana .....	259

Oregon.....	260
Washington .....	261
Wyoming.....	262
Yellowstone National Park .....	263
Supplementary Material A .....	264
Technical Details of Modeling to Estimate Parameters for Forecasting .....	264
Model Code for Estimating Parameters .....	264
Supplementary Material B .....	266
Literature Cited.....	269

## List of Figures

Figure 1. Analysis area for SSA for the gray wolf in the Western United States.....	2
Figure 2. Historical (green) and current (yellow) gray wolf range in the Western United States. .....	14
Figure 3. A conceptual model for the primary stressors that may affect individuals or cumulatively influence the resiliency of the gray wolf in the Western United States.....	33
Figure 4. Number of wolves harvested through regulated public harvest in Idaho by method of take and season (for completed seasons only) from the 2009/2010 season through the 2022/2023 season.....	61
Figure 5. Number of wolves harvested through regulated public harvest in Montana by method of take and season (for completed seasons only) from the 2009/2010 season through the 2022/2023 season.....	73
Figure 6. Primary Federal land management agencies in our analysis area. ....	111
Figure 7. Federal land and wilderness areas within our analysis area. [Source for Federal land ownership: BLM 2022; Source for wilderness areas: U.S. Geological Survey (USGS) Gap Analysis Project (GAP) 2020] .....	113
Figure 8. Potentially suitable gray wolf habitat, Federal land, and current range of the gray wolf in the Western United States.....	117
Figure 9. Minimum number of gray wolves counted or estimated in the Western United States, 1985–2022, both inside of the NRM (blue) and outside of the NRM (green).....	131
Figure 10. Ecoregional provinces, as defined by Bailey (2016), comprising potentially suitable habitat and the current range of wolves in the Western United States. ....	146
Figure 11. Schematic of density-dependent wolf population model. ....	151
Figure 12. Yellowstone National Park wolf population estimates from 1995–2022.....	155
Figure 13. Schematic of forecasting, including future scenarios.....	159
Figure 14. Example output graph.....	184
Figure 15. Visual representation of the area in which the model projection results in this section apply (blue outline).....	186
Figure 16. Median projected wolf population size (solid line) and 95% credible interval (shaded area) in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) in Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations.....	187

Figure 17. Visual representation of the area in which the model projection results in this section apply (blue outline). ..... 190

Figure 18. Median projected wolf population size (solid lines) and 95% credible interval (shaded area) in the NRM in Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations. .... 191

Figure 19. Visual representation of the area in which the discussion in this section applies (blue outline). ..... 195

**List of Tables**

Table 1. Comparison of Idaho’s wolf harvest regulations between the 2020/2021 and 2021/2022 seasons. .... 59

Table 2. Comparison of Montana’s wolf harvest regulations between the 2020/2021 and 2021/2022 seasons. .... 71

Table 3. Annual number of gray wolves known to have died by various causes, percent annual total mortality, and end-of-year statewide minimum wolf counts or population estimates in Idaho, Montana, Wyoming, Oregon, and Washington from 2009–2022. .... 89

Table 4. Estimated area of modeled suitable gray wolf habitat by state..... 116

Table 5. Gray wolf year-end minimum population counts or population estimates in the Western United States. .... 137

Table 6. Estimated growth rate ( $\lambda$ ) in: Idaho, Montana, Oregon (both the portion inside the NRM and the entire state), Washington (both the portion inside the NRM and the entire state), and Wyoming..... 139

Table 7. Our assessment of 12 “core” adaptive capacity attributes for the gray wolf in the Western United States..... 144

Table 8. Estimated input parameter values for simulations (i.e., intrinsic rate of growth, effect of harvest and lethal depredation control (the overall effect per removed wolf on population growth), maximum population size, and initial population size)..... 158

Table 9. Harvest rates (percent of wolves killed annually through legal hunting and trapping) in each modeled state under each of the three harvest scenarios in our forecasting. .... 165

Table 10. Six combinations of future scenarios evaluated in future condition modeling..... 166

Table 11. Lethal depredation control rates from 2019, 2020, 2021, and 2022 (percentage of wolves removed) in each state included in our forecasting. .... 168

Table 12. Summary of uncertainties or assumptions in future condition modeling, and potential effect on model’s projections of abundance. .... 178

Table 13. Median, lower 95% credible interval, and upper 95% credible interval for population size in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) at the end of the a) 10 year and b) 100-year timeframes of our simulations in all six future disease and harvest scenario combinations..... 188

Table 14. Median, lower 95% credible interval, and upper 95% credible interval for population size in the NRM at the end of the a) 10-year and b) 100-year timeframes of our simulations in all six future disease and harvest scenario combinations..... 192

## Executive Summary

The purpose of this document is to provide an assessment of the status of the gray wolf (*Canis lupus*) in the Western United States. The geographic scope of our analysis includes: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming. While individual gray wolves from this 11-state area have been known to disperse outside of it, the primary remaining habitat for the gray wolf in the Western United States occurs within these states. The Mexican wolf, a subspecies of the gray wolf, occupies parts of the Southwestern United States (see *Taxonomy* below) but is not considered in this assessment. Currently, gray wolves in the Western United States are listed as endangered under the Endangered Species Act (Act), except within the delisted Northern Rocky Mountains (NRM) distinct population segment (DPS), which includes Idaho, Montana, Wyoming, eastern Oregon and Washington, and a small portion of north-central Utah.

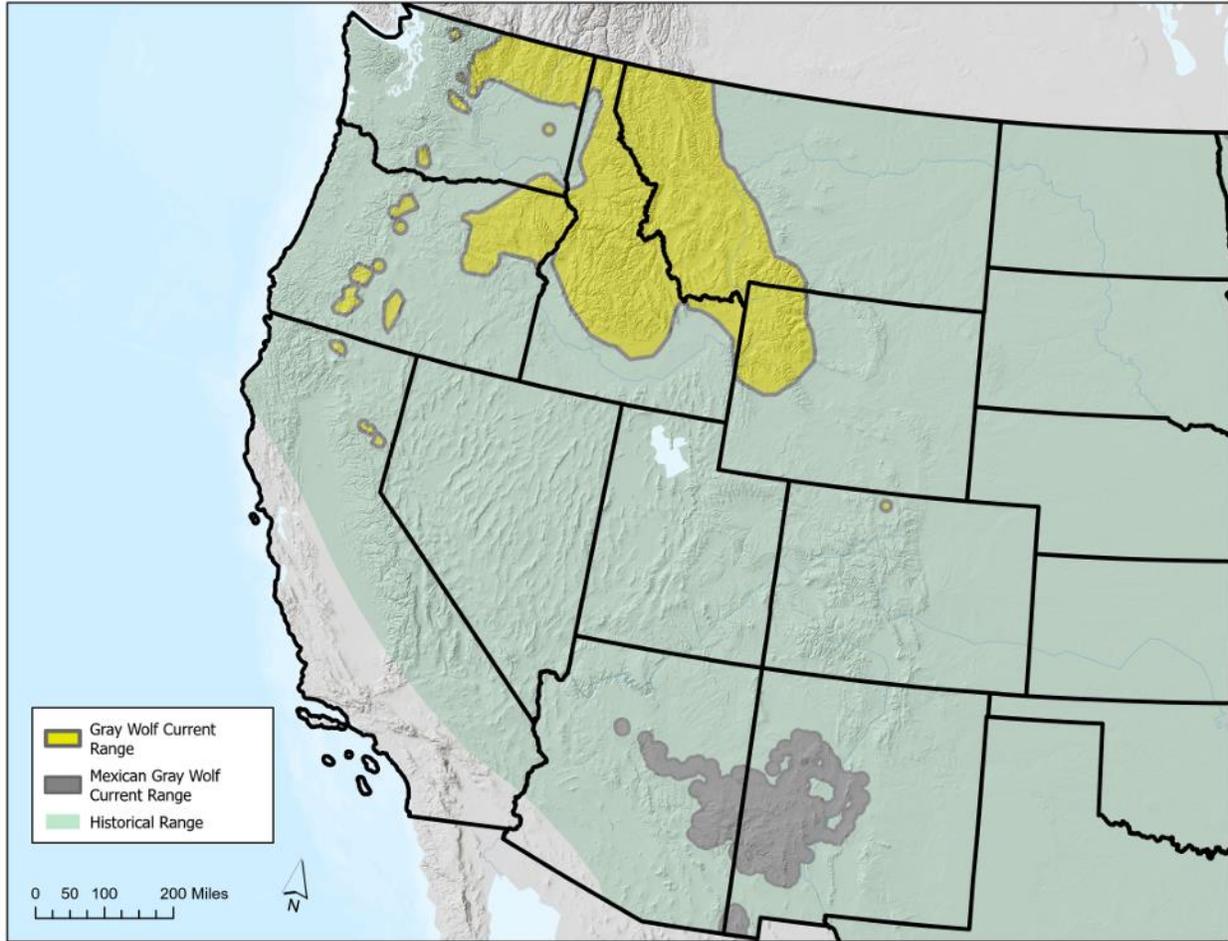
This Species Status Assessment (SSA) uses the conservation biology principles of **resiliency**, **redundancy**, and **representation**, collectively known as the “3Rs,” as a lens to evaluate the viability of the species (U.S. Fish and Wildlife Service (Service) 2016, p. 6). **Resiliency** is the ability 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 Western United States’ cultural or ecological significance (with the exception of an appendix summarizing indigenous knowledge on the gray wolf), nor does it discuss ethical dimensions of wolf management.

## Biology, Life History, and Ecology

Gray wolves are the largest wild members of the *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. Gray wolves are highly territorial, social animals and group hunters, normally living in packs of seven or fewer, but sometimes attaining pack sizes of 20 or more wolves (Mech 1970, pp. 38–43; Mech and Boitani 2003, p. 8; Stahler et al. 2020, p. 46). 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, wolf populations can overcome severe disruptions, such as intensive human-caused mortality or disease. Wolf populations can also quickly expand and recolonize vacant 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 conterminous United States, except the Southeast. We consider suitable wolf habitat to be areas containing adequate wild ungulate populations (e.g., elk and deer) and a low risk of conflict with humans and livestock (conflict generally increases the likelihood of human-caused wolf mortality) (see Mech 2017, pp. 312–315). Gray wolves are efficient at using available food resources (Newsome et al. 2016, pp. 260–261; Janeiro-Otero et al. 2020, p. 2).

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) (Figure ES 1). In the Western United States, wolves were historically common and widely distributed (Young and Goldman 1944, pp. 9–58). Estimates of historical populations are notoriously difficult to verify, but genetic data and extrapolations of known wolf densities have been used to estimate that there were likely hundreds of thousands of gray wolves once occupying the Western United States (Hampton 1997, pp. 22, 258; Leonard et al. 2005, pp. 14–15). As a result of poisoning, unregulated trapping and shooting, and the public funding of wolf extermination efforts, gray wolf populations were essentially eliminated from the Western United States by the 1930s (Young and Goldman 1944, pp. 56–58). After human-caused mortality of wolves in Southwestern Canada was regulated in the 1960s, populations expanded southward (Carbyn 1983, p. 240). Dispersing wolves occasionally reached the Rocky Mountains of the United States (Service 1994, pp. 4–5), but they lacked legal protection there until 1973 when they were first listed under the Endangered Species Preservation Act of 1969, a predecessor of the Act (38 FR 14678, June 4, 1973).



*Figure ES 1. Historical (green) and current (yellow) gray wolf range in the Western United States. The U.S. portion of Mexican wolf range is depicted in gray. Historical range based on Nowak (1995). Current range based on most recent state distribution data (see Chapter 1 for references and details).*

The reintroduction of wolves to central Idaho and Yellowstone National Park (YNP) in 1995 and 1996, along with natural recolonization of wolves from Canada into northern Montana in the 1980s and 1990s, led to increased numbers and distribution of wolves in the northern Rocky Mountains of the United States. Over the course of the last several decades, wolves have continued to expand their range in the Western United States, and wolf packs have become established in California, Oregon, and Washington, and, more recently, wolves have been documented in Colorado (see Chapter 4). Within our analysis area, dispersing wolves have also been observed in Arizona, Nevada, New Mexico, and Utah but they have not established packs there.

In general, to maintain populations in the wild over time, wolves in the Western United States need well-connected and genetically diverse subpopulations that function as a

metapopulation<sup>1</sup> 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 the NRM and population viability analyses on other wolf populations can provide further insight into the viability of wolf populations in the Western United States. Overall, the majority of population viability analyses that have been conducted on wolf populations around the globe indicate that several hundred individuals likely provide for a viable 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 (Rolley et al. 1999, p. 43; Nilsson 2003, p. 236; Liberg 2005, p. 6; Wisconsin Department of Natural Resources (WI DNR) 2006, pp. 8–11; Wiles et al. 2011, p. 9; Chapron et al. 2012, pp. 37–41; Liberg and Sand 2012, pp. 5–12; Oregon Department of Fish and Wildlife (ODFW) 2015b, pp. 17–19; Swedish Environmental Protection Agency 2015, unpaginated; Faust et al. 2016, pp. 3–4; Maletzke et al. 2016, pp. 372–374; Miller 2017, pp. 41–44; Petracca et al. 2023a, entire; Petracca et al. 2023b, entire).

## Stressors and Conservation Efforts

A stressor is that which causes a change in a habitat or demographic resource that can lead to an adverse individual response. The stressors that we evaluate for wolves in the Western United States include: human-caused mortality, disease and parasites, inbreeding depression, 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 wolves in the Western United States by reducing the influence of a stressor, improving the condition of wolf habitat, or improving wolf demographic factors.

In 2021, the state legislatures of Idaho and Montana both passed legislation intended to reduce the size of wolf populations in their states to minimize conflicts with livestock and impacts on ungulate populations. These statutes and the associated regulatory changes for the 2021/2022 wolf hunting and trapping seasons in Idaho and Montana were the primary subject of the 2021 petitions to list the gray wolf in the Western United States under the Act.

In the Western United States, the primary stressor influencing wolf populations is human-caused mortality. The main sources of human-caused mortality are regulated harvest in Idaho, Montana, Washington, and Wyoming, lethal control of wolves depredating livestock throughout the NRM, and illegal take. Within current wolf range, most states, tribal nations, and Federal agencies have management protocols and regulations that govern conservation and take of wolves. Overall, harvest rates have not always increased as harvest regulations have become less

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<sup>1</sup> 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.

restrictive in Idaho and Montana (e.g., extended seasons, removal of harvest limits, increased bag limits), and populations remained relatively stable through the end of 2020, with slight population decreases observed in Idaho and Montana at the end of 2021 and 2022. Furthermore, current levels of mortality in the NRM have not prevented the continued natural recolonization of suitable habitat in Oregon and Washington (where known wolves now total close to 400 individuals), California, or, more recently, in Colorado. According to the best available science, disease in wolves has caused episodic, yet short-term and localized population decreases. In some circumstances, disease outbreaks can interact with density-dependent mortality to regulate population sizes at lower levels than prior to the introduction of the disease(s) (e.g., DeCandia et al. 2021, p. 430). In our SSA, we project the future condition of wolves in the Western United States considering potential increased rates of harvest and disease (given the regulatory changes in Idaho and Montana); we also discuss the potential for future climate-related changes in disease distribution, frequency, and severity. Finally, we consider the current and future status of inbreeding, inbreeding depression, connectivity, and genetic diversity in our analysis of current and future condition. We also considered the potential effects of diseases in prey species, climate change, or other sources of habitat modification on gray wolves in the Western United States, but we do not further analyze their future effect on gray wolf viability because, based on the best available scientific information, these stressors have not negatively influenced gray wolf viability nor are they anticipated to do so in the future.

## Current Condition

Habitat and prey for wolves are abundant and well distributed in the Western United States. This, in conjunction with the high reproductive potential of wolves and their innate behavior to disperse and locate social openings or vacant suitable habitats, has allowed wolf populations to withstand relatively high rates of human-caused mortality. Based on the best available scientific information, our analysis of the current condition of gray wolves in the Western United States demonstrates that, despite current levels of regulated harvest, lethal control, and episodic disease outbreaks, wolf abundance in the Western United States has generally continued to increase and occupied range has continued to expand since reintroduction in the 1990s, with the exception of three years during which wolf abundance in the Western metapopulation decreased slightly (i.e., a decrease of approximately 50 to 100 wolves in one year). As of the end of 2022, states estimated that there were 2,797 wolves distributed among more than 286 packs in seven states (see Chapter 4 for detailed population estimates and references). This large population size and broad distribution contributes to the resiliency and redundancy of wolves in the Western United States. Moreover, wolves in the Western United States currently have high levels of genetic diversity and connectivity, further supporting the resiliency of wolves throughout the West. Finally, wolves in the Western United States have adaptive capacity characterized by life history traits that confer dispersal and colonization capability, and phenotypic and behavioral plasticity, with contributing factors such as their current population size, distribution, connectivity, and genetic diversity, that allows for evolutionary genetic adaptation. These traits, in combination with a range that extends into five different ecoregional provinces, demonstrate that wolves in the Western United States currently retain the ability to adapt to changes in their environment.

## Future Condition

We developed a density-dependent population growth model to project the future population size of wolves in: Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) under a range of future scenarios. We modeled the annual size of the wolf population in these states for every year between 2022 and 100 years into the future. We then used these projections to conduct a population viability analysis by evaluating the likelihood of falling below several thresholds related to extinction risk and genetic health. Our model structure and thresholds were chosen to specifically evaluate the ability of wolves to persist in multiple areas under various harvest scenarios and disease rates (resiliency and redundancy), and to evaluate the ability of wolves to maintain effective population sizes above those needed to prevent inbreeding depression, which is another component of resiliency. We qualitatively discuss (1) resiliency in the states for which we were unable to model future population size (i.e., Arizona, California, Colorado, Utah, New Mexico, and Nevada) and (2) potential future changes in factors related to suitable habitat, prey availability, genetic diversity, connectivity, and representation.

We quantitatively projected the future population size of wolves at two geographic scales under multiple future scenarios. Future scenarios allow us to explore a range of possible future conditions for wolves in the Western 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 harvest and disease, the two primary stressors that could influence wolf populations in the future. 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.

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 wolf population dynamics. First, we applied the frequency and severity of disease that we have recently observed in a wolf population in the Western United States. This first level of disease (i.e., “observed YNP disease rates”) was estimated from data on wolves in 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). 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.

Our future scenarios also included variation in harvest rates, which we define as the annual percent of wolves killed through legal hunting and trapping. For Washington and Wyoming, we used the average of past observed harvest rates from the most recent 4 years for each state across all scenarios; in other words, we assumed that harvest in Washington and Wyoming would stay the same as current levels into the future. Due to many factors that affect hunter/trapper effort and success, uncertainty remains as to how the new harvest regulations in Idaho and Montana may affect future harvest rates in these states. Therefore, to examine a range of potential effects of these recent changes to harvest regulations in Idaho and Montana, we projected future population sizes for these two states under three different harvest scenarios. Under Harvest Scenario 1, the harvest rate in each state reflected the average estimated harvest

rates from the most recent 4 years. Under Harvest Scenario 2, the harvest rate in Idaho and Montana reflected the maximum harvest rate observed in the state (since delisting) plus 20 percentage points, to represent an increase in harvest over previously observed rates. Under Harvest Scenario 3, harvest rates in Idaho and Montana reflected the harvest rate necessary to reduce the population in Idaho and Montana to 150 wolves each within 5 years, a timeframe reflecting a rapid (within approximately one wolf generation) decline from the current population size to the management buffer above the recovery criteria (i.e., 150 wolves), a level both states have repeatedly committed to manage above and which the new regulations uphold (Groen et al. 2008, p. 1; Talbott and Guertin 2012, p. 1). We also varied the rate at which wolves that primarily reside in YNP would be harvested in areas surrounding YNP.

Therefore, in our projections we estimated the future number of wolves in each state under six total combinations of disease and harvest scenarios, all starting with the current estimated population size in each state and spanning two disease scenarios and three harvest scenarios.

It is unlikely that an individual scenario will play out exactly as we describe above in the future; not all scenarios are equally likely to accurately represent future harvest rates. Moreover, new state regulatory mechanisms indicate states will or could manage for population sizes larger than our model assumes under these future scenarios. Additionally, factors such as the high reproductive rates of wolves, the amount of refugia habitat for wolves, and the high costs of control efforts make the increased harvest rates modeled in Harvest Scenarios 2 and 3 unlikely throughout an entire state over an extended period of time, even though these harvest rates are legally allowable under current state laws (though inconsistent with Idaho's new 2023 state management plan) (Idaho Fish and Game (IDFG) 2023a, pp. 38–44). Therefore, our projections of future abundance under Harvest Scenarios 2 and 3 likely underestimate true future abundance, given the difficulty of achieving and sustaining the harvest rates in these scenarios at the temporal and/or spatial scales we modeled and given the expressed objectives of Idaho to manage for a population larger than our model assumes.

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 one year during the 100-year timeframe. These values illustrate the probability that the population will fall below critical thresholds that represent a key reduction in viability (quasi-extinction) or a potential risk of inbreeding depression (effective population size of 50).

### **Future Resiliency and Redundancy**

According to the assumptions and parameters in our modeling, neither the projected future wolf population in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) nor the projected future wolf population in the NRM reached quasi-extinction levels (i.e., fewer than 5 wolves) in 100 years. Additionally, there was a maximum of a 0.02 percent probability of falling below an effective population size of 50 (i.e., 192 to 417 wolves) in 100 years, demonstrating a negligible risk of future inbreeding (see Figure ES 2 and Figure ES 3). Our models project that wolf populations are extremely likely to remain above both thresholds

(quasi-extinction or a level at which inbreeding may occur) in the future, even if Idaho and Montana immediately increase harvest to over 65 percent and catastrophic levels of disease occur throughout the range (the most impactful combination of harvest and disease scenarios we analyzed). Our model results project that, although the number of wolves in Idaho and Montana will decline in the future, when taken together, the wolves in the Western states we modeled and in the NRM will likely maintain the ability to withstand stochastic and catastrophic events into the future, provided Idaho, Montana, and Wyoming cease harvesting wolves if the populations in those states decline to 150 wolves each (and as long as the other assumptions in our model are satisfied).

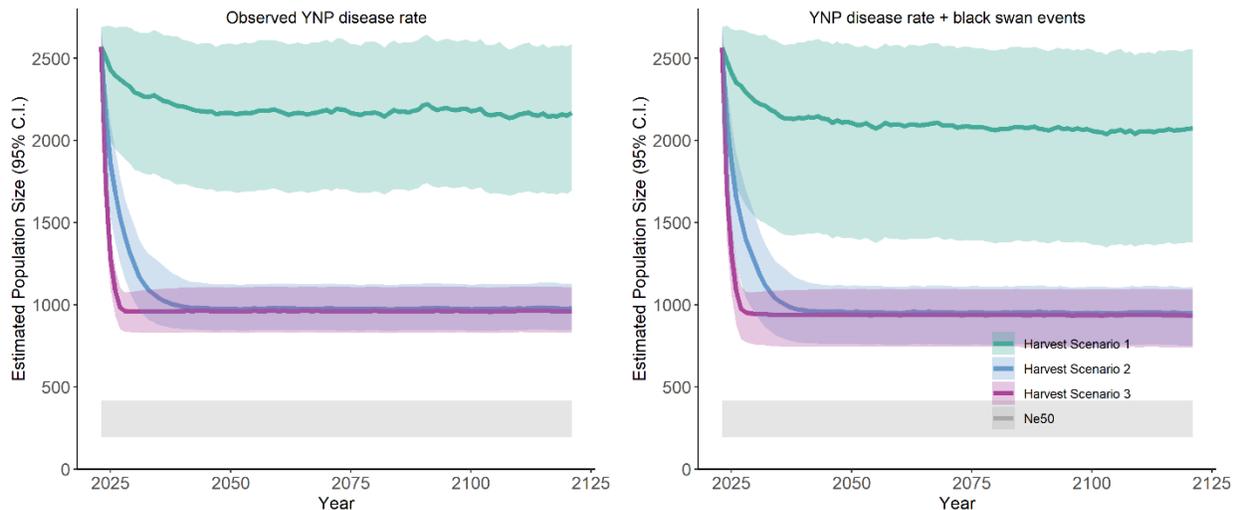


Figure ES 2. Median projected wolf population size (solid line) and 95% credible interval (shaded area) in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) in Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations. The shaded gray box represents the range of estimated wolf population sizes (192–417 wolves) we calculated to be equivalent to an effective population size of 50.

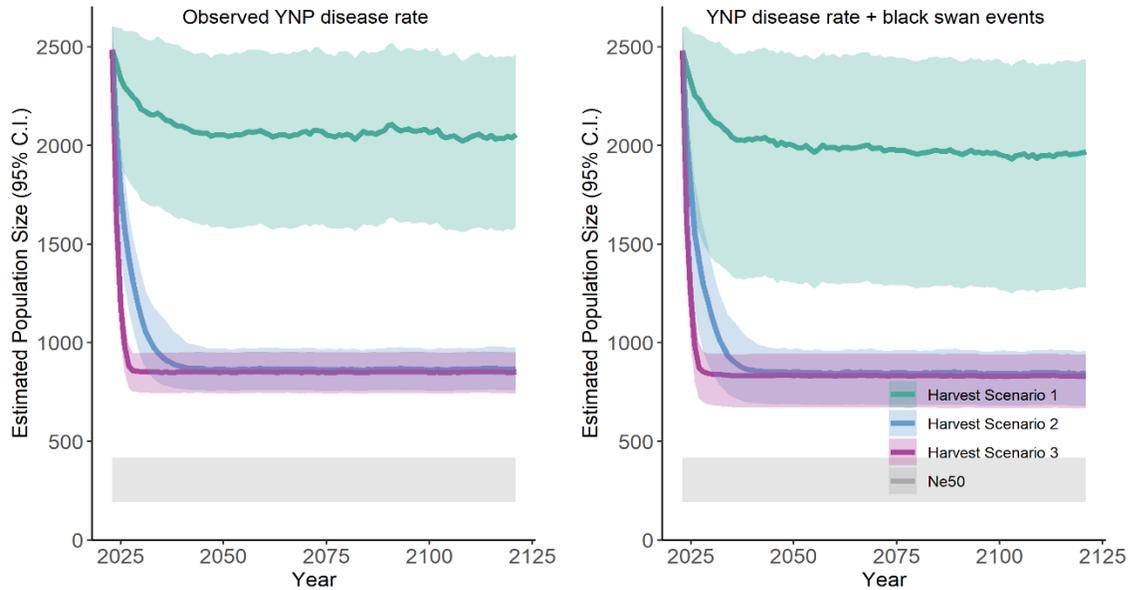


Figure ES 3. Median projected wolf population size (solid lines) and 95% credible interval (shaded area) in the NRM in Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations. The shaded gray box represents the range of estimated wolf population sizes (192–417 wolves) we calculated to be equivalent to an effective population size of 50.

In the other parts of our analysis area where we lacked sufficient data to quantitatively forecast future gray wolf abundance (i.e., Arizona, California, Colorado, Utah, New Mexico, and Nevada), we qualitatively describe how the number of wolves may change in the future. Under all of our future scenarios, the number of wolves in California and Colorado will likely increase in the future due to dispersal from neighboring states, the growth of resident packs already in the states, and, in the case of Colorado, a state statute that requires the reintroduction of wolves to the state. This likely future increase in wolf abundance in California and Colorado would further expand the number and distribution of wolves relative to current condition and would further contribute to the future resiliency and redundancy of wolves in the Western metapopulation; redundancy may be higher in the future than it is currently given this expanding range. Thus, the model results, combined with our expectations for the number of wolves outside of the modeled Western states, demonstrate that the wolves in the Western population are likely to maintain the ability to withstand stochastic and catastrophic events (i.e., disease) into the future even with the projected declines in the number of wolves in Idaho and Montana.

Our expectations for habitat and prey availability and genetic health further support the maintained resiliency of wolves in the Western United States and the NRM 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 United States in the future. Given our expectation of continued connectivity in the Western United States 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 wolves and the projections for changes in population sizes in the future scenarios we model, it is likely that wolves will remain capable of adapting to environmental change. Such capability will be comprised, as it is currently, of: (1) a strong ability to disperse and colonize suitable habitat; (2) tolerance to a range of environmental conditions, facilitated in part by 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 our projections display a wide range of outcomes for future population size and the primary stressor, human-caused mortality, is one for which sufficient adaptation is unlikely, we expect wolves in the Western United States 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 limits described in our future scenarios.

## Summary of Future Condition

Given our stated assumptions and accounting for uncertainty, our model projections indicate that wolves will avoid extirpation in the NRM and Western United States over the next 100 years (as long as future mortality rates are within the bounds we evaluate in our analysis). Even in the extremely unlikely scenarios in which harvest substantially increases and is maintained at high rates over time in Idaho and Montana, while population sizes decrease in these states, overall populations remain well above quasi-extinction levels in the NRM and Western United States. More generally, gray wolves in the NRM and the Western metapopulation will retain the ability to withstand stochastic and catastrophic events in the future (resiliency and redundancy) despite the decrease in the number of wolves relative to current condition under our future scenarios. We also expect the population size to remain large enough, with sufficient connectivity and genetic diversity, to avoid consequential levels of inbreeding or inbreeding depression in the future. Given this maintained connectivity, combined with wolves' adaptable life history characteristics, we expect wolf populations in the NRM and Western United States will be able to maintain their evolutionary potential and adapt to future change (representation). The likelihood of additional wolves in California and Colorado (and possibly in Arizona, New Mexico, and Utah in the long term), the continued recolonization of Western Oregon and Washington, and the availability of suitable wolf habitat and prey further support the continued viability of the gray wolf in the NRM and the Western metapopulation under the existing management commitments, albeit at potentially reduced population sizes compared to current numbers. Significant deviations from the mortality rates we analyzed, or violations of other model assumptions, could alter our confidence in this conclusion.

## Introduction

### Purpose and Geographic Scope

The purpose of this document is to provide an assessment of the status of the gray wolf (*Canis lupus*) in the Western United States. The geographic scope of our analysis includes: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming (Figure 1). We only include the portions of Arizona and New Mexico north of Interstate-40 (I-40) in our analysis area because the Service has promoted the recovery of the Mexican wolf subspecies (*Canis lupus baileyi*), rather than the gray wolf (*Canis lupus*), in areas south of I-40 (Service 2022b, entire). Although individual gray wolves from this 11-state area have been known to disperse outside of this area, the primary remaining habitat for the gray wolf in the Western United States occurs within these states. The Mexican wolf, a subspecies of the gray wolf, occupies parts of the Southwestern United States (see *Taxonomy* below) but is not a part of this assessment.

Currently, gray wolves in the Western United States are listed as endangered under the Endangered Species Act (Act), except within the delisted Northern Rocky Mountains (NRM) distinct population segment (DPS) (Figure 1). Gray wolves in the NRM DPS are not federally protected under the Act. The NRM DPS area includes: Idaho, Montana, and Wyoming as well as the eastern one-third of Oregon, a small portion of north-central Utah, and the eastern one-third of Washington (we describe these boundaries in detail in the 2009 rule originally delisting the DPS, with the exception of Wyoming; 74 FR 15123, April 2, 2009). The Service reissued this final rule, in 2011; gray wolves in Wyoming were delisted in 2012 and again 2017. For more details on the regulatory history of gray wolves, see the 2020 final rule removing the protections of the Act from gray wolves in the conterminous states (85 FR 69778, November 2, 2020).

Throughout this Species Status Assessment (SSA), we refer to the wolves within the boundaries of the NRM DPS described in the 2009 rule as the “NRM” or the “NRM population” when we discuss the biological status of wolves in this delisted portion of the range; however, in using the term “NRM” or “NRM population” to refer to this area, we are not indicating that this area is a biologically-separate population, nor are we claiming whether or not this area still qualifies as a DPS. We will conduct any necessary DPS analyses in later regulatory documents; we will use the information in this SSA to inform these analyses. Furthermore, throughout this SSA, we often refer to the wolves in each state as a “population” and frequently discuss each state’s population separately, as wolves are managed at this state scale in the Western United States. However, the wolves in each state are connected to wolf populations in other states in the Western U.S. metapopulation; in using the term “population” as shorthand to refer to the wolves in each state, we are not concluding each state represents a biologically-separate population.



Figure 1. Analysis area for SSA for the gray wolf in the Western United States. Analysis area includes the States of California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Washington, and Wyoming; and portions of the States of Arizona and New Mexico. The gray shading of the analysis area on this map does not indicate historical, current, or potential range, nor does it indicate a DPS; rather, this map only illustrates the area we are considering in our SSA. The black hatched area on the map depicts the delisted NRM area. The yellow shaded area indicates current range of the gray wolf within the analysis area (as of December 31, 2022, except California, which is current as of May 2023). The black cross-hatched area delineates the Mexican Wolf Nonessential Experimental Population Area, which is not part of our analysis.

## 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 Western United States. We recognize there are other aspects of gray wolf conservation and management that are of interest to a diverse set of stakeholders, including—but not limited to—ethical questions surrounding wolf 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 distinct

population segments) 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 Western 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 in the Western United States' habitat and demographics and the probable explanations for past and ongoing changes in abundance and distribution (*Chapters 3 and 4*).
3. **Future Species Condition.** Lastly, we use a quantitative model to forecast the estimated abundance of wolves under 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 gray wolf in the Western United States' viability (*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 species status assessments. 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 (the 3Rs) 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; Sgro 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 species status assessment, we assessed all three facets to the best of our ability based on available data.

## Traditional Ecological Knowledge

Over the course of the status review of the gray wolf in the Western United States and the development of this SSA, we corresponded and met with various Tribes across the west, including sending “Dear Interested Party” letters requesting information for this SSA from over 370 Tribes within the analysis area. We also specifically spoke with tribal representatives from seven Tribes to discuss traditional ecological knowledge surrounding the gray wolf.

Native American knowledge about the gray wolf is passed down orally from one generation to the next, which is often referred to in the literature as traditional ecological knowledge. Traditional ecological knowledge refers to the knowledge base acquired by indigenous and local peoples over many hundreds of years through direct contact with the environment. Traditional knowledge is based in the ways of life, belief systems, perceptions, cognitive processes, and other means of organizing and transmitting information in a particular culture. Traditional ecological knowledge includes an intimate and detailed knowledge of plants, animals, and natural phenomena; the development and use of appropriate technologies for hunting, fishing, trapping, agriculture, and forestry; and a holistic knowledge, or “world view”, which parallels the scientific discipline of ecology (Inglis 1993, p. vi; Cajete 2000, entire; Berkes 2012, p. 7). New scientific knowledge can be derived from perceptive investigations of traditional knowledge with respect to species natural history, behavior, and life cycles. For example, traditional ecological knowledge regarding several arctic species coming from the Inuit of Belcher Islands in Canada exceeded that of the Western scientists who were limited to seasonally-scheduled research periods (Berkes 1999, p. 29). Furthermore, Ramos (2022, entire) explored Yurok traditional ecological knowledge and wildlife management, articulating the need for more inclusivity of indigenous peoples’ knowledge in Western science.

Native American relationships with the gray wolf in the Western United States predates modern Western knowledge of the gray wolf by thousands of years (Pierotti 2011, p. 58). Carnivores are recognized as being powerful creatures, not unlike humans, and, in the case of wolves, are very similar to humans in the structure of their family units (Pierotti 2011, p. 21). The gray wolf is known by many names among Tribal Nations throughout this land, and for time immemorial has held an esteemed place in the cultures and lifeways of the original inhabitants of this continent. Indeed, for some Tribal Nations, the gray wolf has guided and influenced their people in a foundational way, since the beginning of time. The cultural, spiritual, and ceremonial importance of the gray wolf is profound; suffice to say, the gray wolf is, for many Tribes, foundational to their place upon and understanding of the earth and stars (Rocky Mountains Tribal Leaders Council 2019, in litt., p. 2). We summarize the traditional ecological knowledge on the gray wolf in the Western United States that tribal members shared with us in Appendix 1; where appropriate, we incorporate this traditional ecological knowledge into the SSA report to further illustrate the species’ life history, ecology, or current condition.

## 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., NRM 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 Tribes and state agencies to the conservation and management of wolves in the Western United States, 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.

### Taxonomy

The gray wolf is a member of the canid family (*Canidae*) in a global 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*). Wolves share an evolutionary history with other mammalian carnivores (Order *Carnivora*), or meat eaters, which are distinguished by their long, pointed canine teeth, sharp shearing fourth upper premolars and first lower molars, 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, the forerunners of all modern wolves, coyotes, and domestic dogs (Nowak 2003, p. 241). The lineage of wolves and coyotes diverged between 1.8 and 2.5 million years ago based on fossil evidence (Nowak 2003, p. 241) and 1.0 million years ago based on genetic evidence (vonHoldt et al. 2011, p. 1294; vonHoldt and Aardema 2020, p. 249). Domestication of wolves led to all modern domestic dog breeds, which probably occurred between 20,000–40,000 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).

Among *Canis* species found in North America, taxonomic relationships have been studied extensively, though with a notable lack of consensus, even on issues such as the phylogenetic history of dogs, wolves, and coyotes (e.g., Cronin et al. 2014, 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 or hybridization 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 (Koblmuller et al. 2009, pp. 2321–2323; vonHoldt and Aardema 2020, entire; Sacks et al. 2021, p. 4301; Wilson and Rutledge 2021, 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).

There is general 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 area (vonHoldt et al. 2011, p. 1301), wolves in North America have consistently been divided and arranged into different types of subgroupings throughout much of their range. Early taxonomic work, based on morphological differences, led to the designation of numerous subspecies across the continent, which have been revised and, primarily, consolidated over time (reviewed in Chambers et al. 2012, pp. 10–13). Of these, the Mexican wolf (*Canis lupus baileyi*) 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; though see Cronin et al. 2014, p. 34; Fredrickson et al. 2015, entire; Fan et al. 2016, p. 169). Other generally recognized subspecies identified in the continental United States include *C. l. nubilus*, which historically ranged from eastern Canada down through the Great Plains and up the west coast, and *C. l. occidentalis*, whose range stretches from interior Alaska south into the Rocky Mountains (Nowak 1995, p. 396; Chambers et al. 2012, pp. 34–41). Researchers hypothesize that these three subspecies represent three distinct migration events from Eurasia, with *C. l. baileyi* being the oldest, followed by *C. l. nubilus* and then *C. l. occidentalis* (Chambers et al. 2012, p. 42).

While some discussion continues on these subspecies' delineations, an increasing body of research has added important insight into genetic variation among wolf populations beyond a traditional taxonomic framework (Cronin et al. 2014, p. 34; Wayne and Shaffer 2016, entire). This work often does not directly address the taxonomic validity of previously designated subspecies and, at times, has shown a lack of strong support for those designations (vonHoldt et al. 2011, pp. 1300–1301; Cronin et al. 2014, p. 34). Nonetheless, this research confirms that wolves in North America are not panmictic (random breeding throughout a population), 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 clades 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) or bioclimatic groups (González-Bernal et al. 2022, p. 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; Munoz-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) and have been linked to putative functional genes that determine morphology, coat color, and metabolism (Schweizer et al. 2016, pp. 396–397).

Although there is ongoing debate about the taxonomy and evolutionary origins of wolves in the lower 48 states (see Service 2020, entire, and references within), there is general agreement within the scientific community that wolves occupying the Rocky Mountains and Pacific Northwest are genetically distinct from those inhabiting the western Great Lakes. This distinction has been clearly demonstrated with genetic markers (vonHoldt et al. 2011, p. 1301;

Sinding et al. 2018, pp. 3–6) and morphological analyses (Nowak 2002, pp. 199–202; Chambers et al. 2012, pp. 14–25 and references therein). Within the western United States, there is further taxonomic differentiation between existing populations. While our understanding of the specific boundaries of the historical range of the Mexican wolf (*C.l. baileyi*), or the current range necessary for recovery of the subspecies, may continue to evolve (e.g., Leonard et al. 2005, p. 15; Hendricks et al. 2016, entire; Heffelfinger et al. 2017, entire; Odell et al. 2018, entire; Martinez-Meyer et al. 2021, entire; González-Bernal et al. 2022, p. 5), the Service considers it a valid subspecies with a range in the Southwestern United States and Mexico (80 FR 2488, January 16, 2015). Wolves currently occupying the NRM are the result of natural immigration from Canada into Northwest Montana and reintroduction from inland Alberta and British Columbia into central Idaho and Yellowstone National Park (YNP) (Bangs and Fritts 1996, entire; Fritts et al. 1997, entire). Both of these source populations have traditionally been classified as *C. l. occidentalis*. As these populations have grown, wolves have expanded into Northern California, Oregon, and Washington; more recently, wolves have been documented in Colorado. A genetic study in the Pacific Northwest found that all wolves in Oregon and the majority of wolves in Washington descended exclusively from wolves in the NRM and interior Alberta and British Columbia (Hendricks et al. 2018, p. 140). Oregon wolves are naturally recolonizing California (California Department of Fish and Wildlife (CDFW) 2021a, entire), and adult wolves that became the first known reproductively-active pack in Colorado in modern history likely dispersed from Wyoming, including a female confirmed to be from the Snake River Pack in Wyoming (Colorado Parks and Wildlife (CPW) 2022, unpaginated).

While the vast majority of wolves in the Western United States appear to share a taxonomic history consistent with *C.l. occidentalis* in the NRM, there is also wide recognition that coastal wolves from British Columbia into Southeastern Alaska represent a distinct group, possibly even separate subspecies (Goldman 1944, pp. 452–455; Service 2023a, pp. 6–13; Weckworth et al. 2005, entire; Weckworth et al. 2010, entire) (we refer to this group as “coastal wolves” in the remainder of this SSA). Studies have shown coastal wolves are genetically and morphologically distinct and display distinct habitat and prey preferences, despite relatively close proximity to inland wolves (Carmichael et al. 2001, pp. 2796–2797; Weckworth et al. 2005, entire; Muñoz-Fuentes et al. 2009, p. 1525; Weckworth et al. 2010, pp. 368–170; vonHoldt et al. 2011, p. 1298; Schweizer et al. 2016, p. 381). As noted in the review by Chambers et al. (2012, p. 41), as many as three distinct coastal wolf subspecies have been recognized in the past: (1) *C.l. ligoni* in Southeast Alaska, (2) *C.l. fuscus* in coastal British Columbia down through Washington and into Oregon, and (3) *C.l. crassodon* on Vancouver Island. Nowak (1995, pp. 382–384) subsequently consolidated all three subspecies into *C.l. nubilus*, though Muñoz-Fuentes et al. (2009, p. 1527) point out that no samples from coastal British Columbia were included in that analysis. Several studies have concluded that coastal wolves from Southeastern Alaska into coastal British Columbia appear closely related genetically and occupy a similar bioclimatic niche, indicating that they likely represent a single taxonomic group (Breed 2007, pp. 28–30; Weckworth et al. 2011, entire; González-Bernal et al. 2022, p. 5–7). The Service, in its 2023 12-month finding on Alexander Archipelago wolves, recognized them as the subspecies *C.l. ligoni*, with a range that extends from Southeast Alaska down the coast to the Washington border, while acknowledging that there is still uncertainty about the correct taxonomic status (88 FR 57388, August 23, 2023). Further discussion of the taxonomy of these wolves is available in the Service’s 2023 SSA for Alexander Archipelago Wolf (Service 2023, pp. 6–13).

Genetic markers associated with coastal wolves have been identified in historical, museum specimens from as far south as Southwestern Oregon (Hendricks et al. 2015, p. 763), indicating the presence of coastal wolves in that area prior to extirpation. Contemporary data do not indicate such a southernly extent of coastal wolf range, however, as wolves currently found in California and Oregon all appear to be of NRM origin (Hendricks et al. 2018, p. 143). While the same is largely true in Washington, where most wolves show NRM ancestry, two wolves sampled there appear to be admixed with both NRM and coastal wolf origins (Hendricks et al. 2018, p. 141). It is not clear from the data whether the admixture occurred in Washington or whether admixed individuals dispersed into the state. Nevertheless, this admixture is consistent with the view that the borders between wolf subdivisions, whether identified as ecotypes or subspecies, may be porous, particularly where suitable habitat exists between them (Chambers et al. 2012, p. 43; Schweizer et al. 2016, p. 395; Hendricks et al. 2018, p. 143; González-Bernal et al. 2022, p. 6). While Western Washington may represent an area of potential overlap between coastal wolves and gray wolves in the Western United States, there is little coastal habitat remaining to support a viable population of coastal wolves in the Western United States (Carroll et al. 2006, p. 32; Larsen and Ripple 2006, pp. 26–27, 31) when compared to their roughly 84,595 square mile (mi<sup>2</sup>) (219,101 square kilometer (km<sup>2</sup>)) range in Alaska and British Columbia (Service 2015, Appendix I). Therefore, while we acknowledge there is likely to be admixture of wolf genes across ecotype or subspecies boundaries, the vast core of the coastal wolf’s range is outside of our analysis area. We conducted a rangewide status assessment of coastal wolves (a.k.a., Alexander Archipelago wolves) in 2015 (Service 2015, entire) and recently completed a new assessment of the same entity (Service 2023a, entire).

In summary, wolf taxonomy and evolutionary history are complex and controversial in North America. The science around 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 wolves are subdivided, to some degree, based on ecological and climatic factors. In the Western United States, these subdivisions are represented by the Mexican wolf and wolves in the NRM, which have expanded into portions of California, Oregon, and Washington; more recently, wolves have been detected in Colorado. While there is some evidence of admixture with coastal wolves, there is not yet any confirmation that such admixture is common or has occurred within our analysis area. Nor is there evidence of non-admixed coastal wolves in the conterminous United States. Because the specific taxonomic and evolutionary relationships within the gray wolf are not yet fully resolved, for the remainder of this report we use the term “gray wolf in the Western United States” to describe wolves that occur in the Western United States, excluding the Mexican wolf.

## Species Description

Gray wolves are the largest wild members of the 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). Gray wolves have a circumpolar range including North America, Europe, and Asia. In North America, wolves are primarily predators of medium and large mammals, such as: moose, elk, white-tailed deer, mule deer, caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*), bison (*Bison bison*), and beaver (*Castor canadensis*), and they are efficient at utilizing 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, wolves also use ambush behavior, especially for smaller prey such as beaver (Gable et al. 2021, p. 340). Wolves also have keen senses of smell, hearing, and vision, which they use to detect prey and one another (Mech 1970, pp. 15–16; see Appendix 1); 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 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; see Appendix 1).

## Species Life History

Gray wolves are highly territorial, social animals and group hunters, normally living in packs of seven or fewer but sometimes attaining pack sizes of 20 or more wolves (Mech 1970, pp. 38–43; Mech and Boitani 2003, p. 8; Stahler et al. 2020, p. 46). Though 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 wolf (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 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 Boitani 2003, pp. 2–3). Research from Idaho and YNP indicates that multiple breeders are observed in approximately 25 percent of packs and are more likely to be observed in larger packs; the occurrence of multiple breeders implies that habitat is saturated (Ausband 2018, pp. 840–842; Stahler et al. 2020, p. 52).

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). Wolves of both sexes typically reach sexual maturity at 2 to 3 years of age but, on rare occasions, can breed as early as one year of age (Fuller et al. 2003, p. 175; Mech et al. 2016, pp. 1–2). Once paired with a mate, 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 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; CDFW 2021a, 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 one 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 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). Overall, with multiple pups reared by a pack on an annual basis, 10 to 40 percent of pack members disperse away from the pack every year (Fuller et al. 2003 p. 181; Mech and Boitani 2003, pp. 2, 11; Jimenez et al. 2017, p. 586). Dispersers may become nomadic and cover large areas as lone animals, or they may establish their own territorial wolf 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 (Boyd and Pletscher 1999, pp. 1102–1103; Mech and Boitani 2003, pp. 14–15; Oregon Department of Fish and Wildlife (ODFW) 2011, pp. 5–6; ODFW 2016, p. 10; Jimenez et al. 2017, p. 585; CDFW 2021a, p. 2). The innate ability of wolves to disperse long distances (Smith et al. 2020a, p. 88) allows wolf populations to quickly expand and recolonize vacant 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<sup>2</sup> (i.e., reduced probability of finding a mate at low densities) are stronger at greater distances from source populations (Hurford et al. 2006, pp. 249–250; Stenglein and Van Deelen 2016, entire).

Wolf packs typically occupy and defend a territory of 13 to more than 1,016 mi<sup>2</sup> (33 to more than 2,600 km<sup>2</sup>), with territories tending to be smaller at lower latitudes (Fuller et al. 2003, pp. 172–175; Mech and Boitani 2003, p. 22; Sells et al. 2021, pp. 5–6; see Appendix 1). The large variability in territory size is likely due to the costs and benefits of differences in 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; Sells et al. 2021, pp. 6–8; Sells et al. 2022b, pp. 6–9).

In wolf populations, pack social structure is very adaptable. In many instances, breeding members can be quickly replaced from either within or outside the wolf pack, and pups can be

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<sup>2</sup> Allee effects are more 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 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).

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 wolf breeding strategies, leads to high potential fecundity and the ability for packs to act as “dispersal pumps” (see discussion of dispersal in paragraph below) (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, wolf populations can overcome severe disruptions, such as intensive human-caused mortality or disease. The likelihood a wolf pack will maintain its territory declines if both breeders are killed; however, if one member of the breeding pair is killed, the wolf pack may hold its territory until a new, unrelated wolf 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 wolf pack may die, disperse, or remain in the territory until an unrelated dispersing wolf arrives and mates with one of the remaining pack members (Mech and Boitani 2003, pp. 28–29; Brainerd et al. 2008, p. 96). 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).

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. 2012a, entire). However, pack and population response to mortality is also influenced by many factors including habitat quality, prey abundance, wolf density, pack size, reproductive rates, and levels of isolation (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. 2023a, entire; and see *Effects of Human-Caused Mortality and Disease and Parasites in Wolves*). In wolf populations, the density of wolves on the landscape can impact specific vital rates such as adult survival, natality rates<sup>3</sup> and recruitment, and dispersal. These vital rates can directly influence population growth and the ability for a wolf population to recolonize vacant habitats or respond to population declines. In general, when suitable habitat is available (e.g., high prey density, low livestock density), these vital rates are positively influenced by low wolf densities, which ultimately results in relatively rapid population growth and expansion. As wolf abundance and distribution increases and wolves begin to occupy most of the available suitable habitat in an area, wolf population growth declines. Examples of this density dependent relationship with population growth can be seen in the NRM and the Western Great Lakes wolf populations (Service et al. 2016, Figure 7a; Service 2020, pp. 15–24). High 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, and age of dispersal (Jimenez et al. 2017, pp. 5–12; Sells et al. 2022a, pp. 7–12). Conversely, when wolf densities decline and suitable habitat remains available, any or all of the above wolf 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. 2020a, pp. 77–92), thus providing opportunity for increased growth.

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<sup>3</sup> A natality rate is the number of pups produced.

## Suitable Habitat

Gray wolves are habitat generalists (Mech and Boitani 2003, p. 163; MacNulty et al. 2020, p. 31); they once occupied or transited most of the conterminous United States, except the Southeast (Nowak 2002, pp. 103–121; Nowak 2009, pp. 242–244; Hohenlohe et al. 2017, pp. 1–2). Wolves can successfully occupy a wide range of habitats, provided adequate prey exists and human-caused mortality is sufficiently regulated (Mech 2017, p. 315). To identify areas of suitable wolf habitat in the conterminous United States, researchers have used models that relate the distribution of wolves to characteristics of the landscape. These models have shown the presence of wolves is positively correlated with prey density, Federal land ownership, large habitat patches, and forest cover; and is negatively correlated with higher livestock density, higher road density, higher human density, presence of agricultural land, and small habitat patches (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; Petracca et al. 2023a, Appendix S4). At finer spatial scales (i.e., within their home range or territory), wolves appear to select simple topography where ungulate prey may be more susceptible (Peterson et al. 2021, pp. 9–19; Sells et al. 2021, pp. 5–8; Sells et al. 2022b, p. 4). Aside from prey density and susceptibility, these environmental variables are proxies for the likelihood of wolf-human conflict and the ability of 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 escape cover without agricultural land) (see Mech 2017, pp. 312–315).

Modeled wolf habitat in the Western United States includes occupied wolf habitat in the NRM, the Cascade mountains and adjacent foothills of Oregon and Washington as well as northern California, and northern Colorado (Carroll et al. 2001, p. 36; Carroll et al. 2003, pp. 551–553; Houts 2003, p. 7; Carroll et al. 2006, p. 32; Larsen and Ripple 2006, pp. 27–31; Oakleaf et al. 2006, p. 559; CDFW 2016b, p. 156; Maletzke et al. 2016, p. 370; ODFW 2019a, Appendix D; Peterson et al. 2021, pp. 9–19; Ditmer et al. 2022a, pp. 7–12; Sells et al. 2022b, supplementary material). However, there are substantial areas of modeled wolf habitat in the Western United States that are currently unoccupied (Switalski et al. 2002, pp. 11–15; Ratti et al. 2004, pp. 12–13; Larsen and Ripple 2006, pp. 27–31; CDFW 2016b, p. 156; Maletzke et al. 2016, p. 370; Mech 2017, pp. 331–315; Nickel and Walther 2019, pp. 387–389; ODFW 2019a, Appendix D; Ditmer et al. 2022a, pp. 7–12), particularly in the central and southern Rocky Mountains in Colorado and Utah, with theoretical predictions indicating these areas could potentially support 600 to 2,000 wolves combined (Bennett 1994, p. 112; Switalski et al. 2002, pp. 11–15; Carroll et al. 2003, pp. 551–553; Carroll et al. 2006, pp. 32–33; Ditmer et al. 2022a, pp. 7–12) (Figure 2). Northern California, Western Oregon, and Western Washington also contain substantial areas of potential wolf habitat, and wolves are currently naturally recolonizing these areas (Larsen and Ripple 2006, pp. 27–31; CDFW 2016b, p. 156; Maletzke et al. 2016, p. 370; Nickel and Walther 2019, pp. 387–389; ODFW 2019a, Appendix D).

## Historical Distribution and Abundance

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).

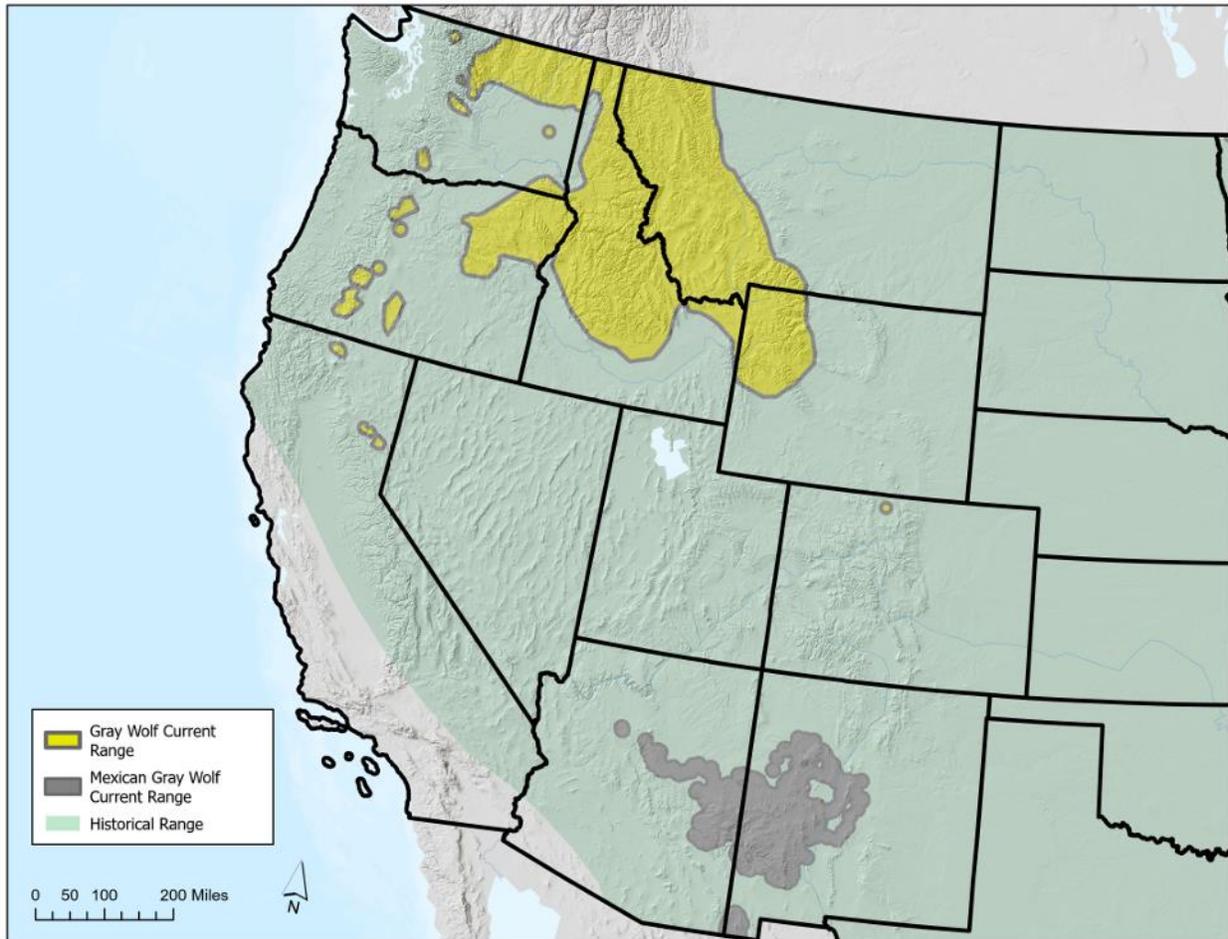


Figure 2. Historical (green) and current<sup>4</sup> (yellow) gray wolf range in the Western United States. The U.S. portion of Mexican wolf range is depicted in gray. Historical range based on Nowak (1995). Current range based on most recent state distribution data (as of December 31, 2022, except California, which is current as of May 2023), among other sources (see footnote below).

<sup>4</sup> The current range depicted in the maps throughout this SSA report was created from several datasets including state sources, Service expert judgement on the potential distribution of the wolf pack in Northern Colorado (which involved placing a 7.5 mi (12 km) buffer around the known wolf pack in Walden, Colorado), and range files from previous wolf rulemakings. The large current range polygon that includes portions of Idaho, Montana, Oregon, Washington, and Wyoming was created by Service personnel in 2013 from several sources but was reviewed and updated for accuracy by Service personnel in 2022, based on the aforementioned additional data sources. State data sources referenced above include Oregon’s Areas of Known Wolf Activity polygons (Brown 2023 in litt.), Wyoming’s 2022 pack polygons (Mills 2023, in litt.), Washington’s 2022 pack polygons (Maletzke 2023, in litt.), and California’s pack polygon locations (which were digitized from a map) (Laudon 2023 in litt.; CDFW 2023a, unpaginated).

In the Western United States, wolves were historically common and widely distributed (Young and Goldman 1944, pp. 9–58) (Figure 2). Estimates of historical populations are notoriously difficult to verify, but genetic data and extrapolations of known wolf densities have been used to estimate that there were likely hundreds of thousands of gray wolves once occupying the Western United States (Hampton 1997, pp. 22, 258; Leonard et al. 2005, pp. 14–15). As a result of poisoning, unregulated trapping and shooting, and the public funding of wolf extermination efforts, gray wolf populations were essentially eliminated from the Western United States by the 1930s (Young and Goldman 1944, pp. 56–58); although there was some evidence of wolf occupancy into the 1940s in the remote parts of central Idaho, along Montana’s Northwestern border with Canada, and the Cascade Mountains of Oregon (Young and Goldman 1944, pp. 56–58; Service 1987, pp. 1–3). After human-caused mortality of wolves in Southwestern Canada was regulated in the 1960s, populations expanded southward (Carbyn 1983, p. 240). Dispersing wolves occasionally reached the Rocky Mountains in the conterminous United States (Service 1994, pp. 4–5), but they lacked legal protection there until 1973, when the subspecies *C.l. irremotus* was first listed under the Endangered Species Preservation Act of 1969, a predecessor of the Act (38 FR 14678, June 4, 1973).

In 1978, when several gray wolf subspecies were consolidated into a single conterminous U.S./Mexico listing and a separate Minnesota listing under the Act, gray wolves occurred in only a small fraction of their historical range in the conterminous United States, and they were very rare in most places where they did exist (43 FR 9607, March 9, 1978). In the Southwestern United States, the Mexican wolf subspecies was present only as an occasional wanderer near the Mexico border (43 FR 9607, March 9, 1978) with no indication of reproducing packs in the United States (Service 2017, p. 7). In the rest of the West, although occasional sightings of gray wolves (*Canis lupus spp.* other than *Canis lupus baileyi*) were documented at the time of the 1978 listing, there was no indication that there were reproducing packs at that time (Service 1994, pp. 4–5). Wolves had been eliminated in much of the eastern half of the United States except for an estimated 1,235 wolves in northeast Minnesota (Berg and Kuehn 1982, p. 11), a few wolves in Wisconsin (Thiel and Welch 1981, pp. 401–402), and a small, isolated population of wolves on Isle Royale, Michigan (Peterson and Page 1988, pp. 89–92).

An interagency wolf recovery team completed the NRM Wolf Recovery Plan in 1980 (Service 1980, entire). The NRM Wolf Recovery Plan focused on wolf recovery efforts on the large contiguous blocks of public land from central Idaho and Western Wyoming through Montana to the Canadian border. In 1982, a wolf pack from Canada began to use a portion of Glacier National Park (GNP) along the U.S./Canada border. In 1986, the first litter of pups documented in the Western United States in over 50 years was born in GNP (Ream et al. 1989, pp. 39–40). In recognition of the ongoing natural recovery of wolves arising from Canadian populations, the NRM Wolf Recovery Plan was revised in 1987 (Service 1987, entire). The revised NRM Wolf Recovery Plan recommended that recovery be focused in areas with large blocks of public land, abundant native ungulates, and minimal livestock. Three recovery areas were identified—central Idaho, the Greater Yellowstone Area (GYA), and Northwestern Montana.

In 1995 and 1996, the Service reintroduced a total of 66 wolves from Southwestern Canada to remote public lands in central Idaho and YNP (Bangs and Fritts 1996, pp. 408–412;

Fritts et al. 1997, pp. 13–25; Bangs et al. 1998, entire). An additional 10 wolves were translocated from northwestern Montana to YNP in 1997. The Service designated the central Idaho and GYA recovery areas as nonessential experimental population areas where increased management flexibility was authorized to address local and state concerns about wolf conflicts with humans and livestock (59 FR 60252, November 22, 1994; 59 FR 60266, November 22, 1994). Wolves that were naturally recolonizing Northwestern Montana remained listed as endangered.

The reintroduction of wolves to central Idaho and YNP in 1995 and 1996, along with natural recolonization of wolves from Canada into Northern Montana in the 1980s and 1990s, led to increased numbers and distribution of wolves in the Western United States (see Table 5 and Figure 9). Because of the reintroduction, wolves soon became established throughout central Idaho and the GYA. In a comparison of the historical and contemporary ranges of carnivores in North America around the turn of the century, gray wolves (inclusive of Mexican wolves) were still absent from over 40 percent of their historical range on the continent, with a large majority of that loss in the conterminous United States and Mexico (Laliberte and Ripple 2004, pp. 126–127). However, over the course of the last several decades, wolves have continued to expand their range in the Western United States and wolf packs have become established in California, Oregon, and Washington. More recently, wolves have been documented in Colorado (see Chapter 4, below). Within our analysis area, dispersing wolves have also been observed in Arizona, Nevada, New Mexico and Utah, but they have not established packs there. Wolves have likely always been scarce in Nevada due to the biogeography of the Great Basin and limited prey resources (Young and Goldman 1944, p. 30).

Worldwide, gray wolves are listed by the International Union for the Conservation of Nature as a species of *Least Concern* with a circumpolar distribution and global population on the order of 200,000 to 250,000 individuals (Boitani et al. 2018, unpaginated). In the conterminous United States, gray wolves exist primarily in two large metapopulations<sup>5</sup>—one in the Western United States and one in the Great Lakes region in the upper Midwest. Subpopulations in the Western United States are connected to each other, as evidenced by habitat connectivity and models predicting wolf movement pathways (Singleton et al. 2002, pp. 18–25; Oakleaf et al. 2006, pp. 559–561; Carroll et al. 2012, pp. 85–86; Mesler 2015, pp. 38–41), tracking data of dispersing wolves (Forbes and Boyd 1996, pp. 1083–1084; Jimenez et al. 2017, p. 583; ODFW 2019a, pp. 10–11; ODFW 2022, p. 6; WDFW et al. 2022, pp. 18–19), and genetic data (vonHoldt et al. 2010, pp. 4421–4424; Hendricks et al. 2018, pp. 138–141; Wildlife Genetics International (WGI) 2021, entire). The gray wolf metapopulation in the Western United States is also interconnected with a much larger Western U.S. and Western Canada metapopulation of wolves that includes thousands of wolves throughout Western Canada and Alaska (Boyd and Pletscher 1999, entire; Mech and Boitani 2003, pp. 322–323; Carroll et al. 2012, pp. 85–86; Kuzyk and Hatter 2014, p. 881; Jimenez et al. 2017, p. 583; Hendricks et al.

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<sup>5</sup> 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.

2018, pp. 138–141). We provide a detailed discussion of the current distribution, population size, and population trends of wolves in the Western conterminous United States in Chapter 4.

## Chapter 2: Needed Resources and Demographic Factors that Support Viability of the Gray Wolf in the Western 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 Western 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 Western 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 NRM and provide a summary of past population viability analyses (PVA) on gray wolves; while viability is context-specific, both the recovery criteria and these analyses can further inform the factors the gray wolf in the Western United States may need to withstand stochastic and catastrophic events and adapt to future change.

### Resiliency

#### Resource Needs

Gray wolves in the Western United States need suitable habitat, including a 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 escape cover without agricultural land), which generally allows for increased wolf 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 wolf populations at any given time. Due to their high reproductive capacity and their ability to disperse long distances, 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). Where human-caused mortality is low or nonexistent, wolf populations may be regulated by the distribution and abundance of prey on the landscape (Fuller et al. 2003, p. 189; McRoberts and Mech 2014, p. 966; Mech and Barber-Meyer 2015, p. 501). However, there is considerable evidence to indicate that 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).

Wolf populations are organized into wolf packs (Mech and Boitani 2003, p. 1). Impacts to wolf 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., wolf density) and extrinsic (e.g., nutritional) factors (Packard and Mech 1980, entire). In general, wolf populations need a sufficient number of wolf packs to support reproduction and connectivity. Impacts to connectivity between wolf 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 wolves. Territoriality in wolves may have evolved to protect pups from infanticide by competing packs and, secondarily, to secure food (Smith et al. 2015a, 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 wolf numbers through mortality of individuals when packs defend their territories (Cassidy et al. 2020, p. 66). The loss of adult wolf members may reduce the competitive strength of the pack and failure to defend against intruding 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. In low-density populations or in areas where 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***

Wolf populations are also regulated by the number of breeders within each pack. Within a wolf 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 wolf densities multiple breeding females within a pack are more common, leading to a higher potential reproductive rate than packs with a single breeding female. For example, in Idaho and YNP, up to 25 percent of packs have multiple litters per year (Ausband 2018, pp. 839–840; Stahler et al. 2020, p. 52; Ausband and Mitchell 2021, pp. 996–997; Cassidy et al. 2021, p. 7; WGFD et al. 2023, pp. 14–15).

### ***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), 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) (Stahler et al. 2013, pp. 226–231; Smith et al. 2020a, p. 91). Adult wolf survival rates typically decrease as wolf densities increase (density-dependent intrinsic population regulation), whereas recruitment appears to be more dependent on food availability (extrinsic regulation) (Smith et al. 2020a, 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 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 immigration add new alleles, while genetic drift, or the random loss of alleles, can remove them from the population. A sufficiently large population or metapopulation promotes a positive 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 preferable to these generalized targets (Frankham et al. 2014, p. 61). Despite their generalized nature, these guidelines highlight that genetic diversity is critical both in the short term, to avoid inbreeding and inbreeding depression, as well as in the long term as the foundation upon which natural selection may act for adaptation. Furthermore, while the effective population size capable of retaining genetic diversity in the short term and long term is different, both are important considerations in assessing viability.

Because the effective population size is often smaller than census population size, estimates of the ratio between the two measures can be important for assessing a given species’ genetic health. For gray wolves in YNP, the ratio of effective to census population size was estimated as approximately 0.3 during the decade following reintroduction (vonHoldt et al. 2008, pp. 265–267). However, using more recent data from the NRM (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 2 for this methodology and effective population size calculations). 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. 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, 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 isolation in these general rules of thumb is critical, however, and creates the need to specifically examine the role and importance of connectivity. Wolves in the Western metapopulation are well connected<sup>6</sup> to each other and also linked to wolf populations in Canada (Jimenez et al 2017, p. 585; Ausband 2022, p. 5). This connectivity, as noted in a number of the 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 wolf populations (Wayne and Hedrick 2011, entire; Rääkkönen et al. 2013, entire; Carroll et al. 2014, pp. 81–82). A study of the Scandinavian 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). As noted in the final delisting rule for the NRM, which did not include Wyoming, and in prior expert reviews of the recovery criteria (Bangs 2002, p. 3), connectivity among subpopulations within the Western North American metapopulation, which includes Canada, was an important factor in ensuring the long-term viability of that metapopulation (74 FR 15123, April 2, 2009). In addition, movement of individuals between the metapopulation segments could occur either naturally or by human-assisted migration management (Service 1994, p. 7–67; Bangs 2002, p. 3). 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 wolf metapopulation in the Western United States, we discuss *Inbreeding Depression* in Chapter 3 and methods for evaluating adaptive capacity of gray wolves under *Representation* below and 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 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, 1269–1270; Thurman et al. 2020, p. 521). Many attributes of wolves in the Western United States, 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,

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<sup>6</sup> 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.

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 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 wolves in the Western United States all related to one or more aspects of that overall ability and included the: extent of occurrence, dispersal distance, physiological tolerance, diet breadth, population size, genetic diversity, and fecundity, among others (see *Current Representation* in Chapter 4 below, Appendix 4, 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 wolves in the Western United States will be able to adapt to a range of environmental changes (Thurman et al. 2020, entire).

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 wolf population viability in the NRM and Western United States is dependent on maintaining a minimum number of wolves in multiple core areas. Additionally, greater numbers of packs and breeding pairs spread across the range in the Western United States further enhances redundancy. For example, our recovery criteria for the NRM included maintaining at least 300 wolves and 30 breeding pairs distributed among three core areas (see the *Recovery Criteria for the Northern Rocky Mountains* section below). In general, wolves in the Western United States need multiple, resilient subpopulations with multiple packs distributed across a broad enough area of the Western United States metapopulation 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 Northern Rocky Mountains

The NRM Wolf Recovery Plan was completed in 1980 (Service 1980, p. i) and it was revised in 1987 (Service 1987, p. i). The minimum recovery goal for the NRM was regularly reviewed, reevaluated, and, when necessary, modified as new scientific information warranted it (Service 1987, p. 12; Service 1994, Appendix 8 and 9; Fritts and Carbyn 1995, p. 26; Bangs 2002, p. 1; 73 FR 10513, February 27, 2008; 74 FR 15123, April 2, 2009, pp. 15130–15135). The final recovery criterion for the NRM gray wolf population was 30 or more breeding pairs comprising at least 300 wolves equitably distributed amongst Idaho, Montana, and Wyoming for 3 consecutive years, with genetic exchange (either natural or, if necessary, agency managed) between the populations in each of these three states. To provide a buffer above these minimum recovery levels, Idaho and Montana agreed to manage for at least 15 breeding pairs and 150 wolves in mid-winter (74 FR 15123, April 2, 2009, p. 15132). Wyoming agreed to manage for 10 breeding pairs and 100 wolves in areas of the state under their jurisdiction, and the National Park Service and the Eastern Shoshone and Northern Arapaho Tribes would maintain a minimum of 5 breeding pairs and 50 wolves combined (77 FR 55530, September 10, 2012, pp. 55538–55539). We summarize the process the Service used to develop these recovery criteria, including these various revisions, below. In addition, we also detail critical feedback the Service received on these recovery criteria for NRM wolves.

#### ***History of Developing and Validating Recovery Criteria for the NRM***

The 1980 NRM Wolf Recovery Plan's objective was to re-establish and maintain viable populations of the NRM wolf (*C. l. irremotus*) in its former range where feasible (Service 1980, p. iii), but there were no recovery goals. It recommended recovery actions be focused on the large areas of public land in the GYA, central Idaho, and Northwestern Montana. The 1987 revised NRM Wolf Recovery Plan (Service 1987, p. 57) concluded that the subspecies designations may no longer be valid and simply referred to gray wolves in the NRM. Consistent with the 1980 NRM Wolf Recovery Plan, it also recommended focusing recovery actions on the large blocks of public land in the NRM. The 1987 NRM Wolf Recovery Plan specified a recovery criterion of a minimum of 10 breeding pairs of wolves (defined as two wolves of opposite sex and adequate age capable of producing offspring) for a minimum of 3 successive years in each of three distinct recovery areas. These recovery areas included:

- (3) Central Idaho (Selway-Bitterroot, Gospel Hump, Frank Church River of No Return, and Sawtooth Wilderness Areas; and adjacent, mostly Federal, lands);
- (2) Northwestern Montana (Glacier National Park; Great Bear, Bob Marshall, and Lincoln Scapegoat Wilderness Areas; and adjacent public and private lands); and
- (3) YNP area (including the Absaroka-Beartooth, North Absaroka, Washakie, and Teton Wilderness areas; and adjacent public and private lands).

The 1987 NRM Wolf Recovery Plan encouraged connectivity among the three recovery areas as well as continued recolonization of northwest Montana and potential recolonization of northern Idaho from wolves in Canada (Service 1987, pp. 13–14, 31). Wolf establishment outside of these recovery areas would not be promoted due to the increased potential for conflicts to occur, but no attempts would be made to prevent wolf pack establishment outside of the recovery areas (Service 1987, pp. v, 32–35).

As part of the final EIS evaluating the reintroduction of wolves to YNP and central Idaho, the Service reviewed wolf recovery in the NRM and the adequacy of the recovery goals because the Service was concerned that the 1987 goals might be insufficient (Service 1994, pp. 6:68–78). The Service was particularly concerned about the 1987 definition of a breeding pair, given that any male and female adult wolf are “capable” of producing offspring and lone wolves may not have territories. The Service also believed the relatively small “hard” recovery areas of previous recovery plans greatly reduced the amount of area that could be used by wolves, and they would almost certainly eliminate the opportunity for meaningful natural demographic and genetic connectivity. The Service conducted a thorough literature review of wolf population viability analysis and minimum viable populations; reviewed the recovery goals for other wolf populations; surveyed the opinions of the top 43 wolf experts in North America, of which 25 responded; and incorporated our own expertise into a review of the NRM wolf recovery goal. Our analysis was published as part of the final EIS and in a peer-reviewed paper (“Population viability, nature preserves, and the outlook for gray wolf conservation in North America”) (Service 1994, Appendix 8, 9; Fritts and Carbyn 1995, pp. 26–38).

Our analysis concluded that the 1987 recovery goal was, at best, a minimum recovery goal, and that modifications were warranted on the basis of more recent information about wolf distribution, connectivity, and numbers. We also concluded that “Data on survival of actual wolf populations suggest greater resiliency than indicated by theory” and theoretical treatments of population viability “have created unnecessary dilemmas for wolf recovery programs by overstating the required population size” (Fritts and Carbyn 1995, p. 26). Based on our analysis, we redefined a breeding pair as an adult male and an adult female wolf that have produced at least two pups that survived until December 31 of the year of their birth during the previous breeding season. We also concluded that “Thirty or more breeding pairs comprising some 300+ wolves in a metapopulation with genetic exchange between subpopulations should have a high probability of long-term persistence” because they would contain enough individuals in successfully reproducing packs that were distributed over distinct, but somewhat connected large areas, to be viable for the long term (Service 1994, p. 6:75). We explicitly stated that the required genetic exchange could occur by natural means or by human-assisted migration management and that dispersal of wolves between recovery areas was evidence of that genetic exchange (Service 1994, Appendix 8, 9). In the glossary of the 1994 EIS, a recovered wolf population in the northern Rockies was defined as “10 breeding pairs of wolves in each of three areas for 3 successive years with some level of movement between areas” (Service 1994, pp. 6–7). We further determined that a metapopulation of this size and distribution among the three recovery areas in the NRM would result in a wolf population that would fully achieve our recovery objectives.

In late 2001 and early 2002, we conducted another review of what constitutes a recovered wolf population to reevaluate and update our 1994 analysis and conclusions (Bangs 2002, entire). We attempted to survey the same 43 experts we had contacted in 1994 as well as 43 other biologists from Europe and North America who were recognized experts about wolves and/or conservation biology. There were a total of 53 people who provided their expert opinions regarding a wide range of issues related to the NRM recovery goal. We also reviewed a wide range of literature, including wolf population viability analysis from other areas (Bangs 2002, pp. 1–9). Despite varied professional opinions and a great diversity of suggestions, experts overwhelmingly thought the recovery goal derived in our 1994 analysis was more biologically appropriate than the 1987 NRM Wolf Recovery Plan’s criteria for recovery, and that the 1994 recovery goal represented a viable and recovered wolf population. Specifically, approximately 75 percent of the expert respondents agreed that a metapopulation comprised of 30 breeding pairs and over 300 wolves constituted a viable population (Bangs 2002, pp. 1–2). Reviewers also thought genetic exchange, either natural or human-facilitated, was important to maintaining the metapopulation configuration and wolf population viability; insufficient emphasis on connectivity in favor of the total number of wolves was the primary reason a minority of the reviewers did not believe the recovery criteria represented a viable wolf population (Bangs 2002, pp. 1–2) (see further discussion of *Connectivity and Genetic Diversity* in Chapter 2 above). Reviewers also thought the proven ability of a breeding pair to show successful reproduction was a necessary component of a biologically meaningful breeding pair definition. Reviewers recommended other concepts/numbers for recovery goals, but most were slight modifications to those we recommended in our 1994 analysis. While experts strongly (78 percent) supported that our 1994 conclusions represented a viable wolf population, they also tended to believe that wolf population viability was enhanced by higher rather than lower population levels and longer rather than shorter demonstrated timeframes. Five-hundred wolves and 5 years were common minority recommendations. A slight majority indicated that even the 1987 recovery goal of only 10 breeding pairs (defined as a male and female capable of breeding) in each of three distinct recovery areas may be viable given the persistence of other small wolf populations demonstrated in other parts of the world. Reviewers also commented that population viability is a probability not a single number. A population can be more or less likely to persist, but there is no hard point at which it is either viable or not viable except when there are extreme conditions (Bangs 2002, p. 4). Based on that review, we reaffirmed our more relevant and stringent 1994 definition of wolf breeding pairs, population viability, and recovery (Service 1994, p. 6:75; Bangs 2002, pp. 1–9).

The Service’s development of the recovery goal clearly recognized that the key to wolf recovery was establishing a viable demographically and genetically diverse wolf population in the core recovery areas of the NRM. We would ensure its future connectivity by promoting natural dispersal and genetic connectivity between the core recovery segments and/or by human-assisted migration management in the unlikely event it was ever required (Fritts and Carbyn 1995, entire; Groen et al. 2008, entire) (see further discussion of *Connectivity and Genetic Diversity* in Chapter 2 above).

We measure the wolf recovery goal by the number of breeding pairs as well as by the number of wolves because wolf populations are maintained by wolf packs that successfully raise pups. We use “breeding pairs” (an adult male and an adult female that raised at least two pups

that survived until December 31) to describe successfully reproducing wolf packs (Service 1994, p. 6:67; Bangs 2002, pp. 7–8; Mitchell et al. 2008, p. 881). The breeding pair metric includes most of the important biological concepts in wolf conservation:

- both male and female members together going into the February breeding season;
- successful occupation of a distinct territory (generally 200–500 mi<sup>2</sup> (500–1,300 km<sup>2</sup>) and almost always in suitable habitat);
- enough pups to replace two adults;
- offspring that become dispersers;
- at least four wolves following the point in the year with the highest mortality rates (summer and fall);
- all social structures and age classes represented within a wolf population; and
- adults that can raise and mentor younger wolves.

We also determined that an essential part of achieving recovery was a sufficient distribution of wolf breeding pairs and individual wolves among the three recovery areas. Following the 2002 review of our recovery criteria, we began to use states, in addition to recovery areas, to measure progress toward recovery goals (74 FR 15123, April 2, 2009). Because Idaho, Montana, and Wyoming each contain the vast majority of one of the original three core recovery areas, we determined the metapopulation structure would be best conserved by equally dividing the overall recovery goal between the three states. This approach made each state's responsibility for wolf conservation fair, consistent, and clear; it also avoided any possible confusion that one state might assume the responsibility for maintaining the required number of wolves and wolf breeding pairs in a shared recovery area that is the responsibility of the adjacent state. State regulatory authorities and traditional management of resident game populations occur on a state-by-state basis. Management by state would still maintain a robust wolf population in each core recovery area because they each contain manmade or natural refugia from human-caused mortality (e.g., National Parks, wilderness areas, and remote Federal lands) that guarantee those areas remain strongholds for wolf breeding pairs and sources of dispersing wolves in each state (see Barber-Meyer et al. 2021, pp. 8–11). Establishing recovery targets by state promote connectivity and genetic exchange between the metapopulation segments by avoiding management that focuses solely on wolf breeding pairs in relatively distinct core recovery areas; each state promotes a minimum level of potential natural dispersal to and from each population segment.

As a result of an injunction granted after publication of our 2008 rule delisting the NRM DPS (73 FR 10513, February 27, 2008), we again re-analyzed the NRM recovery criteria and determined they were adequate to ensure recovery of wolves in the NRM. Peer reviewers of the NRM delisting generally agreed that the NRM wolf population was biologically recovered. In our 2009 delisting rule for the NRM wolf population, we expressed that these recovery and post-delisting management goals were designed to provide the NRM gray wolf population with sufficient representation, resiliency, and redundancy for their long-term conservation (74 FR 15123, April 2, 2009, p. 15133).

In summary, after this repeated reevaluation, the Service's resulting recovery goal for the NRM gray wolf population was 30 or more breeding pairs comprising at least 300 wolves

equitably distributed amongst Idaho, Montana, and Wyoming (therefore, 100 wolves per state) for 3 consecutive years with genetic exchange (either natural or, if necessary, agency managed) between the populations in each of these states. To provide a buffer above these minimum recovery levels, Idaho and Montana agreed to manage for at least 15 breeding pairs and 150 wolves in mid-winter (74 FR 15123, April 2, 2009, p. 15132), whereas Wyoming agreed to manage for 10 breeding pairs and 100 wolves in areas of the state under their jurisdiction while national parks and the Eastern Shoshone and Northern Arapaho Tribes would maintain a minimum of 5 breeding pairs and 50 wolves combined (77 FR 55530, September 10, 2012, pp. 55538–55539).

### ***Past Criticism of Recovery Criteria***

Over the past decades, the Service received critical feedback on its recovery criteria for NRM wolves. Criticisms have included but are not limited to: (1) our targets are too low to ensure a demographically minimally viable population, (2) our targets are too low to ensure the genetic health of the population, or (3) we should view recovery of the gray wolf in terms of their ecological effectiveness or evolutionary potential, requiring a broader distribution of wolves across the ecosystems they once occupied in the West.

Conservation targets are often expressed in terms of a minimum population size necessary to ensure a high probability of survival over a given period of time. This is known as a minimum viable population (MVP), and our recovery criteria were developed using this concept. Multiple researchers have cautioned against identifying a single MVP size for wolves given the “complexity of factors affecting population dynamics and the challenges of estimating population processes,” in addition to the fact that future influences on wolf dynamics may be different from those that affected the population in the past (Chapron et al. 2012, p. 41; Eriksen et al. 2020, p. 11) (see further discussion of minimum viable populations and population viability analyses in Chapter 5). However, we determined that numerical recovery criteria for wolves in the NRM served as one important benchmark for defining a recovered population. Those who submitted information to inform this SSA and 12-month finding proposed MVP estimates, based on meta-analyses of population persistence among over 100 vertebrate species, ranging from 2,261 animals to over 6,000 animals (Reed et al. 2003a, entire; Traill et al. 2007, entire; Traill et al. 2010, entire). Traill et al. (2007, p. 159) acknowledged that the determination of an MVP is “context-specific,” and their calculated generic MVPs may not universally apply to all species. To calculate their universal MVPs, Reed et al. (2003a, p. 26) assumed populations were discrete and isolated (i.e., not distributed in a source-sink configuration or metapopulation). Therefore, these MVP values are less applicable to the NRM and the Western United States because these entities do not function as an isolated population given that they are part of larger metapopulation with connectivity to wolf populations in Canada.

Those who have petitioned us to protect the gray wolf under the Act have also posited that we need more wolves in the Western United States to ensure genetic health in perpetuity given the “50/500” rule for effective population size (which we define under *Connectivity and Genetic Diversity* above). Assuming the population is isolated—an effective population size of 50 wolves, the rule of thumb for avoiding inbreeding depression, equates to a census population size of approximately 192 to 417 wolves and an effective population size of 500, the rule of thumb for retaining evolutionary genetic potential, equates to a census population size of

approximately 1,923 to 4,167 wolves, according to the ratio of effective to census population size we calculate in Appendix 2. However, wolves in the Western metapopulation are not isolated. On the contrary, wolves in the Western metapopulation are well connected to each other and also linked to wolf populations in Canada. This connectivity, as noted in a number of the PVAs we discuss below, allows for 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). Moreover, recovery and evaluations of viability involve exploring extinction risk over a biologically meaningful timeframe, rather than perpetuity.

Critics of our recovery criteria for wolves have recommended that ecological effectiveness (Soulé et al. 2005, pp. 171–175)—the ability for a species to maintain critical interactions within ecosystems, communities, or landscapes—be one of the criteria for recovery given the gray wolf’s strong top-down controls within ecosystems (i.e., predation at higher trophic levels regulating the amount of biomass at lower trophic levels) (Soulé et al. 2005, pp. 171–175; Weiss et al. 2007, pp. 300–304; Bergstrom et al. 2009, p. 995; Weiss et al. 2014, p. 7; Beschta and Ripple 2016, entire). These critics argue that the disappearance of strongly interacting species, such as the wolf, can lead to profound changes in ecosystem composition, structure, and diversity. Furthermore, they argue that protecting the ecological effectiveness of species is an ethical obligation of conservation practitioners, even though it is not codified in Federal law. For species whose occupied range is actively expanding, Carroll et al. (2021, pp. 78–82) propose that recovery criteria should also evaluate future evolutionary potential across the range of ecosystems the species is capable of recolonizing. While we respect the viewpoints of the above authors, the Service’s 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, p. 303). Other critics have emphasized that quantitative assessments of population persistence (e.g., PVAs) alone are an insufficient measure of recovery and that we should instead reassess wolf recovery based on the conservation biology principles of resiliency, redundancy, and representation (see Wolf et al. 2015, p. 204). This SSA includes a comprehensive analysis of the gray wolf’s current and future viability using the conservation biology principles of resiliency, redundancy, and representation.

### **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 in other regions can provide further context for the needs and conservation targets of wolf populations in the Western United States. For example, a PVA on red wolves (*Canis rufus*) indicated that increasing the population size to 330 to 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 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). A PVA for wolves in Wisconsin found a completely isolated population of 300 to 500 wolves would have a high probability of persisting for 100 years under all scenarios evaluated (Rolley et al. 1999, p. 43; WI DNR 2007, pp. 7–8). Managing wolves at a hypothetical “cultural carrying capacity”<sup>7</sup> of 300 wolves instead of allowing the population to reach the “biological carrying capacity”<sup>8</sup> of 500 wolves had little effect on the estimated risk of extinction of wolves in Wisconsin (Rolley et al. 1999, pp. 42–43; WI DNR 2007, pp. 7–8).

Petracca et al. (2023a, entire) conducted a PVA to estimate the probability of Washington State achieving their recovery goals for gray wolves. They also evaluated the risk of falling below the state’s management goal of 92 gray wolves (Wiles et al. 2011, p. 279; Petracca et al. 2023a, p. 14). They concluded that the probability Washington would achieve their recovery goals by 2030 was 99 percent and that, with a starting population of 172 gray wolves in 2020, the risk of falling below their management goals was approximately zero (Petracca et al. 2023a, entire). Petracca et al. (2023b, entire) evaluated gray wolf recovery in Washington State under a variety of management strategies. Under all of these management scenarios, the gray wolf population in Washington either achieved stability or increased, depending on the scenario (Petracca et al. 2023b, p. 1). However, the probability of achieving the state’s recovery goals declined if 5 percent of the population was removed every 6 months through harvest, if 30 percent of the population was removed every 4 years through lethal control, or if immigration into the state ceased. Regardless, given a starting population size of 172 gray wolves in 2020, the probability of achieving the state’s recovery goals, was greater than 92 percent in all scenarios through 2070 (Petracca et al. 2023b, p. 12).

Researchers have also conducted multiple PVAs on the Scandinavian wolf population, which can further inform the demographic needs of wolves in the Western United States. PVAs conducted in the late 1990s to early 2000s for wolves in Sweden concluded approximately 200 wolves would be sufficiently viable (Swedish Environmental Protection Agency 2015, unpaginated). However, another PVA for wolves in Scandinavia that incorporated the effects of hunting, catastrophes, and inbreeding found that at least 400 wolves would be needed for a minimum viable population (Nilsson 2003, p. 236). That analysis also found that increasing

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<sup>7</sup> Cultural carrying capacity is the maximum population size tolerated by a given community’s social and cultural norms.

<sup>8</sup> Biological carrying capacity is the maximum population size supported by available abiotic and biotic resources (e.g., food, habitat).

hunting pressure at small population sizes (e.g., 100 or 150 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 wolves) would be necessary to maintain 95 percent of genetic variation in the Scandinavian wolf 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 wolf populations of 100 individuals in Scandinavia have over a 90 percent chance of persistence for 100 years, if current genetic issues are ignored; they found that only small 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 two to three 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 wolves would maintain at least 90 percent of current genetic diversity and current inbreeding coefficients in the Scandinavian wolf population (Bruford 2015, pp. 10, 25–26). However, the metapopulation to which the Scandinavian 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, 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 in small populations and using a single MVP 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 necessitate more wolves to increase their ability to withstand stochastic and catastrophic events and to ensure genetic health. However, populations that are connected to other wolf populations (e.g., the population in the Western United States and its connection to Canada) need fewer wolves to ensure viability. For example, in a PVA conducted on the Oregon population of wolves, which allowed for emigration and immigration, the modeled wolf population never fell below a biological extinction threshold (fewer than five 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 2015b, 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; the recovery goal for Washington is 15 breeding pairs for 3 consecutive years distributed across three recovery regions or 18 breeding pairs distributed across the three recovery areas for a single year (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 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 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 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 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 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

Wolves in the Western United States need suitable habitat, which includes sufficient prey resources, to withstand stochastic events. Wolf populations also need a sufficient number of wolf packs to sustain reproduction, survivorship, and connectivity. In general, to maintain populations in the wild over time, wolves in the Western 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 the NRM and results of PVAs on other wolf populations can provide further insight into the viability of wolf populations in the Western United States.

## Chapter 3: Stressors and Conservation Efforts

Before we evaluate the current and future condition of wolves in the Western 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 that which 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 wolves in the Western United States include:

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

Figure 3 below illustrates the relationships between these stressors, relevant conservation efforts, and the species' needs.

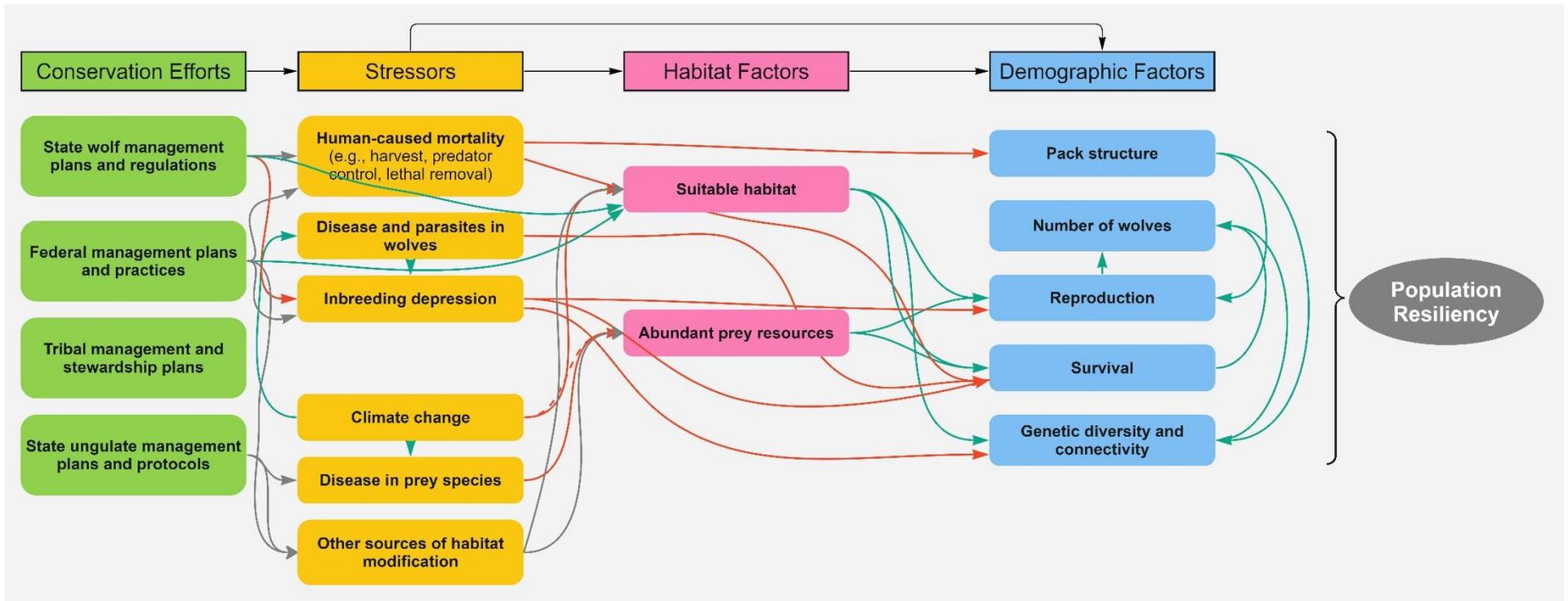


Figure 3. A conceptual model for the primary stressors that may affect individuals or cumulatively influence the resiliency of the gray wolf in the Western United States. Green arrows represent positive relationships between nodes and red arrows represent negative relationships between nodes. Gray arrows indicate the relationship between nodes could be either positive or negative. Dotted lines indicate where there is uncertainty or debate in current research regarding the relationship between the conservation efforts, stressors, and/or resource needs.

In the sections below, we evaluate the stressors of gray wolves and summarize the state, tribal, and Federal management that have provided for the conservation of wolves in the Western United States. These conservation efforts reduced the influence of a stressor, improved the condition of wolf habitat, or improved wolf demographic factors.

## Human-Caused Mortality

Causes of 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 wolf populations exist with no to minimal human influence, mortalities from natural causes are the primary cause of death. For example, over 80 percent of known wolf mortalities documented in YNP since reintroduction were a result of natural causes, with intraspecific strife accounting for approximately 40 percent of known adult mortality (Cubaynes et al. 2014, pp. 7–8; Smith et al. 2020a, p. 83). 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. 2020a, p. 83; Chakrabarti et al. 2022, pp. 7, 9). Human-caused mortality is estimated to account for 60 to 80 percent of all mortalities in the conterminous 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).

In the Western United States, the primary stressor influencing 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 the wolf entirely. Bounties were used to incentivize the destruction 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. 2009, p. 88; Service 2020, pp. 10–13). Unregulated hunting and trapping, the excessive use of poison in the Great Plains and the Western United States, and the activities of government trappers eradicated wolves across much of their historical range in the conterminous 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 conterminous United States (43 FR 9611, March 9, 1978).

After the gray wolf was listed under the Act, its protections, along with state endangered-species statutes, prohibited the intentional killing of wolves except under very limited circumstances. These circumstances included defense of human life, scientific or conservation purposes, and special regulations intended to mitigate repeated 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 is the primary reason the number and range of wolves have increased and expanded since the mid- to late-

1970s (Smith et al. 2010a, entire; O’Neil et al. 2017, entire; Stenglein et al. 2018, entire). However, a “natural” wolf population free from 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 wolf mortality and how this mortality plays a role as a driver of wolf population dynamics, including survival, population growth, and persistence, is an active area of research. The risk of human-caused mortality is not uniform, however, and tends to be highest for younger age classes of wolves (Ballard et al. 1987, p. 28; Adams et al. 2008, p. 14; Smith et al. 2010a, 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. 2010a, pp. 630–631; Schmidt et al. 2017, p. 23; Morales-González et al. 2022, pp. 473, 477), and for wolves that occupy more fragmented habitats with less escape cover (which are generally found on the peripheries of occupied wolf range) (Murray et al. 2010, pp. 2522–2523; Smith et al. 2010a, 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). Wolf survival rates were higher for wolves that inhabited protected areas, such as National Parks or wilderness areas, where human access was limited and where the potential for conflict was 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 survival 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 killed by humans, 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. 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 wolves to compensate for increased human-caused mortality. Although debate continues about which is most important, the three primary mechanisms with which 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. 2020a, 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; Ausband et al. 2023, p. 11).

Due to strong compensatory mechanisms in many wolf populations, the additive or compensatory nature of human-caused mortality and its effects on wolf populations remains unclear. Some studies have documented that 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 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 superadditive through the loss of dependent offspring or future reproductive output (Creel and Rotella 2010, pp. 3–6); however, other researchers have noted that evidence for this 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, mortality was found to be additive during recolonization then transitioned to compensatory as the 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 public harvest (i.e., hunting or trapping by private citizens) to manipulate 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 wolf abundance, especially when the wolf population is large and well-distributed. For example, although human-caused mortality increased compared to other sources of mortality, little changes in wolf survival and abundance were documented in Minnesota between 2012 and 2014 when wolf harvest was authorized (Erb et al. 2016, unpaginated; Chakrabarti et al. 2022, pp. 1, 6–9). Similarly, at current observed levels of harvest in Idaho, little change in wolf occupancy was documented between 2016 and 2021 (Ausband et al. 2023, entire); however, year-end abundance estimates decreased slightly in 2021 and 2022 when compared to 2020 estimates (Thompson et al. 2022, entire; IDFG 2023b).

Given the partially compensatory nature of human-caused mortality, a much higher percentage of the wolf population must be annually killed over multiple years to significantly reduce wolf abundance (Mech 2006, p. 1482). For example, a total of 337 wolves were killed over a seven-year period to reduce a wolf population from 239 to approximately 143 wolves in one Alaskan study (Boertje et al. 1996, pp. 479–480). Managers have documented intentional wolf reductions over a 3 to 7 year period of up to around 80 percent of the pre-control population levels; however, when control efforts were completed, wolf populations returned to, and sometimes exceeded, pre-control levels in fewer than 5 years because large source populations were adjacent to the affected population (Ballard et al. 1987, p. 30; Boertje et al. 1996, pp. 479, 487; Hayes and Harestad 2000, pp. 43–45; Hayes et al. 2003, pp. 14, 25–26; Boertje et al. 2017, p. 437). Another more recent example of wolves’ resilience to population reduction efforts comes from predator control in British Columbia, Canada to support caribou recovery (B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development (B.C. Ministry) 2021, entire). The goal of these efforts was to remove up to 80 percent of wolves within each of nine treatment areas and evaluate caribou demographic responses. Depending on the treatment area, wolf reduction efforts were conducted over a 2- to 7-year period, and based on pre-control

numbers, between 30 and 97 percent of the wolves in each treatment area were removed. However, wolves recolonized treatment areas at rates of 30 to 100 percent of pre-control levels within one year.

There is considerable research and continued debate surrounding the level of human-caused mortality for which wolf populations can compensate and maintain population stability. Dependent on the analysis, researchers estimate that human-caused mortality rates between 17 to 48 percent result in 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 2015b, p. 31; Hebblewhite and Whittington 2020, pp. 7–8). A general rule of thumb is that 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 develop this rule of thumb were based on autumn/winter minimum 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. Other researchers have posed that because growth rates used to estimate this wolf population stability threshold were obtained from a relatively small sample of the entire population, extrapolation to the larger population is questionable (Morales-González et al. 2022, pp. 471–472). As discussed in greater detail later in this section, estimates of average rates of human-caused wolf mortality in Idaho, Montana, and Wyoming are similar to or slightly below the 29 percent threshold; however, our human-caused mortality rate estimates may be lower than other studies discussed in this document because we calculated rates based on known, annual abundance (i.e., end of year wolf count/estimate plus known total mortality) rather than the autumn/winter population size only. As part of their state management and monitoring efforts, Idaho, Montana, and Wyoming document cause-specific mortality for all wolves that are known to have died in the state annually beyond those that die due to harvest and lethal depredation control. This has allowed the Service to calculate an absolute minimum number of wolves known to be alive in each state in a given year (by adding the year-end minimum count or population estimate and the total number of known wolf mortalities that occurred during that same year) and to use this information to estimate harvest and lethal depredation control rates for a given year. The Service used this method in past NRM annual reports to estimate cause-specific mortality rates for each state so that we could make comparisons among states and years and, as a result, we chose to use the same method in this SSA Report.

Ultimately, wolf population sustainability is a function of the productivity of the population and its proximity to other wolf populations (Fuller et al. 2003, p. 185). Where productivity is average to high and source populations are near, 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 wolf survival when mortality is partially compensatory (O’Neil 2017, p. 220), and the risk of inadvertently reducing wolf abundance to a level that compromises population resiliency through regulated harvest is low (Boertje et al. 1996, p. 479; Mech 2001, pp. 75–76; Adams et al. 2008, pp. 1, 20–22). For further information specific to wolf populations in Idaho, Montana, Oregon, Washington, and Wyoming, please see *Levels of Human-Caused Mortality in Idaho, Montana, Oregon, Washington, and Wyoming* below and refer to Table 3.

### ***Effects on Wolf Dispersal***

Increased human-caused mortality may either increase or decrease wolf dispersal rates, depending on various factors. If 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 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 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 control) removed individual wolves and entire packs, and thereby provided a constant source of social openings or vacant habitat for dispersing wolves to fill or recolonize. Long-distance dispersals continue from populations with low 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 wolf densities were high, wolf 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 wolf densities and were lowest at moderate wolf 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 wolves to disperse, based on an integrated population model constructed from data from 197 Global Positioning System (GPS)-collared wolves from 65 wolf 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 Wolf Social Structure***

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

First, 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. 2023a, 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. 2023a pp. 3–4). Additionally, the likelihood a wolf pack will maintain its territory declines if both breeders are killed; however, if a single breeder is killed, the wolf pack may hold its territory until a new, unrelated 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 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. 2023a, pp. 5–6).

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 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. 2023a, 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, 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 wolf populations as a whole are less pronounced. In some 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. 2023a, p. 5). Breeder replacement and subsequent reproduction in colonizing populations greater than 75 wolves was similar to that of core populations at or near carrying capacity, whereas small recolonizing populations ( $\leq 75$  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 wolf population with little immigration from elsewhere, age of first reproduction declined as wolf 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 wolf abundance, immigration from neighboring areas was found to be the most important determinant in the speed with which wolf populations rebounded (Bergerud and Elliot 1998, pp. 1554–1559, 1562; Hayes and Harestad 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). Consequently, 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). We acknowledge that 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 Western United States is likely to be minimal, as long as a sufficiently large population is maintained that is well-connected to other wolf 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 which may have long-term implications for the affected individuals. Stress comes from many sources that may include environmental conditions, availability of food resources, disease, social interactions, and human activities. As wolf abundance and distribution has increased, wolves have increasingly interacted with humans to varying degrees, which can result in a certain level of habituation as some wolves become more comfortable living around humans (Heilhecker et al. 2007, entire). Social interactions among wolves surrounding breeding and the birth of pups results in greater stress hormone levels than other potential stressors, including human activity (Eggermann et al. 2013, pp. 172–174). Relatively low stress hormone levels and habituation of wolves to human presence provide evidence of adaptability that has allowed them to survive 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 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 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 affected the rate of female pregnancy or pseudopregnancy and the number of interactions among male 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 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 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 wolf when dealing with the specific stressors.

### **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 Western United States. We focus our discussion on regulated public harvest, lethal control of depredating wolves, and illegal take because these are the most common forms of mortality in Western U.S. wolf populations.

#### ***Discretionary Sources of Mortality: Regulated Public Harvest***

Regulated public 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 wildlife) 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, managers may use a trajectory/trend objective instead of a numerical objective. 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, 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 managers to evaluate population responses over a set time 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 first ever regulated wolf harvest seasons in the conterminous United States in Idaho and Montana in 2009 and within the Wolf Trophy Game Management Area (WTGMA) in Wyoming in 2012. 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 stakeholder groups with different values regarding wolves and wolf management (Mech 2010, p. 1422). When the harvest season concluded, managers used multiple harvest and population metrics from current and past seasons to inform future harvest decisions based on management objectives. At present, the Wyoming Game and Fish Department (WGFD) adaptively manages wolves to maintain a numerical objective of 160 wolves within the WTGMA. This objective is based on rigorous data collected from the population and ensures Wyoming can maintain Federal recovery levels in the portion of Wyoming under the management jurisdiction of WGFD. Idaho and Montana manage wolf abundance primarily based on a trajectory/trend objective because the primary objective is to reduce wolf abundance in each state by creating negative population growth through increased harvest. However, if wolf abundance is reduced, managers may set a numerical objective for wolves in these respective states and use harvest strategies designed to maintain wolf abundance at a specific numerical objective, similar to WGFD's management in Wyoming.

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 2010, 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).

For some harvested species, accurate information related to catch per unit hunter effort may be used by managers, in conjunction with other metrics, as a relative index of species abundance. Although other factors may affect measures of catch per unit effort, in general, if catch per unit effort is high, it may mean there are less of a particular species available for harvest or that hunters are highly selective. If catch per unit effort is low, it may mean that the particular species is highly available or that hunter selectivity is concurrently low. Measures of harvest effort and success are most useful when the species being evaluated is the primary species being targeted. However, when a species is harvested opportunistically or secondarily to other targeted species (e.g., as is often the case with wolf hunting), metrics of hunter effort and success become a less useful indicator of abundance. This is because the number of days hunters spend attempting to harvest the particular species may not be accurately reported given that it was not the targeted species. In one study that evaluated wolf harvest and its correlation with wolf population trends in British Columbia, Canada, hunter effort and success were found to be poor indices of wolf abundance due to the opportunistic nature of wolf harvest in the province (Mowat et al. 2022, pp. 2, 15–16). Trapper harvest was more targeted and less variable annually, but challenges in accurately evaluating trapper effort and success remain (Mowat et al. 2022, pp. 13–15). As such, Idaho, Montana, and Wyoming require mandatory reporting and checks of all harvested wolves to obtain near real-time harvest information as well as to collect demographic, biological, and geographic information related to harvest. Even though annual variability in harvest can be expected, where wolf harvest is relatively high, the total number and locations of harvested wolves may be a useful index to evaluate general trends in wolf abundance and distribution over time, but it becomes less useful as an index of abundance where the number of wolves harvested is low (Mowat et al. 2022, pp. 15–16). Given these challenges with using catch per unit effort as an indicator of wolf abundance, states and provinces do not rely solely on measures of hunter and trapper effort and success or total harvest to inform management decisions. Rather, this and other harvest information is used in combination with wolf minimum counts or population estimates from the most recent season and past seasons to inform future harvest management decisions and to assist in achieving their management objectives.

### ***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, managers work with livestock owners to minimize conflict risk as much as is practical using a combination of nonlethal and lethal methods.

There are certain circumstances in which preventative and nonlethal techniques have been shown to be effective. 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). Subsequently, lethal control may also 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 minimizing conflict risk because a relatively high proportion of depredations in any given year occur over a relatively small area (Olson et al. 2015, entire; DeCesare et al. 2018, pp. 9–11). If wildlife managers use lethal control to reduce pack size shortly after a depredation occurred, it has been effective at minimizing recurrent depredations at the local scale; for example, 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, at least in the NRM, complete pack removal can be more effective than removal of a few pack members (Bradley et al. 2015a, pp. 6–9).

Nonetheless, the use of lethal control to mitigate wolf conflicts with livestock has been criticized for lacking long-term effectiveness and for being too costly (Wielgus and Peebles 2014, entire; McManus et al. 2015, entire; Lennox et al. 2018, entire; Santiago-Ávila et al. 2018, entire). Though, 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 one year exacerbated the conflict cycle, which resulted in an increased number of livestock killed by wolves the following year. 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. 2015a, entire; DeCesare et al. 2018, pp. 8, 10).

Researchers disagree on whether lethal or nonlethal 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.

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 it, with the exception of 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). Similarly, the number of cattle depredations confirmed in the WTGMA in Wyoming has declined from 141 in 2016 (prior to delisting) to 38 in 2021 (post-delisting) (WGFD et al. 2022, pp. 20–21). 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 3). In Montana, in addition to these decreases in the total number of wolves removed, under state management, 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).

The Service has long recognized that control of depredating wolves was an important aspect of wolf recovery and management in the NRM (Service 1980, entire; Service 1987, entire; Service 1994, pp. xiii–xvi). As a result, the Service developed control plans for wolves, which provided guidance for when depredating wolves could be harassed, moved, or killed by agency personnel (Service 1988, entire; Service 1999, entire; Bangs et al. 2009, pp. 107–114). Furthermore, the central Idaho and GYA recovery areas in the NRM were designated as nonessential experimental population areas, which provided increased management flexibility to control depredating wolves than would normally be allowed for a species listed as federally endangered (59 FR 60252, November 22, 1994; 59 FR 60266, November 22, 1994; 70 FR 1286, January 6, 2005; 73 FR 4320, January 28, 2008). This designation allowed for agency control of wolves and also allowed livestock owners to control wolves that were observed physically attacking livestock. The Service used an incremental approach to the control of depredating

wolves and removed an average of 7 percent of the population annually between 1987 and 2006 (Bangs et al. 2009, pp. 107–111).

Overall, a relative few wolf packs are implicated in livestock or pet depredations on an annual basis (e.g., approximately 17 percent of known packs in the NRM in 2015) (Olson et al. 2015, entire; Service et al. 2016, p. 2). Furthermore, Stenglein et al. (2015a, 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 to mitigate livestock conflicts in the Western United States, see *Levels of Human-Caused Mortality in the Western United States* below.

### ***Illegal Take (i.e., Poaching) of Wolves and Other Sources of Mortality***

While some illegal take may be considered accidental due to vehicle collisions, mistaken identity, or other causes, some illegal take is intentional and, by its very nature, can be challenging to document, regulate, and limit even with 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 (1) 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; Louchouart et al. 2021, entire; Santiago-Ávila and Treves 2022, p. 1738) and (2) in fragmented habitats with reduced escape cover (Hill et al. 2022, pp. 4, 6–7). Federal managers in the NRM estimated that around 10 percent of the known wolf population was illegally killed annually prior to delisting, the second highest source of mortality behind lethal control to resolve wolf conflicts with livestock. Studies estimated that illegal take accounted for 24 percent of all mortalities in the NRM (annually removing approximately six percent of the known population); however, 12 percent of all documented mortalities were attributed to unknown causes, so it is highly plausible that the number of wolves illegally taken may have been higher (Smith et al. 2010a, p. 625; Treves et al. 2017b, p. 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 conterminous United States (Murray et al. 2010, p. 2519; Smith et al. 2010a, 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 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, contrary to assumptions made by some researchers (Treves et al. 2017b, pp. 7–8), 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 four percent of missing wolves in Wisconsin may have actually died (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-Ávila et al. 2020, entire; Treves et al. 2021, p. 9; Santiago-Ávila and Treves 2022, pp. 1738–1739; Oliynyk 2023, entire), although the claims of these studies 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). In Wyoming, although the number of wolves illegally killed has not significantly changed under Federal versus state management, the reasons for the illegal take have changed; most illegal take that occurs at present are regulatory infractions related to hunting seasons rather than intentional killing or mistaken identity (Thompson 2022, in litt.).

As has been noted in the Scandinavian wolf population (Liberg et al. 2020, pp. 4–6), illegal take may have contributed to a localized reduction in wolf population growth in the Western United States to some extent, including in Oregon in 2021 (ODFW 2022, pp. 4–7). However, based on wolf minimum counts, population estimates (Table 3), and distribution across the Western United States, illegal take alone or in combination with all other forms of mortality has not prevented the continued recolonization of vacant, suitable habitat in the Western United States.

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. Overall, these types of mortality are rare, and they are not expected to have a significant impact on gray wolf populations in the Western United States now or in the future.

In general, when compared to the early twentieth century when take was unregulated, the regulation of human-caused mortality has reduced the number of wolf mortalities caused by humans, which has allowed wolves to recolonize areas within their former range. Illegal and accidental killing of wolves are likely to continue in the future, and at current levels those mortalities have minimal impact on wolf abundance in the Western United States.

### **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 who values other things more than wolves is likely to have a more negative perception than an individual who believes wolves are beneficial. This perception 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 (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. 2022b, entire; Niemiec et al. 2022, entire).

Wolves often invoke deep-seated issues related to identity, fear, knowledge, empowerment, and trust that are not directly related to the issues raised in this SSA (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).

There is much debate about the role regulated wolf harvest has 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; Slagle et al. 2022, entire). Hogberg et al. (2016, p. 50) documented an overall decline in tolerance for wolves after public 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 public 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, which can, in turn, influence 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 Western United States. These increases in human-caused mortality could be caused by changes in public attitudes, in addition to a multitude of other influencing factors.

### **Levels of Human-Caused Mortality in Idaho, Montana, Oregon, Washington, and Wyoming**

Before the delisting of wolves in the NRM, it was long recognized that the future conservation of a delisted wolf population in the NRM depended almost entirely on state regulation of human-caused mortality. In 1999, the governors of Idaho, Montana, and Wyoming agreed that regional coordination in wolf management planning among the states, Tribes, and other jurisdictions was necessary. They signed a memorandum of understanding (MOU) to facilitate cooperation among the three states to develop adequate state wolf management plans so that delisting could proceed (IDFG 2002, pp. 17, 31; Service et al. 2003, p. 31; MFWP 2008, unpaginated). In this agreement, which was renewed in April 2002, all three states committed to maintain at least 10 breeding pairs and at least 100 wolves per state (i.e., the recovery level) (74 FR 15123, April 2, 2009, pp. 15166–15167). Further, to ensure the NRM wolf population remained above this recovery level, Idaho, Montana, and the combination of YNP, the Eastern Shoshone and Northern Arapaho Tribes, and the WGFD in Wyoming<sup>9</sup> agreed to manage for at least 15 breeding pairs and at least 150 wolves each (Groen et al. 2008, p. 1; 74 FR 15123, April 2, 2009; Talbott and Guertin 2012, p. 1; 77 FR 55530, September 10, 2012).

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<sup>9</sup> In Wyoming, different jurisdictions have large portions of management responsibility, which is not the case in the other states. As a result, the Service agreed to allow WGFD to manage for at least 10 breeding pairs and 100 wolves in the WTGMA whereas YNP and the Eastern Shoshone and Northern Arapaho Tribes combined would maintain at least five breeding pairs and 50 wolves (77 FR 55530, September 10, 2012).

In 2009, the Service determined that Idaho and Montana had state laws, management plans, and regulations that met the requirements of the Act to maintain their respective wolf populations above recovery levels into the foreseeable future (74 FR 15123, April 2, 2009). A similar determination was made for Wyoming in 2012 (77 FR 55530, September 10, 2012). The three states agreed (1) to manage above the recovery level and (2) to adapt their management strategies and adjust allowable rates of human-caused mortality should the population be reduced to near recovery levels per their management objectives. As part of post-delisting monitoring in the NRM, the Service conducted annual assessments of the NRM wolf population and noted that it remained biologically recovered and well above Federal recovery levels with no identifiable threats that imperiled its recovered status under state management in 2009 (Bangs 2010, entire) and between 2011 and 2015 (Jimenez 2012, 2013a, 2014, 2015, 2016, entire). Similar assessments and determinations were made for Wyoming after delisting in 2017 (Becker 2018a, entire; Becker 2019, entire).

Between 2009 and 2015 (the years for which we have consistent NRM information as a result of post-delisting monitoring), during the times when wolves were under state management, Idaho, Montana, and Wyoming (which make up the majority of the NRM) began to manage wolves with the objective of reversing or stabilizing population growth while continuing to maintain wolf populations well above Federal recovery targets. The primary method these states have used to manage wolf populations and achieve management objectives was through regulated public harvest. The management of wolf populations through regulated harvest had never been attempted in the conterminous United States until 2009 when Idaho and Montana conducted the first regulated wolf hunts. Due to legal challenges, no regulated harvest occurred in Idaho, Montana, or Wyoming during the 2010/2011 season but, in Idaho and Montana, it has occurred each year since the 2011/2012 season. Regulated harvest occurred within the WTGMA in northwest Wyoming during the fall of 2012 and 2013, then has occurred each year since 2017. With the introduction of regulated wolf harvest, total wolf mortality in Idaho, Montana, and Wyoming increased from 14 percent of the minimum known or estimated population (the average between 2000 and 2010, excluding 2009, when regulated wolf harvest did not occur) to 31 percent of the minimum known population (the average in 2009 and from 2011 to 2015, when regulated wolf harvest did occur) (Service et al. 2010–2016, entire). During these same time periods, human-caused mortality increased from 11 percent of the minimum known or estimated population to 29 percent (Service et al. 2010–2016, entire). Concurrent with increased total and human-caused mortality, population growth declined from 17 percent (the average between 2000 and 2010, with the exclusion of 2009) to an annual average of approximately one percent in 2009 and from 2011 to 2015 (Service et al. 2010–2016, entire). These results are very similar to a review of human-caused mortality in North American wolves where researchers found that wolf population growth rates remained stable to slightly increasing with human-caused mortality rates of approximately 29 percent or less (Adams et al. 2008, pp. 19–20).

Overall, harvest rates have not always increased as harvest regulations have become less restrictive in Idaho and Montana (e.g., extended seasons, removal of harvest limits, increased bag limits), and populations remained relatively stable through the end of 2020. This demonstrates that the life-history characteristics of wolf populations can provide natural resiliency to certain levels of human-caused mortality. Consistent with current wolf management objectives in Idaho and Montana, the year-end wolf abundance estimates in 2021 and 2022 in both states decreased

slightly compared to the year-end estimate from the previous years (a 44-wolf decrease in Idaho and a 33-wolf decrease in Montana between year-end 2020 and year-end 2021 and an 86-wolf decrease in Idaho and a 56-wolf decrease in Montana between year-end 2021 and year-end 2022); however, in Montana, the confidence intervals around these year-end estimates for 2021 and 2022 encompass the previous years' estimates, suggesting that uncertainty remains in the exact trajectory of the population between year-end 2020 and year-end 2022 (see Appendix 3 for citations).

Our detailed discussion of the history of wolf harvest regulations in the 2020 delisting rule (85 FR 69778, November 3, 2020) illustrates the adaptive style of management that Idaho, Montana, and Wyoming use to manage wolves above Federal recovery criteria while meeting, or attempting to meet, wolf population objectives at the state level. At present, Idaho is using a trajectory/trend objective to reduce the estimated wolf population in the state to fluctuate around an average of 500 wolves, at which time they intend to adaptively manage the population around this numerical objective (see *Management of Wolves in Idaho* below for more discussion of this objective). In Montana, the trajectory/trend objective is to reduce wolf populations but not to less than the number needed to support at least 15 breeding pairs. WGFD has fewer wolves within their jurisdiction and manages them based on a numerical population objective of 160 wolves within the WTGMA, so harvest regulations and harvest totals are relatively conservative compared to Idaho and Montana to ensure that the numerical objective is achieved and that the number of wolves stays above Federal recovery levels. Below, we summarize state law, regulations, and the management plans relevant to wolf management, particularly focusing on human-caused mortality in each state in our analysis area. Outside of very remote or large protected areas, regulated harvest and lethal control of depredating wolves has accounted for the majority of the known wolf mortalities in the NRM since 2009; 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 and, except for a few instances, they are not discussed specifically, but are incorporated into discussions of total human-caused mortality for each state (Table 3). For comparative purposes, all rates have been calculated at the statewide scale regardless of any potential management differences within each state. All estimated cause-specific and total mortality rates discussed below were calculated by dividing the number of wolves that died from each type of mortality by the population count/estimate for the end of the calendar year plus the known number of animals 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, or the number of wolves that were available for mortality during that year).<sup>10</sup>

### ***Human-Caused Mortality in Idaho***

#### **Management of Wolves in Idaho**

Since Federal delisting, wolves have been classified and managed as a big game species in Idaho, which allows for controlled take and enforcement for illegal take under big game rules

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<sup>10</sup> For example, we calculated the total mortality rate as: Total Mortality Rate = [Total # of Wolves Died From All Known Causes in 20XX]/[Year-End Population Count/Estimate for the State for 20XX + Total # of Wolves Died From All Known Causes in 20XX]

and regulations. Until recently, wolf management in Idaho was guided by the legislatively adopted *2002 Idaho Wolf Conservation and Management Plan (2002 Idaho Plan)* (Idaho Legislative Wolf Oversight Committee (ILWOC) 2002, entire). The primary goal of the *2002 Idaho Plan* was to manage for a viable, self-sustaining wolf population that was well-connected to neighboring states and provinces while, concurrently, working to minimize negative impacts to livestock and ungulates (ILWOC 2002, p. 4, 18; 74 FR 15123, April 2, 2009, pp. 15166–15167). Under the *2002 Idaho Plan*, when there were more than 15 packs documented in the state, wolf management was similar to management of other predators in the state, whereas management became more restrictive when 15 or fewer packs were documented (ILWOC 2002, p. 5). Wolf management in Idaho was also guided by a memorandum of agreement between the State of Idaho and the Nez Perce Tribe that defined roles and responsibilities for the conservation and management of wolves in the state (State of Idaho and Nez Perce Tribe 2005, entire).

In a May 2023, Idaho Fish and Game (IDFG) completed an updated *Idaho Gray Wolf Management Plan (2023 Idaho Plan)* that will guide wolf management from 2023 through 2028 (IDFG 2023a, entire), at which time the state expects to develop and implement a new plan. If a new plan is not completed by the end of 2028, we expect, based on past practice, that this 2023 plan would continue to guide wolf management in Idaho until an updated plan is completed. Similar to the *2002 Idaho Plan*, IDFG states its continued commitment to maintaining a viable, self-sustaining wolf population that is well-distributed across suitable habitat in the state and remains well connected to neighboring states and provinces (IDFG 2023a, p. 38). IDFG will closely monitor wolf populations to ensure they remain well above the state’s previous commitment to manage for at least 150 wolves and 15 breeding pairs (Groen et al. 2008, p. 1; 74 FR 15123, April 2, 2009; IDFG 2023a, p. 38). The four primary goals of the *2023 Idaho Plan* are to: (1) manage for a viable wolf population that fluctuates around 500 wolves annually (they expect that wolf numbers would fluctuate from a high of 650 wolves after the birth pulse in the spring to a low of 350 wolves just prior to the birth pulse in the spring); (2) monitor wolf population dynamics annually and continue to improve wolf monitoring and population abundance estimation methods; (3) reduce wolf depredations on livestock; and (4) reduce wolf depredations on ungulate populations not meeting objective (IDFG 2023a, pp. 38–44). To achieve these goals, IDFG intends to increase wolf mortality in the state to reduce the wolf population so that the population fluctuates around an average of 500 wolves annually by the end of 2028 (IDFG 2023a, p. 39). This management goal exceeds the state’s previous commitments to manage for at least 150 wolves and 15 breeding pairs (Groen et al. 2008, p. 1; 74 FR 15123, April 2, 2009; IDFG 2023a, p. 38). IDFG projected that a total mortality rate of 37 percent for each of the next six years would result in wolf population reductions that would achieve the new numerical objective of an average of 500 wolves by the end of 2028 (IDFG 2023a, pp. 39–41). Public hunting and trapping will continue to be the primary methods IDFG uses to achieve its wolf population objective (IDFG 2023a, p. 39). When it achieves this population objective, IDFG will adjust hunting and trapping to maintain the population around an average of 500 wolves annually (IDFG 2023a, p. 41).

### **Regulated Harvest in Idaho**

Idaho has managed a regulated hunting season for wolves every year since 2009, with the exception of the 2010/2011 season when wolves were briefly relisted. Although IDFG has not developed models to make predictions about harvest outcomes based on different harvest scenarios on an annual basis, they adaptively managed wolf harvest seasons to achieve their

desired management objective of reducing wolf abundance in specific hunt units in order to address conflicts with livestock and impacts to ungulate populations (Oelrich 2022, in litt.). Harvest regulations have gradually become less restrictive over time in Idaho with the intent to reduce overall wolf abundance in the state. Some of these regulatory changes included the removal of harvest limits statewide, season length extensions, increased bag limits, and implementation of a trapping season in 2011 (both footholds and snares allowed; trappers are required to complete a wolf trapper education course).

Between 2011 and 2015, as part of the post-delisting monitoring period, the Service evaluated regulatory changes to Idaho's wolf harvest seasons and assessed wolf populations in the state. Although the Service noted that regulatory changes could result in increased harvest, our evaluation determined that these changes did not represent a significant threat to the wolf population or the recovered status of wolves in Idaho (Cooley 2011, entire; Cooley 2012, entire; Cooley 2013, entire; Cooley 2014, entire).

After the post-delisting monitoring period ended in 2015, wolf harvest regulations continued to become gradually less restrictive to meet population management objectives of reducing wolf abundance by increasing harvest through expanded hunting season lengths, opening additional areas to trapping, increasing bag limits, and increasing the number of tags a hunter or trapper could purchase, among other changes. Wolves were also managed across 99 hunt units (HU) rather than the larger wolf management zones of previous years to better direct harvest, if deemed necessary (for further details about the regulatory history of wolf harvest regulations in Idaho, please see the 2020 delisting rule (85 FR 69778, November 3, 2020)). Although the formal post-delisting monitoring period ended in 2015, interest in wolves and wolf management remains high in Idaho. As a result, the Service has continued to review wolf harvest and population trends in Idaho since the post-delisting monitoring period ended to keep abreast of current status.

During the 2021 Idaho Legislative session, legislators introduced and approved language that revised and amended Idaho Senate Bill (SB) 1211, which guides wolf management in Idaho. The revised legislation amended several Idaho Codes (IC) to: (1) authorize a year-round trapping season on private property (IC 23-201(3)); (2) authorize additional methods of take previously prohibited<sup>11</sup> (IC 201(2)); (3) remove any limit to the number of wolf tags an individual may purchase (IC 36-408(1)); (4) allow a livestock or domestic animal owner to use a private contractor to control wolves (IC 36-1107(c)); (5) allow the Idaho Wolf Depredation Control Board to enter into agreements with private contractors, in addition to state and Federal agencies, to implement the provisions of SB 1211; and (6) direct wolf control assessments (\$110,000 annually) collected from the Idaho livestock industry to be combined with \$300,000 the state would transfer from the IDFG fund annually beginning on July 1, 2021. The IDFG Commission would direct the Wolf Depredation Control Board in the use of this funding for wolf control. These statutes and the associated regulatory changes for the 2021/2022 wolf

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<sup>11</sup> These expanded methods of take included (1) no weapons restrictions; (2) use of bait on private property only; (3) allowing hunters to take wolves outside of hunting hours (i.e., at night) on private property with landowner permission and on public land with a permit from IDFG; (4) no vehicle restrictions, although Federal regulations and private landowner permissions still apply; and (5) the use of dogs to pursue wolves.

hunting and trapping season were the primary subject of the 2021 petitions to list wolves in the NRM or Western United States under the Act.

The IDFG Commission incorporated the new provisions of SB 1211 into regulation and, on July 1, 2021, implemented the new wolf hunting and trapping regulations for the 2021/2022 season. (For additional detail on how these new regulations compare to the 2020/2021 season prior to statutory changes, see Table 1). Wolf harvest regulations for the 2022/2023 season were the same as those promulgated for the 2021/2022 season. Most regulations remained unchanged for the 2023/2024 wolf harvest season with the following exceptions: (1) all HUs are open year-round for hunting wolves on public lands (expanded methods of take are allowed in 44 HUs between November 15, 2023, and March 31, 2024, on public land) and (2) 92 HUs are open to trapping (footholds only) on public lands beginning September 10, 2023 (see Table 1 for comparison with recent wolf harvest seasons).

Notwithstanding the new revisions and amendments to SB 1211, IC 36-104(b)(2) continues to provide the IDFG Commission discretionary authority to open/close hunting or trapping seasons and set harvest limits on public lands, open/close hunting seasons and set harvest limits on private lands, and set harvest limits for trapping seasons on private lands. IC 36-104(b)(3) allows the IDFG Commission to adopt emergency closures or restrictions, if necessary, and IC 106(e)(6) provides similar authority to the IDFG Director.

The Foundation for Wildlife Management (F4WM) is a non-profit organization founded in northern Idaho in 2012 to “promote ungulate population recovery in areas negatively impacted by wolves,” among other objectives. Since its inception, F4WM has managed a reimbursement program to compensate members for the cost associated with the legal harvest of a wolf in Idaho. Reimbursement amounts are based on actual expenses from receipts submitted to F4WM after the legal harvest of a wolf, up to a specified amount dependent on the location of the harvest. In Idaho, the reimbursement program is funded through membership dues, private donations, and, more recently, funding from the state. Beginning with the 2021/2022 wolf harvest season, the IDFG Commission routed \$200,000 through the Idaho Wolf Depredation Control Board to F4WM to increase program reimbursement amounts in priority areas identified by IDFG. Using these funds, reimbursement amounts during the 2021/2022 wolf harvest season were up to \$2,500 per wolf in 21 HUs that experience chronic depredations, up to \$2,000 per wolf in 22 HUs where elk numbers are below objective, up to \$1,000 per wolf in HU 1 in northern Idaho, and up to \$500 per wolf in the remainder of the state. During the 2021/2022 season, Wolf Depredation Control Board funds were depleted by November 29, 2021, so reimbursement payments reverted back to standard reimbursement rates of up to \$1,000 in HU 1, up to \$750 for 25 HUs where elk numbers are below objective, and up to \$500 for the remainder of the state.

For the 2022/2023 Idaho wolf harvest season, changes were made to the reimbursement program in an attempt to prolong the timeline of increased reimbursement payments using state funds. Through a cooperative agreement between IDFG and F4WM (IDFG 2023a, in litt.), in HUs identified as priority areas by IDFG (those that experience chronic depredations or where elk are below objective), reimbursement amounts paid up to \$1,000 for the first wolf harvested by an individual through F4WM funds only. If an individual hunter or trapper harvested additional wolves, all subsequent reimbursement amounts used state funds routed through

F4WM and paid up to \$2,000 per wolf in 19 HUs experiencing chronic livestock depredations, up to \$1,500 per wolf in 26 HUs where elk are below objective, and up to \$1,000 per wolf in HU 1. In the remaining 53 HUs, reimbursements paid up to \$500 per wolf, regardless of whether it was the first or any subsequent wolf harvested. Furthermore, F4WM was awarded additional funds to support their wolf hunter and trapper reimbursement program in Idaho from the regional and statewide Commission Challenge Grant during the 2022/2023 wolf harvest season, the terms of which were outlined in a second cooperative agreement between IDFG and F4WM (IDFG 2023b, in litt.). Under the terms of each cooperative agreement, successful hunters and trappers did not need to be members of F4WM to receive reimbursements using state funds for the legal harvest of a wolf in one of the priority areas (IDFG 2023a, in litt.; IDFG 2023b, in litt.). For the 2023/2024 wolf harvest season, the total number of priority areas and reimbursement rates for these priority areas remained unchanged from the previous season. As with the previous wolf harvest season, F4WM was awarded funds from the Idaho Commission Challenge Grant to support the wolf harvest reimbursement program, but, again, hunters and trappers do not need to be members of F4WM to receive reimbursement from this grant (Atkins 2023, in litt.).

Between the 2012/2013 and the 2018/2019 wolf seasons, wolf harvest fluctuated between 231 and 333 wolves per season in Idaho. Wolf harvest sharply increased to 462 wolves during the 2019/2020 season then declined to 411 wolves in the 2020/2021 season. A total of 412 wolves were harvested during the 2021/2022 season (general hunt = 176 wolves and trapping = 236), the first season after the legislative changes described above were incorporated into wolf harvest regulations. The expanded legal methods of take incorporated into regulation for the 2021/2022 season resulted in three additional wolves harvested and included one wolf taken during extended hours, one wolf taken from a motorized vehicle, and one wolf taken over bait. An additional eight wolves were harvested with foothold traps through extended trapping seasons on private property during the 2021/2022 season (IDFG 2023c, in litt.; see Figure 4 and Table 3 for further details about total harvest in Idaho since the 2009/2010 season). During the 2022/2023 wolf harvest season, a total of 388 wolves were harvested in Idaho (general hunt = 197 wolves and trapping = 191 wolves). Similar to the previous season, the expanded methods of take that the 2021 legislative changes authorized resulted in few additional wolves harvested as five wolves were harvested using the expanded methods and six wolves were harvested through extended trapping seasons on private lands during the 2022/2023 season (IDFG 2023c, in litt.). A total of 124 and 120 reimbursement payments were made by F4WM to members who successfully harvested a wolf during the 2021/2022 and 2022/2023 wolf harvest seasons, respectively, under the cooperative agreement with IDFG (IDFG 2022a, in litt.; IDFG 2023d, in litt.). In addition, for the 2022/2023 wolf harvest season, through the Commission Challenge grant, 67 harvested wolves were reimbursed and F4WM used their own funds to reimburse hunters and trappers for an additional 95 wolves (IDFG 2023d, in litt.). In total, of the 388 wolves harvested in Idaho, 283 harvested wolves were reimbursed during the 2022/2023 season.

Although correlative in nature, funds that Idaho contributed to F4WM to deliberately increase harvest in priority HUs by increasing reimbursements to successful hunters and trappers (described above) may have contributed to a shift in the spatial distribution of wolf harvest in Idaho during the 2021/2022 and the 2022/2023 season, without increasing overall wolf harvest statewide (IDFG 2023d, in litt.). When compared to average harvest during the three harvest seasons prior to the 2021/2022 season, HUs identified as chronic depredation areas observed a

25-wolf increase in the mean number of wolves harvested (approximately 61 wolves to 86 wolves) while HUs identified as having both chronic depredations and elk below objective observed a 12-wolf increase in the mean number of wolves harvested (from 24 wolves to 36 wolves). In HUs where elk were below objective, the number of wolves harvested declined from a mean of 215 wolves between 2018/2019 and 2020/2021 wolf harvest seasons to a mean of 198 wolves harvested over the 2021/2022 and 2022/2023 harvest seasons (IDFG 2023d, in litt.). In non-priority HUs where standard reimbursements were provided, the mean number of wolves harvested declined from 96 wolves to 81 wolves. Although increased reimbursements may have contributed to observed changes to the spatial distribution of harvest in Idaho over the past few years, the exact reasons for the shift remain unknown. Whether or not these pattern shifts in the distribution of harvest will be maintained over time and will result in reduced wolf-livestock conflicts or increased elk abundance is yet to be determined.

The spatial distribution of harvest in Idaho may also illustrate the presence of refugia for wolves (i.e., areas that are difficult to access where human-caused mortality is low). Since the 2016/2017 season, most wolf harvest has occurred in the northern half of the state, particularly in heavily roaded areas near population centers (IDFG 2023a, pp. 21–22). During the 2021/2022 and 2022/2023 seasons, on average, approximately 84 percent of wolf harvest occurred on public land in Idaho (IDFG 2023c, in litt.), but, at least during the 2021/2022 season, those HUs that contained more than 30 percent designated wilderness accounted for only 13 percent of the total statewide wolf harvest (IDFG 2022b, in litt.). Although this only represents a single year of data, these results are consistent with a 50-year long study showing that wilderness areas can act as a refugia for wolves, with higher survival rates inside wilderness areas, even when compared to other Federal lands outside of wilderness boundaries (Barber-Meyer et al. 2021, pp. 10–11).

In Idaho, the harvest success rate of individual trappers is significantly higher than the success rate of individual hunters (IOSC and IDFG 2022, in litt.; IDFG 2023a, p. 19). Most successful hunters generally harvest a single wolf opportunistically in the fall, incidental to deer and elk seasons (Ausband 2016, p. 501; IDFG 2017, p. 15; IDFG 2023a, pp. 19–21). However, primarily due to sheer volume of hunters, hunters harvested a greater number of wolves in the state until the 2019/2020 season (Figure 4; IDFG 2023a, p. 20). Since the 2019/2020 season, the total number of wolves harvested by trapping has outpaced hunter harvest except for the 2022/2023 season, where hunter harvest exceeded trapper harvest by six wolves. Although the exact mechanisms remain speculative (Ausband 2016, p. 504), and most successful trappers each harvest fewer than two wolves per season (IOSC and IDFG 2022, in litt.), the increased proportion of trapped wolves in the harvest may be a result of increased harvest opportunity (IDFG 2023a, p. 20).

Over the last decade, Idaho has gradually increased individual hunter and trapper harvest limits by increasing the number of tags an individual hunter and/or trapper may purchase in the state as a method to increase wolf harvest. However, this has not resulted in a significant increase in the number of tags purchased or the number of wolves harvested (IDFG 2023a, p. 19). Even with increases in the number of tags an individual may purchase, the average number of tags an individual hunter and trapper purchased was still 1.1 and 2.1, respectively, between 2018 and 2022 (IDFG 2023a, p. 19). The most tags any single individual has purchased to date has been 16 hunting tags and 16 trapping tags and the most wolves any single individual has

harvested in Idaho to date was 20 wolves during the 2019/2020 season (which preceded the new regulatory changes for the 2021/2022 season; IDFG 2023a, p. 19). Thus, the removal of individual harvest limits and the number of tags an individual may purchase beginning with the 2021/2022 season may not result in increased harvest because, in most cases, these harvest limits were not limiting take in prior seasons. Since the 2021/2022 season when an individual could purchase an unlimited number of tags, the highest harvest recorded by a single individual has been 10 wolves.

Treves et al. (2022, in litt.) assumed regulatory changes in Idaho also increased hunter and trapper effort that should have resulted in increased harvest during the 2021/2022 season; because total harvest was similar to the previous season, Treves et al. (2022, in litt.) thus assumed wolf abundance must be lower than estimated. These assumptions may be incorrect for several reasons. First, although Idaho hunters and trappers purchased over 54,000 tags during the 2021/2022 season (IOSC and IDFG 2023, in litt.), there is no information to indicate that regulatory changes in Idaho resulted in increased hunter effort during the 2021/2022 season because it is unknown how many individuals who purchased a tag actually attempted to hunt a wolf. Although a slight increase in the number of trapping tags sold has been noted over the years (even prior to regulatory changes), the number of active trappers has remained relatively constant over time (IDFG 2023a, pp. 19–20). Second, measures of catch per unit effort may be a particularly poor indicator of wolf abundance given that wolves are often harvested opportunistically or secondarily to other hunted species (see *Discretionary Sources of Mortality: Regulated Public Harvest* above). As a result, metrics collected to measure hunter effort and success after each season may not be accurate and should be used with caution because they have been found to be poor predictors of trends in wolf abundance (Mowatt et al. 2022, p. 16). Managers can use total wolf harvest to detect significant changes in wolf abundance and distribution at large spatial scales, but harvest data is less useful for detecting changes at smaller spatial scales, such as the hunt unit level (Mowat et al. 2022, pp. 13–17). Furthermore, a host of complex factors affect hunter and trapper effort and success in any given season. Many of these factors are wholly unrelated to regulatory changes designed to increase harvest opportunity and may include, but not be limited to, changes in wolf behavior and susceptibility to harvest, environmental conditions, economics (i.e., gas prices, fur prices), and social and political factors that affect individual choices (Fritts et al. 2003, p. 301; Adams et al. 2008, pp. 17–18; Cluff et al. 2010, entire; Mech 2010, pp. 1422–1423; Webb et al. 2011, p. 750; Kapfer and Potts 2012, pp. 240–241; F4WM 2022, unpaginated). Due to the challenges of using a single metric (e.g., catch per unit effort or total harvest in a single year) to base management decisions upon, managers use multiple harvest and population metrics from the most recent season, in addition to past harvest and population trends, to make informed decisions about future harvest management with the goal of achieving a specific management objective.

Between 2009 and 2015, harvest removed, on average, approximately 20 percent of Idaho’s minimum estimated wolf population annually. After 2015, IDFG transitioned away from providing minimum estimates of wolves in the state and explored the use of multiple alternative methods to evaluate population performance, including modeled abundance and distribution estimates using statewide camera surveys (see *Methods for Counting and Estimating Annual Population Size in Each State* in Chapter 4). Although not directly comparable to harvest rates calculated based on minimum wolf population estimates, wolf harvest averaged 27 percent of the

estimated year-end wolf population based on space-to-event modeling efforts in the state between 2019 and 2022. Despite regular changes to harvest regulations that expanded opportunities for take, harvest rates have not necessarily increased commensurately, but rather have continued to fluctuate between 22 and 35 percent. Moreover, observed levels of harvest did not result in population reductions through the end of 2020. During the 2021/2022 and 2022/2023 harvest seasons, the harvest rates in Idaho were 26 and 28 percent, respectively, within the range of harvest rates from seasons that predated the new law prompting less restrictive harvest regulations. At the end of 2021 and 2022, the year-end estimates for wolf abundance in Idaho indicated a slight population decrease relative to the previous years' estimate (i.e., a 44-wolf decrease between year-end 2020 and year-end 2021 and an 86-wolf decrease between year-end 2021 and year-end 2022), which is consistent with IDFG's stated objective to reduce the wolf population size to around 500 wolves (Table 3; IDFG 2023b, entire; IDFG 2023a, p. 39).

Table 1. Comparison of Idaho’s wolf harvest regulations between the 2020/2021 and 2021/2022 seasons. Regulations for the 2022/2023 season are identical to the regulations for the 2021/2022 season described below. The 2023/2024 harvest regulations are similar to previous seasons with a few minor changes that include: (1) all HUs are open year-round for hunting wolves on public lands (expanded methods of take are allowed in 44 HUs between November 15, 2023, and March 31, 2024, on public land) and (2) 92 HUs are open to trapping (footholds only) on public lands beginning September 10, 2023.

	2020/2021 Season (before new law/regulatory changes)	2021/2022 Season (after new law/regulatory changes)
<b>Season dates</b>	<ul style="list-style-type: none"> <li>• <u>Hunting</u> <ul style="list-style-type: none"> <li>○ July 1–June 30: private land only in 57 HUs</li> <li>○ July 1–June 30: public/private land in 30 HUs</li> <li>○ Aug. 1–June 30: public/private land in 69 HUs</li> </ul> </li> <li>• <u>Trapping</u> <ul style="list-style-type: none"> <li>○ Sept. 10–Oct. 9: footholds only (3 HUs)</li> <li>○ Oct. 10–Nov. 14: footholds (91 HUs); snares on private land only (19 HUs) and public/private land (6 HUs)</li> <li>○ Nov. 15–March 31: footholds and snares on public and private land in most HUs; snares allowed on private land only in 23 HUs</li> </ul> </li> </ul>	<ul style="list-style-type: none"> <li>• <u>Hunting (private land): July 1–June 30</u> <ul style="list-style-type: none"> <li>○ expanded methods of take [see row below] allowed year-round statewide</li> </ul> </li> <li>• <u>Hunting (public land)</u> <ul style="list-style-type: none"> <li>○ July 1–June 30 (59 HUs); Aug. 1–June 30 (40 HUs)</li> <li>○ expanded methods of take allowed in 43 HUs only from Nov. 15–March 31</li> </ul> </li> <li>• <u>Trapping (private land): July 1–June 30</u> <ul style="list-style-type: none"> <li>○ Footholds allowed year-round</li> <li>○ Oct. 10 or Nov. 15–March 31: snares allowed in 97 of 99 HUs</li> </ul> </li> <li>• <u>Trapping (public land)</u> <ul style="list-style-type: none"> <li>○ Sept. 10–Oct. 9: footholds only (41 HUs)</li> <li>○ Oct. 10–Nov. 14: footholds (92 HUs) and snares (six HUs)</li> <li>○ Nov. 15–March 31: footholds (97 HUs) and snares (93 HUs)</li> </ul> </li> </ul>
<b>Key Hunting Regulations</b>	<ul style="list-style-type: none"> <li>• Separate tag required for each wolf harvested; hunting tags valid for calendar year</li> <li>• Individuals who possess valid hunting and trapping license may use trapping tag to harvest unrestrained wolf as long as the hunting and trapping season is open in unit</li> <li>• Weapons restrictions apply (type of weapon, caliber, etc.)</li> <li>• Prohibited methods of take includes: <ul style="list-style-type: none"> <li>○ Bait</li> <li>○ Night hunting</li> <li>○ Use of dogs to attract or pursue</li> </ul> </li> </ul>	<ul style="list-style-type: none"> <li>• Separate tag required for each wolf harvested; hunting tags valid for calendar year</li> <li>• Individuals with a valid hunting license may use tags purchased under either a hunting or trapping license to take wolves as long as both hunting and trapping seasons are open in unit</li> <li>• Expanded methods of take allowed in some areas at some times of year (see above) include: <ul style="list-style-type: none"> <li>○ No weapons restrictions</li> <li>○ Use of bait on private property only</li> <li>○ Night hunting allowed on private property and public land with permit</li> <li>○ No vehicle restrictions (though Federal regulations still apply)</li> <li>○ May use dogs to pursue wolves</li> </ul> </li> </ul>
<b>Key Trapping Regulations</b>	<ul style="list-style-type: none"> <li>• Must attend wolf trapper education class and have valid wolf trapping license to purchase trapping tags.</li> <li>• Individual with valid trapping license may use either a valid hunting or trapping tag to harvest trapped wolf, as long as both hunting and trapping seasons are open in unit. Limits based on tag type used for harvest still apply (see below).</li> </ul>	<ul style="list-style-type: none"> <li>• Must attend wolf trapper education class and have valid wolf trapping license to purchase trapping tags.</li> <li>• Individual with valid trapping license may use either a valid hunting or trapping tag to harvest trapped wolf, as long as both hunting and trapping seasons are open in unit.</li> <li>• Separate tags are required for each wolf trapped</li> </ul>

	2020/2021 Season (before new law/regulatory changes)	2021/2022 Season (after new law/regulatory changes)
	<ul style="list-style-type: none"> <li>• Separate tag required for each wolf trapped; tags valid for trapping season (July 1–June 30)</li> <li>• Footholds and snares permitted</li> </ul>	<ul style="list-style-type: none"> <li>• Trapping tags valid for trapping year (July 1–June 30)</li> </ul>
<b>Harvest limits</b>	<ul style="list-style-type: none"> <li>• No harvest limits in any of the 99 HUs</li> </ul>	<ul style="list-style-type: none"> <li>• No harvest limits in any of the 99 HUs</li> </ul>
<b>Bag limits</b>	<ul style="list-style-type: none"> <li>• 15 wolves/hunter/calendar year</li> <li>• 15 wolves/trapper/trapping season</li> </ul>	<ul style="list-style-type: none"> <li>• No bag limits for hunters or trappers</li> <li>• Hunters/trappers may purchase an unlimited number of tags</li> </ul>
<b>Commission authorities</b>	<ul style="list-style-type: none"> <li>• Commission has discretion under IC (36-104(b)(2) and 36-104(b)(3)) to adjust seasons and/or methods of take, or adopt emergency closures if wolf harvest is greater than expected</li> </ul>	<ul style="list-style-type: none"> <li>• Commission has discretion under IC (36-104(b)(2) and 36-104(b)(3)) to adjust seasons and/or methods of take or adopt emergency closures if wolf harvest is greater than expected.</li> </ul>
<b>Wolf Population Requirements and State Mgmt. Thresholds<sup>a</sup></b>	<ul style="list-style-type: none"> <li>• Federal Recovery Criteria for ID: <math>\geq 10</math> breeding pairs (BP) and <math>\geq 100</math> wolves</li> <li>• Post-Delisting Management: manage for <math>\geq 15</math> BPs and <math>\geq 150</math> wolves to ensure population is maintained above Federal recovery criteria. Service may review status if wolf population drops below this threshold for 3 consecutive years</li> <li>• The <i>Idaho Wolf Plan</i> states that the wolf population will be managed at levels to ensure a viable, self-sustaining wolf population until it can be established that increasing numbers of wolves will not adversely affect big game populations</li> <li>• Management (harvest and control) thresholds described in Idaho's wolf management plan <ul style="list-style-type: none"> <li>○ <math>&gt; 15</math> packs: mgmt. less restrictive</li> <li>○ <math>&lt; 15</math> packs: mgmt. more restrictive</li> </ul> </li> </ul>	<ul style="list-style-type: none"> <li>• All wolf population requirements and management thresholds remain the same as those described under the 2020/2021 season.</li> </ul>
<b>Harvest Reimbursement<sup>b</sup></b>	<ul style="list-style-type: none"> <li>• allowed</li> </ul>	<ul style="list-style-type: none"> <li>• allowed</li> </ul>
<b>Other</b>	<ul style="list-style-type: none"> <li>• Allowed to enter into agreements with state and Federal agencies to implement management actions (both nonlethal and lethal)</li> </ul>	<ul style="list-style-type: none"> <li>• Allowed to enter into agreements with private contractors, in addition to state and Federal agencies, to implement management actions (both nonlethal and lethal)</li> <li>• IDFG Fund increased funding to the ID Wolf Depredation Control Board from \$110,000 to \$300,000</li> </ul>

<sup>a</sup>IDFGs updated wolf management objective is to reduce wolf populations in the state so they fluctuate around an average of 500 wolves annually (IDFG 2023a, p. 39); therefore, the objective for the 2023/2024 season is different than described in the table above.

<sup>b</sup>Provided by outside organization (Foundation for Wildlife Management)

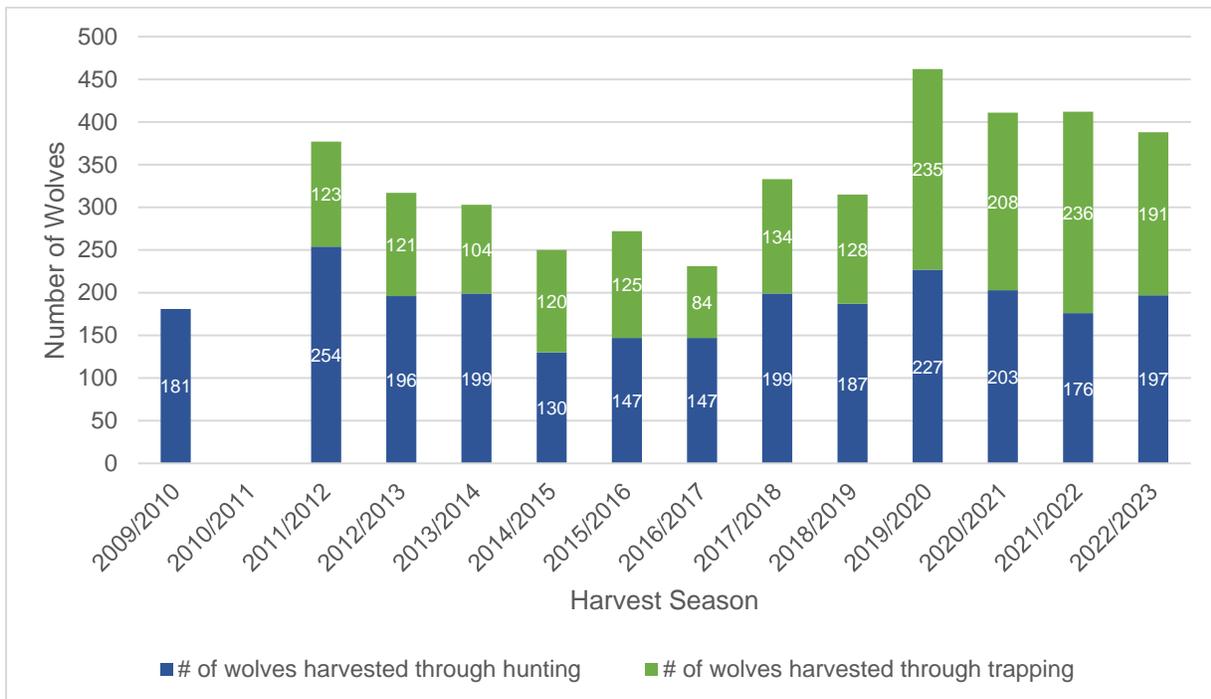


Figure 4. Number of wolves harvested through regulated public harvest in Idaho by method of take and season (for completed seasons only) from the 2009/2010 season through the 2022/2023 season. These totals do not include removals for lethal control; we discuss lethal control below and include wolves removed through lethal control in the total mortality in Table 3 below.

### Depredation Control in Idaho

Wolf-livestock depredation management in Idaho is guided by Idaho Statute (I.S.) 36-1107 and the provisions in the *2023 Idaho Plan* (IDFG 2023a, pp. 43–44). I.S. 36-1107 authorizes the IDFG Director or his designated authorities to control, trap, and/or remove animals doing damage to or destroying any property (e.g., depredating livestock). Section (c) of the statute permits owners of livestock or domestic animals, their employees, agents, or agency personnel to lethally remove wolves molesting or attacking livestock without the need for a permit from IDFG. Private individuals or their contractors must obtain a permit from IDFG to lethally remove wolves that are not attacking or molesting livestock or domestic animals or to remove wolves when not already pursuant to IDFG wolf harvest rules. In addition, along with the other revisions and amendments to SB 1211 discussed above, Idaho extended the reporting window for wolves taken for depredation control purposes from 10 days to 30 days in 2021. A primary goal of the *2023 Idaho Plan* is to reduce wolf depredation on livestock (IDFG 2023a, p. 43). Although the state will encourage the voluntary use of nonlethal and prevention methods, wolf-livestock conflict mitigation will favor the use of lethal control as well as hunter and trapper incentives to direct harvest to areas that have high levels of wolf-livestock conflicts until the wolf population reaches the goal of fluctuating around 500 individuals (IDFG 2023a, p. 43). Once the wolf population goal is achieved, the agency may consider nonlethal responses to resolve conflicts in some circumstances (IDFG 2023a, p. 43).

In most years, the total number of individual sheep killed by wolves is greater than the total number of individual cattle killed by wolves in Idaho (Service et al. 2016, see Table 7b). Although there has been annual variability among years, a general downward trend in the number of wolf-sheep conflicts has occurred since 2009, whereas cattle depredations initially declined then rose slightly during the same time period (IDFG 2016, pp. 12–16; USDA-WS 2021, entire; USDA-WS 2022, entire; USDA-WS 2022, in litt.). In calendar years 2020 and 2021, most depredations were documented on private land (USDA-WS 2021, entire; USDA-WS 2022, entire). The total number of wolves removed in lethal control actions described below includes take from agency actions to mitigate conflicts, take by private citizens under a permit, or take by private citizens when wolves were killed in the act of attacking or molesting livestock (through 2015 only). Between 2011 and 2022, on average, 60 wolves were removed annually to resolve conflicts with livestock in Idaho (Table 3). IDFG conducted minimum wolf counts through 2005, calculated minimum wolf population estimates between 2006 and 2015, and has estimated wolf abundance using a space-to-event modeling framework since 2019 (see *Methods for Counting and Estimating Annual Population Size in Each State* in Chapter 4). This allowed for the calculation of annual control rates as a percentage of the minimum known or estimated population during all years except 2016–2018. Although the total number of wolves removed to resolve livestock conflicts was higher in Idaho under state management (2009 and 2011–2015; n = 396) when compared to a similar period under Federal management (2004–2008 and 2010; n = 331), as a percentage of the minimum known or estimated wolf population, a slightly smaller percentage of wolves was removed under state authority (six percent) than under Federal management (seven percent). Although not directly comparable to above percentages due to changes in methods used to estimate wolf abundance in Idaho, between 2019 and 2022, an average of four percent of the estimated year-end wolf population in Idaho was removed annually in control actions to mitigate conflicts with livestock; however, the total number of wolves removed annually over this same time period declined from 62 wolves in 2019 to 34 wolves in 2022 (Table 3).

Under the IDFG Policy for Avian and Mammalian Predator Management (IDFG 2000, entire) where there is evidence that predation is a significant factor limiting prey populations from achieving management objectives, management actions to mitigate the effects of predators may be developed in a predation management plan. Initial management options may include habitat improvements, changes to regulations governing take of the affected species, or regulatory changes that increase hunter/trapper opportunity for predators. If these methods are implemented and do not achieve the desired management objective, predator management may be used to reduce predator populations where predator effects are most significant, but only when wolves are managed under state authority. To date, predator management plans have been developed for five elk management zones in Idaho with wolves being one of, if not the primary, targeted predators (IDFG 2011, entire; IDFG 2014a, entire; IDFG 2014b, entire; IDFG 2014c, entire). Between 2011 and May 2023, 184 wolves were removed under these predation management plans to benefit ungulate populations.

### **Wolf Population and Human-Caused Mortality in Idaho Summary**

Between 2000 through 2010 (excluding 2009), while wolves were primarily federally protected in Idaho, human-caused mortality removed, on average, approximately eight percent of the minimum known/estimated wolf population each year. This allowed the wolf population to increase on average 17 percent annually during those same years. In 2009 and between 2011 and

2015, when wolves were federally delisted and primarily under state management authority (the exception being August 2010 to May 2011), human-caused mortality increased to 27 percent annually. This increase in human-caused mortality was one of a multitude of factors that likely contributed to the relative stabilization of wolf numbers in Idaho since 2010 (despite changes in harvest regulations intended to reduce wolf abundance over this time period). Although some variation in annual wolf abundance was documented, minimum estimates of wolves in Idaho ranged from 684 to 786 wolves between 2010 and 2015 (Table 3).

Beginning in 2019, wolf abundance in Idaho has been estimated using a space-to-event modeling framework (Ausband et al. 2022, entire; Thompson et al. 2022, entire). While recent population estimates—and, thus, percent mortality calculated from these estimates—may not be directly comparable to minimum counts or estimates used through 2015, they can still provide useful information. Human-caused mortality removed approximately 32 percent of the estimated year-end wolf population in Idaho between 2019 and 2022. Similar to the years under state management authority up to 2015, regulated public harvest and lethal control of depredating wolves accounted for the majority of known human-caused and total wolf mortalities. Despite regular changes to harvest regulations that expanded opportunities for take, harvest rates have not necessarily increased commensurately, but rather have continued to fluctuate between 22 and 35 percent. Moreover, observed levels of harvest did not result in population reductions through the end of 2020; rather, this mortality stabilized population growth, based on the best available scientific information on population size and trends. During the 2021/2022 and 2022/2023 harvest seasons, the harvest rates in Idaho were 26 and 28 percent, respectively, within the range of harvest rates from seasons that predated the new law prompting less restrictive harvest regulations. Additionally, between 2016 and 2021, researchers did not detect any significant changes in wolf occupancy across Idaho (Ausband et al. 2023, p. 9). At the end of 2021 and 2022, Idaho wolf abundance estimates indicated a slight decrease relative to the previous years' estimates (a 44-wolf decrease between year-end 2020 and year-end 2021 and an 86-wolf decrease between year-end 2021 and year-end 2022), which is consistent with IDFG's stated objective to reduce the wolf population to around 500 wolves (Table 3; IDFG 2023b, entire; IDFG 2023a, p. 39).

### ***Human-Caused Mortality in Montana***

#### **Management of Wolves in Montana**

##### **State Management**

The 2001 Montana Legislature passed Senate Bill 163 (SB163), which amended several statutes in Montana Title 87 pertaining to fish and wildlife species and oversight. SB163 called for the removal of wolves from the Montana list of endangered species concurrent with Federal delisting. After removal as a state endangered species, wolves were classified as a “Species in Need of Management” under the Montana Nongame and Endangered Species Conservation Act of 1973 (Montana Code Annotated (MCA) 87-5-101 to 87-5-123). This classification created the legal mechanisms to protect wolves and regulate human-caused mortality (including regulated public harvest) beyond the allowances for immediate defense of life/property situations under Montana State law. Illegal human-caused mortality is prosecuted under state law and regulations issued by the Montana Fish and Wildlife (MFW) Commission.

Although the “Species in Need of Management” classification for wolves provides the framework necessary to regulate wolf take in Montana, it does not provide some statutory protections afforded to other species that are classified as game animals. For example, MCA 87-6-208 and 87-6-401 prohibit the take of game animals with the use of aircraft and tracking devices, respectively, but these statutes do not apply to animals classified as a species in need of management. However, Federal law continues to prohibit aerial hunting of any species without a Federal permit.

The primary goal of the *Montana Wolf Conservation and Management Plan (Montana Plan)* is to manage gray wolves as a native species in sufficient numbers to preclude Federal relisting (MFWP 2004, p. 2). The *Montana Plan* specifies a management threshold whereby wolf management will be less restrictive when 15 or more packs are documented in the state, but it will become more restrictive if the number of packs is at or below 15 (MFWP 2004, pp. 61–63). Wolves are not deliberately confined to any specific geographic areas of Montana, nor is the population size deliberately capped at a specific level. However, wolf abundance and distribution are managed adaptively based on biological and social factors (MFWP 2004, pp. 21–22). According to the *Montana Plan*, wolves will be managed in a manner that encourages connectivity among resident wolves in Montana as well as to wolf populations in Canada, Idaho, and Wyoming to maintain metapopulation structure in the NRM. Overall, wolf management in Montana includes: population monitoring, routine analysis of population health, management in concert with prey populations, law enforcement, control of domestic animal/human conflicts, implementation of a wolf-damage mitigation and reimbursement program, research, information dissemination, and public outreach.

In January 2023, the governor of Montana directed MFWP to draft a new, updated wolf management plan (Montana Governor’s Office 2023, unpaginated). In October 2023, MFWP completed a draft Montana Gray Wolf Conservation and Management Plan (*Draft 2023 Montana Plan*; MFWP 2023, entire). The *Draft 2023 Montana Plan* highlights nine gray wolf management objectives that include: “(1) maintain a viable and connected wolf population in Montana; (2) maintain authority for the State of Montana to manage wolves; (3) maintain positive and effective working relationships with all stakeholders; (4) reduce wolf impacts on livestock and big game populations; (5) maintain sustainable hunter opportunity for wolves; (6) maintain sustainable hunter opportunity for ungulates; (7) increase broad public acceptance of sustainable harvest and hunter opportunity as part of wolf conservation; (8) enhance open and effective communication to better inform decisions; and (9) learn and improve as we [MFWP] go” (MFWP 2023, pp. 41–42). The *Draft 2023 Montana Plan* uses 450 wolves as a “benchmark” to ensure the population in Montana maintains at least 15 breeding pairs (MFWP 2023, p. 43). Although there is no specific management objective, if the plan is finalized as drafted, wolves in Montana would be managed above this “benchmark” (MFWP 2023, pp. 41–46; Service 2023a, pp. 164–165). If wolf numbers in Montana approach the 450-wolf level, MFWP would increase monitoring intensity and may transition to methods that document minimum counts and the number of breeding pairs to ensure that numbers remain well above 15 breeding pairs and 150 wolves (the management buffer above the Federal recovery level) (MFWP 2023, p. 44). In addition, wolf harvest and lethal control of depredating wolves may become more restrictive if wolf numbers in Montana approach the 450-wolf level (MFWP 2023, pp. 52, 70).

### **Confederated Salish and Kootenai Tribes (Flathead Indian Reservation)**

The Confederated Salish and Kootenai Tribes (CSKT) Tribal Wildlife Management Program finalized the *Northern Gray Wolf Management Plan for the Flathead Indian Reservation (CSKT Plan)* in Western Montana in 2015 (CSKT 2015, entire). The *CSKT Plan* was updated in 2020, and it will be reviewed again after five years of implementation (CSKT 2020, entire), with any recommended changes requiring Tribal Council approval before being finalized. Wolf activity is concentrated in the Western half and around the southern boundary of the Reservation (CSKT 2020, p. 7). The management of wolves is coordinated with state and Federal agencies with the goal of long-term persistence of wolves in Montana and preventing the need for Federal relisting, while also minimizing conflicts between wolves and humans and adverse impacts to big game (CSKT 2020, p. 8).

The *CSKT Plan* does not specify maximum or minimum population sizes; instead, abundance is dictated by wolf behavior and the level of conflict. For example, low levels of conflict with a high wolf population will be tolerated without efforts to reduce the wolf population (CSKT 2020, p. 9). Lethal control may be considered for wolves that threaten human safety or kill livestock or domestic animals (CSKT 2020, p. 9). The Tribal Council can authorize hunting and trapping of wolves on the reservation (CSKT 2020, p. 9).

### **Blackfeet Nation (Blackfeet Indian Reservation)**

Wolves on the Blackfeet Indian Reservation exist on the Reservation's Western boundary, which has a high predicted probability of use (Inman et al. 2021, p. 13). The *Blackfeet Tribe Wolf Management Plan (Blackfeet Plan)* was finalized in 2008 (Blackfeet Tribal Business Council (BTBC) 2008, entire). The goal of the *Blackfeet Plan* is to manage wolves on the Blackfeet Reservation in Montana to provide for their long-term persistence. This is accomplished by minimizing wolf-human conflict while incorporating cultural values and beliefs (BTBC 2008, p. 3). For example, low levels of conflict with a high wolf population will be tolerated without resulting in efforts to reduce the wolf population (BTBC 2008, p. 4).

Wolves on the Blackfeet Reservation are classified as big game animals and they are managed by Blackfeet Fish and Wildlife Department similar to other wildlife species on the reservation (BTBC 2008, p. 4). The *Blackfeet Plan* does not specify maximum or minimum population sizes. Rather abundance will be driven by wolf behavior and the level of conflict. Lethal control may be considered for wolves that repeatedly kill livestock even if there are low numbers of wolves on the reservation (BTBC 2008, pp. 4–5).

### **Regulated Harvest in Montana**

Regulated public harvest of wolves in Montana was first endorsed by the Governor's Wolf Advisory Council in 2000 and it was recommended as a population management tool in the *Montana Plan* (MFWP 2004, pp. 27–28). Wolf harvest may only be authorized when (1) wolves are federally delisted and under state management authority and (2) when greater than 15 packs are documented in the state the previous year (MFWP 2004, p. 27). The MFWP uses an adaptive management process to develop wolf harvest recommendations to achieve management objectives (MFWP 2004, pp. 21–22; Sells et al. 2020, pp. 60–74; Parks et al. 2022, pp. 35–41; Parks et al. 2023, pp. 34–41). The Montana public has the opportunity for input regarding wolf harvest recommendation alternatives through a public season-setting process prior to adoption of season regulations by the MFW Commission. The MFW Commission maintains authority to

make emergency regulatory changes (such as changes in take methods, harvest limits, or season closures) outside of the public season setting process, if necessary.

Montana held its first-ever regulated wolf hunt in 2009 and, with the exception of the 2010/2011 season when wolves were briefly relisted in the NRM, regulated harvest has occurred every year since. The first two seasons were relatively conservative and they included a statewide harvest limit with hunting as the only legal method of take. During these first few harvest seasons, wolf numbers in Montana remained relatively stable to slightly increasing. As a result, wolf harvest regulations gradually became less restrictive over the next several years with the objective of reversing wolf population growth. For the 2012/2013 wolf season, trapping (foothold traps only) was added as a legal method of take, hunting seasons were extended, and statewide harvest limits were removed (with the exception of specific wolf management units (WMU) to the west of GNP and the north of YNP). The following season, the maximum number of wolves hunters and trappers could take or possess (i.e., bag and harvest limit) was increased. All wolf trappers were, and still are, required to attend a wolf trapping education course to become certified prior to purchasing a wolf trapping license.

Between the years of 2011 and 2015, as part of post-delisting monitoring for Montana, the Service evaluated significant regulatory changes to assess the level of impact to wolves; the Service concluded that, although harvest would likely increase over previous years, these changes did not pose a significant threat to wolves in Montana, and they would ensure wolf numbers remained well above Federal minimum recovery levels (Sartorius 2012, entire; Jimenez 2013b, entire). Very few, if any, notable changes occurred to hunting and trapping regulations between the 2014/2015 and 2020/2021 wolf harvest seasons. For further details about the regulatory history of wolf harvest in Montana through 2020, please see the 2020 delisting rule (85 FR 69778, November 3, 2020).

During the 2021 Montana Legislative session, legislators introduced two House bills (HB224 and HB225) and two Senate bills (SB267 and SB314) intended to increase individual harvest opportunities and reduce wolf abundance in the state. However, as SB314 stated, any population reduction should not result in fewer than the number of wolves necessary to support 15 breeding pairs; in other words, Montana law requires that the state's management support at least 15 breeding pairs of wolves. The bills were approved by the legislature and signed into law by the governor in April 2021. The provisions of the new statutes: (1) authorized the use of snares to take wolves by licensed trappers (MCA 87-1-901); (2) provided the MFW Commission authority to extend trapping season dates (MCA 87-1-304); (3) allowed for the reimbursement of costs incurred to harvest a wolf or wolves in Montana (MCA 87-6-214); and (4) allowed MFW Commission discretion to implement unlimited bag limits, allow unlimited take on a single hunting license, authorize the use of bait to hunt wolves, and allow hunting wolves at night on private property only (MCA 87-1-901).

MCA 87-6-214 (based on SB267) opened the door for F4WM to legally function in the state. In Montana, member dues and private donations are used to reimburse F4WM members for the cost associated with the documented legal harvest of a wolf, up to a specified amount, based on receipts submitted to F4WM. During the 2021/2022 season, reimbursements paid up to a flat rate of \$500 statewide for the cost of harvesting a wolf. For the 2022/2023 season,

reimbursement amounts of up to \$750 per wolf was paid to F4WM members that legally harvested a wolf in MFWP Regions 1 and 2 and amounts of up to \$500 per wolf were paid to members who submitted receipts for reimbursement in the remainder of the state. For the 2023/2024 wolf harvest season, reimbursement amounts increased statewide. F4WM members who legally harvest a wolf in MFWP Regions 1 and 2 may be reimbursed up to \$1,000 per wolf and amounts of up to \$750 will be paid to members who legally harvest a wolf in the remainder of the state.

The new state statutes provided the MFW Commission discretion to determine how to implement the extension of trapping seasons, the setting of bag limits, allowance of a full bag limit on a single hunting license, use of bait to hunt wolves, and night hunting, but no discretion regarding the use of snares or reimbursements to individuals who successfully harvested a wolf or wolves. MFWP did not interpret the specific statutory language in SB314 to require wolf populations be reduced to the minimum number to support 15 breeding pairs (MFWP 2021a, p. 1). MFWP used an adaptive management approach that analyzed past and present harvest data and developed models to predict different harvest scenario outcomes to prepare proposed harvest recommendations for the MFW Commission prior to the 2021/2022 season (MFWP 2021a, pp. 7–14; Messmer 2022, in litt.). These harvest recommendations, which incorporated the new state statutes, included limited, intermediate, and maximum harvest options, along with universal regulatory components that were recommended to minimize human safety concerns, minimize overharvest potential, and minimize the potential for take of federally threatened lynx and grizzly bears, regardless of the harvest option selected (MFWP 2021a, pp. 1–5). The MFW Commission accepted public comments on the recommendations and voted to approve most of the maximum harvest option recommendations, as well as all universal regulatory components, with some modifications prior to the wolf harvest season. The universal regulatory components included MFW Commission review with the potential for rapid in-season adjustments to wolf hunting and trapping regulations if: (1) a statewide harvest of 450 wolves occurs prior to the close of the season and at intervals of every 50 additional wolves harvested thereafter; (2) wolf harvest in any one region exceeds, or is likely to exceed, a specified harvest review threshold (Region 1 = 195 wolves; Region 2 = 116 wolves; Region 3 = 82 wolves; Region 4 = 39 wolves; Region 5 = 11 wolves; Region 6 = 3 wolves; Region 7 = 4 wolves); or (3) one lynx or one grizzly bear are incidentally captured in a wolf trap or snare and each time thereafter if a single lynx or grizzly bear continue to be incidentally captured. Although MCA 87-1-901 allowed the MFW Commission discretion to permit unlimited individual bag limits and the use of a single hunting license to harvest up to an unlimited number of wolves, the MFW Commission chose to require hunters to purchase separate licenses for each wolf an individual intended to harvest up to an individual limit of 10 wolves via hunting and 10 wolves via trapping (Table 2). For additional detail on how these new regulations compare to the 2020/2021 season, see Table 2. These statutes, and the associated regulatory changes for the 2021/2022 wolf harvest season, were the primary subject of the 2021 petitions to list wolves in the NRM or Western United States under the Act.

Due to regulatory similarities between wolf and furbearer harvest, MFWP combined wolf and furbearer harvest regulations for the 2022/2023 season. Wolf harvest recommendations for the 2022/2023 season were similar to regulations in the previous season except that MFWP recommended removing all WMUs statewide with the exception of combining WMU 313 and

316 north of YNP into a new WMU 313 that would have a separate harvest quota of 10 wolves. The MFW Commission voted to approve MFWP's recommendations for the 2022/2023 season with the following changes: (1) reduce the harvest quota to 6 wolves in WMU 313 and (2) change the state and regional harvest review thresholds to harvest quotas whereby the season closes when the harvest quota is reached at the statewide-level of 450 wolves or in any region (see Table 2). All other regulations are similar to the 2021/2022 season.

For the 2023/2024 wolf harvest season, the MFW Commission approved a reduction in the statewide wolf harvest quota to 313 wolves with separate quotas for Regions 1, 2, 3, and 4, a single quota for the combination of Regions 5, 6, and 7, and a single quota of 6 wolves for WMU 313. If wolf harvest in regions 1, 2, and 3 is within 25 percent of the quota being reached prior to the close of the season on March 15, 2024, or a non-target capture of a single lynx or grizzly bear occurs, the MFW Commission shall initiate a review with potential for in-season changes to hunting and trapping regulations. Dependent upon grizzly bear activity, gray wolf trapping seasons may begin anywhere between November 27 and December 31, 2023, and close when regional wolf harvest quotas are met or on March 15, 2024, whichever occurs first. However, due to a recent court order, the 2023/2024 wolf trapping season dates have been changed to January 1 through February 15, 2024 (Flathead-Lolo-Bitterroot Citizen Task Force v. State of Montana, Robinson, and Gianforte; Nov. 21, 2023, D. Mont CV 23-101-M-DWM). All other regulations are similar to the previous two wolf harvest seasons.

Between the 2012/2013 season, when trapping was added as a legal method of take, and the 2019/2020 season, hunters and trappers in Montana harvested an average of 245 wolves per season (range: 206 to 295 wolves) (Figure 5 and Table 3). Although few significant changes occurred to hunting and trapping regulations during this same time period, a general upward trend in total harvest was documented that was driven primarily by increased trapper harvest (Figure 5). Total harvest peaked at 327 wolves during the 2020/2021 season with hunters taking 169 wolves and trappers taking an additional 158 wolves. This was the first-time total harvest in Montana topped 300 wolves and this increase occurred with no significant regulatory changes prior to the season. Estimated wolf numbers in Montana remained relatively stable over this same time period, fluctuating from a high of 1,210 wolves in 2013 to a low of 1,117 wolves in 2017 (Table 3). To date, no wolves have been harvested in Montana with the use of tracking devices or aircraft. Table 3 details the amount of harvest that has occurred in Montana since 2009, by harvest season.

A total of 273 wolves were harvested in Montana during the 2021/2022 season (the first season the new legislation was incorporated into harvest regulations that we discussed above). Hunters took 148 wolves (which included three wolves taken at night; no wolves were harvested over bait) and trappers harvested 125 (which included 20 wolves taken with snares; Figure 5). Only MFWP Region 3 approached the wolf harvest thresholds that prompted a review by the MFW Commission. As a result of this review, six WMUs that comprise MFWP Region 3, which included WMUs north of YNP, were closed on February 18, 2022, after 85 wolves were harvested. This closure of one-third of the WMUs in Montana a month early likely contributed to the reduced harvest totals observed during the 2021/2022 season.

At the close of the 2022/2023 wolf harvest season in Montana, a total of 258 wolves were harvested. Hunters harvested 121 wolves (which included a single wolf harvested at night; no wolves were harvested over bait) and trappers harvested 137 wolves (which included 12 wolves taken with snares). A reduction in hunter harvest compared to the 10-year average across MFWP Regions 1, 3, and 4 likely contributed to overall lower hunter and total harvest across the state for the season (Parks et al. 2023, p. 15). WMU 313 north of YNP closed to hunting on February 7, 2023, after the harvest quota of six wolves was met. No other harvest quotas were reached, and all other areas closed at the end of the wolf harvest season on March 15, 2023.

During the 2021/2022 season, a total of 21 wolves were harvested in WMUs 313 and 316, which are north of YNP and which lacked harvest limits. Nineteen of the 21 wolves that were legally harvested in these WMUs were members of known packs that resided primarily in YNP (YNP 2022, in litt.). This was the highest total number of wolves whose territories were primarily in YNP that were harvested in Montana since wolf harvest began in 2009 (excluding the 2021/2022 season, an average of 3.5 wolves (range: zero to seven wolves) that reside mostly in YNP were harvested in Montana per harvest season since 2009). During the 2022/2023 season, four wolves that lived mostly in YNP were legally harvested in WMU 313 in Montana (WGFD et al. 2023, p. 15; YNP 2023, in litt.). Given that most of YNP is in Wyoming, the wolves that reside primarily in YNP count towards Wyoming's end-of-year minimum counts; thus, wolves that live primarily in YNP that are legally harvested in Montana (or Idaho) reduce the total number of wolves documented in Wyoming at the end of that year. Although MFWP combined WMUs 313 and 316 into a single WMU 313 and implemented a harvest quota of six wolves for the WMU, it remains unclear how continued legal harvest of wolves that live primarily in YNP might affect long-term abundance, pack social structure, reproduction, pack interactions, and interactions with prey within YNP (see *Regulated Harvest of Wolves that Live Primarily in YNP* below for additional discussion) (YNP 2022, in litt.); we model potential future effects of harvest of wolves that live primarily in YNP in Chapter 6.

Although trapper harvest has increased in recent years, the number of wolves taken by hunters exceeded the number of wolves taken by trappers every season until the 2022/2023 season (Figure 5). The number of hunting licenses issued and the estimated number of active hunters peaked in 2013 and 2014, respectively, and were followed by a period of decline (Parks et al. 2023, pp. 43–44). An increase in the number of wolf hunting licenses issued occurred in 2021 following the new legislation and MFW Commission regulations to increase wolf harvest opportunities in Montana; however, the estimated number of active hunters continued to decline (Parks et al. 2023, pp. 43–44). Similarly, the number of wolf trapping licenses and the estimated number of active wolf trappers peaked in 2013, a year after wolf trapping was first authorized in Montana, then declined slightly and remained relatively stable through 2020 (Parks et al. 2023, pp. 45–47). Since 2020, the number of trapping licenses issued has declined by approximately 500 licenses each year (from 2,851 issued in 2020 to 1,846 issued in 2022) while the estimated number of active trappers has also slightly decreased over the same time period (Parks et al. 2023, pp. 45–47).

While most hunters and trappers harvest a single animal, trappers are more likely than hunters to harvest multiple animals, indicating that hunter harvest is more opportunistic while

trapping is more targeted. A slightly greater percentage of wolves are harvested on public lands (state and Federal) than on private lands in Montana (MFWP 2022, entire).

The CSKT of the Flathead Reservation provide hunting and trapping opportunities in three wolf hunting and trapping zones on the Flathead Reservation (CSKT 2021, entire). Harvest has occurred almost annually on the reservation since 2013. The Blackfeet Nation also provides gray wolf hunting opportunities for its tribal members and descendants as well as to non-members at the discretion of the Blackfeet Nation Fish and Wildlife Department (BTBC 2021, entire). The Blackfeet Nation is divided into five hunting zones. Hunting is only allowed in two of five hunting zones on the Blackfeet Reservation. Although it is unknown if any wolves have been harvested from either Reservation, given the relatively small proportion of wolf habitat that exists on these Tribal lands, harvest levels are presumed to be low and would add little to total harvest in Montana.

The Integrated Patch Occupancy Model (iPOM) (see *Methods for Counting and Estimating Annual Population Size in Each State* in Chapter 4 for additional detail about population estimation techniques used in Montana) estimate of wolf population size in 2021 was 1,143 wolves in 191 packs (Parks et al. 2023, p. 10) and was 1,087 wolves in 181 packs at the end of 2022 (Parks et al. 2023, p. 10). Based on these estimates, approximately 20 percent and 18 percent of Montana's estimated wolf population was harvested in 2021 and 2022, respectively, which is within the range of annual harvest rates that occurred in Montana between prior to the 2021 legislation that was incorporated into regulation to increase wolf harvest opportunities (i.e., between 2011 and 2020, annual harvest rates ranged from 8 percent to 20 percent). Even though annual harvest rates have fluctuated in Montana, there was a general overall upward trend in harvest rates between 2011 and 2021 followed by a slight decline in 2022. Despite some changes to harvest regulations that expanded opportunities for take, estimated wolf abundance in Montana remained relatively stable through 2020, with a slight decrease of 41 wolves between year-end 2020 and year-end 2021 and a slight decrease of 56 wolves between year-end 2021 and year-end 2022 (Table 3). However, the confidence intervals around these year-end estimates for 2021 and 2022 encompass the previous years' estimates, suggesting that uncertainty remains in the exact trajectory of the population between year-end 2020 and year-end 2022 (see Appendix 3 for citations).

Table 2. Comparison of Montana’s wolf harvest regulations between the 2020/2021 and 2021/2022 seasons. We discuss the regulatory changes between the 2021/2022 and 2022/2023 season in the text above, which primarily included instituting harvest limits in WMU 313. We discuss regulatory changes for the 2023/2024 wolf harvest season in the text above; they primarily included a reduction in statewide and regional harvest quotas.

	2020/2021 Season	2021/2022 Season
<b>Season dates</b>	<ul style="list-style-type: none"> <li>• <u>Archery</u>: Sept. 5–14</li> <li>• <u>General</u>: Sept. 15–March 15</li> <li>• <u>Trapping</u>: Dec. 15–Feb. 28</li> </ul>	<ul style="list-style-type: none"> <li>• <u>Archery</u>: Sept. 4–14</li> <li>• <u>General</u>: Sept. 15–March 15</li> <li>• <u>Trapping</u>: Dec. 15–March 15 (1 WMU); Dec. 21–March 15 (nine WMUs); Dec. 27–March 15 (remaining eight WMUs)</li> <li>• In future years, trapping start dates may begin as early as Nov. 29 or as late as Dec. 31, dependent on known grizzly bear activity in specific WMUs</li> </ul>
<b>Key Hunting Regulations</b>	<ul style="list-style-type: none"> <li>• May harvest up to five wolves; separate license required for each wolf harvested</li> <li>• Use of bait not permitted</li> <li>• Hunting outside of daylight hours not permitted</li> </ul>	<ul style="list-style-type: none"> <li>• May harvest up to 10 wolves; separate license required for each wolf harvested</li> <li>• Use of bait permitted to hunt wolves statewide with some restrictions in lynx protection zones</li> <li>• Hunting outside of daylight hours permitted on private property only</li> </ul>
<b>Key Trapping Regulations</b>	<ul style="list-style-type: none"> <li>• Completion of mandatory wolf trapper certification required</li> <li>• May harvest up to five wolves with single trapping license</li> <li>• Foothold traps only</li> <li>• Snares not authorized</li> </ul>	<ul style="list-style-type: none"> <li>• Completion of mandatory wolf trapper certification required</li> <li>• May harvest up to 10 wolves with single trapping license</li> <li>• Foothold traps allowed</li> <li>• Snares permitted on public and private lands statewide, EXCEPT on public lands within lynx protection zones</li> </ul>
<b>Harvest limits</b>	<ul style="list-style-type: none"> <li>• WMU 110 = two wolves (west of GNP)</li> <li>• WMU 313 = one wolf (north of YNP)</li> <li>• WMU 316 = one wolf (north of YNP)</li> <li>• No harvest limits in remaining 15 WMUs</li> </ul>	<ul style="list-style-type: none"> <li>• No harvest limits in any WMU</li> </ul>
<b>Bag limits</b>	<ul style="list-style-type: none"> <li>• Five wolves/person in any combination of hunting/trapping</li> <li>• One wolf/person in WMUs with harvest limits</li> </ul>	<ul style="list-style-type: none"> <li>• 20 wolves/person with no more than 10 via hunting and 10 via trapping</li> <li>• NOTE: MT SB314 provided MFW Commission discretion to authorize unlimited bag limits; the Commission did not choose to authorize unlimited bag limits for the 2021/2022 season</li> </ul>
<b>Commission authorities</b>	<ul style="list-style-type: none"> <li>• MFW Commission reserves authority to amend seasons, limits, and regulations, if deemed necessary for wildlife management purposes</li> </ul>	<ul style="list-style-type: none"> <li>• MFW Commission reserves authority to amend seasons, limits, and regulations, if deemed necessary for wildlife management purposes</li> </ul>

	2020/2021 Season	2021/2022 Season
	<ul style="list-style-type: none"> <li>• MFW Commission authorizes MFWP to initiate emergency closure of any WMU at any time</li> </ul>	<ul style="list-style-type: none"> <li>• MFW Commission authorizes MFWP to initiate emergency closure of any WMU at any time</li> <li>• MFW Commission will conduct review with potential for rapid in-season adjustments to hunting and trapping regulations: <ul style="list-style-type: none"> <li>○ If a statewide harvest of 450 wolves occurs prior to the close of the season; the commission will review again if additional 50 wolves are harvested</li> <li>○ If wolf harvest in any one region exceeds: Region 1 = 195 wolves; Region 2 = 116 wolves; Region 3 = 82 wolves; Region 4 = 39 wolves; Region 5 = 11 wolves; Region 6 = three wolves; Region 7 = four wolves</li> <li>○ If one lynx or one grizzly bear is incidentally captured, and with any additional lynx or grizzly capture</li> </ul> </li> </ul>
<b>Wolf Population Requirements and State Management Thresholds</b>	<ul style="list-style-type: none"> <li>• Federal Recovery Criteria for MT: <math>\geq 10</math> breeding pairs and <math>\geq 100</math> wolves</li> <li>• Post-Delisting Management: manage for <math>\geq 15</math> breeding pairs and <math>\geq 150</math> wolves to ensure population is maintained above Federal recovery criteria. Service may review status if wolf population drops below this threshold for 3 consecutive years</li> <li>• <i>Montana Plan</i>: 15 breeding pairs and 150 wolves is the management threshold, not a minimum or maximum number of wolves allowed in the state <ul style="list-style-type: none"> <li>○ <math>&gt; 15</math> breeding pairs/150 wolves: management less restrictive</li> <li>○ 10 to 15 breeding pairs/100 to 150 wolves: management more restrictive</li> </ul> </li> </ul>	<ul style="list-style-type: none"> <li>• MFWP did not interpret the statutory language in the various 2021 statutes as requiring wolf population reduction to the minimum number of wolves necessary to support only 15 breeding pairs</li> <li>• All wolf population requirements and management thresholds remain the same as those described under the 2020/2021 season.</li> </ul>
<b>Harvest Reimbursements<sup>a</sup></b>	<ul style="list-style-type: none"> <li>• Not allowed</li> </ul>	<ul style="list-style-type: none"> <li>• State statute allows individual hunters/trappers to be reimbursed for costs associated with legal wolf harvest</li> </ul>

<sup>a</sup>Provided by outside organization (Foundation for Wildlife Management)

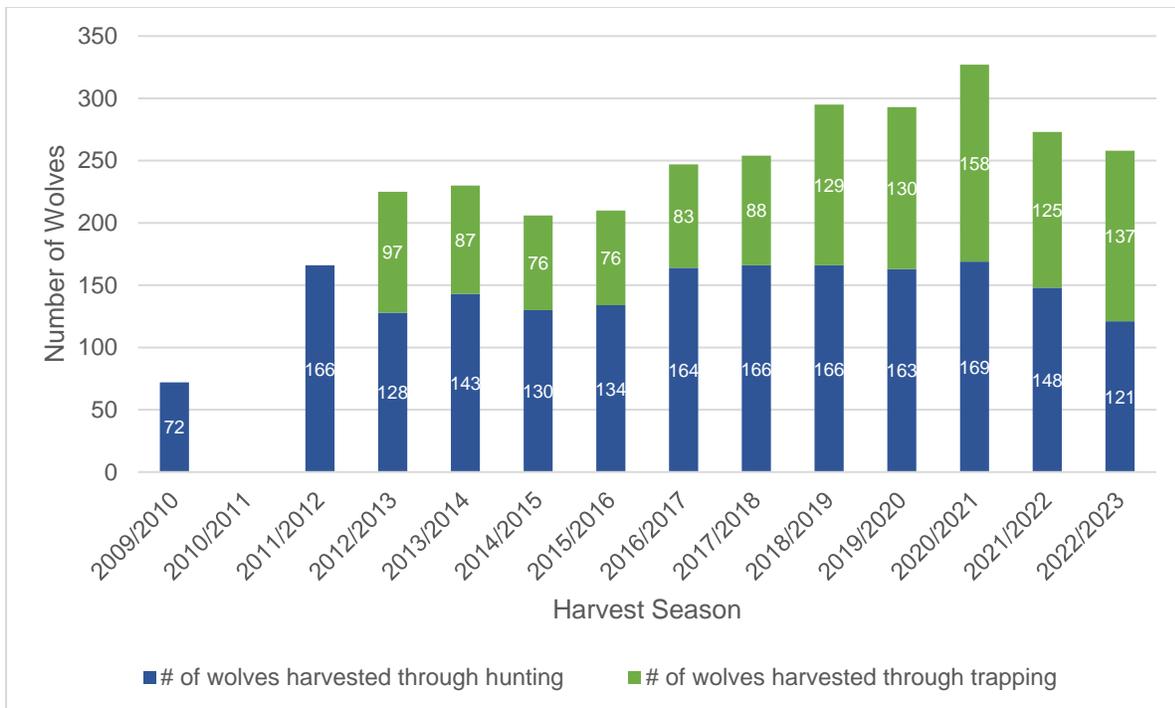


Figure 5. Number of wolves harvested through regulated public harvest in Montana by method of take and season (for completed seasons only) from the 2009/2010 season through the 2022/2023 season. These totals do not include removals for lethal control; we discuss lethal control below and include wolves removed through lethal control in the total mortality in Table 3 below.

### Regulated Harvest of Wolves that Live Primarily in YNP

While wolf harvest is not authorized within YNP, wolves that have territories primarily within YNP may be harvested in surrounding states if they leave YNP, consistent with rules and regulations that guide wolf management in each surrounding state. If a wolf originating from YNP is harvested in a surrounding state, the wolf is included in the total number of wolves harvested in the state the mortality occurred (Table 3). Prior to the winter of 2021/2022, the number of wolves that lived primarily in YNP, left the park, and were harvested in surrounding states ranged from 0 to 12 wolves annually (YNP 2022a, in litt.). However, during the winter of 2021/2022, 24 wolves that lived primarily in YNP and left the park were legally harvested outside of YNP boundaries: two in Idaho, 19 in Montana, and three in Wyoming (YNP 2022a, in litt.). The increased number of wolves harvested in Montana was a direct result of the removal of harvest limits in WMUs 313 and 316 for the 2021/2022 harvest season, units that border YNP’s northern boundary, as all 19 wolves harvested in Montana that lived primarily in YNP were harvested in these two WMUs. As a result, the MFW Commission combined WMU 313 and 316 into a single WMU 313 and implemented a harvest limit of six wolves for the 2022/2023 wolf harvest season. Although it is possible that a high number of wolves could still be harvested in other areas of Montana outside of WMU 313 or in surrounding states when they leave YNP, based on past harvest totals and locations of wolves originating from YNP that were harvested in surrounding states, it is unlikely the level of harvest observed in the 2021/2022 season will be repeated, especially if harvest limits in WMU 313 in Montana are retained. We analyze potential future harvest scenarios for wolves that live primarily in YNP, including a

scenario in which harvest levels similar to those in the 2021/2022 season continue in the future, in Chapters 5 and 6.

Some hypothesized that the increased harvest in Montana may affect population dynamics of wolves that live primarily in YNP through disruptions to the social dynamics of some packs, causing more instances of packs producing multiple litters in spring 2022 (Koshmrl 2022, entire), while others disagreed with this hypothesis (Urbigkit 2022, entire) because there is already a relatively high incidence of packs producing multiple litters in YNP (Stahler et al. 2020, p. 52). The 2022 end-of-year data for YNP do include instances of multiple litters per pack in YNP; however, the best available information does not indicate if this is in response to increased harvest (WGFD et al. 2023, pp. 14–15). In 2022, YNP observed an increase in the dissolution and creation of packs (two packs dissolved and four new packs were formed) compared to average rates of one pack dissolving and one new pack forming (WGFD et al. 2023, p. 14). Although increased harvest of wolves residing primarily in YNP during the 2021/2022 season may partially explain the changing pack dynamics in YNP, other possible reasons include several years of successful reproduction, large numbers of offspring from 2019 and 2020 dispersing, shifting prey dynamics, and other factors (WGFD et al. 2023, p. 14).

Data on the resulting population size in the winter of 2022/2023 indicates the population in YNP remained stable after the higher level of harvest of wolves residing primarily in YNP that occurred during the 2021/2022 harvest season; there were at least 108 wolves in YNP by the end of calendar year 2022, a population size comparable to previous years. Thus, while there is some evidence that less restrictive harvest regulations result in decreased *individual* wolf survival in YNP (Cassidy et al. 2022a, p. 5), the population size in YNP for the winter of 2022/2023 indicates that this increased individual mortality may not result in overall *population* declines, and that other processes (e.g., increased immigration or recruitment) can partially compensate for this mortality, which may account for the lack of observed population change after the 2021/2022 harvest season (Brainerd et al. 2008, entire; Borg et al. 2015, entire).

### **Depredation Control in Montana**

MFWP encourages the use of preventative and nonlethal methods to address conflicts. It also actively participates and cooperates in many preventive conflict reduction programs (Wilson et al. 2017, p. 247; Inman et al. 2019, p. 14; Parks et al. 2023, pp. 20–21). Current rules and regulations to address wolf-livestock conflicts provide opportunity for livestock producers and/or private landowners to address wolf-related conflicts. These methods become more restrictive when there are fewer than 15 packs in the state, but they will be more liberal when 15 packs or more are documented (MFWP 2004, pp. 26, 55–57). Nonlethal harassment is allowed at all times; however, if nonlethal methods do not discourage wolves from harassing livestock, landowners may request a special kill permit from MFWP that is valid on lawfully occupied public and private lands. Montana Code Annotated 87-6-106 provides authorization for individuals to kill a wolf without a permit if it is threatening, attacking, or killing a person, livestock, or a domestic dog on either public or private lands. The MFW Commission may adopt rules that allow a landowner or the landowner's agent to take a wolf on the landowner's property at any time without the purchase of a wolf license when the wolf is a potential threat to human safety, livestock, or dogs (MCA 87-1-901). Agency-directed lethal control of depredating wolves may be considered to resolve repeated conflict situations, but it will only be used in

extreme circumstances if 15 or fewer packs are documented in Montana. In Montana, conflict resolution using nonlethal and/or lethal means is a cooperative effort between MFWP and USDA-WS.

The *CSKT Plan* and *Blackfeet Plan* each provide similar management responses based on potential wolf conflict scenarios that may occur on their respective reservations (see Table 1 in BTBC 2008, p. 7; see Table 1 in CSKT 2020, p. 11). In most instances, initial management responses emphasize preventative and nonlethal methods to resolve conflicts (BTBC 2008, pp. 6–7; CSKT 2020, pp. 10–11). If these methods are unsuccessful at resolving the conflict, more aggressive techniques, including agency-directed lethal control, may be implemented until the conflict is resolved.

Lethal removal of wolves in response to livestock depredations has declined under state management authority in Montana. Between 2005 and 2015, 83 percent of confirmed livestock depredations occurred on private lands, 14 percent occurred on public lands, and three percent occurred on Tribal lands (DeCesare et al. 2018, p. 5), a trend that continues to the present (Inman et al. 2021, p. 16; Parks et al. 2023, p. 17). Although fluctuations have occurred, a general overall downward trend in the number of wolf complaints has been documented since 2009, while the number of confirmed depredations of both cattle and sheep declined between 2009 and 2015; while the number of confirmed depredations has increased slightly between 2015 and 2022, they still remain well below 2009 levels (Inman et al. 2021, pp. 16–18; Parks et al. 2023, p. 18). This general downward trend in the number of complaints and depredations has tracked closely with the time period wolves have been under state management authority in Montana (Parks et al. 2023, p. 18) and may be a result of more aggressive management of depredating wolves (DeCesare et al. 2018, pp. 8, 10–11; Parks et al. 2023, p. 19). Even though management may have become more aggressive, the average annual percentage of Montana wolves lethally removed in depredation control actions (including agency control and removal by private individuals) has also declined in Montana under state management (Inman et al. 2021, pp. 16–18; Parks et al. 2023, pp. 18–19). Between 2002 and 2010 (excluding 2009), corresponding to the years wolves were primarily under Federal authority, 511 wolves were removed to address conflicts with livestock, which equated to an average of 15 percent of Montana’s minimum wolf count annually). In 2009 and between 2011 and 2017, when wolves were primarily under state management authority, a total of 618 wolves were removed to resolve conflicts with livestock, which equated to an average of 9 percent of the minimum wolf count annually.

More recently, Montana developed a patch occupancy model (POM; Rich et al. 2013, entire) and used this model as the primary method to estimate year-end wolf abundance and distribution in 2018 and 2019; they then refined this technique and began using an Integrated Patch Occupancy Model (iPOM) to estimate year-end wolf abundance and distribution in the state beginning in 2020 (Sells et al. 2020, entire; Sells et al. 2021, entire; Sells et al. 2022a, entire; Sells et al. 2022b, entire; Sells et al. 2022c, entire). Wolf abundance estimates based on iPOM are back-estimated through 2007 and are higher than minimum counts of known individuals or estimates obtained by POM. As a result, estimated mortality rates are lower for the iPOM estimated wolf population in Montana (Table 3) (see *Methods for Counting and Estimating Annual Population Size in Each State* in Chapter 4 for additional detail about population estimation techniques used in Montana). Based on iPOM wolf population estimates,

the rate of wolves lethally removed to mitigate conflicts with livestock in Montana has declined under state management (when compared to Federal management) and has been less than seven percent of the estimated population since 2013 (Sells et al. 2022c, p. 12).

### **Wolf Population and Human-Caused Mortality in Montana Summary**

Based on minimum counts, wolf numbers in Montana continued to annually increase two percent on average (range: -12 percent to 33 percent), between 2011 (when consistent state management began) and 2017 (the final year MFWP conducted minimum counts of wolves in the state). Also, between 2011 and 2017, the rate of human-caused mortality in Montana averaged 33 percent of the minimum known population (range: 23 percent to 41 percent). Based on iPOM estimates rather than minimum counts, the rate of human-caused mortality ranged between 14 and 25 percent, and it averaged 21 percent, between 2011 and 2022. Also based on iPOM population estimates, from 2011 to 2022, the population averaged zero percent growth (range: negative six percent to positive 10 percent) in Montana; thus, the best available science indicates that current levels of human-caused mortality through 2022 have resulted in a general stabilization of the Montana wolf population rather than a substantial population reduction, despite gradually less restrictive wolf harvest regulations. However, consistent with recent Montana statutes and state objectives, year-end population estimates in Montana have decreased slightly since the end of 2020 (after which, Montana changed their harvest regulations in accordance with new state laws), with a 41-wolf decrease between year-end 2020 and year-end 2021 and a 56-wolf decrease between year-end 2021 and year-end 2022.

Note that, in a recent research paper, Sells et al. (2022c, pp. 11–12) used a different method to calculate the rate of human-caused mortality in Montana, which produced slightly higher human-caused mortality rates in Montana relative to our calculations. The difference in the human-caused mortality rate of 30.4 percent between 2016 and 2020 reported in Sells et al. (2022c, pp. 11–12) and the mortality rates reported in this SSA do not affect the conclusions of our analysis; Sells et al. (2022c, pp. 10–11) still reports relative stability in the Montana wolf population and only minor population reductions since harvest began, and the harvest rates we evaluate in our future condition analysis (see Chapters 5 and 6) conservatively examine large increases in harvest above past observed rates (well above the higher mortality rates Sells et al. (2022c) reports). Throughout this SSA, when we refer to “observed” mortality rates in Montana, we are referring to the rates calculated according to the equation in the footnote below.<sup>12</sup>

### ***Human-Caused Mortality in Wyoming***

#### **Management of Wolves in Wyoming**

##### **State Management**

The WGFD and Wyoming Game and Fish Commission (WGFC) manage wolves under the 2011 *Wyoming Gray Wolf Management Plan (Wyoming Plan)* (WGFC 2011, entire), as amended in 2012 (WGFC 2012, entire). Per WGFC Chapter 21 regulations, the regulations that govern the management of wolves in Wyoming outside of national parks and the Wind River Reservation (WRR), wolves are classified as trophy game animals and are actively managed by

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<sup>12</sup> Total Human-Caused Mortality Rate = [Total # of Wolves Died From Human Causes in 20XX]/[Population Count/Estimate for the State for 20XX + Total # of Wolves Died From Human Causes in 20XX]

WGFD in the WTGMA in the northwest part of the state where most wolves reside. Wolves outside of the WTGMA, national parks, and the WRR, except for non-Indian owned fee title lands, are classified as predatory animals and are managed by the Wyoming Department of Agriculture under title 11, chapter 6 of the Wyoming Statutes. We provide a map of these various management areas in the 2012 final rule delisting wolves in Wyoming (77 FR 55530, September 10, 2012, p. 55534). As we have previously concluded (73 FR 10514, February 27, 2008; 74 FR 15123, April 2, 2009; 77 FR 55530, September 10, 2012), wolf packs are unlikely to persist long-term in portions of Wyoming where they are designated as predatory animals. However, the WTGMA is large enough to support Wyoming's management goals (77 FR 55530, September 10, 2012; WGFD et al. 2022, entire).

Wolves within Grand Teton National Park and YNP are managed under the National Park Service (NPS) authority and, for the most part, are allowed to naturally fluctuate within National Park borders. When wolves leave National Park boundaries, they are managed under the rules and regulations of the jurisdiction they entered (see *Conservation Efforts on Federal Lands in the Western United States* below for additional detail on Federal management).

As wolf management in northwest Wyoming falls under different Federal, state, and tribal jurisdictions, the Service agreed to allow WGFD to maintain a minimum of at least 10 breeding pairs and 100 wolves within the WTGMA. Furthermore, WGFC Chapter 21 regulations, state statute, and the *Wyoming Plan* (WGFC 2011, p. 1; WGFC 2012, p. 4) all codify WGFD's commitment to manage for these levels. In addition, YNP and the WRR combined would maintain at least five breeding pairs and 50 wolves, so that the totality of Wyoming's wolf population is managed at or above 15 breeding pairs and 150 wolves (which provides the buffer above the 10-breeding pair and 100-wolf Federal recovery level). The WGFD manages wolf abundance in the WTGMA above the 10-breeding pair and 100-wolf level to ensure (1) the number of wolves in Wyoming stays above Federal recovery criteria, (2) regulated public harvest and agency control to resolve conflicts is not limited, and (3) genetic connectivity is maintained (WGFC 2011, p. 23; WGFC 2012, pp. 3–5). Furthermore, Wyoming wolf management regulations commit to the management of wolves so that genetic diversity and connectivity issues do not negatively influence the population. To accomplish this, WGFC Chapter 21 regulations provide for a seasonal expansion of the WTGMA from October 15 through the end of February to facilitate natural dispersal of wolves between Wyoming and Idaho (WGFC 2011, Figure 1, pp. 2, 8, 52).

#### **Wind River Reservation**

The WRR typically contains a small number of wolves relative to the remainder of Wyoming (approximately 10 to 20 wolves annually for the past 10 years). The WRR adopted a *Wolf Management Plan (WRR Plan)* in 2007 (Eastern Shoshone and Northern Arapaho Tribes, 2007, entire) and updated the *WRR Plan* in 2008 (Eastern Shoshone and Northern Arapaho Tribes, 2008, entire). Wolves are managed as game animals on the WRR (Eastern Shoshone and Northern Arapaho Tribes 2008, pp. 3, 9). The Eastern Shoshone and Northern Arapaho Tribes govern this area and the Shoshone and Arapaho Tribal Fish and Game Department manages wildlife on the WRR, with assistance from the Service's Fish and Wildlife Conservation Office in Lander, Wyoming.

Wyoming claims management authority of non-Indian fee title lands and on Bureau of Reclamation lands within the external boundaries of the WRR. Thus, wolves are classified as game animals within about 80 percent of the reservation and as predators on the remaining 20 percent of the reservation (Hnilicka 2020, in litt.). To date, predator status has had minimal impact on wolf management and abundance on the WRR because these inholdings tend to be concentrated on the eastern side of the reservation in habitats that are less suitable for wolves (Eastern Shoshone and Northern Arapaho Tribes 2008, p. 5, Figure 1).

### **Regulated Harvest in Wyoming**

Wyoming Statute (W.S.) 23-1-304 provides authority for the WGFC to promulgate rules and regulations related to the management of wolves in Wyoming where they are classified as trophy game animals, as described in W.S. 23-1-101. Wolf harvest regulations within the WTGMA are annually evaluated and revised based on current population objectives and past demographic and mortality information. An internal review and an extensive public input process occur prior to WGFC approval and implementation of Chapter 47 wolf harvest regulations in Wyoming.

WGFD manages significantly fewer wolves than Idaho and Montana, so the state has less margin for error to ensure wolf numbers remain above Federal wolf recovery criteria (i.e., 100 wolves and 10 breeding pairs). As a result, regulated take is managed more conservatively than other states that allow wolf harvest and it is used to adaptively manage wolves at or near a population objective of 160 wolves within the WTGMA. Each year, a WTGMA harvest limit is calculated by using abundance and mortality data from wolves in the WTGMA to predict the percentage of the population that can be harvested each season to maintain wolf numbers at or near the objective of 160 wolves (WGFD et al. 2022, p. 17; WGFD et al. 2023, p. 18). Once calculated, this harvest limit is distributed across all hunt areas within the WTGMA so each hunt area, or groups of hunt areas, have a specific harvest limit. Hunting is the only legal method of take allowed for harvesting a wolf within the WTGMA; trapping is not permitted to harvest a wolf within the WTGMA. Wolf hunting seasons close on the season closing date or once the harvest limit is reached, whichever occurs first. We describe past harvest regulations within the WTGMA (e.g., hunt areas, season lengths, tag limits) in further detail in the 2020 delisting rule (85 FR 69778, November 3, 2020).

Between the 2017/2018 and 2021/2022 harvest seasons, an annual average of 34 wolves (range = 25 to 43 wolves) were legally harvested in the WTGMA each year. During the 2022/2023 wolf hunting season, a total of 29 wolves were harvested in the WTGMA in Wyoming.

On the WRR, wolves are classified as a trophy game animal. Regulated take was not permitted on the WRR until 2019 when the Eastern Shoshone and Northern Arapaho Joint Business Council approved the first regulated wolf hunting season. A total harvest limit of six wolves was distributed evenly across two hunt areas. No wolves were harvested on the WRR until the 2022/2023 season when a single wolf was legally harvested.

Wolves outside of the WTGMA, national parks, and the WRR, except for non-Indian owned fee title lands, are classified as predatory animals as defined in W.S. 23-1-101(a)(viii)(B). W.S. 23-2-303(d), 23-3-103(a), 23-3-112, 23-3-304(b), 23-3-305, and 23-3-307 govern

management of wolves where they are designated as predatory animals; these wolves may be taken by any legal means year-round and without limit. Any person who harvests a wolf in the predatory animal area is required to report the kill to WGFD within 10 days. Between 2017 and 2022, an annual average of 28 wolves (range = 21 to 42 wolves) have been legally harvested where they are designated as predators in Wyoming. Wolves harvested in the predatory animal area are included in the harvest totals and estimations of harvest rates for Wyoming (Table 3).

Overall, during all or portions of those years when wolves were under state management authority (i.e., 2008, 2012 through 2014, and 2017 to the present; this includes 2008 and 2014 when wolves were legally harvested only where they were designated as predatory animals, but no regulated hunting occurred in the WTGMA due to litigation), an average of 12 percent of Wyoming's wolf population was annually removed through harvest. If 2008 and 2014 are removed (the years that harvest was limited to the predatory animal area) and we evaluate only the eight years that included regulated harvest, an average of 14 percent of the wolf population in Wyoming was annually removed through harvest. As a result of WGFD's adaptive management approach to managing wolves and wolf harvest, the best available scientific information indicates that wolf populations in Wyoming have remained well above minimum recovery levels (i.e., 100 wolves and 10 breeding pairs) under state management authority, despite public harvest. Between 2017 and 2020, as part of post-delisting monitoring for Wyoming, the Service evaluated the status of the wolf population in Wyoming and any significant regulatory changes that may affect population status. The Service concluded that the wolf population in Wyoming remained secure above Federal minimum recovery levels during the post-delisting monitoring period and that regulatory changes made prior to the 2018/2019 season (the last time a regulatory change was sufficiently significant to prompt a review) did not pose a significant threat to wolves in Wyoming (Becker 2018a, entire; Becker 2018b, entire; Becker 2019, entire).

### **Depredation Control in Wyoming**

Within the WTGMA, WGFD places emphasis on conflict prevention and minimization of livestock depredation risk through education and outreach (WGFC 2011, p. 30). However, when depredations do occur, agency response is evaluated on a case-by-case basis and it may include: no action, nonlethal control (if it is deemed appropriate or the landowner requests it), capture and radio-collaring a wolf or wolves, issuance of a lethal take permit to the property owner, or agency-directed lethal control. The use of lethal control to resolve wolf-livestock conflicts by WGFD and their designated agents or private citizens is authorized under W.S. 23-1-304, W.S.23-3-115, and WGFC Chapter 21 regulations. However, agency-directed lethal control will not be used, and any take permits issued may be revoked, if wolf removal would result in wolf abundance falling below the 10-breeding pair and 100-wolf threshold within the WTGMA in the state (WGFC 2012, p. 7).

In Wyoming, lethal control of depredating wolves generally increased concurrent with increases in wolf numbers and distribution for about the first decade of wolf recovery (i.e., 1995–2005). Under Service direction, management of depredating wolves became more aggressive towards packs that repeatedly depredated livestock in the mid- to late-2000s, which moderated the number of depredations and subsequent wolf removals so that the number of depredations no longer tracked with wolf population growth. Between 1995 and 2008, as a percentage of the total wolf population, five percent of the Wyoming minimum wolf count was annually removed through agency-directed control actions. Between 2009 and 2022, the percentage of Wyoming's

known wolf population lethally removed to resolve conflicts with livestock has averaged 10 percent. However, the percentage of the minimum known number of wolves removed since 2009 was greater under Service direction than under state management. Since 2009, during those years when wolves were federally listed (including years when harvest occurred under predator status only), approximately 12 percent of Wyoming's minimum known wolf population was removed annually to resolve conflicts with livestock (range: 9 to 22 percent). The annual average percentage of wolves removed to resolve conflicts with livestock during years wolves were managed under state authority was nine percent of the minimum known number of wolves in Wyoming (range: 5 to 14 percent).

Since 2017, when Federal protections were most recently removed for wolves in Wyoming, and as wolf abundance within the WTGMA has approached and been managed at the objective of 160 wolves, the total number of wolves and the percentage of the population lethally removed to resolve livestock conflicts has trended downward. In 2022, 21 wolves were removed to mitigate livestock conflicts in Wyoming (WTGMA = 15 wolves and predatory animal area = 6 wolves; WGFD et al. 2023, pp. 3, 21–22), which equals approximately five percent of the minimum known population. Similarly, damage compensation payments for wolf-caused livestock losses have declined from an average of just over \$300,000 between 2014 and 2017 to an average of under \$200,000 since 2018 (WGFD et al. 2022, pp. 23–24; WGFD et al. 2023, p. 24).

In addition to wolf control for livestock depredations, WGFC Chapter 21 Section 6(c) provides WGFD authorization to lethally remove wolves should it be determined that they are causing unacceptable impacts to wildlife or when wolves displace elk from state-managed feedgrounds. Displaced elk may result in damage to privately stored crops, commingling with domestic livestock, or human safety concerns due to their presence on public roadways. To date, no wolves have been removed in Wyoming under these provisions. However, in some cases WGFD used regulated public harvest of wolves to better direct hunters to areas where wolves may have affected the distribution of bighorn sheep and elk or to areas where elk recruitment has declined.

Wolf-livestock conflict resolution on the WRR is guided by the *WRR Plan* (Eastern Shoshone and Northern Arapaho Tribes 2008, entire). Under this *WRR Plan*, lethal take by private citizens or agencies is authorized if a wolf or wolves are caught in the act of depredating livestock or if it is deemed necessary to resolve repeated conflicts with livestock. To date, three wolves have been removed within the external boundaries of the WRR to mitigate conflicts with livestock. These wolves were included in the above totals when discussing lethal wolf control in Wyoming.

### **Wolf Population and Human-Caused Mortality in Wyoming Summary**

During those years when wolves were removed from Federal protections, human-caused mortality increased in Wyoming as WGFD implemented regulated harvest to manage wolf populations within the WTGMA. The WGFD set a population objective of 160 wolves within the WTGMA and it has adaptively managed harvest to achieve this objective when wolves were federally delisted. As the wolf population within the WTGMA approached this objective, human-caused mortality declined and has been relatively stable since 2019. Since 2009, during those years when wolves were federally listed (including years when harvest occurred under

predator status only), the average rate of human-caused mortality was 14 percent of the minimum known number of wolves in Wyoming. The average rate annually increased to 25 percent during years when WGFD managed wolf populations with regulated public harvest (i.e., when wolves have been delisted in the state) although it has remained relatively stable at an average of 21 percent since 2019 (range: 19 percent in 2022 to 23 percent in 2020) as wolf populations within the WTGMA approached and have been managed at the objective of 160 wolves. State management resulted in an overall negative growth rate for the wolf population in Wyoming. This gradual decline was expected as WGFD began to use harvest to reduce and then stabilize wolf populations to meet wolf population objectives, while also maintaining wolf numbers above agreed upon and statutorily required management levels within the WTGMA (77 FR 55530, September 10, 2012, p. 55553; WGFD et al. 2022, p. 4).

### ***Human-Caused Mortality in Oregon***

Wolf abundance is greatest in the Eastern one-third of Oregon, which was removed from Federal protections with the remainder of the NRM (except Wyoming) in 2011 (76 FR 25590, May 5, 2011). As a result, most wolf mortalities occur in this portion of the state. Currently, directed human take is restricted where wolves are federally listed in Oregon; however, our analysis addresses human-caused mortality at the state-level regardless of Federal status. Wolf management in Oregon is guided by the *Oregon Wolf Conservation and Management Plan (Oregon Plan)* (ODFW 2019a, entire), but some aspects of the *Oregon Plan*, in particular regulated public harvest and lethal control to resolve wolf-livestock conflicts, are not permitted where wolves remain federally-listed. This has been noted below for clarification when necessary.

### **Management of Wolves in Oregon**

Currently, wolves are listed as endangered under the Act in the Western two-thirds of Oregon, whereas wolves inhabiting the Eastern one-third of Oregon are federally delisted and managed under state authority. Thus, management differs in these two portions of the state. Wolves in Oregon achieved state-defined recovery and were delisted from the State Endangered Species Act in 2015. The *Oregon Wolf Conservation and Management Plan (Oregon Plan)*, its associated regulation (Oregon Administrative Rule 665-110), and Oregon's wildlife policy guide current wolf management in the federally delisted portion of Oregon and illustrate how the State would manage wolves statewide should their Federal protected status change. In sum, the *Oregon Plan* and Oregon's wildlife policy (Oregon Revised Statute 496.012) guide long-term management of wolves into the future in Oregon (ODFW 2019a, p. 6).

The *Oregon Plan* was developed prior to wolves becoming established in Oregon. The *Oregon Plan* was first finalized in 2005 and it contains provisions that require it to be updated every five years. The first revision occurred in 2010 and a second revision was completed in June of 2019. ODFW is required by state regulations to follow the *Oregon Plan*. The *Oregon Plan* includes program direction, objectives, and strategies to manage gray wolves in Oregon and it defines the gray wolf's special status game mammal designation (Oregon Administrative Rule 635-110).

The *Oregon Plan* includes two wolf management zones (WMZ) that roughly divide the state into western and eastern halves. The two management zones do not align with the boundary between the federally listed and delisted portions of Oregon; the division line between

the state-defined management zones is further to the west. Each WMZ has a “conservation population objective” and a “management population objective,” which are used to determine when the state will shift to a different phase of management within a specific WMZ (ODFW 2019a, pp. 14–17). The conservation population objective is defined as a minimum of four breeding pairs of wolves for three consecutive years and any WMZ that has not met this population objective is managed under Phase I. Phase II management is for any WMZ that has met the requirements of the conservation population objective, but has not yet achieved the management population objective of at least seven breeding pairs for three consecutive years. Any WMZ that has achieved and maintained the management population objective may be managed under Phase III. As WMZs progress from Phase I to Phase III, wolf management options gradually become less restrictive. Currently, wolves in the West WMZ are managed under Phase I, which provides a level of protection comparable to that of the Oregon Endangered Species Act. Wolves in the East WMZ are managed under Phase III (a maintenance phase), which strikes a balance such that populations do not decline to Phase II levels or reach unmanageable levels resulting in conflicts with other land uses.

In addition to the state management described above, biologists from the Confederated Tribes of Warm Springs are actively participating in radio-collaring and monitoring wolves on the Warm Springs Reservation in western Oregon.

### **Regulated Harvest in Oregon**

Gray wolves throughout Oregon are delisted at the state-level, but they are federally listed in the western two-thirds of the state. To date, regulated wolf harvest has never been permitted anywhere in Oregon, but it could be considered in the future in any portion of the state where wolves are federally delisted. Currently, the *Oregon Plan* only discusses and considers public involvement in controlled take as a management tool in specific areas in response to repeated livestock depredation incidents (ODFW 2019a, pp. 51–52); this controlled take would be highly regulated, require a permit, and would only be allowed under Phase III. We discuss management direction and regulations regarding depredation control in more detail below. The ODFW Commission would need to go through a public season-setting process before regulated public wolf harvest could be authorized (ODFW 2019a, p. 31).

### **Depredation Control in Oregon**

When addressing wolf-livestock conflicts, ODFW’s primary objective is to implement a three-phased approach based on population status that minimizes conflicts with livestock while ensuring conservation of wolves in Oregon (ODFW 2019a, p. 44). This phased approach to wolf management emphasizes preventive and nonlethal methods in Phase I, and it provides for increased management flexibility when the wolf population is managed under Phase III guidelines. Nonlethal methods will be prioritized to address wolf conflicts with livestock regardless of wolf population status (ODFW 2019a, p. 45). Under Phase III wolf management (Oregon Administrative Rule 635-110-0030), lethal force may be used by property owners, livestock producers, or their designated agents to kill a wolf that is in the act of biting, wounding, killing, or chasing livestock or working dogs, if wolves are not federally protected. If nonlethal methods were implemented following depredation events, but were unsuccessful at deterring recurrent depredations, ODFW may also issue a lethal take permit of limited duration to a livestock producer to kill a wolf, if wolves are not federally protected. Similarly, as long as wolves are not federally protected, ODFW, or their agents, may conduct lethal removal on

private and public lands to minimize recurrent depredation risk. If wolves are taken by private citizens, take must be reported to ODFW within 24 hours. Through a public process, the ODFW Commission may also authorize controlled take in specific areas to address long-term, recurrent depredations or significant wolf-ungulate interactions in areas where wolves are not federally protected.

Control options are currently limited to preventative and nonlethal methods within the federally listed portion of Oregon. In the eastern one-third of Oregon where the state has full management authority, agency directed lethal control of depredating wolves has been authorized to resolve wolf-livestock conflicts following guidelines outlined in Oregon's management plan (ODFW 2019a, pp. 41–54). Thus, while the east WMZ is currently in Phase III, lethal control may be authorized only in the eastern half of the east WMZ, where wolves are under state management authority per Oregon Administrative Rule 635-110-0030.

Between 2009 and 2022, agency-directed lethal control resulted in the removal of 25 wolves in Oregon to resolve repeated conflicts with livestock (see Appendix 3 for citations). Additionally, four wolves have been legally taken by livestock producers or their designated agents when they were caught in the act of attacking livestock or herding dogs. Five wolves have been removed in Oregon as a result of ODFW issuing a limited duration kill permit to a landowner to resolve repeated livestock depredations. Since 2009, lethal control of depredating wolves (including wolves removed by livestock producers or their designated agents to resolve conflicts) has removed an average of three percent of Oregon's total wolf population annually (range: 0 to 13 percent). This amount is much lower than was documented in Idaho, Montana, and Wyoming when the Service was managing the species in these states (i.e., when they were federally listed and managed under a section 10(j) rule).

### **Wolf Population and Human-Caused Mortality in Oregon Summary**

Known human-caused mortality from all causes resulted in the death of 86 wolves in Oregon between 2009 and 2022. The number of human-caused wolf mortalities documented in Oregon in 2021 ( $n = 21$ ) was the highest on record and it included eight wolves that were illegally killed by poison (ODFW 2022, p. 7). In 2022, 17 human-caused wolf mortalities were documented (ODFW 2023, p. 7). Nonetheless, known human-caused mortality removed an average of five percent of the total wolf population annually between 2009 and 2022 (range: 0 to 13 percent), which represents the lowest percentage of human-caused mortality among Western states that have had wolf populations for more than 10 years. Since 2010, human-caused mortality has not exceeded 10 percent of the statewide wolf population in any given year. Although fluctuations in population growth have occurred every year since wolves were first documented in the state and growth has slowed somewhat in recent years, this level of human-caused mortality has still provided Oregon wolves the opportunity to increase at an average rate of 22 percent annually, since 2010 (see Chapter 4 below for more detail on current population dynamics).

In 2015, using an individual-based predictive population model and vital rate estimates obtained from the literature for established or exploited wolf populations, ODFW estimated that rates of human-caused mortality up to 15 percent would result in positive population growth, while rates of 20 percent would cause population declines (ODFW 2015b, pp. 30–33). These rates of human-caused mortality were in addition to natural and other causes of mortality, which

were held constant at 12 percent. This resulted in a total mortality rate of 27 to 32 percent with which Oregon's wolf population would continue to increase or slightly decrease, respectively. Between 2009 and 2022, the average rates of human-caused and total mortality in Oregon's wolf population were five and seven percent, respectively (see Table 3) and they are well below the modeled levels that could result in a declining population in Oregon. These total mortality rates and their effects on wolf population growth in Oregon are considerably lower than observed rates for other wolf populations in the Western United States (see discussion of Idaho, Montana, and Wyoming above and Service 2020, p. 8). Mortality rates at this level provide opportunity for continued positive population growth and recolonization of suitable habitat in Oregon.

### ***Human-Caused Mortality in Washington***

Wolf abundance is greatest in the eastern one-third of Washington, which was removed from Federal protections as part of the NRM, except Wyoming, in 2011 (76 FR 25590, May 5, 2011). Most known wolf mortalities are documented in the delisted portion of the state. We discuss human-caused mortality at the state-level rather than separately discuss the listed and delisted portions of the state; however, directed human take is more restricted where wolves are currently federally listed in Washington.

### **Management of Wolves in Washington**

#### **State Management**

Currently, wolves are listed as endangered under the Act in the western two-thirds of Washington, whereas wolves inhabiting the eastern one-third of Washington are federally delisted and managed under state or tribal authority. Thus, management differs in these two portions of Washington. Wolves are also classified as endangered under the Washington state Endangered Species Act (Washington Administrative Code 220-610-010). Unlawful taking of endangered fish or wildlife (when a person hunts, fishes, possesses, maliciously harasses, or kills endangered fish or wildlife and the taking has not been authorized by rule of the commission) is prohibited in Washington (Revised Code of Washington (RCW) 77.15.120). In May 2023, WDFW published a draft periodic status review for gray wolves that recommended reclassifying wolves from state endangered to a state sensitive status (Smith et al. 2023, entire). In Washington, a state sensitive species is defined as: "vulnerable or declining and is likely to become endangered or threatened in a significant portion of its range within the state without cooperative management or removal of threats" (WAC 220-610-110). Even if Washington were to downlist wolves to state sensitive status, wolves would continue to be protected from unauthorized taking under RCW 77.15.130 and protections precluding hunting (outside of tribal lands) would remain in place (Smith et al. 2023, pp. 30, 40–42).

The *2011 Wolf Conservation and Management Plan* for Washington (*Washington Plan*) (Wiles et al. 2011, entire) was developed in response to the state endangered status for the species. The plan reflects the expectations that the wolf population in Washington would continue to increase through natural recolonization of vacant suitable habitat from adjacent wolf populations and that the state would be responsible for wolf management after Federal delisting. The purpose of the *Washington Plan* is to facilitate reestablishment of a self-sustaining population of gray wolves in Washington and to encourage social tolerance for the species by addressing and reducing conflicts. An advisory Wolf Working Group was appointed in 2008 to

provide recommendations during the *Washington Plan* development. In addition, the *Washington Plan* underwent extensive peer and public review prior to being finalized.

The *Washington Plan* provides recovery goals for downlisting and delisting the species under Washington state law, and it identifies strategies to achieve recovery and manage conflicts with livestock and ungulates. According to the *Washington Plan*, wolf recovery will be achieved in Washington when a minimum of 15 breeding pairs are equitably distributed across three wolf recovery areas in the state for 3 consecutive years or when 18 breeding pairs are equitably distributed across the state for a single year (Wiles et al. 2011, pp. 58–70).

#### **Confederated Tribes of the Colville Reservation**

The Confederated Tribes of the Colville Reservation (CTCR) is located in north-central Washington (where wolves are federally delisted). The *CTCR Gray Wolf Management Plan (CTCR Plan)* was finalized in 2017, and it guides management and conservation of gray wolf populations and their prey on the CTCR (Colville Confederated Tribes Fish & Wildlife Department (CCTFWD) 2017, p. 5). The goals of the *CTCR Plan* include developing a strategy for maintaining viable wolf populations while also maintaining healthy ungulate populations to support the cultural and subsistence needs of tribal members and their families (CCTFWD 2017, p. 20). The *CTCR Plan* also seeks to resolve wolf-livestock conflicts early to avoid escalation (CCTFWD 2017, p. 24). Wolf management activities that may occur on the CTCR include (CCTFWD 2017, pp. 31–32):

- (1) monitor gray wolf populations;
- (2) monitor ungulate response to gray wolf recolonization;
- (3) educate tribal members and general public about wolves;
- (4) use population goals to develop an annual harvest allocation;
- (5) investigate, document, and provide support to reduce resource or property damage;
- (6) report annual wolf management;
- (7) establish a wildlife parts distribution protocol;
- (8) coordinate on regional wolf management concerns; and
- (9) review and/or modify tribal codes to actively manage gray wolves.

Given the subsistence culture of the Colville tribal members, the impacts wolves may have on ungulate populations are an important consideration of the *CTCR Plan* (CCTFWD 2017, p. 20). To preserve the subsistence culture of Colville Tribal members, if significant ungulate population declines are documented, the Tribes may initiate research to determine the primary cause of the decline. Based on this research, the Tribes may recommend changes to ungulate harvest policies or may consider predator control efforts (including wolf control) (CCTFWD 2017, p. 22). Implementation of the *CTCR Plan* promotes informed decision-making to balance the benefits of wolf recovery and maintenance of existing ungulate populations that are important to Colville tribal members.

#### **Regulated Harvest in Washington**

Upon achieving recovery at the state-level, wolves in Washington may be reclassified as a game animal (or other similar designation). When wolf reclassification occurs at the state-level, regulated public harvest may be considered by the Washington Department of Fish and Wildlife (WDFW) Commission through a public season-setting process (Wiles et al. 2011, pp.

70–71). A majority of Washington residents are supportive of a regulated wolf hunting season once wolf recovery is achieved in the state (Duda et al. 2014, p. 118; Duda et al. 2019, p. 52), but regulated harvest may only be considered in those areas of Washington where wolves are federally delisted. To date, the WDFW Commission has not authorized regulated wolf harvest in the delisted portion of Washington; however, the Colville Business Council of the CTCR and Spokane Tribe of Indians (STOI) have promulgated regulations to allow wolf harvest for tribal members on tribal lands in the federally delisted portions of Washington.

On CTCR tribal lands, wolf harvest regulations have gradually become less restrictive over time to allow for increased harvest opportunities for individuals, but have remained unchanged since 2019. Gray wolf harvest seasons include a year-round hunting season and a four-month trapping season with no daily or seasonal bag limits for individual hunters or trappers (CTCR 2022, pp. 18–20). As of December 31, 2022, 44 wolves have been legally harvested on CTCR lands since regulated harvest was first authorized by the Colville Business Council of the CTCR in 2012.

Regulated wolf harvest is also allowed on the Spokane Indian Reservation for tribal members only and it was first authorized by the Tribal Council in 2013. Between 2013 and 2017, harvest quotas and individual harvest limits increased, but harvest seasons have remained unchanged since 2017. Gray wolf harvest seasons include a year-round hunting season and a five-month trapping season. Annual allowable take is a maximum harvest of 10 wolves within the calendar year (STOI 2023, entire). If the maximum allowable take is reached, the season closes until the start of the next calendar year. Between 2013 and 2022, 19 wolves have been legally harvested on the Spokane Indian Reservation.

Despite less restrictive regulations for harvest on tribal lands in Washington, the total number of wolves legally harvested has been low relative to total wolf population size and it has had minimal impact on wolf populations in the state (see Table 3). Since 2012, when regulated take was first permitted on CTCR, an average of three percent of the total statewide wolf population in Washington has been legally harvested annually (range: 0 to 9 percent) and the population of wolves in the state has continued to increase by an average of 23 percent each year (WDFW et al. 2023, p. 3).

### **Depredation Control in Washington**

A primary goal of wolf management in Washington is to minimize livestock losses in a way that continues to provide for the recovery and long-term perpetuation of a sustainable wolf population (Wiles et al. 2011, p. 14). Nonlethal management of wolf conflicts is prioritized in the state (Wiles et al. 2011, p. 85; WDFW 2017, pp. 2–9). WDFW personnel work closely with livestock producers to implement conflict prevention measures suitable to each producers' operation. Interested livestock producers may also enter into a Depredation Prevention Cooperative Agreement with WDFW, which provides a cost-share for the implementation of conflict prevention tools (WDFW et al. 2020, p. 24).

Control options are currently limited to preventative and nonlethal methods within the federally listed portion of Washington. In the eastern one-third of Washington, where wolves are federally delisted and under the management authority of WDFW, state law (RCW 77.12.240) provides WDFW authority to implement lethal control to resolve repeated wolf-livestock

conflicts when other methods have been unsuccessful at preventing conflicts. The WDFW wolf-livestock interaction protocol provides specific guidelines for when lethal control may be implemented (WDFW 2017, pp. 17–19). When lethal control is implemented, WDFW uses an incremental removal approach followed by an evaluation period to determine the effectiveness of any control action (WDFW 2017, pp. 18–19).

Under state law (RCW 77.36.030 and RCW 77.12.240), administrative rule (Washington Administrative Code 220-440-080), and the provisions of the *Washington Plan*, a private individual may kill a wolf attacking livestock under certain conditions in the federally delisted portion of Washington. Any removal of a wolf under these provisions must be reported to WDFW within 24 hours of take and the carcass must be surrendered to the agency.

Lethal control of depredating wolves was first used to mitigate wolf conflicts with livestock in Washington in 2012. Between 2012 and 2022, a total of 41 wolves have been removed in Washington through agency-directed control actions to resolve repeated conflicts with livestock. Additionally, one wolf was legally removed in 2021 under the authority of a lethal take permit issued to a livestock producer after a documented depredation and seven wolves have been legally killed by owners of domestic animals under the caught-in-the-act rule, two each in 2017 and 2019 and three in 2022.

The goal of wolf-livestock conflict management on the Colville Reservation is to resolve conflicts before they become chronic (CCTFWD 2017, p. 24). Potential livestock depredations on the Colville Reservation will be investigated by CCTFWD personnel. The CCTFWD personnel will work with livestock owners proactively and reactively to prevent and/or resolve conflicts as they arise (CCTFWD 2017, p. 24). Through 2022, no wolves have been removed to resolve conflicts with livestock on the CTCR.

The effect of lethal control of depredating wolves on Washington’s wolf population has been relatively minor to date. Overall, the percentage of wolves annually removed through lethal control (includes agency-directed control and legal take by livestock producers) in Washington is lower than what was documented in the core of the NRM in the years following wolf reintroduction when wolves were managed under Federal authority. In Washington, as a percent of the minimum known population, an average of two percent of the total statewide wolf population has been annually removed due to conflicts with livestock since 2008 (range: 0 to 12 percent; see Table 3).

Analyses of factors that contribute to wolf-livestock conflicts in Washington indicate that, in general, areas having a high abundance of livestock (Hanley et al. 2018a, pp. 8–10) or high densities of both wolves and livestock (Hanley et al. 2018b, pp. 8–11) are at higher risk for conflict. Between 2009 and 2021, 51 percent of documented wolf depredations in Washington occurred on public lands (WDFW 2022, p. 9). Also, persistent wolf presence has not been documented in some Washington counties with the highest risk of wolf-livestock conflicts based on cattle abundance alone (Hanley et al. 2018a, p. 10), thus the potential exists for increased levels of conflict as wolves continue to recolonize portions of the state.

### **Wolf Population and Human-Caused Mortality in Washington Summary**

Despite human-caused mortality, wolf populations in Washington have continued to grow and expand. Since 2009, the year after wolves were first documented in Washington, human-caused mortality has been responsible for the average removal of seven percent of the minimum known wolf population annually (range: zero to 13 percent). Over the same time period, the mean total wolf mortality rate has been 9 percent and ranged between zero percent and 15 percent (see Table 3). Concurrent with generally increasing numbers of human-caused mortality, wolf numbers and distribution have continued to increase in Washington, although the rate of increase has slowed somewhat in recent years as suitable habitat in eastern Washington has become increasingly saturated (Smith et al. 2023, p. 17). Since wolves were first documented in the state in 2008, wolf populations have increased an average of 23 percent annually (WDFW et al. 2023, p. 3) as dispersing wolves originating from both inside and outside of Washington continue to recolonize vacant suitable habitat in the state, including the first documented pack in the Southern Cascades and Northwest Coast recovery area in 2022 (WDFW et al. 2023, pp. 13–18) (see Chapter 4 below for more detail on current population dynamics). Population growth has been most rapid in the eastern Washington recovery area due to its proximity to large wolf populations in the NRM and Canada.

Table 3. Annual number of gray wolves known to have died by various causes, percent annual total mortality, and end-of-year statewide minimum wolf counts or population estimates in Idaho, Montana, Wyoming, Oregon, and Washington from 2009–2022. (See Appendix 3 for citations.)

Year	IDAHO					MONTANA					WYOMING <sup>e</sup>					OREGON					WASHINGTON				
	# Control <sup>a</sup>	# Harvest <sup>b</sup>	# Total Mort. <sup>c</sup>	% Total Mort. <sup>d</sup>	Yr. End Min. Count/Estimate	# Control <sup>a</sup>	# Harvest <sup>b</sup>	# Total Mort. <sup>c</sup>	% Total Mort. <sup>d</sup>	iPOM Estimate	# Control <sup>a</sup>	# Harvest <sup>b,f</sup>	# Total Mort. <sup>c</sup>	% Total Mort. <sup>d</sup>	Yr. End Min. Count	# Control <sup>a</sup>	# Harvest	# Total Mort. <sup>c</sup>	% Total Mort. <sup>d</sup>	Yr. End Min. Count	# Control <sup>a</sup>	# Harvest <sup>b,g</sup>	# Total Mort. <sup>c</sup>	% Total Mort. <sup>d</sup>	Yr. End Min. Count
2009	94	181	286	<b>25%</b>	856	145	72	258	<b>20%</b>	1,028	32	0	53	<b>14%</b>	320	2	0	2	<b>13%</b>	14	0	0	0	<b>0%</b>	14
2010	84	0	158	<b>17%</b>	777	141	0	179	<b>13%</b>	1,149	40	0	69	<b>17%</b>	343	0	0	1	<b>5%</b>	21	0	0	0	<b>0%</b>	19
2011	59	377	305	<b>28%</b>	768	64	166	216	<b>15%</b>	1,259	37	0	62	<b>16%</b>	328	2	0	3	<b>9%</b>	29	0	0	0	<b>0%</b>	35
2012	62	317	431	<b>37%</b>	722	108	225	324	<b>21%</b>	1,205	43	66	135	<b>33%</b>	277	0	0	1	<b>2%</b>	48	7	0	9	<b>15%</b>	51
2013	82	303	478	<b>41%</b>	684	75	230	335	<b>22%</b>	1,210	33	62	108	<b>26%</b>	306	0	0	3	<b>4%</b>	64	0	1	5	<b>9%</b>	52
2014	42	250	367	<b>32%</b>	785	57	206	306	<b>21%</b>	1,143	37	12	76	<b>19%</b>	333	0	0	0	<b>0%</b>	81	1	0	11	<b>14%</b>	68
2015	57	272	365	<b>32%</b>	786	51	210	276	<b>19%</b>	1,190	54	0	86	<b>18%</b>	382	0	0	7	<b>6%</b>	110	0	3	7	<b>7%</b>	90
2016	54	231	368	NA	NA	61	247	334	<b>23%</b>	1,126	113	0	133	<b>26%</b>	377	5	0	7	<b>6%</b>	112	7	3	15	<b>12%</b>	115
2017	75	333	379	NA	NA	57	254	305	<b>21%</b>	1,117	62	76	168	<b>33%</b>	347	5	0	13	<b>9%</b>	124	5	3	14	<b>10%</b>	122
2018	67	315	414	NA	NA	60	295	341	<b>23%</b>	1,153	66	81	177	<b>38%</b>	286	3	0	7	<b>5%</b>	137	4	6	12	<b>9%</b>	126
2019	62	462	475	<b>32%</b>	1,020	72	293	395	<b>25%</b>	1,159	30	48	96	<b>24%</b>	311	1	0	7	<b>4%</b>	158	11	6	21	<b>13%</b>	145
2020	77	411	512	<b>32%</b>	1,088	52	327	369	<b>24%</b>	1,184	43	53	119	<b>27%</b>	327	1	0	10	<b>5%</b>	173	3	8	16	<b>8%</b>	178
2021	43	412	515	<b>33%</b>	1,044	39	273	349	<b>23%</b>	1,143	32	51	107	<b>25%</b>	314	8	0	26	<b>13%</b>	175	2	22	30	<b>13%</b>	206
2022	34	388	404	<b>30%</b>	958	45	258	309	<b>22%</b>	1,087	21	56	95	<b>22%</b>	338	7	0	20	<b>10%</b>	178	9	11	37	<b>15%</b>	216

<sup>a</sup>Wolves killed through agency-directed actions or by private individuals to minimize wolf-livestock conflict risk. Does not include wolves removed to benefit ungulates.

<sup>b</sup>Harvest reported by harvest season for Idaho and Montana (example: 2011/2012 harvest season reported in 2011); by calendar year for Wyoming and Washington.

<sup>c</sup>Total mortality is the sum of all known wolf mortalities from all causes. This sum does not include unknown or undocumented mortalities (including undocumented illegal take).

<sup>d</sup>The total mortality rate was calculated by dividing the total number of wolves that died from all known causes during the calendar year by the population counts/estimates for the end of the calendar year plus the known number of animals that died from all causes that same year. Represented in equation form: Total Mortality Rate = [Total # of Wolves Died From All Known Causes in 20XX]/[Year-End Population Count/Estimate for the State for 20XX + Total # of Wolves Died From All Known Causes in 20XX]. We used the same method to

calculate the rate of human-caused mortality throughout this SSA. Note that Sells et al. (2022c, pp. 11–12) used a different method to calculate the rate of human-caused mortality in Montana, which produced slightly higher mortality rates in Montana relative to our calculations. The difference between the mortality rates reported in Sells et al. (2022c) and in this SSA do not affect the conclusions of our analysis; Sells et al. (2022c, pp. 10–11) still reports relative stability in the Montana wolf population and only minor population reductions since harvest began, and the harvest rates we evaluate in our future condition analysis (see Chapters 5 and 6) conservatively examine large increases in harvest above past observed rates (well above the higher mortality rates Sells et al. (2022c) reports). Throughout this SSA, when we refer to “observed” mortality rates, we are referring to the rates calculated according to the equation above.

<sup>e</sup>Includes wolves in YNP.

<sup>f</sup>Includes harvest in Wolf Trophy Game Management Area and predatory animal area.

<sup>g</sup>Harvest permitted on the Confederated Tribes of the Colville Reservation and the Spokane Reservation. Harvest not authorized where WDFW is responsible for management.

## Human-Caused Mortality in Arizona, California, Colorado, New Mexico, and Utah

We do not detail the levels of human-caused mortality in Arizona, California, Colorado, New Mexico, and Utah in Table 3 because the number of gray wolves in these states is small or, in some cases, nonexistent. Instead, we summarize below wolf management regulations, plans, and practices in each of these states, which influence current and future mortality. We also discuss known mortalities in these states.

### *Management of Wolves in Arizona, California, Colorado, New Mexico, and Utah*

#### California

Wolves in California are classified as endangered under the California Endangered Species Act (CESA; California Fish and Game Commission 2014, entire). Under CESA, take (defined as hunt, pursue, catch, capture, kill, or attempts to hunt, pursue, catch, capture, or kill) of listed wildlife species is prohibited (California Fish and Game Codes § 86 and § 2080). California also adopted a wolf-management plan intended to provide for the conservation and reestablishment of wolves in the state (CDFW 2016a, entire; CDFW 2016b, entire). The 2016 *Conservation Plan for Gray Wolves in California (California Plan)* includes education and public outreach goals, damage-management strategies, and monitoring and research plans. Wolves will remain on the state endangered species list in California until state recovery objectives have been reached, though such objectives have not yet been defined.

The *California Plan* was developed in coordination with stakeholder groups in anticipation of the return of wolves to California (CDFW 2016a, p. 2). The *California Plan* included direction to develop alternatives for wolf management, specified that CDFW would not reintroduce wolves to California, and acknowledged that historical distribution and abundance of wolves in California are not achievable (CDFW 2016a, pp. 3–4). The goals include the conservation of biologically sustainable populations, management of wolf distribution, management of native ungulates for wolf and human uses, management of wolves to minimize livestock depredations, and public outreach (CDFW 2016a, p. 4). The *California Plan* recognizes that wolf numbers in the state will increase with time, and the *California Plan* needs to be flexible to account for information that is gained during the expansion of wolves into the state (CDFW 2016a, pp. 19–24). Similar to plans for other states, the *California Plan* uses a three-phase strategy for wolf conservation and management.

**Phase I** is a conservation-based strategy to account for the reestablishment of wolves under both state and Federal Endangered Species Acts (CDFW 2016a, pp. 21–22). Phase I will end when there are four breeding pairs for two consecutive years in California. The CDFW defines a breeding pair as at least one adult male, one adult female, and at least two pups that survive to the end of December (CDFW 2016a, p. 21). California is currently in Phase I, with two breeding pairs documented for two consecutive years as of the end of 2022 (CDFW 2023b, entire).

**Phase II** is expected to represent a point at which California's wolf population is growing more through reproduction of resident wolves than by dispersal of wolves from other states (CDFW 2016a, p. 22). This phase will conclude when there are eight breeding pairs for two

consecutive years. During Phase II, CDFW anticipates gaining additional information and experience with wolf management, which will help inform future revisions to the state plan. During Phase II, managing wolves for depredation response or predation on wild ungulates may be initiated. Wolf management may include injurious harassment and/or lethal control under specific conditions (CDFW 2016b, pp. 281–282). However, this aspect of the plan cannot be implemented while wolves are listed as endangered at either the Federal or at the state-level.

**Phase III** is less specific due to the limited information available to CDFW at the time of the *California Plan*'s development (CDFW 2016a, p. 22). This phase moves toward longer-term management of wolves in California. Specific aspects of Phase III are more likely to be developed during Phase II when more information on wolf distribution and abundance in the state are available. Towards the end of Phase II and the beginning of Phase III, information should be available to inform a status review of wolves in California to determine if continued state listing as endangered is warranted (CDFW 2016a, p. 22).

Currently, harvest and lethal control of depredating wolves is not permitted in California because the species is listed as endangered under the Act and classified as a state endangered species. The 2016 *California Plan* does not contemplate harvest in the state.

## **Colorado**

Wolves are currently listed as endangered at the Federal level in Colorado; therefore, harvest is not allowed in the state. However, due to designation as an experimental population under section 10(j) of the Act, gray wolves may be lethally removed under certain circumstances, in accordance with the final 10(j) rule (88 FR 77014, November 8, 2023), which we discuss in more detail below. Gray wolves are also listed as an endangered species by the State of Colorado and they are protected under Colorado Revised Statutes ((CRS) 33–6–109), making it illegal for any person to hunt, take, or possess a gray wolf in Colorado.

Recognizing the potential for increasing numbers of wolves to enter Colorado from growing populations in the NRM, the Colorado Division of Wildlife (now CPW) convened a multi-disciplinary Wolf Management Working Group in 2004 to formulate management recommendations for wolves that naturally enter and possibly begin to recolonize the state. The Working Group did not evaluate what would constitute wolf recovery in Colorado but did recommend that wolves that enter or begin to recolonize Colorado should be free to occupy available suitable habitat and that managers should balance the ecological needs of the wolf with the social aspects of wolf management (Colorado Wolf Management Working Group 2004, pp. 1, 3–5). Although the Working Group's recommendations were not a formal management plan, they were adopted by the CPW Commission in 2005 and were reaffirmed in 2016 (CPW Commission Resolution 16-01).

In November 2020, Colorado voters passed a ballot initiative (Proposition 114) that later became CRS 33-2-105.8, which required the CPW Commission to prepare a plan to restore and manage gray wolves in Colorado and take the steps necessary to begin reintroductions by December 31, 2023. The CPW Commission convened a Technical Working Group and a Stakeholder Advisory Group which provided input and recommendations for CPW staff during development of the draft Colorado Wolf Restoration and Management Plan. The final Colorado Wolf Restoration and Management Plan was presented to and approved by the CPW

Commission in May 2023 (*Colorado Plan*; CPW 2023, p. 3). The primary goal of the *Colorado Plan* is to “identify the steps needed to recover and maintain a viable, self-sustaining wolf population in Colorado while concurrently working to minimize wolf-related conflicts with domestic animals, other wildlife, and people” (CPW 2023, p. 3). Wolf restoration and management in Colorado is guided by a three-phased approach that ensures wolf populations progress towards self-sustainability while also providing flexibility to manage conflicts in the state (CPW 2023, pp. 23–25).

**Phase I** corresponds to state endangered status when wolves will be managed in accordance with state law to conserve endangered species. To transition to Phase II, a minimum of 50 wolves must be documented anywhere within Colorado for four successive years. Once this is documented, the CPW Commission must downlist wolves from state endangered to state threatened.

**Phase II** corresponds to state threatened status. To transition to Phase III, a minimum of 150 wolves must be documented anywhere in the state for two successive years or a minimum of 200 wolves must be documented anywhere in the state for a single year. Phase II can progress concurrently with Phase I should Phase II numerical requirements be reached prior to wolf populations exceeding 50 wolves for the four successive years required to proceed out of Phase I. Therefore, depending on the speed of wolf population growth in Colorado, the CPW Commission may transition directly from Phase I to Phase III. After achieving Phase II status, should the state document fewer than 50 wolves in any two successive years, a review will be initiated to determine if wolves in Colorado should be relisted as endangered and managed under Phase I or remain in Phase II.

**Phase III** management corresponds to the removal of gray wolves from the state endangered and threatened list and the reclassification of wolves to a nongame species. After achieving Phase III status and being reclassified as a nongame species, should the lower 80 percent confidence limit of a population estimate be fewer than 150 wolves for any two successive years, a review would be initiated to determine if wolves in Colorado should be relisted as threatened and managed under Phase II or remain a nongame species that continues to be managed under Phase III.

The long-term management of wolves in Colorado may only be considered once the wolf population in Colorado reaches Phase III levels and wolves have been reclassified to a nongame species. Any future discussions regarding the long-term management of wolves in Colorado will consider both biological and social factors in an adaptive management framework. At this time, the *Colorado Plan* does not consider wolf management beyond Phase III and it does not take a position on whether the “CPW Commission has the statutory authority to reclassify wolves as a game species or take other appropriate management actions” (CPW 2023, p. 25). Regulated public harvest of gray wolves may only be considered in Colorado if wolves are reclassified as a game species at some point in the future (and are federally delisted). Any possible harvest recommendations that may be considered in the future will be vetted through a public process prior to CPW Commission approval, similar to harvest recommendations for all other game species in the state.

Concurrent with the development of the *Colorado Plan*, the Service embarked on a rulemaking process to designate wolves reintroduced into Colorado as an experimental population under section 10(j) of the Act. On November 8, 2023, the Service published a final rule designating wolves that will be reintroduced into Colorado as a nonessential experimental population; this rule clearly defines under what circumstances take may be allowed, up to and including lethal control of depredating wolves (88 FR 77014, November 8, 2023). As long as wolves remain federally listed in Colorado, wolf management in the state must be consistent with this final 10(j) rule.

If wolves were to be federally delisted, the *Colorado Plan* would guide all aspects of wolf conflict management in the state (CPW 2023, pp. 26–30). The state will prioritize prevention and nonlethal management of wolf conflicts in Colorado during the early phases of wolf restoration. However, under the *Colorado Plan*, CPW may authorize lethal control of depredating wolves during all phases of wolf management. The CPW Commission would need to approve any rules concerning the take of wolves while they are on the state endangered and threatened list.

The Southern Ute and the Ute Mountain Ute Tribes in southwestern Colorado have embarked on a process to develop wolf management plans for their respective tribal lands. It is anticipated that these plans will be completed in late 2023 or in 2024.

#### **Arizona and New Mexico**

Although non-Mexican gray wolves are not known to occur in Arizona, any gray wolves that disperse to this state would be federally listed as endangered north of I-40; therefore, harvest and lethal depredation control of gray wolves is not authorized. Additionally, all wolves receive protections from illegal take under Arizona statutes regulating management of game and fish (Arizona Revised Statutes (A.R.S.) 17-309 and A.R.S. 17-314) (Gray in litt. 2021, p. 4). If gray wolves were to be federally delisted, an Arizona statute allows “the taking of a wolf that is actively threatening or attacking a person, livestock or other domestic animal” (A.R.S. 17-302.01).

As in Arizona, gray wolves north of I-40 in New Mexico are currently listed as endangered under the Act and have been listed as endangered under New Mexico’s Wildlife Conservation Act (WCA) (§17-2-37 through §17-2-46 New Mexico Statutes Annotated) since 1975 (New Mexico Department of Game and Fish 2022, p. iv). Therefore, harvest and lethal depredation control of gray wolves is not authorized. If gray wolves were to be federally delisted in New Mexico, the WCA would continue to provide protections for gray wolves. Under the WCA, it is illegal “for any person to take, possess, transport, export, process, sell or offer for sale or ship any species of wildlife” that is listed as endangered (WCA §17-2-41). The WCA provides that state endangered species “may be removed, captured or destroyed where necessary to alleviate or prevent damage to property or to protect human health” (WCA §17-2-42D). However, unless such action is in response to “an immediate threat to human life or private property,” prior authorization through a state issued permit would be required (§17-2-42D).

Although non-Mexican gray wolves (*Canis lupus spp.*, other than *Canis lupus baileyi*), the subject of this SSA, are not currently known to occur in Arizona or New Mexico, Mexican

wolves (*Canis lupus baileyi*) have occurred in these states since 1998 and 2000, respectively, following the release of eleven captive-reared Mexican wolves into eastern Arizona in 1998 (Service 2023b, unpaginated; New Mexico Department of Game and Fish 2022, p. 22). The Arizona Game and Fish Department and the New Mexico Department of Fish and Game are active members of the collaborative Inter-agency Field Team working to manage and monitor the wild population of Mexican wolves in the Southwestern United States (Service 2023c, p. 3).

## Utah

Wolves were federally delisted in a small portion of north-central Utah, along with the rest of the NRM (except Wyoming), in 2011 (76 FR 25590, May 5, 2011). Any wolf documented in the remainder of Utah is listed as endangered. Gray wolves are designated as a species of greatest conservation need in Utah. They receive protections under Utah Code (Section 23-20-3) that prohibits the taking of protected wildlife, except as authorized by the Wildlife Board. Wolves are also classified as furbearers and Utah Code (Section 23-18-2) prohibits furbearer take without a license. At present, there is no harvest season authorized for wolves in the federally delisted portion of Utah and take is not allowed in the remainder of the state due to the Federal protected status of wolves. However, wolves may be lethally removed to mitigate wolf conflicts with livestock in the federally delisted portion of Utah (i.e., the portion that was contained within the NRM).

In 2003, the Utah Legislature passed House Joint Resolution 12, which directed Utah Division of Wildlife Resources (UDWR) to draft a wolf management plan for review, modification, and adoption by the Utah Wildlife Board through the Regional Advisory Council process. In June 2005, the Utah Wildlife Board formally approved the *Utah Wolf Management Plan (Utah Plan)* (UDWR and Utah Wolf Working Group 2005, entire). The goal of the *Utah Plan* is to manage, study, and conserve wolves moving into Utah while avoiding conflicts with the elk and deer management objectives of the Ute Indian Tribe; minimizing livestock depredation; and protecting wild ungulate populations in Utah from excessive wolf predation. The Utah Wildlife Board has since extended the implementation of the *Utah Plan* through 2030. The *Utah Plan* is comprised of six adaptive management strategies intended to guide wolf management once the species is federally delisted statewide and until 2030, or until two naturally occurring wolf packs occupy the state. Confirmation of two packs does not represent a population cap, but rather signals that the species has become established in Utah and that UDWR should commence planning for the next phase of wolf management.

The *Utah Plan* recognizes that concerns about livestock depredation by wolves can effectively be addressed using both nonlethal and lethal management tools (UDWR and Utah Wolf Working Group 2005, pp. 35–39). At present, the UDWR may consider lethal control to mitigate wolf conflicts with livestock in the federally delisted portion of the state. The *Utah Plan* recommends a compensation program for livestock owners who experience loss due to wolves (UDWR and Utah Wolf Working Group 2005, pp. 35–39). Under Utah Administrative Code (Rule R657-24), the state may compensate livestock producers for confirmed losses caused by wolves in those areas of the state where wolves are federally delisted.

In 2010, the Utah Legislature passed SB 36 (Wolf Management Act). The Wolf Management Act was passed, in part, because the state concluded they could not “adequately or effectively manage wolves on a pack level in the small area of the state where the species is

currently delisted without significantly harming other vital state interests” (Utah Code 23-29-103). Utah Code 23-29-201 directs UDWR to prevent the establishment of a viable wolf pack in the delisted portion of Utah until wolves are federally delisted in the entirety of the state, at which time the *Utah Plan* would again guide wolf management. To comply with Utah Code 23-29-201, wolves are aggressively managed in the delisted portion of the state when documented. Although individual wolves have been documented, depredations have been confirmed, and some wolves have died from human causes in the delisted portion of Utah, no known wolves have been killed through state action or by private individuals in response to conflicts with livestock in the delisted portion of the state (although one was killed just across the border in Idaho for depredating sheep in Utah).

If wolves were to be delisted in Utah, the *Utah Plan* would guide wolf management in the entirety of the state. Any future wolf harvest recommendations would be vetted through a public process via the Regional Advisory Councils, and they must be approved by the Wildlife Board. Lethal control may be considered statewide to mitigate wolf conflicts with livestock and all livestock producers in the state that experience confirmed wolf-caused livestock losses would be eligible for compensation.

#### ***Mortality in Arizona, California, Colorado, New Mexico, and Utah***

As documented in California’s report “California’s known wolves—past and present,” there are many formerly known wolves that are from or traveled through California whose whereabouts are unknown (CDFW 2023b, entire). However, we only discuss known mortalities that occurred in California. A total of three wolves were known to have died in California since they began to recolonize the state; one died of known causes (gunshot), another died from a vehicle collision, and one mortality remains under investigation (CDFW 2023b, entire).

In 2008, several sightings of a single, black-colored canid in New Mexico were presumed to be a gray wolf from the NRM (Oakleaf 2022, p. 50), given that no black-colored Mexican wolf has ever been documented (Odell et al. 2018, pp. 294–296). The fate of this canid is unknown. In 2014, a gray wolf collared in Wyoming dispersed into northern Arizona where it was regularly sighted during a two-month period before being killed by a coyote hunter in southern Utah due to mistaken identity (Odell et al. 2018, pp. 294–296; Service 2020, unpublished data). In Colorado, three wolves were known to have died from human-causes between 2002 and 2022; one died from a vehicle collision, one died from illegal take (i.e., poison), and one died as a result of mistaken identity (CPW 2023, p. 4). In January 2020, a group of six wolves were documented in extreme northwest Colorado. Two wolves from this group were legally harvested in Wyoming during spring 2020 and by the end of that year, a single individual remained in the territory. This individual was last documented in October 2021 and its fate is currently unknown. In Utah, four dispersing wolves were known to have died from human causes between 2006 and 2015; this total includes the gray wolf described above that was documented in Arizona and later died in Utah (UDWR 2022b, entire). Other dispersers have been documented in California, Colorado, and Utah, but their fates remain unknown.

## 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 2015b, 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). Human-caused mortality is estimated to account for 60 to 80 percent of all known mortalities in the conterminous 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).

Although the intent of new legislation passed in Idaho and Montana in 2021 and incorporated into wolf harvest regulations since then was to decrease wolf abundance, both states continue to maintain a significant amount of regulatory authority to limit wolf harvest, if and when necessary. While amended Idaho Codes (IC) authorize year-round trapping seasons on private property and additional methods of take to harvest wolves in Idaho, IC 36-104(b)(2) and IC 36-104(b)(3) continues to provide the IDFG Commission with discretion to open and close hunting seasons and set harvest limits on both public and private lands; open and close trapping seasons and set harvest limits on public lands; set harvest limits for trapping seasons on private lands; and to adopt emergency closures or restrictions, as necessary (IOSC and IDFG 2022, in litt.). Furthermore, IC 36-106(e)(6) provides the IDFG Director similar emergency authority. The 2021 Montana legislature passed four bills that affected wolf management in the state. With the exception of authorizing the use of snares to take wolves by licensed trappers, the MFW Commission retained discretion to determine how to implement remaining wolf harvest regulations (e.g., season length, method of take, harvest limits, etc.). Furthermore, the MFW Commission maintains authority to amend seasons, limits, and regulations, when necessary, and authorizes the MFWP to initiate emergency closures of any WMU or trapping district at any time, if deemed necessary.

Even though the number of wolves that died as a result of legal, human causes (primarily in the form of regulated public harvest) has increased in the NRM states of Idaho, Montana, and Wyoming since Federal delisting as states have attempted to meet wolf population objectives, the best available scientific information indicates that wolf populations in these states remained relatively stable through the end of 2020, with slight population decreases observed in Idaho and Montana at the end of 2021 and 2022. Furthermore, current levels of mortality in the NRM have not prevented the continued natural recolonization of suitable habitat in Oregon and Washington (where known wolves now total close to 400 individuals), California, or, more recently, in Colorado. While harvest rates documented in Idaho and Montana during the 2021/2022 and 2022/2023 wolf seasons are within the range of harvest rates that occurred during seasons that predated the new laws prompting less restrictive harvest regulations in these states, it remains unclear how recent statutory and regulatory changes will affect wolf abundance and distribution in each state and throughout the West in the long term. To evaluate these possible effects, we analyzed the potential effects of increased take in Idaho and Montana on wolves in the Western United States in greater detail in Chapters 5 and 6.

## Disease and Parasites in Wolves

Disease outbreaks are the most common cause of die-offs 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. 2021, p. 2). Although disease and parasites were not identified as a threat at the time we listed the gray wolf, 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).

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 2016b, pp. 38–41; IDFG 2023a, p. 14). 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, anaplasmosis, ehrlichiosis, echinococcus granulosus, and oral papillomatosis; however, impacts of these diseases on wolf population dynamics are not known to be significant (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; 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; Jara et al. 2016, p. 13; CDFW 2016b, pp. 38–41; Knowles et al. 2017, entire; Carstensen et al. 2017, entire; Bevins et al. 2021, 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: canine distemper virus (CDV), canine parvovirus (CPV), mange, and rabies (CDFW 2016b, 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 in the Western United States. We also discuss the prospect of novel pathogens and the potential implications for wolves in the Western 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) only survivors are available for sampling, (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; Almborg 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) (Almborg et al. 2010, p. 2072; Brandell et al. 2020, p. 126). Outbreaks of CDV are particularly lethal for young wolves, and it has resulted in reduced pup survivorship to as low as 13 percent (Almborg 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) (Almborg 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 (Almborg 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) (Almborg et al. 2016, p. 2). Serological evidence indicates that exposure to CDV is periodically high among some wolf populations, including those in YNP and Montana (Smith and Almborg 2007, p. 18; Almborg et al. 2009, pp. 8–9; Cross et al. 2018, p. 8730; Brandell et al. 2020, p. 123; Brandell et al. 2021a, supplementary material in the citation), probably as a result of spillover from another species that acts as a disease reservoir (Almborg et al. 2010, p. 2068). Exposure rates in other areas of the Western United States have not been reported; however, CDV is present in wild carnivores and domestic dogs across the West and wolves in these areas have the potential to be infected by sympatric wild carnivores and dogs. While distemper can cause localized population decreases in the short term, its effects are acute and wolf populations usually rebound shortly after disease outbreaks (Brand et al. 1995, p. 421; Almborg et al. 2009, pp. 5–9; Almborg et al. 2010, p. 2072; Almborg et al. 2012, p. 2848; Stahler et al. 2013, pp. 227–229); however, the combined effect of reduced elk abundance, CDV, and mange likely contributed to wolf populations declining to a lower long-term average of around 100 wolves in YNP since 2008 (DeCandia et al. 2021, p. 430).

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. Canine parvovirus 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), 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 Almborg 2007, p. 18; Almborg et al. 2009, p. 4), 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. 2009, p. 96).

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 scabiei*) 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; Almbert 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 (Almbert 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; Wydeven et al. 2009, 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 Almbert 2007, p. 19; Jimenez et al. 2010a, 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 (Jimenez et al. 2010a, 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 Western United States, 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 Western 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 one 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 seven 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 United States 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, p. 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 Moreno 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; Gomez-Sanchez 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 National Park Service to translocate 19 wolves from the mainland 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; Akesson 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 Moreno 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 (Gomez-Sanchez 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). Reintroduced and naturally expanding populations in the NRM have shown low levels of inbreeding even in the GYA 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 2023a, p. 11). 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; Akesson et al. 2016, entire). 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, the best available data does not provide evidence of inbreeding or inbreeding depression in wolves in the Western U.S. metapopulation. We discuss whether inbreeding depression could occur in this metapopulation in the future in Chapter 6.

## Climate Change

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 Western 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 (Vose et al. 2018, pp. 270, 273). Climate change may have direct or indirect effects on predators, prey, and their habitats. 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 Western 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. 4). Because of their generalist, adaptable life history, climate change is not likely to strongly affect wolf populations directly throughout North America (van den Bosch et al. 2023, pp. 8–9). 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. The Western United States is roughly in the middle of historical wolf distribution 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). Models project range shifts (approximately 6.8 mi/year (11 km/year)) due to climate change for the gray wolf in North America (Williams and Blois 2018, p. 8). However, recent modeling analysis indicates that wolf habitat in the Western Great Lakes will remain stable or increase during the twenty-first century, with limited or no change to wolf distribution or potential recolonization (van den Bosch et al. 2023, pp. 5–9). Additionally, 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).

While wolves appear to be unaffected by near-term climate change (Barber-Meyer et al. 2021, pp. 1, 11), 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). For example, changes to prey availability could arise from altered phenology of resources for ungulates and diminished foraging benefits (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, affected annual wolf reproductive success (e.g., high snowfall reduced overwinter survival of prey resulting in lower wolf reproductive success 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 Midwest and southern GYA, 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 Midwest under changing climate conditions, where milder winters could increase forage availability.

The increase in frequency and severity of wildfires throughout the Western United States could also potentially change the distribution of wolf prey species across the landscape. Fire and insect outbreaks have killed millions of hectares of forested area across the Western United States in recent decades (Hicke et al. 2016, p. 141). Between 2000 and 2016, with the exception

of 3 years, wildfires burned over 3.7 million acres (1.5 million hectares) every year; between 2017 and 2021, wildfires burned an average of 8.1 million acres (3.3 million hectares) every year (National Interagency Fire Center 2022, unpaginated). However, as we discuss further below under *Other Sources of Habitat Modification*, 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); 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). 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 Western United States. Significant changes in temperature and precipitation patterns due to climate change have already been documented within the wolf's range in the Western United States, while the occupied range of the wolf metapopulation has continued to expand. Gray wolves are highly adaptable and are efficient at exploiting available food resources. 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. Therefore, we do not directly analyze the effects of climate change on the current and future condition of wolves in the Western 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 the most significant diseases with the potential to affect ungulates—the primary prey species for wolves—in the Western United States. These diseases include CWD, brucellosis, and several viral hemorrhagic diseases.

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: Colorado, Idaho, Montana, New Mexico, Utah, and Wyoming (USGS 2022, 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 three 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.

Brucellosis is a zoonotic bacterial disease caused by *Brucella abortus* that is routinely detected in elk and bison in the GYA. Brucellosis in wild ungulates in the Western United States is largely limited to the GYA where bison populations facilitate high seroprevalence of the disease and where high elk population densities serve as a disease reservoir (Cross et al. 2013, p. 79). It is readily transmitted by exposure of susceptible animals to aborted fetuses and exudates from the reproductive tract of an infected mother. Brucellosis does not appear to affect adult survival, but it can cause significant reductions in elk and bison reproductive success and recruitment (Hobbs et al. 2015, pp. 540–544; Cotterill et al. 2018, p. 10739). For example, the seroprevalence of brucellosis in the bison of YNP oscillates around 60 percent and the disease has been shown to depress recruitment (Hobbs et al. 2015, pp. 538–543), although not pregnancy rates (Gogan et al. 2013, pp. 1271, 1274). Depressed recruitment due to brucellosis caused the mean population growth rate of bison in YNP to drop from 1.11 to 1.07 based on infection

probabilities from 1975–2010 (Hobbs et al. 2015, p. 543). In a study of over 1,000 female elk from Wyoming, individuals with brucellosis infections exhibited a 24 percent reduction in the number of calves they birthed, a decrease comparable to that which results from severe winters or droughts (Cotterill et al. 2018, p. 10739). Despite these impacts, brucellosis is not generally considered to be a direct threat to the sustainability of either elk or bison populations (National Academies of Sciences, Engineering, and Medicine 2020, p. 61).

There are three viruses known to cause hemorrhagic diseases in North American wild ruminant species: bluetongue virus (BTV), epizootic hemorrhagic disease virus (EHDV), and *Odocoileus hemionus* adenovirus (OdAdV), which causes adenovirus hemorrhagic disease AHD (Tomaszewski et al. 2021, p. 183). A biting midge (*Culicoides* spp.) transmits BTV and EHDV to prey species (Tomaszewski et al. 2021, p. 183). BTV and EHDV have similar symptoms, and they can result in rapid mortality. EHDV is largely confined to white-tailed deer and pronghorn antelope (*Antilocapra americana*), while BTV can infect domestic animals and deer. Rising temperatures have led to a northward expansion of *Culicoides* and thus have contributed to expansion of the ranges of BTV and EHDV (Rivera et al. 2021, pp. 9–13). In the Western United States, BTV and EHDV transmission is attributed to *Culicoides sonorensis*, which is associated with polluted water and mud sources because the midges often prefer water and mud contaminated with livestock manure for reproduction (Rivera et al. 2021, pp. 9–13). Unlike BTV and EHDV, OdAdV is transmitted through direct contact. It was first identified in the Western United States during an epizootic event in 1993 and 1994 when thousands of deer died in California (Woods et al. 2018, p. 530). It has now spread to other Western states and Western Canada. All age-classes of ungulates are affected by OdAdV, but fawns and juveniles appear to be most susceptible to increased rates of mortality (Woods et al. 2018, p. 530). The disease course is usually rapid and fatal as the virus damages small blood vessels in the lungs and intestines with symptoms of respiratory distress and internal hemorrhaging. All three hemorrhagic diseases can result in occasional outbreaks in various ungulate species, which episodically increases their mortality rates.

To date, diseases in prey species have not resulted in significant, rangewide prey reductions nor have they led to wolf population declines in the Western metapopulation. However, wolf prey in the Western 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., CPW 2018, entire; MFWP 2019a, entire; WGFD 2020, entire; IDFG 2021, entire). They also command significant regulatory authorities to adjust harvest rates seasonally or spatially if disease outbreaks emerge. In the west, state wildlife agencies coordinate on wildlife health issues through the Western Association of Fish & Wildlife Agencies' Wildlife Health Committee and nationally through the Association of Fish & Wildlife Agencies' Fish & Wildlife Health Committee. In addition, the U.S. Department of Agriculture (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 escape cover without agricultural land) (see Mech 2017, pp. 312–315). Stressors related to prey and human-caused mortality are described in the preceding sections. Below, we discuss two other potential sources of habitat modification within the range of the gray wolf in the Western United States: the human footprint and wildfire. However, as we discuss further below, habitat modification as a result of the human footprint or wildfire is not a primary stressor on wolf populations; the impacts of these sources are localized relative to the wide range of the species and wolves have been able to adapt to their effects (i.e., wolves are habitat generalists). Thus, we do not further consider these sources of habitat modification in our analysis of current and future condition.

### The Human Footprint

The extent of the impacts of human presence and actions on the landscape have been collectively called the human footprint (Janzen 1998, entire). In an analysis of the human footprint in the Western United States, Leu et al. (2008, p. 1125) found that the physical effect area of the 14 anthropogenic features they analyzed (human habitation, interstate highways, Federal and state highways, secondary roads, railroads, irrigation canals, powerlines, linear feature densities, agricultural land, campgrounds, highway rest stops, landfills, oil and gas development, and human induced fires) covered 13 percent of the land area in the Western United States, with agricultural land being the most dominant (9.8 percent) human use. Accounting for the indirect effects radiating out from the direct human footprint, Leu et al. (2008, p. 1125) categorized 52 percent of the Western United States as having medium or high-intensity impacts from the human footprint (both direct and indirect impacts), while low intensity impact areas covered the remaining 48 percent of the landscape (Leu et al. 2008, pp. 1125–1127). We overlaid the current range of the gray wolf with the human footprint map and found that 36 percent of current range was within the medium- or high-intensity categories (35 percent medium, 1 percent high) and 64 percent was in the low-intensity category.

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 (e.g., 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). 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).

## Wildfire

Gray wolves appear to be remarkably resilient to wildfire, persisting and breeding in human-dominated landscapes under intense fire regimes (e.g., Lino et al. 2019, entire). In a systematic review of predator response to fire, the gray wolf showed a positive response to fire (Geary et al. 2019, p. 961). Ballard et al. (2000, p. 246) documented successful denning by a wolf pack on the edge of a 322 mi<sup>2</sup> (845 km<sup>2</sup>) wildfire in Northwestern Alaska. They found that collared wolves used the area during the burn and the summer after the burn proportionally more than expected (Ballard et al. 2000, pp. 243–246). The wolves used the area less in the following winters, likely due to shifts in caribou distribution as a result of the wildfire (Ballard et al. 2000, pp. 243–246). After 3 years, wolf use of the burned area returned to pre-fire levels (Ballard et al. 2000, pp. 243–246). The authors concluded that the fire did not appear to have short-term effects because the effects to prey were within normal annual variation and unburned areas within the fire continued to attract prey (Ballard et al. 2000, p. 246). Predators with large territories, like wolves, have more flexibility to exploit resources in burned and unburned landscapes (Geary et al. 2019, p. 956). Moreover, in conifer-dominated forest ecosystems, wildfires transition forest to earlier succession stages, which can increase prey densities due to increases in the availability of vegetative food resources (Snobl et al. 2022, pp. 14–15). Gray wolf response to fire is likely a combination of behavior and morphology (e.g., fewer obstacles allowing for pursuit of prey) and environmental context (e.g., scale, severity, and patchiness of fire) (Geary et al. 2019, p. 956). However, if wolves are attracted to burned areas to exploit higher densities of prey (Geary et al. 2019, p. 964), they may be more exposed to human disturbance and persecution due to limited escape cover in these areas (Lino et al. 2019, p. 111).

## 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 in the Western United States and gray wolf habitat discussed above are interrelated and could be synergistic, and thus may cumulatively affect the gray wolf in the Western 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 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.

## Conservation Efforts on Federal Lands in the Western United States

Federal lands in the Western United States cover approximately 63 percent of the gray wolf's current range (i.e., 89,635 mi<sup>2</sup> (232,153 km<sup>2</sup>) of Federal land out of 142,451 mi<sup>2</sup> (368,946 km<sup>2</sup>) total current range). These lands are primarily managed by the National Park Service, National Wildlife Refuge System, U.S. Forest Service, and Bureau of Land Management (BLM) (Figure 6; Congressional Research Service 2020, pp. 7–12).

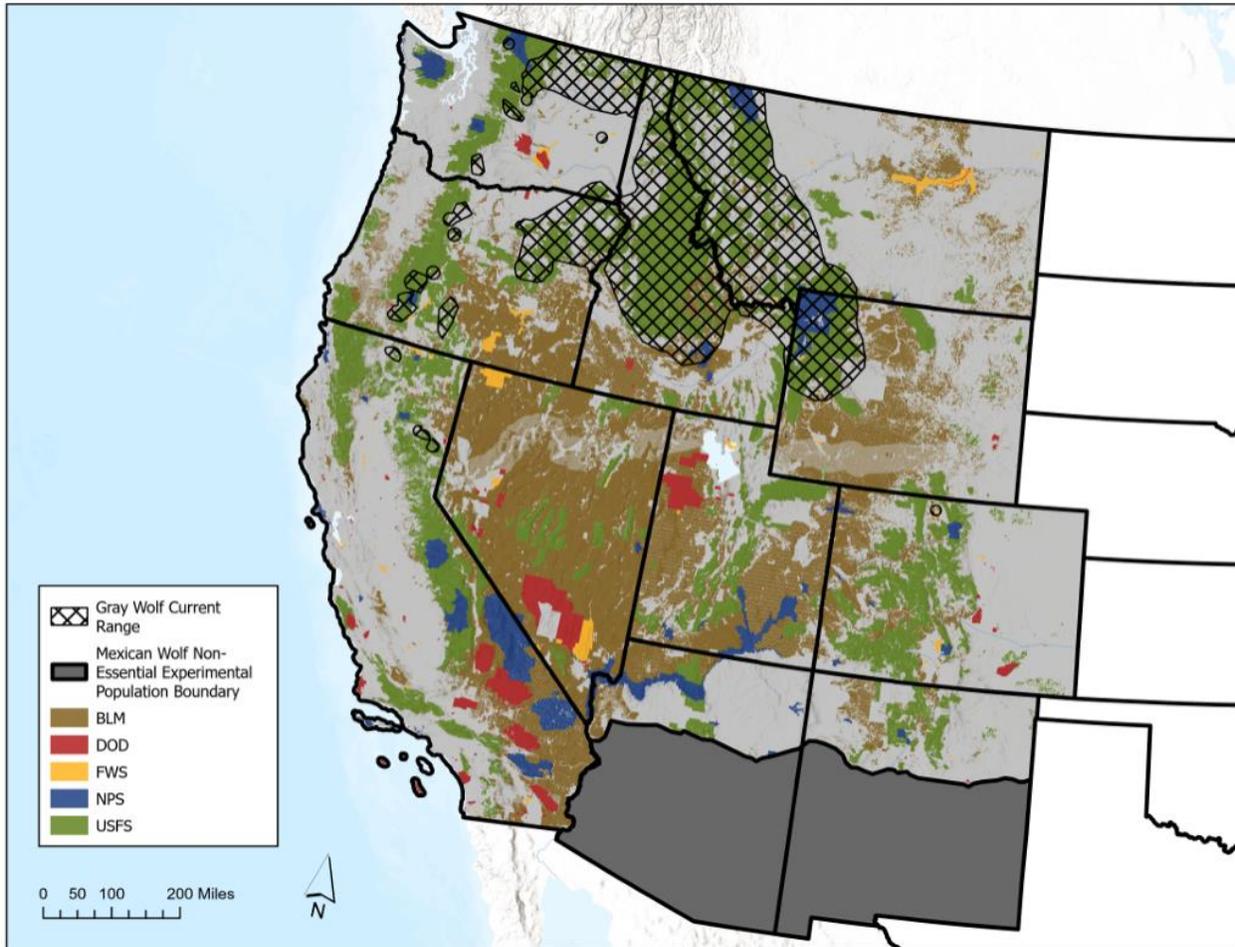


Figure 6. Primary Federal land management agencies in our analysis area. Federal land ownership includes BLM, Department of Defense (DOD), the Service (FWS above), NPS, and the U.S. Forest Service (USFS). [Source for Federal land ownership data: BLM 2022].

Some wolves inhabit National Parks (four percent of current wolf range in the Western United States, or approximately 6,087 mi<sup>2</sup> (15,765 km<sup>2</sup>)) and National Wildlife Refuges (less than 1 percent of current wolf range in the Western United States, or approximately 244 mi<sup>2</sup> (632 km<sup>2</sup>)) in the Western United States. Within National Parks, hunting is not allowed unless the authorizing legislation specifically provides for hunting. National Wildlife Refuges operate under individual Comprehensive Conservation Plans, which guide their management. None of the National Parks within the current distribution of the wolf in the Western United States allow wolf hunting within their boundaries. Hunting 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>). Wolves in National Parks and National Wildlife Refuges in the Western United States are monitored in coordination with the wildlife agencies in those states. Some wolves on the border of National Parks or National Wildlife Refuges may be available to hunting and other forms of human-caused mortality when they leave these Federal land management units. Overall, National Parks and National Wildlife Refuge lands are managed in such a way as to provide habitat for wildlife, including wolves and their prey.

The Forest Service manages 52 percent of current wolf range in the Western United States and the BLM manages 6 percent of current wolf range in the Western United States (approximately 74,150 mi<sup>2</sup> (192,047 km<sup>2</sup>) and 8,797 mi<sup>2</sup> (22,784 km<sup>2</sup>), respectively). The Forest Service and BLM manage for multiple uses, including providing habitat for fish and wildlife such as wolves. The other uses include, but are not limited to, providing opportunities for outdoor recreation (including hunting and trapping), livestock grazing, 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 wolves, the Forest Service and BLM work with Federal and state partners to identify and implement management strategies consistent with state plans to minimize wolf conflict risk on Federal lands. Forest Service Manual 2670.22 requires National Forests to develop and implement practices to ensure species do not become federally listed, and to maintain viable populations of all native and desired nonnative wildlife, fish, and plant species in habitats on National Forest System lands. Manual guidance also directs the Forest Service to assist states in achieving their species conservation goals.

On some Forest Service and BLM lands, livestock grazing increases the likelihood of wolf-livestock conflict, which may increase the chances of wolf mortality from lethal removal of wolves that repeatedly deplete livestock where the species is under state management in the Western United States (see *Lethal Control of Depredating Wolves* and *Levels of Human Caused Mortality*, above). In recent years, 216,217 mi<sup>2</sup> (560,000 km<sup>2</sup>) of BLM land and 120,078 mi<sup>2</sup> (311,000 km<sup>2</sup>) of Forest Service land were used for livestock grazing (Congressional Research Service 2017, p. 2). Within the current range of the gray wolf in the West, approximately 25 percent (35,673 mi<sup>2</sup> (92,393 km<sup>2</sup>)) is within a Forest Service grazing allotment and approximately 10 percent (13,936 mi<sup>2</sup> (36,094 km<sup>2</sup>)) is within a BLM grazing allotment. We discuss the effects of addressing conflicts between wolves and livestock in our overview of human-caused mortality above (see *Lethal Control of Depredating Wolves*). While lethal control can result in disruption of packs, or even the removal of entire packs, overall, the level of lethal removal in response to livestock depredations across the wolf's range in the Western United States has not prevented the growth and expansion of wolf populations.

The Wilderness Act of 1964 established a system for preserving wilderness areas on Federal lands. Wilderness areas 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 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 wolves in the upper Midwest, wolf survival rates were higher within wilderness areas compared to surrounding Federal land (Barber-Meyer et al. 2021, pp. 10–11). It is likely that large wilderness areas also provide refugia for wolves in the Western United States. Of the 63 percent of the wolf's current

range that is Federal land, 21 percent is designated as a wilderness area (18,595 mi<sup>2</sup> (48,161 km<sup>2</sup>) of designated wilderness areas within the current range of wolves) (Figure 7). Overall, 13 percent of the gray wolf's current range in the Western United States is designated as a wilderness area.

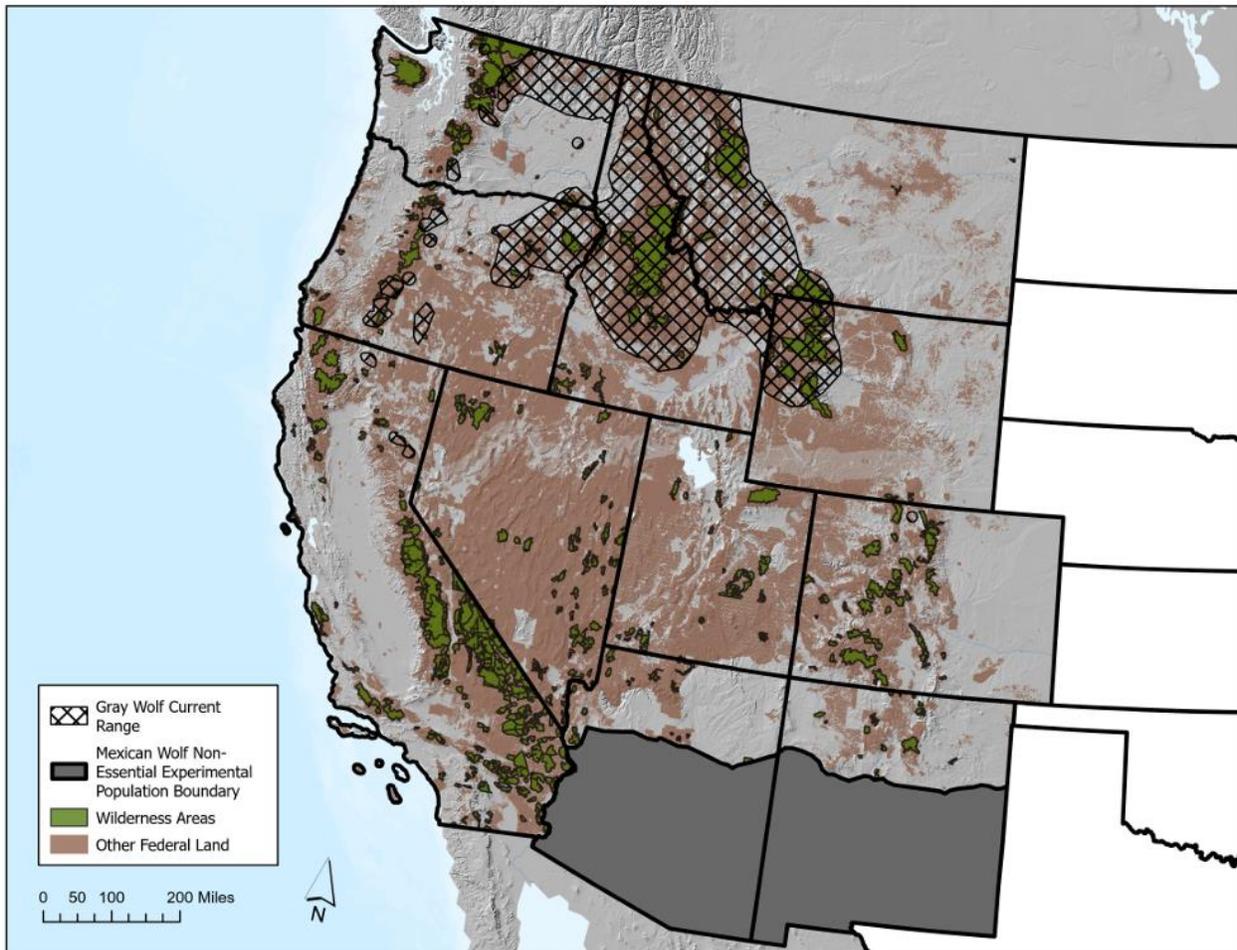


Figure 7. Federal land and wilderness areas within our analysis area. [Source for Federal land ownership: BLM 2022; Source for wilderness areas: U.S. Geological Survey (USGS) Gap Analysis Project (GAP) 2020]

## Summary of Stressors and Conservation Efforts

In the Western United States, the primary stressor influencing wolf populations is human-caused mortality. The main sources of human-caused mortality are harvest (regulated by states and some Tribes in Idaho, Montana, Washington, and Wyoming), lethal control of wolves depredate livestock in the delisted NRM, and illegal take. All states and some Tribes within the current range of gray wolves have statutes and regulations that govern take and conservation 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 substantial reductions in wolf abundance throughout

the Western United States; in fact, despite ongoing human-caused mortality, wolves were able to expand into previously unoccupied habitat in Western Oregon and Washington, California, and, more recently, wolves have been documented in Colorado. Additionally, the best available science indicates that disease in wolves has caused episodic, yet short-term and localized population decreases. In some circumstances, disease outbreaks can interact with density-dependent mortality to regulate population sizes at lower levels than prior to the introduction of the disease(s) (e.g., DeCandia et al. 2021, p. 430). Chapters 5 and 6 present information on modeled future scenarios with increased rates of harvest and disease, and they include a discussion of the potential for future climate-related changes in disease distribution, frequency, and severity. Finally, we also 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 depression in this SSA analysis, we do not specifically analyze the effect of diseases in prey species, climate change, or other sources of habitat modification on 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 wolf population declines in the Western 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 wolf populations. Moreover, each state within the range of wolf species in the Western United States has comprehensive ungulate management plans and strategies to address disease outbreaks and manage for sustainable populations of ungulates. 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 Western United States, nor do we expect it to do so in the future. Habitat modification as a result of the human footprint or wildfire is not a primary stressor on wolf populations; based on the best available scientific information, the impacts of these sources are localized relative to the 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.

## Chapter 4: Current Condition

### Current Resiliency

The current availability of the gray 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 the Western United States characterizes the current resiliency of wolves in the Western United States. In Chapter 3, we summarized our evaluation of potential stressors and conservation efforts that influence the condition of wolves in the Western United States. Human-caused mortality is the primary stressor that currently influences the resiliency of wolves in the Western United States. According to the best available science, disease also causes episodic, yet short-term and localized population decreases. Below, we discuss the current condition of the resource and demographic factors that gray wolves require and examine whether these stressors are compromising the gray wolf's current viability in the Western United States.

### Current Habitat Availability

Gray wolves are habitat generalists, meaning they can thrive in a variety of habitats (Mech and Boitani 2003, p. 163). To identify areas of suitable wolf habitat in the conterminous United States, researchers have used computational models that relate the distribution of wolves to characteristics of the landscape. These models have shown the presence of wolves is positively correlated with prey density; large, contiguous areas of Federal land ownership; large habitat patches; and forest cover (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; Rich et al. 2013, pp. 1284–1286; Ausband et al. 2014, pp. 341–342; Mech 2017, pp. 312–315; Hanley et al. 2018a, pp. 8–11; Petracca et al. 2023a, Appendix S4). The presence of wolves is negatively correlated with higher livestock density; higher road density; higher human density; presence of agricultural land uses; and small, fragmented habitat patches (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; Rich et al. 2013, pp. 1284–1286; Ausband et al. 2014, pp. 341–342; Mech 2017, pp. 312–315; Hanley et al. 2018a, pp. 8–11; Petracca et al. 2023a, Appendix S4). At finer spatial scales (i.e., within their home range or territory), wolves appear to select simple topography where ungulate prey may be more susceptible (Peterson et al. 2021, pp. 9–19; Sells et al. 2021, pp. 5–8; Sells et al. 2022b, p. 4). Aside from prey availability and susceptibility, these environmental variables are proxies for the likelihood of wolf-human conflict and the ability of 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 limited human access, high amounts of escape cover, or relatively low numbers of wolf-livestock conflicts. 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 escape cover without agricultural land) (see Mech 2017, pp. 312–315). Table 4 below summarizes the estimates of suitable habitat in each state in our analysis area from each of these modeling efforts.

Table 4. Estimated area of modeled suitable gray wolf habitat by state.

State	Estimated Area of Suitable Gray Wolf Habitat mi <sup>2</sup> (km <sup>2</sup> )	Data Source(s)
Idaho	27,804–46,111 (72,012–119,428)	Oakleaf et al. 2006; Ausband et al. 2014
Montana	26,830 (69,490) <sup>a</sup>	Oakleaf et al. 2006
Wyoming	11,091 (28,725) <sup>b</sup>	Oakleaf et al. 2006
Washington	16,900–41,500 (43,770–107,485)	Wiles et al. 2011; Maletzke et al. 2016
Oregon	26,448–41,256 (68,500–106,853)	Larson and Ripple 2006; ODFW 2019a
California	23,200 (60,088) <sup>c</sup>	CDFW 2016b
Colorado	24,770–50,781 (64,155–131,522)	Bennett 1994; Ditmer et al. 2022a
Utah	13,900 (36,000)	Switalski et al. 2002
Arizona and New Mexico (N. of I-40)	30,973 (80,219)	Service 2014

<sup>a</sup>Estimate for Western Montana only.

<sup>b</sup>Estimate for Northwest Wyoming only.

<sup>c</sup>Estimate for Northern California only.

We developed a generalized map of potentially suitable habitat by identifying ecological subregions (McNab et al. 2007, entire)—a national framework of ecological units (Bailey 1995, entire; Bailey 2016, map)—containing relatively large blocks of modeled suitable habitat based on the above gray wolf modeling studies (Figure 8). We used these ecological subregions to delineate suitable habitat because they represent regions with unique ecological characteristics that have relatively homogenous physical and biological components, landscape productivity, and responses to disturbance; they also provided a common mapping scale. We did not include those ecoregional provinces where there were relatively small patches of modeled habitat that were fragmented or isolated (e.g., in Northern and Southeastern Nevada; see Carroll et al. 2006, pp. 27–32). Habitat and population models show that, if human-caused wolf mortality is sufficiently regulated, wolves will likely continue to recolonize areas of the Pacific Northwest (Larson and Ripple 2006, p. 31; Maletzke et al. 2016, entire; ODFW 2019a, entire), California (CDFW 2016b, pp. 153–162; Nickel and Walther 2019, pp. 386–389); and the central and southern Rocky Mountains (Bennett 1994, pp. 56–112; Switalski et al. 2002, pp. 11–15; Carroll et al. 2006, pp. 27, 31–32; Ditmer et al. 2022a, pp. 7–12).

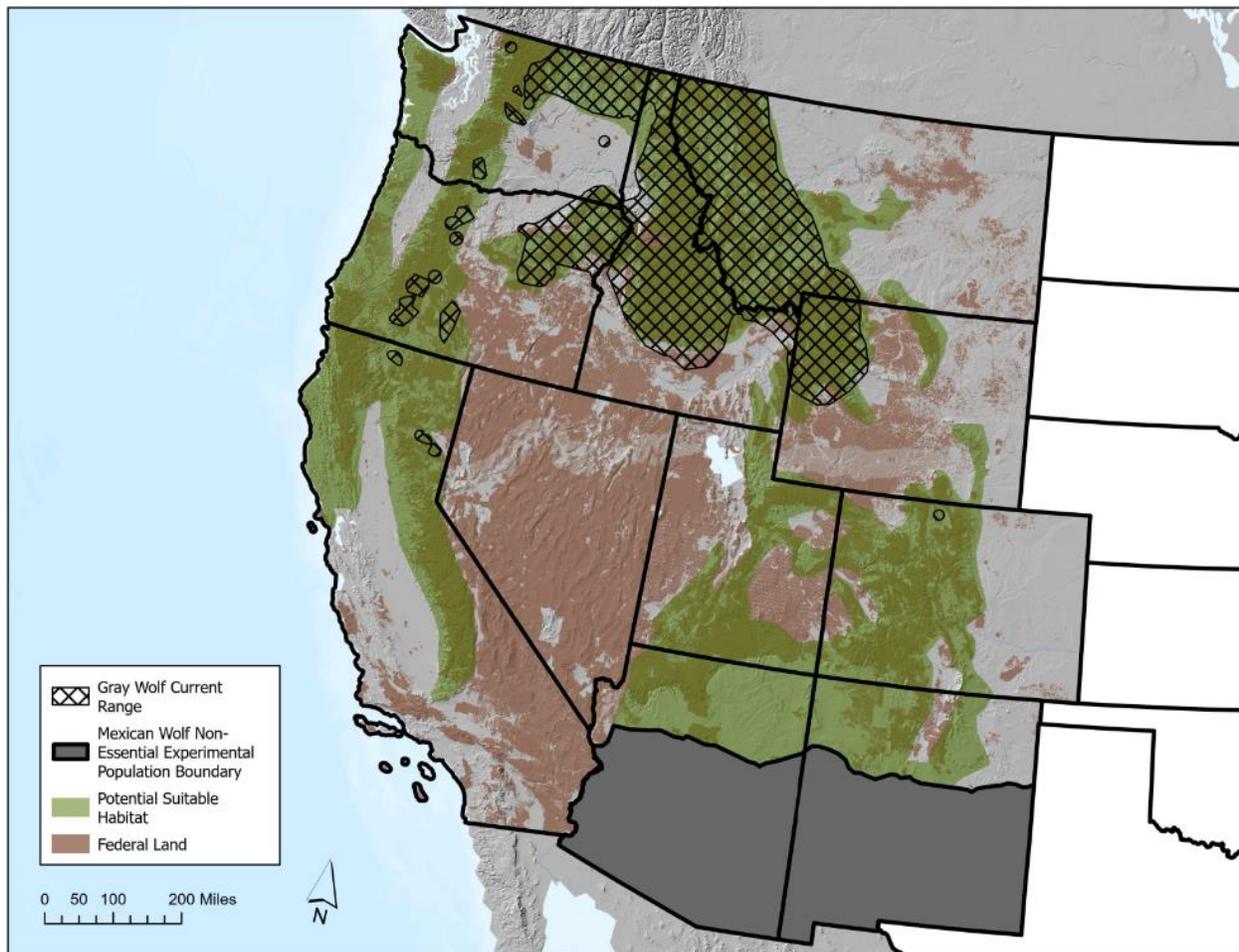


Figure 8. Potentially suitable gray wolf habitat, Federal land, and current range of the gray wolf in the Western United States. Our potentially suitable habitat map was developed as a coarse-scale visual aid based on ecological subregions and is not intended to provide a fine-scale rendering of gray wolf suitable habitat across the Western United States. The gray wolf's current range in the Western United States is in the cross-hatched area. The Mexican Wolf Nonessential Experimental Population Area is colored in dark gray.

Idaho, Montana, and Wyoming were selected for wolf reintroduction and recovery because they contained some of the best suitable habitat for wolves in the Western United States (Carroll et al. 2006, Figure 6; 74 FR 15123, April 2, 2009; 77 FR 55530, September 10, 2012). Suitable wolf habitat in these states is characterized by relatively large blocks of undeveloped public lands that contain some of the largest wilderness areas in the conterminous United States, abundant year-round wild ungulate populations, low road densities, relatively low numbers of seasonally grazed domestic livestock, low agricultural land uses (i.e., irrigated fields, crops, etc.), and few people (Carroll et al. 2006, pp. 27–31; Oakleaf et al. 2006, pp. 555–558). Large wilderness areas, which have more limited human access, provide refugia for wolves (Barber-Meyer et al. 2021, pp. 10–11); in a 50-year study of wolves in the upper Midwest, wolf survival rates were higher within wilderness areas, even compared to surrounding Federal land (Barber-Meyer et al. 2021, pp. 10–11). Some large national parks can also provide refugia in this region. Based on a wolf habitat model that considered: roads accessible to two-wheel and four-wheel drive vehicles, topography (slope and elevation), land ownership, relative ungulate density

(based on state harvest statistics), cattle (*Bos* sp.) and sheep density, vegetation characteristics (ecoregions and land cover), and human density, there is an estimated 65,725 mi<sup>2</sup> (170,228 km<sup>2</sup>) of suitable habitat in Idaho, Montana, and Wyoming (Oakleaf et al. 2006, pp. 555–559) (see Table 4). The current distribution of wolves in Idaho, Montana, and Wyoming generally mirrors Oakleaf et al.’s (2006, p. 559) prediction of suitable habitat, indicating that their analysis is a reasonable approximation of where suitable habitat exists in these three states. Carroll et al. (2004, p. 1118) predicted a 26.4 percent loss in long-term carrying capacity of the wolf in the NRM based on forecasted land use changes and human population growth from 2000–2025. However, regulated harvest and wolf control efforts are more likely to set the wolf carrying capacity in the NRM than the landscape features evaluated by Carroll et al. (2004, entire).

In Washington, wolves are expected to maintain packs and become established in habitats with similar characteristics to those identified by Oakleaf et al. (2006) (see Wiles et al. 2011, p. 50) and as described above. Several modeling studies have estimated potentially suitable wolf habitat in Washington with most predicting suitable habitat in northeastern Washington, the Blue Mountains, the Cascade Mountains, and the Olympic Peninsula (Ratti et al. 2004, entire; Wiles et al. 2011, pp. 51, 53; Maletzke et al. 2016, p. 370; Petracca et al. 2023a, Appendix S4). Total area estimates of suitable habitat in Washington range from approximately 16,900 mi<sup>2</sup> (43,770 km<sup>2</sup>) to 41,500 mi<sup>2</sup> (107,485 km<sup>2</sup>) (Wiles et al. 2011, pp. 51, 53; Maletzke et al. 2016, p. 370).

In Oregon, ODFW estimated suitable habitat to cover an area of approximately 41,256 mi<sup>2</sup> (106,853 km<sup>2</sup>) primarily in northeast Oregon, the Cascade Mountains and foothills, the Klamath-Siskiyou region in southwest Oregon, and the Coast Range. Their assessment considered land-cover type, elk range, human population density, road density, and land types altered by humans (ODFW 2019a, p. 147, Appendix D). Another model that included information on prey availability, human presence, landscape characteristics, and the additive effects of these factors, estimated that there were approximately 26,448 mi<sup>2</sup> (68,500 km<sup>2</sup>) of suitable habitat for gray wolves in Oregon, in the same general regions of the state identified by ODFW (Larsen and Ripple 2006, pp. 25–26).

In California, CDFW projected wolf habitat using models from other areas of the Western United States (Carroll et al. 2006, entire; Larsen and Ripple 2006, entire; Oakleaf et al. 2006, entire; CDFW 2016b, pp. 153–157). They found that wolves are most likely to occupy three general areas: (1) the Klamath Mountains and portions of the northern California Coast Ranges; (2) the southern Cascades, the Modoc Plateau, and Warner Mountains; and (3) the Sierra Nevada Mountain Range (CDFW 2016b, p. 20). CDFW (2016b, p. 159) estimated potential wolf habitat in the northern part of California to encompass approximately 23,200 mi<sup>2</sup> (60,088 km<sup>2</sup>). Using a different approach and modeling technique, Nickel and Walther (2019, pp. 387–398) largely affirmed CDFW’s conclusions regarding areas likely to have a high potential for wolf recolonization.

In Colorado, Bennett (1994, pp. 56–112) used a series of screening and ranking criteria—including prey availability, human access and density, and livestock use—to estimate the area of suitable habitat in “potential wolf recovery areas.” Using these methods, Bennett (1994, pp. 56–112) identified seven potential wolf recovery areas in Colorado totaling 24,770 mi<sup>2</sup> (64,155 km<sup>2</sup>). The seven potential wolf recovery areas, which roughly correspond to National Forests of the

same names, were identified as: (1) Grand Mesa Uncompahgre-Gunnison, (2) Rio Grande, (3) Arapaho-Roosevelt, (4) Routt, (5) Pike-San Isabel, (6) San Juan, and (7) White River (Bennett 1994, pp. 94–107). Carroll et al. (2003, entire) examined multiple models to evaluate suitable wolf habitat, occupancy, and the probability of wolf persistence given various landscape changes and potential increases in human density in the southern Rocky Mountains, which included portions of Colorado, Northern New Mexico, and Southeast Wyoming. Using a resource selection function model developed for wolves in the Greater Yellowstone Ecosystem and projecting it to Colorado, Carroll et al. (2003, pp. 541–542) identified potential wolf habitat across north-central and northwest Colorado and also in the Southwestern part of the state. Resource selection function model predictions indicate that 87 percent of the area available for wolves to occupy in Colorado is on public lands. Recently, Ditmer et al. (2022a, entire) developed a habitat suitability model for Colorado that incorporated seasonal livestock use, prey availability, land ownership, and perceived human tolerance to identify relative habitat suitability for wolves across the state. They found that Western Colorado had significant areas of potentially ecologically and socially suitable habitat for wolves. Specifically, they reported that northwest Colorado had the highest relative ecological suitability for wolves in the state, but also the highest potential for conflict with livestock (Ditmer et al. 2022a, pp. 7–9). Southwest Colorado had lower ecological suitability than northwest Colorado, although still relatively high ecological suitability and relatively large areas of connected protected lands, as well as less potential for conflict with livestock (Ditmer et al. 2022a, pp. 7–9). The Front Range also contained some areas of suitable wolf habitat but in lower proportions than found in Western Colorado (Ditmer et al. 2022a, pp. 7–9).

In Utah, a wolf habitat suitability model was developed to identify areas most likely to support wolf occupancy in the state (Switalski et al. 2002, pp. 11–15). The model evaluated five habitat characteristics that included estimates of prey abundance, estimates of road density, proximity to year-round water sources, elevation, and topography. Although the resulting model identified primarily forested and mountainous areas of Utah as suitable wolf habitat, an area over 13,900 mi<sup>2</sup> (36,000 km<sup>2</sup>), it was highly fragmented as a result of high road densities. Nonetheless, six relatively large core areas of contiguous habitat were identified that ranged in size from approximately 127 mi<sup>2</sup> to 2,278 mi<sup>2</sup> (330 km<sup>2</sup> to 5,900 km<sup>2</sup>) (Switalski et al. 2002, p. 13).

Arizona and New Mexico have large areas (Table 4) of unoccupied suitable wolf habitat north of I-40 (30,973 mi<sup>2</sup> (80,219 km<sup>2</sup>)) (Service 2014, p. 5); however, the quality of habitat in northern Arizona is fragmented with limited prey (Gray 2021, in litt., p. 1, 4). In areas south of I-40, the Service has promoted the recovery of the Mexican wolf (Service 2022b, entire) within an area of suitable wolf habitat equivalent in size to the areas north of I-40 (32,244 mi<sup>2</sup> (83,512 km<sup>2</sup>)) (Table 4) (Service 2014, pp. 1–25).

There are no habitat models for wolves specific to Nevada. Carroll et al. (2006, pp. 27, 32) included Nevada in their assessment of wolf habitat across the Western United States and found very little suitable habitat there, much of which was fragmented or isolated. Therefore, we did not include any ecoregional provinces in Nevada in our maps of suitable wolf habitat (Figure 8).

In summary, based on our evaluation of the extent of suitable habitat in the Western United States (Table 4), sufficient suitable habitat remains for a viable gray wolf metapopulation.

### 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 exist at densities 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. 2020a, p. 92). Based on a meta-analysis of 41 studies from across North America, the relationship of wolves/1,000km<sup>2</sup> (y) to a prey index of deer equivalents/1,000km<sup>2</sup> (x) was  $y = 5.12 + 0.0033x$  ( $r^2 = 0.71$ ) (Mech and Peterson 2003, p. 148) meaning that a 1,000km<sup>2</sup> area with 10,000 deer equivalents could theoretically support roughly 38 wolves. However, the numerical response of wolves to prey density is not always linear and there are real world complexities not captured in this coarse-scale relationship, especially in multi-prey systems (Mech and Peterson 2003, pp. 147–155; Cariappa et al. 2011, pp. 728–729). 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. 2020a, 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). To provide a basic assessment of the amount of prey available for wolves in the Western United States, we reviewed ungulate population estimates from state fish and game 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. We also discuss wolf population growth and expansion over the past several decades in the Western United States as evidence of the sufficiency of the current prey base.

Wild ungulate prey in Idaho, Montana, and Wyoming is composed mainly of elk, but also includes deer, moose, and—in the GYA—bison (Metz et al. 2020, pp. 159–162). Bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and pronghorn antelope are also common, but they are relatively unimportant as wolf prey. For the last several decades, ungulate populations have been sufficient to grow and sustain a population of over 2,000 wolves spread across Idaho, Montana, and Wyoming (Table 5). These states have sustainably managed resident ungulate populations for decades and continue to manage ungulate populations to provide public harvest and viewing opportunities. In total, recent state population estimates indicate that, in Idaho, there are approximately 120,000 elk (range: 114,000–124,000), 250,000 mule deer, 300,000–350,000 white-tailed deer, and 6,000–10,000 moose (IDFG 2022c, in litt.); in Montana, there are approximately 142,000 elk (MFWP 2021b, entire), over 294,000 mule deer (MFWP

2021c, entire), and almost 214,000 white-tailed deer (MFWP 2021d, entire); and, in northwest Wyoming there are an estimated 50,000 elk outside of YNP, approximately 10,000 to 20,000 elk in YNP in summer, 4,000 elk in YNP in winter (NPS 2020a, entire), and 5,000 bison (NPS 2020b, entire; WGFD 2022a, entire; WGFD 2022b, entire; WGFD 2022c, entire; WGFD 2022d, entire). Although regional estimates of deer in northwest Wyoming were not readily available, there are approximately 396,000 mule deer in the state (Mule Deer Working Group 2018, p. 1).

In Washington, WDFW recently conducted a Wildlife Program 2015–2017 Ungulate Assessment to identify ungulate populations that are below management objectives or may be negatively affected by predators (WDFW 2016, entire). The assessment covered: white-tailed deer, mule deer, black-tailed deer (*Odocoileus hemionus columbianus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), Roosevelt elk (*Cervus elaphus roosevelti*), bighorn sheep, and moose (WDFW 2016, p. 12). Washington defines an at-risk ungulate population as one that falls 25 percent below its population objective for 2 consecutive years and/or one in which the harvest decreases by 25 percent below the 10-year-average harvest rate for 2 consecutive years (WDFW 2016, p. 13). Based on available information as of 2021, no ungulate populations in Washington were at-risk (WDFW 2021, entire). However, a severe drought in 2015 followed by a severe winter in 2016 caused declines in harvest estimates for white-tailed deer and mule deer (WDFW 2021, entire). As of 2020, elk populations were below management objectives in 4 of the 10 elk herds (WDFW 2021, entire). The mule deer population estimate in 2021 for Washington was 90,000 to 110,000 deer (Western Association of Fish and Wildlife Agencies 2021, p. 2). There were an unknown number of black-tailed deer. Elk populations numbered in the tens of thousands, although no statewide estimate was provided in WDFW’s 2021 statewide *Game Status and Trend Report* (WDFW 2021, entire).

In Oregon, ODFW recently estimated there were approximately 60,000 Roosevelt elk and 72,000 Rocky Mountain elk in the state (ODFW 2019a, p. 66). Mule deer and black-tailed deer populations peaked in the mid-1900s and have since declined, likely due to human development, changes in land use, predation, and disease (ODFW 2019a, p. 66). In 2021, the mule deer population in Oregon was estimated at 163,007 deer (ODFW 2021a, unpaginated). The most recent black-tailed deer estimate for Oregon was approximately 320,000 deer (ODFW 2019a, p. 66). White-tailed deer populations, including Columbian white-tailed deer (*Odocoileus virginianus leucurus*), are small, but are increasing in distribution and abundance (ODFW 2019a, p. 69).

In California, areas with ungulate densities most likely to support wolf recolonization, include the Klamath Mountains, Coast Ranges, and Sierra Nevada (Nickel and Walther 2019, p. 386). Prey densities in these areas ranged from 0.17 to 1.39 deer-equivalent units/mi<sup>2</sup> (0.45 to 3.6 deer-equivalent units/km<sup>2</sup>), with deer forming the vast majority of available ungulate prey (Nickel and Walther 2019, pp. 386–387). Deer populations (mule deer and black-tailed deer, combined) are estimated at approximately 175,000 deer within the area of northern California most likely to be initially recolonized by wolves (CDFW 2016b, p. 89). In addition, there are an estimated 5,100 tule elk throughout California in 22 separate herds; and four populations of Rocky Mountain elk totaling 1,500 to 2,000 animals, which occur in portions of Modoc, Kern, San Luis Obispo, Lassen, Shasta, and Siskiyou counties (CDFW 2016b, p. 82). Roosevelt elk populations currently exist in areas of Del Norte, Humboldt, Mendocino, and Shasta counties, as

well as within the Cascade and Klamath mountains in Siskiyou and Trinity counties; CDFW currently estimates the Roosevelt elk population at 5,000 to 6,000 individuals (CDFW 2016b, p. 82).

CPW manages ungulate populations using *Herd Management Plans*, which establish population objective minimums and maximums for each ungulate herd in the state (CPW 2019, unpaginated). The *Herd Management Plans* consider both biological and social factors when setting herd objective ranges. The following information on ungulates is from unpublished data provided by CPW (CPW 2022). Similar to other Western states, mule deer in Colorado have declined due to a multitude of factors since the 1970s to a statewide post-hunt population estimate of 416,430 animals in 2021, which was well below the target statewide population objective of 484,100. In 2021, of 54 mule deer herds in Colorado, 18 were below their population objective minimum with the Western part of the state being the most affected. In contrast, elk populations in Colorado are stable with a 2021 post-hunt population estimate of 308,920 elk. Although 34 of 42 elk herds are within or above the population objective range, the ratio of calves per 100 cows (a measure of overall herd fitness) has been on the decline in some Southwestern herd units (CPW 2019, p. 8). Moose are not native to Colorado so, to create hunting and wildlife viewing opportunities, CPW transplanted moose to the state beginning in 1978. Since then, they transplanted moose on four other occasions through 2010. The 2021 post-hunt moose population was estimated at 3,510 animals and continues to increase as moose expand into new areas of Colorado. In summary, while deer and elk numbers are down from their peak populations in some parts of Colorado, they still number in the hundreds of thousands of individuals, and the state is actively managing populations to meet objectives. Introduced moose provide an additional potential food resource for wolves in some parts of Colorado.

The UDWR manages ungulate populations by establishing population objectives at the herd unit level and directing management efforts, primarily through public harvest, to achieve population goals for each herd unit. The summation of herd unit objectives can be considered a statewide objective for the species. The mule deer population in Utah consists of approximately 312,900 deer, which is below the state's objective of 404,900 deer (Hersey 2022, in litt.). Recently mule deer numbers have been declining due to drought. Elk populations in Utah have increased from an average of slightly over 60,000 from 1995 to 2005 to approximately 80,000 between 2012 and 2020 (UDWR 2021, pp. 111–112). The 2020 statewide elk population estimate was 80,320 elk, which is marginally higher than the statewide population objective of 78,990 elk. Moose are relatively recent migrants to Utah, first being documented in the early 1900s. Since that time, moose have dispersed, or been transplanted, to occupy suitable habitats primarily in the northern half of the state (UDWR 2021, p. 178).

The primary prey species for wolves in Arizona and New Mexico north of I-40 are elk and mule deer. Elk are abundant in Arizona and New Mexico, inhabiting mixed habitat types including mountain meadows, ponderosa pine woodlands, spruce-fir forests, and other high elevation habitats between 7,000–10,500 feet (ft) (~2134–3200 meters (m)) in elevation. Arizona Game and Fish Department (AGFD) and New Mexico Department of Game and Fish (NMDGF) manage elk herds to stabilize or slightly increase herds (Service 2022c, pp. 47–51). In areas south of I-40, approximately 74,500 to 87,600 elk occur in the two states (Service 2022c, pp. 47–51). Additional elk herds occur north of I-40 (Service 2022c, p. 48; New Mexico

Game and Fish 2023, p. 8–9), although, in Arizona, herds are primarily limited to the south rim of the Grand Canyon and north of Flagstaff (Gray in litt. 2021, p. 4). Mule deer are found throughout Arizona and New Mexico in the higher elevation forests and shrublands in the northern parts of the states and chaparral, desert grasslands, and deserts in the southern portions. Mule deer population trajectories in the arid Southwest are primarily related to moisture events. Frequent droughts can keep population sizes relatively low; however, when there are consecutive years of normal precipitation, mule deer populations respond quickly and increase. Populations of mule deer are estimated to exceed 160,000 animals in the two states (Service 2022c, pp. 51–52).

Other species of potential prey include white-tailed deer, bighorn sheep, and antelope. In Arizona, there is only one subspecies of white-tailed deer, the Coues' white-tailed deer (*O.v. couesi*). Coues' deer are most common in Arizona's southeastern mountains, inhabiting all of the Sky Islands south of I-10, but range up to the Mogollon Rim and into the White Mountains. The Arizona statewide population of white-tailed deer, not including tribal lands, was estimated at 60,000–85,000 post-hunt adults in 2018 (Service 2022c, p. 53 and references therein). In New Mexico, Coues white-tailed deer occupy the western half of the state and Texas white-tailed deer (*O.v. texanus*) occupy the eastern half of the state. Overall, we do not expect white-tailed deer to contribute substantially to total prey biomass for wolves in these two states because of their low densities and scattered distribution in areas of suitable wolf habitat (Service 2022c, p. 53). Other prey species exist in Arizona and New Mexico (e.g., bighorn sheep, antelope), but we do not expect wolves to prey on these species on a consistent basis.

In summary, prey availability is an important factor in maintaining wolf populations. Native ungulates (e.g., deer, elk, and moose) are the primary prey within the range of gray wolves in the Western United States. Each state within wolf-occupied 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., MFWP 2021e, entire). Based on decades of sustained wolf range expansion in the Western United States, as well as our evaluation of prey numbers, 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***

From the outset of wolf recolonization and reintroduction in the NRM, significant effort was placed on using traditional monitoring techniques (e.g., capture and radio-collar wolves, monitor from the ground and air) to document wolf abundance and distribution by providing minimum counts at the end of each calendar year (Jimenez and Cooley 2012, entire). Although approved and effective capture and monitoring protocols minimize the risk of injury or death, there is always a certain amount of risk associated with the capture and monitoring of wildlife (Sasse 2003, entire; Sikes et al. 2016, entire). Furthermore, capturing and monitoring wolves

from the air and ground is costly and time-consuming, and counts become less precise as wolf abundance and distribution increase (i.e., managers cannot directly count every animal) (Gude et al. 2012, p. 116; Sells et al. 2020, p. 5; Thompson et al. 2022, pp. 3–4). The Service was aware of these constraints in providing accurate minimum counts, especially where populations were large, well-distributed, and in which a high proportion of radio collars were lost due to public harvest (Jimenez and Cooley 2012, entire).

Due to these constraints, both Idaho and Montana have been at the forefront in developing methodologies more applicable to estimating abundance of widely distributed and larger wolf populations than minimum counts could accurately document. For example, in 2006, based on similar methodology used to estimate wolf abundance in Minnesota, Idaho began using an equation that provided a minimum estimate of wolves in the state (Nadeau et al. 2007, pp. 66–67). Similarly, beginning in 2007, Montana began work to develop alternative population estimation techniques based on patch occupancy modeling methods (Miller et al. 2013, entire; Rich et al. 2013, entire). Both before and after delisting, Idaho and Montana explored alternate methods to monitor wolf populations and continued to refine and improve on the new methodologies to estimate wolf abundance in their respective states. As a result, numerous peer-reviewed manuscripts have been published on the topic (Ausband et al. 2010, entire; Stenglein et al. 2010, entire; Stenglein et al. 2011, entire; Miller et al. 2013, entire; Rich et al. 2013, entire; Ausband et al. 2014, entire; Stansbury et al. 2014, entire; Loonam et al. 2020, entire; Sells et al. 2020, entire; Loonam et al. 2021, entire; Sells et al. 2021, entire; Ausband et al. 2022; Sells et al. 2022a, entire; Sells et al. 2022b, entire; Sells et al. 2022c, entire). Although these new methods to estimate abundance involve detection rates that are less than 100 percent, in which not all animals included in the population estimate are directly observed/counted, they can improve on accuracy and are more cost-effective than minimum counts (Sells et al. 2022c, p. 13; Thompson et al. 2022, p. 15). The Service fully supported state efforts to develop alternate methodologies to estimate wolf abundance in the NRM (Jimenez and Cooley 2012, entire). Based on this work in Idaho and Montana, other states, specifically Wisconsin, have developed and incorporated similar methodologies into their wolf management programs to estimate wolf abundance and distribution (Stauffer et al. 2021, entire; WI DNR 2022, entire), while other researchers continue to explore alternative wolf monitoring techniques that provide accurate counts/estimates, but do not require the use of radio collars (Brennan et al. 2013, entire; Stansbury et al. 2014, entire; Barber-Meyer et al. 2020, entire; O’Gara et al. 2020, entire; WDFW et al. 2022, pp. 35–36). Below, we provide a detailed summary of the methods for counting or estimating population size in each state in the Western United States.

Between 1995 and 2005, Idaho conducted minimum counts to document the number of wolves in the state. As wolf abundance and distribution increased, the ability to obtain accurate minimum counts became increasingly challenging (Nadeau et al. 2007, p. 66). Beginning in 2006, Idaho started to use an equation to estimate the minimum number of wolves in the state. This equation estimated wolf abundance by (1) obtaining an average pack size from packs with complete counts; (2) multiplying the average pack size by the number of known packs with incomplete counts; (3) adding these estimates to the total number of wolves in packs with complete counts; and (4) adding an estimate of lone wolves in the state (Nadeau et al. 2007, pp. 66–67). This method was used to estimate the minimum number of wolves and packs in the state through 2015. Between 2016 and 2018, Idaho did not estimate the total number of wolves or

packs in the state, but continued to explore, develop, and use other methods to estimate wolf abundance and monitor population trends. These other methods included:

- collecting biological samples of wolves at den and rendezvous sites to identify individuals through genetic analysis (Ausband et al. 2010, entire; Stenglein et al. 2010, entire; Stenglein et al. 2011, entire; Stansbury et al. 2014, entire);
- requiring mandatory checks of all harvested wolves to collect biological and genetic samples, which were then used to estimate the minimum number of reproductively active packs (i.e., packs that had litters) in the state each year (Clendenin et al. 2020, entire; Hebdon et al. 2022, in litt.);
- collecting incidental observations by the public and agency personnel (IDFG 2020, p. 5);
- monitoring the location and number of lethal control actions authorized by IDFG (IDFG 2020, p. 5);
- conducting limited wolf tracking via radio transmitters (IDFG 2020, p. 5);
- using multiple survey methods to estimate wolf occupancy in the state (Ausband et al. 2014, entire) and later using camera-based occupancy analyses (IOSC and IDFG 2022, in litt.; Thompson et al. 2022, pp. 4–10); and
- conducting camera-based monitoring to estimate wolf abundance in the state (“space-to-event modeling”) (Ausband et al. 2022, entire; IOSC and IDFG 2022, in litt.; Thompson et al. 2022, pp. 4–10).

As noted above, between 2016 and 2018, Idaho evaluated and developed camera-based methodology to estimate wolf occupancy across the state (“occupancy study”) (Ausband et al. 2022, entire; Thompson et al. 2022, pp. 4–6). Concurrent with this occupancy study, Idaho evaluated the use of a space-to-event (STE) model to estimate wolf abundance across three study areas in the state during summer 2016 to 2018 (Ausband et al. 2022, entire). Idaho selected an STE model because (1) it does not require identification of individuals or a count of the number of animals (it only requires information about presence) and (2) estimates are not affected by animal movement (Ausband et al. 2022, p. 2). Moreover, the STE model can be scaled up to larger areas, such as the entirety of the state of Idaho (Ausband et al. 2022, p. 2). STE models rely on various assumptions, including that cameras capturing animal presence are placed randomly, that each observation is independent of another, and that all animals within the viewshed of a camera are photographed (Thompson et al. 2022, p. 13). Between 2016 and 2018, when Idaho was testing the STE methodology, they chose to place cameras non-randomly (i.e., they stratified habitat based on predicted occupancy to place cameras in particular locations to ensure that an adequate number of detections occurred) (Thompson et al. pp. 4–7).

Since 2019, Idaho has used the STE model to estimate wolf abundance across the state (Thompson et al. 2022, entire). To do so, Idaho deploys remote cameras during the summer months (July 1 to August 31) (Thompson et al. 2022, pp. 6–8); Idaho continues to place these cameras non-randomly to ensure an adequate number of detections occur (e.g., they place more cameras in areas with a lower probability of occupancy) (Thompson et al. 2022, p. 6). After Idaho analyzes all of the images, they use the STE model to estimate wolf abundance across the state (Ausband et al. 2022, entire; Thompson et al. 2022, pp. 8–10). Using this method, IDFG estimates wolf populations near their peak in late summer and then uses a combination of known

and estimated mortality by month to calculate monthly wolf population estimates through the end of March of the following year (IDFG 2022b, entire). The wolf population estimate at the end of March may be considered a minimum estimate just before the birth pulse in April, when populations increase once again after the birth of pups. Throughout this chapter, we report the calendar year-end estimates (i.e., December estimates) for Idaho to be consistent with other states' annual reporting.

Loonam et al. (2020, entire) presented evidence that, in general, STE methods could be used to estimate densities of mountain lions, another sparsely distributed carnivore. Leo (2022, pp. 8–9) documented that STE methodologies used to estimate feral sheep abundance underestimated abundance when compared to aerial estimates. However, Leo (2022, pp. 8–9) also noted that STE estimates provided acceptable levels of accuracy and precision that reduced cost, time, and model complexity in the long term compared to aerial surveys of radio-collared individuals (provided that STE model assumptions are met).

Additionally, Loonam et al. (2021, entire) evaluated the robustness of time-to-event modeling (closely related to STE modeling) and determined that time-to-event modeling produces accurate estimates even when certain assumptions are violated (e.g., assumptions of no immigration/emigration, no territoriality, and no clustering). However, models were less accurate when cameras were placed non-randomly or when movement speed was inaccurately estimated (e.g., when managers use motion triggered cameras instead of time lapse cameras, they can inaccurately estimate this movement speed) (Loonam et al. 2020, pp. 7–8). As we discuss above, currently, Idaho places their cameras non-randomly in order to ensure adequate detection, which is a violation of these STE assumptions (Thompson et al. 2022, pp. 6–7). Furthermore, Thompson et al. (2022, pp. 6–7) describe the use of both motion triggered and time-lapse cameras to produce Idaho's STE estimates; however, they report how the detections from motion-triggered cameras are adjusted to account for potential bias used by these types of cameras. There are no quantifications of how much bias, if any, this non-random placement of cameras or the use of motion-triggered cameras (with the detections corrected as Thompson et al. (2022, pp. 6–7) describes) could produce. Ausband et al. (2022, pp. 4–5) compared estimates from the use of STE models in a portion of Idaho, and determined that in two of three years, the STE estimates closely matched the estimates from genetic mark-recapture efforts in the same portions of Idaho. However, it is not known how well these estimates from STE or genetic mark-recapture methods compare to the true numbers of wolves in the areas Ausband et al. (2022, pp. 4–5) studied. Idaho is continuing to evaluate STE methodology and how violations of model assumptions may bias STE abundance estimates (Thompson et al. 2022, pp. 13–15). Additionally, although population estimates obtained from STE methods are more economically feasible than Idaho's previous minimum count or estimation methods, these methods remain costly and labor intensive (Thompson et al. 2022, p. 15; IDFG 2023a, p. 36). As a result, IDFG continues to explore alternative wolf abundance estimation techniques (IDFG 2023a, pp. 36–37).

Montana used minimum counts to estimate wolf abundance through 2017 then transitioned to estimating wolf distribution and abundance solely using Patch Occupancy Modeling (POM) after 2017 (Rich 2010, entire; Miller et al. 2013, entire; Rich et al. 2013, entire). Montana began development of POM methods in 2007 and, as a result, much of the information needed to estimate wolf populations using this method was readily available starting

that year, which allowed them to retrospectively estimate wolf populations back to 2007 using POM. POM relies on accurate information on territory size, territory overlap, and pack size, which requires intensive field-based monitoring (Sells et al. 2020, pp. 9–10). As populations grew over time, intensive field monitoring became less effective and less reliable for providing accurate estimates of wolf territory size, territory overlap, and pack size (values that were necessary as POM inputs) (Sells et al. 2020, p. 5; Sells et al. 2022c, p. 13). Moreover, POM assumed wolf territory size did not vary across space and time (Sells et al. 2020, p. 47; Sells et al. 2022c, p. 13); however, wolf territory size does vary in Montana due to a host of factors, including ungulate and competitor densities, wolf group size, energetic costs of travel, and risk of mortality (Sells et al. 2021, pp. 5–8). Thus, MFWP adjusted POM and developed a multi-model approach called the integrated patch occupancy model (iPOM) that became the primary method to estimate wolf abundance and distribution in Montana beginning in 2020. iPOM incorporates an occupancy, territory, and group size model to estimate annual wolf occupancy and abundance in Montana based primarily on knowledge of wolf biology and behavior rather than intensive field monitoring (Sells et al. 2020, p. 5; Sells et al. 2022c, entire). Relative to POM, iPOM methods provide improved estimates of the number of packs and wolf abundance at statewide and regional scales, which allows managers to make more informed decisions regarding wolf management at multiple, relatively large spatial scales (Sells et al. 2022c, pp. 13–14). However, iPOM estimates may not be appropriate for estimating abundance and developing management strategies at a smaller spatial scale (such as specific hunt areas adjacent to YNP) (Stauffer et al. 2021, p. 1420). iPOM estimates of wolf abundance are higher than those resulting from POM, because POM did not accurately represent the spatial-temporal dynamics of wolf behavior (Sells et al. 2020, p. 47; Sells et al. 2022c, p. 13). Therefore, estimates of wolf abundance for Montana detailed in our 2020 Biological Report (Service 2020, Appendix 2, pp. 32–33) are different than the estimates we provide in Table 5 because the estimates in the 2020 Biological Report were based on POM rather than iPOM methods (the estimates in Table 5 were derived from iPOM methods).

Minimum counts, which Montana and Idaho used to estimate wolf population size prior to the mid-2000s and which Oregon, Washington, and Wyoming currently use, are obtained through direct monitoring. Minimum counts fail to account for imperfect detection (i.e., not all wolves are directly detected using direct counting methods) and have no quantifiable method for estimating error; this method has been criticized in the past for these reasons (Mallonee 2011, pp. 176–180). Given these sources of bias, minimum counts likely represent underestimates of wolf population size, especially as wolf population size and distribution increases. As we describe above, state management agencies in Idaho and Montana therefore developed new methods to estimate wolf populations that account for imperfect detection and produce quantifiable error (e.g., STE methods, POM methods). However, there is some concern that estimated abundance from unmarked populations in Idaho and Montana may be biased (Creel 2022, pp. 3–14; Leo 2022, entire; Treves et al. 2022, in litt.), and it has been suggested that direct monitoring of wolves, rather than the methods currently employed by the states, may be necessary to produce reliable estimates of abundance (Creel 2022, p. 14). POM (Gude et al. 2012, pp. 109–111; Miller et al. 2013, entire; Rich et al. 2013, entire; Ausband et al. 2014, entire; Latham et al. 2014, entire), iPOM (Gude et al. 2012, pp. 109–111; Miller et al. 2013, entire; Rich et al. 2013, entire; Ausband et al. 2014, entire; Latham et al. 2014, entire; Sells et al. 2020, pp. 39–51; Inman et al. 2021, pp. 3–13; Stauffer et al. 2021, pp. 1410, 1420–1421; Sells et al. 2022c, entire) and STE

methods (Hurley and Roberts 2020, pp. 37–40; Ausband et al. 2022, entire; Leo 2022, entire; Thompson et al. 2022, entire) are estimation techniques that have been developed, tested, and published in the peer-reviewed literature and have been refined over time. These techniques can reduce financial and logistical constraints as wolf populations increase yet still provide reliable population estimates on which to base management decisions (Leo 2022, pp. 8–9). Although Leo (2022, pp. 8–9) noted that STE estimates were lower than aerial estimates for feral sheep, this result is somewhat unexpected. Model estimates that account for detection probability (i.e., include unobserved animals in the estimate) should, by definition, result in estimates that are higher than minimum counts, which are biased low. Therefore, it is not unexpected that wolf population estimates increase when these modeling techniques are employed. Moreover, states use population estimates, rather than direct monitoring, to successfully manage populations of many other species (including ungulates) (CPW 2019, unpaginated).

However, when assumptions are violated, as with any modeling technique, results can be biased (Amburgey et al. 2021, pp. 14–16; Creel 2022, entire; Treves et al. 2022, in litt., unpaginated). A rigorous quantification of bias in these techniques, or in the estimates Idaho and Montana have produced (if any), has not been conducted. However, in an unpublished report and a letter to the Department of the Interior, Creel (2022, entire) and Treves et al. (2022, in litt., unpaginated) provided detailed assessments of the assumptions Idaho and Montana may be violating in their use of these monitoring techniques. As Creel (2022, entire) and Treves (2022, in litt., unpaginated) note, these violations of assumptions may result in biased estimates. Additionally, bias in modeled abundance estimators may be greatest when using these techniques to monitor small populations (Stouffer et al. 2021, p. 1420). Montana has committed to increase monitoring intensity if harvest and population metrics indicate wolf abundance is significantly reduced, especially if they near the 15-breeding pair and 150-wolf management buffer (MFWP 2004, pp. 29–30). This commitment is reiterated in the *Draft 2023 Montana Plan*; however, MFWP intends to manage for no less than 450 wolves, rather than 150, to ensure a minimum of 15 breeding pairs are maintained in the state (MFWP 2023, p. 44). Additionally, IDFG continues to investigate other methods of estimating wolf abundance (IDFG 2023a, pp. 36–37) that are less costly and labor intensive.

As mentioned above, despite these criticisms of the methods used to estimate wolf abundance in Idaho and Montana, currently there are no published estimates of potential bias, if any, for the population estimates reported in Idaho and Montana, just as there are no definitive estimates of bias for minimum counts of wolves in these states. Thus, the best available scientific information does not allow us to determine if correcting the estimates from Idaho or Montana 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 these states produced from different methods. Therefore, the current estimates provided by the states represent the best available science, and thus we rely on these estimates in this SSA. However, we also conducted a sensitivity analysis to examine the effect of uncertainty in the current population size (i.e., starting population size) on our future condition modeling results (see Appendix 5).

Wyoming's wolf population is much smaller and occurs over a smaller area within the state when compared to wolf populations in Idaho or Montana. As such, minimum counts

continue to be a cost-effective and reliable method to ensure wolf populations in Wyoming remain above Federal recovery and management criteria; WGFD also used minimum counts to develop wolf harvest recommendations to annually achieve population objectives. WGFD, YNP, and the Eastern Shoshone and Northern Arapaho Tribal Fish and Game Department coordinate to capture and radio collar a large proportion of the wolf population in the state each winter. For example, 41 to 49 percent of the minimum known wolf population in the WTGMA were fitted with a radio transmitter after WGFD completed winter capture efforts between 2018 and 2021 (WGFD et al. 2019, p. 7; WGFD et al. 2020, p. 7; WGFD et al. 2021, p. 10; WGFD et al. 2022, p. 11). Even though some lone or dispersing wolves may be unaccounted for, this allows biologists to consistently, and as accurately as possible, locate wolves from the ground and the air to obtain a minimum count of the known number of wolves in Wyoming each winter. Similar techniques are used to document a minimum known number of wolves at the end of each calendar year in California, Colorado, Oregon, Washington, and YNP.

For Oregon and Washington, where each state contains wolves both inside and outside of the NRM, we evaluated information in annual monitoring reports to determine whether packs, groups of wolves, and lone wolves occurred inside or outside of the NRM boundary for the purposes of our SSA analysis below. In both states, lone wolves are accounted for when reliable information is available, and these individuals are assigned to the specific wolf management zone or recovery region where they are documented at the end of the calendar year. However, it has been estimated that between 10 to 15 percent of the known winter wolf population is composed of lone individuals (Fuller et al. 2003, p. 170). As a result, Washington multiplies their minimum count by 0.125 to estimate the number of lone wolves in the state each year, but they do not indicate whether these lone wolves occur inside or outside the boundary of the NRM. To produce an estimate of the number of lone wolves that occur inside and outside of this boundary, we used the proportion of known wolves in the state that occur within the NRM in Washington to allocate estimates of lone or miscellaneous wolves to both areas. The data for the number of wolves in the portion of Washington outside of the NRM in Table 5 are slightly different than the data presented in our 2020 Biological Report (Service 2020, Appendix 2, pp. 32–33). This difference is due to a more precise attribution of lone wolves to areas inside and outside of the NRM in this SSA. Oregon’s annual reports include numbers of lone wolves by management zone. All lone wolves in the West Wolf Management Zone were allocated to the total number of wolves outside of the NRM in Oregon. For lone wolves in the East Wolf Management Zone of Oregon, which is bisected by the NRM, we used the proportion of known wolves in the state that occur within the NRM to allocate estimates of lone wolves inside and outside of the NRM boundary in this management zone. Finally, new groups of wolves have been documented in Oregon and Washington in 2022; however, ODFW or WDFW will not include these wolves in the year-end state totals for 2022 unless they remain in those states when minimum counts are conducted at the end of 2022.

### ***Current Population Size and Trends***

In the Western United States, wolves currently occur as one large metapopulation that consists of the delisted NRM wolf population, which is biologically connected to a small number of colonizing wolves in northern California, Colorado, Western Oregon, and Western Washington, which remain federally listed. Wolf populations in the NRM states of Idaho, Montana, and Wyoming increased by an average of 24 percent per year through 2008 then

appeared to stabilize as wolves colonized most of the available suitable habitat in the region and as human-caused mortality increased, primarily due to regulated harvest, post-delisting (Service et al. 2016, tables 6a and 6b, figures 7a and 7b). At the end of 2015, there were more than 1,700 wolves in these three states alone based on minimum counts. As core wolf populations in Idaho, Montana, and Wyoming increased in abundance and range, wolves began to recolonize portions of California, Oregon, Washington, and, more recently, Colorado. Since the reintroduction of gray wolves in the NRM, lone dispersing wolves have been detected in all states within their historical range west of the Mississippi River, except Oklahoma and Texas (Wydeven 2019, in litt.). At the end of 2022, there were approximately 2,682 wolves inside of the NRM and 115 wolves outside of the NRM for an estimated total of 2,797 wolves in the Western United States (Table 5). Currently, wolves occupy 142,451 mi<sup>2</sup> (368,946 km<sup>2</sup>) in the Western United States.

Table 5 and Figure 9 below detail the estimated total number of wolves in each state from 1982 to 2022, both inside and outside the NRM. Chapter 6 (*Future Condition*) presents modeled results illustrating how increased harvest in Idaho and Montana may affect population estimates beyond 2022.

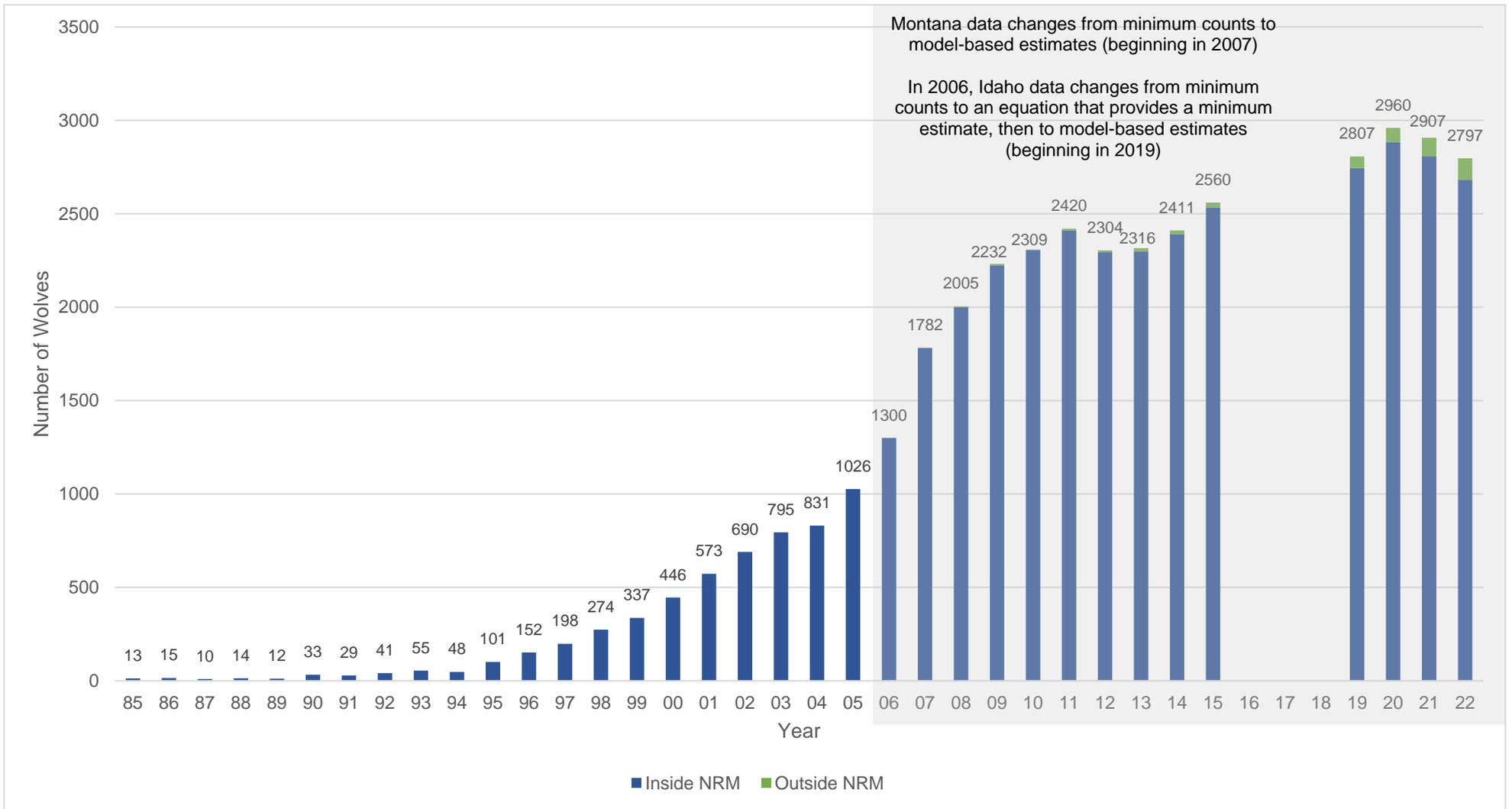


Figure 9. Minimum number of gray wolves counted or estimated in the Western United States, 1985–2022, both inside of the NRM (blue) and outside of the NRM (green). Total number of wolves in the Western United States metapopulation indicated at the top of each year’s bar. These estimates do not include Mexican wolves. Note that this graph does not include estimates for the total number of wolves in 2016, 2017, or 2018, as we do not have population estimates from Idaho for these years so could not produce a total estimate for the Western United States. Idaho and Montana also changed their monitoring strategies during the time period depicted on this graph. After 2017, Montana began exclusively using an occupancy modeling framework, rather than minimum counts; they were also able to apply the framework retrospectively to produce wolf population estimates from occupancy modeling back to 2007. In 2006, Idaho began using an equation to provide a minimum estimate of the number of wolves in the state that accounted for incomplete counts as the population size grew. Idaho then began using an STE modeling framework to estimate their population in 2019 (see above discussion of monitoring methods for more details). We cannot accurately compare the minimum counts in Idaho and Montana to the estimated population size derived from other techniques. See Appendix 3 for sources for this data.

We also estimated recent population growth rates for: Idaho, Montana, Oregon, Washington, and Wyoming by calculating lambda ( $\lambda$ ), or  $N_t/N_{t-1}$  (where  $N_t$  is the year-end population size during the current year and  $N_{t-1}$  is the year-end population size the previous year), from minimum counts or the population estimates for each state (Gotelli 2001, Chapter 2, pp. 25–45). We averaged this value over the most recent 4 years of year-end population data available for each state to obtain a mean lambda and confidence interval (with the exception of Idaho, this is the average of the lambda values between 2018–2019, 2019–2020, 2020–2021, 2021–2022).<sup>13</sup> Four years represents approximately one generation of wolves (Mech and Barber-Meyer 2017, entire; vonHoldt et al. 2010, p. 4422). Generally, a lambda greater than one indicates populations that are increasing, while a lambda less than one indicates declining populations. We did not report lambda values for California and Colorado due to the short time spans of available data and the small number of individuals in these states. Nor did we report lambda values for the Western portions of Oregon and Washington (those areas outside of the NRM). With small population sizes, small changes in the number of wolves translates to large changes in lambda and wide confidence intervals for the estimate of lambda.

### **Current Population Size and Trends within the NRM**

Based on minimum counts and population estimates used through 2015, the wolf population in Idaho peaked in 2009 at an estimated 870 animals. Under state management, including public harvest in most years since 2009, the population declined slightly and stabilized between 659 to 786 wolves between 2010 and 2015 (see Service et al. 2016, Table 6b). Between 2012 and 2015, the mean lambda in Idaho was 1.01, with a 95% confidence interval between 0.90 and 1.12 (Table 6). This estimate for lambda indicates that, on average, the population increased 1 percent each year, but, considering the 95% confidence interval for lambda, it could have been declining by 10 percent annually or increasing by 12 percent annually. Population estimates are not available for the years between 2016 and 2018. However, IDFG estimated a minimum of 63 litters during the summer of 2015, a minimum of 81 packs during summer 2016, 59 litters in 2017, 76 litters in 2018, and 97 litters in 2019 (IDFG 2017, pp. 7–6; Clendenin et al. 2020, pp. 496–501; Hebdon et al. 2022, in litt.). Ausband et al. (2023, p. 14) determined that wolf occupancy in Idaho remained stable between 2016 and 2021. As of the latest year-end estimates, based on new methodology described previously, there were approximately 958 wolves in Idaho at the end of 2022 (Table 5) (IDFG 2023b, entire). Between 2019 and 2022 (the time period for which we have STE-based estimates in Idaho), the mean lambda in Idaho was 0.98, indicating an average annual population decrease of two percent over this timeframe. Accounting for the 95% confidence interval for lambda (0.84–1.12), the wolf population in Idaho could have been decreasing up to 16 percent annually or increasing up to 12 percent annually between 2019 and 2022. The population estimate for year-end 2022 (958 wolves) was 8.2 percent lower than the previous year’s population estimate, which is consistent with IDFG’s stated objective of wolf population reduction, an objective we factored into our future condition analysis in this SSA (IDFG 2023a, pp. 39–41). However, we need additional years of data to interpret if this decrease is an overall trend that will continue.

The minimum count of wolves in Montana peaked in 2011 and stabilized around 500 to 650 wolves between 2012 and 2017 (Inman et al. 2021, p. vi; Table 5). At the end of 2017, the

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<sup>13</sup> For Idaho, we evaluated lambda between 2019 and 2021 (the most recent three years of data), given the transition to model-based estimation methods in 2019.

final year Montana conducted minimum counts of wolves, there were a minimum of 633 wolves in 124 packs including 63 breeding pairs (MFWP 2018a, p. 12). Based on the latest iPOM estimates, there were approximately 1,087 wolves distributed in 181 packs in Montana in 2022 (Table 5) (Parks et al. 2023, p. 10). Between 2018 and 2022, the mean lambda in Montana was 0.99, indicating an average annual population decrease of one percent over this timeframe. Accounting for the 95% confidence interval for lambda (0.96–1.02), the wolf population in Montana could have been decreasing up to four percent annually or increasing up to two percent annually between 2018 and 2022 (Table 6). The above estimates of wolf population growth in Montana are similar to the period between 2016 and 2020, where wolf population growth stabilized around zero growth despite various sources of human-caused mortality (Sells et al. 2022c, pp. 11–12). The population estimate for year-end 2022 (1,087 wolves) was 4.9 percent lower than the previous year’s population estimate (Table 5), which is consistent with state statutes in Montana directing wolf population reduction (e.g., MCA 87-1-901), an objective we factored into our future condition analysis in this SSA (see Chapters 5 and 6). However, we need additional years of data to interpret if this decrease is an overall trend that will continue.

Wolves were delisted in Wyoming in 2017 (82 FR 20284, May 1, 2017). The number of wolves is substantially lower in Wyoming than in Idaho and Montana, given the lower amount of suitable habitat available (see *Current Habitat Availability* above) (Oakleaf et al. 2006, entire). In Wyoming, the majority of wolves inhabit the northwest part of the state where they are managed by WGFD as a trophy game animal within the WTGMA, managed by the Eastern Shoshone and Northern Arapaho Tribal Fish and Game as a trophy game animal on the WRR, or are protected by Federal rules and regulations in Grand Teton National Park and YNP. Managers in YNP and the WRR have not set population objectives and have, for the most part, allowed wolves to naturally fluctuate. As a result, the number of wolves in YNP appears to have reached an equilibrium and has fluctuated around 100 wolves since 2009, while the number of wolves on the WRR has varied between 10 and 20 wolves over the same time period. At the end of 2022, a minimum of 338 wolves in 41 packs with 23 breeding pairs were documented in Wyoming (Table 5) (WGFD et al. 202, p. i). The statewide total includes a minimum of 108 wolves in YNP at the end of 2022, which is slightly higher than the average of 98 wolves counted between 2009 and 2021 (WGFD et al. 2023, p. 14). Slightly over 14 percent (49 of 338) of known wolves in Wyoming were documented in the predatory animal area, which is largely considered unsuitable wolf habitat (Oakleaf et al. 2006, p. 559) and where wolves may be taken year-round by any legal means (WGFD et al. 2023, p. i). Between 2018 and 2022, the wolf population in Wyoming had a mean lambda of 1.04, indicating an average annual population increase of four percent over this timeframe (Table 6). Accounting for the 95% confidence interval for lambda (0.99–1.10), the wolf population in Wyoming could have been decreasing by up to 1 percent annually or increasing up to 10 percent annually between 2018 and 2022.

At the end of 2022, there were a minimum of 140 wolves in the eastern one-third of Oregon, where wolves are federally delisted and managed under state authority (ODFW 2023, pp. 6; Table 5). These 140 wolves were distributed between 17 packs (defined as four or more wolves traveling together in winter) and 10 additional groups of two to three wolves (ODFW 2023, p. 6). The total number of wolves in the NRM portion of Oregon includes 13 known lone wolves that are either occupying a territory or actively dispersing in this part of Oregon (ODFW 2023, p. 6). Inside of the NRM, as calculated between 2018 and 2022, the mean lambda in

Oregon was 1.05, indicating an average annual population increase of 5 percent over this timeframe. Accounting for the 95% confidence interval for lambda (0.98–1.11) (Table 6), the wolf population inside the NRM in Oregon could have been decreasing by up to 2 percent annually or increasing up to 11 percent annually between 2018 and 2022.

At the end of 2022, there were a minimum of 159 wolves in 27 packs in the eastern one-third of Washington, where wolves are federally delisted and managed under state authority (WDFW et al. 2023, pp. 16–17; Table 5). The total number of wolves in the NRM portion of Washington includes 18 known individuals that are either occupying a territory or actively dispersing in this part of Washington. Inside of the NRM in Washington, as calculated between 2018 and 2022, wolves had a mean lambda of 1.12, indicating an average annual population increase of 12 percent over this timeframe. Accounting for the 95% confidence interval for lambda (1.02–1.20) (Table 6), the wolf population inside of the NRM in Washington could have been increasing at an annual rate between 2 and 20 percent between 2018 and 2022.

Overall, within the NRM, the mean lambda between 2019 and 2022 was 0.99, indicating an average annual population decrease of one percent over this time period. Accounting for the 95% confidence interval for lambda (0.92–1.07) (Table 6), the wolf population inside the NRM could have been decreasing at an annual rate of eight percent or increasing at an annual rate of seven percent between 2019 and 2022.

#### **Current Population Size and Trends outside of the NRM**

In the Western two-thirds of Oregon, where wolves are federally listed (i.e., outside of the NRM), at the end of 2022, there were a minimum of 38 wolves distributed between six packs and four additional groups of two to three wolves (ODFW 2023, p. 5). The total number of wolves in the Western two-thirds of Oregon includes one lone wolf that is either occupying a territory or actively dispersing in this part of Oregon (ODFW 2023, p. 5).

In the Western two-thirds of Washington, where wolves are federally listed (i.e., outside of the NRM), at the end of 2022, there were a minimum of 57 wolves in 10 packs. The total number of wolves includes six known individuals that are either occupying a territory or actively dispersing in this part of Washington, calculated based on the lone wolf factor used by WDFW and the methods described above (WDFW et al. 2023, pp. 16–17; Table 5). Increases in wolf abundance and distribution continue at a moderate pace in the North Cascades recovery area. WDFW confirmed a resident pack of wolves in the state’s Southern Cascades and Northwest Coast recovery area in 2022 (WDFW et al. 2022, p. 13). Slow recolonization of this recovery area was anticipated by WDFW (Wiles et al. 2011, p. 69). Factors that may be contributing to the slow recolonization in southwest Washington may include its distance from large wolf population centers and the availability of intervening suitable habitat between it and those population centers.

In California at the end of 2022, there were a minimum of 18 wolves in two packs and at least one individual dispersing wolf (CDFW 2022, entire). The packs are located in the northern part of the state, east of Interstate-5 in the area with the most wolf activity in California (see Figure 2). However, in 2021, a dispersing wolf ventured as far south as Ventura County (north of Los Angeles) but has not been observed since (CDFW 2021b, p. 1). In addition, CDFW detected a new breeding pack of wolves in 2023 in Tulare County which is in the southern Sierra

Nevada Mountains, approximately 200 miles south of all other known packs; this new breeding pack in Tulare County is not included in the two total packs documented at the end of 2022 (CDFW 2023c, entire). These records from 2021 and 2023 are examples of the ongoing expansion of known areas of wolf activity in California (CDFW 2021b, p. 1; CDFW 2023c, entire). Additionally, preliminary information indicates that, in 2023, the number of packs in California may have increased to seven, five of which produced pups in 2023, the highest number recorded since the recolonization of wolves in California began in 2015 (CDFW 2023d, entire).

Until recently, only lone wolves had been confirmed in Colorado, beginning with a dispersing individual that died as a result of a vehicle collision in 2004 (CPW 2023, p. 4). A disperser from Wyoming was first documented in north-central Colorado during the summer of 2019 and paired up with another wolf during the winter of 2020/2021 (Odell 2022, pers. comm.). This pair produced offspring in spring 2021, becoming the first documented reproductively active pack in Colorado in recent history. In January of 2020, CPW personnel also confirmed at least six wolves traveling together in Moffatt County in northwest Colorado (Odell 2022, pers. comm.). This group was down to a single individual later that year and, at the end of 2021, there was no indication that any wolf or wolves remain in this part of Colorado (Table 5). At the end of 2021 and 2022, a minimum of eight wolves and two wolves were confirmed in Colorado, respectively, all in the northcentral part of the state (Odell 2022, pers. comm.; Odell 2023, pers. comm.). In accordance with CRS 33-2-105.8 and the *Colorado Plan*, during the week of December 18, 2023, CPW began releasing wolves translocated from Oregon into Colorado.

As mentioned above, we do not report mean lambdas for California or Colorado, nor do we report mean lambdas for the Western portions of Oregon and Washington (i.e., areas outside of the NRM). We instead report mean lambdas for the entire states of Oregon and Washington based on the minimum counts of wolves in those states (Table 6). In Oregon, between 2018 and 2022, wolves had a mean lambda of 1.07, indicating an average annual population increase of seven percent in Oregon over this timeframe. Accounting for the 95% confidence interval for lambda (1.00–1.14) (Table 6), the wolf population in Oregon could have been increasing at an annual rate between zero and 14 percent between 2018 and 2022 (ODFW 2022, p. 5). In Washington, between 2018 and 2022, wolves had a mean lambda of 1.15, indicating an average annual population increase of 15 percent in Washington over this timeframe. Accounting for the 95% confidence interval for lambda (1.07–1.22) (Table 6), the wolf population in Washington could have been increasing at an annual rate between 7 and 22 percent between 2018 and 2022 (WDFW et al. 2022, pp. 16–17).

Within our analysis area, dispersing wolves have also been observed in Arizona, Nevada, New Mexico, and Utah, but they have not established packs there. At present, wolves are not known to inhabit any of these four states. In 2014, a gray wolf collared in Wyoming dispersed into northern Arizona where it was regularly sighted during a two-month period before being killed by a coyote hunter in southern Utah due to mistaken identity (Odell et al. 2018, pp. 294–296; Service 2020, unpublished data). In 2008, several sightings of a single, black-colored canid in New Mexico were presumed to be a gray wolf from the NRM (Oakleaf 2022, p. 50), given that no black-colored Mexican wolf has ever been documented (Odell et al. 2018, pp. 294–296). The fate of this canid is unknown. Wolves have likely always been scarce in Nevada (Young

and Goldman 1944, p. 30). In Utah, at least 20 probable or confirmed sightings of wolves have been documented since 1995 (UDWR 2022a, entire; UDWR 2022b, entire).

Overall, considering all wolves in Idaho, Montana, Oregon, Washington, and Wyoming (both inside and outside of the NRM), the mean lambda between 2019 and 2022 was 1.00, indicating an average annual population increase of zero percent over this time period. Accounting for the 95% confidence interval for lambda (0.93–1.07) (Table 6), the wolf population in these five states combined could have been decreasing at an annual rate of seven percent or increasing at an annual rate of seven percent between 2019 and 2022.

The gray wolf metapopulation in the Western United States is also interconnected with a much larger “Western United States and Western Canada” metapopulation of wolves that includes wolves throughout Western Canada (see *Current Genetic Diversity and Connectivity* discussion below) (Boyd and Pletscher 1999, entire; Carroll et al. 2012, entire; Jimenez et al. 2017, entire; Hendricks et al. 2018, entire). British Columbia and Alberta have an estimated 8,500 (range 5,300–11,600) (B.C. Ministry 2014, p. 6) and 7,000 wolves (Frame 2022, pers. comm.), respectively. Wolves in Idaho, Montana, and Washington have been, and continue to be, documented dispersing to Canada and vice versa; wolves from Canada naturally recolonized northwest Montana beginning in the 1980s and they formed at least half of the first pack documented in Washington in recent history in 2008 (Wiles et al. 2011, pp. 20–24).

Table 5. Gray wolf year-end minimum population counts or population estimates in the Western United States.<sup>a</sup> (See Appendix 3 for all relevant citations.)

Year	ID (inside NRM)	MT <sup>b</sup> (inside NRM)	WY (inside NRM)	WA (inside NRM)	OR (inside NRM)	WA (outside NRM)	OR (outside NRM)	CA (outside NRM)	CO (outside NRM)	Total (inside NRM)	Total (outside NRM)	Total in all Western States
1985	0	13	0	0	0	0	0	0	0	13	0	13
1986	0	15	0	0	0	0	0	0	0	15	0	15
1987	0	10	0	0	0	0	0	0	0	10	0	10
1988	0	14	0	0	0	0	0	0	0	14	0	14
1989	0	12	0	0	0	0	0	0	0	12	0	12
1990	0	33	0	0	0	0	0	0	0	33	0	33
1991	0	29	0	0	0	0	0	0	0	29	0	29
1992	0 <sup>c</sup>	41	0	0	0	0	0	0	0	41	0	41
1993	0 <sup>c</sup>	55	0	0	0	0	0	0	0	55	0	55
1994	0 <sup>c</sup>	48	0	0	0	0	0	0	0	48	0	48
1995	14	66	21	0	0	0	0	0	0	101	0	101
1996	42	72	38	0	0	0	0	0	0	152	0	152
1997	71	56	71	0	0	0	0	0	0	198	0	198
1998	114	63	97	0	0	0	0	0	0	274	0	274
1999	156	83	98	0	0	0	0	0	0	337	0	337
2000	196	97	153	0	0	0	0	0	0	446	0	446
2001	261	123	189	0	0	0	0	0	0	573	0	573
2002	289	184	217	0	0	0	0	0	0	690	0	690
2003	362	182	251	0	0	0	0	0	0	795	0	795
2004	418	153	260	0	0	0	0	0	0	831	0	831
2005	518	256	252	0	0	0	0	0	0	1,026	0	1,026
2006	673 <sup>d</sup>	316	311	0	0	0	0	0	0	1,300	0	1,300
2007	764 <sup>d</sup>	422 (659)	359	0	0	0	0	0	0	1,782	0	1,782

<b>Year</b>	<b>ID</b> <i>(inside NRM)</i>	<b>MT<sup>b</sup></b> <i>(inside NRM)</i>	<b>WY</b> <i>(inside NRM)</i>	<b>WA</b> <i>(inside NRM)</i>	<b>OR</b> <i>(inside NRM)</i>	<b>WA</b> <i>(outside NRM)</i>	<b>OR</b> <i>(outside NRM)</i>	<b>CA</b> <i>(outside NRM)</i>	<b>CO</b> <i>(outside NRM)</i>	<b>Total</b> <i>(inside NRM)</i>	<b>Total</b> <i>(outside NRM)</i>	<b>Total in all Western States</b>
2008	849 <sup>d</sup>	497 (849)	302	0	0	5	0	0	0	<b>2,000</b>	<b>5</b>	<b>2,005</b>
2009	856 <sup>d</sup>	524 (1,028)	320	7	14	7	0	0	0	<b>2,225</b>	<b>7</b>	<b>2,232</b>
2010	777 <sup>d</sup>	566 (1,149)	343	16	21	3	0	0	0	<b>2,306</b>	<b>3</b>	<b>2,309</b>
2011	768 <sup>d</sup>	653 (1,259)	328	26	29	9	0	1	0	<b>2,410</b>	<b>10</b>	<b>2,420</b>
2012	722 <sup>d</sup>	625 (1,205)	277	43	48	8	0	1	0	<b>2,295</b>	<b>9</b>	<b>2,304</b>
2013	684 <sup>d</sup>	627 (1,210)	306	38	61	14	3	0	0	<b>2,299</b>	<b>17</b>	<b>2,316</b>
2014	785 <sup>d</sup>	554 (1,143)	333	55	74	13	7	1	0	<b>2,390</b>	<b>21</b>	<b>2,411</b>
2015	786 <sup>d</sup>	536 (1,190)	382	77	99	13	11	2	0	<b>2,534</b>	<b>26</b>	<b>2,560</b>
2016	NA	477 (1,126)	377	97	100	18	12	2	0	<b>NA</b>	<b>32</b>	<b>NA</b>
2017	NA	633 (1,117)	347	106	110	16	14	6	0	<b>NA</b>	<b>36</b>	<b>NA</b>
2018	NA	(1,153)	286	104	117	22	20	5	0	<b>NA</b>	<b>47</b>	<b>NA</b>
2019	1,020 <sup>e</sup>	(1,159)	311	123	131	22	27	7	7	<b>2,744</b>	<b>63</b>	<b>2,807</b>
2020	1,088 <sup>e</sup>	(1,184)	327	144	141	34	32	7	3	<b>2,884</b>	<b>76</b>	<b>2,960</b>
2021	1,044 <sup>e</sup>	(1,143)	314	163	144	43	31	17	8	<b>2,808</b>	<b>99</b>	<b>2,907</b>
2022	958 <sup>e</sup>	(1,087)	338	159	140	57	38	18	2	<b>2,682</b>	<b>115</b>	<b>2,797</b>

<sup>a</sup> Does not include the Mexican wolf subspecies.

<sup>b</sup> Montana Integrated Patch Occupancy Modeling (iPOM) results in parentheses.

<sup>c</sup> Information provided by IDFG, and confirmed with former Service personnel, indicates that a single wolf was in central Idaho at the end of 1992, 1993, and 1994 prior to reintroduction (Rachael 2022, in litt.). This wolf did not constitute a population. Written reference to this wolf could not be found in any past document so it was not included in the table.

<sup>d</sup> Estimate based on an equation that accounted for incomplete minimum counts as the wolf population grew.

<sup>e</sup> Estimate based on STE modeling framework and not directly comparable to prior years.

Table 6. Estimated growth rate ( $\lambda$ ) in: Idaho, Montana, Oregon (both the portion inside the NRM and the entire state), Washington (both the portion inside the NRM and the entire state), and Wyoming. Lambda values calculated from states' provided population estimates (see Table 5). The 5-state total represents the growth rate for all of Idaho, Montana, Oregon, Washington, and Wyoming combined.

State	Years Evaluated	Mean $\lambda$	Lower Bound of 95% CI	Upper Bound of 95% CI
Montana	2018–2022	0.99	0.96	1.02
Idaho	2012–2015	1.01	0.90	1.12
Idaho	2019–2022	0.98	0.84	1.12
Wyoming	2018–2022	1.04	0.99	1.10
Oregon ( <i>in NRM</i> )	2018–2022	1.05	0.98	1.11
Washington ( <i>in NRM</i> )	2018–2022	1.12	1.02	1.20
<b>Overall NRM</b>	<b>2019–2022</b>	<b>0.99</b>	<b>0.92</b>	<b>1.07</b>
Oregon ( <i>statewide</i> )	2018–2022	1.07	1.00	1.14
Washington ( <i>statewide</i> )	2018–2022	1.15	1.07	1.22
<b>5-state Total</b>	<b>2019–2022</b>	<b>1.00</b>	<b>0.93</b>	<b>1.07</b>

### Summary of Current Population Distribution and Demographics

State agencies' minimum counts of wolves at the end of 2015 (the final year combined minimum counts were available), indicated that there were more than 1,900 gray wolves in the Western United States, the vast majority of which were within the NRM. In 2022, the best available science indicates there were an estimated 2,682 wolves inside of the NRM and 115 wolves outside of the NRM, though monitoring methodologies have changed since 2015, complicating any comparison between these estimates and previous years. Mean lambdas over the most recent four years, derived from the best available scientific information on population counts, indicate populations are increasing in Washington and Oregon. Mean lambdas in Idaho, Montana, and Wyoming, derived from the best available scientific information on population estimates or counts through the end of 2022, indicate populations in these states are slightly decreasing or slightly increasing; confidence intervals for Idaho, Montana, and Wyoming include lambda values less than and greater than one, which indicates that the populations in these states could be annually declining at a rate of 16 percent, 4 percent, or 1 percent or increasing at a rate of 12 percent, 2 percent, or 10 percent, respectively. This fluctuation of lambdas around one in Idaho, Montana, and Wyoming is typical of populations fluctuating around a maximum population size. However, because wolf populations in the Western United States are highly managed and influenced by human activities, both environmental and societal factors likely limit maximum population sizes in these states; we discuss this concept of a “maximum population size” further in Chapter 5. Idaho no longer reports the number of packs in the state; however, as of the end of 2022, there were at least 286 packs distributed between the remaining states in the Western U.S. metapopulation. Overall, the best available scientific information indicates that the metapopulation in the Western United States remains large and the occupied range has continued to expand despite current levels of human-caused mortality.

The NRM wolf population achieved the Service's numerical and distributional recovery goals at the end of 2000 (Service et al. 2008, Table 4). The temporal portion of the recovery goal was achieved in 2002, when the numerical and distributional recovery goals were exceeded for the third consecutive year (Service et al. 2008, Table 4). Post-delisting and subsequent

monitoring, and the expansion of the NRM population into northern California, Western Oregon, Western Washington, and more recently into Colorado, indicate that the wolf population in the NRM remains well above the minimum recovery levels to which each state committed (Groen et al. 2008, p. 1; Talbott and Guertin 2012, p. 1). In other words, as of the most recent estimates for each state, the number of wolves in Idaho, Montana, and Wyoming each exceeds the minimum recovery goal of 100 wolves and the management buffer of 150 wolves in each state.

### **Current Genetic Diversity and Connectivity**

As discussed in greater detail above, the ability to disperse long distances allows wolf populations to quickly expand and recolonize vacant, suitable habitats, as long as a minimum number of wolves are tolerated in these new areas (i.e., human-caused mortality is sustainable in these new areas); this dispersal can provide for gene flow among colonized areas (e.g., Mech 1995, pp. 272–273; Boyd and Pletscher 1999, entire; Treves et al. 2009, entire; Mech 2017, p. 310; Hendricks et al. 2019, pp. 37–38). Despite being colonized by a limited number of translocated and naturally dispersing founders, the population in the NRM has maintained high levels of genetic diversity and low levels of inbreeding in the decades since their establishment, without any indications of negative genetic effects (vonHoldt et al. 2010, pp. 4420–4421; WGI 2021, p. 8; Ausband 2022, p. 5; IDFG 2023a, p. 11; see Appendix 2). Three factors likely contribute to these characteristics.

First, the 66 wolves reintroduced into Idaho and Wyoming (and the 10 wolves translocated from northwest Montana to YNP in 1997), combined with the naturally dispersing wolves in Montana, constituted a much larger group of founders than most of the examples of small wolf populations that have experienced deleterious genetic effects (described above under *Inbreeding Depression* in Chapter 3). These wolves also seemed to be representative of large and genetically-diverse source populations in Canada (Bang and Fritts 1996, pp. 407–408; vonHoldt et al. 2010, p. 4421). This representation, combined with a relatively rapid population expansion, mean the genetic signature of a population bottleneck or significant founder effects appear to have been minimized or avoided (vonHoldt et al. 2008, p. 267; vonHoldt et al. 2010, pp. 4420–4421; WGI 2021, entire; Ausband 2022, p. 539).

Second, wolves appear to avoid inbreeding when possible, preferentially mating with unrelated individuals (vonHoldt et al. 2008, pp. 267–268; Ausband 2022, p. 539). Research in Scandinavian wolves demonstrated that the most heterozygous individuals consistently established themselves as breeders, which worked to reduce the loss of genetic diversity even as the level of inbreeding increased (Bensch et al. 2006, entire). Such behaviors can work to preserve important genetic diversity at higher levels than expected if there were random mating.

Finally, researchers have concluded that there has been consistent gene flow within and among the NRM states and Canada (vonHoldt et al. 2010, pp. 4421–4422; Jimenez et al. 2017, entire; Clendenin et al. 2019, entire; Ausband and Waits 2020, pp. 3192–3193; WGI 2021, entire; Ausband 2022, p. 539; IDFG 2023a, p. 11). The population is not panmictic, in that there is detectable population structure (vonHoldt et al. 2010, p. 4421; Hendricks et al. 2018, pp. 139–141; Ausband and Waits 2020, entire; WGI 2021, entire), but the relatively low levels of differentiation indicate effective dispersal among groups. Such dispersal has been documented

not only while wolves were federally listed in the NRM (i.e., when harvest was not allowed) (vonHoldt et al. 2010, pp. 4421–4422), but also during a recent 10-year study across Idaho that specifically examined the effects of harvest on genetic diversity (Ausband and Waits 2020, entire). That study concluded that harvest led to no change in individual genetic diversity but an increase in relatedness among groups and a decrease in relatedness within groups (Ausband and Waits 2020, pp. 3190). These results indicate wolves are dispersing to nearby groups and successfully breeding, thereby providing connectivity and gene flow; however, the impacts of harvest on longer distance dispersal, between states for example, were not specifically examined.

Moreover, Idaho and Montana each signed an MOU with the Service that committed to monitoring and managing the population to ensure sufficient connectivity (Groen et al. 2008, entire); Idaho reaffirms this commitment in the *2023 Idaho Plan* (IDFG 2023a, p. 38). Wyoming signed a nearly identical MOU in 2012, prior to the final rule delisting wolves there (Talbot and Guertin 2012, entire). With each MOU, the States, in cooperation with the Service, agree to regularly collect and analyze genetic data. The States each have protocols for the collection and storage of such samples and the 2021 unpublished report from Wildlife Genetics International (WGI 2021, entire) provides an example of the resulting analysis. Future analyses may differ based on available techniques and changing circumstances, but the focus on assessing genetic diversity and connectivity should remain consistent. In addition, in these MOUs, a range of management options, up to and including translocation of individual wolves, was made available to address any significant deficiencies in effective dispersal uncovered by the genetic analyses, thereby mitigating concerns of negative genetic effects due to delisting those wolves. Translocation or other mediated dispersal has not been necessary since the MOUs were signed, as natural dispersal within the metapopulation has been sufficient to maintain connectivity within the NRM.

More broadly, wolves have dispersed from Idaho, Montana, and Wyoming to form packs in Oregon and Washington (Jimenez et al. 2017, entire; Hendricks et al. 2018, entire). Meanwhile, individuals from Oregon and Washington have dispersed both within and across their respective state borders as well as to California, other NRM states, and Canada to join existing packs or to find a mate and form a new pack (Service 2020, pp. 16–18). Although founder effects are possible at the edges of expanding populations, no available data have shown discrepancies in genetic diversity between these advancing edges and the source populations in the NRM. In our review of the best available information, we also found no evidence of inbreeding. In addition, the presence of admixed coastal/NRM individuals in Washington indicates that coastal wolves, or their admixed progeny, have dispersed successfully from Canada into the state (Hendricks et al. 2018, entire) and are living in Washington’s interior, further increasing the genetic diversity of wolves in the Western United States.

Such evidence of dispersal and connectivity does not indicate that wolves have been readily or rapidly dispersing into all peripheral or unoccupied habitat throughout our analysis area, nor that we expect them to do so in the future; the dynamics or drivers of such range expansion are not necessarily well understood and can be difficult to assess. It took longer for documentation of pack formation in Colorado following dispersal from the GYA, for example, than in northern California after dispersal from eastern Oregon, despite relatively comparable distance. Such differences could be due to management, habitat, or a number of other factors.

Nevertheless, wolves have consistently continued to disperse from established populations and recolonize vacant suitable habitats, both dispersing into new areas and effectively providing gene flow between those populations.

These factors, combined with a population size consistently above the management threshold of 450 wolves set for the NRM, indicate that, to date, the effective population size and connectivity of the current population have been more than sufficient for retaining high levels of genetic diversity and avoiding inbreeding and inbreeding depression in the Western United States.

## 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 United States 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 a standardized scoring rubric for each attribute (see Appendix 4 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 4 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 7). 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 in the Western United States’ 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 7). 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 7). While not considered a “core” attribute, early sexual maturity of wolves (two 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 7). 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 NRM states and into neighboring states in the Western United States, while effective dispersal has been consistently documented among subpopulations (vonHoldt et al. 2010, pp. 4421–4422; Jimenez et al. 2017, entire; Ausband and Waits 2020, pp. 3192–3193). Because of these factors, we do not find wolves' dispersal and colonization ability to be limiting current adaptive capacity in the Western 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 7). 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; Munoz-Fuentes et al. 2009, pp. 1525–1526; Schweizer et al. 2016, p. 398). While two such populations (coastal and Rocky Mountain) appear to be mixing to a limited degree in our analysis area in Washington, there is not yet any indication that such admixture has led to adaptive changes or that it is likely to be widespread, given the relatively limited coastal habitat in the conterminous United States compared with British Columbia and Alaska. Nonetheless, 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 United States (McKelvey and Buotte 2018, p. 360). We do not find wolves' phenotypic and behavioral plasticity to be limiting current adaptive capacity in the Western United States.

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 consistently high genetic diversity in the gray wolf in the Western United States (*genetic diversity* is “high”) (vonHoldt et al. 2010, pp. 4420–4421; Ausband and Waits 2020, pp. 3192–3193; WGI 2021, p. 8) and their *life span* is “moderate,” according to the generalized scale in Thurman et al. (2020, WebTable 2) (Table 7). 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 7). 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 Western 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. That connectivity has, thus far, precluded the loss of genetic diversity and any concerns about inbreeding (see *Current Genetic Diversity and Connectivity* above). As such, the

evolutionary genetic capacity of wolves in the Western United States appears to 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 United States.

Overall, our assessment of wolves in the Western United States using the framework established by Thurman et al. (2020, entire) resulted in only two attributes in the “low” category. One was *parental investment*, 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). 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. As a result, wolves are very unlikely to colonize human-dominated habitat in a significant way, 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 United States 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 7. Our assessment of 12 “core” adaptive capacity attributes for the gray wolf in the Western United States. 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 Western 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). See Appendix 4 for complete scoring of all 36 attributes, including justification.*

Core Attribute	Category	Adaptive capacity rating for gray wolf in Western United States
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
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). For wolves in the Western United States, that phenomenon may be especially true as the population expands into unoccupied habitat and smaller founding subpopulations are established, which can sometimes diverge rapidly under strong selection (Carroll et al. 2021, pp. 76–77). 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). As shown in Figure 10, wolves in the Western United States are currently found in five ecoregional provinces:

- (1) Southern Rocky Mountain Steppe—Open Woodland—Coniferous Forest—Alpine Meadow;
- (2) Rocky Mountain Steppe—Open Woodland—Coniferous Forest—Alpine Meadow;
- (3) Northern Rocky Mountain Steppe—Open Woodland—Coniferous Forest—Alpine Meadow;
- (4) Cascade Mixed Forest—Coniferous Forest—Alpine Meadow; and
- (5) Sierran Steppe—Mixed Forest—Coniferous Forest—Alpine Meadow.

Occurrence in these different ecoregional provinces not only demonstrates the ecological flexibility of the species, which has become established in two new provinces (i.e., Cascade Mixed Forest and Sierran Steppe) since the NRM DPS (without Wyoming) was delisted in 2011, but also that the evolutionary processes that result from different selection regimes in these differing provinces are likely to positively contribute to the adaptive capacity of the species.

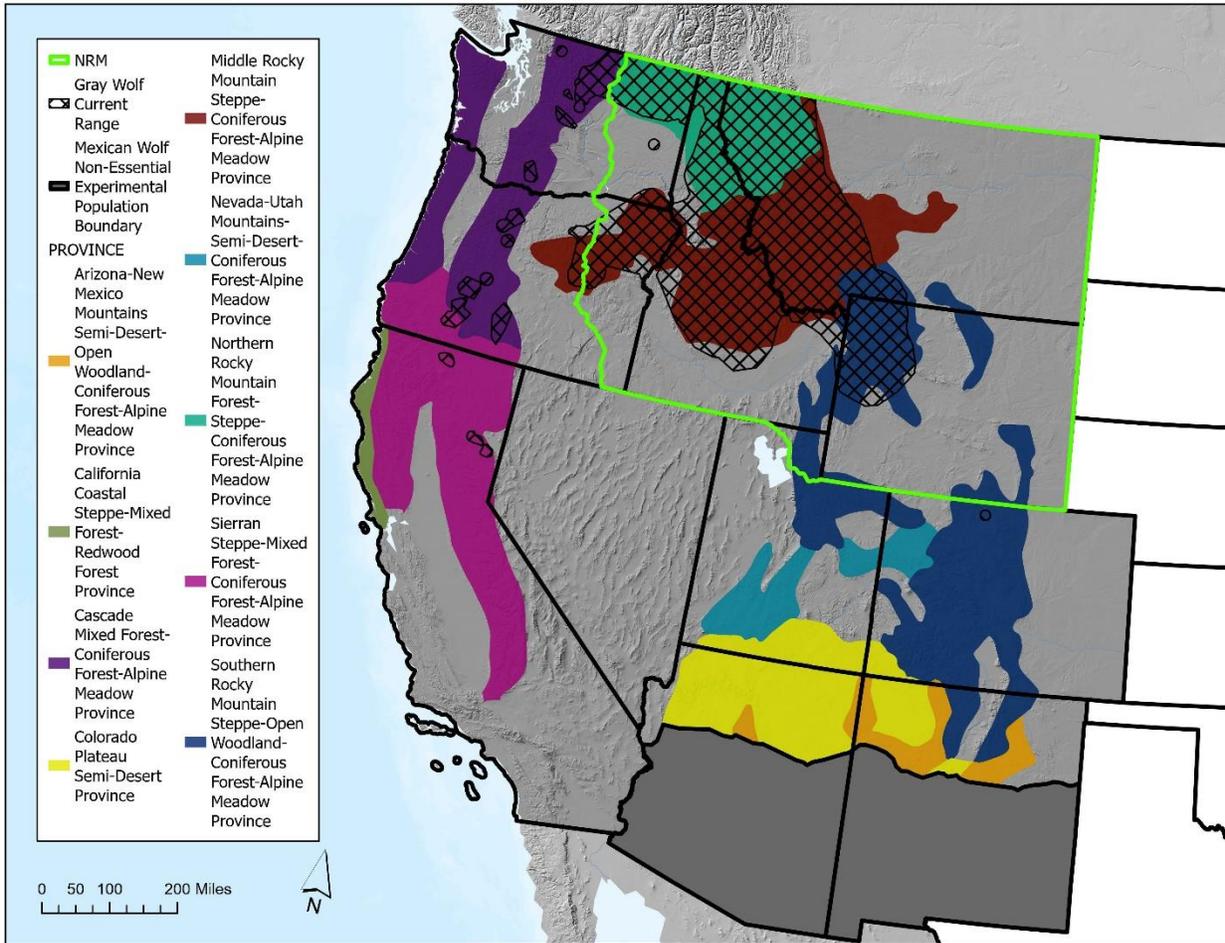


Figure 10. Ecoregional provinces, as defined by Bailey (2016), comprising potentially suitable habitat and the current range of wolves in the Western United States. The NRM is delineated in green. The Mexican Wolf Nonessential Experimental Population Area is colored in dark gray.

Considering these components of adaptive capacity, wolves in the Western United States 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 two 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. In addition, wolves occupy a diversity of ecoregional provinces, which further contributes to evolutionary potential. Consistent with conventional wisdom about wide-ranging, habitat generalist species, the gray wolf in the Western United States can adapt to environmental changes with a range of behavioral, physiological, or evolutionary responses.

### Current Redundancy

Wolves in the Western United States currently occur in one metapopulation, structured in a constellation of subpopulations spread across six states (and one known pack in Colorado); this metapopulation is also connected demographically to a larger population of wolves in Canada. At the end of 2022, there were at least 286 packs distributed between: California, Colorado,

Montana, Oregon, Washington, and Wyoming,<sup>14</sup> further contributing to redundancy of the species. The best available scientific information does not provide a minimum number of wolf packs in Idaho for the end of 2022. 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 United States in the recent past, population decreases have been localized to specific regions, with the overall metapopulation continuing to expand to new areas (see *Disease and Parasites in Wolves* in Chapter 3). Although it is possible a novel disease may arise, given the wolf's wide distribution in the Western United States (i.e., redundancy) and our understanding of current wolf disease ecology, it is unlikely that a disease outbreak would cause the wolf metapopulation in the entire Western United States to crash, even given current management objectives to reduce wolf abundance in some states.

## Summary of Current Condition

Habitat and prey for wolves are abundant and well distributed in the Western United States. This, in conjunction with the high reproductive potential of wolves and their innate behavior to disperse and locate social openings or vacant suitable habitats, has allowed wolf populations to withstand relatively high rates of human-caused mortality (Service 2020, pp. 8–9). Our analysis of the current condition of gray wolves in the Western United States demonstrates that, despite current levels of regulated harvest, lethal control, and episodic disease outbreaks, wolf abundance in the Western United States has generally continued to increase and occupied range has continued to expand since reintroduction in the 1990s, with the exception of three years during which wolf abundance in the Western metapopulation decreased slightly (i.e., a decrease of approximately 50 to 100 wolves in one year) (Table 5). As of the end of 2022, states estimated that there were 2,797 wolves distributed between at least 286 packs in seven states. This large population size and broad distribution contributes to the resiliency and redundancy of wolves in the Western United States. Moreover, wolves in the Western United States currently have high levels of genetic diversity and connectivity, further supporting the resiliency of wolves throughout the West. Finally, based on several metrics for assessing adaptive capacity, wolves in the Western United States currently retain the ability to adapt to changes in their environment.

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<sup>14</sup> Idaho no longer reports the number of packs in the state at the end of the calendar year. There are likely considerably more than 290 packs in the Western United States, if Idaho's numerous packs are considered.

## Chapter 5: Methods for Evaluating Future Condition

We developed a population model to (1) project the future population size of wolves in: Idaho, Montana, Oregon, Washington, and Wyoming under a range of future scenarios (see *Future Scenarios* below) and (2) conduct a PVA by evaluating the likelihood of falling below several 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. Montana (Messmer 2022, in litt.) and Wisconsin (Johnson and Schneider 2021, entire) have both used population-level models to estimate the effects of harvest on wolf populations. Our model structure and thresholds were chosen to specifically evaluate the ability of wolves to persist in multiple areas under various harvest scenarios and disease rates, and to evaluate the ability of 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. We qualitatively discuss resiliency in the states for which we were unable to model future population size in Chapter 6 (i.e., for Arizona, California, Colorado, Nevada, New Mexico, and Utah). We also discuss potential future changes in factors related to suitable habitat, prey availability, genetic diversity, connectivity, and representation qualitatively in Chapter 6.

Below we describe our methods for the wolf population modeling and forecasting; we summarize the uncertainties and assumptions involved in our model in *Key Uncertainties and Assumptions* and in Table 12 below. The results of our modeling and forecasting for the total wolf population in all Western states we modeled, and in the NRM, are presented in Chapter 6. Results for individual analysis units are presented in Appendix 6.

### Analysis Units

We quantitatively projected the total future population size of wolves in two different geographic areas: (1) Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) and (2) within the boundaries of the NRM (excluding the small portion of Utah within the NRM). For each area, we estimated the total number of wolves over time under each future scenario up to 100 years into the future. To develop these future projections for areas that contained multiple states or portions of multiple states, we separately projected future wolf population size in smaller analysis units (Appendix 6). We describe these analysis units below:

- For the multi-state area comprised of Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP), analysis units included:
  - Idaho
  - Montana
  - Oregon
  - Washington
  - Wyoming (without the wolves in YNP)

- YNP<sup>15</sup>
- For the NRM, analysis units included:
  - Idaho
  - Montana
  - The portion of Washington within the NRM boundary
  - The portion of Oregon within the NRM boundary
  - Wyoming (without the wolves in YNP)
  - YNP

Throughout Chapter 5 and Chapter 6, we generically refer to our analysis units as “states,” even though some of our analysis units were only portions of states (i.e., portions of Oregon and Washington for the NRM analysis; YNP). We summed the individual projections for each of these analysis units to determine the total number of wolves that would occur in a multi-state area in the future.

We did not use our model to quantitatively project the future number of wolves in Arizona, California, Colorado, New Mexico, or Utah. Considering the small number of, or lack of, wolves in each of these states, the best available scientific information did not allow us to estimate the necessary parameters to quantitatively model the number of wolves in these states given uncertainties regarding future management (i.e., harvest and control rates and population goals); the future sustainable number of wolves in each of these states (i.e., unknown maximum population size); and wolf population growth rates in these states. Thus, our projections for the total future population size in the NRM, developed from our model, do not include the small, unoccupied area of Utah within the NRM boundary, because we did not quantitatively project the future population size in Utah. We also did not quantitatively model the future number of wolves in Nevada, given insufficient information to estimate necessary parameters; limited amounts of suitable habitat in the state; and historical scarcity of wolves in the state. In Chapter 6, we qualitatively discuss the best available information regarding potential changes in the number of wolves in Arizona, Colorado, California, Utah, New Mexico, and Nevada in the future.

## 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

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<sup>15</sup> We treated YNP as its own unit of analysis, separate from Wyoming, given differences in agency missions, management objectives, and regulations for wolves that live primarily within YNP relative to wolves that live outside of YNP.

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 wolf population sizes provided by Idaho, Montana, Oregon, Washington, YNP, and Wyoming (Table 5), we assessed both density-dependent (**Equation 1**) and density-independent (**Equation 2**) growth models for each state. We compared model results (see Supplementary Material A for details of model fitting) to determine which model best fit the wolf population data for each state. We then used the parameter estimates from the model that best described the population dynamics of wolves in each state to project future wolf population size under several scenarios (as we describe in further detail under *Future Scenarios* below).

Negative 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 wolf population dynamics.

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

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

where  $\lambda$  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 under Equation 1 above.

Negative density-dependent models (hereafter density-dependent models) were a better statistical fit than density-independent models to the empirical data for all states, except Montana (see Supplementary Material A for details of model fitting). However, for multiple reasons we describe below, we determined that the best available information supported using a density-dependent model framework for Montana, rather than the density-independent model that

seemed to provide a better statistical fit. First, density-dependence provided the better statistical fit for all other states, including states with minimal harvest and lethal depredation control (e.g., Oregon and Washington). Second, multiple scientific studies have concluded that density dependence occurs in wolf populations, though the exact cause of the density dependent response is debatable (Van Deelen 2009, pp. 146–149, Cariappa et al. 2011, p. 729, Cubaynes et al. 2014 p. 8–10, O’Neil et al. 2017, p. 9525). Several studies hypothesize that intra-specific aggression results in density dependence even if prey densities are high (Cariappa et al. 2011, p. 729, Cubaynes et al. 2014 p.8–10), while others cite conflicts with humans (O’Neil et al. 2017, p. 9525), expansion into marginal habitat, or prey availability (Van Deelan et al. 2019, pp. 146–149) as the primary reasons for limitations on wolf population growth. Third, previous wolf PVAs that considered density-independent versus density-dependent models have noted that density-dependent models are the more likely biological mechanism in wolf populations (Patterson and Murray 2008, p. 676, Chapron et al. 2012, unpaginated). However, PVAs conducted for small populations of wolves often do not assume that the growth rate decreases as the population size increases (i.e. they assume that growth rates observed for small populations continue as the population increases until a carrying capacity is reached) (Chapron et al. 2012, unpaginated; ODFW 2015b, p. 12; Faust et al. 2016, p. 7; also see Rolley et al. 1999, p. 41 where density dependence is incorporated by reducing the percentage of breeding females as the population increases).

Therefore, given that the data from all other states indicated that a density dependent model was the best fit (with or without harvest) and given that other studies have indicated density dependence is an appropriate descriptor of wolf population dynamics, we selected a density-dependent model for the state of Montana to generate projections of future wolf populations. In sum, we used density-dependent models when estimating future population size for each of our analysis units in our model projections.

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

Figure 11 provides a graphical depiction of the density-dependent growth model we used to project wolf population size in the future (**Equation 1** above). Below, we further describe the model parameters in this equation.

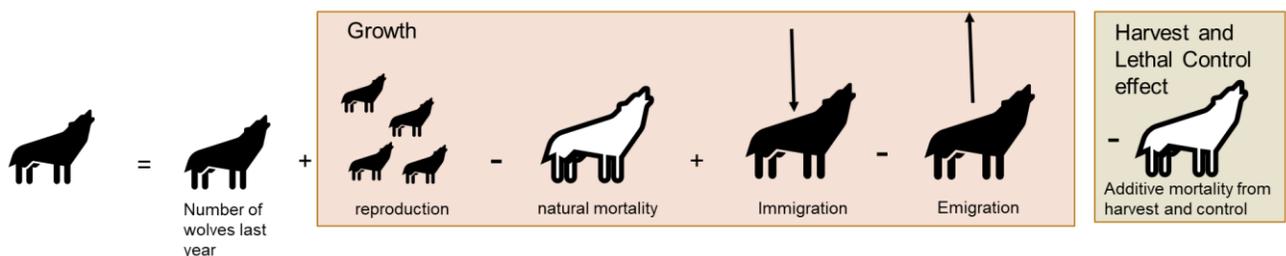


Figure 11. Schematic of density-dependent wolf population model. Arrows indicate direction of movement into (immigration) or out of (emigration) the population.

In 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 wolf populations in the Western 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 social and cultural norms, in addition to biotic conditions) rather than a biological carrying capacity; the maximum population size is likely limited by both environmental and societal factors.

Our density-dependent growth model also included a measure of the additive effect of harvest and lethal depredation control ( $h$ ) (Figure 11). In our models, we used reported annual harvest plus the reported number of wolves removed through lethal depredation control efforts in each state to estimate this additive effect parameter from observed data. There is significant debate regarding whether wolf harvest and 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 (**Equation 1**), as the estimate of  $h$  approaches zero, harvest and lethal depredation control efforts do not exceed losses that otherwise would have occurred through natural mortality and dispersal; in other words, as  $h$  approaches zero, harvest and lethal depredation control has no effect on the growth rate of the population either because the wolf that was removed would have died from natural causes or because recruitment or immigration rates increase in response to wolf harvest 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 wolf killed by harvest or lethal depredation control is subtracted from the population; in other words, as  $h$  approaches one, any 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 would imply “superadditive” effects of harvest and lethal depredation control (see *Effects on Wolf Social Structure* in Chapter 3 above); this means that for each wolf removed through harvest or lethal depredation control more than one wolf is lost from the population due to the effects of the removed wolf’s loss on pack dynamics and future reproductive success and recruitment.

## Estimating Parameters for Projections

To project the future population size of wolves, we first needed to estimate the input parameters in the density-dependent growth equation (**Equation 1**) above, because density-dependent growth generally provided the best fit to the data. For each state, we separately estimated a distribution for: (1) initial population size ( $N_i$ ); (2) maximum intrinsic rates of growth ( $r_{max}$ ); (3) effects of harvest and lethal depredation control ( $h$ ); and (4) the maximum population size ( $K$ ). We estimated these parameters separately for each state using monitoring data provided by the states to account for the unique characteristics of each state’s population. Below, we discuss how we estimated these parameters for each state.

## Estimating Starting Population Sizes

We used our density-dependent models to estimate the starting population size parameter ( $N_i$ ) for each state from the population data provided by state agencies (either minimum counts or modeled estimates, see Appendix 7). We estimated a distribution for starting population size, which allowed us to develop estimates of error for these starting population sizes (see code in Supplementary Material A).

Specifically for Idaho, we did not use the reported year-end population estimates to derive this starting population size from our models. Population data estimated from Idaho's STE models (i.e., modeled population estimates for 2019–2022) represents the best available science on the number of wolves currently in the state. Idaho conducts surveys for this STE modeling during the summer months, and it provides a wolf population estimate for August, near the annual peak in the wolf population; they then use data on known and estimated wolf mortalities to extrapolate the wolf population size for each month thereafter through March of the following year (see Chapter 4 Current Conditions for a more detailed explanation of these methods). These extrapolated estimates provide an indication of population size in late March, which represents the annual low point for the wolf population in Idaho, as March is just prior to the birth pulse when populations substantially increase in size. Thus, through its new methods, Idaho is producing a wolf population estimate for August (when wolf populations are near their annual maximum), and extrapolated population estimates by month through March (when wolf populations are at their annual minimum). We used our density-dependent model to estimate the initial starting population size from the March estimates provided by IDFG. Using these March estimates rather than the calendar year-end estimates or the August estimates for 2019 through 2022 allowed for the most conservative approach in projecting population trend for Idaho, given the March estimates represent the estimate of the population low point.

We used these starting population sizes estimated from our density-dependent models for all five states rather than the latest population sizes reported by each state because three states (Oregon, Washington, and Wyoming) monitor wolf populations using minimum counts, which do not include estimates of error; 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. As such, the starting population sizes we used for our future projections (which we estimated from these density-dependent models using observed population data) differ slightly from the population estimates or counts outlined in Table 5 in Chapter 4 (see Table 8 below for the modeled initial population sizes we used as input values in our forecasting). For Idaho, the starting population size in Table 8 below is lower than the population estimate in Table 5 in Chapter 4 not only because we estimated this value from our density-dependent models but also because the starting population size in Table 8 represents the conservative low point of the population (i.e., the March estimates) and the estimate in Table 5 represents the calendar year-end estimate (i.e., the December 2022 estimate).

## Estimating Parameters for Idaho Projections

In order to estimate  $r_{max}$ ,  $h$ , and  $K$  for Idaho, we used population data provided by the State of Idaho through 2022. This population data included minimum counts up through 2005,

estimates from a combination of minimum counts and an estimation equation for 2006–2015, and estimates from STE models for 2019–2022 (see Chapter 4 for details). Due to methodological changes and development of new monitoring techniques, Idaho did not count or estimate population size between 2016 and 2018, and thus we do not have population data for Idaho for these years. Idaho derived abundance estimates for 2019, 2020, 2021, and 2022 using a new method developed to estimate wolf numbers in the state (i.e., STE methods) (Ausband et al. 2022, entire; Thompson et al. 2022, entire; see Chapter 4). The new estimator incorporates data collected from remote cameras and STE modeling (Moeller et al. 2018, pp. 3–7; Moeller and Lukacs 2021, entire) to estimate wolf abundance. Comparing these estimates to minimum counts when calculating population growth could produce unreliable results. Therefore, we used a “piece-wise” model (McGee and Carleton 1970, entire) to estimate the intrinsic rate of growth through 2015 and then from 2019–2022, effectively removing the trend between 2015 and 2019 from the estimation of  $r_{max}$ .

### Estimating Parameters for Montana Projections

As described above, we used a density-dependent model to estimate the starting population size ( $N_t$ ) in Montana from estimates provided by MFWP. Prior to 2007, minimum counts of the number of wolves in Montana were conducted at the end of each calendar year. Between 2007 and 2017, wolf abundance was obtained through minimum counts and estimated by patch occupancy models (Rich et al. 2013, entire) (see *Methods for Counting and Estimating Annual Population Size in Each State* in Chapter 4 above). Beginning in 2018, wolf abundance was only estimated using patch occupancy or integrated patch occupancy models (Sells et al. 2020, pp. 39–47). Comparing wolf abundance 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) to estimate  $r_{max}$ ,  $h$ , and  $K$  using trends calculated between 1995–2006 and between 2007–2022. This method effectively removes the trend between the years 2006 and 2007 (when estimation methods changed from minimum counts to patch occupancy modeling) from the overall estimates of  $r_{max}$ ,  $h$ , and  $K$ .

### Estimating Parameters for Wyoming Projections

In Wyoming, no harvest takes place in YNP; therefore, we removed the number of wolves counted in YNP from the total number of wolves documented in Wyoming at the end of each year to separately estimate  $r_{max}$ ,  $h$ , and  $K$  for the State of Wyoming with our density-dependent models. As explained above, we estimated the starting population size ( $N_t$ ) for Wyoming from observed minimum count data (total Wyoming population minus YNP estimates) using our density-dependent models. These models, provide an estimate of error for this starting population size. We separately projected the future number of wolves in YNP (Table 8) (explanation of methods for YNP below). However, in Appendix 6, we include estimates for the future population size of YNP in our projections for the total number of wolves in Wyoming because most of YNP (96 percent) is in Wyoming.

## Estimating Parameters for Yellowstone National Park Projections

We modeled the wolves that live primarily in YNP separately from wolves in the remainder of Wyoming due to the differences in agency missions and regulations that guide wolf management between WGFD and YNP. We estimated the initial population size for YNP from minimum counts provided by YNP using our density-dependent models, which then provided an estimate of error for this initial population size. We also used our density-dependent growth model to estimate  $r_{max}$ ,  $h$ , and  $K$  for the wolves that live within YNP, similar to the methods we used to estimate input parameters and project future population size in each of the states we modeled. We estimated the intrinsic rate of growth ( $r_{max}$ ) from observed population data using the entire time series of observed population data from YNP (1995 to 2022).

The wolf population in YNP increased rapidly after reintroduction in 1995 and 1996. The population reached a peak of slightly over 170 wolves in 2003, 2004, and again in 2007. Primarily due to reductions in prey abundance, and possibly disease factors (DeCandia et al. 2021, p. 430), YNP wolf numbers declined and has ranged between 80 and 123 wolves annually since 2009 (Smith et al. 2020a, pp. 77–78; Cassidy et al. 2021, p. 4; WGFD et al. 2023, p. 14; see Figure 12 below). Due to the observed change in the maximum number of wolves in YNP after 2009 (likely due to changes in the carrying capacity induced by decreased prey populations and disease), we estimated two different  $K$ 's for YNP, one for the period between 1999 and 2009 and one for the period between 2009 and 2022. We used the  $K$  estimates from 2009–2022 in our projections of future wolf population size given that this represents the lower, more recent carrying capacity of the population. Similar to the states that we modeled, we used information from documented wolf count data to estimate the distribution of  $K$ .

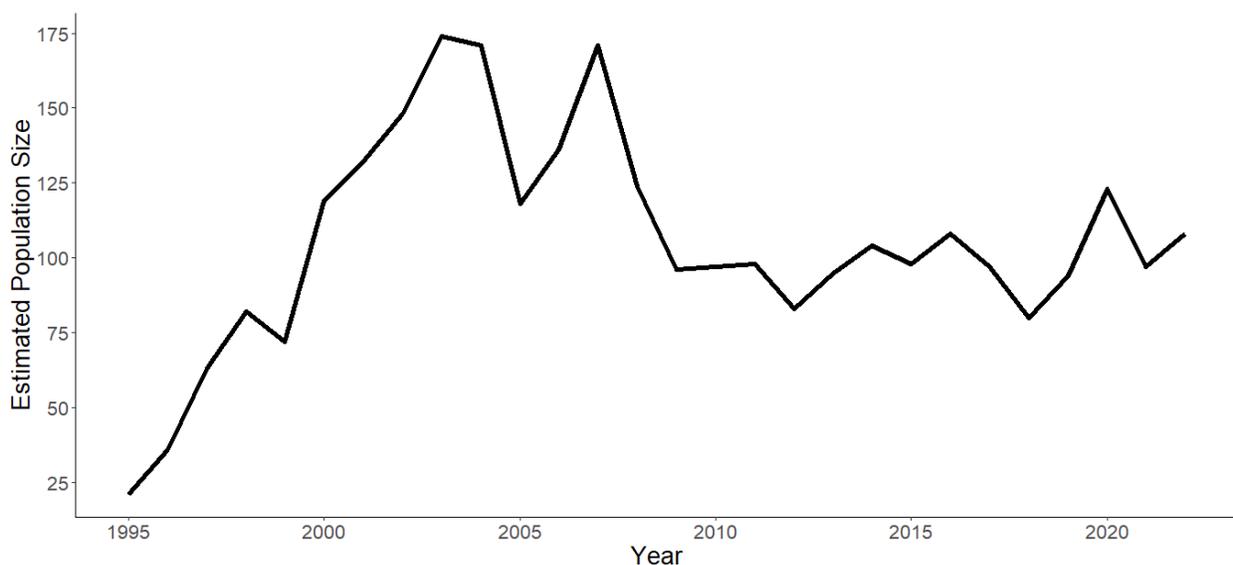


Figure 12. Yellowstone National Park wolf population estimates from 1995–2022.

While wolf harvest is not authorized within YNP, wolves that have territories primarily within YNP may be harvested in surrounding states if they leave YNP, consistent with rules and regulations that guide wolf harvest in each surrounding state. If a wolf originating from YNP is

harvested in a surrounding state, the wolf is included in the total number of wolves harvested in the state the mortality occurred. Although wolves originating from YNP that died from regulated harvest were included in mortality totals for the state where that mortality occurred, to estimate the effects of harvest mortality on wolves that live primarily in YNP, we separately used these known mortalities of wolves originating from YNP to evaluate the effects of harvest on wolves living primarily in YNP.<sup>16</sup> Since delisting and the implementation of wolf harvest in Idaho and Montana in 2009 and Wyoming in 2012, the leading cause of mortality for wolves that leave YNP is regulated harvest, rather than lethal depredation control; therefore, we only modeled mortalities from regulated harvest to estimate  $h$  and evaluate future effects of harvest (see *Future Idaho, Montana, and YNP Harvest Rates* below).

Prior to the winter of 2021/2022, the number of wolves that lived primarily in YNP, left the park, and were harvested in surrounding states ranged from 0 to 12 wolves annually (YNP 2022a, in litt.). However, during the winter of 2021/2022, 24 wolves that lived primarily in YNP and left the park were legally harvested outside of YNP boundaries: two in Idaho, 19 in Montana, and three in Wyoming (YNP 2022a, in litt.). The increased number of wolves harvested in Montana was a direct result of the removal of harvest limits in WMUs 313 and 316 for the 2021/2022 harvest season, units that border YNP's northern boundary, as all 19 wolves harvested in Montana that lived primarily in YNP were harvested in these two WMUs. However, data on the resulting population size in the winter of 2022/2023 indicates the population in YNP remained stable after the higher level of harvest of wolves residing primarily in YNP that occurred during the 2021/2022 harvest season; there were at least 108 wolves in YNP by the end of calendar year 2022, a population size comparable to previous years. Thus, while there is some evidence that less restrictive harvest regulations result in decreased *individual* wolf survival in YNP (Cassidy et al. 2022a, p. 5), the population size in YNP for the winter of 2022/2023 indicates that this increased individual mortality may not result in overall *population* declines, and that other processes (e.g., increased immigration or recruitment) can partially compensate for this mortality, which may account for the lack of observed population change after the 2021/2022 harvest season (Brainerd et al. 2008, entire; Borg et al. 2015, entire).

While the population information from winter 2022/2023 in YNP indicates that the wolves in YNP may be able to partially compensate for wolves lost to harvest, information on wolves removed due to harvest, and the population response in YNP, is too limited to precisely inform the population-level effect of harvest and lethal depredation control parameter ( $h$ ) (i.e., we could not estimate  $h$  directly from the YNP data). Thus, we used a diffuse uniform distribution from -0.1 to 1 to capture the entire range of possible estimates of  $h$  for our YNP projections. This distribution captures the range of values that represent effects of harvest and lethal depredation control from completely compensatory to completely additive.

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<sup>16</sup> This means that, in our modeling, we double-counted the harvest of wolves that primarily reside in YNP, leave the park, and are harvested outside of the park; these wolves are counted both as harvested wolves in our analysis of YNP, and as wolves harvested in the state where they were legally hunted or trapped (i.e., Idaho, Montana, or Wyoming). We included all other forms of mortality in our analysis of wolves primarily residing in YNP only if this mortality was documented within the boundaries of YNP.

## Estimating Parameters for Oregon and Washington Projections

For Oregon and Washington, wolves are located both inside and outside of the boundaries of the NRM (Chapter 4). We used the same methods to separately estimate the initial population size,  $r_{max}$ , and  $K$  for Oregon and Washington as we used for Montana and Wyoming. We estimated the initial population size,  $r_{max}$ , and  $K$  from observed data for both (1) all wolves in each state and (2) the subset of wolves located inside the NRM in each state. However, despite the fact that density-dependent models fit the data best, the wolf populations in Oregon and Washington are still growing; therefore, our estimates of  $K$  may be biased low for these states because we have not yet observed their maximum population size. The rates of lethal depredation control in both of these states and the limited tribal harvest in Washington were not high enough to provide reliable estimates of  $h$  for either state; therefore, we used a combined distribution of  $h$  values from Montana, Idaho, and Wyoming to inform the value for the effect of harvest and lethal depredation control ( $h$ ) in these states.

## Assumptions Regarding Immigration, Emigration, Natural Mortality, Reproduction, and Harvest and Lethal Depredation Control Effects

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 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 through our estimates of  $h$  and the number of animals harvested 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). Instead, in our models we assume that  $h$  is density-independent (i.e., the per-wolf effect of harvest and lethal depredation control is the same at all population sizes). The best available science does not inform the relationship between  $h$  and population size, and this relationship is likely complex and potentially population specific; therefore, the best available science did not provide a mechanism by which to relate  $h$  to population size in our model. In addition, if the ability of wolf populations to compensate for human-caused mortality declines in small populations, it is possible these effects are more prominent in small, *isolated* populations. Populations in the Western United States are connected to each other as well as Canada, buffering individual populations from the effects of small population dynamics. Moreover, previous researchers have also modeled the per-wolf effect of harvest and lethal depredation control as a constant value, as we do in our models (ODFW 2015b, p. 14, Petracca et al. 2023b, p. 8). Further our estimates of  $h$  include uncertainty to capture a range of possible values and convert to 1 (i.e., fully additive mortality) when harvest rates are between 20 and 40 percent (see *Future Scenarios: Harvest* below). We included a sensitivity analyses (see Appendix 5) to explore the effect of variation in

our estimates of all parameters, including  $h$ . Finally, 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% credible interval around a median) rather than a single median or mean value.

## Estimated Parameters

In Table 8 below, we summarize the input parameters (i.e., intrinsic rate of growth ( $r_{max}$ ), effect of harvest and lethal depredation control ( $h$ ), maximum population size ( $K$ ), and starting population size ( $N_i$ )) we estimated for each state or part of a state for our forecasting modeling. (See Supplementary Material A for additional technical details on our methods for estimating these parameters.)

*Table 8. Estimated input parameter values for simulations (i.e., intrinsic rate of growth, effect of harvest and lethal depredation control (the overall effect per removed wolf on population growth), maximum population size, and initial population size). These parameters were estimated from observed data using a density-dependent model. See above for explanation of model parameters and estimation methods. The 95% Bayesian credible intervals (CI) reported below represent the interval in which 95 percent of the values are expected to fall (Gelman et al. 2020, Chapter 1).*

Entity	Intrinsic rate of growth ( $r_{max}$ ) (95% credible interval (CI))	Per wolf effect of harvest ( $h$ ) (95% CI)	Maximum population size ( $K$ ) (95% CI)	Starting population size ( $N_i$ ) (95% CI)
Idaho	0.45 (0.38–0.54)	0.10 (-0.01–0.18)	848 (778–928)	743 (690–794)
Montana	0.27 (0.24–0.28)	0.38 (0.25–0.47)	2,001 (1,685–2,226)	1,167 (1,103–1,232)
Wyoming	0.46 (0.36–0.59)	0.18 (-0.02–0.33)	270 (227–329)	226 (210–238)
Oregon	0.40 (0.33–0.47)	0.18 (0.01–0.39) <sup>a</sup>	186 (173–206)	178 (169–188)
Oregon (NRM)	0.42 (0.35–0.51)	0.18 (0.01–0.39) <sup>a</sup>	144 (136–156)	141 (135–149)
Washington	0.28 (0.22–0.35)	0.18 (0.01–0.39) <sup>a</sup>	294 (235–453)	217 (202–231)
Washington (NRM)	0.33 (0.23–0.43)	0.18 (0.01–0.39) <sup>a</sup>	192 (162–300)	165 (153–181)
Yellowstone National Park	0.62 (0.46–0.82)	0.28 (-0.08–0.93) <sup>b</sup>	100 (90–112)	92 (77–105)

<sup>a</sup> Composite estimate from Idaho, Montana, and Wyoming; effects of harvest and lethal depredation control were not able to be estimated from Oregon or Washington data.

<sup>b</sup> Note this estimate closely resembles our input distribution of the parameter (-0.1–1) (i.e., the best available science does not provide sufficient information to inform this parameter)

## Future Scenarios

We projected the future population size of wolves at two geographic scales under multiple future scenarios. Future scenarios allow us to explore a range of possible future conditions for wolves in the Western 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 harvest (see *Harvest*, below) and disease (see *Disease*, below), the two primary stressors that could influence wolf populations in the future; our analysis also included application of consistent rates of lethal depredation control. 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. We illustrate the various geographic scales and future scenarios we explored in Figure 13, and explain each further below.

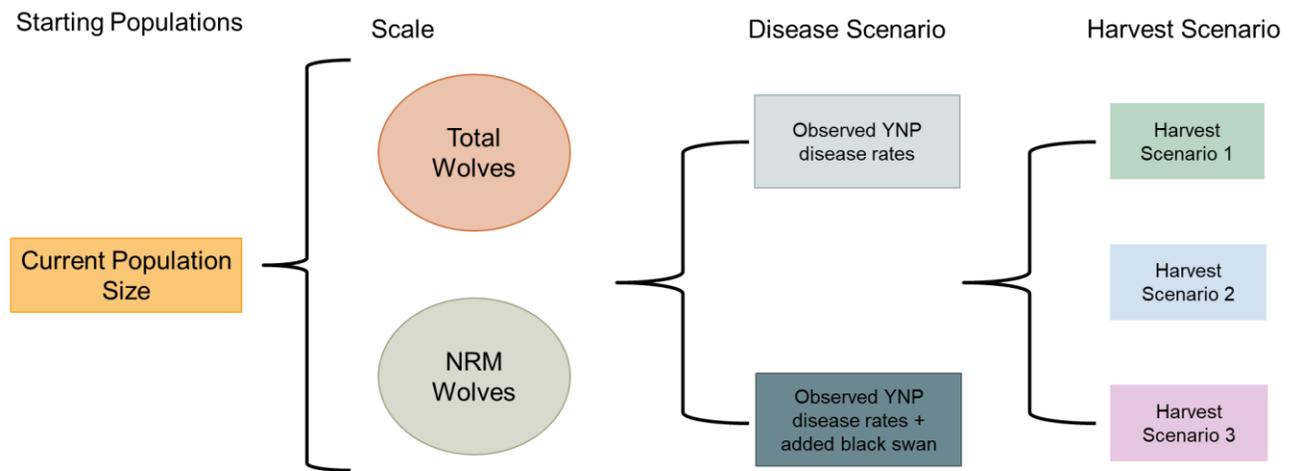


Figure 13. Schematic of forecasting, including future scenarios. Total wolves included wolves in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP). NRM wolves excludes wolves in the portions of Oregon and Washington outside of the NRM; these projections for the NRM also did not include the small portion of northern Utah within the NRM boundary (there are currently no resident wolves in Utah and we did not quantitatively model future population size for this state). See text below for description of disease and harvest scenarios.

## Disease

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 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 wolf populations across the West 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) in our model. (See 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 wolf population in the Western United States. This first level of disease (i.e., “observed YNP disease rates”) was estimated from data on wolves in 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). We applied this level of disease in all of our future scenario combinations.

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. Black swan events are statistically improbable events that have potentially severe consequences. Ignoring black swan events 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 their effect 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 United States 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 that included “added vertebrate black swan events” included—for each analysis unit—a one 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. In the future scenario combinations that included these added black swan events, we applied these mortality rates in addition to the observed YNP disease rates.

## Harvest

Our future scenarios also included variation in harvest rates, which we define as the percent of wolves killed through legal hunting and trapping annually (Table 9). Because increased wolf harvest in British Columbia, Canada through the 1990s and 2000s generally corresponded to increases in wolf abundance and distribution across the province (Mowat et al. 2022, pp. 15–16), we assumed that a similar trend in total harvest would occur if wolf abundance was reduced. 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 west during the late 1800s and early 1900s (Wiles et al. 2011, pp. 16–18). Where wolves are the targeted species, increased harvest pressure and higher rates of harvest may reduce wolf abundance in some areas, but it can also result in changes to wolf behavior that result in smarter wolves that are more challenging to harvest in subsequent years (Young and Goldman 1944, pp. 275–285; Webb et al. 2011, p. 750). Therefore, we chose to model harvest levels as a consistent proportion of the population versus a

fixed number of 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.

As we explain in detail under *Assumptions Regarding Immigration, Emigration, Natural Mortality, and Reproduction, and Harvest and Lethal Depredation Control Effects* above, we estimated the effects of harvest and lethal depredation control (assessed by our estimates of  $h$ ) as density-independent (i.e., harvest and lethal depredation control do not become more or less compensatory as population sizes change). Models with a density-independent effect of harvest and lethal depredation control provided adequate fit to the population estimates, lethal depredation control, and harvest data, and they required fewer assumptions regarding the nature of the relationship between harvest and population size. Finally, as the combined rate of harvest and lethal depredation control increases, our models assume that, at some point, this rate becomes fully additive as wolf populations can no longer partially compensate for these higher levels of harvest and lethal depredation control. We model the transition from partially compensatory to fully additive harvest and lethal depredation control 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 portion of the combined harvest and lethal depredation control rate above the 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 8 above).

For all states for which we included a harvest rate, we calculated average harvest rates from the most recent four years in which both population and harvest estimates were available on a state-by-state basis. Generally, we calculated harvest rates by dividing the number of wolves harvested by the population counts/estimates for the calendar year plus the known number of animals that died from all causes that year (i.e., we added the total number of known wolf mortalities back to the population count/estimate for the calendar year to determine the denominator for our calculation of harvest rate, see Appendix 7 for rate calculations). 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. As we explain further below, we applied this formula slightly differently in Wyoming and Washington.

### ***Future Wyoming Harvest Rates***

For Wyoming, we used the average past observed harvest rates calculated for this state across all future scenarios; in other words, we assumed that harvest in Wyoming would stay the same as current levels into the future (see Chapter 3 for more detail on harvest regulations in these states). The WGFD manages wolves within the WTGMA based on a numerical objective of 160 wolves. To achieve this objective, WGFD manages harvest using harvest limits that will maintain population objectives. At present, Wyoming conducts an annual public season-setting process before the WGFD Commission finalizes wolf harvest regulations prior to each season. At the end of 2022, there were 163 wolves in the WTGMA (WGFD et al. 2023, p. i); given this

objective, and the number of wolves currently in the WTGMA, unless wolf abundance significantly increases in the WTGMA, wolf harvest is unlikely to increase substantially in the WTGMA, supporting this assumption regarding the continuation of average observed harvest rates into the future. We calculated the harvest rate in Wyoming as the number of wolves harvested in Wyoming divided by the estimated population size in Wyoming (not including the wolves in YNP) plus the estimated total mortality in Wyoming (not including YNP) for each calendar year.

### ***Future Oregon and Washington Harvest Rates***

Oregon and Washington wolf populations are currently not subject to regulated harvest open to the general public. In Washington, harvest is currently permitted for tribal members on tribal lands of the Confederated Tribes of the Colville Reservation and the Spokane Tribe of Indians. Oregon has had no regulated harvest to date. Although it is possible that Oregon and Washington could authorize public harvest of wolves at some point in the future, too much uncertainty existed in the timing of when harvest may be authorized and at what level this harvest would occur for us to include this harvest in our future scenarios. Both Oregon and Washington would need to go through a public rule-making process prior to their respective Commission approval of any potential, future harvest regulations being implemented in each state (ODFW 2019a, p. 31; WDFW 2011, pp. 70–71). Therefore, in all of our future scenarios, we assumed that harvest in Oregon and Washington would stay the same as it is currently into the future (no harvest in Oregon and limited tribal harvest in Washington).

Therefore, for all of our future scenarios, harvest rates are zero in Oregon, for both the NRM portion of the state and the statewide analysis unit. For Washington, harvest only occurs on the tribal lands of the Confederated Tribes of the Colville Reservation and the Spokane Tribe of Indians, both within the NRM portion of the state (see *Regulated Harvest in Washington* in Chapter 3). We assumed that the current levels of harvest that occur on these tribal lands continue to occur annually into the future, under all of our future scenarios. However, we calculated the harvest rate this tribal harvest represents differently for the NRM portion of the state and the statewide analysis unit. We assumed that the number of wolves removed through harvest in the future would be the same in the NRM portion of the state as the number removed statewide (i.e., if wolves were delisted and available for harvest statewide, rather than only in the NRM, the total number of wolves harvested would remain the same because harvest would continue to occur only on the Confederated Tribes of the Colville Reservation and the Spokane Tribe of Indians tribal lands in the NRM portion of the state). Thus, we estimated the harvest rate for Washington statewide as the total number of wolves harvested in the NRM portion of Washington divided by the statewide population size of Washington plus the total mortality in Washington State.<sup>17</sup> We estimated the harvest rate for the NRM portion of Washington as the total harvest in the NRM portion of Washington divided by the estimated population size in the NRM portion plus the total mortality in the NRM portion.<sup>18</sup> This results in the harvest rate for

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<sup>17</sup> Harvest rate we apply to the entire state of Washington = number wolves harvested in NRM portion of Washington/(total number of wolves in Washington + total mortality in Washington)

<sup>18</sup> Harvest rate we apply to the NRM portion of Washington = number of wolves harvested in NRM portion of Washington/(number of wolves in the NRM portion of Washington + total mortality in NRM portion of Washington)

the NRM portion of Washington being slightly higher than the harvest rate for the statewide population of Washington.

### ***Future Idaho, Montana, and YNP Harvest Rates***

Due to many factors that affect hunter/trapper effort and success, uncertainty remains as to how the new harvest regulations in Idaho and Montana (discussed in detail in Chapter 3) may affect future harvest rates in these states and of wolves that live primarily in YNP but leave the park and become available for harvest. Therefore, to examine a range of potential effects of these recent changes to harvest regulations in Idaho and Montana, we projected future population sizes for these three areas (Idaho, Montana, and the wolves that reside primarily in YNP) under three different harvest scenarios in which harvest rates reflected:

- *Harvest Scenario 1*: the average estimated annual harvest rates from the most recent four years in Idaho and Montana; and the average harvest rate of individual wolves that lived primarily in YNP, left the park, and were harvested in surrounding states from the most recent four harvest seasons, excluding the harvest rate from 2021 (i.e., average of harvest rates individual wolves that lived primarily in YNP, left the park, and were harvested in surrounding states from 2018, 2019, 2020, and 2022).<sup>19</sup>
- *Harvest Scenario 2*: the maximum annual harvest rate observed in Idaho and Montana (since 2009) plus 20 percentage points, to represent an increase in harvest over previously observed rates. Furthermore, modeling an increase of 20 percentage points over the maximum observed harvest rates allowed us to better examine the impact of a transition from partially compensatory harvest effects to fully additive harvest and lethal depredation control effects. For YNP, under this scenario, we used the maximum observed harvest rate of wolves that left YNP and were harvested in surrounding states between 2009 and 2022 (excluding the harvest rate from 2021).<sup>20</sup>

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<sup>19</sup> For harvest of wolves that reside primarily in YNP but leave the park and become available for harvest, we calculated annual harvest rates as the estimated number of wolves that originated from YNP, left the park, and were harvested in Idaho, Montana, or Wyoming during a given harvest season divided by the total YNP minimum count (end-of-year count provided by YNP) for the first calendar year in the season plus total mortality for the calendar year (e.g., harvest rate for 2020 = number of wolves originating from YNP harvested during 2020/2021 hunting season/YNP population estimate for 2020 + total mortality in YNP in 2020). For Scenario 1, we then averaged these harvest rates for 2018, 2019, 2020, and 2022 to determine the overall average annual harvest rate. The 2021/2022 harvest season was the only harvest season, before or since, in which Montana did not set harvest limits in the WMUs surrounding YNP. Therefore, we excluded the harvest rate from 2021, the annual harvest rate that reflected the higher level of harvest that occurred during the 2021/2022 season, from the calculation of the average for this scenario given that the lack of harvest limits from this season was anomalous. Essentially, Harvest Scenario 1 assumes Montana will continue to employ a harvest limit in the WMU(s) that surround YNP into the future, limits they reinstated after the 2021/2022 harvest season. In our modeling, we double-counted the harvest of wolves that primarily reside in YNP, leave the park, and are harvested outside of the park; these wolves are counted both as harvested wolves in our analysis of YNP, and as wolves harvested in the state where they were legally hunted or trapped (i.e., Idaho, Montana, or Wyoming).

<sup>20</sup> We used the maximum observed harvest rate in YNP under this scenario, rather than the maximum observed harvest rate plus 20 percentage points, given that not all YNP wolves are available for harvest because many individuals do not leave YNP and harvest is not allowed within the park itself. Thus, we assumed that increased harvest in Montana and Idaho would not lead to a corresponding 20-percentage point increase in harvest of wolves originating from YNP under this scenario. We excluded the 2021 harvest rate from the identification of a maximum harvest rate for this scenario given that the lack of harvest limits from the 2021/2022 season was anomalous;

- *Harvest Scenario 3*: the harvest rate necessary to reduce the population in Idaho and Montana to 150 wolves each within five years, a timeframe reflecting a rapid (within approximately one wolf generation) decline from the current population size to the management buffer above the recovery criteria (i.e., 150 wolves), a level both states have repeatedly committed to manage above and which the new laws or harvest regulations uphold (see *Levels of Human-Caused Mortality* in Chapter 3 above) (Groen et al. 2008, p. 1; Talbott and Guertin 2012, p. 1). For YNP, under this scenario, we used the harvest rate for 2021, which reflected the harvest that occurred during the 2021/2022 season, the harvest season with the highest observed number of wolves that resided in YNP, left the park, and were harvested outside the park; essentially, this scenario examines mortality in YNP should Montana consistently choose to remove harvest limits in WMU(s) surrounding the park in the future, as it did during the 2021/2022 harvest season.

In all scenarios, we assumed that legal public harvest ceased in Idaho, Montana, and Wyoming once the populations reached 150 wolves in the respective state. This was based on commitments to manage wolf populations above the management buffer of 150 wolves each (Groen et al. 2008, p. 1; Talbott and Guertin 2012, p. 1). However, once regulated harvest ceases in the model, lethal depredation control and disease continue to affect the populations, which means populations in each state can drop below 150 wolves each, should lethal depredation control or disease further reduce population size.

### **Harvest Scenarios**

We detail the specific harvest rates in each state under each of these three harvest scenarios in Table 9 below. Only the harvest rates in Idaho, Montana, and YNP vary between scenarios. As we explain in more detail above, we assume harvest in Oregon, Washington, and Wyoming will stay the same as current average levels (or, in the case of Oregon, will remain nonexistent) into the future. It is unlikely that an individual future scenario will occur exactly as we describe above because not all scenarios are equally likely to accurately represent future harvest rates. Moreover, new state regulatory mechanisms indicate states will or could manage for population sizes larger than our model assumes or projects under these future scenarios (see “Conservation Measures and Existing Regulatory Mechanisms” above). For example, Idaho’s new 2023 gray wolf management plan (*2023 Idaho Plan*), which was released after we developed these scenarios, indicates that Harvest Scenarios 2 and 3 are extremely unlikely for Idaho because they would result in population sizes below Idaho’s stated objective of managing for a viable wolf population that fluctuates around an average of 500 wolves annually (varying between a low of 350 wolves just prior to spring reproduction and a high of 650 wolves following spring reproduction) (IDFG 2023, pp. 39–42). Similarly, the recently released *Draft 2023 Montana Plan* uses 450 wolves as a “benchmark” to ensure the population in Montana maintains at least 15 breeding pairs (MFWP 2023, p. 43). Although there is no specific management objective, if the plan is finalized as drafted, wolves in Montana would be managed above this “benchmark” (MFWP 2023, pp. 41–46; Service 2023a, pp. 164–165). Because our future scenarios were developed before these new management plans were available, our models do not incorporate the objective in Idaho’s new management plan or the benchmark in

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essentially, Harvest Scenario 2 assumes Montana will continue to employ a harvest limit in the WMU(s) that surround YNP into the future, limits they reinstated after the 2021/2022 harvest season.

Montana’s draft management plan. However, although these management plans indicate that some of our scenarios may be extremely unlikely, we elected to retain the original construction of our future scenarios because any revisions to our future scenarios to reflect these new state population objectives would have resulted in higher population projections; we wanted to retain our more conservative future scenarios, consistent with the conservative approach we took elsewhere in the analysis, such as our estimate of starting population size for Idaho. We also determined that the higher population projections would not appreciably alter our conclusions regarding viability (which we discuss in Chapter 6) because higher population sizes in the future would only increase the gray wolf’s ability to withstand stochastic and catastrophic events and adapt to future changes in the environment.

*Table 9. Harvest rates (percent of wolves killed annually through legal hunting and trapping) in each modeled state under each of the three harvest scenarios in our forecasting. Harvest in our future scenarios stops once populations reach 150 wolves; therefore, the harvest rates below no longer apply once a population reaches 150 wolves. Harvest rates for Scenario 3 were designed to reduce the population size to 150 wolves in Idaho and Montana within five years. This scenario assumes the maximum population size in these states thereafter is 150 wolves and that harvest ceases when wolf populations are below 150.*

Harvest Scenario	Idaho	Montana	Wyoming, without YNP	Oregon, statewide and within the NRM	Washington statewide (within NRM)	YNP
<b>Harvest Scenario 1</b>	32%	19%	16%	0%	5% (7%)	4%
<b>Harvest Scenario 2</b>	53%	40%	16%	0%	5% (7%)	11%
<b>Harvest Scenario 3</b>	65%	65%	16%	0%	5% (7%)	19%

Therefore, in our projections we estimated the future number of wolves in each state under six total combinations of future scenarios, spanning two disease scenarios and three harvest scenarios (as depicted in Figure 13 above and Table 10 below, and described in more detail above).

Table 10. Six combinations of future scenarios evaluated in future condition modeling. All scenario combinations also include a past observed lethal depredation control rate randomly selected from the most recent 4 years (see Lethal Depredation Control below).

	Disease Scenario	Harvest Scenario
1	<i>Observed YNP disease rates</i>	<p><b>Harvest Scenario 1:</b></p> <ul style="list-style-type: none"> <li>• Average past observed annual harvest rates in Idaho, Montana, Washington, and Wyoming;</li> <li>• Average past observed annual harvest rate of wolves that live primarily in YNP, leave the park, and are harvested in surrounding states (excluding the harvest rate from 2021);</li> <li>• No harvest in Oregon</li> </ul>
2	<i>Observed YNP disease rates</i>	<p><b>Harvest Scenario 2:</b></p> <ul style="list-style-type: none"> <li>• Maximum past observed annual harvest rates in Idaho and Montana, plus 20 percentage points;</li> <li>• Maximum past observed annual harvest rate of wolves that live primarily in YNP, leave the park, and are harvested in surrounding states (excluding the harvest rate from 2021);</li> <li>• Average past observed annual harvest rates in Washington and Wyoming;</li> <li>• No harvest in Oregon</li> </ul>
3	<i>Observed YNP disease rates</i>	<p><b>Harvest Scenario 3:</b></p> <ul style="list-style-type: none"> <li>• Harvest rate necessary to reduce the populations in Idaho and Montana to 150 wolves each within five years;</li> <li>• 2021 harvest rate for wolves that lived primarily in YNP, left the park, and were harvested in surrounding states (which reflects the harvest rate from the 2021/2022 season, when highest number of wolves residing primarily in YNP left the park and were harvested);</li> <li>• Average past observed annual harvest rates in Washington and Wyoming;</li> <li>• No harvest in Oregon</li> </ul>
4	<i>Observed YNP disease rates + added vertebrate black swan events</i>	<p><b>Harvest Scenario 1:</b></p> <ul style="list-style-type: none"> <li>• Average past observed annual harvest rates in Idaho, Montana, Washington, and Wyoming;</li> <li>• Average past observed annual harvest rate of wolves that live primarily in YNP, leave the park, and are harvested in surrounding states (excluding the harvest rate from 2021);</li> <li>• No harvest in Oregon</li> </ul>
5	<i>Observed YNP disease rates + added vertebrate black swan events</i>	<p><b>Harvest Scenario 2:</b></p> <ul style="list-style-type: none"> <li>• Maximum past observed annual harvest rates in Idaho and Montana, plus 20 percentage points;</li> <li>• Maximum past observed annual harvest rate of wolves that live primarily in YNP, leave the park, and are harvested in surrounding states (excluding the harvest rate from 2021);</li> <li>• Average past observed annual harvest rates in Washington and Wyoming;</li> <li>• No harvest in Oregon</li> </ul>
6	<i>Observed YNP disease rates + added vertebrate black swan events</i>	<p><b>Harvest Scenario 3:</b></p> <ul style="list-style-type: none"> <li>• Harvest rate necessary to reduce the populations in Idaho and Montana to 150 wolves each within five years;</li> <li>• 2021 harvest rate for wolves that lived primarily in YNP, left the park, and were harvested in surrounding states (which reflects the harvest rate from the 2021/2022 season, when highest number of wolves residing primarily in YNP left the park and were harvested);</li> <li>• Average observed annual harvest rates in Washington and Wyoming;</li> <li>• No harvest in Oregon</li> </ul>

## Lethal Depredation Control

Our models also included the rate of lethal depredation control as an influence on future population size (see **Equation 1** above); we define the rate of lethal depredation control as the percent of wolves killed through removals to mitigate conflicts with livestock and through removals for management of ungulates, annually. We calculated annual lethal depredation control rates for each of the most recent four years in which both population estimates and reports of the number of animals removed through lethal depredation control efforts were available on a state-by-state basis. We calculated these lethal depredation control rates for each state by dividing the number of wolves removed through lethal depredation control in that state, by the population counts/estimates for the calendar year plus the known number of animals that died from all causes that year (i.e., we added the total number of known wolf mortalities back to the population count/estimate for the calendar year to determine the denominator for our calculation of lethal depredation control rate); 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.<sup>21</sup>

In each of our future scenarios, we consistently used the current rate of lethal depredation control (i.e., we did not vary rates of lethal depredation control between scenarios for any state). In order to represent the continued effect of recent and current lethal depredation control rates on wolf populations in each state for each year of our models, and to allow for interannual variation, we randomly drew an annual lethal depredation control rate from the values for the most recent four years (i.e., 2019, 2020, 2021, and 2022) (Table 11) and applied this selected lethal depredation control rate to the population in the state for that model run (one simulation). Using this range of possible values for the annual rate of lethal depredation control captures some of the uncertainty associated with future rates of control (see Table 11). Our methods for inclusion of lethal depredation control assume that the annual levels of lethal depredation control from the most recent four years will continue to occur into the future (i.e., rates of lethal depredation control will remain within levels recently observed). Lethal depredation control was used to resolve repeated wolf-livestock conflicts, even when wolves were federally listed. It was first used in 1987 (Service et al. 2016, Table 7b in Chapter 3); therefore, we assumed that, when necessary, states would continue to address depredation events using lethal depredation control,

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<sup>21</sup> Currently, in Oregon and Washington, lethal depredation control can only occur in the NRM portions of the states where gray wolves are federally delisted and under state management. Thus, mortality information from the most recent four years does not provide any data on lethal depredation control in the non-NRM portions of these states, given this control is not authorized. Therefore, we assumed that, if lethal depredation control were authorized statewide (i.e., if wolves throughout Oregon were delisted), the lethal depredation control rate would be the same across the entire state of Oregon as it currently is in the NRM portion of Oregon. In other words, we assumed that if wolves were delisted throughout Oregon, the total number of wolves available for lethal depredation control (i.e., the total population size) and the number of wolves removed due to lethal depredation control would increase relative to the numbers in the NRM portion of the state, but the proportion of all wolves in Oregon removed due to lethal depredation control would remain the same as the proportion removed in the NRM portion of the state. Therefore, we calculated the rate of lethal depredation control as the number of wolves removed due to lethal depredation control in the NRM portion of Oregon divided by the estimated population size in the NRM portion of Oregon plus total mortality (all sources) in the NRM portion of Oregon; we then applied this lethal depredation control rate to the statewide population of Oregon. This results in an increased total number of wolves removed through lethal depredation control in our statewide analysis versus our NRM portion analysis for Oregon. We applied the same method to Washington.

even when populations in the state are small (i.e., when there are fewer than 150 wolves). We did not apply mortality from lethal depredation control to the population in YNP because our reason for modeling YNP separately was to investigate potential impacts that the changes in Idaho and Montana’s harvest regulations might have on wolves that primarily reside in YNP.

*Table 11. Lethal depredation control rates from 2019, 2020, 2021, and 2022 (percentage of wolves removed) in each state included in our forecasting. Rates in Oregon and Washington are calculated as number of wolves removed through lethal depredation control divided by the population estimate in the NRM portion of the state. These rates are applied in statewide and NRM scenarios (see footnote above).*

Year	Idaho	Montana	Wyoming, without YNP	Oregon, statewide and within the NRM	Washington, statewide and within the NRM	YNP
<b>2019</b>	5%	5%	7%	1%	8%	0%
<b>2020</b>	6%	3%	10%	1%	2%	0%
<b>2021</b>	3%	3%	13%	5%	1%	0%
<b>2022</b>	3%	3%	10%	4%	5%	0%

Illegal take and 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,  $h$ , 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 wolf population in our two geographic areas for every year between 2022 and 100 years into the future (i.e., our graphical depictions of projected 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 and 100 years into the future. When selecting future timeframes for future condition analysis in SSAs, 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 infrequent catastrophes (e.g., novel diseases) or black swan events that might severely impact the population. A ten-year time frame represents approximately two generations of wolves and informs our evaluation of the viability of the Western metapopulation in the near-term. 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 increases in 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 one year during the 100-year timeframe. This analysis illustrates the probability that the population will fall below critical thresholds that represent a key reduction in viability (quasi-extinction) or a potential risk of inbreeding depression (effective population size of 50). In the past, wolf populations have rebounded from significant population reductions (e.g., growing from 100 wolves to over 2,000 wolves in 20 years in the Western United States; growing from zero resident wolves to over 1,500 wolves in Wisconsin and Michigan within around 40 years (Service 2020, p. 30–31); also see Harding et al. 2016, Table 2). However, we selected these thresholds to provide a conservative estimate of the probability the projected population size would consistently remain above estimated population sizes needed to retain genetic health or avoid complete extirpation. We examined the probability of the total wolf population in the Western states that we modeled or in the NRM 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, PVA practitioners 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 wolves based on a previous PVA for gray wolves that used five wolves as the definition of “biological extinction” (ODFW 2015b, p. 15).<sup>22</sup> Also, a population of only five 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 populations falling below this quasi-extinction threshold of five wolves for scenarios that projected the total wolf population in: Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP), as well as for scenarios that projected the future number of wolves within the NRM.

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<sup>22</sup> We recognize that, based on information in the *Washington Plan* (Wiles et al. 2011, p. 278), Petracca et al. (2023a, p. 10) used a quasi-extinction threshold of up to 92 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. (2023a), 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. (2023a, p. 10) 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.

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. For gray wolves in the NRM, based on an analysis of WGI genetic data (WGI 2021, unpublished data), we estimated the average ratio of effective to census population size as approximately 0.17, with a 95% confidence interval between 0.12 and 0.26 (see Appendix 2 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 metapopulation are well connected to each other and to wolf populations in Western 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 United States, 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).<sup>23</sup>

Our effective population size threshold should not be viewed as a size for an MVP. An MVP represents the population size at which society would consider the risk of extinction unacceptably high for any smaller population size (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 United States in this SSA, because MVPs require normative (value-based) decisions around acceptable levels of risk. Additionally, in Appendix 6, we describe our evaluation of post-delisting monitoring thresholds for the populations in Idaho and Montana (which we also do not consider MVPs).

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<sup>23</sup> Note that for the Wisconsin-Michigan wolf population, Stenglein and Van Deelen (2016, p. 8) estimated that a population size of fewer than 20 wolves would cause an Allee effect; this estimate was generated from wolves located in a much smaller geographic area than all gray wolves in the Western United States and therefore is not directly comparable. However, even if it was relevant, our threshold for the evaluation of potential inbreeding depression (192 to 417 wolves), derived from genetic data from WGI (WGI 2021, unpublished data; see Appendix 2), is considerably higher than this level at which Allee effects could occur. Therefore, if there is a low probability of wolves in the Western United States crossing this effective population size/inbreeding depression threshold (i.e., if there is a low probability of having fewer than 192 to 417 wolves), there would be an even lower probability of Allee effects occurring (i.e., of having fewer than 20 wolves).

## 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 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 two major stressors on gray wolf populations in our models (human-caused mortality and disease). Given our uncertainty about future disease and harvest rates, scenarios reflect estimates of the potential range of these stressors in the future and their effects on future population sizes based on the best available science. 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 our models 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 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 various uncertainties 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.

### Disease Scenarios

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., canine distemper

virus) in the intensively monitored YNP wolf population in our model. However, 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 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. Therefore, we simulated disease events at the statewide scale (or portions of eastern Washington and eastern Oregon for our NRM analysis) 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 disease rates in the Western United States have not, to date, had observable population-level effects at this statewide scale.

The frequency and impact of black swan events is inherently difficult to predict, but failure to account for them can lead to underestimates of extinction risk. We included the possibility of black swan disease events to address the possibility for severe, but improbable, catastrophic events in the future. In our modeling, we included the rate, impact, and geographic extent of black swan disease, which 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 wolves (Reed et al. 2003b, p. 110). We have not, thus far, observed disease impacts at the catastrophic level we modeled in North American gray wolf populations.

## **Harvest Scenarios**

It is unlikely that an individual scenario will play out exactly as we framed in our model in the future; moreover, Harvest Scenarios 2 and 3 are inconsistent with Idaho’s new management plan. Recent changes in states’ management objectives, spatial heterogeneity in human access and wolf harvest, and constraints on sustaining high levels of harvest all indicate that the harvest rates we modeled statewide likely do not present an exact illustration of how harvest will occur in the future, and our projections of future abundance may thus be over- or underestimates of the true future population size. Given the research and past experience described below, in addition to new information on state management plans, it is more likely that our projections of future abundance under Harvest Scenarios 2 and 3 underestimate rather than overestimate true future abundance, given the difficulty of achieving and sustaining the harvest rates in Harvest Scenarios 2 and 3 at the temporal and/or spatial scales we modeled and Idaho’ stated objective to manage for a larger population than our model assumes or projects.

## ***Recent Changes in State Management***

As discussed in Chapter 3, although the intent of new legislation passed in Idaho and Montana in 2021, and incorporated into wolf harvest regulations for the 2021/2022 season, was to decrease wolf abundance to reduce wolf conflicts with livestock and minimize detrimental effects to ungulate populations, both states continue to maintain a significant amount of regulatory authority and discretion to limit wolf harvest, when necessary, to achieve their wolf management objectives.

In our modeling, we assume that Idaho and Montana will not reduce wolf populations below approximately 150 wolves each, a level both states have repeatedly committed to manage above and which the new regulations uphold (see *Levels of Human-Caused Mortality* in Chapter 3 above) (Groen et al. 2008, p. 1; Talbott and Guertin 2012, p. 1). Moreover, Montana law specifically states, “the commission shall establish by rule hunting and trapping seasons for wolves with the intent to reduce the wolf population in this state to a sustainable level, *but not less than the number of wolves necessary to support at least 15 breeding pairs*” (emphasis added) (MCA 87-1-901); Montana law requires that the state’s management support a minimum 15 breeding pairs of wolves. Similarly, Idaho’s new 2023 management plan (*2023 Idaho Plan*) states that management of wolves “will be closely monitored and regulated to maintain annual abundance and reproduction that stays well above the USFWS’s 2009 recovery/delisting criteria (>150 wolves and >15 breeding pairs with  $\geq 2$  pups at year end)” (IDFG 2023a, p. 38).

However, even if wolf population reductions are achieved and sustained, based on Idaho’s current management plan (*2023 Idaho Plan*) and Montana’s draft plan (*Draft 2023 Montana Plan*), the states intend to use their regulatory authorities to adjust wolf harvest opportunities to ensure that wolf abundance remains well above this 150-wolf level (IDFG 2023a, pp. 39–42; MFWP 2004, pp. 29–30; MFWP 2023, pp. 41–46). States retain more management flexibility when they manage populations above their minimum commitments. For example, state statute and WGFC Chapter 21 regulations commit WGFD to manage for at least 100 wolves in the WTGMA, but they manage wolf abundance in the WTGMA using a numerical objective of 160 wolves, 60 wolves in excess of this minimum commitment. Managing wolves at this objective allows WGFD to maintain full management flexibility to resolve conflicts and continues to provide for public wolf harvest opportunities. We expect Idaho and Montana will also continue to manage for populations above these minimum commitments to retain management flexibility. In fact, Idaho’s new 2023 management plan (*2023 Idaho Plan*) includes a primary goal of managing for a viable wolf population that fluctuates around 500 wolves annually, a population size far above the management buffer of 150 wolves to which we assume Idaho will manage in Harvest Scenario 3 (IDFG 2023a, pp. 39–42). This population objective renders Harvest Scenarios 2 and 3 extremely unlikely for Idaho, when combined with our disease scenarios, because they would result in population sizes contrary to their objective. Our assumption that Idaho would continue to harvest wolves until 150 remain is also inconsistent with the objectives and intentions in the *2023 Idaho Plan*. Although the current Montana wolf management plan identifies 15 packs as a threshold by which management will become more or less restrictive (MFWP 2004, pp. 26, 55–57), their draft management plan uses 450 wolves as a “benchmark” to ensure the population in Montana maintains at least 15 breeding pairs; while Montana does not identify a specific population size objective, the wolf population in Montana would likely be managed above this “benchmark” (MFWP 2023, pp. 41–46), again reducing the likelihood of Harvest Scenarios 2 and 3 for Montana, should the state finalize a management plan with this stipulation (MFWP 2023, pp. 41–46).

In addition, we have observed adaptive changes in harvest regulations in response to increased take in wolf management units in Montana. For example, the increase in the number of wolves that left YNP and were legally harvested in Montana during the 2021/2022 season resulted in the MFW Commission reinstating a harvest limit in WMU 313 (WMU 313 and 316 in

past seasons) for the 2022/2023 season (a harvest limit of 6 wolves). Harvest Scenario 3 assumes that the higher level of harvest of wolves residing primarily in YNP, but that leave the park and are harvested, that occurred during the 2021/2022 season would continue for the next one hundred years. Although it is possible that a high number of wolves could still be harvested in other areas of Montana outside of WMU 313 or in surrounding states when they leave YNP, based on past harvest totals and locations of wolves originating from YNP that were harvested in surrounding states, it is unlikely the level of harvest observed in the 2021/2022 season will be repeated, especially if harvest limits in WMU 313 in Montana are retained.

If Idaho and Montana are successful in reducing wolf abundance, but manage for populations in excess of 150 wolves, as the 2023 Idaho Plan and 2023 draft management plan in Montana indicate, the population sizes and probabilities in our model outputs would represent an underestimation of wolf abundance.

### ***Spatial Heterogeneity in Human Access and Wolf Harvest***

In our model, we assumed that harvest would occur at the same rate statewide every year for 100 years into the future. However, wolves can be found over broad expanses of Idaho and Montana and, because areas within these states have varied levels of human access, harvest is not uniform. This circumstance results in areas that provide refugia where harvest is low in these states, even under increased human pressure elsewhere (IDFG 2023a, p. 13), which may act to limit total harvest across each state. For example, 85 percent of wolves harvested in Idaho were harvested on public land during the 2021/2022 season, but game management units with substantial wilderness areas ( $\geq 30$  percent wilderness) accounted for only 13 percent of the total wolf harvest in Idaho as of April 2022 (IDFG 2022b, in litt.). This disproportionate harvest of wolves outside of wilderness areas may be because human access is more difficult in wilderness areas that lack road networks or because harvest was directed away from these areas through the state's reimbursement program (IDFG 2023d, in litt.). This pattern in Idaho is consistent with a 50-year study showing that wilderness areas act as refugia for wolves, with higher survival rates inside wilderness areas when compared to other Federal lands outside of wilderness boundaries (Barber-Meyer et al. 2021, pp. 10–11). Therefore, these refugia may make it difficult to achieve a consistently high harvest rate statewide. 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. This could result in overestimating the number of wolves removed in a state in any given year in our modeling for scenarios with increased harvest rates.

### ***Constraints on Sustaining High Harvest Rates***

We modeled future population trajectories for Idaho and Montana at sustained, statewide annual harvest rates of 53 to 65 percent and 40 to 65 percent, respectively (Harvest Scenarios 2 and 3). However, as we describe in detail below, harvest and control rates at these levels have only been achieved at relatively small scales (e.g., specific game management units or ungulate summer/winter ranges) and over limited periods of time in the past 100 years, if managers were able to achieve high harvest or control rates at all. Wolf harvest or control at the sustained levels represented in Harvest Scenarios 2 and 3 at the spatial (statewide) and temporal scale we modeled is extremely challenging to achieve given the biological and logistical constraints we describe below.

While managers have been able to achieve high harvest rates of wolves in the past, they were only achieved in a small area. For example, while wolf population reduction was not the intent, nor was population reduction achieved, the highest mean sustained wolf harvest rate ever documented was 74 percent in the Portneuf Wildlife Reserve in Quebec, Canada from 1990–1997 (Lariviere et al. 2000, pp. 146, 148; Fuller et al. 2003, p. 185); however, the reserve was very small (298 mi<sup>2</sup> (774 km<sup>2</sup>)) compared to the area of the entirety of Idaho (83,642 mi<sup>2</sup> (216,631 km<sup>2</sup>)) and Montana (147,040 mi<sup>2</sup> (380,832 km<sup>2</sup>)). The authors indicated that persistence of wolves in the reserve, given this high harvest rate, was probably due to immigration from adjacent areas. The distribution of harvest in Idaho during the 2021/2022 season provides another example of targeting wolf reduction efforts through harvest over a smaller scale (i.e., hunt units), rather than at a large, statewide scale. Idaho provided funding for increased reimbursements to incentivize harvest in certain areas of the state for the 2021/2022 harvest season. While the number of wolves harvested increased in these specifically targeted hunt units, the overall number of wolves harvested statewide remained similar to past seasons (IDFG 2022b, in litt.); Idaho was only able to increase harvest in small, targeted areas, not statewide. Overall, especially when wolf populations are well connected, achieving significant wolf population reduction through regulated public harvest programs alone can be difficult (Boertje et al. 1996, p. 479; Mech 2001, pp. 75–76; Adams et al. 2008, pp. 1, 20–21) because, in many cases, large carnivore harvest regulations are seldom correlated with harvest outcomes (Bischoff et al. 2012, pp. 828–830). This is primarily due to extrinsic factors that affect individual hunter and trapper effort and success in any given season (Adams et al. 2008, pp. 17–18; Cluff et al. 2010, entire; Mech 2010, pp. 1422–1423; Kapfer and Potts 2012, pp. 240–241; Mowat et al. 2022, pp. 14–16). See *Discretionary Sources of Mortality: Regulated Public Harvest* in Chapter 3 for more detail.

Given that regulated public harvest alone seldom results in significant wolf reductions, a combination of public harvest and high-intensity, agency-directed aerial control efforts are generally used to reduce wolf abundance and maintain wolf numbers below pre-control levels in a specified geographic area for a particular number of years. However, high intensity control efforts conducted over multiple years require a significant amount of logistical planning, effort, and funding to complete (B.C. Ministry 2021, pp. 3–5), which most agencies cannot maintain over the long term. Similar to the patterns we have observed for harvest rates (described in the paragraph above), due to these logistical challenges, we have only observed high rates of wolf removal through agency control over relatively small geographic scales (significantly smaller than the scale of an entire state) and over relatively short timeframes. For example, in Alaska and Canada, wolf control efforts have typically been conducted over relatively small, targeted areas, such as specific game management units or ungulate summer/winter ranges, that have ranged between 1,043 to 8,880 mi<sup>2</sup> (2,700 to 23,000 km<sup>2</sup>) and occurred over timeframes of 3 to 7 years (Ballard et al. 1987, p. 7; Boertje et al. 1996, pp. 475–476; National Research Council 1997, p. 91; Hayes and Harestad 2000, p. 7; Hayes et al. 2003, pp. 5–8; Boertje et al. 2017, p. 437).

Another more recent example of wolf population reduction efforts through agency-directed control is that of predator management in British Columbia, Canada to support caribou recovery (B.C. Ministry 2021, entire). The goal of these efforts was to remove up to 80 percent of wolves within each of nine treatment areas that, approximately, ranged in size between 965 to

9,845 mi<sup>2</sup> (2,500 to 25,500 km<sup>2</sup>) and to evaluate caribou demographic responses. Dependent upon the treatment area, wolf reduction efforts were conducted over a 2- to 7-year period and results indicated that between 30 and 97 percent of the wolves in each treatment area were removed relative to pre-control numbers. While managers in British Columbia were able to meet their reduction targets in some treatment areas, this was only over a small area with significant effort and costs (i.e., removing up to 97 percent of the population). Although overall cost estimates for the duration of these efforts are not available, B.C. Ministry spent over \$1.5 million in 2020 alone on predator reductions to benefit caribou in the province (B.C. Ministry 2021, pp. 4–5). Wolves recolonized treatment areas at rates of 30 to 100 percent of pre-control levels within one year (B.C. Ministry 2021, p. 5).

Based on the above examples, achieving and maintaining population reductions through a combination of agency control and public harvest over the long term, even at these relatively small spatial scales, while possible, has proven challenging in landscapes with well-connected and moderate- to high-density wolf populations because dispersers rapidly replace wolves lost through control, because a higher proportion of dispersers rather than resident wolves may be removed through these actions, and because of the high reproductive capacity of wolves (Ballard et al. 1987, pp. 30, 44; Boertje et al. 1996, pp. 485–487; National Research Council 1997, pp. 183–184; Hayes and Harestad 2000, pp. 44–45; Adams et al. 2008, pp. 16–17, 20–21; B.C. Ministry 2021, pp. 3, 5). Moreover, reduction efforts (either through public harvest or agency control) are extremely costly and labor-intensive. While we assumed Idaho and Montana would implement similar methods to attempt intensive wolf reduction in their states (in our Harvest Scenario 3), they would likely face very similar logistical, spatial, temporal, financial, and biological constraints that may make achieving the harvest and/or control rates necessary to accomplish long-term population reduction objectives unlikely, especially at the scale of an entire state (which would be an order of magnitude larger geographic area than any of these past observed reduction efforts).

Idaho and Montana have generally relied on regulated public harvest as the primary tool to manage wolf populations in their states. Idaho and Montana use agency-directed lethal depredation control to address conflicts with livestock or, in the case of Idaho only, to minimize negative impacts to ungulate populations. Moreover, as discussed in greater detail in Chapter 3, the percentage of the known or estimated wolf population removed through lethal depredation control has declined slightly since wolves were delisted in Idaho and Montana, further illustrating the states' ongoing intent to use public harvest as the primary wolf population management tool. The laws and regulations promulgated in 2021 reduced restrictions on wolf harvest and changed some aspects of the states' practices regarding lethal depredation control (i.e., longer reporting period for private citizens and added the ability to use contractors to carry out permitted control efforts). However, to date, these changes have had little effect on the number of wolves removed through agency-directed lethal depredation control. Therefore, in our model, we assumed that any increase in wolf take in Idaho and Montana would occur through increased hunting and trapping; we assumed that lethal depredation control would occur at the same rate as it currently does into the future.

However, it is possible that a proportion of the 40 to 65 percent take in Harvest Scenarios 2 and 3 could occur through increased lethal depredation control, rather than increased harvest.

If Idaho and Montana were successfully able to use increased agency control, in addition to harvest, to achieve the removal rates in Scenarios 2 and 3, the results of our projections of future abundance would not change (as long as the levels of increased lethal depredation control and harvest, taken together, do not exceed 65 percent). However, it would likely still be extremely difficult for Idaho and Montana to achieve the removal rates and population reductions projected under Scenarios 2 and 3 (even through this combination of harvest and lethal depredation control), given the research above on the limited scope of past successful harvest and control efforts.

While we have observed broad-scale reductions in wolf abundance in the historical past (i.e., when wolves were almost extirpated from the conterminous United States in the early twentieth century), these eradication programs relied on unregulated and widespread use of poisons in the Western United States, along with unregulated harvest incentivized through bounty programs and the use of professional trappers. Currently, the regulatory landscape in the Western United States does not allow the widespread use of poison to take wolves nor does it authorize bounty programs. Although the intentional and illegal use of poison results in the death of some wolves each year, these events tend to be rather localized and affect a relatively small number of wolves (ODFW 2022, p. 7) (see discussion of illegal take in Chapter 3 above). 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. Further, in the *2023 Idaho Plan*, the State of Idaho indicated it will not use poison to manage wolf populations (IDFG 2023a, p. 40). The draft 2023 Montana gray wolf conservation and management plan also states the state would not use poison as a response to wolf depredations (MFWP 2023, p. 70). Additionally, while Idaho and Montana law allows individuals who successfully harvest a wolf to be reimbursed by an outside foundation (i.e., F4WM) for the cost of the harvest, these payments differ from bounty programs used in the past in that the amount of the reimbursement is based on receipts of actual expenditures that hunters or trappers submit documenting costs associated with the harvest (i.e., the reimbursement program is intended to defray the costs of the hunt, not to serve as an income-generating process). Finally, harvest is currently regulated in the Western United States (e.g., regulatory bodies with management authority can change season regulations and open and close seasons as needed).

Given the evidence above, sustaining statewide harvest (and/or lethal depredation control) rates of 53 to 65 percent and 40 to 65 percent over the entirety of Idaho and Montana over five years, respectively, as we model under Harvest Scenarios 2 and 3, while possible, is highly unlikely. While harvest regulations have become less restrictive since delisting in Idaho and Montana, they have not consistently achieved significant increases in the number of wolves harvested, nor substantial commensurate reductions in wolf abundance. If states cannot achieve and sustain the harvest rates presented in Scenarios 2 and 3, our model outputs for these scenarios would present an underestimate of future wolf viability.

Table 12. Summary of uncertainties or assumptions in future condition modeling, and potential effect on model's projections of abundance.

Area of Uncertainty or Assumption	Potential Effect on Projection of Abundance
<p><b>Assumption of density-dependence for Montana</b>            We determined that the best available information supported using a density-dependent model framework for Montana, rather than the density-independent model that seemed to provide a better statistical fit. We made this choice because the data from all other states indicated that a density dependent model was the best fit (with or without harvest) and because other studies have indicated density dependence is an appropriate descriptor of wolf population dynamics.</p>	<p>If the best available science had instead indicated that selection of a density-independent model for Montana was appropriate, the use of a density-independent model would have resulted in the same rate of population growth being applied to large population sizes as small populations. This means our density-dependent model could be overestimating growth in Montana at small population sizes but underestimating growth in Montana at large population sizes, with complex consequences for the projection of abundance.</p>
<p><b>Effects of harvest and lethal depredation control</b></p> <ul style="list-style-type: none"> <li>• <b>Additive versus compensatory:</b> 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 (<math>h</math>) directly from observed data, so that this effect in our model could be specific to observed dynamics in each state. However, if harvest and/or lethal depredation control rates increase outside of the past observed range (as we model in two of our future scenarios), we do not know if the value of <math>h</math> 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 <math>h</math> outside of the range observed in the past (a completely additive value for <math>h</math>) 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).</li> <li>• <b>Density-independence of <math>h</math>:</b> Further we assumed that <math>h</math> 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 <math>h</math> 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. 2023b, p. 8).</li> <li>• <b>Estimates of <math>h</math> for Oregon and Washington:</b> Sufficient data was not available to estimate the effect of harvest and lethal depredation control in these states (<math>h</math>). Therefore, we estimated an effect of harvest and lethal depredation control in these states from the estimates of harvest and lethal depredation control in Wyoming, Montana, and Idaho.</li> </ul>	<p>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 Idaho and Montana may be <b>overestimates</b>; future population projections may be <b>underestimates</b> 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.</p> <p>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 <b>overestimates</b> (for example, in Harvest Scenario 3) or <b>underestimates</b> (for example, in Harvest Scenario 1) depending on the strength of the density dependent effects of <math>h</math>, and the harvest scenario.</p> <p>If the effects of harvest and lethal depredation control are greater in Oregon and Washington than in Montana, Idaho, and Wyoming, our population projections may be <b>overestimates</b>. If the effects of harvest and lethal depredation control are smaller in Oregon and Washington than in Montana, Idaho, and Wyoming, our population estimates may be <b>underestimates</b>.</p>

Area of Uncertainty or Assumption	Potential Effect on Projection of Abundance
<p><b>Uncertainty in future <math>r_{max}</math>, <math>h</math>, and <math>K</math> values</b></p> <p>We estimated our parameters of <math>r_{max}</math>, <math>h</math>, and <math>K</math> 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 populations, 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. In addition, the wolf populations in Oregon and Washington are still growing; therefore, estimates of <math>K</math> for these states are likely low.</p>	<p>Model projections will potentially <i>overestimate</i> future population sizes if conditions become less favorable to growth or <i>underestimate</i> future population sizes if conditions become more favorable to growth.</p>
<p><b>Future management of populations</b></p> <ul style="list-style-type: none"> <li> <p><b>Management of reduced populations:</b> We assume that Idaho, Montana, and Wyoming will stop all legal public harvest when 150 gray wolves or fewer are documented in their respective state, but lethal depredation control will continue. However, if gray wolf population reductions are achieved and sustained, Montana may use and Idaho will use their regulatory authorities to adjust gray wolf harvest opportunities to ensure gray wolf abundance remains considerably above this 150-wolf level.</p> </li> <li> <p><b>Future harvest in Oregon, Washington, and Wyoming:</b> Based on current state and tribal gray wolf management goals and objectives, wolves in Oregon, Washington, and Wyoming are unlikely to experience significantly increased harvest in the future; therefore, we did not analyze the effects of increased harvest in these states.</p> </li> <li> <p><b>Future rates of lethal depredation control:</b> Research is inconclusive as to whether lethal depredation control activities increase or decrease as harvest of wolves increases; however, the best available science on populations in the Western United States indicates that the levels of lethal depredation control while wolves are under state management have been lower than control rates prior to the transition to state management authority (see discussion of lethal depredation control in Chapter 3). Therefore, we assume that, in the future, lethal depredation control will occur at the same rate as it currently does, even as harvest increases under two of our Harvest Scenarios. Nevertheless, if Idaho and Montana use increased agency control, in addition to harvest, to achieve the population reductions in Harvest Scenarios 2 and 3 (contrary to our assumption), the results of our projections of future abundance would not change (as long as the level of increased lethal depredation control and harvest collectively does not exceed approximately 65 percent of the wolf population).</p> </li> </ul>	<p>Model projections will be <i>underestimates</i> for Idaho, Montana, and Wyoming, if these states stop harvest/control when there are more than 150 gray wolves in each state.</p> <p>Model projections will be <i>overestimates</i> if harvest, illegal removal, or lethal depredation control efforts in Oregon, Washington, or Wyoming significantly increase over average/recent (or nonexistent) rates in the future. Another possibility is that model projections of abundance could be <i>underestimates</i> for Washington and Wyoming if harvest, illegal removal, or lethal depredation control in these states declines in the future compared to the current average/most recent four years.</p> <p>Model projections could be <i>overestimates</i> if rates of control change in the future such that increased lethal depredation control plus increased harvest exceeds approximately 65 percent mortality. On the other hand, model projections could be <i>underestimates</i> if rates of lethal depredation control continue to decline relative to current rates in the future.</p>

Area of Uncertainty or Assumption	Potential Effect on Projection of Abundance
<p><b>Estimating current harvest for model scenarios</b></p> <p>We estimated current harvest and lethal depredation control as a proportion of the population size available for harvest and lethal depredation control (i.e., year-end population estimates plus all known mortalities from that year) rather than a fixed number of animals. We estimated harvest and lethal depredation control in this way because past evidence has shown that, if wolf abundance begins to decline, removing a consistent number of wolves through harvest and/or lethal depredation control becomes more difficult due to access, changes in wolf behavior, and fewer opportunities to encounter wolves.</p>	<p>If states are able to sustain harvest as a fixed number of wolves over time (rather than a constant proportion), our model projections will be <i>overestimates</i> of abundance.</p>
<p><b>Illegal take and wolf removals for health and human safety</b></p> <p>Current levels of illegal take and gray wolf removal for health and human safety are a component of the intrinsic rate of growth (<math>r_{max}</math>) and the estimated effect of harvest and lethal depredation control (<math>h</math>) 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.</p>	<p>Model projections will <i>overestimate</i> the future size of wolf populations if rates of illegal take and wolf removal for health and human safety were to increase in the future and <i>underestimate</i> future population size if rates of illegal take and wolf removal for health and human safety were to decline.</p>
<p><b>Frequency, severity, and scope of future disease events</b></p> <ul style="list-style-type: none"> <li> <p><b>Observed Disease Rate Scenarios:</b> We use the observed rates (frequency and impact) of canine distemper virus outbreaks in YNP (the disease with the most acute impact on the wolf population in YNP) as the future rate of disease in wolf populations in every Western state in our model because this is the only area within the Western United States where we had data on disease frequency and impact on 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 wolf population density in YNP, which can increase disease transmission.</p> </li> <li> <p><b>Added Vertebrate Black Swan Events:</b> 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, thus far, observed disease impacts at the catastrophic level we modeled in North American gray wolf populations.</p> </li> <li> <p><b>Scale of Disease Events:</b> Estimating the scale of disease events in 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, p. 2–5). The best available science on 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 wolves in an entire state.</p> </li> </ul>	<p>Model projections could <i>underestimate</i> the future size of wolf populations by overestimating the effects and scale of disease and catastrophes. They could <i>overestimate</i> the future size of wolf populations if a novel disease outbreak causes impacts not previously observed in wolves in the Western United States or if the actual frequency or impact of black swan events is higher than the vertebrate averages we used.</p>

Area of Uncertainty or Assumption	Potential Effect on Projection of Abundance
<p><b>Choice of thresholds</b></p> <p>There is no widely accepted, established quasi-extinction threshold for gray wolves. Therefore, we chose a quasi-extinction threshold of 5 wolves based on the best available science because this was a threshold that researchers previously used in a PVA (ODFW 2015b, p. 15).</p>	<p>Model projections will <b>overestimate</b> viability (underestimate risk of quasi-extinction) if population sizes larger than five are needed to maintain population viability.</p> <p>Model projections will <b>underestimate</b> viability (overestimate risk of quasi-extinction) if populations always rebound after falling below this threshold with no deleterious consequences.</p>
<p><b>Small population effects</b></p> <p>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 thresholds 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 2). 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.</p>	<p>Model projections could <b>overestimate</b> wolf abundance if deleterious effects of small populations (e.g., loss of genetic diversity and inbreeding depression) occur at population sizes greater than 417 wolves or if our model simulations fail to capture the dynamics of small populations.</p> <p>Model projections will <b>underestimate</b> 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.</p>
<p><b>Changes in connectivity and genetic diversity</b></p> <ul style="list-style-type: none"> <li>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 <math>r_{max}</math> 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 future viability of wolves in the Western United States, in greater detail in Chapter 6.</li> <li>We do not explicitly model genetic composition of gray wolves, 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 informed by an evaluation of the best available science to reflect a minimum population size required to avoid deleterious genetic effects of small populations.</li> </ul>	<p>Model projections will <b>overestimate</b> abundance if connectivity is lower in populations reduced by harvest than in small populations. Model projections will underestimate abundance if states that did not have wolf populations during early recolonization in Idaho and Montana (e.g., Oregon and Washington) serve as source populations for Idaho and Montana in the future.</p> <p>Model projections will <b>underestimate</b> risk of extinction if deleterious genetic effects are experienced by wolf populations at sizes &gt;417 wolves.</p>

Area of Uncertainty or Assumption	Potential Effect on Projection of Abundance
<p><b>Monitoring and population estimate accuracy</b></p> <p>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 Idaho, Montana, and Wyoming would close all harvest seasons when 150 wolves remained in their respective states, which is contingent on accurate minimum counts or estimates of population size. If populations approach recovery thresholds in Montana, MFWP has committed to increase monitoring intensity; MFWP also reiterates this commitment in the <i>2023 Draft Montana Plan</i> (MFWP 2004, pp. 29–30; MFWP 2023, p. 44). Wolf management in Idaho will be closely monitored and regulated to maintain a population that remains well above Federal recovery criteria and fluctuates around 500 wolves annually (IDFG 2023a, pp. 38–42). IDFG also continues to evaluate alternative population estimation techniques that are accurate, reliable, and cost efficient (IDFG 2023a, pp. 36–37).</p> <p>Harvest Scenario 3 results are robust to starting population sizes; therefore, these scenarios represent lower bounds of possible future conditions for wolf populations in these states.</p>	<p>Model projections of abundance will be <i>overestimates</i> or <i>underestimates</i> if states are unable to accurately estimate wolf population sizes in the future or if current estimates are biased. We developed a sensitivity analysis (Appendix 5) to specifically examine the effect of error in the initial population size in Idaho and Montana, and in other parameters.</p>
<p><b>Wolf population dynamics outside of Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP)</b></p> <p>The best available science is not sufficient to provide key demographic data for gray wolves in Arizona, California, Colorado, Nevada, New Mexico, and Utah. Therefore, the total population projections from the model do not include gray wolves outside of Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP).</p>	<p>Model projections will <i>underestimate</i> total population sizes in the entire Western United States.</p>

## Chapter 6: Future Condition

In this chapter, we discuss the future viability of wolves in the Western United States. As described in Chapter 5, we used simulation modeling and scenario analysis to project the future population size of wolves under various rates of disease and harvest. This approach allowed us to quantify the range of effects of these stressors on gray wolf abundance 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 portions of our analysis area for which we had sufficient data on wolf demographic rates and other model parameters (i.e., in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP); and in the NRM).

In the other parts of our analysis area where we lacked sufficient data to quantitatively forecast future wolf abundance (i.e., Arizona, California, Colorado, Nevada, New Mexico, and Utah), we qualitatively describe how the number of wolves may change in the future. We also qualitatively discuss future expectations for suitable habitat and prey availability in the Western 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. Additionally, the inclusion of these variables would likely have required a spatially-explicit model (i.e., a model that included information about the spatial location of wolves on the landscape at a smaller scale than the analyses unit), which the best available science did not allow us to construct. 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

For each scenario, we produced two million simulations from our models. We then estimated the median future population size and a 95% credible interval for this population size (Chen and Shao 1999, entire) based on the results of these two million simulations (see example in Figure 14 and Supplementary Materials A and B for technical details on these simulations). Median values represent the value for which 50 percent of the 2 million projected estimates are above and 50 percent of the 2 million 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). The lower 95% credible interval is the value for which 2.5 percent of the 2 million projected estimates are below and 97.5 percent of the 2 million projected estimates are above. The upper 95% credible interval is the value for which 2.5 percent of the 2 million projected estimates are above and 97.5 percent of the 2 million projected estimates are below.

We used figures to depict the projected wolf population size over a 100-year timeframe for the three different harvest scenarios and two different disease scenarios, as described in Chapter 5. We produced separate figures for our two geographic scales: (1) all of Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) and (2) the NRM. 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 14 below for an example.

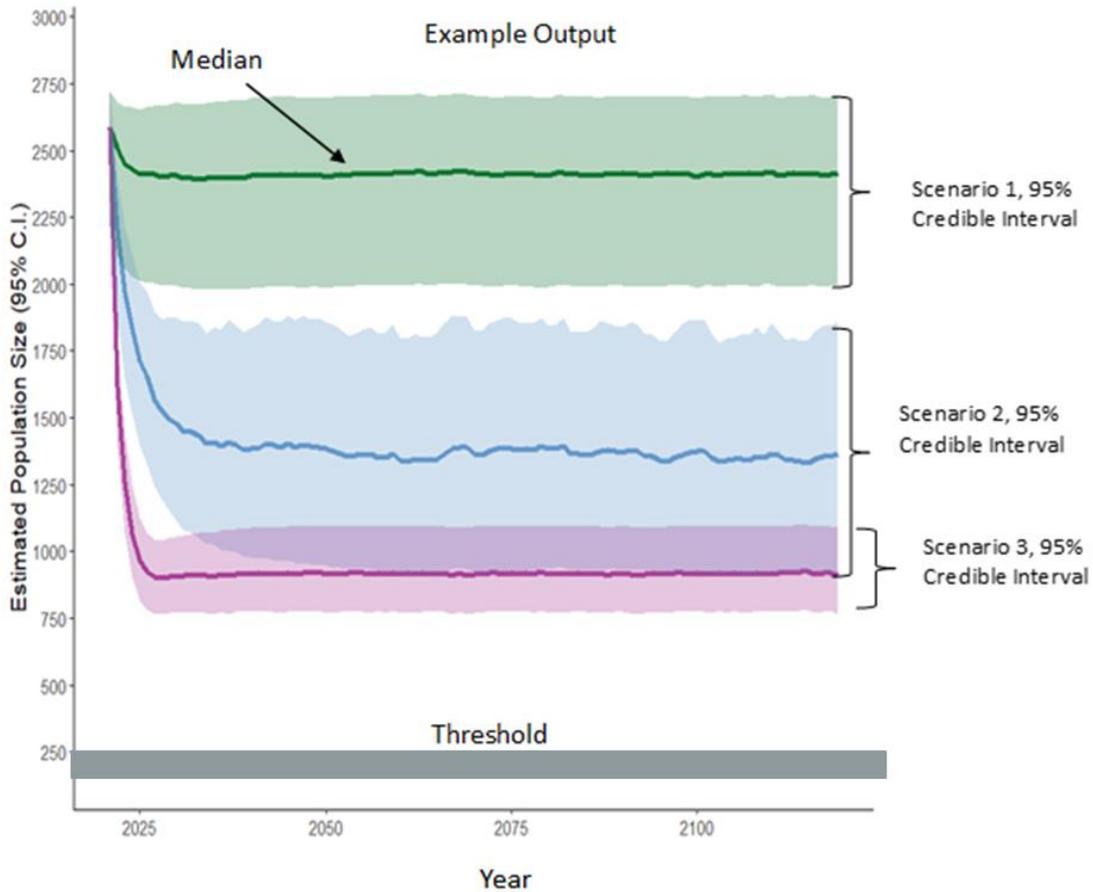


Figure 14. Example output graph depicting the median (line) and 95% credible intervals (shaded area) for three different scenarios (green, blue, and pink); gray bar represents the range of threshold values for demonstration purposes.

In the text, we report the median and upper and lower credible intervals of the estimated population size at 100 years for only two of our six future scenario combinations; namely, we report these values in the text for the combination of disease and harvest scenarios that results in the largest number of wolves (Harvest Scenario 1 combined with the observed YNP rates of disease) as well as the combination of disease and harvest scenarios that results in the smallest number of wolves (Harvest Scenario 3 combined with observed YNP disease rates and added black swan levels of disease). Results from the remaining four 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 projected population size at 100 years and the starting population size for each of the 2 million simulations. We then subtracted the starting population size from the ending population size and divided by the starting population size for each simulation to get a distribution of population change for all of our simulations; we report the median and the 95% credible interval of this distribution as the percent change from the initial population size in our tables below.

In addition to reporting median estimates of projected abundance along with the 95% credible intervals for abundance, we evaluate the number of simulations out of 2 million for which at least one simulated population falls below specific thresholds during the 100-year timeframe of our analysis (i.e., below our quasi-extinction threshold of 5 wolves or below our effective population size thresholds of 192 to 417 wolves). To estimate a probability of falling below each of these thresholds, we simply divided the number of simulated populations that crossed the threshold at least once during the 100-year timeframe by the total number of simulated populations.

## **Results of Forecasting Model: Resiliency and Redundancy in Idaho, Montana, Oregon, Washington, and Wyoming**

### ***Population Size Projection for Idaho, Montana, Oregon, Washington, and Wyoming***

In this section, we report the results of our model projections for the area depicted in Figure 15 (the total number of wolves in all of Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP)), though we modeled these as the separate analysis units depicted in Figure 15 below. 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 2,621 wolves (95% credible interval 2,535–2,708) (see Table 8 in Chapter 5). In Appendix 6, we detail the projected population size (median and 95% credible intervals) in each individual state we modeled (i.e., Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP)).

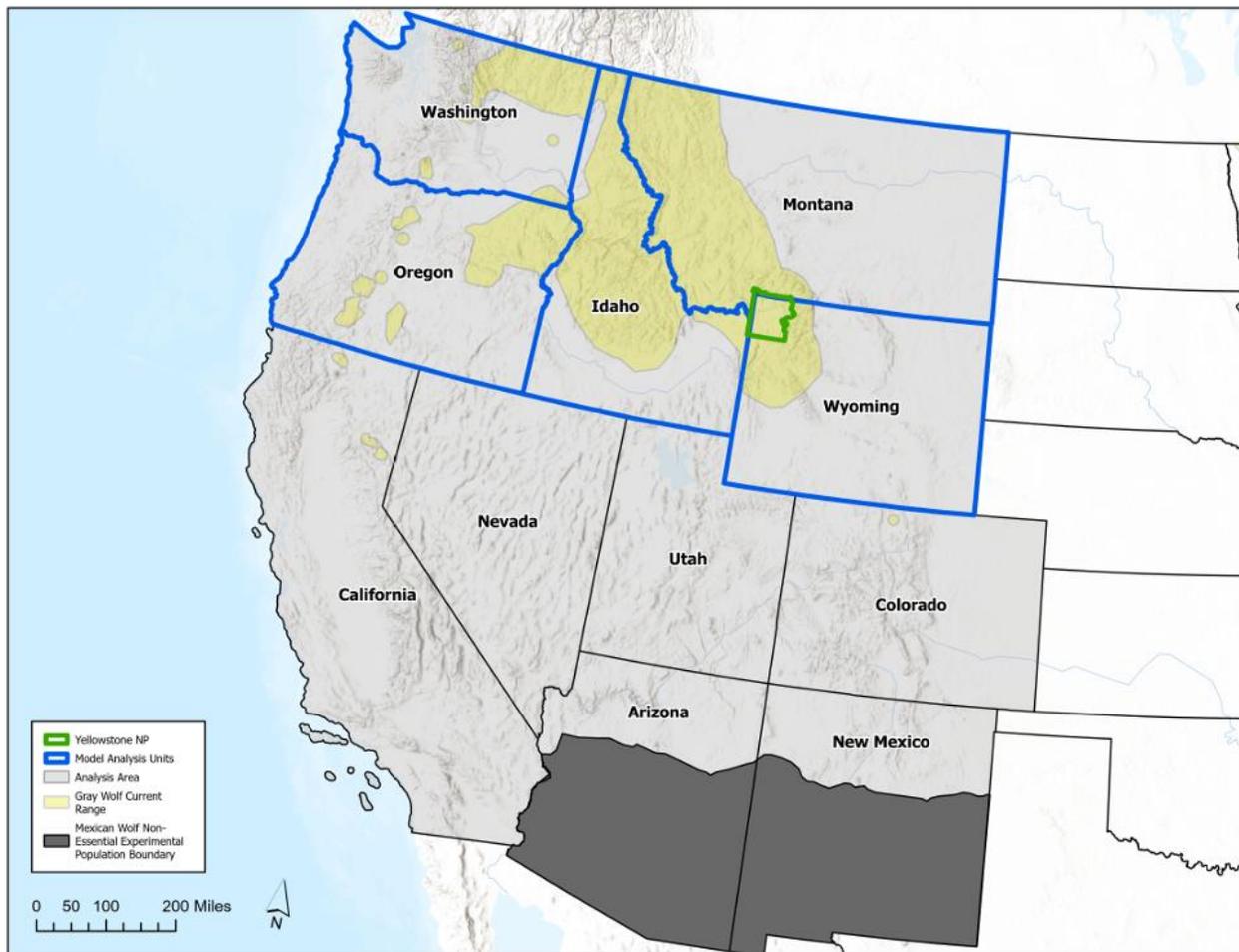


Figure 15. Visual representation of the area in which the model projection results in this section apply (blue outline). Analysis area for the entire SSA is depicted in light gray, with the current range of the gray wolf in the Western United States highlighted in yellow. The Mexican Wolf Nonessential Experimental Population Area is colored in dark gray.

We report the median projected population size and 95% credible intervals for the total population of wolves in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) in 100 years under each of our six future scenario combinations in Table 13. Under Harvest Scenario 1 with observed YNP disease rates (the least impactful scenario combination), the median projected population size for this geographic area in 100 years was 2,161 wolves (95% credible interval 1,684–2,586) (Figure 16, Table 13b). This resulted in a 2 to 36 percent (median 18 percent) decline relative to the total starting population size in these states. Under Scenarios 1 and 2, the vast majority of the population decline took place in the first 10 years of the simulation, regardless of the disease scenario (see Figure 16 and Table 13a). Under Harvest Scenario 3 with observed YNP disease rates and added black swan events, the most impactful combination of harvest and disease scenarios we analyzed, the median projected population size at 100 years was 935 wolves (95% credible interval 739–1,091) (Figure 16, Table 13b), which was a 58 to 72 percent (median 64 percent) decline relative to the total starting population size in these states. As expected, based on the intent and design of Harvest Scenario 3, the vast majority of this population decline took place over the initial five years of the simulation.

The percentage of simulations that included all wolves in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) that fell below our upper threshold for an effective population size of 50 (417 wolves) at least once over the course of 100 years was 0.01 percent for Harvest Scenario 2 with observed YNP disease rates and added black swan events and 0.02 percent for Harvest Scenario 3 with observed YNP disease rates and added black swan events; the probability of dropping below 417 wolves in 10 years would be even lower. For all other harvest and disease scenario combinations, the percentage of simulations falling below 417 wolves in 100 years was zero. No individual simulated population that included all wolves in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) 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 scenarios we analyzed (Figure 16).

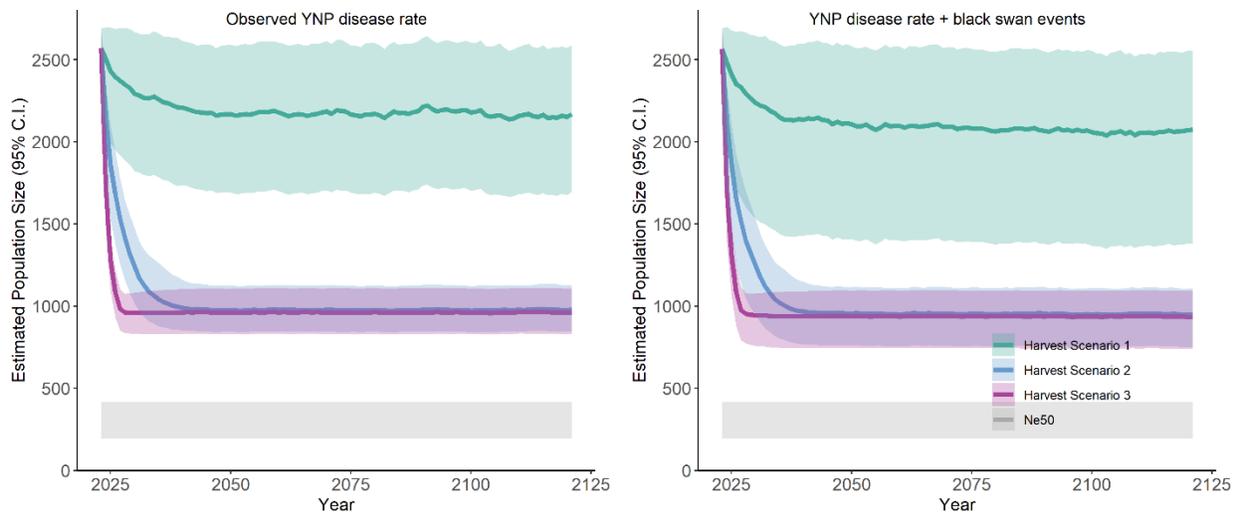


Figure 16. Median projected wolf population size (solid line) and 95% credible interval (shaded area) in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) in Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations. The shaded gray box represents the range of estimated wolf population sizes (192–417 wolves) we calculated to be equivalent to an effective population size of 50.

Table 13. Median, lower 95% credible interval, and upper 95% credible interval for population size in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) at the end of the a) 10 year and b) 100-year timeframes of our simulations in all six future disease and harvest scenario combinations. We also report the median percent change between this projected population size 100 years into the future and the starting population size in this geographic area, including the 95% credible interval (CI) for this percent change in parentheses. These values were calculated by subtracting the starting population size from the ending population size for all two million simulations for each scenario and dividing by the starting population size for that simulation. We then calculated the median and the credible intervals from these two million estimates of the percent change.

a)

Disease Scenarios	Harvest Scenarios	Median Projected Population Size at 10 years	Lower Credible Interval (LCI)	Upper Credible Interval (UCI)	Median Percent Change from Initial Population Size (95% CI)
Observed YNP disease rates	Scenario 1	2,261	1,786	2,657	-14% (-32 to 1%)
Observed YNP disease rates	Scenario 2	1,122	931	1,339	-57% (-64 to -49%)
Observed YNP disease rates	Scenario 3	959	830	1,089	-63% (-68 to -58%)
YNP + added black swan	Scenario 1	2,211	1,498	2,645	-16% (-43 to 1%)
YNP + added black swan	Scenario 2	1,116	863	1,367	-57% (-67 to -48%)
YNP + added black swan	Scenario 3	944	753	1,084	-64% (-71 to -59%)

b)

Disease Scenarios	Harvest Scenarios	Median Projected Population Size at 100 years	Lower Credible Interval (LCI)	Upper Credible Interval (UCI)	Median Percent Change from Initial Population Size (95% CI)
Observed YNP disease rates	Scenario 1	2,161	1,684	2,586	-18% (-36 to -2%)
Observed YNP disease rates	Scenario 2	976	843	1,127	-63% (-68 to -57%)
Observed YNP disease rates	Scenario 3	961	830	1,108	-63% (-68 to -58%)
YNP + added black swan	Scenario 1	2,073	1,382	2,556	-21% (-47 to -3%)
YNP + added black swan	Scenario 2	947	751	1,107	-64% (-71 to -58%)
YNP + added black swan	Scenario 3	935	739	1,091	-64% (-72 to -58%)

These models 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 negative density-dependent growth, reproductive rates increase as population size decreases. Simultaneously, in our simulations, because we modeled harvest and lethal depredation control as a constant annual proportion, as the population declines, the actual number of gray wolves removed through harvest or lethal depredation control decreases. Therefore, as the number of wolves added to the population increases (due to increasing intrinsic rates of growth as population sizes decrease) and the number removed decreases (due to declining population size), at some point the number of wolves removed from the population due

to mortality will be the same as the number of wolves added to the population due to reproduction and immigration (i.e., the population reaches an equilibrium point).<sup>24</sup> If harvest was sufficiently high or if growth rates were low, this equilibrium point could be a population size of zero wolves. However, in the case of wolves in the Western United States, growth equilibrates with mortality at population sizes greater than zero under all of the harvest 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, after reaching this approximate equilibrium point, the projected population size bounces slightly above and below this equilibrium point over time. Stochasticity is included in our models through catastrophic disease events, random selection of control rates from the most recent four years of observed control rates for each state, 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). Note that, while regulated harvest ceases in Idaho, Montana, and Wyoming once population size reaches 150 wolves in each state, lethal depredation control and disease continue to affect the populations when fewer than 150 wolves remain in a state, which means populations in each state can drop below 150 wolves each.

### ***Population Size Projection for the NRM***

In this section, we report the results of our model projections for the area depicted in Figure 17 (the total wolves in the NRM excluding the small portion of the NRM in Utah, though we modeled these as the separate analysis units depicted in blue in Figure 17 below). The median estimated starting population size for this area was 2,534 wolves (95% credible interval 2,448–2,620) (see Table 8 in Chapter 5).

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<sup>24</sup> Mathematically, eventually  $r_{max}N_t(1-N_t/K)=h(m+c)$ .

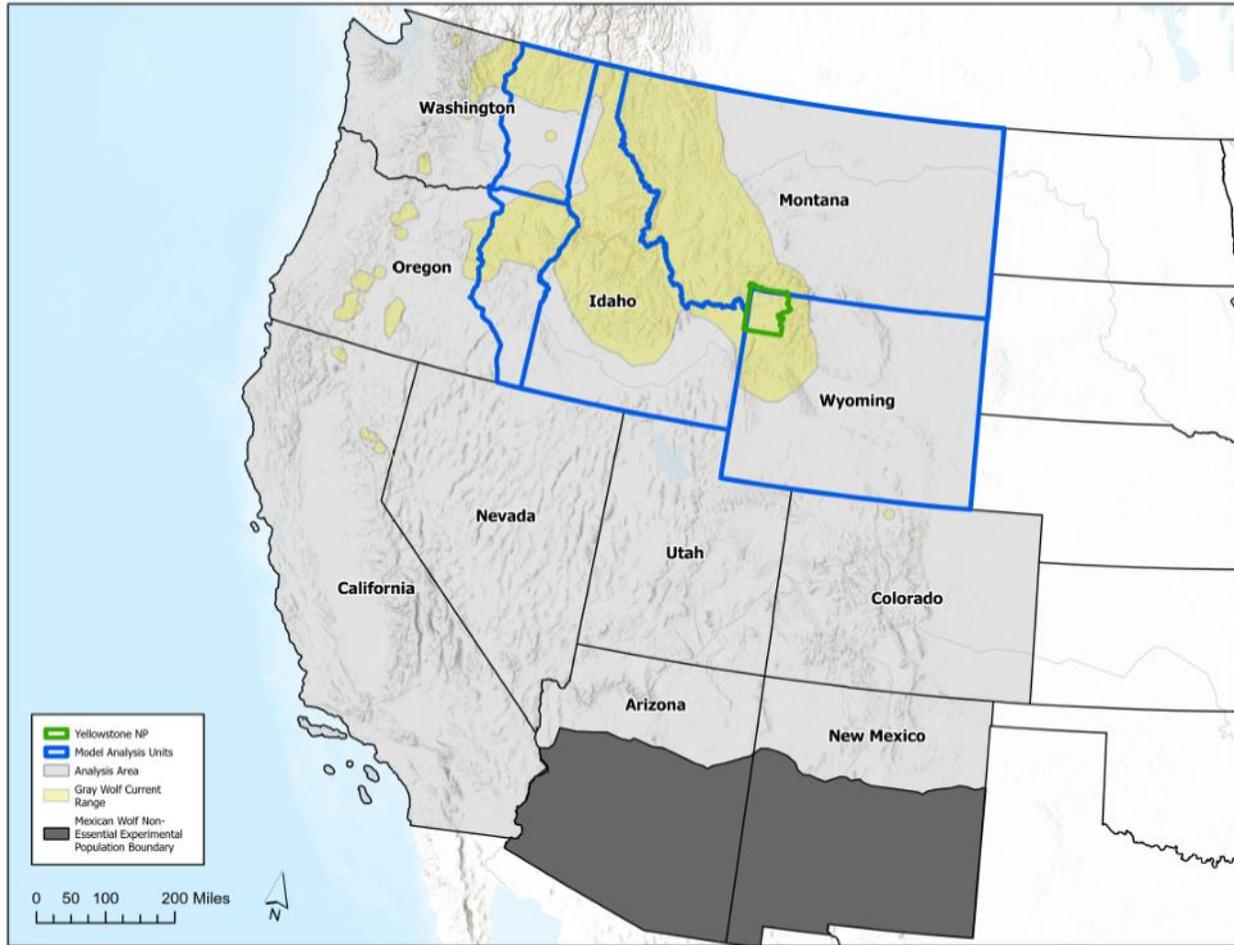


Figure 17. Visual representation of the area in which the model projection results in this section apply (blue outline). Analysis area for the entire SSA is depicted in light gray with the current range of the gray wolf in the Western United States highlighted in yellow. Note that while we report the results in this section as the projection for the NRM, these modeled projections do not include results for the small portion of northern Utah within the NRM boundary. The Mexican Wolf Nonessential Experimental Population Area is colored in dark gray.

The median projected population size for wolves in the NRM at 100 years under Harvest Scenario 1 with observed YNP disease rates, the least impactful combination of harvest and disease scenarios we analyzed, was 2,048 wolves (95% credible interval 1,579–2,462), resulting in a 6 to 40 percent decline (median 22 percent decline) in the future NRM population size relative to the starting population size in the NRM (Figure 18, Table 14b). Under Harvest Scenarios 1 and 2, the vast majority of the population decline took place in the first 10 years of the simulation, regardless of the disease scenario (see Figure 18, Table 14a). Under Harvest Scenario 3 with observed YNP disease rates and added black swan events, the most impactful combination of harvest and disease scenarios we analyzed, the median projected population size at 100 years was 829 wolves (95% credible interval 667–940) (see Figure 18 and Table 14), a decline of 64 to 75 percent (median 68 percent) relative to the total starting population size in the NRM. As expected, based on the intent and design of Harvest Scenario 3, the vast majority of this population decline took place over the initial five years of the simulation.

The percentage of simulations that included all wolves in the NRM (excluding the small portion of the NRM in Utah) that fell below our upper threshold for an effective population size of 50 (417 wolves) at least once over the course of 100 years was 0.01 percent for Harvest Scenario 2 with observed YNP disease rates and added black swan events and 0.02 percent for Harvest Scenario 3 with observed YNP disease rates and added black swan events; the probability of dropping below 417 wolves in 10 years would be even lower. For all other harvest and disease scenario combinations, the percentage of simulations falling below 417 wolves in 100 years was zero. No individual simulated population in the NRM 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 scenarios we analyzed (Figure 18).

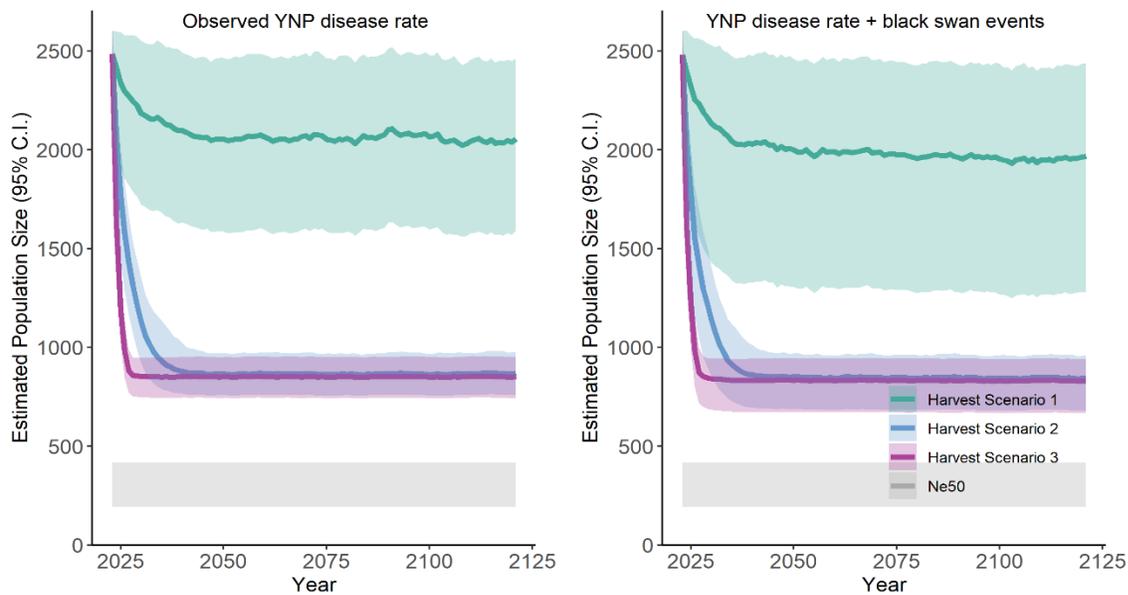


Figure 18. Median projected wolf population size (solid lines) and 95% credible interval (shaded area) in the NRM in Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations. The shaded gray box represents the range of estimated wolf population sizes (192–417 wolves) we calculated to be equivalent to an effective population size of 50.

Table 14. Median, lower 95% credible interval, and upper 95% credible interval for population size in the NRM at the end of the a) 10-year and b) 100-year timeframes of our simulations in all six future disease and harvest scenario combinations. We also report the median percent change between this projected population size 100 years into the future and the starting population size in this geographic area, including the 95% credible interval (CI) for this percent change in parentheses. These values were calculated by subtracting the starting population size from the ending population size for all two million simulations for each scenario and dividing by the starting population size for that simulation. We then calculated the median and the credible intervals from these two million estimates of the percent change.

a)

Disease Scenarios	Harvest Scenarios	Median Projected Population Size at 10 years	Lower Credible Interval (LCI)	Upper Credible Interval (UCI)	Median Percent Change from Initial Population Size (95% CI)
Observed YNP disease rates	Scenario 1	2,152	1,684	2,538	-18% (-36 to -3%)
Observed YNP disease rates	Scenario 2	1,014	840	1,216	-61% (-68 to -54%)
Observed YNP disease rates	Scenario 3	852	746	948	-68% (-72 to -64%)
YNP + added black swan	Scenario 1	2,107	1,398	2,529	-20% (-47 to -4%)
YNP + added black swan	Scenario 2	1,011	781	1,245	-61% (-70 to -53%)
YNP + added black swan	Scenario 3	840	680	945	-68% (-74 to -64%)

b)

Disease Scenarios	Harvest Scenarios	Median Projected Population Size at 100 years	Lower Credible Interval (LCI)	Upper Credible Interval (UCI)	Median Percent Change from Initial Population Size (95% CI)
Observed YNP disease rates	Scenario 1	2,048	1,579	2,462	-22% (-40 to -6%)
Observed YNP disease rates	Scenario 2	865	757	973	-67% (-71 to -63%)
Observed YNP disease rates	Scenario 3	851	744	952	-68% (-72 to -64%)
YNP + added black swan	Scenario 1	1,967	1,283	2,437	-25% (-51 to -7%)
YNP + added black swan	Scenario 2	842	678	957	-68% (-74 to -63%)
YNP + added black swan	Scenario 3	829	667	940	-68% (-75 to -64%)

### Sensitivity Analysis

As we discuss in greater detail in Chapter 4, some have expressed concern that abundance estimates from unmarked populations in Idaho (Amburgey et al. 2021, p. 14) and Montana may be biased (Creel 2022, pp. 3–14; Treves et al. 2022, pers comm). However, as discussed in Chapter 4, despite these criticisms of the methods used to estimate wolf abundance in Idaho and Montana, currently there are no published estimates of potential bias, if any, for the population estimates reported in Idaho and Montana, just as there are no definitive estimates of bias for minimum counts of wolves in these states. Thus, the best available scientific information does not allow us to determine if correcting the estimates from Idaho or Montana 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 these states produced from different methods. Therefore, the current estimates provided by the states represent the best available science, and thus we rely on these estimates in this SSA.

However, we conducted a sensitivity analysis (Lonsdorf et al. 2015, p. 1143) to evaluate the effect of uncertainty in the starting population size,  $h$ , and  $r_{max}$  values in Idaho and Montana on the median projected population size 100 years into the future for all future scenarios (see Appendix 5). None of the variation in parameter estimates we evaluated in this sensitivity analysis resulted in a median projected population size in all Western states modeled or in the NRM below 192 wolves (our minimum effective population size threshold) or 5 wolves (our quasi-extinction threshold); the variation in parameter estimates we evaluated in our sensitivity analysis resulted in a maximum of 0.020% of simulations falling below 417 wolves (the upper bound of our threshold evaluating a risk of inbreeding depression) under any of the harvest or disease scenarios we analyzed (results comparable to the results we report above). In sum, Harvest Scenario 1 is most sensitive to uncertainty in values of intrinsic rate of growth ( $r_{max}$ ) or effects of harvest ( $h$ ) in Idaho and Montana, and Harvest Scenario 3 is least sensitive to uncertainty in these values (differences in projected population sizes between the range of parameter values we explored were essentially zero). Changes in the initial population size in Montana and Idaho, within the range of the minimum and maximum values we estimated from observed data, did not result in substantial changes to the projected population size for any scenario. See Appendix 5 for more information on this sensitivity analysis.

### ***Discussion and Summary of Future Condition Modeling Results***

Our model projections demonstrate that even with large increases in harvest in Idaho and Montana (Harvest Scenarios 2 and 3), the wolf population in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP), and the wolf population in the NRM, maintain their ability to withstand stochastic and catastrophic events—albeit at substantially reduced population sizes in Harvest Scenarios 2 and 3—given the assumptions in our model. There were no simulations in which the population size in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) or in the NRM dropped below our quasi-extinction threshold (5 wolves), even considering these increases in harvest. Additionally, there was a negligible risk (maximum of 0.02 percent) of these wolf populations falling below our thresholds for an effective population size of 50 (192 to 417 wolves) during our 100-year timeframe under all of the scenario combinations we analyzed, indicating a negligible risk of future inbreeding depression, despite projected decreases in population size. As we discuss in greater detail in Chapter 3, ultimately wolf population sustainability is a function of the productivity of the population and its proximity to other wolf populations (Fuller et al. 2003, p. 185). Where productivity is average to high and source populations are near, wolf populations can sustain higher rates of mortality than populations with lower productivity. According to our model projections, as long as future wolf population productivity and connectivity remain consistent with past observed data and as long as Idaho and Montana close harvest seasons if their wolf populations fall below 150 wolves, the increases in human-caused mortality that we considered are unlikely to have a meaningful impact on overall wolf resiliency and redundancy in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) or in the NRM. In short, our modeling indicates that the population of gray wolves in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP), and the wolf population in the NRM, have sufficient levels of

productivity to prevent extirpation across a gradient of average to high harvest scenarios, assuming current levels of connectivity are maintained and our other assumptions are satisfied.

Even though the harvest and disease scenarios we analyzed are not likely to result in quasi-extinction in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) or in the NRM, harvest and lethal depredation control at the rates applied in Harvest Scenarios 2 and 3 would still result in large population declines. Under Harvest Scenario 3 with observed YNP disease rates and added black swan events, there could be an approximately 64 percent (95% credible interval 58 to 72 percent) decline in the total population size or 68 percent (95% credible interval 64 to 75 percent) decline in the NRM 100 years into the future. Additionally, the populations in Idaho and Montana could individually decline by approximately 80 to 90 percent under the level of harvest in Harvest Scenario 3, when combined with either disease scenario; this level of reduction could result in fewer than 100 wolves in each state (the results of analyzing the probability of crossing post-delisting monitoring thresholds in Idaho and Montana are reported in Appendix 6). We discuss the potential implications of these population reductions on the gray wolf's genetic health, connectivity, and adaptive capacity below. However, as we discuss in greater detail under *Key Uncertainties* in Chapter 5, the best available science indicates that the levels of harvest projected in Harvest Scenarios 2 and 3 would be extremely challenging to achieve. Factors such as the high reproductive rates of wolves, wolves' dispersal capability, the amount of refugia habitat for wolves, and the logistical constraints associated with efforts designed to reduce wolf population numbers make the increased harvest rates modeled in these scenarios unlikely throughout an entire state over an extended period of time (as we modeled), even though these harvest rates are legally allowable under current state laws (though inconsistent with Idaho's new state management plan).

### **Future Expectations of Populations in States Not Analyzed in the Model (Arizona, California, Colorado, Nevada, New Mexico, and Utah)**

As we discuss in Chapter 5, we did not quantitatively project the future number of wolves in Arizona, California, Colorado, Nevada, New Mexico, or Utah due to the lack of demographic data that would be needed to do so. Below, we provide a brief discussion of our expectations for the future number of wolves in these states (depicted in Figure 19).



Figure 19. Visual representation of the area in which the discussion in this section applies (blue outline). Analysis area for the entire SSA is depicted in light gray, with the current range of the gray wolf in the Western United States highlighted in yellow. The Mexican Wolf Nonessential Experimental Population Area is colored in dark gray.

### California

Wolves are currently listed as endangered under the California Endangered Species Act, which prevents any lethal depredation control or harvest of gray wolves in the state; this protection supports the future growth of the wolf population in the state. We expect that status to continue until the state has a more established, stable population. Although in *California's Conservation Plan for Gray Wolves (California Plan)* there is no population size specified at which delisting might occur, the *California Plan* indicates a status review might be appropriate when six breeding pairs have been confirmed for two successive years (CDFW 2016b, p. 175).

As noted in Chapter 4, California has a significant amount of vacant, suitable wolf habitat. The current population of wolves in California is largely the result of natural recolonization from dispersing wolves that originated in Oregon. As California's wolf population continues to grow, dispersers from resident California packs and from packs outside the state (i.e., primarily from Oregon) will likely continue to recolonize the state and contribute to wolf population growth under all of our future scenarios. While our model projects the abundance of wolves in Oregon is likely to remain approximately the same under all scenarios

we examined (see Appendix 6), we expect Oregon to continue to serve as a source population for California in the future under all scenarios due to the fact that our model results for Oregon are likely biased low (see Chapter 5 and Appendix 6) and given the significant amount of unoccupied suitable habitat in California.

This continued immigration into the state, combined with reproduction and population growth of existing packs within California, is likely to result in continued population growth in the state under all of our future scenarios. CDFW (2016b, pp. 155–160) provided preliminary estimates of biological carrying capacity of wolves in northern California using prey-based estimates as well as a spatial approach that analyzed the likely number of territories and wolves within those territories. They estimated northern California could support 497 wolves based on prey densities and 371 wolves based on territory size. However, CDFW (2016b, p. 157) noted that accurately estimating the potential carrying capacity in the state is difficult because of a multitude of factors that differ from the other regions that informed their models (e.g., differences in prey abundance and diversity, habitat and climatic conditions, and anthropogenic influence); therefore, they strongly cautioned that these estimates were preliminary characterizations of what might occur but will probably be substantially revised as they obtain more information from resident California wolves. Overall, while specific projections are difficult to develop, the extent of suitable habitat and available prey make continued recolonization of vacant suitable habitat in California very likely under all of our future scenarios.

### **Colorado**

Gray wolves are listed as an endangered species by the State of Colorado and they are protected under CRS 33-6-109, making it illegal for any person to hunt, take, or possess a gray wolf in Colorado. They are also federally listed as endangered under the Act. Therefore, harvest is not allowed in the state. However, due to designation as an experimental population under section 10(j) of the Act, gray wolves may be lethally removed under limited circumstances, in accordance with the final 10(j) rule (88 FR 77014, November 8, 2023). In November 2020, Colorado voters passed a ballot initiative (Proposition 114) that later became CRS 33-2-105.8, which required the CPW Commission to prepare a plan to restore and manage gray wolves in Colorado and take the steps necessary to begin reintroductions by December 31, 2023. The CPW Commission convened a Technical Working Group and a Stakeholder Advisory Group which provided input and recommendations for CPW staff during development of the draft Colorado Wolf Restoration and Management Plan. The final Colorado Wolf Restoration and Management Plan (*Colorado Plan*) was presented to and approved by the CPW Commission in May 2023 (CPW 2023, entire).

Concurrent with the development of the *Colorado Plan*, the Service embarked on a rulemaking process to designate wolves reintroduced into Colorado as an experimental population under section 10(j) of the Act. On November 8, 2023, the Service published a final rule designating wolves that will be reintroduced into Colorado as a nonessential experimental population; this rule clearly defines under what circumstances take may be allowed, up to and including lethal control of depredating wolves (88 FR 77014, November 8, 2023). As long as wolves remain federally listed in Colorado, wolf management in the state must be consistent with this final 10(j) rule. In accordance with CRS 33-2-105.8 and the *Colorado Plan*, during the

week of December 18, 2023, CPW began releasing wolves translocated from Oregon into Colorado.

If wolves are federally delisted, the *Colorado Plan* will guide all aspects of wolf conflict management in the state (CPW 2023, pp. 26–30). The state will prioritize prevention and nonlethal management of wolf conflicts in Colorado during the early phases of wolf restoration. However, under the *Colorado Plan*, CPW may authorize lethal control of depredating wolves during all phases of wolf management. The CPW Commission would need to approve any rules concerning the take of wolves while they are on the state endangered and threatened list. For legal public harvest to be considered in Colorado, several regulatory and procedural steps would be required: (1) wolves would need to be reclassified as a game animal (rather than a state endangered, threatened, or nongame species); (2) season recommendations would need to be developed and vetted through a public process; and (3) the CPW Commission would need to approve and implement the harvest regulations.

Models developed to assess habitat suitability and the probability of wolf occupancy indicate that Colorado contains adequate habitat to support a population of wolves; however, the exact number of wolves is difficult to predict. Based on mule deer and elk biomass and distribution and based on a pack size of between five and 10 wolves, Bennett (1994, pp. 112, 275–280) estimated that the probable number of wolves in Colorado would range between 407 and 814 wolves. Using an individual-based population model of suitable habitat and wolf occupancy, Carroll et al. (2006, pp. 32–33) estimated that Colorado contained substantial amounts of suitable habitat that could potentially support several hundred wolves; however, they also found that wolf persistence in some areas would likely be vulnerable to predicted landscape changes in road density and human population density (Carroll et al. 2006, pp. 33–36). The authors proposed that habitat improvements, primarily in the form of road removal or closures, could mitigate these effects (Carroll et al. 2006, p. 36). Finally, Carroll et al. (2003, p. 545; 2006, pp. 32–34) cautioned that their model predictions may overestimate potentially suitable habitat in Colorado because they did not account for the presence of livestock and the potential use of lethal removal to mitigate wolf conflicts, which may affect wolf persistence and distribution in some areas. Based on a variety of influencing factors, including conflict risk, habitat quality, dispersal probabilities, and management regimes, Ditmer et al. (2023, pp. 2329, 2335) found that, of the 21 Federal public land units in Colorado that were analyzed (i.e., wilderness areas and national parks), a complex of wilderness areas in west-central Colorado ranked the highest and was the area most likely to support wolf occupancy in the state.

Given current statutory and regulatory protections, state law that requires wolf reintroduction, and the availability of suitable wolf habitat in Colorado, it is likely that the number of wolves in Colorado will increase in the future under any of the scenarios we considered. While the predator zone in Wyoming can make dispersal more difficult between Wyoming and Colorado, it has not completely prevented dispersers from entering Colorado. Moreover, under all future scenarios we modeled, the number of wolves in Wyoming will remain approximately the same as the current population size and we do not anticipate, nor do we model, any change in the predator zone in the future. Therefore, we expect that dispersal from the rest of the larger metapopulation into Colorado will likely remain relatively consistent with current levels into the future under any of our future scenarios.

## Utah

As we discuss in greater detail in Chapter 4, suitable wolf habitat exists in Utah (Switalski et al. 2002, p. 13). One estimate predicted there is enough high-quality suitable habitat in six core areas to support up to 214 wolves, while all of Utah could theoretically support over 700 wolves (Switalski et al. 2002, pp. 15–16). However, there are currently no documented resident wolves in the state.

Outside of a small portion of north-central Utah that is currently federally delisted, wolves in the remainder of Utah are federally protected as endangered. If the Federal status of wolves changed in the future in the remainder of the state, the provisions of the *Utah Plan* would be fully implemented (SB 36; UDWR and Utah Wolf Working Group 2005, p. 28). Moreover, when wolves are removed from the protections of the Act, the UDWR will have full management authority to consider and implement actions to manage wolves in the state (UDWR and Utah Wolf Working Group 2005, p. 34). At that point, any potential harvest recommendations would be vetted through the public process via the Regional Advisory Councils, and they must be approved by the Utah Wildlife Board. If wolves were federally delisted in Utah, lethal depredation control could be considered statewide to mitigate wolf conflicts with livestock.

Without concerted efforts to minimize human-caused mortality in Utah and with low levels of immigration from neighboring populations, wolves recolonizing Utah would likely exist in small numbers and increase slowly (Switalski et al. 2002, p. 16). However, given the number of dispersing wolves that have already been documented in Utah (Service 2020, p. 19), coupled with the state efforts to actively restore wolves in Colorado, it is probable that there could be wolves in Utah during our analysis timeframe (i.e., 100 years) in any of our future scenarios. However, wolf occupancy in Utah within the next 5 years seems unlikely because the States of Arizona, New Mexico, and Utah signed a Memorandum of Understanding (MOU) with Colorado and the Service stating their “intent to relocate gray wolves that leave the Colorado nonessential population area back to Colorado, should they disperse to Utah, Arizona, or New Mexico and establishes mutual agreement for the 10(a)(1)(A) permits issued by the [Service] that would provide authority for Arizona, Colorado, New Mexico, and Utah to return both gray wolves and Mexican wolves back to their nonessential population areas” (Gray et al. 2023, p. 2). The purpose of the MOU is “to maintain geographic separation of the gray wolf and Mexican gray wolf subspecies to prevent hybridization that may threaten the genetic integrity of the Mexican gray wolf population” (Gray et al. 2023, p. 2). On November 7, 2023, the Service signed a 10(a)(1)(A) permit under the Act authorizing the capture and transport gray wolves originating from Colorado back to Colorado should they disperse to Arizona, New Mexico, and Utah. Thus, given this permit and MOU, gray wolves are unlikely to establish in Utah for the duration of the permit and/or MOU agreement (i.e., 5 years). However, in the long-term, if the permit and/or MOU change or populations expand considerably in areas surrounding Utah, there would likely be dispersal of gray wolves to and establishment of wolves in Utah in the next 100 years. Future wolf abundance in Utah is difficult to predict; as elsewhere, the number and distribution of wolves will be influenced by social and biological constraints.

## **Arizona and New Mexico**

There are currently no documented resident gray wolves (*Canis lupus spp.* other than *Canis lupus baileyi*) north of I-40 in Arizona or New Mexico. Given the efforts to actively restore wolves in Colorado, gray wolves could occupy the northern portions of Arizona and New Mexico, outside of the Mexican Wolf Experimental Population Area, during our analysis timeframe (i.e., 100 years). However, this establishment depends on the success of the reintroduction and how the States of Arizona and New Mexico manage gray wolves if they disperse to these states. Arizona, New Mexico, and Utah signed an MOU with Colorado and the Service to clarify their intent to capture and transport gray wolves that leave the Colorado nonessential population area back to Colorado, should they disperse to Arizona, New Mexico, or Utah (Gray et al. 2023, entire). On November 7, 2023, the Service signed a 10(a)(1)(A) permit under the Act authorizing the capture and transport gray wolves originating from Colorado back to Colorado should they disperse to Arizona, New Mexico, and Utah. Thus, given this permit and MOU, gray wolves are unlikely to establish in Arizona and New Mexico for the duration of the permit and/or MOU (i.e., five years). However, in the long-term, if the permit and/or MOU change or populations expand considerably in areas surrounding Arizona and New Mexico, there would likely be dispersal of gray wolves to and establishment of gray wolves in the Northern portions of Arizona and New Mexico in the next 100 years.

## **Nevada**

Wolves have likely always been scarce in Nevada (Young and Goldman 1944, p. 30). There is only a very limited amount of modeled suitable habitat in the state, and these areas are largely isolated or fragmented (Carroll et al. 2006, p. 27); therefore, we do not expect more than the occasional, disperser, border pack, or breeding pair in Nevada in any of the future scenarios we consider.

## **Future Habitat and Prey Availability**

Sufficient suitable habitat exists in the Western United States to continue to support wolves into the future. We do not anticipate overall habitat changes will occur at a magnitude that would affect gray wolves across their range in the Western United States because the wolf is broadly distributed in a large metapopulation, and it is a habitat generalist. Furthermore, a large proportion of the area occupied by gray wolves occurs on Federal public land (63 percent) (see *Conservation Efforts on Federal Lands in the Western United States* in Chapter 3). We anticipate wilderness areas and large national parks will continue to provide refugia for wolves into the future. Livestock grazing will likely continue on Forest Service, BLM, and other lands (including private lands) resulting in wolf-livestock conflicts. These conflicts will likely continue to result in wolf control efforts in an attempt to reduce the number of livestock killed by wolves.

Prey availability is one of the most important factors in determining wolf abundance and distribution. Native ungulates (e.g., deer, elk, and moose) are the primary prey within the range of gray wolves in the Western United States. Each state within wolf-occupied 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. 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. Therefore, we do not anticipate prey populations will decline to the extent that they would measurably affect the wolf's risk of extinction in the Western United States.

While we are aware of emerging contagious disease threats 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. While there is considerable uncertainty regarding the precise impacts of diseases in prey in the future, we expect that wolf abundance and distribution will continue to be more a function of human tolerance than prey availability in many areas of the West, especially near the edges of human dominated landscapes where wolf-human conflicts are likely to be highest. In addition, 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 wolf population in the Western United States.

Given that 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 wolf prey (Barber-Meyer et al. 2021, pp. 10–11; see also *Climate Change* in Chapter 4). Climate change may also influence prey's vulnerability to 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 wolf distribution and abundance is difficult to predict due to large 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 substantial and 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). The precise impacts of these shifts on wolf populations are likely to be complex and spatially heterogeneous. Nevertheless, we anticipate that states will continue to be incentivized to retain relatively large populations of ungulates for a variety of stakeholders, and that they will respond adaptively to mitigate any future declines in these populations.

### Future Genetics and Connectivity

In our models evaluating future condition, we assume that genetic diversity does not decrease to an extent that it would negatively affect population demographics, as might occur with inbreeding, given the highly connected nature of the Western metapopulation, the life history of wolves, and uncertainty about the thresholds under which we would see such effects in wolf populations. Instead, we discuss here qualitatively the possibility of impacts to genetic diversity under the future scenarios. As discussed in Chapter 3, genetic diversity in gray wolf populations is linked to effective population size and is often driven in large part by connectivity among subpopulations (Liberg et al. 2005, p. 19; Råikkönen et al. 2006, pp. 70–71; Jansson et al.

2012, pp. 5188–5189; Carroll et al. 2014, pp. 81–82; Fabbri et al. 2014, pp. 144–146; Hedrick et al. 2014, p. 1119; Akesson et al. 2016, pp. 5753–5754). Within the Western United States, such connectivity includes gene flow among subpopulations in the United States and between the United States and Canada (vonHoldt et al. 2010, pp. 4421–4422; Hendricks et al. 2018, p. 143; WGI 2021, pp. 11–14); successful dispersal facilitates this connectivity and gene flow.

In the future scenarios we examined, it is possible that dispersal rates or distance, and therefore connectivity, could be affected to some degree compared with the current situation; effects we do not model in our forecasting above. Although some change in connectivity is possible due to anthropogenic changes to habitat, including new roads or altered land use, such changes are not likely to be at a scale that would affect a significant proportion of the projected range. Conversely, we do expect human-caused mortality to continue to impact large portions of the range. As noted in Chapter 3, however, the effects of increased human-caused mortality on dispersal are not necessarily consistent and they include the possibility of decreased dispersal due to mortality of dispersing individuals or other factors (Packard and Mech 1980, p. 144; Smith et al. 2010a, p. 631; Rick et al. 2017, pp. 1100–1102) or increased dispersal at some scale due to increased social and territorial openings (Jimenez et al. 2017, pp. 588–590; Ausband and Waits 2020, pp. 3191–3192). Some evidence indicates that wolves tend to show more frequent long-range dispersal during periods of population expansion and recolonization, as opposed to periods of population stability, which instead tend towards shorter dispersal and more limited gene flow (Randi 2011, pp. 102–103; Szewczyk et al. 2019, pp. 9–11; Jarausch et al. 2021, p. 102). If so, the ongoing recolonization of habitat in Western states (e.g., California and Colorado) might correlate to a pattern of long-range dispersal, thereby facilitating connectivity over larger scales. However, dispersal between Colorado and Wyoming may be impacted to some degree by the predatory animal area in Wyoming. This designation may have the effect of decreasing the likelihood of successful dispersal across the area. Nonetheless, that designation is already in place and wolves have successfully dispersed across the region into Colorado, albeit in limited numbers. Therefore, we expect wolves will likely continue to do so to some extent in all of our future scenarios (given that our future scenarios do not consider any changes to the predator animal area in Wyoming and future population size in Wyoming is projected to remain relatively stable under all of our scenarios). While uncertainty about specific impacts of increased human-caused mortality on dispersal makes precise projection difficult, it is unlikely that dispersal would be completely prevented in areas in which wolves are currently well-established under any future scenario we analyzed above.

In addition, existing MOUs between the Service, Idaho, Montana, and Wyoming establish a commitment to monitoring and maintaining minimum levels of effective dispersal among those states (Groen et al. 2008, entire; Talbott and Guertin 2012, entire); state management plans from Idaho, Montana, and Wyoming also reaffirm this commitment (IDFG 2023a, p. 38; MFWP 2004, p. 24, 36; WGFC 2012, pp. 6–7). These agreements add assurance of continued gene flow within the Western U.S. metapopulation in the future, with associated benefits for genetic diversity. Rigorous implementation of their terms, including robust analyses of both genetic diversity and connectivity between geographic areas, will continue to be important for understanding the dynamics and resiliency of the wolf metapopulation in the Western United States as it continues to change.

Such continued dispersal may also lead to new areas of connectivity within the United States. For example, our expectation that the number of wolves in Colorado will continue to grow and expand increases the likelihood that those wolves will disperse southward and contact Mexican wolves in the long-term; however, the likelihood of effective dispersal into areas where Mexican wolves occur is reduced while MOUs are in place that direct return of any dispersing wolves to Colorado. The details of that contact, including the timing or extent, are difficult to predict. As discussed in the *Taxonomy* section in Chapter 1, wolf taxa often have contiguous or slightly overlapping ranges, with varying degrees of interbreeding. In the case of the gray wolf in the Western United States (*Canis lupus* spp. other than *Canis lupus baileyi*) and Mexican wolves (*Canis lupus baileyi*), interbreeding would be unlikely to have significant effects on the gray wolf in the Western United States, given the narrow geographic range in which such contact would likely occur relative to the overall range. We do not explicitly consider that possibility further, however, as existing data cannot reduce the considerable uncertainties surrounding this potential interbreeding such that we could make reasonable assumptions.

Connectivity between the United States and Canada is also likely to continue given extensive suitable habitat along the border. Not only did wolves from Canada naturally recolonize portions of Montana in the 1980s prior to the reintroductions in YNP and Idaho in the mid-1990s (Ream et al. 1989, entire), but there are also wilderness areas that may act as refugia from human-caused mortality and, subsequently, serve as corridors between the United States and Canada in several parts of the range, including Montana near Glacier National Park and in eastern Washington (see Figure 7 in Chapter 3). Although we expect wolves' propensity for dispersal to continue to facilitate connectivity, it is difficult to predict the specific, perhaps localized, effects on connectivity that future stressors (e.g., increases in harvest) could have. Assurance of continued connectivity, especially to Canada, would benefit from standardized genetic monitoring to specifically investigate the effectiveness of connectivity at a regional scale (vonHoldt 2022, in litt).

Some level of continued connectivity among subpopulations and with Canada has important implications for genetic diversity. All of our projections show decreases in median population size to some extent compared with the current population size. In highly structured populations with relatively little gene flow and significant differentiation among subpopulations, declines in abundance are likely to cause steeper declines in genetic diversity, as subpopulations that may become extirpated are more likely to harbor unique genetics that would be lost from the population (Moura et al. 2014, pp. 414–415). While wolves in the Western United States demonstrate detectable population structure, differentiation between subpopulations appears low, indicative of consistent connectivity (Clendenin et al. 2019, entire; Ausband and Waits 2020, pp. 3191–3193; WGI 2021, pp. 11–14). As such, while we expect a correlation between abundance and genetic diversity, that relationship may not be as strong as in a highly structured population (Fabbri et al. 2014, pp. 144–146; Moura et al. 2014, pp. 414–415). In the wolf metapopulation in the Western United States, genetic diversity is likely to be driven by continued connectivity and effective population size more than strictly abundance.

Several examples in European wolves highlight the relationship between population decline, genetic diversity, connectivity, and inbreeding. In Croatia, the population was reduced to 30 to 50 wolves before rebounding to 175 to 240 wolves as of 2014 (Fabbri et al. 2014, p.

139). Despite this bottleneck and overall low population size, genetic diversity has remained high, likely due to connectivity with neighboring populations (Fabbri et al. 2014, p. 144). The Finnish wolf population, likely founded by dispersal from Russia, also maintained high genetic diversity and low inbreeding for several decades following a severe population bottleneck (Aspi et al. 2006, p. 1571). Subsequent reductions in connectivity, however, led to dramatic increases in inbreeding and decreases in diversity within a short period (Jansson et al. 2012, p. 5184). Wolves in Italy appear to have been almost completely isolated for several millennia and were reduced in abundance to fewer than 100 individuals (Lucchini et al. 2004, p. 533; Fabbri et al. 2014, pp. 138–139; Montana et al. 2017, p. 2), leading to a 30 to 40 percent reduction in genetic diversity compared with other European wolf populations (Montana et al. 2017, p. 12). However, the Italian wolf population now numbers between 1,200 and 1,800 wolves and dispersers from this population have recolonized areas of France and other neighboring countries (Galaverni et al. 2016, p. 21). Lastly, the wolf population in Bulgaria was reduced to 100 to 150 wolves in the 1970s before rebounding to 700 to 800 wolves (Moura et al. 2014, p. 406). Although genetic diversity is currently high and the population seems stable, Moura et al. (2014, p. 413) noted relatively high inbreeding, which they attribute to heavy hunting pressure (25 to 50 percent harvest); they hypothesize this may lead to reduced genetic diversity in the future. Connectivity was not specifically examined in that study. These examples demonstrate that wolf populations can maintain genetic diversity and rebound even following relatively dramatic population reductions, particularly if connectivity with other populations is maintained.

Several of these studies also highlight that the ratio of effective population size to census size is not globally consistent across wolf populations, which can influence the number of wolves deemed necessary to avoid inbreeding depression. The lower the ratio of effective to census population size, the more wolves are needed to meet an effective population size of 50 wolves. Sastre et al. (2011, p. 710) found the ratio to be very small (0.025) for the isolated Iberian population and 0.12 for a Russian population previously believed to be large and well connected, concluding that the Russian population may in fact be fragmented. In Finnish wolves, there has been striking variation in measurements over time as the census size and degree of connectivity have fluctuated. During population growth, the ratio was measured as high as 0.42, when inbreeding was low (Aspi et al. 2006, p. 1569). Using a different method, Jansson et al. (2012, pp. 5184–5185) found a ratio of 0.28 during this period, but a much smaller ratio of 0.097 only a few years later after the population declined and inbreeding was higher. The ratio was measured as 0.12 for the Bulgarian wolf population, which was noted to have high diversity but also inbreeding (Moura et al. 2014, p. 414). As we discuss in Appendix 2, we estimated the 95% confidence interval for the ratio in the Western United States as 0.12 to 0.26, with an average of 0.17 (see Appendix 2). While we use this value to inform our assessment of the risk of inbreeding depression, it is not clear under which circumstances this ratio might change, emphasizing that census population estimates alone will likely not be sufficient for monitoring genetic health.

To specifically evaluate the risk of inbreeding depression in our future scenarios, our forecasting (discussed above) quantitatively evaluated the potential of the population in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) or in the NRM declining to a level where we might expect deleterious genetic effects by reporting the proportion of simulations that fall below an effective population size of 50 (192 to 417 wolves, calculated

based on the ratios we report in the preceding paragraph, and in Appendix 2). Based on the results of our modeling for all future scenarios, it is extremely likely the wolf population in the Western United States and in the NRM will remain above these thresholds. The lower credible interval for the smallest projected population size in all Western states modeled (Harvest Scenario 3 with observed YNP disease rates and added black swan events – 739 wolves) is still almost double 417 wolves (the upper bound of our threshold values for an effective population size of 50), and it would be above an effective population size of 50 even if the ratio of effective to census population size was considerably smaller. This result indicates that concerns about significant inbreeding or inbreeding depression within Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP), or within the slightly smaller NRM, should be minimal. Nonetheless, genetic monitoring is likely to be critical for ensuring that genetic diversity remains high and inbreeding remains low into the future, particularly because changes in connectivity can be difficult to detect and have significant consequences (Sastre et al. 2011, pp. 710–711; Jansson et al. 2012, pp. 5189–5190).

Despite our projection of minimal risk of inbreeding depression across the Western United States or NRM, wolves at or near the edge of population expansion (e.g., California, Colorado, Western Oregon, or Western Washington) might be affected differently by impacts to connectivity and dispersal in the future. For example, if population reductions in Idaho and Montana were to reduce dispersal to northern California and Western Oregon, those small, recolonizing peripheral populations could experience more significant founder effects (Fabbri et al. 2007, p. 1662). However, we lack sufficient data to accurately predict specific changes in dispersal patterns in response to potentially increased harvest in Idaho and Montana. Wolves' tendency to avoid or mitigate impacts of inbreeding (Bensch et al. 2006, entire; vonHoldt et al. 2008, pp. 267–268; Ausband 2022, entire), combined with the observed benefits of even a small number of effective dispersers (Vilà et al. 2003, entire; Wayne and Hedrick 2011, entire; Akesson et al. 2016, entire) indicate that, even if it were to occur, reduced connectivity of peripheral wolf packs is not likely to be widespread or prolonged; however, there may be specific cases of extirpations of colonizing packs. Lastly, if certain peripheral areas do become isolated and experience inbreeding or inbreeding depression, it is unlikely that such effects could impact the larger, more genetically diverse and well-connected portions of the gray wolf's range in the Western United States.

### **Summary of Future Resiliency and Redundancy**

According to the assumptions and parameters in our modeling (described above in Chapter 5 and in Table 12), neither the projected future wolf population in Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP) nor the projected future wolf population in the NRM reached quasi-extinction levels (i.e., fewer than 5 wolves) in 100 years. Additionally, depending on the scenario, there was either a zero percent probability or a less than 0.02 percent probability of falling below an effective population size of 50 (192 to 417 wolves) in 100 years, demonstrating a negligible risk of future inbreeding depression. Our models project that wolf populations are extremely likely to remain above both thresholds (quasi-extinction or a level at which inbreeding may occur) in the future, even if Idaho and Montana immediately increase harvest to over 65 percent and catastrophic levels of disease occur throughout the range (the most impactful combination of harvest and disease scenarios we

analyzed). Therefore, based on the results of our model, although the number of wolves in Idaho and Montana will decline in the future, when taken together, the wolves in the Western states we modeled and in the NRM will maintain the ability to withstand stochastic and catastrophic events into the future. Our assumptions regarding future management (i.e., that Idaho and Montana will stop harvest of wolves when 150 wolves remain), future harvest levels (i.e., that harvest will occur as a proportion of the population), our chosen thresholds for quasi-extinction and inbreeding depression, and sustained connectivity are key conditions for these conclusions.

Moreover, the number of wolves in California and Colorado will likely increase in the future due to dispersal from neighboring states, the growth of resident packs already in the states, and, in the case of Colorado, state statute that requires the reintroduction of wolves to the state. This likely future increase in wolf abundance in California and Colorado would further expand the number and distribution of wolves relative to current condition, and would contribute to increased resiliency and redundancy of wolves in the Western metapopulation. Thus, the model results, combined with our expectations for the populations of wolves outside of the modeled Western states, demonstrate that the wolves in the Western population are likely to maintain the ability to withstand stochastic and catastrophic events into the future, even with the projected declines in the number of wolves in Idaho and Montana.

Our expectations for habitat and prey availability and genetic health further support the maintained resiliency of wolves in the Western United States and the NRM 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 United States and the NRM in the future. Given our expectation of continued connectivity in the Western United States and the NRM and given wolves' life history, we do not expect any significant decreases in genetic diversity or increased risks from inbreeding depression under any of our future scenarios.

## 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 7 in *Current Representation*). Many of the attributes that contribute to those abilities are consistent among 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 allowed the wolf population in the Western United States to expand in number and range relatively quickly since reintroduction in the mid-1990s without specific management (e.g., habitat restoration or disease control), other than a reduction in human-caused mortality. 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 (vonHoldt et al. 2008, p. 267; vonHoldt et al. 2010, pp. 4420–4421; WGI 2021, entire). As such, we expect gray wolves to continue to be able to adapt to environmental

changes by dispersing to and exploiting available habitat, and establishing and reproducing 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, as discussed above (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 wolves for either geographic configuration under any scenario we examined. Similarly, although we project population decline under Harvest Scenario 1 relative to the starting population size, the decline in median population sizes is not dramatic enough to result in a “*low*” population score under Thurman et al.’s definition. In Harvest Scenarios 2 and 3, for either disease projection, the entire 95% credible intervals are more than a 25 percent reduction from current population sizes. While we did not calculate the percentage of simulations in which that decline occurred in a single generation, it is likely substantial. This evaluation of population decline in Thurman et al. (2020, WebTable 2) serves as an indicator of potential loss of genetic diversity. However, there are other methods of analyzing the future of genetic diversity of gray wolves in the Western United States, which we discussed above under *Future Genetics and Connectivity*, and detail more below.

The projected reductions in population size in all our scenarios indicate wolves in the Western United States may experience some loss of evolutionary genetic potential (see Flagstad et al. 2003, p. 878; Kardos et al. 2021, pp. 3–7; Ausband 2022, p. 539 for information regarding the relationship between population size and genetic diversity or evolutionary genetic potential). Using the generalized threshold that an effective population size of 500 is a reasonable target to ensure retention of evolutionary genetic potential (Franklin 1980, p. 147) (1,923 to 4,167 wolves, based on the ratios we calculated in Appendix 2), our projected population sizes for all Western states modeled largely fall below this threshold range. 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, our projections generally 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)). In addition, our models do not consider the number of wolves in California or Colorado, which are both likely to contribute to overall population size to some degree in the future under all of our scenarios. Perhaps most importantly, the generalized threshold of an effective population size of 500 for the retention of evolutionary genetic potential is predicated on the assumption of a single, isolated population. As discussed previously, connectivity and gene flow have been shown to be critical components in maintaining long-term genetic diversity in wolves, including for wolves in the Western United States (Ausband 2022, p. 535; Ausband and Waits 2020, p. 3192). In fact,

our analysis area is not a single, isolated population but is effectively connected to Western Canada (where there are currently an estimated 8,500 wolves in British Columbia and 7,000 wolves in Alberta; see Chapter 4). Such connectivity will likely continue to provide dispersers and gene flow that will act to buffer any potential losses of genetic diversity. As such, considering this lack of isolation and the wolf-specific PVAs regarding genetic diversity, although reductions in abundance may lead to some decreases in genetic diversity, such decreases are unlikely to be significant or sustained under the scenarios we analyzed (see *Future Genetics and Connectivity*), and thus are unlikely to negatively affect adaptive capacity in the future. As outlined in MOUs between the Service and Idaho, Montana, and Wyoming (Groen et al. 2008, entire; Talbott and Guertin 2012, entire), management and monitoring that explicitly consider the importance of genetic diversity and connectivity within the metapopulation and with Canada will be critical to ensure gray wolf evolutionary genetic potential is retained into 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 examined the degree to which wolf occurrence in different ecoregional provinces in the Western 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 wolves to remain present in each of the five ecoregional provinces that are currently occupied. Most of the population reductions projected in our future scenarios are expected to occur in Idaho and Montana, neither of which contain unique ecoregional provinces. As a result, we expect the different selective pressures and evolutionary processes facilitated by different ecoregional provinces to be maintained within the Western United States into the future.

Overall, given the adaptable nature of wolves and the projections for changes in population sizes in the future scenarios we model, it is likely that wolves will remain capable of adapting to environmental change. Such capability will be comprised, as it is currently, of: (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 our projections display a wide range of outcomes for future population size and the primary stressor, human-caused mortality, is one for which sufficient adaptation is unlikely, we expect wolves in the Western United States 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 limits described in our future scenarios.

## Summary of Future Condition

Given our stated assumptions and accounting for uncertainty, our model projections indicate that wolves will avoid extirpation in the NRM and Western United States over the next 100 years (as long as future mortality rates are within the bounds we evaluate in our analysis). Even in the extremely unlikely scenarios in which harvest substantially increases and is maintained at high rates over time in Idaho and Montana, while population sizes decrease in these states, overall populations remain well above quasi-extinction levels in the NRM and

Western United States. More generally, gray wolves in the NRM and the Western metapopulation will retain the ability to withstand stochastic and catastrophic events in the future (resiliency and redundancy) despite the decrease in the number of wolves relative to current condition under our future scenarios. We also expect the population size to remain large enough, with sufficient connectivity and genetic diversity, to avoid consequential levels of inbreeding or inbreeding depression in the future. Given this maintained connectivity, combined with wolves' adaptable life history characteristics, we expect wolf populations in the NRM and Western United States will be able to maintain their evolutionary potential and adapt to future change (representation). The likelihood of additional wolves in California and Colorado (and possibly in Arizona, New Mexico, and Utah in the long term), the continued recolonization of Western Oregon and Washington, and the availability of suitable wolf habitat and prey further support the continued viability of the gray wolf in the NRM and the Western metapopulation under the existing management commitments, albeit at potentially reduced population sizes compared to current numbers. Significant deviations from the mortality rates we analyzed, or violations of other model assumptions, could alter our confidence in this conclusion.

# Appendix 1: Report: Indigenous Knowledge and Cultural Significance of the Gray Wolf to Tribal Nations with Lands in Idaho, Montana, and Wyoming

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## Introduction

Indigenous Knowledge is one of many important bodies of knowledge that contributes to the scientific, technical, social, and economic advancements of the United States and to our collective understanding of the natural world. It is applied to phenomena across biological, physical, cultural, and spiritual systems. Indigenous Knowledge has evolved over millennia, continues to evolve, and includes insights based on evidence acquired through direct contact with the environment and long-term experiences, as well as extensive observation, lessons, and skills passed from generation to generation. Indigenous Knowledge is owned by Indigenous people including, but not limited to, Tribal Nations, Native Americans, Alaska Natives, and Native Hawaiians (Draft Guidance for Federal Agencies on Indigenous Knowledge 2022, entire).

Indigenous Knowledge, often referred to in the literature as Traditional Ecological Knowledge or TEK, includes an intimate and detailed knowledge of plants, animals, and natural phenomena; the development and use of appropriate technologies for hunting, fishing, trapping, agriculture, and forestry; and a holistic knowledge, or “world view,” which parallels the scientific discipline of ecology (Inglis 1993; Cajete 2000; Berkes 2012). The term TEK was coined in Western academia, not from Indigenous communities (McGregor 2004). Indigenous people throughout the world have always had “science,” defined as a body of practical empirical knowledge of their environment because without it a society could not survive (Cajete 2000; Nadasdy 2003). Indigenous Knowledge has in it a foundation that includes a process of environmental learning in order to survive and passing learned knowledge to the next generation. Indigenous people who have been living for generations in a particular environment develop intimate familiarity with the land. As Native American peoples developed through observations of their fellow beings, they noted that each species had characteristics that set them apart from other species and enhanced their chances of survival (Marshall 1995). The way for humans to survive and prosper was to pay careful attention and learn as much as possible about strengths and weaknesses of all the other organisms, so that they could take them as food and avoid being taken by them as food. The body of knowledge acquired through careful observations was passed on to others through detailed conversations and stories, which had to be repeated constantly so that the knowledge would be passed on to future generations (Pierotti and Wildcat 1997, 1999; Pierotti 2011).

Indigenous Knowledge includes holistic approaches to complex systems and includes inextricably linked cultural, social, and ecological contexts. The importance of stories cannot be understated or minimized by Western science. Indigenous oral histories, traditions, and stories inform everyday life about the natural world. For example, according to The Blackfoot Gallery Committee (2013), their ancient stories tell how traditions were given to the Blackfoot people. These teachings show how to live and explain relationships with the other beings in creation, and

they are a record of their history since the beginning of time. The stories and legends of the Nez Perce, passed down from generation to generation, are the repository of their collected knowledge and wisdom. Furthermore, stories told to children not only explained the world around the Nez Perce, but they also taught people how to live (Josephy 2007).

Native peoples depended upon the animals and plants of these environments for food, clothing, shelter, and companionship and, as a result, developed strong ties to the fish and land animals, forests, and grasslands (Pierotti and Wildcat 1999). The gray wolf is just one example. The gray wolf is known by many names among Tribal Nations within North America, and for time immemorial has held and esteemed place in the cultures and lifeways of the original inhabitants of this continent. Indeed, for some Tribal Nations, the gray wolf has guided and influenced their people in a foundational way, literally since the beginning of time. The cultural, spiritual, and ceremonial importance of the gray wolf is profound; suffice to say, the gray wolf is, for many Tribes, foundational to their place upon and understanding of the earth and stars (Rocky Mountain Tribal Leaders Council 2019).

This report includes only a fragment of the Indigenous Knowledge and cultural significance of the gray wolf to Tribes and Nations within the Western United States. According to the Executive Office of the Presidential Memorandum on Indigenous Traditional Ecological Knowledge and Federal Decision Making (November 15, 2021) this Federal undertaking (i.e., this SSA Report and the 12-month finding it will inform) could not be adequately prepared without including information from Indigenous people who have a deep connection with the species. The objective was to include the Indigenous Knowledge of the gray wolf into the Service's SSA Report and 12-month finding for the gray wolf. Information was gathered from Natural Resource directors, Tribal Historic Preservation Officers (THPO), and Indigenous Knowledge holders during June and August of 2022 both in person and virtual over Microsoft Teams or over the phone. Unstructured interviews occurred with Indigenous Knowledge holders from the Nez Perce Tribe and Blackfoot Nation in-person, and Shoshone, Crow, and Chippewa Cree virtually or over the phone. Information was collected from the designated THPOs of the Confederated Salish and Kootenai Tribes and Northern Arapaho Tribe. The Service also worked closely with the Rocky Mountain Tribal Leaders Council. During conversations with Indigenous Knowledge holders, questions included inquiries about the tribal name of the wolf, the translation of this name, knowledge about the wolf, stories that include the wolf, and how the wolf is viewed culturally. In the report that follows, we organize Indigenous Knowledge and cultural significance about the gray wolf in the Western United States by Tribe. In the sections for each Tribe that follow, text explaining the history of the Tribe and the Tribe's Indigenous Knowledge regarding the gray wolf are almost always verbatim from tribal websites, articles, or books (when this text was available) or directly reported from interviews with Tribes. This text does not represent the position of the Service, but it serves to accurately catalogue these Tribes' histories and Indigenous Knowledge, in their own words. We denote this verbatim text with quotations below.

## Confederated Salish and Kootenai Tribes *Séliš (Salish), Qlispé (Pend d'Oreille), and Ksanka (Kootenai)*

The *Séliš*, *Qlispé*, and *Ksanka*, who were given the name “Confederated Salish and Kootenai Tribes” by the Federal government pursuant to the Treaty of 1855, reside on the 1.3 million-acre (526,091 ha) Flathead Reservation located in northwest Montana. The Flathead Indian Reservation is home to three Tribes, the Bitterroot Salish, Upper Pend d’Oreille, and Kootenai. The territories of these three Tribes covered all of Western Montana and extended into parts of British Columbia, Idaho, and Wyoming. The Hellgate Treaty of 1855 established the Flathead Reservation, but over half a million acres transferred from tribal ownership during land allotment that began in 1904.

“The subsistence patterns of Tribal people developed over generations of observation, experimentation and spiritual interaction with the natural world, created a body of knowledge about the environment closely tied to seasons, locations and biology. This way of life was suffused with rich oral history and a spiritual tradition in which people respected the animals, plants and other elements of the natural environment. By learning from Elders and teaching children, Tribal ways of life continue to this day” (CSKT 2023, unpaginated).

### Salish and Pend d’Oreille

“The Salish-Pend d’Oreille name for wolf is *Nči cn*. There are distinct names for black wolf (*Ntłane?*) and white wolf is (*íq<sup>w</sup>nšó*). It was said that long ago it was common to hear the wolves singing in the mountains. Wolves were heard during family hunting trips in the Blackriver Valley into the 1920s. Wolves coexisted in balance with other animals, such as elk. They are the loudest in the woods, work well together in a group, and have keen hearing. In recent years, they have been reintroduced. They are important animals in the circle of life and the health of the land and the people because they clean up disease, sickness, and death, taking it into their bodies and purifying it. Some of the elders say the black wolf is kind of like the boss. The other wolves bring food back to the black wolf. He is kind of a glutton” (CSKT 2014, unpaginated).

The wolf is within the Salish and Pend d’Orielle (Qelispé-Upper Kalispell) Coyote stories. These stories are an important part of history, and they also hold important teachings. These stories are told in the winter months when snow is on the ground. Telling these stories outside of the winter months is considered dangerous. Wolf is a character in two stories of the Salish and Qelispé Coyote stories, “Four Wolves and a Deer” and “Wolves and Salmon.” These stories are meant to teach tribal children morals and the value of critically thinking. As adults, these stories are reminders of the role adults play in the upbringing of children (McDonald 2022, pers. comm.).

### Kootenai

“The Kootenai name for wolf is *Ka·kin*. Wolf is an important character in the animal stories of the Kootenai. In one story the author teaches by example the importance of family relationships and he has great spiritual power” (CSKT 2014, unpaginated).

## Nez Perce Tribe

### *Nimí pu*

“Originally, the *Nimiipuu* people occupied an area that included parts of present-day Idaho, Oregon, and Washington. They moved throughout this region and parts of what are now Montana and Wyoming to fish, hunt, and trade” (Nez Perce Tribe 2022, unpaginated). The 770,000 acre (311,608 ha) Nez Perce Reservation is located in northern Idaho. The stories and legends of the Nez Perce, passed down from generation to generation, are the repository of their collected knowledge and wisdom. And by listening to the world around them, the Nez Perce created a language that was truly the voice of the land and its creatures—indeed, many Tribal people see that as their special gift back to the land that sustains them (Josephy 2007, p. xi).

The Tribe’s deep commitment to gray wolf management was based on the Tribe’s biological and technical expertise, as well as the cultural significance of the wolf to the Tribe (Nez Perce Tribal Executive Committee 2019, p. 2). The Nez Perce Wolf Reintroduction Program reflected the importance that the Nez Perce people place on the land and all its inhabitants, which was considered a success by the Nez Perce Tribal Natural Resource Department (Miles 2022 pers. comm.; Josephy 2007, xvi). To the Nez Perce people, the wolf has always been a symbol of strength, hunting prowess, and power. The wolf’s haunting calls were often heard in the forests of their homeland and their exploits were recounted in Nez Perce stories. The Nez Perce, out of duty and honor to the wolf, took it upon themselves to restore this important part of the ecosystem (Josephy 2007, p.xvi).

In the language of the Nez Perce Tribe, the wolf is *Him’iin*, roughly translated to “him with a mouth,” a reference to wolves howling. The wolf is an important figure in many Nez Perce stories. In one story about deer, the wolf insisted that the humans remember that deer could once fly, a reference to the way deer can jump while running; furthermore, this story emphasized that the wolf cleans the land by taking the weaker individual deer. In another story five wolf brothers venture to the stars and become the five stars within the Big Dipper (with two stars that represent two grizzly bears). This story explains the different seasonal positions of the Big Dipper representing the four seasons (Josiah Pinkham 2022, pers. comm.).

An important historic Nez Perce warrior was called Yellow Wolf, who had wolf power in that he had an incredible sense of smell and he refused to ever smoke (Pinkham 2022, pers. comm.). As the wolf is unsurpassed in the sense of smell, so was Yellow Wolf who could detect the presence of an enemy at a considerable distance by the olfactory sense alone. Yellow Wolf was described as adroitly circumspective and as having fierce fighting qualities of the timber wolf. Furthermore, as the wolf is the greatest hunter among all the wilderness denizens, Yellow Wolf excelled as a hunter (McWhorter 2020, entire).

## Blackfeet Nation

### *Siksika, Kainai, Piikuni*

The Buffalo People and Star People, known as the Blackfeet, include *Siksika*, *Kainai*, and *Piikuni*. The roughly 1.5 million-acre (607,028 hectare) Blackfeet Reservation in north-central

Montana is bordered by Canada to the north and Glacier National Park to the west. The reservation was established in 1855. Traditional Blackfeet territory spanned from Alberta and Saskatchewan, Canada south to modern day Montana. “In 2009, the Iinnii Initiative was launched by leaders of the four Tribes that make up the Blackfoot Confederacy (Blackfeet Nation, Kainai Nation, Piikani Nation, and Siksika Nation) to conserve traditional lands, protect Blackfeet culture, and create a home for the buffalo to return to” (Blackfeet Nation 2022, unpaginated).

In the Blackfeet language, the wolf is known as *Makoiyi*. Although the wolf is also known by other names, all roughly translate in English to “big coyote.” The story of *The Wolf Trail: Makoi-yohsokoyi* tells the story of the wolves as the first Earth Beings to pity the people. One winter, when the people were starving, wolves invited the people to come live with them. The wolves became human and wore wolf skins on their heads. The wolves taught the people how to hunt buffalo and elk. The Blackfeet people were disciplined and listened to what the wolves told them. The people could turn into wolves while hunting in order to become good hunters, but the people started to become undisciplined and disobeyed a rule that the wolves told them; the wolves howled and then disappeared into the sky. The story states that there will be a day when the wolves can come back and help the people. The footprint of wolves is in the Milky Way (Running Wolf 2022, pers. comm.).

The story of the Wolf Trail is also referenced in The Blackfoot Gallery Committee (2013, pp. 19–20). In this story, a young man and his family camped by themselves as they searched for food. The wolves found the family and appeared to them as young men bringing fresh meat to the tipi. The wolves took this family with them, showing the man how to cooperate with other people. The man then hunted buffalo and other animals. The wolves told our ancestors that animals with hoofs and horns were all right to eat, but that animals with paws and claws should be left alone. *Makoiyi* taught the Blackfeet people the value of living and working together. The wolves disappeared in the spring, but they are still seen in the sky as *makoi-yohsokoyi*, the Wolf Trail (i.e., the Milky Way). The stars in the Milky Way are a reminder to the people how to live together (The Blackfoot Gallery Committee 2013, pp. 19–20).

## Crow Tribe *Apsáalooke*

The *Apsáalooke* or Crow People (federally recognized as the Crow Tribe of Montana), currently reside in south-central Montana on an approximately 2.2 million-acre (890,308 hectare) reservation. In historical times, the Crow lived in the Yellowstone River Valley, which extends from present day Wyoming through Montana and into North Dakota, where it joins the Missouri River (Governor’s Office of Indian Affairs 2022a, unpaginated). The wolf is known as *Cheéte*; specifically, the gray wolf or timber wolf is known as *Cheét x iilisee*. A wolf pup is called *Cheéte daa ka*. There was a famous Chief named after a wolf. There is a mountain range called Cheetah, translated as Wolf Teeth. Before the time of horses, wolves were used as a means of transportation when harvesting plants and animals. Belongings and harvested items were loaded on travois, which were pulled by wolves and later by horses and they were introduced by the Spanish in the sixteenth century. Wolves were also raised as pets and some were trained to be hunters. The wolf is also considered a protector; specifically, the significance of the wolf is

evident as it is portrayed on one side of the entrance to a tipi lodge to protect the family. The wolf portrayed on the doorway of the lodge guards the doorway so not to allow evil to enter the lodge. The other animals portrayed on the lodge doorway include mountain lions and grizzly bears (Left Hand 2022, pers. comm.).

The wolf, mountain lion, and grizzly bear were never hunted for game meat. The Tribe believes the wolf should not be shot because he is a brother to the Crow People. When the wolf was seen while hunting, the Crow would offer prayers and leave some tobacco as an offering. Wolves have the ability to take unhealthy, sick, or old prey items. Oftentimes, wolves would kill a sick animal, but they would not eat it because they knew it was sick and not healthy to eat. In Crow stories told by elders, if someone, especially a young person is lost, the wolf acted as a protector and a guide. Wolves were observed in wolf packs, with particular rankings in the pack as they hunted. The alpha pair is first and then others as they ranked in the pack. Wolf packs also fought for territory, similar to the past tribal warfare days. Furthermore, wolves are part of the solar system Left Hand 2022, pers. comm.).

## Arapaho *Hinoni'ei*

“Since 1878, the Northern Arapaho have lived with the Eastern Shoshone on the Wind River Reservation in Wyoming and are federally recognized as the Arapaho Tribe of the Wind River Reservation. The *Hinono'ei*, or Arapaho, are known as the mother Tribe due to their extensive ties to the land within the North American continent. Arapaho People were natural stewards of the land and learned of the plants and wildlife very quickly when coming to a new area because of this way of life. Today, the Arapaho can be found throughout the world, but their primary locations are the Wind River Indian Reservation in Wyoming and the Cheyenne and Arapaho Reservation in Oklahoma. The Arapaho claim seventeen states in their migratory territory. These states include Wyoming, Montana, Colorado, New Mexico, Nebraska, Kansas, South Dakota, North Dakota, Minnesota, Wisconsin, Michigan, Illinois, Oklahoma, Arkansas, Iowa, and numerous Texas Counties.” (Fowler 2004, entire).

In the language of the Arapaho, the wolf is known as *hooxei*. There are different names for wolf pups (*hooxelihilisoo*), wolves of different sizes (*heebetotees*), and for “rutting wolves” (*nookotees*) (i.e., wolves in their breeding season). The Arapaho considered the wolf a very good provider for their families. One story describes wolves helping starving children and then later as protectors of the children’s lodge (C’ Bearing 2022, pers. comm).

## Shoshone *Newe*

“The Eastern Shoshone Tribe, now living on the Wind River Reservation in Wyoming, has been living, some say, in the Wind River mountain range and its environments for some 12,000 years. Recently discovered ancient cliff dwellings, attributed to Eastern Shoshone builders, in the Wind River Mountains are evidence of just how long the Shoshone Tribe has dwelled and hunted in these lands. By the early 1800s, the Eastern Shoshone band ranged along the eastern slope of the Rocky Mountains from Southwestern Wyoming to Southwestern

Montana. In the 1860s, the band camped for most of the year in the Wind River Valley, which the Shoshones call "Warm Valley," moving to the Fort Bridger area in Wyoming for the summer months" (Eastern Shoshone Tribe 2022, unpaginated).

In the language of the Shoshone people, the wolf is known as *Bia-ee-sah-pah*, which translates to big coyote in English. The Shoshone language is very descriptive such that other names for the wolf describe coat colors, (i.e., silver, white, and black). Furthermore, there are wolf names for various life stages, i.e., pups, young adult wolves, and old wolves. In the Creation story of the Shoshone, *Bia-ee-sah-pah* (wolf) was considered "a father." The wolf gave the people his amenities (i.e., knowledge, etc.). The wolf is respected and given great honor because of his cunning and fortitude. The Shoshone do not consider the wolf to be an animal that should be hunted and thus, he should be left alone. The Wolf Dance is part of Shoshone culture to honor the wolf. The Wolf Dance is synonymous with the War Dance for warriors because of the great reverence for the wolf's strength and endurance. The Shoshone also watched how they captured their prey and emulated the wolves' hunting techniques; specifically, the Shoshone observed where wolves hunted, their habitats, hunting habits, and their hunting formation (i.e., alpha hunters followed by the younger wolves). Wolves are considered Nature's way of culling weak and sick animals (Barney 2022, pers. comm.).

## Chippewa Cree *Ne Hiyawak*

The Chippewa Cree Tribe resides on the Rocky Boy Reservation in Montana; they are descendants of Cree who migrated south from Canada and Chippewa (Ojibwe) who moved west from the Turtle Mountains in North Dakota in the late nineteenth century. The name "Rocky Boy" was an inaccurate English translation of Chief Asiniiwin (Chippewa), whose name was Stone Child. The Rocky Boy Reservation encompasses approximately 122,000 acres in north-central Montana (Governor's Office of Indian Affairs 2022b, unpaginated).

In the language of the Chippewa Cree, the wolf is called *Ma-he-kahn*, which directly translates to wolf in English. The wolf is a highly significant individual. We as humans and animals and insects are all connected. At the beginning, the wolf plays a significant role in the Creation story. During the time of Creation long ago, all the four-legged beings (including wolves) were created and existed before humans. The four-legged beings all had different responsibilities to assist humans. These different responsibilities were considered commitments from the Creator. Wolves had the responsibility of providing the humans with survival, natural instinct, and guidance. These covenants equated to the natural laws of the earth and universe, such that when humans disrespect these laws, humans are hurt. Humans and the four-legged beings are all created equal and, thus, all connected both physically and spiritually (Windy Boy 2022, pers. comm.).

## Discussion

In the Indigenous Knowledge holder's worldview, the Creation story begins with animals and humans in spirit form with the ability to communicate with each other. Therefore, in a spiritual sense, animals are viewed as people (Ramos 2022). The Tribes interviewed in the

Rocky Mountain Region of the Western United States have an understanding and worldview of the wolf that differs from Euro-American, Western science. Their engagements with wolves on the landscape was based in a rich blend of ecological observations and sociocultural and cosmological knowledge and beliefs. The seven Tribal Nations discussed above have their Indigenous science regarding wolves, which is “that body of traditional environmental and cultural knowledge unique to a group of people which has served to sustain that people through generations of living within a distinct bioregion” (Cajete 2000, p. 2).

As documented above, wolves are enormously significant sentinel beings to the Tribes that are included in this report. The wolf plays an important role in Creation stories and cosmology, having a synergistic relationship with human beings. Wolves were called by different names that described wolves’ various colors traits, specific ages, and life-history traits. Shared themes from Indigenous Knowledge holders that were documented in this report include the following: (1) the wolf is a central figure in many stories and significantly important culturally; (2) the wolf is an important part of the ecosystem in that they are healers and cleansers of the land because they take weak and sick prey; (3) wolves should be respected; (4) wolves have a strict pack order when hunting prey; and (5) wolves were teachers and taught people how to hunt and survive. While important knowledge and cultural information was documented in this report, it should be noted that the author of this report was new to the communities and to the Indigenous Knowledge holders and, thus, detailed information about the wolf could not be shared. Specifically, some information is considered too culturally sensitive to share outside of their society. Furthermore, within Tribes, strict protocols exist for sharing culturally sensitive information, especially Creation stories; specifically, tribal members often cannot share these stories with individuals outside of their Tribes or even outside of their families.

It must be noted that the return of the bison (*Bison bison*, buffalo) was a momentous subject when discussing the wolf to Indigenous Knowledge holders and THPOs during this project. Bison hold an important place in the cultures and spiritual lives of many modern native Tribes. As stated above, the Blackfoot Confederacy is one example of a large, landscape restoration effort to bring bison back to fill their ecological niche and the historical cultural role for native peoples. The goal of the Iinnii Initiative is to restore bison, which are central to the historical, cultural, and ecological legacy of the region, conveying multiple benefits to the Blackfeet and providing native peoples the opportunity to reconnect with a living symbol of their ancient culture. The Iinnii Initiative also seeks to connect restoration efforts to the economic sustainability of communities (Montana Fish, Wildlife, and Parks, 2019, p. 59). In 2017, the Blackfeet Reservation received 89 genetically pure bison from Elk Island in Canada. Additionally, in 2020, National Bison Range, located on the Flathead Reservation but administered by the Service, was returned to, and is now managed by, the Confederated Salish and Kootenai Tribes. This is noted because of the close association between bison, wolves, and the Indigenous people in the Rocky Mountain region.

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- C’Bearing, C. 2022. In-Person meeting with Crystal C’Bearing, Tribal Historic Preservation Officer, Arapaho Tribe, dated July 26, 2022

Left Hand, L. 2022. Phone conversation with Les Left Hand, Crow Tribe Rocky Mountain Tribal Leadership Council, Project Director, All Nation Youth Partner for Success, dated August 3, 2022.

McDonald, K. 2022. Phone conversation with Katie McDonald, Tribal Historical Preservation Officer, Confederated Salish Kootenai Tribes, dated August 19, 2022.

Miles, A. Sr. 2022. In-person meeting with Aaron Miles, Sr., Director, National Resources Department, Nez Perce Tribe, dated June 22, 2022.

Pinkham, J. 2022. In-person meeting with Josiah Pinkham, Cultural Director, Nez Perce Tribe, dated June 22, 2022.

Running Wolf, T. 2022. In-person meeting with Tyson Running Wolf, Blackfeet Tribe, House of Representatives, District 16, State of Montana, dated June 24, 2022.

Windy Boy, J. 2022. Phone conversation with Jonathan Windy Boy, Tribal Historical Preservation Officer, Rocky Boy Tribe, dated September 22, 2022.

## Appendix 2: Analysis of Wildlife Genetics International Data Set

Brenna Forester  
Branch of SSA Science Support  
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 ( $N_e$ ), 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.

### 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 ( $PHt = \text{number of heterozygous loci} / \text{number of genotyped loci}$ ) 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.

#### Analysis of effective population size

We calculated contemporary  $N_e$  for all states with a sufficient sample size (i.e.,  $\geq 50$  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  $N_e$  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  $N_e$  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 ( $N_e:N_c$ ), 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.

**Proportion of heterozygous loci in an individual by year and location**

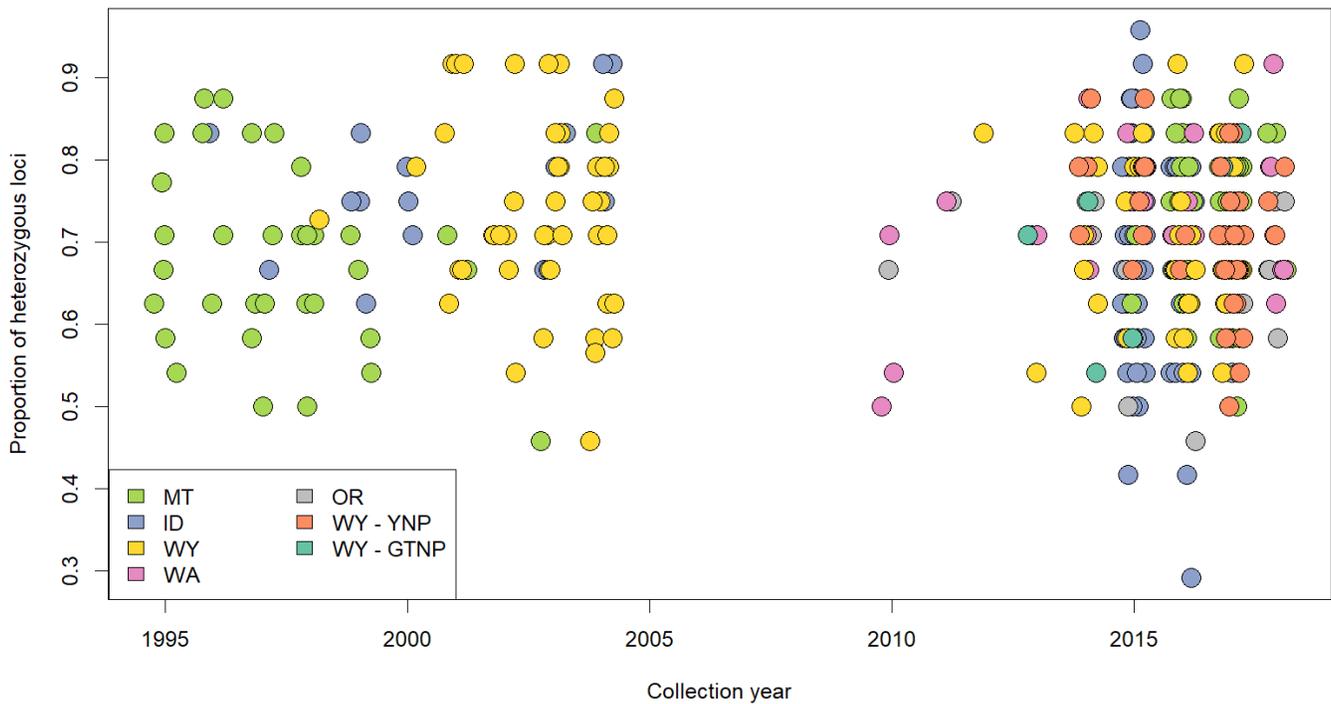


Figure A 1. Individual heterozygosity measured as the proportion of heterozygous loci in 427 individual NRM wolves (circles), color-coded by location region where the sample was collected. Individual points are jittered slightly to illustrate number and location of samples per year. YNP = Yellowstone 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  $N_e$  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  $N_e$  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  $N_e:N_c$  ratios across states, including 95% confidence intervals was: 0.171 (0.121–0.264; Table A 4).

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

	Idaho	Montana	Wyoming
<b>Years of samples used</b>	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
<b>2015</b>	786	NA	NA
<b>2016</b>	Not available	1119	377
<b>2017</b>	NA	1107	347
<b>Average</b>	<b>786</b>	<b>1113</b>	<b>362</b>

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

	Idaho	Montana	Wyoming	Average
<b><math>N_e:N_c</math> ratio</b>	0.159	0.167	0.186	0.171
$N_e:N_c$ 95% lower CI	0.124	0.114	0.125	0.121
$N_e:N_c$ 95% upper CI	0.212	0.278	0.303	0.264

As mentioned above, there are a number of biases associated with estimating contemporary  $N_e$  for wild populations, including NRM wolves. One potential bias is that associated with grouping individuals across population substructure; we mitigated this bias by calculating  $N_e$  estimates 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  $N_e$  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  $N_e$  estimation approach allows for a direct comparison with state-provided census size estimates to calculate  $N_e:N_c$  ratios.

A bias in  $N_e$  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  $N_e$  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  $N_e$  that is about 75% of the true  $N_e$  value (i.e., reported value above could be ~25% lower than the true  $N_e$  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  $N_e$  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  $N_e:N_c$  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  $N_e:N_c$  ratios may be biased downward.

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

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### Appendix 3: Citations for Population Monitoring and Mortality Data

Year	Citation(s) for population monitoring and/or mortality data
1985	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1986	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1987	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1988	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1989	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1990	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1991	Bangs et al. 2009; Fritts et al. 1995; U.S. Fish and Wildlife Service et al. 2016
1992	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1993	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1994	Bangs et al. 2009; U.S. Fish and Wildlife Service et al. 2016
1995	IDFG 2016; Phillips and Smith 1997; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 1995 and 2016
1996	IDFG 2016; Phillips and Smith 1997; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 1996 and 2016
1997	IDFG 2016; Smith 1998; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2016
1998	IDFG 2016; Smith et al. 1999; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2016
1999	IDFG 2016; Smith et al. 2000; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2000 and 2016
2000	IDFG 2016; Smith et al. 2001; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2001 and 2016
2001	IDFG 2016; Smith and Guernsey 2002; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2002 and 2016
2002	IDFG 2016; Smith et al. 2003; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2003 and 2016
2003	IDFG 2016; Smith et al. 2004, Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2004 and 2016
2004	IDFG 2016; Smith et al. 2005; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2005 and 2016
2005	IDFG 2016; Jimenez et al. 2006; Nadeau and Mack 2006; Sime et al. 2006; Smith et al. 2006; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2006 and 2016
2006	IDFG 2016; Jimenez et al. 2007; Nadeau et al. 2007; Sime et al. 2007; Smith et al. 2007; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2007 and 2016
2007	IDFG 2016; Jimenez et al. 2008; Nadeau et al. 2008; Parks et al. 2023; Sime et al. 2008; Smith et al. 2008; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2008 and 2016
2008	IDFG 2016; Jimenez et al. 2009; Nadeau et al. 2009; Parks et al. 2023; Sime et al. 2009; Smith et al. 2009; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2009 and 2016

Year	Citation(s) for population monitoring and/or mortality data
2009	IDFG 2016; IDFG 2023e, in litt; Jimenez et al. 2010b; Mack et al. 2010; MFWP 2010; Parks et al. 2023; Sime et al. 2010; Smith et al. 2010b; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2010 and 2016
2010	IDFG 2016; IDFG 2023e, in litt; Holyan et al. 2011; Jimenez et al. 2011; Parks et al. 2023; Sime et al. 2011; Smith et al. 2011; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2011 and 2016
2011	CDFW 2018 in litt.; Frame and Allen 2012; Hanauska-Brown et al. 2012; IDFG 2016; IDFG 2023e, in litt; IDFG and Nez Perce Tribe 2012; Jimenez et al. 2012; MFWP 2012; ODFW 2011; Parks et al. 2023; Smith et al. 2012; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2012 and 2016
2012	Becker et al. 2013; Bradley et al. 2013; CDFW 2018 in litt.; IDFG 2016; IDFG 2023e, in litt; IDFG and Nez Perce Tribe 2013; Inman et al. 2021; MFWP 2013; ODFW 2013; Parks et al. 2023; Smith et al. 2013; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2013 and 2016; WGFD et al. 2013
2013	Becker et al. 2014; Bradley et al. 2014; CDFW 2018 in litt.; IDFG 2016; IDFG 2023e, in litt; IDFG and Nez Perce Tribe 2014; Inman et al. 2021; MFWP 2014; ODFW 2014; Parks et al. 2023; Smith et al. 2014; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2014 and 2016; WGFD et al. 2014
2014	Becker et al. 2015; Bradley et al. 2015b; CDFW 2018 in litt.; IDFG 2016; IDFG 2023e, in litt; IDFG and Nez Perce Tribe 2015; Inman et al. 2021; MFWP 2015; ODFW 2015a; Parks et al. 2023; Smith et al. 2015b; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2015 and 2016; WGFD et al. 2015
2015	Becker et al. 2016; CDFW 2018 in litt.; Coltrane et al. 2016; IDFG 2016; IDFG 2023e, in litt; Inman et al. 2021; Jimenez and Johnson 2016; MFWP 2016; ODFW 2016; Parks et al. 2023; Smith et al. 2016; Smith et al. 2020a; U.S. Fish and Wildlife Service et al. 2016
2016	Boyd et al. 2017; CDFW 2018 in litt.; IDFG 2017; IDFG 2023e, in litt; MFWP 2017; Inman et al. 2021; ODFW 2017; Parks et al. 2023; Smith et al. 2017; Smith et al. 2020a; U.S. Fish and Wildlife Service et al 2017; WDFW et al. 2017
2017	CDFW 2018 in litt.; IDFG 2020; IDFG 2023e, in litt; Inman et al. 2021; MFWP 2018a and 2018b; ODFW 2018; Parks et al. 2023; Smith et al. 2018; Smith et al. 2020a; WDFW et al. 2018; WGFD et al. 2018
2018	CDFW 2018 in litt.; IDFG 2020; IDFG 2023e, in litt; Inman et al. 2019; MFWP 2019b; ODFW 2019b; Parks et al. 2023; Smith et al. 2019; Smith et al. 2020a; WDFW et al. 2019; WGFD et al. 2019
2019	CDFW 2020; IDFG 2022b; IDFG 2023b; IDFG 2023e, in litt; IDFG 2023f, in litt; Inman et al. 2020; MFWP 2020; Odell 2022 pers. comm.; ODFW 2020; Parks et al. 2023; Smith et al. 2020b; WDFW et al. 2020; WGFD et al. 2020
2020	Cassidy et al. 2021; CDFW 2021a; IDFG 2022b; IDFG 2023b; IDFG 2023e, in litt; IDFG 2023f, in litt; Inman et al. 2021; MFWP 2021f; Odell 2022 pers. comm.; ODFW 2021b; Parks et al. 2023; WDFW et al. 2021; WGFD et al. 2021
2021	CDFW 2021b; Cassidy et al. 2022b; CPW 2022; IDFG 2022b; IDFG 2023b; IDFG 2023e, in litt; IDFG 2023f, in litt; MFWP 2022; ODFW 2022; Parks et al. 2022; Parks et al. 2023; WDFW et al. 2022; WGFD et al. 2022

Year	Citation(s) for population monitoring and/or mortality data
2022	CDFW 2022; Cassidy et al. 2023b; IDFG 2023b; IDFG 2023e, in litt.; IDFG 2023f, in litt.; Odell 2022, pers. comm.; Odell 2023, pers. comm.; ODFW 2023; Parks et al. 2023; WDFW et al. 2023; WGFD et al. 2023

## Appendix 4: 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 5, we present all 36 attributes as scored for wolves in the Western United States.

*Table A 5. Attributes of adaptive capacity, an explanation of each attribute, the score we assessed for wolves in the Western 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
<b>Extent of occurrence</b>	The area that encompasses all known, inferred, or projected sites of present occurrence	High	Area is greater than 20,000 km <sup>2</sup>
Area of occupancy	The area of currently occupied suitable habitat	High	Area is greater than 2,000 km <sup>2</sup>
<b>Habitat specialization</b>	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
<b>Commensalism with humans</b>	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
Dispersal syndrome	The degree of flexibility in either the timing or mechanism of dispersal	High	Facultative (flexible timing, or no cue dependence)
<b>Dispersal distance</b>	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”
Migration frequency	Timing of migration or dispersal	High	Throughout lifetime (annually or seasonally)

Attribute	Explanation	Score	Justification
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)
<b>Genetic diversity</b>	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
<b>Population size</b>	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
<b>Diet breadth</b>	The ability to use a range of food resources	Moderate	More than 90% 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	Moderate	Moderate dependence on environmental cue, but species is capable of adjusting the timing or duration of life-cycle events.
<b>Climate niche breadth</b>	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
<b>Physiological tolerances</b>	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)

Attribute	Explanation	Score	Justification
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
<b>Reproductive phenology</b>	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 or reproduction
<b>Fecundity</b>	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])
<b>Life span</b>	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	High	Large proportion

## Appendix 5: Sensitivity Analysis of the Effects of Uncertainty in the Initial Population Size, $h$ , and $r_{max}$ Values for Montana and Idaho

**Summary:** *Because of peer and partner review feedback received concerning the accuracy of wolf population estimates from Montana and Idaho, 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 ( $h$ ) and the initial population size parameters in Montana and Idaho 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 (three harvest scenarios and two disease scenarios) at the minimum and maximum estimated values of the  $r_{max}$ ,  $h$ , and initial population size parameters in Montana and Idaho (for a total of 72 projections, resulting from running each of the 6 future scenario combinations 6 times for Idaho (with the minimum and maximum  $r_{max}$ ,  $h$ , and initial population sizes) and 6 times for Montana (with the minimum and maximum  $r_{max}$ ,  $h$ , and initial population sizes)). Overall, results of Harvest Scenario 1 regardless of disease scenario, were most sensitive to changes in  $r_{max}$  and  $h$  in Montana and Idaho, while results of Harvest Scenario 3 were least sensitive to changes in these parameters. Changes in the initial population size in Montana and Idaho within the range of the minimum and maximum values we estimated from observed data (i.e., between 1,002 and 1,345 wolves for Montana and between 596 and 871 wolves for Idaho), did not result in substantial changes to the projected population size for any scenario. Overall, our analysis indicates that results of Harvest Scenario 3 are robust to uncertainty associated with  $r_{max}$  and  $h$ , and all scenarios are robust to uncertainty associated with the initial population sizes in Idaho and Montana. 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 all Western states modeled or in the Northern Rocky Mountain (NRM) population. 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 maximum and minimum initial population size,  $r_{max}$ , and  $h$  values for Idaho and Montana (Table A 6) 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% 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 596 or as high as 871 wolves in Idaho (the minimum and maximum initial population sizes we estimated for Idaho) and as low as 1,002 or as high as 1,345 wolves in Montana (the minimum and maximum initial population sizes we estimated for Montana). 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 8). For example, to examine the effect of initial population size in Idaho, we first held the initial population size in Idaho constant at the minimum value, and allowed all other parameters (i.e.,  $r_{max}$ ,  $h$ , and  $K$  in Idaho; initial population size,  $r_{max}$ ,  $h$ , and  $K$  in Montana; and all parameters for all other states) to vary across the distributions reported in Chapter 5 (Table 8). We then held the initial population size in Idaho constant at the maximum value, and allowed all other parameters (i.e.,  $r_{max}$ ,  $h$ , and  $K$  in Idaho; initial population size,  $r_{max}$ ,  $h$ , and  $K$  in Montana; and all parameters for all other states) to vary across the distributions reported in Chapter 5 (Table 8). We then compared these results to determine the effect initial population size on the population projections. We repeated this for the maximum and minimum initial population size,  $r_{max}$ ,  $h$  values for both Idaho and Montana.

We ran the model for each of the 72 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 states modeled (Idaho, Montana, Oregon, Washington, and Wyoming (inclusive of YNP)). The results for the NRM were comparable to what we report for all Western states modeled below.

*Table A 6. Minimum and maximum values evaluated in our sensitivity analyses (i.e., minimum and maximum values estimated from fitting our density-dependent population model to observed data).*

	Minimum	Maximum
Idaho Initial Population Size	596	871
Montana Initial Population Size	1,002	1,345
Idaho $r_{max}$	0.33	0.63
Montana $r_{max}$	0.18	0.30
Idaho $h$	-0.24	0.29
Montana $h$	-0.21	0.58

## Sensitivity Analysis for Initial Population Size

We examined the effect of varying the initial population size in Idaho and Montana on the median projected population size in all Western states modeled. Overall, projected population sizes were similar for a particular scenario, regardless of whether the initial

population size in Idaho or Montana was the maximum or minimum estimate from the density-dependent models described in Chapters 5 and 6 (Table A 7, Figure A 2, and Figure A 3). The largest differences between the projected population sizes estimated from the minimum initial population size versus the maximum initial population size are under Harvest Scenario 1, and these differences are relatively minimal; the difference between the projected population size with Idaho's maximum initial population size and minimum initial population size for Harvest Scenario 1 is 44 wolves when combined with observed YNP disease rates and 37 wolves when combined with observed YNP disease rates and added black swan events. All other scenario combinations resulted in a less than 10-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 (0.020%) for Harvest Scenario 3 with added black swan disease events, when Idaho's population size was at its minimum or maximum initial population size; this probability is the same as what results from our projections using the full distribution of the parameter values in Chapters 5 and 6.

Table A 7. Results of population projections for the total wolf population in Idaho, Montana, Wyoming (including YNP), Washington, and Oregon when the initial population sizes in Idaho and Montana 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	Harvest Scenario	State	Starting 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	Harvest Scenario 1	Idaho	Minimum	2142	1670	2558	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Idaho	Maximum	2098	1634	2506	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Montana	Minimum	2140	1669	2558	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Montana	Maximum	2146	1673	2564	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Idaho	Minimum	976	843	1128	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Idaho	Maximum	966	836	1113	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Montana	Minimum	980	847	1128	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Montana	Maximum	982	849	1131	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Idaho	Minimum	961	830	1107	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Idaho	Maximum	959	828	1106	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Montana	Minimum	959	828	1106	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Montana	Maximum	960	828	1106	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Idaho	Minimum	2101	1416	2577	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Idaho	Maximum	2064	1383	2536	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Montana	Minimum	2109	1412	2592	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Montana	Maximum	2110	1417	2594	0.000%	0.000%
YNP + added black swan	Harvest Scenario 2	Idaho	Minimum	963	764	1126	0.010%	0.000%
YNP + added black swan	Harvest Scenario 2	Idaho	Maximum	949	751	1105	0.010%	0.000%
YNP + added black swan	Harvest Scenario 2	Montana	Minimum	953	755	1110	0.010%	0.000%
YNP + added black swan	Harvest Scenario 2	Montana	Maximum	954	756	1111	0.010%	0.000%
YNP + added black swan	Harvest Scenario 3	Idaho	Minimum	941	745	1098	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Idaho	Maximum	940	744	1097	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Montana	Minimum	940	743	1097	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Montana	Maximum	940	744	1098	0.010%	0.000%

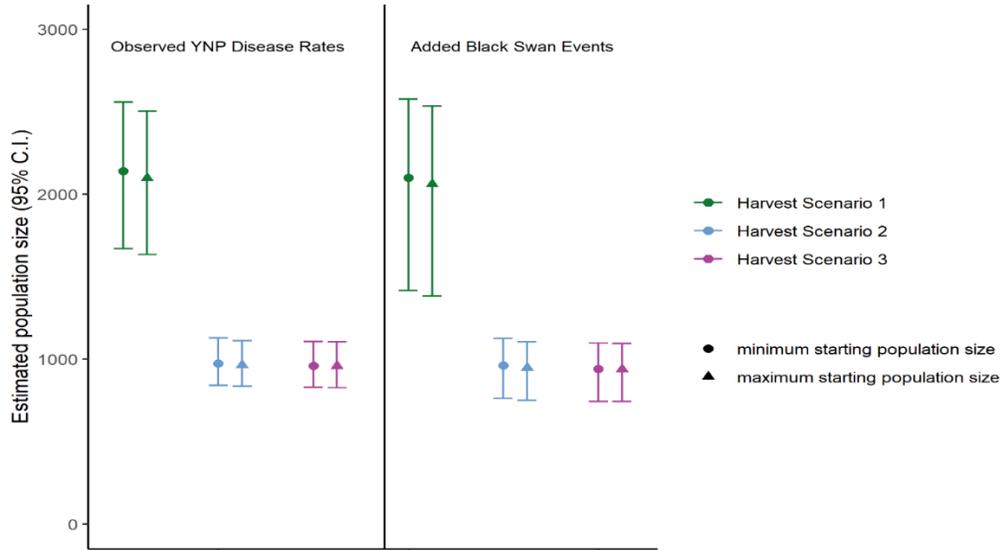


Figure A 2. Median projected population size with 95% credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western states modeled under three different harvest scenarios (Harvest Scenario 1 – green, Harvest Scenario 2 – blue, Harvest Scenario 3 – pink), when initial population size in Idaho was either the minimum (circles) or maximum (triangles) value estimated from the density-dependent models described in Chapter 5.

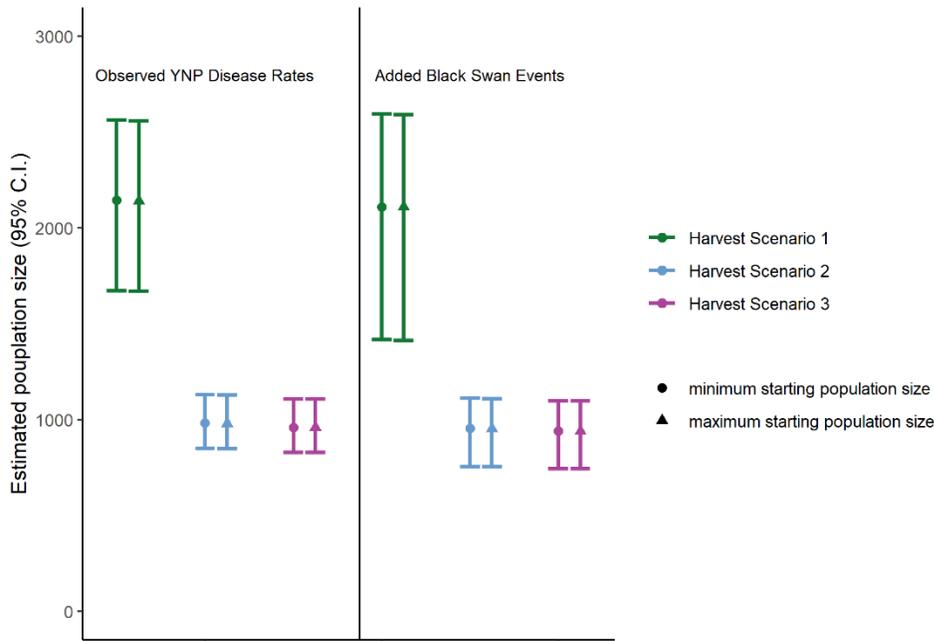


Figure A 3. Median projected population size with 95% credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western states modeled under three different harvest scenarios (Harvest Scenario 1 – green, Harvest Scenario 2 – blue, Harvest Scenario 3 – pink), when initial population size in Montana was either the minimum (circles) or maximum (triangles) 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 maximum and minimum values used in the simulations for Idaho (596–871 wolves) and Montana (1,002–1,345 wolves), there is minimal effect of the initial population size in Idaho or Montana on the median projected population size in all Western states modeled or in the NRM for all Harvest Scenarios. In other words, the total future projected population size is only slightly different (i.e., within 44 wolves) for Harvest Scenario 1 combined with either disease scenario, whether we start with 596 wolves in Idaho (the minimum value we estimated from observed data) or 871 wolves in Idaho (the maximum value). For Harvest Scenarios 2 and 3 for Idaho, and for all future scenario combinations for Montana, the differences are negligible between the projected population size at minimum or maximum initial population size values (i.e., differences <10 wolves). However, this analysis does not provide an estimate of the potential decrease in the total projected population size in all Western states modeled or in the NRM if the initial population size in Idaho was fewer than 596 wolves or if the initial population size in Montana was fewer than 1,002 wolves.

### Sensitivity Analysis for Intrinsic Rate of Growth ( $r_{max}$ )

We examined the effect of the  $r_{max}$  value in Idaho and Montana on the median projected population size in all Western states modeled. Overall, differences between projected population sizes at the maximum and minimum values of  $r_{max}$  were greatest under Harvest Scenario 1 (differences ranging between 171 wolves and 633 wolves, depending on whether we varied Idaho or Montana's  $r_{max}$  and depending on the disease scenario) and minimal under Harvest Scenarios 2 and 3 (all but one difference between the outputs for minimum and maximum  $r_{max}$  values were fewer than 10 wolves) (Table A 8, Figure A 4, and Figure A 5). The percent of simulations falling below 192 total wolves at any time during our 100-year simulation period was zero regardless of the value of  $r_{max}$ . The percent of simulations falling below 417 total wolves was highest (0.020%) for Harvest Scenario 3 with added black swan disease events when Idaho's  $r_{max}$  was at its minimum or maximum or Montana  $r_{max}$  was at its minimum.

Table A 8. Results of population projections for the total wolf population in Idaho, Montana, Wyoming (including YNP), Washington, and Oregon when the intrinsic rate of growth ( $r_{max}$ ) in Idaho and Montana were at their maximums (maximum  $r_{max}$ ) or minimums (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 (200,000 projections) will produce slightly different results.

Disease Scenario	Harvest Scenario	State	$r_{max}$ 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	Harvest Scenario 1	Idaho	Minimum	2073	1603	2491	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Idaho	Maximum	2244	1776	2649	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Montana	Minimum	1640	1269	2143	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Montana	Maximum	2262	1767	2670	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Idaho	Minimum	965	835	1111	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Idaho	Maximum	1049	893	1225	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Montana	Minimum	979	845	1128	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Montana	Maximum	986	852	1137	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Idaho	Minimum	960	828	1107	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Idaho	Maximum	959	827	1105	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Montana	Minimum	958	825	1104	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Montana	Maximum	960	829	1107	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Idaho	Minimum	1937	1262	2419	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Idaho	Maximum	2201	1513	2668	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Montana	Minimum	1607	1155	2158	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Montana	Maximum	2240	1485	2712	0.000%	0.000%
YNP + added black swan	Harvest Scenario 2	Idaho	Minimum	946	747	1103	0.010%	0.000%
YNP + added black swan	Harvest Scenario 2	Idaho	Maximum	953	756	1112	0.010%	0.000%
YNP + added black swan	Harvest Scenario 2	Montana	Minimum	949	749	1108	0.010%	0.000%
YNP + added black swan	Harvest Scenario 2	Montana	Maximum	958	761	1116	0.010%	0.000%
YNP + added black swan	Harvest Scenario 3	Idaho	Minimum	938	741	1096	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Idaho	Maximum	941	745	1098	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Montana	Minimum	936	736	1095	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Montana	Maximum	941	746	1098	0.010%	0.000%

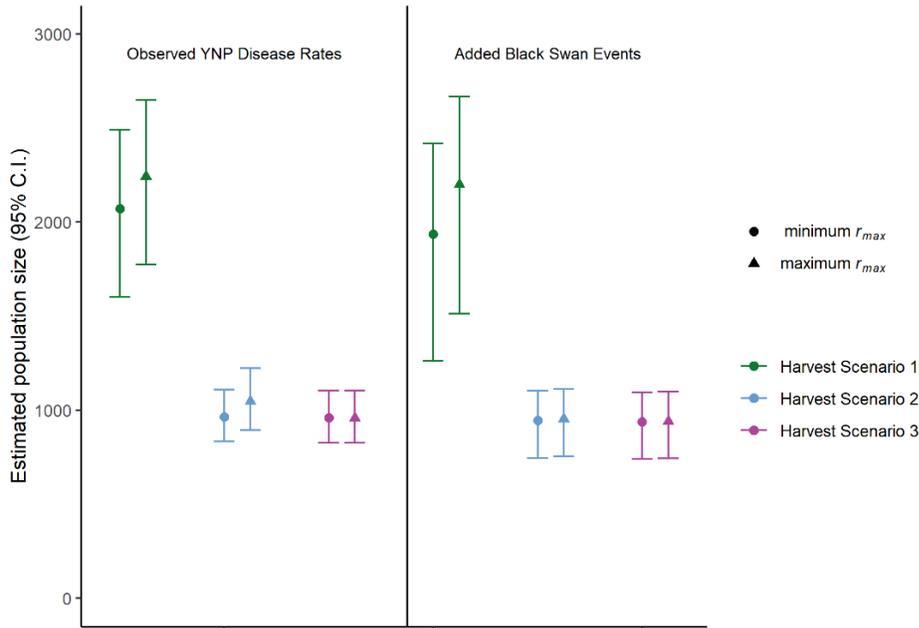


Figure A 4. Median projected population size with 95% credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western states modeled under three different harvest scenarios (Harvest Scenario 1 – green, Harvest Scenario 2 – blue, Harvest Scenario 3 – pink), when  $r_{max}$  in Idaho was either the minimum (circles) or maximum (triangles) value estimated from the density-dependent models described in Chapter 5.

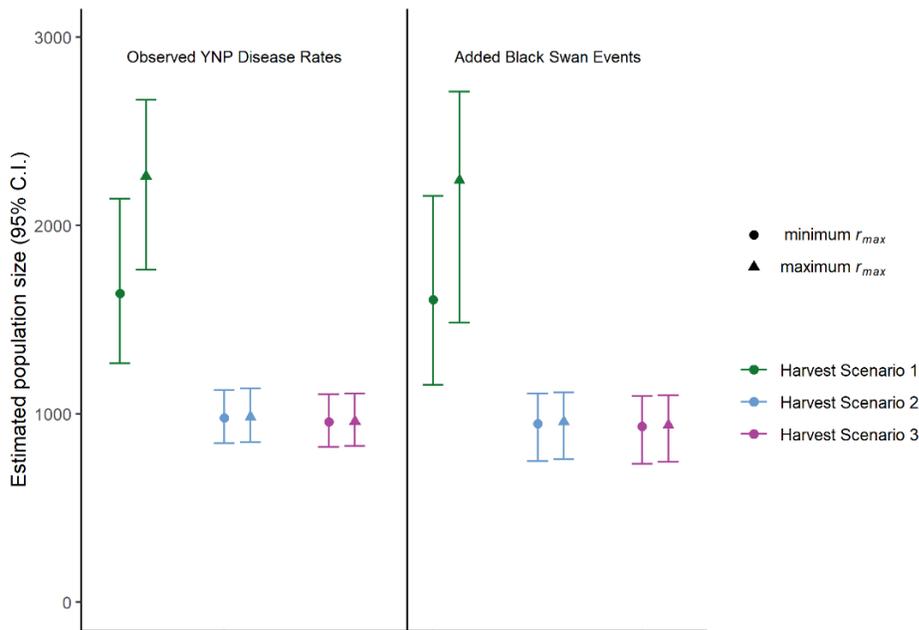


Figure A 5. Median projected population size with 95% credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western states modeled under three different harvest scenarios (Harvest Scenario 1 – green, Harvest Scenario 2 – blue, Harvest Scenario 3 – pink), when  $r_{max}$  in Montana was either the minimum (circles) or maximum (triangles) value estimated from the density-dependent models described in Chapter 5.

The results of this analysis indicate that, when examining the range of  $r_{max}$  values within the maximum and minimum values used in the simulations for Idaho (0.33–0.63) and Montana (0.18–0.30), there is an effect of  $r_{max}$  in Idaho or Montana on the median projected population size in all Western states modeled or in the NRM under Harvest Scenario 1, and minimal effect of  $r_{max}$  under Harvest Scenarios 2 and 3. As expected, minimum values of  $r_{max}$  lead to smaller population sizes than maximum values of  $r_{max}$ . For Harvest Scenario 1, the difference in the projected population size when using a maximum value of  $r_{max}$  versus a minimum value of  $r_{max}$  is approximately 620 to 630 wolves for Montana (depending on the disease scenario) and approximately 170 to 260 wolves for Idaho (depending on the disease scenario). If the  $r_{max}$  value we included in our models was 0.33 for the State of Idaho (approximately 27 percent less than the median of the distribution of  $r_{max}$  values we used in our modeling in Chapters 5 and 6) or 0.18 for Montana (approximately 33 percent less than the median of the distribution of the  $r_{max}$  value we used in our modeling in Chapters 5 and 6), the output total population size in 100 years in all Western states modeled and the NRM would be approximately the same under Harvest Scenarios 2 and 3 as if we used the  $r_{max}$  value of 0.63 for Idaho (approximately 40 percent over the median of the distribution of  $r_{max}$  values we used in our modeling in Chapters 5 and 6) or 0.30 for Montana (approximately 11 percent over the median of the distribution of  $r_{max}$  value we used in our modeling in Chapters 5 and 6). Regardless of the value of  $r_{max}$ , the percentage of scenarios falling below the threshold values of 417 or 192 total wolves was negligible. However, this analysis does not provide an estimate of the potential decrease in the total projected population size in all Western states modeled or in the NRM if the  $r_{max}$  in Montana was less than 0.18 or if  $r_{max}$  in Idaho was fewer than 0.33.

### Sensitivity Analysis for Effect of Harvest and Lethal Depredation Control ( $h$ )

We examined the effect of the  $h$  value in Idaho and Montana on the median projected population size in all Western states modeled. Overall, differences between projected population sizes at the maximum and minimum values of  $h$  were greatest under Harvest Scenarios 1 and 2 (differences ranging between 83 wolves and 1,554 wolves, depending on whether we varied Idaho or Montana's  $h$  value and depending on the scenario combination) and minimal for Harvest Scenario 3 (differences between the outputs for minimum and maximum  $h$  values were fewer than 5 wolves) (Table A 9, Figure A 6, and Figure A 7). The percent of simulations falling below 192 total wolves at any time during our 100-year simulation period was zero regardless of the value of  $h$ . The percent of simulations falling below 417 total wolves was highest (0.020%) for Harvest Scenario 3 with added black swan disease events with both the minimum and maximum values of  $h$  for Idaho and Montana.

Table A 9. Results of population projections for the total wolf population in Idaho, Montana, Wyoming (including YNP), Washington, and Oregon when the intrinsic rate of growth ( $r_{max}$ ) in Idaho and Montana were at their maximums (maximum  $r_{max}$ ) or minimums (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 (200,000 simulations) will produce slightly different results.

Disease Scenario	Harvest Scenario	State	$h$ 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	Harvest Scenario 1	Idaho	Minimum	2373	1889	2791	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Idaho	Maximum	2011	1548	2420	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Montana	Minimum	3258	2503	3780	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 1	Montana	Maximum	1704	1333	2108	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Idaho	Minimum	1042	886.14	1228	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Idaho	Maximum	966	836	1111	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Montana	Minimum	1706	1296	2090	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 2	Montana	Maximum	979	846	1127	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Idaho	Minimum	961	830	1107	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Idaho	Maximum	959	827	1105	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Montana	Minimum	963	832	1109	0.000%	0.000%
Observed YNP disease rates	Harvest Scenario 3	Montana	Maximum	959	828	1106	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Idaho	Minimum	2403	1680	2895	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Idaho	Maximum	1868	1202	2329	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Montana	Minimum	3187	1965	3764	0.000%	0.000%
YNP + added black swan	Harvest Scenario 1	Montana	Maximum	1669	1205	2121	0.000%	0.000%
YNP + added black swan	Harvest Scenario 2	Idaho	Minimum	1030	808	1238	0.000%	0.000%
YNP + added black swan	Harvest Scenario 2	Idaho	Maximum	947	750	1103	0.010%	0.000%
YNP + added black swan	Harvest Scenario 2	Montana	Minimum	1812	1082	2267	0.000%	0.000%
YNP + added black swan	Harvest Scenario 2	Montana	Maximum	952	754	1109	0.010%	0.000%
YNP + added black swan	Harvest Scenario 3	Idaho	Minimum	940	744	1098	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Idaho	Maximum	939	744	1097	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Montana	Minimum	942	746	1099	0.020%	0.000%
YNP + added black swan	Harvest Scenario 3	Montana	Maximum	939	742	1097	0.020%	0.000%

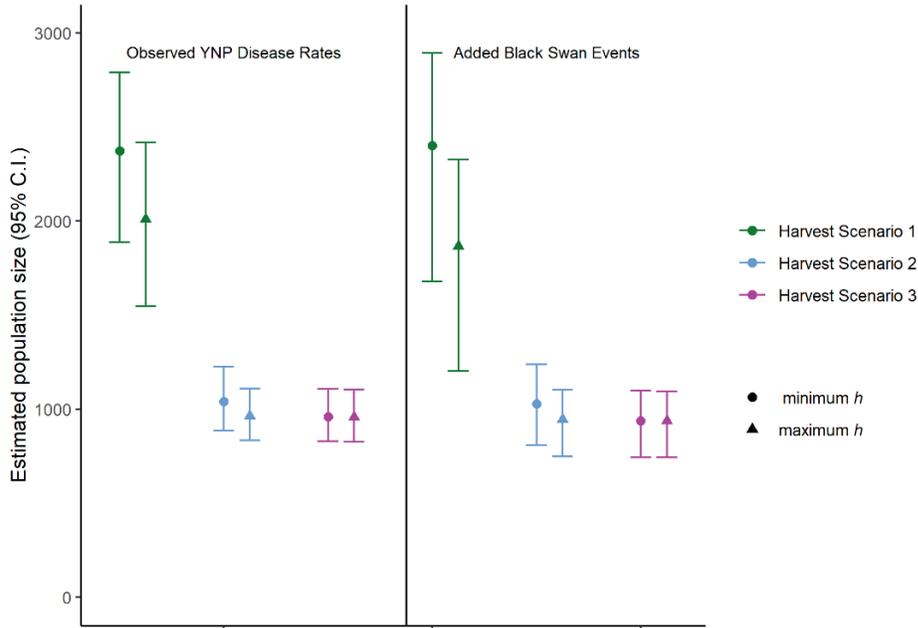


Figure A 6. Median projected population size with 95% credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western states modeled under three different harvest scenarios (Harvest Scenario 1 – green, Harvest Scenario 2 – blue, Harvest Scenario 3 – pink), when  $h$  in Idaho was either the minimum (circles) or maximum (triangles) value estimated from the density-dependent models described in Chapter 5.

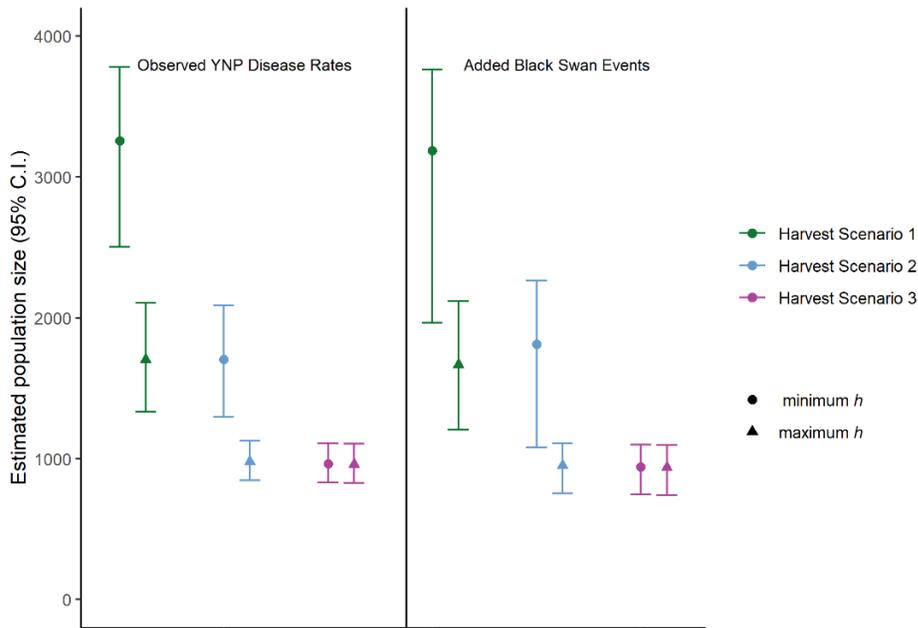


Figure A 7. Median projected population size with 95% credible interval at 100 years with Observed YNP disease rates (left side) and with added black swan events (right side) in all Western states modeled under three different harvest scenarios (Harvest Scenario 1 – green, Harvest Scenario 2 – blue, Harvest Scenario 3 – pink), when  $h$  in Montana was either the minimum (circles) or maximum (triangles) 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 maximum and minimum values used in the simulations for Idaho (-0.24–0.29) and Montana (-0.21–0.58), there is an effect of  $h$  in Idaho or Montana on the median projected population size in all Western states modeled and in the NRM for Harvest Scenarios 1 and 2, and an extremely minimal effect of the  $h$  for Harvest Scenario 3. As expected, minimum values of  $h$  lead to larger population sizes than maximum values of  $h$ . If the  $h$  value we included in our models was 0.29 for the State of Idaho (approximately 3 times greater than the median of the distribution of  $h$  values we used in our modeling in Chapters 5 and 6) or 0.58 for Montana (approximately 53 percent greater than the median of the distribution of  $h$  values we used in our modeling in Chapters 5 and 6), the output total population size in 100 years in all Western states modeled and the NRM would be the same under Harvest Scenario 3. For Harvest Scenario 1, the difference in the projected population size when using a maximum value of  $h$  versus a minimum value of  $h$  is approximately 1,500 to 1,550 wolves for Montana (depending on the disease scenario) and approximately 360 to 530 wolves for Idaho (depending on the disease scenario). For Harvest Scenario 2, the difference in the projected population size when using a maximum value of  $h$  versus a minimum value of  $h$  is approximately 730 to 860 wolves for Montana (depending on the disease scenario) and approximately 75 to 85 wolves for Idaho (depending on the disease scenario). Regardless of the value of  $h$ , the percentage of scenarios falling below the threshold values of 417 or 192 total wolves was negligible. However, this analysis does not provide an estimate of the potential decrease in the total projected population size in all Western states modeled or in the NRM if the  $h$  in Montana was greater than 0.58 or if  $h$  in Idaho was greater than 0.29.

## Conclusion

Overall, the decreases in the median projected population size in 100 years (if the minimum initial population sizes, minimum  $r_{max}$  values, or maximum estimated values of  $h$  were realized) would not result in a median projected population size in all Western states modeled or in the NRM below 192 wolves (our minimum effective population size threshold) or 5 wolves (our quasi-extinction threshold), and would result in a maximum of 0.020% of simulations falling below 417 wolves (the upper bound of our threshold evaluating a risk of inbreeding depression) under any of the harvest or disease scenarios we analyzed. In sum, Harvest Scenario 1 is most sensitive to uncertainty in values of intrinsic rate of growth ( $r_{max}$ ) or effects of harvest ( $h$ ) in Idaho and Montana, and Harvest Scenario 3 is least sensitive to uncertainty in these values (differences in projected population sizes were essentially zero). Changes in the initial population size in Montana and Idaho, within the range of the minimum and maximum values we estimated from observed data, did not result in substantial changes to the projected population size for any scenario. However, this analysis does not provide an estimate of the potential increase or decrease in the median projected population size if the initial population size, intrinsic rate of growth ( $r_{max}$ ), or effects of harvest ( $h$ ) in Idaho and Montana were lower than the minimums or higher than the maximums we evaluated above.

## Appendix 6: State-Level Modeling Results

In this Appendix, we report the results of our model projections for each individual state we modeled (i.e., for Idaho, Montana, Oregon, Washington, and Wyoming, which includes YNP) and evaluate post-delisting monitoring thresholds to provide more detailed information on the future projected spatial distribution of wolves.

### Post-Delisting Monitoring Thresholds for Individual States

We calculated the probability of crossing two 2009 post-delisting monitoring thresholds in Idaho and Montana given that, at the time of their development over a decade ago, they provided some indication of extinction risk (see *Recovery Criteria for the Northern Rocky Mountains in Chapter 2* for more detail). First, we calculated the probability of Idaho's or Montana's projected population falling below 100 wolves for one year (i.e., we estimated the number of simulations out of two million in which the projected population in Idaho or Montana fell below 100 wolves at least once during the 100-year timeframe). Second, we calculated the probability of Idaho's or Montana's projected population falling below 150 wolves for at least three years in a row (i.e., we estimated the number of simulations out of two million in which the population in Idaho or Montana fell below 150 wolves for at least 3 years in a row during the 100-year timeframe). These values represent the post-delisting monitoring thresholds established for Idaho, Montana, and Wyoming in the 2009 delisting rule, as well as the states' commitments, formalized in MOUs, to maintain at least 10 breeding pairs and at least 100 wolves and manage for a "buffer" population size of at least 15 breeding pairs and at least 150 wolves (Groen et al. 2008, p. 1; Talbott and Guertin 2012, p. 1). These results are reported below.

#### Idaho

For Harvest Scenario 1, which included a 32 percent harvest rate in Idaho, combined with observed YNP disease rates, the least impactful combination of harvest and disease scenarios we analyzed, the median projected population size in Idaho 100 years in the future was 569 wolves (95% credible intervals 356–687), a 9 to 51 percent (median 23 percent) decrease relative to the starting population size (see Figure A 8 and Table A 10b). Under Harvest Scenario 3, we subjected the population to a harvest rate that reduced the population size to 150 wolves within five years (i.e., a harvest rate of 65 percent); when we included observed YNP disease rates and added black swan events with the harvest rate in Harvest Scenario 3, the most impactful combination of harvest and disease scenarios we analyzed, the median projected population size 100 years into the future was 145 wolves (95% credible interval 84–148), a 79 to 89 percent (median 81 percent) decrease in population size relative to the starting population size (see Figure A 8 and Table A 10b).

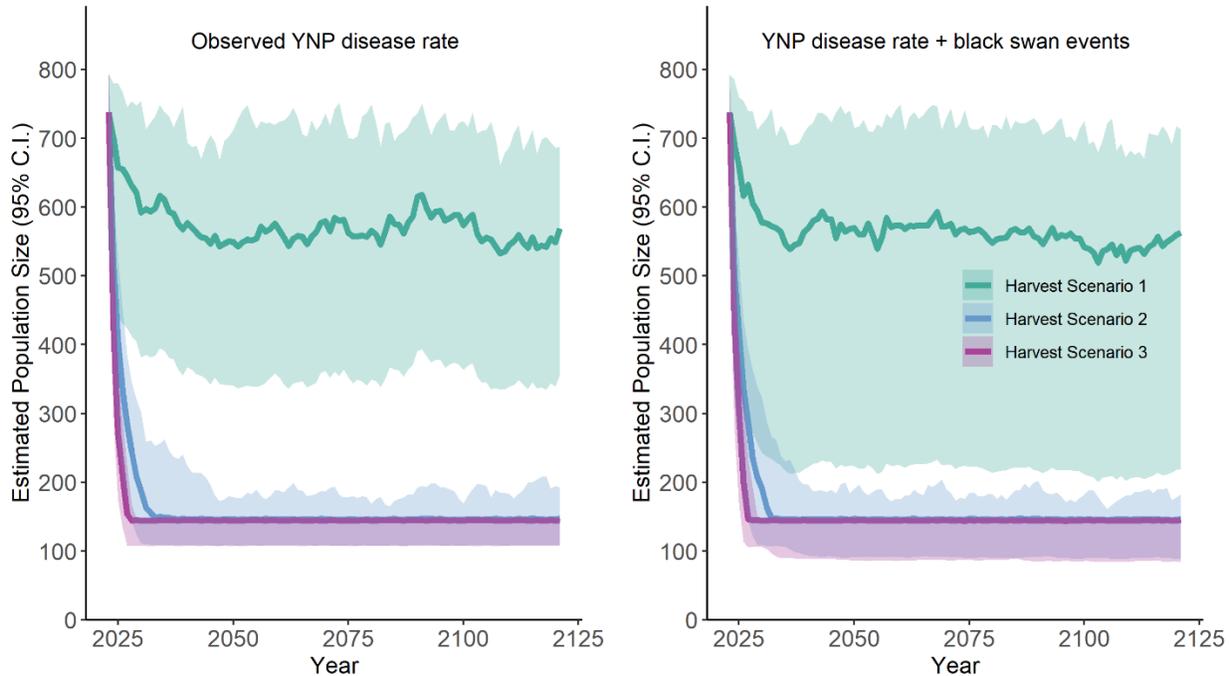


Figure A 8. Median projected wolf population size (solid lines) and 95% credible interval (shaded area) in Idaho under Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations.

Additionally, none of the harvest scenarios, when combined with observed YNP disease rates, resulted in fewer than 100 wolves in Idaho at any point in the 100-year timeframe. For all scenarios that included observed YNP disease rates and added black swan events, 6 (Harvest Scenario 1) to 43 percent (Harvest Scenario 3) of simulated populations fell below 100 wolves at least once during the 100-year timeframe (Table A 10b). Under Harvest Scenario 1, when combined with YNP disease rates, no simulations resulted in a population size with fewer than 150 wolves for three years in a row during the 100-year timeframe; when combined with observed YNP disease rates and added black swan events, 16 percent of simulations fell below 150 wolves for at least three years in a row (Table A 10b). Under Harvest Scenario 2, all simulations (100 percent) fell below 150 wolves for at least three years in a row, with and without added black swan events (Table A 10b). As designed under Harvest Scenario 3, all simulated populations remained below 150 wolves after the first 5 years of the simulation, with and without added black swan events; under this harvest scenario, we assumed that Idaho would use harvest or other means to maintain populations below 150 wolves after the first 5 years of the simulation.

Table A 10. Median and upper and lower 95% credible interval for population size in Idaho at the end of the a) 10-year and b) 100-year timeframes of our simulations in all six future disease and harvest scenario combinations. We also report the median percent change between the starting population size in Idaho and the projected population size in Idaho a) 10 years and b) 100 years into the future, including the 95% credible interval (CI) for these percent changes in parentheses. In addition, in b) we report the percent of simulations in which the population in Idaho (1) fell below 100 wolves at least once during the 100-year timeframe or (2) fell below 150 wolves for three years in a row during the 100-year timeframe.

a)

Disease Scenario	Harvest Scenario	Median Projected Population Size at 10 years (95% CI)	Median Percent Change from Initial Population Size (95% CI)
Observed YNP disease rates	Scenario 1	594 (382–723)	-20% (-48 to -4%)
Observed YNP disease rates	Scenario 2	155 (109–261)	-78% (-85 to -66%)
Observed YNP disease rates	Scenario 3	145 (107–148)	-81% (-86 to -79%)
YNP + added black swan	Scenario 1	572 (234–744)	-22% (-68 to -2%)
YNP + added black swan	Scenario 2	148 (107–266)	-78% (-86 to -62%)
YNP + added black swan	Scenario 3	145 (97–148)	-81% (-87 to -79%)

b)

Disease Scenario	Harvest Scenario	Median Projected Population Size at 100 years (95% CI)	Median Percent Change from Initial Population Size (95% CI)	Threshold 100 (100 years)	Threshold 150 (100 years)
Observed YNP disease rates	Scenario 1	569 (356–687)	-23% (-51 to -9%)	0%	0%
Observed YNP disease rates	Scenario 2	147 (108–193)	-80% (-85 to -75%)	0%	100%
Observed YNP disease rates	Scenario 3	145 (107–147)	-81% (-86 to -79%)	0%	100%
YNP + added black swan	Scenario 1	563 (219–713)	-24% (-70 to -5%)	6%	16%
YNP + added black swan	Scenario 2	146 (89–183)	-80% (-88 to -76%)	42%	100%
YNP + added black swan	Scenario 3	145 (84–148)	-81% (-89 to -79%)	43%	100%

## Montana

For Harvest Scenario 1, which included a 19 percent harvest rate in Montana, combined with observed YNP disease rates, the least impactful combination of harvest and disease scenarios we analyzed, the median projected population size in Montana 100 years into the

future was 919 wolves (95% credible intervals 507–1,259), representing between a 56 percent decrease to a 7 percent increase (median 21 percent decrease) relative to the starting population size (see Table A 11b and Figure A 9). Under Harvest Scenario 3, we subjected the population to a harvest rate that reduced the population size to 150 wolves within five years (i.e., a harvest rate of 65 percent); when we included observed YNP disease rates and added black swan events with the harvest rate in Harvest Scenario 3, the most impactful combination of harvest and disease scenarios we analyzed, the median projected population size in Montana 100 years into the future was 145 wolves (95% credible interval 50–147), an 87 to 96 percent (median 88 percent) decrease in population size relative to the starting population size (see Table A 11b and Figure A 9).

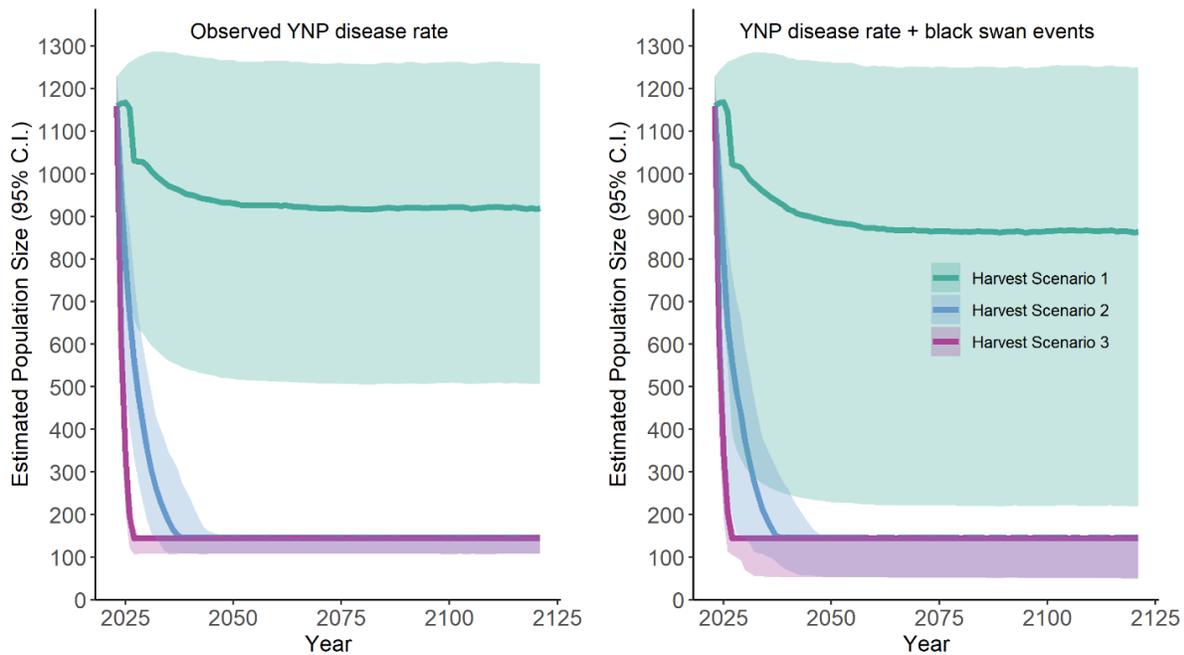


Figure A 9. Median projected wolf population size (solid lines) and 95% credible interval (shaded area) in Montana under Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations.

When combined with observed YNP diseases rates, Harvest Scenario 1 did not result in any simulations falling below 100 wolves at any point during the 100-year timeframe. Harvest Scenario 2 and Harvest Scenario 3 resulted in 7 to 11 percent of the simulations projecting fewer than 100 wolves in Montana at least once during the 100-year timeframe (Table A 11b). For all scenarios that included observed YNP disease rates and added black swan events, 4 (Harvest Scenario 1) to 44 percent (Harvest Scenario 3) of simulated populations fell below 100 wolves at least once during the 100-year timeframe (Table A 11b). Under Harvest Scenario 1, when combined with YNP disease rates, no simulations resulted in a population size with fewer than 150 wolves for three years in a row during the 100-year timeframe; when combined with observed YNP disease rates and added black swan events, 18 percent of simulations fell below 150 wolves for at least three years in a row (Table A 11b). Under Harvest Scenario 2, all simulations (100 percent) fell below 150 wolves for at least three years in a row, with and without added black swan events (Table A 11b). As designed under Harvest Scenario 3, all

simulated populations remained below 150 wolves after the first 5 years of the simulation, with and without added black swan events; under this scenario, we assumed that Montana would use harvest or other means to maintain populations below 150 wolves after the first 5 years of the simulation.

*Table A 11. Median and upper and lower 95% credible interval for population size in Montana at the end of the a) 10-year and b) 100-year timeframes of our simulations in all six future disease and harvest scenario combinations. We also report the median percent change between the starting population size in Montana and the the projected population size in Montana a) 10 years and b) 100 years into the future, including the 95% credible interval (CI) for these percent changes in parentheses. In addition, in b) we report the percent of simulations in which the population in Montana (1) fell below 100 wolves at least once during the 100-year timeframe or (2) fell below 150 wolves for three years in a row during the 100-year timeframe.*

a)

Disease Scenario	Harvest Scenario	Median Projected Population Size at 10 years (95% CI)	Median Percent Change from Initial Population Size (95% CI)
Observed YNP disease rates	Scenario 1	996 (588–1,287)	-14% (-49 to 9%)
Observed YNP disease rates	Scenario 2	265 (145–433)	-74% (-86 to -59%)
Observed YNP disease rates	Scenario 3	145 (108–147)	-88% (-91 to -87%)
YNP + added black swan	Scenario 1	979 (290–1,286)	-15% (-74 to 8%)
YNP + added black swan	Scenario 2	281 (114–477)	-72% (-89 to -55%)
YNP + added black swan	Scenario 3	145 (57–147)	-88% (-95 to -87%)

b)

Disease Scenario	Harvest Scenario	Median Projected Population Size at 100 years (95% CI)	Median Percent Change from Initial Population Size (95% CI)	Threshold 100 (100 years)	Threshold 150 (100 years)
Observed YNP disease rates	Scenario 1	919 (507–1,259)	-21% (-56 to 7%)	0%	0%
Observed YNP disease rates	Scenario 2	146 (108–150)	-88% (-91 to -87%)	7%	100%
Observed YNP disease rates	Scenario 3	145 (107–147)	-88% (-91 to -87%)	11%	100%
YNP + added black swan	Scenario 1	863 (220–1,250)	-26% (-81 to 7%)	4%	18%
YNP + added black swan	Scenario 2	146 (51–149)	-88% (-96 to -87%)	42%	100%
YNP + added black swan	Scenario 3	145 (50–147)	-88% (-96 to -87%)	44%	100%

## Alternative Models of Population Dynamics in Montana

Our models project future population sizes in Montana in different scenarios of disease and harvest based on the following assumptions:

- the rate of harvest is proportional to population size;
- the state will stop harvest when the population size reaches 150 wolves; and
- growth occurs according to a density-dependent growth equation (Equation 1; see Chapter 5 for more detail on these assumptions).

In 2021, the Montana State legislature directed the MFW Commission (via revisions to MCA 87-1-901) to reduce the size of the wolf population in the state to a sustainable level; MCA 87-1-901 defines “sustainable” as “not less than the number necessary to support at least 15 breeding pairs.” To inform the season setting under these new regulations for the 2021/2022 season, MFWP proactively modeled their expectation for wolf populations under several different harvest scenarios (Messmer 2022, in litt.). These models were intended to demonstrate that population reduction of wolves could be achieved through increases in the total number of animals harvested. These results also illustrated that, even in the short term, these modeled increases in harvest, if left unchecked, would potentially reduce population sizes below 100 wolves and result in extirpation of wolves from the state. MFWP staff concluded that “If any of these simulated human-caused mortality levels could be achieved, the MFW Commission would likely be required to intervene after 1 or 2 years to prevent the population from decreasing below the minimum level of 15 breeding pairs set in state and Federal law” (Messmer 2022, in litt.).

Contrary to our models, these model projections provided by MFWP (1) assume that a constant number of animals will be removed from the population through harvest (i.e., harvest numbers are not adjusted as the population declines); (2) assume that harvest will continue regardless of population size (i.e., harvest would not stop when 15 packs or breeding pairs remain, as the Montana Plan and Montana law (MCA 87-1-901) require); and (3) model growth rates as a function of harvest, removal rate, and the previous year’s population size assuming a linear relationship (rather than a mechanistic density-dependent logistic relationship) between these variables. These simulations demonstrate that, if harvest is modeled according to these three assumptions, rather than our model’s framework, wolf populations: (1) would decrease by approximately 50 percent in five years under a scenario with a 15 percent increase in the number of wolves harvested; (2) would decrease by approximately 77 percent in five years under a scenario with a 30 percent increase in the number of wolves harvested; or (3) would likely be extirpated from Montana under a scenario with a 45 percent or more increase in the number of wolves harvested. Given the guidance in the *Montana Plan*, the language in MCA 87-1-901 requiring at least 15 breeding pairs, and the difficulty of maintaining harvest of a fixed number of wolves as populations get smaller, we find that the assumptions in our model (namely, stopping harvest when 150 wolves remain and harvesting a fixed proportion of the population) are reasonable.

## Wyoming

We did not vary harvest rates or levels of lethal depredation control above recent past observed levels in Wyoming (excluding YNP) in our forecasting (see Chapter 4 for details), so the only difference between the future scenarios for Wyoming were the rates of disease (see Figure A 10 and Table A 12b). However, we did vary harvest rates for wolves primarily residing in YNP in each of the three harvest scenarios. We report the total future projected number of wolves statewide in Wyoming, including YNP. For the scenario combination that included observed YNP disease rates and average past observed harvest rates of wolves that live primarily in YNP, leave the park, and are harvested in surrounding states (i.e., Harvest Scenario 1 for YNP wolves), the median projected population size 100 years into the future for Wyoming (which includes YNP) was 301 wolves (95% credible interval 228–341), representing between a 28 percent decrease and a 9 percent increase (median 5 percent decrease) relative to the starting population size. Under Harvest Scenario 3 for YNP wolves with observed YNP disease rates and added black swan events, the median projected population size in Wyoming (inclusive of YNP) at 100 years was similar (284 wolves) (95% credible interval 171–334), representing between a 46 percent decrease and a 5 percent increase in population size (median 10 percent decrease) relative to the starting population size.

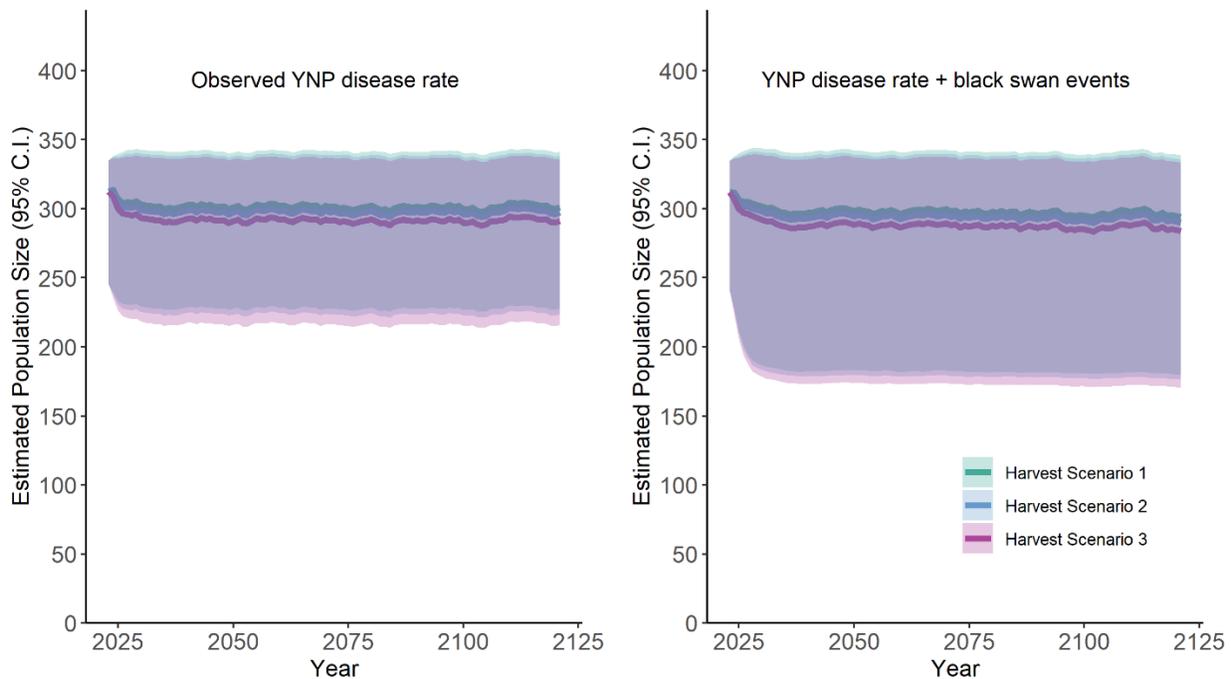


Figure A 10. Median projected wolf population size (solid lines) and 95% credible interval (shaded area) in Wyoming with average level of harvest (16 percent) (all harvest scenarios in Wyoming) and including YNP under Harvest Scenario 1 (green), Harvest Scenario 2 (blue), and Harvest Scenario 3 (pink) for the 100-year timeframe of our simulations.

Table A 12. Median and upper and lower 95% credible interval for population size in Wyoming at the end of the a) 10-year and b) 100-year timeframes of our simulations (harvest rate was the same in Wyoming outside of YNP for all scenarios but varied for YNP wolves). We also report the median percent change between the starting population size in Wyoming (including YNP) and the projected population size in Wyoming (including YNP) a) 10 years and b) 100 years into the future, including the 95% credible interval (CI) for these percent changes in parentheses.

a)

Disease Scenario	Harvest Scenario	Median Projected Population Size at 10 years (95% CI)	Median Percent Change from Initial Population Size (95% CI)
Observed YNP disease rates	Scenario 1	302 (228–342)	-5 (-28 to 9)
Observed YNP disease rates	Scenario 2	298 (224–339)	-6 (-29 to 8)
Observed YNP disease rates	Scenario 3	292 (217–337)	-8 (-31 to 6)
YNP + added black swan	Scenario 1	301 (185–344)	-5 (-42 to 10)
YNP + added black swan	Scenario 2	297 (182–341)	-6 (-43 to 8)
YNP + added black swan	Scenario 3	291 (176–339)	-8 (-44 to 6)

b)

Disease Scenario	Harvest Scenario	Median Projected Population Size at 100 years (95% CI)	Median Percent Change from Initial Population Size (95% CI)
Observed YNP disease rates	Scenario 1	301 (228–341)	-5 (-28 to 9)
Observed YNP disease rates	Scenario 2	297 (224–338)	-6 (-29 to 7)
Observed YNP disease rates	Scenario 3	291 (216–336)	-8 (-31 to 6)
YNP + added black swan	Scenario 1	294 (180–339)	-7 (-43 to 8)
YNP + added black swan	Scenario 2	290 (177–336)	-9 (-44 to 6)
YNP + added black swan	Scenario 3	284 (171–334)	-10 (-46 to 5)

## Oregon and Washington (statewide and within the NRM)

Based on our estimates of lambda in Chapter 4 (the growth rate averaged over the previous four years of observed population data), the statewide populations in Oregon and Washington are still growing at a median rate of 7 to 15 percent annually, respectively; therefore, our estimates of maximum population size estimated from the density-dependent model (see Table 8 in Chapter 5) may be biased low for these two states because we have not yet observed

their maximum population size. In our projections, we did not vary harvest rates or levels of lethal depredation control above recent past observed levels in Oregon and Washington (e.g., zero percent harvest in Oregon; 5 percent harvest in Washington statewide and 7 percent harvest in the NRM portion of the state). Therefore, the only difference between the future scenarios for Oregon and Washington were the rates of disease.

In the scenario with observed YNP disease rates, the median projected population size 100 years into the future was 133 wolves (95% credible interval 88–149) in the NRM portion of Oregon and 169 wolves (95% credible interval 112–195) statewide, representing between a 38 percent decrease and a 2 percent increase within the NRM portion of Oregon, and between a 37 percent decrease and a 6 percent increase statewide (see Figure A 11 and Table A 13b). In this same scenario with observed YNP disease rates, the median projected population size 100 years into the future was 157 wolves (95% credible interval 100–234) in the NRM portion of Washington and 232 wolves (95% credible interval 143–362) statewide, representing between a 39 percent decrease and a 34 percent increase within the NRM portion of Washington, and between a 33 percent decrease and a 61 percent increase statewide (see Figure A 12 and Table A 13b).

In the scenario with observed YNP disease rates and added black swan events, the median projected population size 100 years into the future was 131 wolves (95% credible interval 57–149) for the NRM portion of Oregon and 166 wolves (95% credible interval 70–194) statewide, representing between a 60 percent decrease and a 2 percent increase within the NRM portion of Oregon, and between a 61 percent decrease and a 5 percent increase statewide (see Figure A 11 and Table A 13b). For Washington, in the scenario with observed YNP disease rates and added black swan events, the median projected population size 100 years into the future was 154 wolves (95% credible interval 54–230) for the NRM portion of the state, and 226 wolves (95% credible interval 74–356) statewide, representing between a 67 percent decrease and a 32 percent increase within the NRM portion of Washington, and between a 66 percent decrease and 59 percent increase statewide (see Figure A 12 and Table A 13b).

Overall, our model results indicate that populations within Oregon and Washington, both statewide and within the NRM, will occur at approximately current levels (or slightly increased or decreased population sizes) into the future based on the calculated median percent change in population size (Table A 13). Data provided by the State of Oregon indicates a leveling off of population sizes between 2020 and 2021 (due to large amounts of illegal take), which influenced a potentially low estimate of carrying capacity for the state in our modeling ( $K$ ); therefore, our model estimates, which resulted from parameters derived from this observed data, reflect this leveling off. However, despite our model's projections for Oregon and Washington, we would expect growing populations in both states because: (1) there is a significant amount of unoccupied suitable habitat in both states; (2) current population growth rates are positive; and (3) state-specific PVAs for both states have projected population increases (ODFW 2015b, entire; Converse 2022, entire; Petracca et al. 2023a, entire; Petracca et al. 2023b, entire).

Modeling results from an Oregon-specific PVA shows the potential for wolves to continue to increase to larger population sizes in most scenarios (ODFW 2015b, entire). As we discuss in greater detail in *Wolf Population and Human-Caused Mortality in Oregon* in Chapter

3, a 2015 predictive individual-based population model (where individual wolves are tracked through time) for the wolf population in Oregon indicated that the population would continue to increase in the future. This would occur even if the state introduced human-caused mortality rates of up to 15 percent on top of the 12 percent mortality due to natural and other causes that were occurring in 2015 (ODFW 2015b, pp. 30–33).

Washington-specific PVAs have also projected population increases in the state. For example, Converse (2022, entire), simulated pack dynamics in Washington; they demonstrated the robustness of the Washington population to expected stressors (e.g., disease, harvest), and they predicted the population would continue to grow. Another analysis that also simulated pack dynamics in Washington indicated that once state recovery is achieved (i.e., once there are 15 breeding pairs in the state), Washington’s wolf population would be relatively resilient to increases in human-caused mortality, provided a low level of dispersal from outside the state continues (Maletzke et al. 2016, pp. 372–374). Petracca et al. (2023a, entire) conducted a PVA to estimate the probability of Washington State achieving their recovery goals for wolves. They also evaluated the risk of falling below the state’s management goal of 92 wolves (Wiles et al. 2011, p. 279; Petracca et al. 2023a, p. 14). They concluded that the probability Washington would achieve their recovery goals by 2030 was 99 percent and that, with a starting population of 172 wolves in 2020, the risk of falling below their management goals was approximately zero (Petracca et al. 2023a, entire). Petracca et al. (2023b, entire) evaluated gray wolf recovery in Washington State under a variety of management strategies. Under all of these management scenarios, the gray wolf population in Washington either achieved stability or increased, depending on the scenario (Petracca et al. 2023b, p. 1). However, the probability of achieving the state’s recovery goals declined if 5 percent of the population was removed every 6 months through harvest, if 30 percent of the population was removed every 4 years through lethal depredation control, or if immigration into the state ceased. Regardless, given a starting population size of 172 gray wolves in 2020, the probability of achieving the state’s recovery goals, was greater than 92 percent in all scenarios through 2070 (Petracca et al. 2023b, p. 12).

Therefore, it is possible that our projected population estimates for both states may be biased low because (1) these populations are still growing; (2) there are substantial areas of unoccupied suitable habitat; and (3) our estimates of maximum population size derived from the observed data may be low. However, it is also possible that our estimates are biased high if Oregon and Washington shift management of their wolf populations in the future to either stabilize or decrease the population size (e.g., through hunting and/or increased use of lethal depredation control to minimize conflicts).

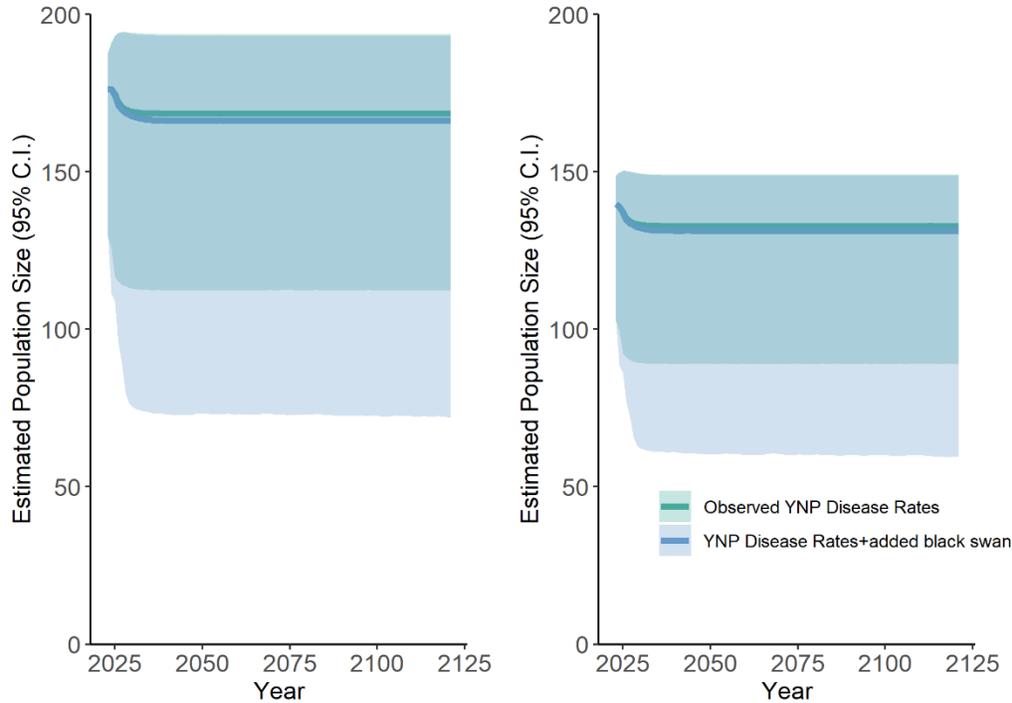


Figure A 11. Median projected wolf population size (solid lines) and 95% credible interval (shaded areas) in Oregon, statewide (left side) and in the portion of the state within the NRM (right side). We assumed no harvest in Oregon.

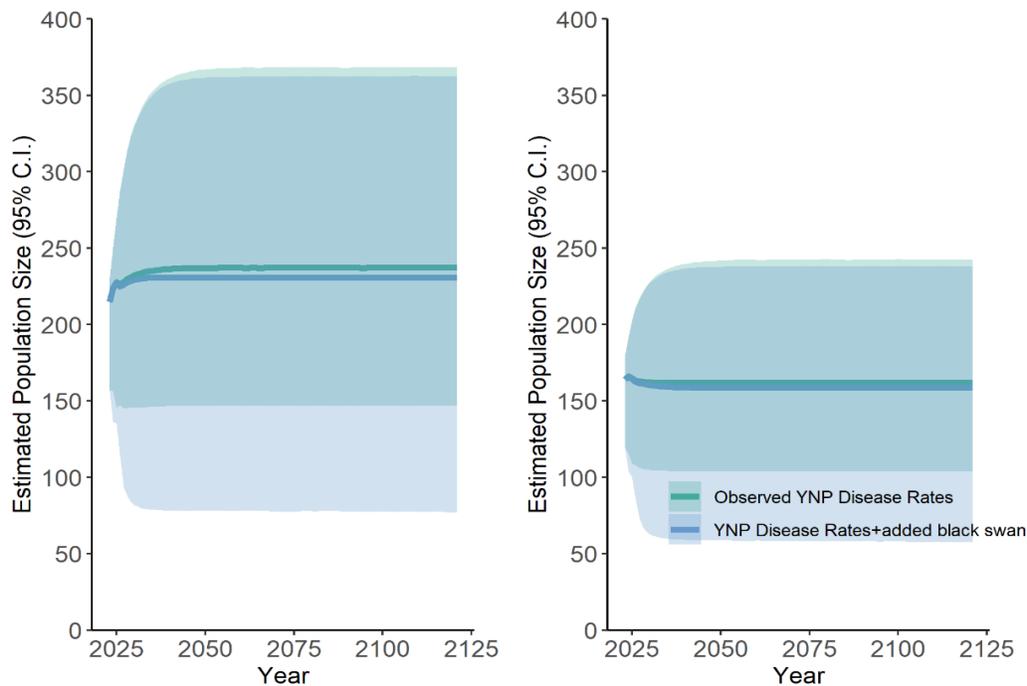


Figure A 12. Median projected wolf population size (solid lines) and 95% credible interval (shaded area) in Washington, both statewide (left side) and in the portion of the state within the NRM (right side). Harvest rates were five percent statewide and 7 percent in the NRM portion of the state under both disease scenarios, representing the continuation of the recent average removal of wolves from two areas of tribal lands.

Table A 13. Median and upper and lower 95% credible interval for population size in Oregon and Washington at the end of the a) 10-year and b) 100-year timeframes of our simulations under the two different disease scenarios, both within the NRM portions of each state and statewide; harvest was the same in Washington under all scenarios (5 percent statewide and 7 percent within the NRM portion of the state) and it did not occur in Oregon under any scenario. We also report the median percent change between the starting population size in Oregon and Washington and the projected population size in Oregon and Washington a) 10 years and b) 100 years into the future, including the 95% credible interval (CI) for these percent changes in parentheses.

a)

Region	Disease Scenario	Median Projected Population Size at 10 years (95% CI)	Percent Change from Initial Population Size (95% CI)
Oregon NRM	Observed YNP disease rates	133 (89–150)	-6% (-37 to 2%)
Oregon NRM	YNP+ added black swan	131 (59–149)	-6% (-58 to 2%)
Oregon statewide	Observed YNP disease rates	169 (112–195)	-5% (-37 to 6%)
Oregon statewide	YNP+ added black swan	167 (73–195)	-6% (-59 to 6%)
Washington NRM	Observed YNP disease rates	158 (101–226)	-3% (-38 to 28%)
Washington NRM	YNP+ added black swan	156 (59–224)	-5% (-64 to 28%)
Washington statewide	Observed YNP disease rates	230 (142–337)	6% (-33 to 48%)
Washington statewide	YNP+ added black swan	226 (78–335)	5% (-64 to 47%)

b)

Region	Disease Scenario	Median Projected Population Size at 100 years (95% CI)	Percent Change from Initial Population Size (95% CI)
Oregon NRM	Observed YNP disease rates	133 (88–149)	-6% (-38 to 2%)
Oregon NRM	YNP+ added black swan	131 (57–149)	-7% (-60 to 2%)
Oregon statewide	Observed YNP disease rates	169 (112–195)	-5% (-37 to 6%)
Oregon statewide	YNP+ added black swan	166 (70–194)	-6% (-61 to 5%)
Washington NRM	Observed YNP disease rates	157 (100–234)	-4% (-39 to 34%)
Washington NRM	YNP+ added black swan	154 (54–230)	-6% (-67 to 32%)
Washington statewide	Observed YNP disease rates	232 (143–362)	8% (-33 to 61%)
Washington statewide	YNP+ added black swan	226 (74–356)	5% (-66 to 59%)

## Appendix 7: Population Monitoring and Mortality Data Used in the Population Projection Model

### Idaho

Calendar year	Year-end wolf minimum count/estimate	Number of wolves harvested in calendar year <sup>a</sup>	Number of wolves removed through lethal control in calendar year	Year-end wolf total mortality (all sources)	Harvest rate <sup>b</sup>	Lethal control rate <sup>c</sup>
1995	14	0	0	1	0.000%	0.000%
1996	42	0	1	1	0.000%	2.326%
1997	71	0	1	2	0.000%	1.370%
1998	114	0	1	5	0.000%	0.840%
1999	156	0	3	21	0.000%	1.695%
2000	196	0	7	19	0.000%	3.256%
2001	261	0	7	16	0.000%	2.527%
2002	289	0	14	24	0.000%	4.473%
2003	362	0	7	17	0.000%	1.847%
2004	418	0	17	55	0.000%	3.594%
2005	518	0	27	46	0.000%	4.787%
2006	673	0	45	68	0.000%	6.073%
2007	764	0	50	77	0.000%	5.945%
2008	849	0	108	155	0.000%	10.757%
2009	856	135	94	286	11.821%	8.231%
2010	777	46	84	158	4.920%	8.984%
2011	768	201	59	305	18.733%	5.499%
2012	722	329	62	431	28.534%	5.377%
2013	684	355	82	478	30.551%	7.057%
2014	785	258	42	367	22.396%	3.646%
2015	786	256	57	365	22.242%	4.952%
2016	NA	268	54	368	NA	NA
2017	NA	291	75	379	NA	NA
2018	NA	329	67	414	NA	NA
2019	768 <sup>d</sup>	400	62	475	32.180%	4.988%
2020	859 <sup>d</sup>	408	77	512	29.759%	5.616%
2021	816 <sup>d</sup>	438	43	515	32.908%	3.231%
2022	710 <sup>d</sup>	351	34	404	31.508%	3.052%

<sup>a</sup>Number of wolves harvested include any wolves that lived primarily in YNP, left YNP, and were legally harvested outside YNP in Idaho during the corresponding calendar year. Note we used number of wolves harvested during a calendar year in our modeling, rather than the number harvested during a harvest season.

<sup>b</sup>Harvest rates are calculated by dividing the number of wolves harvested in a calendar year by the sum of the year-end wolf total mortality (all sources) plus the calendar year-end wolf minimum count/estimate. For example, the 2020 harvest rate of 29.759% =  $100 \times (408/(512+859))$ .

<sup>c</sup>Lethal control rates are calculated by dividing the number of wolves removed due to lethal control in a calendar year by the sum of the year-end wolf total mortality (all sources) plus the calendar year-end minimum count/estimate. For example, the 2020 lethal control rate of 5.616% =  $100 \times (77 / (512 + 859))$ .

<sup>d</sup>Based on March estimates rather than calendar year-end estimates.

## Montana

Calendar year	iPOM Estimate	Number of wolves harvested in calendar year <sup>a</sup>	Number of wolves removed through lethal control in calendar year	Year-end wolf total mortality (all sources)	Harvest rate <sup>b</sup>	Lethal control rate <sup>c</sup>
1985	13	0	0	0	0.000%	0.000%
1986	15	0	0	0	0.000%	0.000%
1987	10	0	4	4	0.000%	28.571%
1988	14	0	0	0	0.000%	0.000%
1989	12	0	1	1	0.000%	7.692%
1990	33	0	1	1	0.000%	2.941%
1991	29	0	0	0	0.000%	0.000%
1992	41	0	0	0	0.000%	0.000%
1993	55	0	0	0	0.000%	0.000%
1994	48	0	0	0	0.000%	0.000%
1995	66	0	0	1	0.000%	0.000%
1996	72	0	5	5	0.000%	6.494%
1997	56	0	18	18	0.000%	24.324%
1998	63	0	4	4	0.000%	5.970%
1999	83	0	19	19	0.000%	18.627%
2000	97	0	7	18	0.000%	6.087%
2001	123	0	8	24	0.000%	5.442%
2002	184	0	26	74	0.000%	10.078%
2003	182	0	34	87	0.000%	12.639%
2004	153	0	40	53	0.000%	19.417%
2005	256	0	35	57	0.000%	11.182%
2006	316	0	53	65	0.000%	13.911%
2007	659	0	73	102	0.000%	9.593%
2008	849	0	110	155	0.000%	10.956%
2009	1,028	72	145	258	5.599%	11.275%
2010	1,149	0	141	179	0.000%	10.617%
2011	1,259	121	64	216	8.203%	4.339%
2012	1,205	175	108	324	11.445%	7.063%
2013	1,210	231	75	335	14.951%	4.854%
2014	1,143	213	57	306	14.700%	3.934%
2015	1,190	205	51	276	13.984%	3.479%
2016	1,126	255	61	334	17.466%	4.178%
2017	1,117	233	57	305	16.385%	4.008%
2018	1,153	259	60	341	17.336%	4.016%
2019	1,159	298	72	394	19.189%	4.636%
2020	1,184	305	52	368	19.652%	3.351%
2021	1,143	299	39	349	20.040%	2.614%
2022	1,087	248	45	309	17.765%	3.223%

<sup>a</sup>Number of wolves harvested include any wolves that lived primarily in YNP, left YNP, and were legally harvested outside YNP in Montana during the corresponding calendar year. Note we used number of wolves harvested during a calendar year in our modeling, rather than the number harvested during a harvest season.

<sup>b</sup>Harvest rates are calculated by dividing the number of wolves harvested in a calendar year by the sum of the year-end wolf total mortality (all sources) plus the calendar year-end wolf minimum count/estimate. For example, the 2020 harvest rate of 19.652% =  $100 \times (305/(368+1,184))$ .

<sup>c</sup>Lethal control rates are calculated by dividing the number of wolves removed due to lethal control number in a calendar year by the sum of the year-end wolf total mortality (all sources) plus the calendar year-end minimum count/estimate. For example, the 2020 lethal control rate of 3.351% =  $100 \times (52/(368+1,184))$ .

## Oregon

Calendar year	Year-end wolf minimum count (statewide)	Year-end wolf minimum count in listed area	Year-end wolf minimum count in NRM portion	Number of wolves harvested in calendar year in NRM portion <sup>a</sup>	Number of wolves removed through lethal control in calendar year in NRM portion	Year-end wolf total mortality in NRM portion (all sources)	Year-end wolf total mortality in listed area (all sources)	Lethal control rate in NRM portion <sup>b</sup>
2009	14	0	14	0	2	2	0	12.500%
2010	21	0	21	0	0	1	0	0.000%
2011	29	0	29	0	2	3	0	6.250%
2012	48	0	48	0	0	1	0	0.000%
2013	64	3	61	0	0	3	0	0.000%
2014	81	7	74	0	0	0	0	0.000%
2015	110	11	99	0	0	7	0	0.000%
2016	112	12	100	0	5	6	1	4.717%
2017	124	14	110	0	5	11	2	4.132%
2018	137	20	117	0	3	6	1	2.439%
2019	158	27	131	0	1	5	2	0.735%
2020	173	32	141	0	1	9	1	0.546% <sup>c</sup>
2021	175	31	144	0	8	21	5	4.848%
2022	178	38	140	0	7	18	2	4.430%

<sup>a</sup>Wolf harvest is not authorized by Oregon in the NRM; therefore, wolf harvest rates are not calculated statewide or in the NRM.

<sup>b</sup>Lethal control rates are calculated by dividing number of wolves removed due to lethal control in the NRM portion of Oregon in a calendar year by the sum of the year-end wolf total mortality in the NRM portion of Oregon (all sources) plus the year-end wolf minimum count in the NRM portion of Oregon. For example, the 2021 lethal control rate of 4.848% =  $100 \times (8/(21+144))$ .

<sup>c</sup>Gray wolves were delisted throughout the state in this year so lethal control rate was calculated using statewide data.

## Washington

Calendar year	Year-end wolf minimum count statewide	Year-end wolf minimum count in listed area	Year-end wolf minimum count in NRM portion	Number of wolves harvested in calendar year in NRM portion	Number of wolves removed through lethal control in calendar year in NRM portion	Year-end wolf total mortality in NRM portion (all sources)	Year-end wolf total mortality in listed area (all sources)	Harvest rate calculated statewide <sup>a</sup>	Harvest rate in NRM portion <sup>b</sup>	Lethal control rate in NRM portion <sup>c</sup>
2008	5	5	0	0	0	0	2	0.000%	NA	NA
2009	14	7	7	0	0	0	0	0.000%	0.000%	0.000%
2010	19	3	16	0	0	0	0	0.000%	0.000%	0.000%
2011	35	9	26	0	0	0	0	0.000%	0.000%	0.000%
2012	51	8	43	0	7	9	0	0.000%	0.000%	13.462%
2013	52	14	38	1	0	2	3	1.754%	2.500%	0.000%
2014	68	13	55	0	1	7	4	0.000%	0.000%	1.613%
2015	90	13	77	3	0	6	1	3.093%	3.614%	0.000%
2016	115	18	97	3	7	14	1	2.308%	2.703%	6.306%
2017	122	16	106	3	5	13	1	2.206%	2.521%	4.202%
2018	126	22	104	6	4	11	1	4.348%	5.217%	3.478%
2019	145	22	123	6	11	21	0	3.614%	4.167%	7.639%
2020	178	34	144	8	3	15	1	4.124%	5.031%	1.546% <sup>d</sup>
2021	206	43	163	22	2	30	0	9.322%	11.399%	1.036%
2022	216	57	159	11	9	37	0	4.348%	5.612%	4.592%

<sup>a</sup>Harvest rates calculated by dividing the number of wolves harvested in the NRM portion of Washington by the sum of the year-end wolf total mortality in the NRM portion of Washington (all sources) plus the year-end wolf total mortality in listed area (all sources) plus the year-end wolf minimum count statewide. For example, the 2021 harvest rate statewide of 9.322% =  $100 \times (22/(30+0+206))$ . Note we used number of wolves harvested during a calendar year in our modeling, rather than the number harvested during a harvest season.

<sup>b</sup>Harvest rates are calculated by dividing the number of wolves harvested in the NRM portion of Washington by the sum of the year-end wolf total mortality in the NRM portion (all sources) plus the year-end minimum count in the NRM portion. For example, the 2021 harvest rate in NRM of 11.399% =  $100 \times (22/(30+163))$ .

<sup>c</sup>Lethal control rates are calculated by dividing the number of wolves removed due to lethal control in the NRM portion in a calendar year by the sum of the year-end wolf total mortality in the NRM portion (all sources) plus the year-end wolf minimum count in the NRM portion. For example, the 2021 lethal control rate of 1.036% =  $100 \times (2/(30+163))$ .

<sup>d</sup>Gray wolves were delisted throughout the state in this year so lethal control rate was calculated using statewide data.

## Wyoming

Calendar year	Year-end wolf minimum count (outside YNP)	Number of wolves harvested in calendar year <sup>a</sup>	Number of wolves removed through lethal control in calendar year	Year-end wolf total mortality (all sources)	Harvest rate <sup>b</sup>	Lethal control rate <sup>c</sup>
1995	0	0	0	0	0.000%	0.00%
1996	2	0	0	2	0.000%	0.000%
1997	8	0	2	4	0.000%	16.667%
1998	15	0	2	2	0.000%	11.765%
1999	26	0	0	1	0.000%	0.000%
2000	34	0	2	3	0.000%	5.405%
2001	57	0	4	4	0.000%	6.557%
2002	69	0	6	7	0.000%	7.895%
2003	77	0	18	27	0.000%	17.308%
2004	89	0	29	36	0.000%	23.200%
2005	134	0	41	51	0.000%	22.162%
2006	175	0	44	59	0.000%	18.803%
2007	188	0	63	75	0.000%	23.954%
2008	178	11	46	77	4.314%	18.039%
2009	224	0	31	41	0.000%	11.698%
2010	246	0	40	58	0.000%	13.158%
2011	230	0	36	51	0.000%	12.811%
2012	194	66	43	125	20.690%	13.480%
2013	211	62	33	102	19.808%	10.543%
2014	229	12	37	73	3.974%	12.252%
2015	284	0	54	77	0.000%	14.958%
2016	269	0	113	128	0.000%	28.463%
2017	250	76	62	163	18.402%	15.012%
2018	206	81	66	174	21.316%	17.368%
2019	217	48	30	93	15.484%	9.677%
2020	204	53	43	115	16.614%	13.480%
2021	217	51	32	101	16.038%	10.063%
2022	230	56	21	88	17.610%	6.604%

<sup>a</sup>Number of wolves harvested include any wolves that lived primarily in YNP, left YNP, and were legally harvested outside YNP in Wyoming during the corresponding calendar year. Note we used number of wolves harvested during a calendar year in our modeling, rather than the number harvested during a harvest season.

<sup>b</sup> Harvest rates are calculated by dividing the number of wolves harvested in a calendar year by the sum of the year-end wolf total mortality (all sources) plus the calendar year-end wolf minimum count. For example, the 2020 harvest rate of 16.614% =  $100 \times (53/(115+204))$ .

<sup>c</sup>Lethal control rates are calculated by dividing the number of wolves removed due to lethal control in a calendar year by the sum of the year-end wolf total mortality (all sources) plus the calendar year-end minimum count. For example, the 2020 lethal control rate of 13.480% =  $100 \times (43/(115+204))$ .

## Yellowstone National Park

Calendar year	Year-end wolf minimum count	Number of wolves primarily residing in YNP harvested outside YNP <sup>a</sup>	Year-end wolf lethal control inside YNP <sup>b</sup>	Year-end wolf total mortality (all sources) <sup>c</sup>	Harvest rate <sup>d</sup>
1995	21	0	0	1	0.000%
1996	36	0	0	5	0.000%
1997	63	0	0	21	0.000%
1998	82	0	0	8	0.000%
1999	72	0	0	4	0.000%
2000	119	0	0	6	0.000%
2001	132	0	0	5	0.000%
2002	148	0	0	5	0.000%
2003	174	0	0	16	0.000%
2004	171	0	0	17	0.000%
2005	118	0	0	18	0.000%
2006	136	0	0	6	0.000%
2007	171	0	0	6	0.000%
2008	124	0	0	17	0.000%
2009	96	4	1	16	3.571%
2010	97	0	0	11	0.000%
2011	98	2	1	13	1.802%
2012	83	12	0	22	11.429%
2013	95	0	0	6	0.000%
2014	104	5	0	8	4.464%
2015	98	1	0	10	0.926%
2016	108	6	0	11	5.042%
2017	97	6	0	11	5.556%
2018	80	4	0	7	4.598%
2019	94	4	0	7	3.960%
2020	123	3	0	7	2.308%
2021	97	24	0	30	18.898%
2022	108	6	0	13	4.959%

<sup>a</sup>Number of wolves harvested reflects the number of wolves that have territories primarily within YNP, left YNP, and were legally harvested outside of YNP (in ID, MT, or WY). Number of wolves harvested is based on harvest season and is reported here by the earlier of the harvest season calendar years (i.e., 2020 harvest in the table corresponds with wolves legally harvested in the 2020/2021 harvest season outside of YNP (in ID, MT or WY)).

<sup>b</sup>Wolves lethally controlled inside YNP due to habituation.

<sup>c</sup>Includes all wolves that died within YNP during the corresponding calendar year plus the number of wolves reported as legally harvested outside YNP during the corresponding harvest season.

<sup>d</sup>Harvest rates calculated by dividing the number of wolves harvested outside YNP during the corresponding harvest season by the sum of the year-end wolf total mortality (all sources) plus the year-end wolf minimum count. For example, the 2020 harvest rate of 2.308% =  $100 \times (3/(7+123))$ .

## 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 2020, Chapter 2).

### Model Code for Estimating Parameters

```
sink("DDmodel.jags")
cat("
model {
  # Priors and constraints
  N.est[1] ~ dunif(0, N.est.initial) # Initial population size
  ### N.est[13]~dunif(min.N,max.N) ### For broken stick modelinitial population size for Montana in 2007
  sigma.obs ~ dgamma(0.25,0.25) ### prior for observations
  tau.obs<-pow(sigma.obs, -2)# precision of observation process

  r~dnorm(0, 0.001)###diffuse prior for growth
  K~dunif(Kmin,Kmax)###informative prior based on observed values for each state
  h~dnorm(0, 0.001)###diffuse prior for harvest effect

  # Likelihood
  # State process for N
  for (t in 1:nYears){
    N.est[t+1]<- N.est[t]+r*N.est[t]*(1-N.est[t]/K)-h*m[t]
  }
  #####State process for broken stick in Montana
  ## for(t in nYears+1:nYears2){
  ## N.est[t+1]<- N.est[t]+r*N.est[t]*(1-N.est[t]/K)-h*m[t]
  ### }
  # Observation process change to nYears 2 for broken stick
  for (t in 1:nYears) {
    y[t] ~ dnorm(N.est[t], tau.obs)
```

```

}
}
}
", fill = TRUE)
sink()

#####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 + control animals
jags.data <- list(y = dat$Estimate, nYears = nrow(dat), m=dat$m)

####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:
Kmin<- ###select a value based on observation
Kmax<- ###select a value based on observations
N.est.initial<- ###select a value based on observations
# Initial values
inits <- function(){list(r = runif(1, 0, 1),
                        K=runif(1,Kmin,Kmax),
                        sigma.obs = runif(1, 0, 10),
                        h=runif(1,0, 1),
                        N.est = c(runif(1, 0, N.est.initial), rep(NA, (nYears-1))))}
####Finally, set the parameters to monitor and the MCMC settings:

# Parameters monitored
parameters <- c("r", "sigma.obs", "N.est","K","h")

# MCMC settings
ni <- 300000
nt <- 3
nb <- 100000
nc <- 3

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

####create objects in R workspace, for the growth, harvest, and start pops for each state

##example

MT.r<-c(ssm.MT$samples[,"r"][[1]],ssm.MT$samples[,"r"][[2]],ssm.MT$samples[,"r"][[3]])
MT.h<-c(ssm.MT$samples[,"h"][[1]],ssm.MT$samples[,"h"][[2]],ssm.MT$samples[,"h"][[3]])
MT.K<-c(ssm.MT$samples[,"K"][[1]],ssm.MT$samples[,"K"][[2]],ssm.MT$samples[,"K"][[3]])
MT.start<-
c(ssm.MT$samples[,"N.est[26]"][[1]],ssm.MT$samples[,"N.est[26]"][[2]],ssm.MT$samples[,"N.est[26]"][[3]])
)

```

## Supplementary Material B

Project the population forward in time using the estimates from the model.

Note that due to stochasticity in individual model runs (i.e., the 200,000 iterations), 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.state` (a vector of harvest rates for each state in order Idaho, Montana, Wyoming, Oregon, Washington statewide, YNP, Washington with the NRM);  
example `h.rate<-c(0.3,0.25,0.2,0.0,0.05, 0.10,0.05)`
- control rates (four by six matrix of the most recent four years of control rates for each state in order Idaho, Montana, Wyoming, Oregon, and Washington)
- `NRM.on` is a TRUE/FALSE value depending on whether we are using a value for the NRM only

`Dis.cat`, `dis.cat=1` is background disease rates, `dis.cat=2` includes additional events from the Reed et al. Values

```
#####Function
```

```
W.rharvest.model<-function(h.rate, control.rates, NRM.on, dis.cat, threshold, scenario){
  index<-scenario
  iters<-199998
  N.pred<-array(0, dim=c(iters, 100, 6))

  states<-c("ID","MT","WY","OR","WA","YNP")
  vec<-list(all=seq(1,6), sub=c(1,2,6), NRM=c(4,5))
  ###Only need to run WY, OR, and WA for scenarios 1 and 4
  check<-
  ifelse(scenario%in%c(1,4)&NRM.on==FALSE,1,ifelse(scenario%in%c(1,4)&NRM.on==TRUE
,3,2))

  for(j in 1:1){
    ###Washington and Oregon NRM on and off
    if(NRM.on==TRUE & (states[j]%in%c("WA","OR"))){
      r<-get(paste(states[j],"NRM.r",sep=""))
      K<-get(paste(states[j],"NRM.K",sep=""))
    }
  }
}
```

```

start.pop<-get(paste(states[j], "NRM.start", sep=""))
h<-get(paste(states[j], "h", sep="."))
}else{
r<-get(paste(states[j], ".r", sep=""))
K<-get(paste(states[j], ".K", sep=""))
start.pop<-get(paste(states[j], ".start", sep=""))
h<-get(paste(states[j], "h", sep="."))
}

N.pred[,1,j]<-start.pop
h.rate.j<-ifelse(states[j]=="WA"&NRM.on==TRUE, h.rate[7], h.rate[j])
h.rate.j<-rep(h.rate.j, iters)

for(i in 2:100){
comp.h<-runif(1,0.2,0.4)#### maybe change this to 0.2
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))
}
##sample control rates
c.rate<-sample(control.rates[,j],length(r), replace=TRUE)

####did the population last year experience a catastrophe?
N.pred[,i-1,j]<-N.pred[,i-1,j]*(1-cat.rate)
#####Grow th population
N.tot<-N.pred[,i-1,j]+r*(N.pred[,i-1,j]*(1-N.pred[,i-1,j]/K)
####harvest rate is zero if the population is less than or equal to threshold[j]
h.rate.t<-ifelse(N.tot<=threshold[j],0,h.rate.j)
comp.rate<-ifelse((h.rate.t+c.rate)<comp.h,(h.rate.t+c.rate),comp.h)
add.rate<-ifelse((h.rate.t+c.rate)>=comp.h,(h.rate.t+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.t/(c.rate+h.rate.t))
control.tot<-(h*comp.m+add.m)*(c.rate/(c.rate+h.rate.t))
check.scenario<-ifelse(scenario%in%c(3,6),1,0)
###if you are in the floor scenario in ID, MT, or WY
if(check.scenario==1&j%in%c(1,2,3)){
###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
}
N.pred[is.na(N.pred)]<-0
}
out<-N.pred
return(out)
}

```

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