

Ecosystems Mission Area—Biological Threats & Invasive Species Research Program, Environmental Health Program, and the Species Management Research Program

Prepared in cooperation with the U.S. Department of Agriculture, National Park Service, U.S. Fish and Wildlife Service, and Wyoming Game and Fish Department

Decision Analysis in Support of the National Elk Refuge Bison and Elk Management Plan

Scientific Investigations Report 2024–5119

U.S. Department of the Interior U.S. Geological Survey

Cover. A group of bull elk forages on grasses on the National Elk Refuge. Photograph taken by Alex Lennon, U.S. Fish and Wildlife Service Volunteer, February 2021.

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Preface

This report was developed to evaluate the performance of a set of proposed alternatives for Cervus elaphus canadensis (elk) and Bison bison (bison) management at the National Elk Refuge (NER) in Wyoming, U.S.A., and to inform a National Environmental Policy Act Environmental Impact Statement focused on developing the next "Bison and Elk Management Plan" (BEMP). The U.S. Geological Survey facilitated a structured decision-making process for the U.S. Fish and Wildlife Service to develop the alternatives and the criteria (performance metrics) for evaluating the alternatives. Chapter A provides scoping details of the report, a summary of the 19 metrics that are used to evaluate the performance of each of 5 alternatives, and methodological details of 2 performance metrics that were not covered in other technical chapters. Chapter B analyzes elk population and chronic wasting disease dynamics under the five alternatives. Chapter C evaluates elk space-use based on data collected from global positioning system collars on elk and expert elicitation for scenarios with limited data. Chapter D evaluates bison population dynamics, conflict, and harvest patterns under the five alternatives. Chapter E assesses social and economic consequences. The alternatives are anticipated to have varying affects on bison and elk population abundance and private land use, wildlife-related recreation and tourism, and hunters and outfitters in the region. Each chapter was developed under advisement of a technical team, made up science experts from U.S. Fish and Wildlife Service, National Park Service, U.S. Forest Service, and Wyoming Game and Fish Department.

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Abbreviations

"BEMP"	"Bison and Elk Management Plan"
CWD	chronic wasting disease
FS	U.S. Department of Agriculture—Forest Service
FWS	U.S. Fish and Wildlife Service
GYE	Greater Yellowstone Ecosystem
JHU	Jackson Elk Herd Unit
NER	National Elk Refuge
PrP ^{cwd}	misfolded prion protein
SD	standard deviation
WGFD	Wyoming Game and Fish Department

Decision Framing Overview and Performance of Management Alternatives for Bison and Elk Feedground Management at the National Elk Refuge in Jackson, Wyoming

By Jonathan D. Cook¹, Gavin G. Cotterill¹, Margaret C. McEachran¹, Tabitha A. Graves¹, Eric K. Cole², Paul C. Cross¹

Executive Summary

This report was developed to evaluate the performance of a set of proposed alternatives for *Cervus elaphus canadensis* (Excleben, 1777; elk) and *Bison bison* (Linnaeus, 1758, bison) management at the National Elk Refuge (NER) in Wyoming, U.S.A., and to inform a National Environmental Policy Act Environmental Impact Statement focused on developing the next "Bison and Elk Management Plan" ("BEMP"). The U.S. Geological Survey facilitated a structured decision-making process for the U.S. Fish and Wildlife Service (FWS) to develop the alternatives and the criteria (performance metrics) for evaluating the alternatives.

The effects of proposed bison and elk supplemental feeding alternatives were estimated for a 20-year period. The study considered outcomes related to bison and elk population abundance, chronic wasting disease (CWD) prevalence in elk, human-wildlife conflict indicators, as well as effects on NER visitors, visitor spending, and hunting-associated revenues. The NER managers developed five future management alternatives:

- 1. *Continue feeding.*—The NER will continue to provision supplemental food to bison and elk during winter months based on forage availability and number of conflicts.
- 2. *No feeding.*—The NER will immediately stop provisioning food to bison and elk during winter months.
- 3. *Increase harvest, then stop feeding (increase harvest).* The NER will continue to provision food to bison and elk during winter months for the next 5 years, then stop feeding. During those 5 years, the NER will work with the Wyoming Game and Fish Department (WGFD) to increase elk harvest and attempt to reduce the population of elk that overwinter at the NER to 5,000 animals.

- 4. *Reduce feeding, then stop feeding (reduce feeding).* The NER will provision a reduced ration to elk during winter months for the next 5 years to reduce the elk population size prior to feedground closures. Exclosures will be designed to protect aspen stands in the south region of the NER, and for willow and cottonwood north of the NER.
- 5. Stop feeding after 3 percent CWD prevalence is measured in Jackson elk (disease threshold).—The NER will continue to provision food to bison and elk during winter months until CWD sampling reveals 3 percent prevalence in the Jackson elk herd, at which point all feeding activities will cease at the NER.

Since at least 1907, elk have been fed in the area that is now the NER during the winter to reduce overwinter mortality. After bison "discovered" supplemental food at the NER in the 1980s, a portion of the herd has overwintered there. In addition to reducing bison and elk overwinter mortality, supplemental feeding may limit human-wildlife conflicts in winter months, including vehicle collisions and private property use by bison and elk. However, it also encourages aggregations of bison and elk that increases the potential for intraspecific disease transmission, such as brucellosis (in bison and elk) and CWD (in elk). Chronic wasting disease is a prion infection that was recently detected in the Jackson Elk Herd Unit (JHU). Out of 1,485 elk tested for CWD between 2020 and 2023 there has been one confirmed positive case. Despite the apparent low prevalence as of 2024, experts expect that prevalence will increase and that the effects of CWD on Jackson elk will exceed what has been observed in other wild elk populations given the dense aggregations of animals that occur at the NER and the long-term persistence and infectivity of the CWD prions in the environment.

Given the benefits and potential drawbacks of supplemental feeding, the alternatives were evaluated under advisement of three separate technical teams. Each team was composed of experts with specific, local knowledge of system attributes; one team focused on wildlife effects (bison and elk), another

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focused on physical landscape effects, and the third on human dimensions, visitor dynamics, and local economic effects. The technical teams helped to develop the methods, provided feedback on assumptions required by the analyses, and provided data. The study area boundaries were created through an expert elicitation process and included the entirety of the JHU, Grand Teton National Park, NER, and the northern third of the Fall Creek Elk Herd Unit, which included three other State elk feedgrounds.

Chapter A (this chapter) provides scoping details of the "BEMP", a summary of the 19 metrics that are used to evaluate the performance of each of five alternatives, and methodological details of two performance metrics that were not covered in other technical chapters. Additional technical details, results, and interpretations are briefly covered in this chapter, but are mostly contained in chapters B–E.

The two metrics covered solely in chapter A are the costs of feedground management to FWS and the risk of invasive species introduction and spread at the NER (for example, *Bromus tectorum*). For evaluating costs, the study calculated that managing the feedground program requires FWS to expend between \$15,213 and \$16,448 per day of feeding activities for the direct costs of feed, labor, fuel, and maintenance of machinery. These daily cost estimates were used to predict that the continue feeding alternative will have an average cumulative cost of \$19,335,000 over 20 years. The reduce feeding and increase harvest alternatives would have an average 20-year cost estimate of \$4,839,000 and the disease threshold would cost \$2,189,000. Finally, the study assumed no additional costs to FWS under the no feeding alternative and did not include any costs associated with constructing exclosures under the reduce feeding alternative.

The cumulative number of feeding days over 20 years were used as a proxy measure to estimate the relative invasive plant species introduction and spread risk across the alternatives. It was assumed that more feeding would require more mechanical damage by feedground equipment and an elevated use of localized areas by bison and elk. The disturbance would negatively affect existing vegetation (mostly sagebrush communities) and allow more opportunities for invasive plant species, such as cheatgrass (*Bromus tectorum*), to expand and establish in new areas. The highest number of feeding days were estimated under the continue feeding alternative (average of 1,243 days) and intermediate feeding days under the reduce feeding and increase harvest (311 days) and disease threshold (140 days). The no feeding alternative was assumed to have 0 feed days on NER over the next 20 years.

Chapter B analyzes elk population and CWD dynamics under the five alternatives. Elk populations are predicted to decline under all alternatives, but timing, cause, and magnitude of those declines differ among alternatives. Alternatives that halt the feeding program had more immediate population declines but fared better by year 20 by partially mitigating future CWD effects. The no feeding alternative resulted in a larger elk population size in 70 out of 100 simulations, with a median elk population decline of 39 percent from the current size, whereas the continue feeding alternative led to a median decline of 55 percent from the current size. The other alternatives resulted in intermediate declines. The continue feeding alternative was predicted to result in a higher CWD prevalence by year 20 in 83 out of 100 simulations, with a median CWD prevalence of 36 percent compared to 23 percent for the no feeding alternative.

Chapter C evaluates elk space-use based on data collected from global positioning system collars on elk and expert elicitation for scenarios with limited data. The resource selection function for fed and unfed elk during average and severe winters was estimated and then used to evaluate metrics including elk use of private property and sensitive vegetation communities at monthly timesteps and under varying winter conditions. Then, monthly estimates of elk under each alternative from chapter B were distributed over the predictive resource selection surfaces developed in this chapter. The continue feeding alternative minimized time spent by elk on private property and brucellosis transmission risk from elk to cattle compared to other alternatives. However, the increase harvest and reduce feeding alternatives minimized elk damage to sensitive aspen, cottonwood, and willow vegetation communities during winter compared to other alternatives. Following the projected population declines, the negative consequences of elk space-use declined by 35-57 percent over the 20 years, and differences among alternatives ranged from 6 to 20 percent.

Chapter D evaluates bison population dynamics, conflict, and harvest patterns under the five alternatives. The bison population is predicted to maintain current population sizes under the continue feeding alternative (median size in year 20 of 541 bison), but it is expected to decline over the next 20 years under all alternatives in which the NER halts feeding (median sizes in year 20 ranged from 469 to 473). Further, these declines are likely to lead to a reduction in available bison harvest by resident, nonresident, and Tribal hunters; the continue feeding alternative leads to a median cumulative harvest estimate across 20 years of 1,879, and the no feeding alternative had a median cumulative harvest estimate of 1,292. Finally, following from results of an expert panel, human-bison conflicts were predicted to increase under no feeding alternatives because bison may venture onto private lands in greater numbers if feed is not provisioned during winter months.

Chapter E assesses social and economic consequences. The alternatives are anticipated to affect bison and elk population abundance and space use dynamics, with potential effects on the wildlife-related recreation and tourism in the area, including winter-season visitors to NER, and hunters and outfitters in the JHU. Limited evidence was found to suggest that NER visitation rates were correlated with historical elk counts at the NER. Projecting this forward, limited differences were found among alternatives in visitation metrics relative to the uncertainty within predictions for each alternative. Larger differences were estimated for elk tag license sales, hunter-associated spending, and outfitter revenues, but these are subject to strong assumptions about human responses to predicted elk changes. The increase harvest alternative was predicted to have higher average revenue from elk tag sales (\$6.6 million compared to \$4.8-5.5 million, on average, for the other alternatives), spending by elk hunters (\$101.3 million compared to \$73.0-88.5 million, on average,

for the other alternatives), and outfitter revenues (\$14.5 million, on average, compared to \$10.4–12.6 million for the other alternatives) because more elk were harvested under this alternative instead of dying from other causes (for example, CWD, severe winters).

The analyses in this report estimated 19 performance metrics that were important to decision makers. No single alternative performed best for all metrics. The next step in a structured decision analysis could be to weight the relative importance of different objectives against one another, such that the overall performance of each alternative can be summarized including all sources of prediction uncertainty.

Introduction

The U.S. Fish and Wildlife Service (FWS) manages the 24,700-acre National Elk Refuge (NER or the Refuge), situated in the Greater Yellowstone Ecosystem (GYE) in northwestern Wyoming (fig. A1). The Refuge was initially established in 1912 as a winter game reserve (16 U.S.C. 673) and later expanded to include the management of habitats for breeding birds, fish, and other big game animals, as well as the conservation of threatened and endangered species. These management purposes have resulted in the protection of important habitats for many species including Cervus elaphus canadensis (Excleben, 1777; elk), Bison bison (Linnaeus, 1758; bison), Canis lupus (Linnaeus, 1758; grey wolves), Ursus arctos (Linnaeus, 1758; grizzly bears), Cygnus buccinator (Richardson, 1831; trumpeter swans), Haliaeetus leucocephalus (Linnaeus, 1766; bald eagles), Ovis canadensis (Shaw, 1804; bighorn sheep), and Oncorhynchus clarkii (Richardson, 1836; cutthroat trout), and have provided recreational opportunities for visitors.

To guide the management of bison and elk populations on NER, FWS has developed a series of planning documents, including a "Bison and Elk Management Plan" ("BEMP"; FWS and National Park Service [NPS], 2007) and a "Step-Down Plan for Bison and Elk Management" ("Step-Down Plan"; FWS, 2019). One of the major elements of the "BEMP" and "Step-Down Plan" is the provisioning of pelleted feed to bison and elk on 5,000 acres of Refuge land during winter months, typically between January and April. Between 2018–2021, the NER fed an average of 7,540 elk out of a population in the Jackson Elk Herd Unit (JHU) that exceeded 12,000 total individuals (fig. A2) Over a similar period (2016–20), NER fed an average of 317 bison out of a total of 550 individuals in the Jackson bison herd (U.S. Fish and Wildlife Service, written comm., 2024).

A total of 22 elk feedground locations in western Wyoming are primarily managed by Wyoming Game and Fish Department (WGFD); the NER feeding program is the only one under the authority of FWS (Wyoming Game and Fish Department, 2024b). Winter feeding is used to reduce overwinter mortality, maintain elk numbers near population objectives, reduce competition between bison and elk, ensure harvest opportunities, and reduce human-wildlife conflicts, such as disease transmission risk among livestock, elk, and bison (Wyoming Game and Fish Department, 2024b). While winter feeding is successful in sustaining animals during harsh winter conditions and sequestering them to reduce private property conflict, the practice also elevates local densities and animal-to-animal contact, thereby increasing the potential for intraspecific disease transmission (National Academies of Sciences, Engineering, and Medicine, 2020; Janousek and others, 2021). Diseases that may be transmitted more quickly in feedground settings include chronic wasting disease (CWD) in elk and brucellosis (caused by *Brucella abortus*) in bison and elk.

The arrival of CWD to the Jackson elk herd, combined with the potential for accelerated spread in dense aggregations of fed elk, has motivated a reevaluation of existing bison and elk feedground management. Chronic wasting disease is a fatal neurodegenerative disease caused by a misfolded prion protein (PrPCWD) that affects members of the Cervidae family (elk, Odocoileus virginianus [Zimmerman, 1780; white-tailed deer], Odocoileus hemionus [Rafinesque, 1817; mule deer], and Alces alces [Linnaeus, 1758; moose]). The disease is transmitted directly during social contact among animals and indirectly when susceptible animals contact a prion-contaminated environment. The PrPCWD protein remains infectious in environments for extended periods of time, possibly years (Williams and Young, 1980; Williams and others, 2002; Miller and others, 2004). As of early 2024, no effective treatments for CWD at the individual, population, or landscape level exist. Previous research has shown population declines in mule deer and white-tailed deer that were correlated with CWD prevalence (Edmunds and others, 2016; DeVivo and others, 2017), and the Jackson elk population was predicted to decline when prevalence reaches 7–13 percent (Monello and others, 2017, Galloway and others, 2021).

Brucellosis, another bacterial disease transmitted in feedground settings, affects elk, bison, and domestic livestock in the Yellowstone region. The disease is mainly transmitted in the spring prior to calving by contact with fetuses aborted from infectious individuals (NAS, 2020). Previous analyses of brucellosis seroprevalence in elk on feedgrounds suggested that longer feeding seasons and higher elk densities were correlated with higher seroprevalence (Cross and others, 2007). Subsequent attempts to mitigate brucellosis transmission on feedgrounds, however, had little success (Cotterill and others, 2020). In addition, increases in brucellosis seroprevalence in elk populations that do not overwinter on feedgrounds suggests that this disease will persist even in the absence of supplemental feeding (Cross and others, 2010a; 2010b; Brennan and others, 2017).

Beyond the disease concerns surrounding fed bison and elk, these species are valued by the many stakeholders for their roles in healthy ecosystems, as a charismatic species for wildlife viewers, and as game. Regionally, bison and elk support local economies and provide viewing and harvest opportunities for Tribes, members of the public, and outfitters. Elk hunting alone has generated more than \$4.9 million in annual income and 269 jobs in Teton County, Wyoming, according to Koontz and Loomis (2005). A more recent study

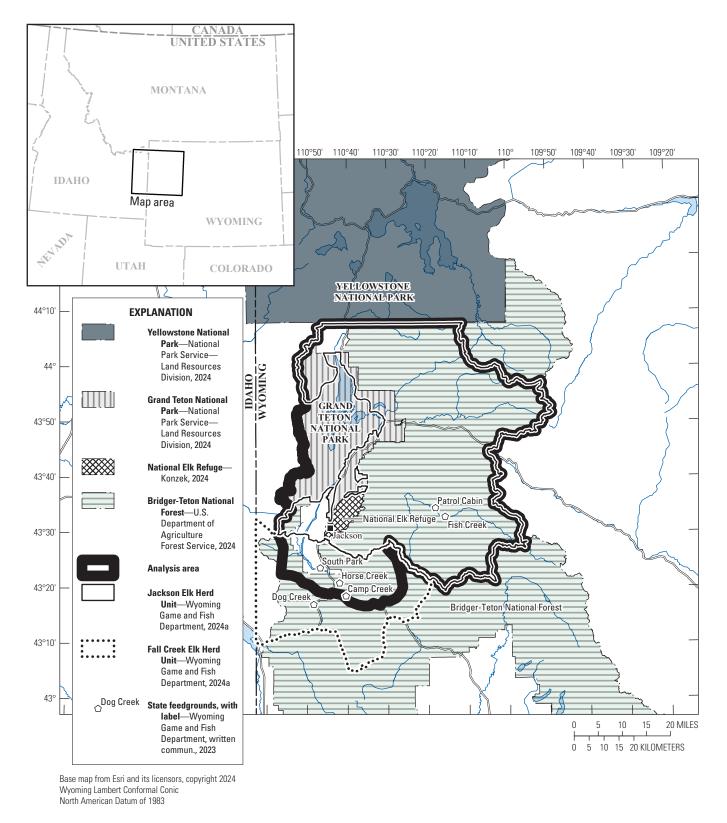


Figure A1. Map showing the study area. The analysis area (thick black polygon) is composed of the Jackson Elk Herd Unit (thin black polygon), part of the Fall Creek Herd Unit (dotted border polygon), the National Elk Refuge and Grand Teton National Park. Also included are the locations of six State feedgrounds, Patrol Cabin, Fish Creek, South Park, Horse Creek, Camp Creek, and Dog Creek, that were considered in the analyses of this report.

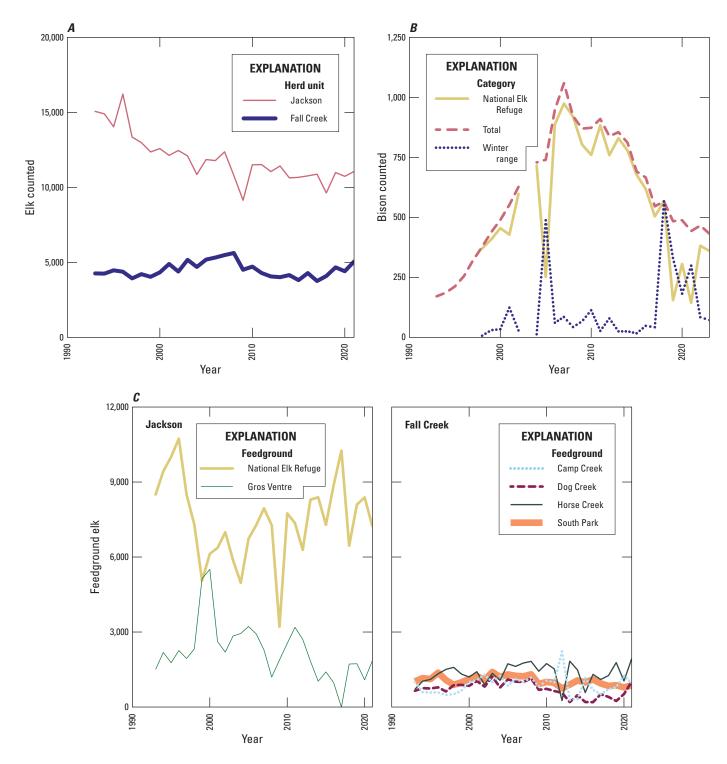


Figure A2. Line graphs showing the population counts of elk (*A* and *C*) and bison (*B*) in the Jackson region from 1993 to 2021 (shown by herd unit [*A*], and by feedground [*C*]). The Gros Ventre feedground in panel *C* includes Patrol Cabin and Fish Creek feedgrounds.

by Dietsch and others (2020) found that visitors continue to visit the NER for opportunities to hunt, fish, and ride horse-drawn sleighs, and that these activities may be affected by any changes to winter feeding of bison and elk.

This multichapter report describes a structured decision-making process that was led by the U.S. Geological Survey to evaluate potential management alternatives and support the drafting of the next "BEMP". This chapter covers the detailed decision-framing elements of the "BEMP" decision, an abbreviated description of methods employed to evaluate alternatives, and presents summarized results for each of four technical chapters on elk disease and population dynamics (Cross and others, 2025, this volume, chap. B), elk space-use patterns including private land use patterns (Cotterill and others, 2025, this volume, chap. C), bison population dynamics and conflict potential (Cook and others, 2025, this volume, chap. D), and human effects including nonhunting and hunting visitation trends and economic effects (McEachran and others, 2025, this volume, chap. E).

Decision Framing

The process of structured decision making was used to frame and evaluate the set of potential bison and elk management alternatives on a set of objectives that were identified by FWS. Structured decision making is a normative process that helps break down and analyze distinct components of decisions using a series of steps. The steps include (and are described in this chapter) defining the problem and identifying objectives, alternatives, consequences, and trade-offs (Hammond and others, 1998).

The decision problem can be described using a formal problem statement that articulates important scoping details about the decision. The details about the following elements are typically included:

- A specific description of the decision itself;
- The decision maker;
- The decision maker's authority to act;
- The scale of the decision (including spatial and temporal scoping); and,
- Any aspects that might make the decision difficult.

Next, the fundamental objectives describe the complete set of concerns that a decision maker has when making a management decision. Fundamental objectives are designed to be a direct expression of the mission and goals of an agency, their motivations, and any relevant values or desires of stakeholders as related to the specific decision context. Then, performance metrics are developed for each fundamental objective to evaluate the performance of the alternatives and to make comparisons against one another. The consequence assessment measures that performance and provides a quantitative comparison of each alternative relative to the others. Finally, tools and strategies from decision analysis can be used to help decision makers evaluate trade-offs and identify the alternative that best meets the full range of concerns specific to the decision context. The process of structured decision making has been successfully used in natural resources settings (for example, refer to Runge and others, 2015), including a recent application to another feedground decision on nearby Bridger-Teton National Forest (fig. A1; Cook and others, 2023). Using this process implemented in a series of facilitated discussions, the following "Problem Statement," "Fundamental Objectives and Performance Metrics," and "Management Alternatives" were developed.

Problem Statement

The physical, biological, and cultural resources of the NER are managed in accordance with several location-specific acts of Congress (for example, 16 U.S.C. 673, establishing an elk reserve), executive orders, and other Federal legislation, such as the National Wildlife Refuge System Administration Act of 1995 (16 U.S.C. 668dd), National Wildlife Refuge System Improvement Act of 1997 (Public Law 105-57), and Endangered Species Act of 1973 (16 U.S.C. 1531). A primary focus of the NER (FWS, 2019) is to help manage the bison and elk herds-both are culturally and ecologically important at the Refuge and throughout the region. To guide the management of these species, FWS uses an existing "BEMP" (FWS and NPS, 2007), and "Step-Down Plan" (FWS, 2019). Decisions at the NER are under the direct authority of the Refuge manager and other leadership of FWS; however, close partnerships exist across State, Federal, local, and Tribal leaders in the GYE that also influence management decisions.

As of 2024, bison and elk are fed at the NER during winter months to reduce overwinter mortality of elk, reduce human-wildlife conflicts, and minimize competition between bison and elk. The NER distributes pelleted feed on 5,000 acres during the months of January-April to offset a loss of native winter range because of human development. Bison and elk feeding is also considered an effective tool to reduce human-wildlife conflicts that can occur when animals seek out alternative food resources in nearby urban areas or comingle with livestock and thereby increase risk of wildlife-to-livestock disease transmission. However, the concentration of elk on feedgrounds has led to loss of diverse woody plant communities that provide habitat for other species and may increase disease transmission as animals are aggregated in high densities on feedgrounds. In addition to feeding, the Refuge acts to improve habitat quality, including large-scale restoration projects and the irrigation of as much as 4,500 acres (FWS, 2019).

The spread of CWD across Wyoming and into the GYE has motivated a reevaluation of bison and elk management, including the practice of bison and elk feeding. Given the potential for CWD to alter the system, the complex setting under which management decisions are made, and the 17 years since the last "BEMP" was drafted, the NER seeks to revise the plan (FWS, 2023) in a manner that considers new knowledge and science, as well as the elevated threat that CWD presents to the Jackson elk herd. The Refuge also wants to better understand the effects that management alternatives might have on bison, physical and cultural resources, and human activities. The temporal scope of the "BEMP" metrics was 20 years to approximately align with the period of implementation for the prior plan. The spatial scope of the "BEMP" is the Refuge, but managers are also interested in considering the effects of the management alternatives on surrounding Federal, State, and private lands (herein called the analysis area, fig. A1). The analysis area was first proposed by WGFD staff using WGFD datasets and local expertise. The analysis area was later confirmed with the interagency team of science experts, including members from the FWS, U.S. Department of Agriculture—Forest Service (FS), National Park Service (NPS), and WGFD.

Fundamental Objectives and Performance Metrics

As established by the NER, fundamental objectives describe the unique set of concerns that a decision maker wants to (or is mandated to) achieve when making a decision (Gregory and others, 2012). As such, the set of fundamental objectives, when comprehensively analyzed, may help a decision maker understand how each alternative might perform and select the option that is expected to provide the best outcomes. The National Elk Refuge used a series of meetings facilitated by the U.S. Geological Survey, as well as feedback from other agencies, stakeholders, and public comments to identify nine fundamental objectives. Many are drawn directly from an interpretation of the mission of the National Elk Refuge and guiding documents such as 16 U.S.C. 673, establishing the NER as an elk reserve, the National Wildlife Refuge System Administration Act of 1995 (16 U.S.C. 668dd), National Wildlife Refuge System Improvement Act of 1997 (Public Law 105-57), as well as prior Refuge plans including the existing "BEMP" (FWS and NPS, 2007) and "Step-Down Plan" (FWS, 2019).

Fundamental Objective 1. Maximize the health and well-being of wildlife.-According to the National Wildlife Refuge System Administration Act of 1995 (16 U.S.C. 668dd) and National Wildlife Refuge System Improvement Act of 1997 (Public Law 105-57)), FWS will manage refuge resources to "ensure that the biological integrity, diversity, and environmental health *** are maintained for the benefit of present and future generations of Americans." The introduction and spread of CWD in elk populations will lead to sick and dying animals and a departure from management goals related to the health and conservation of elk. Further, if elk repeatedly aggregate in the same geographic location because of management activities like supplemental feeding, the NER lands may be contaminated by infectious pathogens, including CWD prions, leading to locally elevated indirect disease transmission and further negative effects.

- Performance metric 1a.—Minimize the prevalence of CWD in elk after 20 years.
- Performance metric 1b.—Maximize the population size of elk after 20 years.
- Performance metric 1c.—Minimize the suffering of elk during the first 5 years of implementation of a new management plan as defined by the cumulative number of natural and disease-induced elk deaths during the winter months (November through March) of the first 5 years.
- Performance metric 1d.—Maximize the population size of bison after 20 years.

National Elk Refuge managers were interested in maintaining long-distance elk migrations (Cole and others, 2015). However, elk population size was used as a proxy because of the high uncertainty in how the management alternatives could affect migration patterns. National Elk Refuge managers were also interested in maintaining the genetic diversity of the bison herd in alignment with the Department of Interior Bison Conservation Initiative (2020), for which bison population size in year 20 was used as a proxy.

- Fundamental Objective 2. Maintain ecosystem fluctuations and processes associated with bison and elk.—Big game populations, including bison and elk, are important to the structure and composition of plant and animal communities across the GYE. For example, elk forage heavily on riparian Salix L. (willow) during winter months and reduce the availability of willow for other species, including songbirds and Castor canadensis (Kuhl, 1820; beaver). The reduction of beavers heavily alters landscapes because beaver dams create ponds, wetlands, and stream channels that retain moisture and create habitat for a diversity of other plants and biota, both terrestrial and aquatic (FWS and NPS, 2007). Bison and elk herbivory similarly affects other woody plants and grasslands, including Populus tremuloides (quaking aspen), Populus angustifolia (narrowleaf cottonwood), and willow.
 - Performance metric 2a.—Minimize elk use of aspen stands on and around NER over the next 20 years.
 - Performance metric 2b.—Minimize elk use of cottonwood stands on and around NER over the next 20 years.
 - Performance metric 2c.—Minimize elk use of willow stands on and around NER over the next 20 years.
- **Fundamental Objective 3.** *Minimize the risk of invasive species introduction and spread associated with bison and elk management activities.*—Human activities associated with bison and elk feeding have the potential to introduce or further spread invasive plant species and alter the dynamics of sensitive ecosystems.

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Performance metric 3a.—Minimize the number of feeding days at the Refuge over the next 20 years as a proxy for invasive plant species introduction and spread risk from mechanized disturbance.

- Fundamental Objective 4. Protect and restore the chemical, physical, and biological quality of water resources.—The NER has a legal mandate and trust responsibility to protect and restore lands and waters for the conservation and enhancement of fish and wildlife, and for the benefit of current and future Americans (National Wildlife Refuge System Administration Act of 1995 [16 U.S.C. 668dd] and National Wildlife Refuge System Improvement Act of 1997 [Public Law 105-57]). Aggregations of big game animals, including bison and elk, can affect the water quality and morphology of waterways in areas of high use (FWS and NPS, 2007). Excessive nutrient inputs from the biological waste of bison and elk may elevate nutrients, fuel algal growth, and elevate the risk of cyanotoxins and harmful algal blooms. Grazing along rivers and stream beds can further affect water quality and morphology by increasing erosion and suspended sediment and altering habitat for riparian plants and aquatic species (FWS and NPS, 2007). In addition, bison and elk aggregations may lead to an elevated prevalence of wildlife diseases whose pathogens can be introduced into streams and rivers, either directly or by surface water runoff (FWS and NPS, 2007). This fundamental objective was raised as important by NER managers (in alignment with FWS and NPS, 2007); however, subject matter experts from the FWS, NPS, FS, and WGFD expected that the effects of bison and elk on the chemical, physical, and biological properties of water resources at the Refuge would be the same under all alternatives and therefore this objective was not considered further in this report.
- **Fundamental Objective 5.** Maintain and enhance multiple use opportunities and public enjoyment.—Abundant and healthy populations of bison and elk help to preserve the multiple uses of cultural, biological, and physical resources of the NER. At the NER, hunting, education, and wildlife viewing are important wildlife-oriented activities to maintain and are listed in the comprehensive conservation plan (FWS, 2015).
 - Performance metric 5a.—Maximize the number of elk harvested in the JHU over the next 20 years.
 - Performance metric 5b.—Maximize the number of visitors using the NER over the next 20 years.
- **Fundamental Objective 6.** *Minimize human-wildlife conflicts.*—During winter months, bison and elk management has been primarily focused on minimizing human-wildlife conflict and maximizing overwinter survival during harsh winter conditions. The bison and elk supplemental feeding program was established to

provide forage, given the large-scale loss of historical winter range because of human developments. If feeding were to stop, bison and elk may redistribute across the landscape in search of other sources of winter forage. The search for winter feed might increase depredation on private haystacks and suburban landscaping. Additionally, it is possible that elk might come into more frequent contact with livestock, and thus increase local rates of brucellosis transmission.

- Performance metric 6a.—Minimize the use of private lands by elk over the next 20 years.
- Performance metric 6b.—Minimize the number of bison expected to conflict with humans over the next 20 years.
- Performance metric 6c.—Minimize the risk of brucellosis transmission events from elk to livestock over the next 20 years. Only the risk that elk present to livestock was evaluated because elk were identified as the primary source of brucellosis transmission in the GYE (NAS, 2020).

NER managers were interested in measuring bison and elk caused vehicle collisions under each alternative (FWS, oral comm., 2024), but data and expert knowledge to inform behavioral responses of bison and elk to feedground operations at fine spatial and temporal scales were unavailable at the time of this study.

- **Fundamental Objective 7.** *Minimize costs of bison and elk management activities.*—Management activities at the NER are limited by annual budgets. Currently, bison and elk management activities require annual monetary costs exceeding \$500,000 (FWS, written comm., 2023). These budgetary allocations compete with other activities and programs, including habitat restoration, public education and outreach, and species conservation.
 - Performance metric 7a.—Minimize direct monetary costs to FWS for bison and elk management activities over the next 20 years.
- **Fundamental Objective 8.** Maximize local economic benefits associated with bison and elk presence at the NER and surrounding lands.—Bison, elk, and other big game animals at the NER are valued among visitors, residents, and Tribes (FWS and NPS, 2007). Bison and elk support local and regional economies by providing millions of dollars in annual revenues to businesses associated with hunting or viewing big game animals (lodging, restaurants, hunting guides, outfitters, and others; FWS and NPS, 2007).
 - Performance metric 8a.—Maximize the annual economic value of elk hunting as measured by harvest tag sales over the next 20 years.

- Performance metric 8b.—Maximize annual spending, in dollars, by elk hunters in the JHU and by nonhunting visitors to the NER over the next 20 years.
- Performance metric 8c.—Maximize annual economic value for outfitters and outfitted hunts over the next 20 years.
- **Fundamental Objective 9.** Maximize opportunities for Tribes to engage in activities related to their buffalo culture.—Bison are important to the traditional cultures, beliefs, and practices of Tribes (Department of Interior Bison Conservation Initiative, 2020). Decisions on how to manage bison and elk must consider how management practices affect opportunities for Tribes to maintain their traditional practices and interactions with bison. This objective also captures bison harvest opportunities for nonTribal resident and nonresident Wyoming hunters.
 - Performance metric 9a.—Maximize the number of harvested bison over the next 20 years.

Management Alternatives

Consistent with the development of the fundamental objectives, the NER used a series of meetings facilitated by U.S. Geological Survey to develop five management alternatives that explore a range of management actions that could be effective at achieving some (or all) of the fundamental objectives. The text in parentheses are the short names for these alternatives.

- *Continue feeding.*—The NER will continue to provision food to bison and elk during winter months. Hunting practices are assumed to remain the same, but the rate of female elk harvest is assumed to decline to zero from current levels if the elk population approaches 80 percent of the Jackson or Fall Creek Herd Unit objectives.
- *No feeding.*—The NER will immediately stop provisioning food to bison and elk during winter months. Following cessation of feeding, restoration will take place on former feedground locations to improve conditions for native plant regeneration.
- Increase harvest then stop feeding (Increase harvest or increased harvest).—The NER will continue to provision food to bison and elk during winter months for the next 5 years, during which time the NER will work with WGFD to increase elk harvest and attempt to reduce population of elk that overwinter on NER feedgrounds to 5,000. After year 5, feeding is ceased. Restoration will occur after year 5 on feedground locations to improve conditions for native plant regeneration. Note that this alternative requires adjustment to the current harvest rates of the JHU and thus is not fully under the authority of FWS.
- *Reduce feeding then stop feeding (Reduce feeding or reduced feeding).*—The NER will provision a fixed daily ration to bison and elk during winter months

for the next 5 years to reduce elk population size prior to feedground closures. After 5 years feeding will stop. Restoration will occur after year 5 on feedground locations to improve conditions for native plant regeneration. Exclosures may be put into place to protect aspen stands in the southern region of the NER, and for willow and cottonwood in the northern region of the NER.

• Stop feeding after 3 percent CWD prevalence (Disease threshold).—The NER will continue to provision food to bison and elk during winter months until CWD sampling reveals 3 percent prevalence in the Jackson elk herd, at which point all feeding activities will cease at the NER. Following cessation of feeding, restoration will take place on former feedground locations to improve conditions for native plant regeneration.

Overview of Analytical Methods Used to Evaluate Consequences of Alternatives

The alternatives were evaluated using several interagency panels of subject matter experts (including staff of FWS, NPS, FS, and WGFD) who focused on physical landscapes and habitats, wildlife effects, hunter and nonhunting visitor groups, and economic effects of bison and elk management. Two expert panels were assembled that used formal methods of elicitation to estimate important but unknown relationships that may affect the performance of management alternatives. The methods are briefly described here (table A1), but full details can be found in Cross and others (2025, this volume, chap. B), Cotterill and others (2025, this volume, chap. C), Cook and others (2025, this volume, chap. D), and McEachran and others (2025, this volume, chap. E; table E1).

To simulate elk population dynamics, CWD, and elk harvest under each alternative, Cross and others (2025, this volume, chap. B) developed a sex- and age-structured population model that included direct and indirect CWD transmission. The model followed several previous studies, including Cross and Almberg (2019), Rogers and others (2022), and Cook and others (2023). The model tracked seven different elk population segments in the Jackson region. The JHU was split into the following three subpopulations: elk that come to the NER in winter, elk that are fed in the Gros Ventre drainage at Patrol Cabin and Fish Creek feedgrounds (fig. Al), and all other elk in the herd unit (referred to as unfed elk). The Fall Creek herd unit was split into four subpopulations-fed and unfed elk inside the analysis area and fed and unfed elk outside the analysis area (fig. Al). Then, the subpopulation results across the JHU or across the analysis area were summarized. The results of Cross and others (2025, this volume, chap. B) were also used to inform population projections for Cotterill and others (2025, this volume, chap. C) and McEachran and others (2025, this volume, chap. E).

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Table A1. Bison and Elk Management Plan objectives and performance metrics related to the bison and elk feeding program. The table also includes a citation for the chapter in this report that develops the technical methods to estimate each performance metric.

[Fundamental objective four was raised as important by NER managers (in alignment with FWS and NPS, 2007); however, subject matter experts from the FWS, NPS, FS, and WGFD expected that the effects of bison and elk on the chemical, physical, and biological properties of water resources at the Refuge would be the same under all alternatives and therefore this objective was not considered further]

Performance metric number	Performance metric	Performance metric units	Reference chapter
	Objective 1—Maximize	the health and well-being of wildlif	e
la	Minimize prevalence of CWD in elk	CWD prevalence in elk in 20 years	Cross and others, 2025 (this volume, chap. B
1b	Maximize population size of elk	Number of elk in 20 years	Cross and others, 2025 (this volume, chap. B
1c	Minimize suffering of elk	Natural and CWD elk mortality in first 5 years	Cross and others, 2025 (this volume, chap. B
1d	Maximize bison population	Number of bison in 20 years	Cook and others, 2025 (this volume, chap. D
	Objective 2—Maintain ecosystem fluct	uations and processes associated v	with bison and elk
2a	Minimize use of aspen habitats	Cumulative elk-use days across 20 years	Cotterill and others, 2025 (this volume, chap. C)
2b	Minimize use of cottonwood habitats	Cumulative elk-use days across 20 years	Cotterill and others, 2025 (this volume, chap. C)
2c	Minimize use of willow habitats	Cumulative elk-use days across 20 years	Cotterill and others, 2025 (this volume, chap. C)
	Objective 3—Minimize risk of invasive species int	roduction associated with bison an	d elk management activities
3a	Minimize invasive species introduction and spread risk	Cumulative feeding days across 20 years	Developed in this chapter
	Objective 4—Protect and restore the chem	iical, physical, and biological qualit	y of water resources
	Objective 5—Maintain and enhance	e multiple use opportunities and pub	lic enjoyment
5a	Maximize elk harvested	Cumulative number of elk harvested over 20 years	Cross and others, 2025 (this volume, chap. B
5b	Maximize NER visitors	Cumulative number of NER visitors over 20 years	McEachran and others, 2025 (this volume, chap. E)
	Objective 6—Mir	nimize human-wildlife conflicts	
6a	Minimize the use of private lands by elk	Cumulative elk-days across 20 years	Cotterill and others, 2025 (this volume, chap. C)
6b	Minimize the use of private lands by bison	Cumulative number of conflict bison across 20 years	Cook and others, 2025 (this volume, chap. D
6c	Minimize the risk of brucellosis transmission	Cumulative number of elk abortions on sensitive properties	Cotterill and others, 2025 (this volume, chap. C)
	Objective 7—Minimize cost	s of bison and elk management act	ivities
7a	Minimize direct monetary costs of bison and elk management	Cumulative cost in U.S. dollars across 20 years	Developed in this chapter
Ob	jective 8—Maximize local economic benefits assoc	iated with bison and elk presence a	t the NER and surrounding lands
8a	Maximize hunting revenues	Cumulative hunting license sale revenue	McEachran and others, 2025 (this volume, chap. E)
8b	Maximize local economic revenues	Cumulative hunting- and nonhunting-associated revenues	McEachran and others, 2025 (this volume, chap. E)
8c	Maximize hunting revenues	Cumulative revenues of outfitters	McEachran and others, 2025 (this volume, chap. E)
	Objective 9—Maximize opportunities for Tril	bes to engage in activities related to	o their buffalo culture.
9a	Maximize bison available to be harvested	Cumulative bison harvested across 20 years	Cook and others, 2025 (this volume, chap. D

To predict elk space-use under each alternative, Cotterill and others (2025, this volume, chap. C) developed a resource selection model that distributed the numbers of elk projected by Cross and others (2025, this volume, chap. B) at monthly intervals. The resource selection model generally followed Cook and others (2023) but, importantly, incorporated additional environmental covariates suggested by subject matter experts. Separate models were developed for "fed" and "unfed" elk that varied according to relative winter severity. Differences among alternatives resulted from varying abundance under the elk CWD model, if and when NER ceased winter feeding operations, and additional assumptions informed by the expert elicitation process. Elk use of sensitive vegetation communities at the NER and across important elk wintering areas in the region were estimated. The number of elk predicted to use private lands and properties where cattle overwinter, as a proxy for brucellosis risk, were summarized.

To model bison population dynamics, harvest, and conflict potential, Cook and others (2025, this volume, chap. D) adapted an existing sex- and age-structured matrix model of ungulate population dynamics (Cross and Almberg, 2019; Cook and others, 2023; Cross and others, 2023). The adapted model incorporated information from the subject matter expert team who had expertise in bison ecology and wildlife management principles. The team described expected changes to bison space-use and population dynamics under the alternatives. Cook and others (2025, this volume, chap. D) then used published literature and expert judgment to estimate vital rates, harvest statistics, and other parameters necessary to predict abundance, harvest, and bison conflicts under the management alternatives.

McEachran and others (2025, this volume, chap. E) integrated bison and elk population and harvest projections, as well as elk space-use patterns, to estimate economic and visitor-related effects that included NER visitation and visit-related spending, and hunting-related spending in the Jackson region. Monthly NER visitor center counts were modeled using predictors typically associated with visits to refuges (Loomis and Caughlan, 2004) and projected changes to visitation and spending according to relationships that these response variables had with elk abundance at the Refuge. McEachran and others (2025, this volume, chap. E) also evaluated the potential for the alternatives to affect sleigh ride businesses using historical data and future elk projections. Lastly, McEachran used harvest projections from Cross and others (2025, this volume, chap. B) and estimates of hunter behavior from Koontz and Loomis (2005), which used best-practice survey methodology, to project future economic revenues from hunting and hunting-associated activities.

Finally, the methods used to calculate the direct costs of the feedground program to FWS (fundamental objective 7) and the total number of feeding days (proxy for fundamental objective 3) are briefly covered in this chapter because they are not covered in a separate technical chapter. First, to estimate costs for each alternative, the average monetary expense of the feedground operations per year for feeding season 2021–22 and 2022–23 was calculated (FWS, written comm., 2024). The annual cost was then divided by the total number of feed days for each of those years to get a cost per day of feedground operations.

Finally, those costs were projected across the 20 years by multiplying the cost per day by 20 randomly drawn feed season lengths from the historical data from 2004 to 2023 and summing the total (FWS, written comm., 2023). Net present value or future expectations about monetary inflation were not adjusted for. The sum of the 20 randomly drawn feed season lengths were used to calculate the proxy measure for invasive species (fundamental objective 3).

Important Modeling Assumptions

All models are simplifications of complex processes that are intended to capture only the most important factors. As such, the following assumptions were made in this study's models:

- The reduction in elk populations because of not feeding at the NER was enforced by the severe winters reducing unfed elk survival rates. Our model's assumptions were based on Hobbs and others (2003), but the frequency and severity of these winter effects are uncertain along with the potential redistribution of previously fed elk to other regions, or potentially other feedgrounds.
- Climate change projections were not incorporated, despite projections of 30–40 percent reductions in April snowpacks in the study area by midcentury (Hostetler and others, 2021). The reduced snowpack may result in shorter feeding seasons under the continue feeding alternative. Other climate effects on bison and elk may include elevated summer temperatures, increasing severity and frequency of drought, shifting forage phenology, and possibly reducing summer growth of winter forage (MacNulty and others, 2020).
- The potential effects that predators, such as wolves and cougars, may have on elk CWD dynamics were not included (Krumm and others, 2010; Brandell and others, 2022). If predators preferentially kill infected individuals and shorten the infectious period, they may reduce transmission and prevalence. However, substantial uncertainty remains in the selectivity of predators for diseased individuals and the relative timing of transmission and disease symptoms (Brandell and others, 2022).
- Other diseases besides CWD and brucellosis and their potential interactions were not evaluated. Other pathogens that this study lacked the data to include but may be important in the future are *Fusobacterium necrophorum* (Flügge, 1886; Moore and Holdeman, 1969) in elk and *Mycoplasma bovis* (Hale et al., 1962; Askaa and Erno, 1976) in bison. It is likely that animal aggregations that result from supplemental feeding may increase the transmission of both diseases.
- Evolutionary changes in either elk or CWD were not included. Some elk genotypes progress to disease and CWD-induced death more slowly than others (Moore

and others, 2018). Similarly, some CWD strains develop and cause mortality more quickly than others depending on host genotype and species (Pritzkow, 2022). The evolution and interaction of hosts and strains are still unclear.

- Any management changes other than those evaluated by NER or attempts to predict land-use changes that may affect bison and elk habitat selection were also not included. Many potential management actions could be taken by agencies that manage bison, elk, as well as public and private lands, which could affect the performance of the alternatives. For example, although concern exists over the potential for increases in traffic accidents, it was unclear whether and how surrounding land management agencies would respond to any changes in bison and elk distribution (for example, erect new fencing, conduct hazing operations).
- For the socioeconomic analyses, historical relationships between wildlife presence and visitation to the NER were assumed to adequately predict future dynamics, and that historical patterns in visitors' trip purpose, general spending patterns, and drivers of visitation are maintained in the future. It is possible that persistent declines in the number of elk available for viewing or hunting in the area could uncouple these relationships in ways not captured by our analyses. Changes in hunting were also assumed to be directly proportional to changes in elk numbers according to historical relationships; in other words, a decline in animals harvested predicted by the elk population model would result in a proportionate decline in hunter spending in the region.

Consequences

We present a summarized set of findings (consequences) for each of the performance metrics under the five alternatives. For complete details and description of the consequences, please refer to Cross and others (2025, this volume, chap. B), Cotterill and others (2025, this volume, chap. C), Cook and others (2025, this volume, chap. D), and McEachran and others (2025, this volume, chap. E; table E1).

The no feeding and disease threshold alternatives had the lowest CWD prevalence estimates in elk at year 20 (table A2). They were 24 (Standard deviation [SD]=8) and 23 percent (SD=7), respectively (Cross and others, 2025, this volume, chap. B). The continue feeding alternative had the highest 20-year CWD prevalence of 35 percent (SD=6), and the reduce feeding and increase harvest alternatives had intermediate values of 26 to 27 percent (SD=9 and 10). Further, the Jackson elk population is predicted to decline under all management alternatives. The continue feeding alternative resulted in the largest declines of elk on average, 54 percent, from 14,500 to 6,700 elk (SD=1,600), whereas the disease threshold alternative resulted in the smallest decline of 40 percent to 8,600 (SD=1,600; table A2). The no feeding alternative performed similarly to the disease threshold alternative and only had a few hundred less individuals in year 20. The reduce feeding and increase harvest alternatives resulted in intermediate outcomes between continue feeding and disease threshold alternatives. Finally, the increase harvest alternative had the lowest number of CWD and natural elk mortalities in the first 5 years of plan implementation (mean=7,100, SD=700), and the continue feeding had intermediate values (mean=8,000, SD=700). The disease threshold, reduce feeding, and no feeding and increase harvest alternatives were all expected to perform worse than continue feeding and increase harvest alternatives in terms of elevating natural mortality from a variety of sources, not limited to harsh winter conditions, increasing human-elk conflicts, and competition with other large ungulates (fig. A3).

For bison population performance, the continue feeding alternative would result in the largest population of bison after 20 years (median=541, SD=57), and the no feeding (median=469, SD=65), disease threshold (median=470, SD=67), increase harvest (median=472, SD=70), and reduce feeding (median=473, SD=65) alternatives had smaller population size estimates that were indistinguishable from one another (Cook and others, 2025, this volume, chap. D).

Negative effects of elk space-use declined over time as elk numbers fell. For sensitive vegetation communities at the NER, effects were reduced by all alternatives that ceased feeding compared to continuing to feed. Across the broader study area, the alternatives had a mixed performance where the continue feeding alternative performed better for willow and worse for aspen (Cotterill and others, 2025, this volume, chap. C). Considering the degree of variation across simulations, increase harvest and reduce feeding were the alternatives that most consistently performed well for these metrics. Importantly, the reduce feeding alternative called for exclosures to be installed surrounding aspen, willow, and cottonwood stands at the NER, which primarily improved the performance of this alternative with respect to aspen.

For invasive species introduction and spread risk, the number of feeding days over the next 20 years was highest under the continue feeding alternative with an average of 1,243 days (SD=100). Fed days were intermediate under the reduced feeding and increased harvest (311 days, SD=50) and disease threshold (140 days, SD=43) alternatives. The no feeding alternative was assumed to have 0 fed days at the Refuge over the next 20 years.

The effect of elk monthly counts on visitation was small and the Bayesian posterior substantially overlapped 0. The small effect size (median=0.03) led to no differences among alternatives even when elk numbers changed substantially in the underlying data. Although it is certainly possible that elk abundance changes at the NER influence winter visitation under the alternatives, the historical data do not support that conclusion (FWS, written comm., 2023).

For human-wildlife conflicts, the continue feeding alternative had the least private land use by elk, whereas disease threshold and no feeding had the highest use of private lands (in other words, performed the worst; Cotterill and others, 2025, this

Table A2. Consequence table showing the performance metrics and alternatives.

[See Table A1 for full performance metric details. Measures for 1a -c were rounded to two significant figures. Fundamental objective four was raised as important by NER managers (in alignment with FWS and NPS, 2007); however, subject matter experts from the FWS, NPS, FS, and WGFD expected that the effects of bison and elk on the chemical, physical, and biological properties of water resources at the Refuge would be the same under all alternatives and therefore this objective was not considered further. min., minimum; CWD, chronic wasting disease; max., maximum SD, standard deviation]

Deutermanne metric dimetion and unit	Continue	feeding	Disease t	hreshold	Reduced	feeding	Increase	harvest	No fee	eding
Performance metric, direction and unit	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	Objective 1-	—Maximize t	he health and	well-being o	f wildlife					
1a, CWD prevalence, min. at year 20	0.35	0.05	0.26	0.06	0.27	0.08	0.28	0.08	0.26	0.07
1b, elk population size, max. at year 20	6,700	1,600	8,600	1,600	7,700	1,800	7,600	1,900	8,400	1,700
1c, minimize elk suffering, min. mortality in first 5 years	8,000	730	8,100	830	8,100	740	7,100	650	8,100	850
1d, bison population size, max. at year 20	546	57	464	67	469	65	467	70	462	65
Objective 2—I	Maintain ecos	ystem fluctua	ations and pro	cesses asso	ciated with bi	son and elk				
2a, elk use of aspen, min. cumulative elk days ^{1,2}	616	61	585	48	539	51	518	44	532	43
2b, elk use of cottonwood, min. cumulative elk days ^{1,2}	1,615	179	1,657	187	1,591	178	1,547	154	1,616	198
2c, elk use of willow, min. cumulative elk days ^{1,2}	385	36	441	39	406	40	393	35	440	36
Objective 3—Minimize ri	isk of invasive	species intro	duction asso	ciated with b	ison and elk n	nanagement a	activities			
3, invasive species risk, min. cumulative feeding days ¹	1,243	100	140	43	311	50	311	50	0	0
Objective 5	5 Maintain a	nd enhance r	nultiple-use o	pportunities	and public en	joyment				
5a, elk harvest, max. cumulative elk harvested ¹	13,181	1,885	13,215	2,082	11,834	2,036	14,276	1,467	12,603	2,071
5b, number of visitors, max. visitors ^{1,3}	3.4	0.8	3.3	0.8	3.3	0.8	3.3	0.8	3.3	0.8
	Objec	tive 6—Minir	nize human-v	vildlife conflic	cts					
6a, elk use of private lands, min. elk days ^{1,3}	12.4	1.0	13.8	1.2	13.1	1.2	12.8	1.0	13.8	1.2
6b, human-bison conflict, min. number of conflict bison	143	16	905	482	756	442	756	473	1,077	474
6c, Brucellosis risk, min. abortions on private lands ¹	161	16	181	21	173	19	170	17	180	21
Ot	jective 7—Mi	nimize costs	of bison and	elk managem	ent activities					
7, cost of management, min. dollars ^{1,3}	19.3	1.6	2.2	0.7	4.8	0.8	4.8	0.8	0	0
Objective 8—Maximize local	economic ben	efits associa	ted with bisor	n and elk pres	sence on the l	NER and surro	ounding lands			
8a, elk harvest tags, max. dollars ^{1,3}	5.5	0.6	5.2	0.7	4.8	0.8	6.6	0.6	5.0	0.8
8b, regional economic inputs for hunting activities, max. dollars $^{\rm l,3}$	88.6	12.2	82.0	14.3	73.0	14.1	101.3	9.6	76.1	14.8
8b, regional economic inputs for nonhunting, max. dollars ^{1,3}	3.0	0.7	2.9	0.7	2.9	0.7	2.9	0.7	2.9	0.7
8c, revenue of outfitters, max. dollars ^{1,3}	12.6	1.7	11.7	2.0	10.4	2.0	14.5	1.4	10.9	2.1
Objective 9—Max	imize opportu	nities for Trib	es to engage	in activities r	elated to their	buffalo cultu	re			
9, bison harvest, max. bison harvested	1,879	197	1,387	248	1,508	234	1,496	245	1,292	247

¹Cumulative across the 20-year simulation.

²Rounded, in thousands.

³Rounded, in millions.

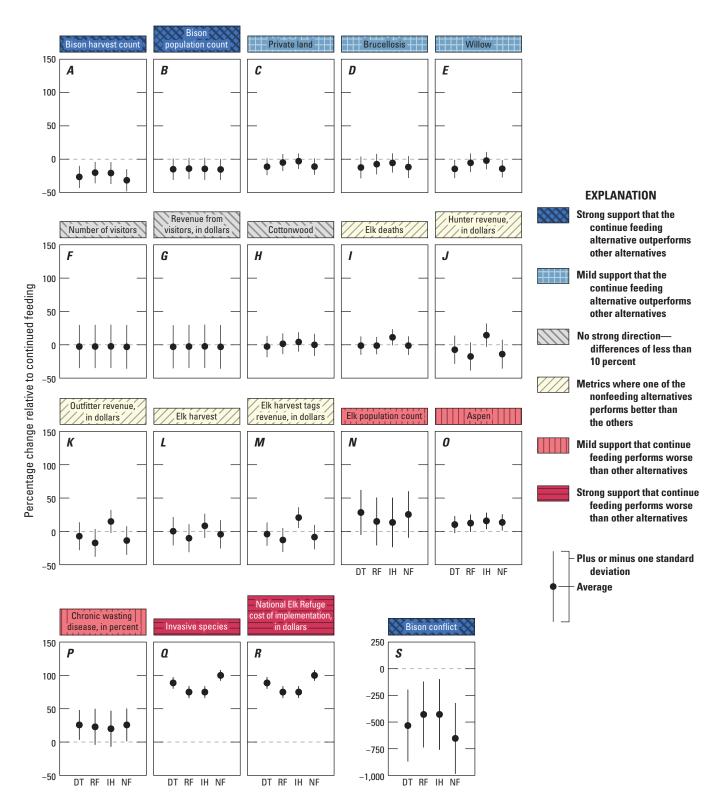


Figure A3. Graphs showing the percentage change in different performance metrics across management alternatives relative to the continue feeding alternative. Performance metrics where minimizing the value is preferred were multiplied by –1 so that negative values indicate the alternative does worse than continue feeding, but positive values indicate that the alternative does better than continue feeding across all metrics. Note that bison conflict is on a different scale for the y-axis. DT=disease threshold; RF=reduce feeding; IH=increase harvest; NF=no feeding.

volume, chap. C). However, the differences between continue feeding, reduce feeding, and increase harvest were small considering the overall magnitude of the estimates, declines in elk numbers, and the associated uncertainty in outcomes. In contrast, substantial differences, in terms of the potential for human-bison conflict, were found between the continue feeding alternative and the other four alternatives that stopped feeding. Over the next 20 years under the continue feeding alternative, 143 bison were estimated to be involved in conflict, whereas between 756 and 1,077 bison were in conflict under reduce feeding, disease threshold, increase harvest, and no feeding alternatives (Cook and others, 2025, this volume, chap. D). Finally, the brucellosis risk to livestock was assessed to be lowest under the continue feeding alternative (Cotterill and others, 2025, this volume, chap. C); however, the median estimates across all five alternatives were similar considering the uncertainty across simulations (table A2).

For the monetary costs of bison and elk management activities, the program was calculated to cost the FWS between \$15,210 and \$16,450 per day of feeding activities for the direct costs of feed, labor, fuel, and maintenance for machinery. In terms of feed season length, days of feeding varied between 0 days in 2017–18 to 101 days in 2010–11. The average length was 62 days (SD=24). In terms of total costs over 20 years, the continue feeding alternative was the most expensive, with an average cost of \$19.3 million (SD=1.6 million), and the lowest cost was no feeding, which was assumed to have no direct costs (in other words, \$0). The other alternatives varied according to the number of years until feeding stopped with reduce feeding and increase harvest alternatives costing \$4.8 million (SD=\$0.78 million) over the next 20 years and disease threshold having a cumulative 20-year cost of \$2.2 million (SD=\$0.67 million). The cost of exclosures that are included in the reduce feeding alternative was not considered.

Elk harvest tag sales, spending by hunters, and outfitter revenues were found to be highest under the increase harvest alternative. Although the increase harvest alternative did have initial hunting rates and hunting-related revenues that were higher than the other alternatives, revenues dropped after a few years. When considering changes over time, the increased harvest alternative had higher predicted tag revenues (mean=\$6.60 million, SD=\$574,000) and hunter-related spending (mean=\$101.3 million, SD=\$9.6 million), but like other performance metrics, the estimated ranges of the alternatives overlapped.

Projecting effects on outfitters over the next 20 years, the increase hunting alternative had the highest predicted number of clients with an average estimate of 3,758 clients (SD=416 clients) served over the next 20 years and a cumulative outfitter revenue of \$14.5 million (SD=\$1.4 million). The next highest performing alternative was the continue feeding alternative with an average of 3,480 clients (SD=565 clients) and \$12.6 million (SD=\$1.7 million) in revenue, followed by the disease threshold alternative, with an average of 3,319 clients (SD=627 clients) and \$11.7 million (SD=\$2.0 million) in revenue. The lowest cumulative number clients and revenues were predicted under the reduce feeding alternative, with 2,879 clients (SD=575 clients) and \$10.4 million (SD=\$2.0 million) in revenue over the next 20 years.

The last fundamental objective associated with bison harvest and Tribal ceremonial take had the best performance under the continue feeding alternative (median=1,879 bison harvested; SD=197) and the worst performance under the no feeding alternative (mean=1,292, SD=247). The reduced feeding (mean=1,508, SD=234), increase harvest (mean=1,496, SD=245), and disease threshold (mean=1,387, SD=248) all performed intermediate between continue feeding and no feeding.

In terms of tradeoffs, the largest differences among alternatives were measured in bison and elk population sizes at year 20, the cumulative invasive species risk as measured by feeding days, cumulative number of bison that conflict with humans, management costs, and cumulative harvest of bison. The continue feeding alternative was the worst alternative for elk population size, CWD prevalence, invasive species, and NER costs but was the best alternative for bison abundance, bison harvest, bison conflict, private land issues, and disease risks to cattle. The management alternatives did not have notably different consequences for visitor numbers, visitor spending, or effects on cottonwoods (fig. A3). The increased harvest alternative tended to perform best on elk harvest metrics as well as minimizing natural and CWD mortality of elk in the first 5 years.

Conclusions and Science Directions

Our results suggest that Jackson elk abundance will decline under all evaluated alternatives but that the mechanism, timing, and degree of declines depend on the specific management actions being taken. Under continue feeding, it is expected that chronic wasting disease (CWD) prevalence will increase over time and reduce abundance from the current population size of around 11,000 down to a median of 4,900 elk in year 20. In contrast, no feeding alternatives may lead to more rapid declines in the near term from natural, harvest, and conflict-associated causes, but after 20 years are projected to have a median size of 6,700 elk. The near-term consequences on elk populations from no longer feeding and the longer term effects of increases in disease mortality crossover between years 7 and 13. The continue feeding alternative predicts more elk initially, but the no feeding alternative predicts the highest elk abundance in year 20.

The disease dynamics that drive these patterns for fed and unfed elk were provided by an expert panel that estimated that direct transmission of CWD would be 1.9 times higher and indirect transmission would be 4 times higher in feedground settings (Cook and others, 2023). These transmission dynamics among fed and unfed elk resulted in the no feeding alternative performing better (in other words, have lower prevalence) than continue feeding in 70 percent of model simulations (Cross and others, 2025, this volume, chap. B). Further, the expert panel was convened to consider CWD dynamics on State feedgrounds that host fewer elk than the National Elk Refuge (NER). The NER elk may have higher (or lower) transmission rates depending on local aggregations of elk, social dynamics, and feed season lengths.

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The effect of severe winters on elk mortality, however, remains a source of substantial uncertainty as it is unclear how snowfall and snowpack might affect elk populations under no feeding alternatives. For the purposes of this study, the results of Hobbs and others (2003) were used to enforce a severe winter penalty that led to higher mortality rates with an annual probability of 0.25 once NER stopped feeding operations. This increase in mortality resulted in an average of 38 percent declines projected for Jackson herd elk, compared to estimates of 23 percent for elk in other western Wyoming herd units (Cook and others, 2023). Although the true magnitude of declines remains uncertain, it seems reasonable to expect the Jackson Elk Herd Unit to perform worse than other units that have more critical winter range available relative to the number of elk overwintering in those units.

The population effects and the spatial structuring of different elk populations across the study area under the different alternatives led to some consistent patterns in elk use of private lands and sensitive habitats. Continue feeding is predicted to result in having fewer elk days on private property and lower brucellosis risk (measured by number of abortions on private property where cattle overwinter) across the 20 years of plan implementation. However, continue feeding also led to a higher degree of use of sensitive areas, particularly at the NER. Further, across all alternatives, the negative effects associated with Jackson elk are predicted to decrease because of population declines projected in the elk CWD model. Depending on the alternative, these declines resulted either from CWD, elevated natural mortality associated with severe winters, or in conjunction with specific management efforts to reduce elk abundance.

Translating the proxy measure of brucellosis risk to an actual change in the magnitude of risk to cattle producers is difficult because there has not been a documented instance of elk infecting cattle in the Jackson region. Doing so would require data to inform the connection between the number of abortions and a successful elk-to-cattle transmission event in the Jackson Elk Herd Unit. As a result, it is unclear how meaningful 19 or 20 additional abortions projected under the no feeding or disease threshold alternatives are compared to continuing to feed.

In terms of bison, the continue feeding alternative is predicted to be best, on average, for the three metrics associated with population size, harvest, and conflict potential. However, it is important to acknowledge the limitations of the available data in this study. First, data from the Yellowstone region was relied on to inform bison vital rates. These vital rates produced model behavior (in other words, harvest, population performance) that matched historical data, but may not necessarily be reflective of future conditions. Second, there was a high degree of uncertainty expressed by the expert panels in how human-bison conflicts might occur, and change, over time. As a result, two hypotheses about trends in those conflicts were incorporated: one where conflicts were stable over time, and another where human-bison conflicts changed according to learned behavior or active management activities. It is unclear which hypothesis is a better representation of future dynamics. Finally, it was assumed that there were no high mortality events from Mycoplasma bovis over the 20 years in either fed or unfed bison populations

because it is uncommon in free-ranging wildlife ungulates (Malmberg and others 2020), even though the bacterial disease has led to 20–40 percent mortality in captive bison herds elsewhere (Janardhan and others 2010).

No discernable pattern for sleigh ride participation or NER visitation rates or spending was found under the different alternatives; however, elk could change their distribution under no feeding alternatives in unpredictable ways such that they become less visible to sleigh riders without supplemental feeding. Further, predicting future visitation to NER is difficult based on the projected changes in bison and elk numbers and the small effect that these species have relative to broader system dynamics, like U.S. human population size and economic conditions that have a greater influence on travel. As expected, NER feeding costs were minimized by alternatives that limited feeding. The increased harvest alternative tended to perform best on elk harvest metrics as well as minimizing the number of natural or CWD-related elk deaths in the first 5 years. As of 2024, however, it is not clear whether increasing harvest tags alone would successfully reduce the number of elk using the NER in winter to 5,000 individuals in 5 years.

Additional work may include NER managers, cooperating agencies, and other stakeholders navigating the tradeoffs embedded in this decision on whether and how to feed bison and elk under threat of CWD and given the range of other effects that are presented in this work. Deliberative tools from decision analysis (for example, swing weighting) could be used to estimate the relative value of the objectives against one another and develop an overall score for each alternative given those weights. This weighting could also help to fully incorporate the many sources of uncertainty embedded in these analyses and explore the role that those uncertainties have on distinguishing the best performing alternative for the next "Bison and Elk Management Plan."

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Predictions of Elk and Chronic Wasting Disease Dynamics in the National Elk Refuge in Jackson, Wyoming, and Surrounding Areas

By Paul C. Cross, Jonathan D. Cook, and Eric K. Cole

Chapter B of Decision Analysis in Support of the National Elk Refuge Bison and Elk Management Plan

Edited by Jonathan D. Cook and Paul C. Cross

Ecosystems Mission Area—Biological Threats & Invasive Species Program and the Environmental Health Program

Prepared in cooperation with the U.S. Department of Agriculture, National Park Service, U.S. Fish and Wildlife Service, and Wyoming Game and Fish Department

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Conversion Factors

International System of Units to U.S. customary units

Multiply	Ву	To obtain
	Length	
kilometer (km)	0.6214	mile (mi)
	Area	
square kilometer (km ²)	247.1	acre
square kilometer (km ²)	0.3861	square mile (mi ²)

Abbreviations

CWD	chronic wasting disease
FCHU	Fall Creek Elk Herd Unit
JHU	Jackson Elk Herd Unit
NER	National Elk Refuge
WGFD	Wyoming Game and Fish Department

Predictions of Elk and Chronic Wasting Disease Dynamics in the National Elk Refuge in Jackson, Wyoming, and Surrounding Areas

By Paul C. Cross,¹ Jonathan D. Cook,¹ and Eric K. Cole²

Abstract

The U.S. Fish and Wildlife Service National Elk Refuge (NER) in Jackson, Wyoming, supplementally feeds Cervus elaphus canadensis (Erxleben, 1777; elk) and Bison bison (Linnaeus, 1758; American bison) during winter months, but the costs and benefits of this management strategy are being reevaluated considering the potential effects of chronic wasting disease (CWD) on elk. U.S. Geological Survey scientists worked with the U.S. Fish and Wildlife Service on a structured decision-making process that considered five alternative feeding strategies and their effects on bison, elk, and humans. This chapter focuses on elk population dynamics and CWD using computer models. Our modeling results highlight a shortversus long-term tradeoff between the continue feeding and no feeding alternatives. Management alternatives associated with a cessation of supplemental feeding were assumed to make elk more susceptible to severe winters, resulting in initially lower population sizes and less CWD transmission. The increased CWD prevalence and transmission associated with the continue feeding alternative resulted in lower elk population sizes by year 20 (mean=6,700, standard deviation=1,600 in the analysis area) in 70 percent of simulations compared to no feeding (mean=8,400, standard deviation=1,500). No feeding alternatives resulted in higher elk populations than the continue feeding alternative between years 7 and 13 when CWD prevalence exceeded 20 percent in the Jackson elk herd. The increased harvest alternative minimized CWD and natural mortality in 83 out of 100 simulations compared to the continue feeding alternative.

Introduction

The National Elk Refuge (NER) in Jackson, Wyoming (fig. B1), is managed by the U.S. Fish and Wildlife Service. The NER has been supplementally feeding *Cervus elaphus canadensis* (Erxleben, 1777; elk) during the winter for over a century (16 U.S.C. §673, Wyoming Elk Reserve). Supplemental feeding was intended to mitigate elk mortality during severe winters and reduce private-property damage in and around Jackson, Wyoming, but aggregates thousands of elk in the NER, which may increase the transmission of pathogens such as chronic wasting disease (CWD). Chronic wasting disease was detected in elk at Grand Teton National Park for the first time in 2020 and has the potential to alter the costs and benefits of the NER supplemental feeding program.

Chronic wasting disease is spread through direct contact with an infectious individual and by way of environmental contamination with prions, which can persist for years in the environment (Miller and others, 2004). Chronic wasting disease prevalence has been observed as much as 29 percent in free-ranging elk of Wind Cave National Park (Sargeant and others, 2021). Galloway and others (2021) predicted that a CWD prevalence of more than 7 percent would lead to elk population declines in the Jackson elk herd even without a harvest. The predicted sensitivity of the Jackson elk herd to CWD is due, in part, to the low recruitment rates of elk calves that are observed in the region (Foley and others, 2015).

Previous studies of free-ranging Odocoileus virginianus (Zimmerman, 1780; white-tailed deer) suggest that CWD transmission is not strongly correlated with regional measures of host density (Storm and others, 2013) likely because broad-scale changes in population size may not correlate with changes in local measures of density or group size (Cross and others, 2009). The discovery of CWD on captive Cervidae (Goldfuss, 1820; cervid) farms typically results in immediate quarantine of the premises and herd depopulation (Haley and others, 2021). The few available studies of affected cervid farms show higher CWD prevalence in captive populations compared to free-ranging populations but typically lack data on how long the disease was present prior to sampling. Keane and others (2008) found a CWD prevalence of 79 percent in a captive white-tailed deer population. Peters and others (2000) found that 67 percent of the 17 elk (average age 2.6 years) tested in a captive facility were infected. Haley and others (2020) found a CWD prevalence of over 37 percent in a captive elk herd (approximately 450 elk in a 14 square kilometer [km²] facility [32 elk per km²]) and over 60 percent in some genotypes. Williams and others (2014) noted that 37 out of 39 elk died from CWD in their study of captive elk at the Tom Thorne/Beth Williams Wildlife Habitat Management Area in Wheatland, Wyoming. The median lifetime of the captive elk in the Williams and others (2014) study was 4.1 years for methionine-methionine at codon 132 in the prion protein gene

¹U.S. Geological Survey.

²U.S. Fish and Wildlife Service.

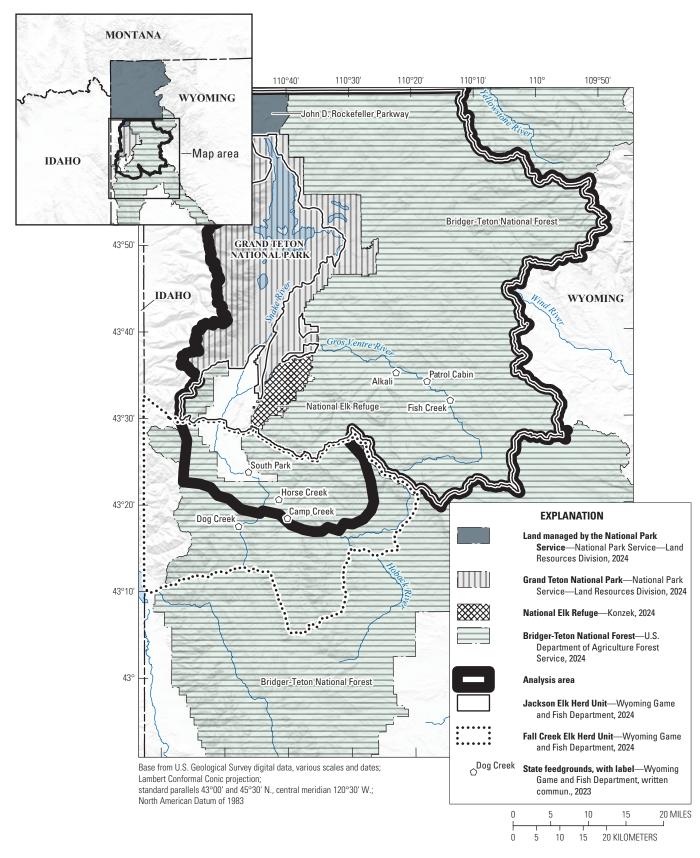


Figure B1. Map showing the location of the National Elk Refuge, Grand Teton National Park, Jackson Elk Herd Unit, Fall Creek Elk Herd Unit, and feedgrounds within the study analysis area.

and 7.1 years for methionine-leucine or leucine-leucine genotypes. These observations from captive populations suggest that local host densities may enhance CWD transmission in a high-density feedground. Previous studies of elk suggest that contact rates among elk on feedgrounds can be many times higher than among individuals overwintering on native winter ranges (Creech and others, 2012; Cross and others, 2013; Janousek and others, 2021). These higher rates are likely because of short-term densities on feedgrounds, such as the NER, reaching as high as 1,089 elk per km² (Graves and others, 2022). The repeated visitation of the same areas and the potential for the long-term persistence of CWD prions in the environment may also increase transmission. Therefore, CWD could reach higher prevalence and have a larger effect on the Jackson elk herd than has been observed in other free-ranging elk herds if the herd continues to be supplementally fed.

Chapter A of this volume provides context on the NER, CWD, and the structured decision-making process used to develop the management alternatives, objectives, and metrics for the supplemental winter feeding of Bison bison (Linnaeus, 1758; American bison) and elk (this volume, Cook and others, 2025). The structured decision-making process identified five management alternatives: (1) continue feeding, (2) no feeding, (3) increase elk harvest for five years and then stop winter feeding (increase elk harvest), (4) reduce the amount of feed for five years and then stop winter feeding (reduce feeding), and (5) phase out feeding after 3 percent CWD prevalence. In this chapter, we develop a computer-simulation model to assess the potential effects of these alternatives on future CWD dynamics and the Jackson elk herd over the next 20 years. We first describe the overall model structure (in the "General Model Structure" subsection of the "Methods" section) and how the model structure represents the five management alternatives (refer to the "Modeling Management Alternatives" subsection of the "Methods" section). The model's temporal predictions of elk numbers and CWD prevalence were used to inform the elk space-use metrics in chapter C (this volume, Cotterill and others, 2025) and some of the socioeconomic metrics in chapter E (this volume, McEachran and others, 2025). The CWD model was developed in consultation with the NER Environmental Impact Statement wildlife subject matter expert team.

Methods

The CWD model was developed to simulate elk and CWD dynamics over time based on several previously published papers (Cross and Almberg, 2019; Brandell and others, 2022; Rogers and others, 2022; and Cook and others, 2023). The model included an environmental transmission component, as in Cook and others (2023), and multiple interacting populations within an elk herd unit. The model is written in R (version 4.4.0; R Core Team, 2024) and is available online (Cross and Cook, 2024).

General Model Structure

The CWD model tracks elk according to their age, winter location, sex, and disease status—susceptible or infectious. The CWD model is stochastic with a discrete monthly timestep, and all simulations begin in May. The model assumes that all births occur in June and hunting occurs only in November. The CWD model has the following order of operations: births and aging individuals, direct CWD transmission, indirect CWD transmission, natural mortality, severe winter mortality, hunting mortality, and disease-induced mortality. Disease transmission and deaths occur in every monthly iteration of the model, but hunting, births, and increasing the age of individuals occur once per year.

Within the model, the category of infectious elk is divided into 10 subcategories of disease progression. We assumed elk would die of CWD when individuals exit the 10th infectious subcategory but not beforehand. Infectious elk that are hunted or died from natural causes are not considered CWD deaths. By assuming individuals progress through multiple stages of infection before dying of disease, substructuring infected categories allows the time for disease-induced death to have an initial delay and then peak later (Wearing and others, 2005). Multiple infectious categories result in a gamma distribution for the time to disease-induced death. As in Cook and others (2023), the probability of progressing to later stages of infection was assumed to be 28 percent such that the time from infection to CWD-induced death was, on average, 2.8 years (standard deviation [SD]=5.29). Twelve age classes were grouped into 5 categories (i) that had similar vital rates: calves (0-1 year, i=1), male yearlings (1-2 years, i=1)i=2), female yearlings (1–2 years, i=3), male adults (>2 years, i=4), and female adults (>2 years, i=5). Elk transitioned between stages according to sex- and age-specific vital rates as defined in Cook and others (2023) unless otherwise noted (app. B1, table B1.1).

The CWD model was structured into k winter subpopulations within two different herd units-the Jackson Elk Herd Unit (JHU) and Fall Creek Elk Herd Unit (FCHU; this volume, chap. A, fig. A1 of Cook and others, 2025). State Highway 22 in Wyoming forms the boundary of these herd units and has historically been a strong barrier to elk movement. The wildlife subject matter expert team believed that if feeding were stopped or reduced in the NER, more elk would relocate from the JHU to the FCHU. We used an expert elicitation process to estimate those potential movement rates (app. B2). The JHU was divided into three groups: elk that winter in the NER (k=1); elk that are fed in the Gros Ventre River drainage (Patrol Cabin, Fish Creek, and the now-closed Alkali feedgrounds [k=2]; and elk that are unfed in the JHU (k=3). The FCHU was divided into four groups: fed and unfed elk that are inside and outside of the analysis area. Within the analysis area were elk fed at South Park, Horse Creek, or Camp Creek feedgrounds [k=4] and an unfed FCHU elk subpopulation (k=5). Outside the analysis area were elk fed at Dog Creek (k=6)and an unfed elk subpopulation (k=7). We assumed the proportion of unfed elk in the FCHU that were in the analysis area was the same as the proportion of the FCHU area that was within the analysis area (36 percent). We summed subpopulations $k \le 5$ to provide results for the analysis area and $k \le 3$ for just the JHU.

In developing our model, we assumed elk could be infected through direct contact with infectious individuals and indirectly through contact with a prion-contaminated environment. These transmission parameters were estimated by an expert panel and reported in Cook and others (2023). As in Cook and others (2023), there were two scenarios for the transmission of CWD among

B4 Predictions of Elk and Chronic Wasting Disease Dynamics

fed and unfed elk subpopulations, and both scenarios were included in the model with equal likelihood by combining an equal number of simulations from each scenario. The first scenario was that elk could transmit CWD between fed and unfed subpopulations within a herd unit during the summer months. In this scenario, fed elk had a higher direct CWD transmission rate during winter months than unfed elk, and the direct CWD transmission rate during the summer months was calculated as the average of fed and unfed elk weighted by the population sizes at the start of the simulation. The second scenario assumed that CWD transmission occurred only within a subpopulation and not among subpopulations. Thus, fed elk would have higher rates of transmission year-round compared to unfed elk. Indirect transmission was assumed to increase linearly during the 20 years of the simulation for fed and unfed elk, where the maximum indirect transmission rate was provided by expert elicitation (Cook and others, 2023). For further modeling details on disease transmission, refer to Cook and others (2023).

The model includes two density-dependent mechanisms to avoid exponential growth or decline of the elk populations. First, calf survival (ϕ_1) depends on the previous year's annual population size in each herd unit, and declines from a maximum of 0.6 to a minimum of 0.05 when the population size is at the herd unit carrying capacity (K_{HU} app. B1), given by the following equation:

$$\phi_1 = max \ (\phi_{max}(1 - c(N_{j-1}/K)^{\delta}, \phi_{min})) \tag{B1}$$

where

- *c* is the proportion reduction when population was at carrying capacity;
- N_{j-1} is the January population size for the previous year in the herd unit;
 - *K* is a parameter related to the carrying capacity of fed and native winter range elk in each herd unit;
 - δ controls the shape of density dependence;
- ϕ_{max} is the maximum calf survival rate; and

 ϕ_{min} is the minimum calf survival rate.

Parameters *c* and δ were drawn from uniform distributions ([0.5, 0.8] and [2, 4], respectively) each year. Carrying capacity, *K*, was set to 1.3 times the population objective of the herd unit so that the population equilibrated at the population objective in the absence of CWD. These parameters resulted in a ratio of calves per adult female at the end of the winter (calf:cow) that ranged from a maximum of 0.6 when populations were less than 5,000 to between 0.3 and 0.5 when the population was at the population objective. The emergent calf:cow ratio in the model was in rough agreement with the maximum calf:cow ratio observed in other Wyoming elk herds. The Northern Bighorn Herd Unit in Wyoming is an example of an increasing elk herd and had a calf:cow

ratio of 0.58 in 2015. The elk population of the Clark's Fork Herd Unit has been stable to slightly decreasing from 2010 to 2020 and had a minimum observed calf:cow ratio of 0.11 (Wyoming Game and Fish Department, written commun., 2010–19; Wyoming Game and Fish Department, 2020). For a visual representation of calf survival expressed as a function of herd unit population size, refer to figure B1.1 in appendix B1.

While tuning the CWD model to the JHU information, the harvest rates were set to match the percentage of different age and sex categories hunted in the JHU from 2016 through 2021, which were approximately 7 percent for female elk and 28 percent for adult male elk (Wyoming Game and Fish Department, written commun., 2016–19; Wyoming Game and Fish Department, 2020, 2021b), and the parameters controlling calf survival (eq. B1) were modified to result in the low calf:cow ratio observed in the Jackson herd (mean=22:100; Wyoming Game and Fish Department, written commun., 2000-19; Wyoming Game and Fish Department, 2021a). This parameter combination, along with the other vital rates set to the values in table B1.1 (app. B1), resulted in a declining population size, which suggests that there may be biases in observed data or some of the vital rates in table B1.1 (app. B1) were not representative of elk in the JHU. The parameter sets used in the CWD model prioritized matching the model results to the elk harvest rates instead of the calf:cow ratios because the elk harvest rates are used by McEachran and others (2025, this volume, chap. E) for some of the economic assessments of the feeding decision. Therefore, the yearling male and adult female harvest rates (app. B1) were matched to observed values, but the density-dependent calf survival rate was allowed to result in a calf:cow ratio that is higher than the ratio that is commonly observed. Yearling females were assumed to be harvested at the same rate as adult female elk. The bull harvest rate was reduced from the observed 28 percent to 8 percent because bulls are commonly in smaller groups that tend to be undercounted.

We assumed that the percentage of female elk harvested annually would decline linearly from a maximum when the elk population was equal to or more than the population objective to zero when the population was at 80 percent of the population objective. The changes to the female harvest rate occurred annually but were based on the previous 3-year average population size in February. This approximates the Wyoming Game and Fish Department harvest setting process (Wyoming Game and Fish Department, oral commun., 2023). Bull harvest rates were assumed to be constant for the duration of each simulation.

One hundred simulations for each management alternative started with elk population sizes drawn from a normal distribution with a coefficient of variation of 0.05, which matches the 2016–21 variation in the JHU. Simulations began with a stable age and sex structure, which we calculated from a Leslie matrix with annual rates using the popbio package (Stubben and Milligan, 2007) in R version 4.4.0 (R Core Team, 2024). We then simulated 5 years of burn-in to reach a stable age and sex structure using the monthly survival rates and seasonal pulses of reproduction and hunting before introducing CWD and recording the results for the subsequent 20 years. The average starting population sizes of fed elk equaled the 2016, 2018, 2019, 2020, and 2021 observed

 $[\]phi_1$ is the annual calf survival rate in the herd unit;

averages. The 2017–18 winter was excluded from these averages because it was a nonfeeding year for the NER and not representative of typical feeding year counts. The starting population size of the unfed elk subpopulations ($k \in \{3, 5, 7\}$) was multiplied by 1.48 to account for the likely undercounting of native winter-range elk (Lubow and Smith, 2004).

All simulations began with a starting CWD prevalence of 1 percent. Setting the prevalence of the modeling analyses modestly higher than current levels was a deliberate choice intended to account for the delay between the completion of analyses, finalization of the Environmental Impact Statement, and any future implementation of management alternatives. Preliminary analyses suggested that model results were not sensitive to starting prevalence because of our assumptions about how indirect transmission of CWD from the environment was modeled as a constantly increasing risk of infection starting at year 1 (Cook and others, 2023).

The effects of severe winters were included in the model to account for the potential demographic effects of not feeding on elk survival. Hobbs and others (2003) estimated elk mortality during different winter conditions based on forage availability in the JHU and across a variety of population sizes. We extrapolated those results across a broader distribution of population sizes (app. B1, fig. B1.2). To use these relationships in the FCHU, the population sizes in each herd unit were converted to the winter range elk density based on the total area of available native winter range (calculated in Cook and others, 2023). In the model, severe winters were included as a random draw with probability ω , which resulted in additional mortality beyond all other causes of death in unfed elk subpopulations ($k \in \{3, 5, 7\}$).

The probability ω of severe winters in the model determined the demographic penalty associated with not feeding in the absence of CWD. Severe winters also affect the spatial distribution of elk (this volume, chap. C, Cotterill and others, 2025). Winter calf mortality in the NER exceeded 5 percent in 4 of the last 15 years (27 percent) when direct measures of snow in the NER were available (fig. B2). In addition, a visual inspection suggested that 5 of 19 years were severe in terms of constraining the movements of elk in the NER (this volume, chap. C, Cotterill and others, 2025). For the model, we assumed that severe winters occurred with an annual probability of 25 percent.

Modeling Management Alternatives

The NER managers defined the following five management alternatives for the elk and bison feeding program (this volume, chap. A, Cook and others, 2025): continue feeding; no feeding; increase elk harvest, then stop feeding (increase harvest alternative); reduce feeding, then stop feeding (reduce feeding alternative); and phase out feeding after a 3 percent CWD prevalence (disease threshold alternative). This section describes how the CWD model incorporated these management alternatives; for a more thorough description of the alternatives, refer to chapter A of this volume (Cook and others, 2025).

Continue Feeding Alternative

In this management alternative, supplemental feeding continues without any changes for 20 years. It was assumed that elk remained in the fed or unfed subpopulations they originated from and did not move across herd unit boundaries. Unfed elk populations were subjected to the demographic effects of severe winters with a probability of 0.25 per year, but supplementally fed subpopulations were unaffected by severe winters.

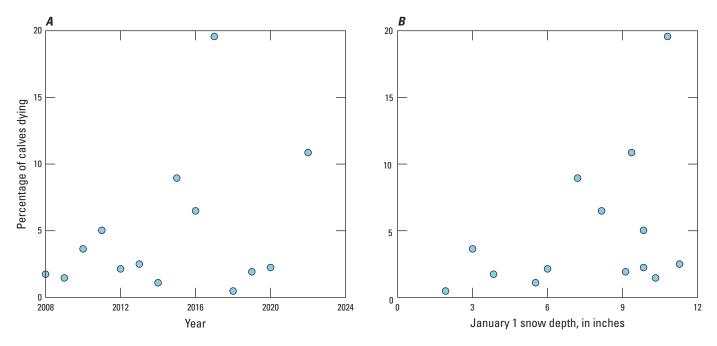


Figure B2. Scatterplots of the percentage of elk calves dying on the National Elk Refuge, Jackson, Wyoming. *A*, during the winter from 2008 to 2022 or, *B*, as a function of snow depth on January 1.

No Feeding Alternative

In the no feeding alternative, the wildlife subject matter expert team expected that elk would redistribute to other areas if the NER stopped feeding elk. To quantify this expectation, we invited a panel of eight experts with specific and localized knowledge about elk behavior and movement dynamics in this ecosystem. We developed a series of questions (app. B2) to inform necessary parameters of the model and used the panel's expert judgment to estimate the percentage of elk that may move from the NER to Gros Ventre feedgrounds (k=2); other areas of the JHU (k=3); and South Park, Horse, or Camp Creek feedgrounds in the FCHU (k=4). We also asked the panel for their estimates of the proportion of elk that would continue to come to the NER even when supplemental feed was not provisioned (app. B2).

A modified Delphi method (Hanea and others, 2017) and four-point Speirs-Bridge elicitation protocol were used to develop estimates (Speirs-Bridge and others, 2010). The four-point estimates were an expert's low, high, and best estimates of a parameter and their confidence that the actual value would fall within the low and high values (figs. B2.1 and B2.2). Each expert's quantiles (based on the expert's four-point estimates) were used to fit a probability distribution by finding the parameters for a beta distribution, which minimized the sum of square differences between the elicited and fitted quantiles. Individual expert distributions were then aggregated by fitting a single Dirichlet distribution, which ensured that the sum of each estimated beta distribution included the upper limit of 1 for the proportional data we elicited (Conroy and Peterson, 2013).

In the no feeding alternative, NER elk were assumed to move to other subpopulations ($k \in \{2, 3, 4\}$) according to the expert panel estimates prior to the start of the simulation. Those elk that we assumed would return to the NER, even though there was no feeding, were treated as unfed elk with lower CWD transmission rates but were exposed to the effects of severe winters.

Increase Harvest Alternative

In the increase harvest alternative, the NER managers' objective was to lower the number of elk using the NER (k=1) to 5,000 within 5 years through increased harvest. The NER would then discontinue the feeding program after those 5 years. To accomplish this in the model, the harvest rate of all age and sex classes was increased by 2.5 times for the NER group compared to the rates in table B1.1 (app. B1). It was assumed that after year 5, the NER would no longer feed elk and elk would redistribute to other subpopulations ($k \in \{2, 3, 4\}$) according to the expert panel estimates (app. B2). Unfed elk at the NER were subjected to the effects of severe winters if they did not move to an alternate feedground where they were fed. After year 5, harvest rates were assumed to return to previous levels, which depended on the herd unit population size relative to the population objective. After year 5, elk that returned to the NER were assumed to have CWD transmission rates of unfed elk.

Reduce Feeding Alternative

In the reduce feeding alternative, the amount of feed provided to elk in the NER was reduced during the first 5 years and discontinued after year 5. We assumed that the reduced feed would be sufficient to mitigate the effects of severe winters on adult elk but that calves would access less food and would, therefore, be exposed to the effects of severe winters. After year 5 of the simulation, the NER halted all feeding. Elk were then redistributed to the other subpopulations ($k \in \{2, 3, 4\}$) as defined by the expert elicitation process (app. B2). After year 5, the elk returning to the NER were assumed to have the CWD transmission rates of unfed elk (table B1.1 of app. B1).

Disease Threshold Alternative

Finally, we modeled an alternative in which feeding in the NER stopped after CWD prevalence reached a disease threshold of 3 percent in the Jackson herd elk. Chronic wasting disease prevalence was estimated based on 400 randomly sampled hunted elk across the JHU, which was approximately the number tested per year from 2020 to 2022 (Wyoming Game and Fish Department, 2020, 2021b, 2022b). If CWD prevalence exceeded 0.03 in that sample, then feeding was halted in the subsequent winter and elk were redistributed to the other subpopulations ($k \in \{2, 3, 4\}$) as defined by the expert elicitation process (app. B2).

Results

The expert panel estimated that 50 percent (SD=8 percent) of the elk fed at the NER would continue to spend their winters in the NER even when no supplemental feed is provided (k=1; app. B2; fig. B3). Eighteen percent (SD=7 percent) of the elk fed at the NER were predicted to move to the Gros Ventre feedgrounds and be fed there (Fish Creek or Patrol Cabin, k=2), and 19 percent (SD=6 percent) would spend winter in other areas of the JHU (k=3; fig. B3). Fourteen percent of the elk from the NER were predicted to move to feedgrounds in the FCHU (k=4) with the South Park feedground being the most likely destination.

Model Checks

To assess the demographic effects associated with severe winters when elk were not being fed, the model was run without disease by setting CWD transmission parameters to zero and evaluating three scenarios. In the first scenario (fig. B4*A*), we assumed continued feeding and that the fed populations would be unaffected by severe winter effects. This scenario established that the model parameters result in a stable population size in the absence of CWD. In the second scenario (fig. B4*B*), we assumed no feeding with severe winters and female elk hunting rates that declined linearly to zero as the population declined from the initial population size to 80 percent of the population objective of 11,000 elk. In the third scenario (fig. B4*C*), we

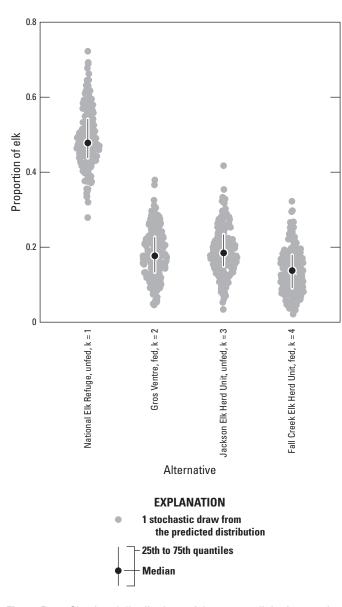


Figure B3. Simulated distributions of the expert elicitation results of how elk may redistribute themselves to other areas if supplemental feeding in the National Elk Refuge (NER) in Jackson, Wyoming, is discontinued. On average, 50 percent of the elk were expected to continue using the NER during the winter (subpopulation [k]=1). The remaining elk were expected to move to the Gros Ventre feedgrounds (k=2), native winter ranges within the Jackson Elk Herd Unit (k=3), or feedgrounds in the Fall Creek Elk Herd Unit (k=4). No elk were expected to move to the unfed elk population of the Fall Creek Elk Herd Unit (k=5).

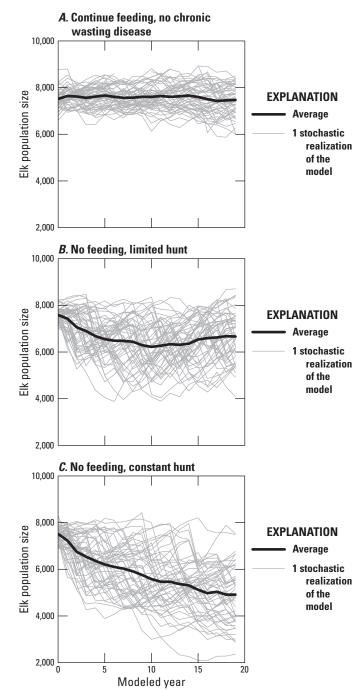


Figure B4. Line graphs showing scenarios describing the demographic effect of severe winters on elk population size over 20 years in the absence of chronic wasting disease (CWD): *A*, severe winters are not included; *B*, severe winters occur with a probability of 0.25, but hunting rates of female elk decline with population size; and, *C*, hunting rates are held constant and severe winters occur with a probability of 0.25. In this example, only a single population starting at 7,500 elk was modeled.

assumed no feeding with severe winters and hunting rates for both sexes that remained at a constant proportion of animals. For demonstration purposes, these scenarios were run for just those elk that visit the NER in winter (k=1) and did not include displacement to other regions.

Simulations with severe winters showed some years when elk populations declined sharply, followed by an increase in calf survival (figs. B4*B*, *C*) and reduced hunting (fig. B4*B*), which led to some population recovery after severe winters. The effect of no feeding reduced the NER elk population by about 14 percent in the absence of CWD when harvest pressure was also reduced in response to the population decline. The elk population in the NER declined by, on average, 38 percent when there was no feeding and harvest rates across both sexes were constant. When a similar analysis was made across all regions and allowed for displacement to other regions according to figure B3, we found that the elk population within the analysis area ($k \le 5$) declined by an average of 21 percent. The effects of severe winters were applied to all elk that were not fed during the winter in the JHU and FCHU.

Model Predictions with Chronic Wasting Disease

Figure B5 shows the results of the increase harvest alternative in which elk are hunted aggressively in the first 5 years to reach an objective of 5,000 elk in the NER in winter. Increasing the harvest rate 2.5 times resulted in an average population size of 5,170 (SD=500) by year 5. The average predicted female elk

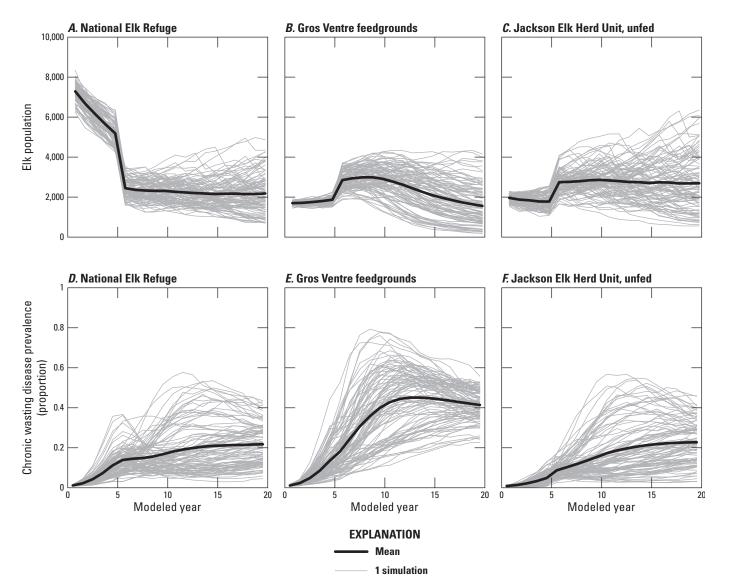


Figure B5. Line graphs showing predicted elk population sizes for, *A*, the National Elk Refuge (NER), *B*, Gros Ventre feedgrounds, and, *C*, Jackson Elk Herd Unit (JHU); and chronic wasting disease prevalence for , *D*, the NER, *E*, the Gros Ventre feedgrounds, and, *F*, the JHU during the 20 modeled years for the three subpopulations within the JHU (subpopulation $[k] = \{1, 2, 3\}$) with the increase harvest alternative. At year 5, elk move to other areas of the JHU ($k = \{2, 3\}$) and Fall Creek Elk Herd Unit (k=4), and the disease transmission in the NER is assumed to be reduced thereafter to levels commensurate with unfed elk populations.

harvest was 840 in the first year, declining to 570 by year 5. The number of female elk hunted in the entire JHU averaged 450 from 2016–21 and 850 from 2000–2004 (Wyoming Game and Fish Department, written commun., 2000–2004; Wyoming Game and Fish Department, 2020, 2021b). Feeding was halted after year 5, and the NER elk were redistributed to other areas of the JHU (fig. B5) or to feedgrounds in the FCHU (not

shown). A fraction of elk was assumed to continue their use of the NER after feeding stopped in year 5, but CWD prevalence and transmission remain lower there than on the Gros Ventre feedgrounds, where elk continue to be fed (fig. B5).

Overall, predicted elk population sizes for the JHU and the analysis area declined across all five management alternatives (table B1; fig. B6). In the JHU, the continue

 Table B1.
 Summary of elk and chronic wasting disease performance metrics for the Jackson Elk Herd Unit and the analysis area in western Wyoming.

Alternative	Modeled year 20 elk population size		Modeled year 20 CWD prevalence		First 5 modeled years of winter elk deaths				
	Mean	SD	% less than SQ ¹	Mean	SD	% less than SQ	Mean	SD	% less than SO
				JHU					
Continue feeding	5,200	1,500		0.35	0.06		6,100	540	
No feeding	6,700	1,600	26	0.24	0.08	86	5,800	600	65
Increase harvest ²	6,000	1,800	30	0.27	0.10	79	5,200	470	88
Reduce feeding ²	6,100	1,700	36	0.26	0.09	84	6,200	580	43
3% disease threshold	6,900	1,400	22	0.23	0.07	91	5,900	620	59
			ļ	Analysis are	a ³				
Continue feeding	6,700	1,600		0.35	0.05		8,000	730	
No feeding	8,400	1,700	30	0.26	0.07	83	8,100	850	45
Increase harvest	7,600	1,900	31	0.28	0.08	76	7,100	650	83
Reduce feeding	7,700	1,800	37	0.27	0.08	87	8,100	740	47
3% disease threshold	8,600	1,600	23	0.26	0.06	89	8,100	830	46

[CWD, chronic wasting disease; SD, standard deviation; %, percent; SQ, status quo; ---, not applicable]

¹Percentage of simulations in which the metric was less than the status quo of continued feeding.

²This alternative assumes there is no feeding after year 5.

³The analysis area includes elk from the JHU and elk within the analysis boundary in the Fall Creek Elk Herd Unit in western Wyoming.

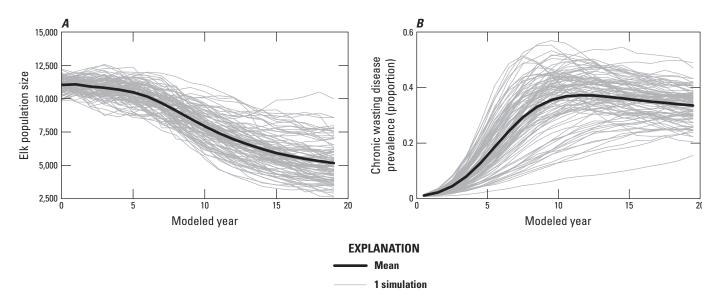


Figure B6. Line graphs of, *A*, predicted elk population size and, *B*, chronic wasting disease prevalence through 20 years for the three populations of the Jackson Elk Herd Unit (subpopulation $[k] = \{1, 2, \text{ and } 3\}$) assuming continued feeding.

feeding alternative resulted in an average decline of 53 percent in population size to 5,200 and a median CWD prevalence of 0.35 (SD=6 percent; fig. B6).

By year 20, the no feeding and disease threshold alternatives resulted in larger populations in the JHU and the larger analysis area (fig. B7A, B). The no feeding alternative started at a lower population size in the JHU than other alternatives because we assumed that elk were already redistributed to the larger analysis area at the start of each simulation of this alternative (fig. B7A). Given the starting CWD prevalence of 1 percent and prior estimates of potential CWD transmission on feedgrounds (Cook and others, 2023), the simulated population in the disease threshold alternative reached 3 percent or greater within the first several years, at which time feeding was stopped. The no feeding and disease threshold alternatives resulted in similar elk and CWD dynamics after the phaseout of NER feeding (figs. B7A-C). The no feeding alternative resulted in an average population size at year 20 of 6,700 (SD=1,600, fig. B7A) and an average CWD prevalence of 24 percent (SD=8 percent, fig. B7C).

The continue feeding alternative usually resulted in lower population sizes and higher CWD prevalence than the other alternatives by year 20 (figs. B7 and B8). Although the model produced a variety of outcomes, the no feeding alternative resulted in lower CWD prevalence than the continue feeding alternative in 86 percent of the simulations (table B1; fig. B8B). In addition, the elk population size in the analysis area was larger in year 20 for the no feeding alternative in 70 percent of simulations compared to the continue feeding alternative (table B1; fig. B8A). The other alternatives can be grouped according to how quickly feeding is ceased, whereby the increase harvest and reduce feeding alternatives resulted in a phaseout of feeding at year 5 whereas the no feeding and 3 percent disease threshold alternatives had earlier phaseouts, which corresponded to differences in year 20 elk population sizes and CWD prevalence (figs. B7 and B8).

The NER managers were also interested in minimizing winter elk mortality and CWD deaths during the first 5 years (this volume, chap. A, Cook and others, 2025). The number and types of elk deaths were tallied across all ages and sexes during the winter months of November through March to exclude baseline summer calf mortality and highlight those deaths that are more likely to be observed by the public. As expected, the increase harvest alternative resulted in higher hunting mortality and lower natural mortality than the other alternatives (fig. B9). The increase harvest and no feeding alternatives tended to have fewer CWD mortalities than the other management alternatives. For CWD and natural deaths, the increase harvest alternative resulted in fewer deaths than the continue feeding alternative in 83 percent of simulations across the analysis area, whereas the other alternatives were approximately equivalent to the continue feeding alternative (table B1).

Figure B10 shows elk mortalities from November through March of every year due to different causes (CWD, fig. B10*A*; natural, fig. B10*B*; and hunting, fig. B10*C*) shifting over time. Model predictions suggested that the number of elk harvested would decline through time for all alternatives. By year 20, the elk harvest was predicted to be about a quarter of 2022 levels and similar in magnitude to the number of CWD deaths from November to April every year (figs. B9*A*, *C*). The higher CWD deaths in the continue feeding alternative coincide with lower harvests by year 20 on average compared to other management alternatives (figs. B10*A*, *C*).

Discussion

We incorporated empirical evidence and formal expert elicitation into our mathematical models of elk and CWD dynamics in Jackson, Wyoming. We then tailored the CWD model to the five supplemental feeding management alternatives identified by the National Elk Refuge managers. The predicted elk population size decreased through time by 42-54 percent for all management alternatives, and the number of elk harvested declined by approximately 75 percent (figs. B7 and B10). The management alternatives associated with cessation of supplemental feeding resulted in lower elk population sizes during the first 5-10 years but higher population sizes by year 20 compared to the continue feeding alternative (figs. B7A, B). The prevalence and effects of CWD were predicted to increase during the 20 years that were modeled, resulting in lower elk population sizes. The predicted elk population size in the analysis area (subpopulations $k \leq 5$) declined by 54 percent, on average, by year 20 in the continue feeding alternative and was lower than the no feeding alternative in 70 percent of the simulations (table B1). The crossover point, when the no feeding or phase-out alternatives resulted in higher populations than the continue feeding alternative, occurred between years 7 and 13 (fig. B7C). The predicted CWD prevalence in year 20 was higher in the continue feeding alternative, 35 percent on average in the JHU, compared to all other alternatives in 80-90 percent of the simulations (table B1). The other management alternatives resulted in an average CWD prevalence of 23 and 27 percent CWD by year 20 (table B1), which is high compared to some free-ranging elk populations (Monello and others, 2017). This high predicted CWD prevalence in the JHU is due, in part, to the assumption that 2,000–3,000 elk would continue to be fed at the Gros Ventre feedgrounds (fig. B5).

Several lines of evidence support the high predicted CWD prevalence and large population declines predicted by the CWD model. First, supplemental feeding results in elk contact rates that are 2–4 times higher than when they are not being fed in winter (Cross and others, 2013; Janousek and others, 2021), which is of similar magnitude to the estimates of increased CWD transmission due to feeding by a panel of experts (Cook and others, 2023). Second, previous work on a free-ranging elk population in Wind Cave National Park in South Dakota estimated an overall CWD prevalence of 18 percent, but as much as 30 percent in some areas (Sargeant and others, 2021). Third, captive cervid farm data suggest that CWD can reach more than 60 percent prevalence when elk are artificially aggregated (Peters and others, 2000; Haley and others, 2020; Williams and others, 2014). Williams and others (2014) noted that 37 out of 39 elk died from CWD in their study of captive elk.

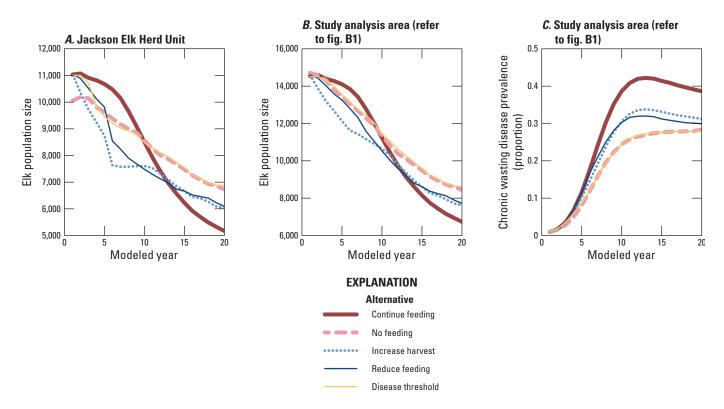


Figure B7. Line graphs of average elk population size in, *A*, the Jackson Elk Herd Unit and, *B*, analysis area; and, *C*, average chronic wasting disease prevalence in the study analysis area for 20 years for the five management alternatives and all simulations.

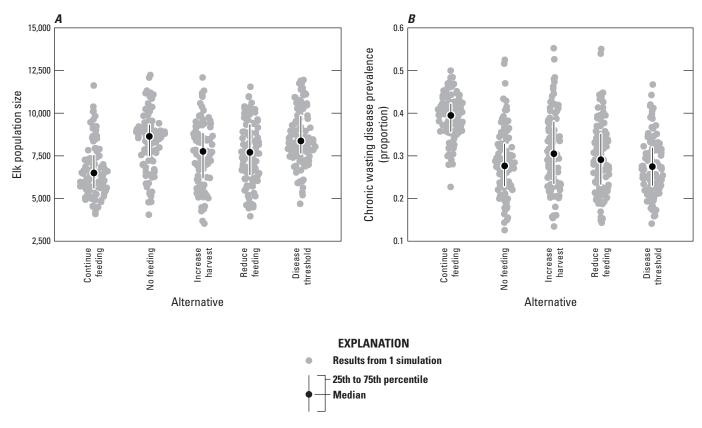


Figure B8. Graphs of the distribution of, A, elk population size across five management alternatives, and, B, chronic wasting disease prevalence at modeled year 20 for the analysis area (subpopulation $[k] \le 5$).

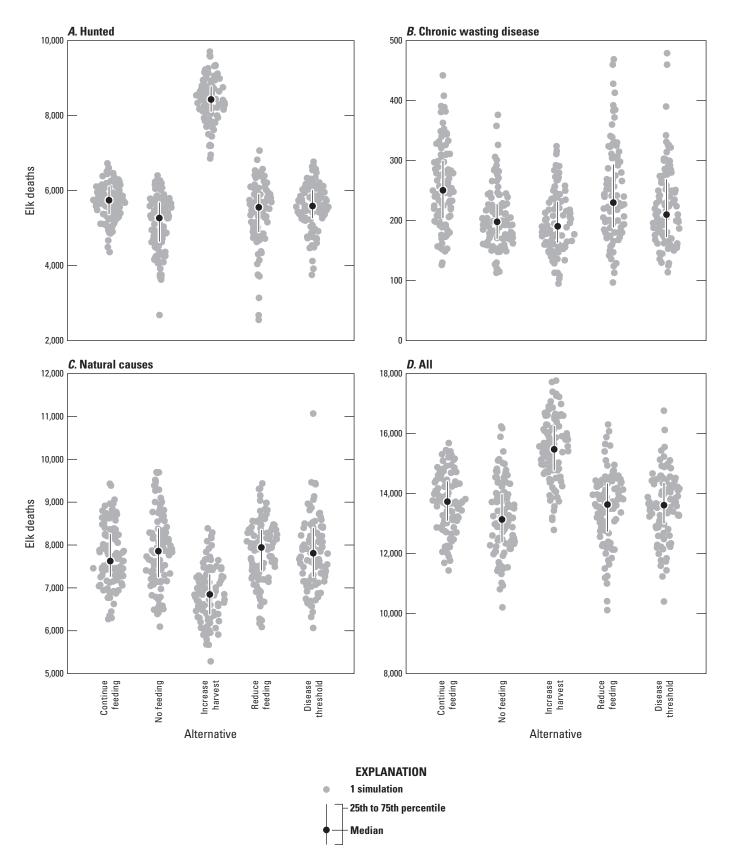


Figure B9. Graphs of the distribution of cumulative elk deaths for the first 5 modeled years by type: A, hunting, B, chronic wasting disease (CWD), C, natural causes, and, D, all deaths for the five management alternatives in the analysis area (subpopulation [k] \leq 5).

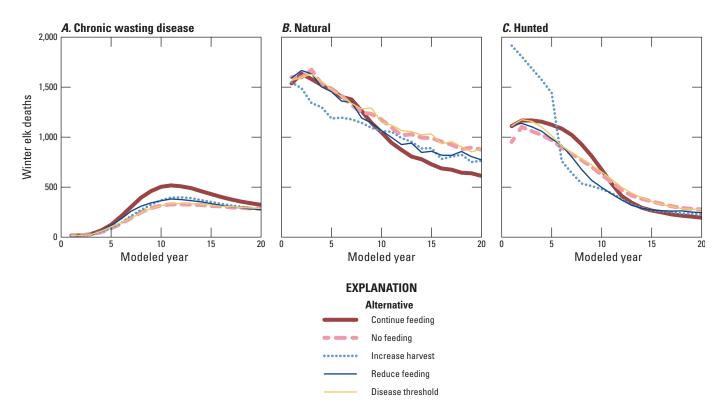


Figure B10. Line graphs showing the average number of elk deaths attributable to, *A*, late-stage chronic wasting disease, *B*, natural causes, or, *C*, hunting, from November through March during the modeled years for the five management alternatives.

In that study, the median elk lifetimes were 4–7 years depending on the elk's genotype, in the absence of predation, starvation, or hunting mortality, whereas MacNulty and others (2020) found that the average age of adult female elk killed by wolves in Yellowstone National Park was 13–16 from 1995–2016.

The CWD model included several important assumptions. First, the demographic penalty for not feeding elk depends on the frequency of severe winters, which reduces the survival of unfed elk in the model. These winter impacts were intended to capture the multiple ways that elk mortality may increase (for example, by vehicle accidents or additional hunts on private lands) if feeding ends so that these mechanisms did not have to be built into the model independently. Wyoming herd units with feedgrounds have higher densities of elk on winter range than the herd units without feedgrounds (Cook and others, 2023), but the evidence that feedgrounds increase elk productivity in Wyoming is mixed (Foley and others, 2015). The no feeding penalty during severe winters in our model resulted in a median decline in elk populations in the NER of 38 percent in the absence of CWD, movement to other feedgrounds, and constant hunting (fig. B4A, C). This penalty is higher than the 23 percent no-feeding penalty predicted in Cook and others (2023), which was based on the average difference in winter elk densities in fed and unfed herd units of western Wyoming. The increase from 23 percent to 38 percent may be appropriate given the much higher number of elk that use the NER and the proximity of human development compared to other Wyoming feedgrounds. Nevertheless, the effects of stopping NER supplemental feeding on elk survival rates is an important source of uncertainty in the model.

The second important assumption was that model simulations started with a CWD prevalence of 1 percent across all sex and age classes because this matched the conditions and model given to the panel of experts (Cook and others, 2023) to predict transmission rates for a fed elk population. However, only one elk has been documented as CWD positive out of the 1,209 elk tested from 2020 to 2022 in the JHU (0.1 percent, 95-percent confidence interval=[0.002 percent, 0.5 percent]; Wyoming Game and Fish Department, 2020, 2021a, 2022a). The 1 percent CWD prevalence that was previously used in Cook and others (2023) was deliberately maintained to account for the delay between the completion of analyses, finalization of the Environmental Impact Statement, and any future implementation of management alternatives. We explored the sensitivity of our model results to starting at 0.1 percent CWD prevalence instead of 1 percent. The results at 0.1 percent prevalence were not noticeably different than the results at 1 percent prevalence because of the assumption that environmental transmission linearly increases as a function of time and does not depend on the starting prevalence (Cross and Cook, 2024). If CWD transmission from the environment grows exponentially rather than linearly, then it would take a similar amount of time for CWD to increase from 0.1 percent to 1 percent as it does from 1 percent to 10 percent, which was about 4-10 years for fed elk in this model. Our model predictions are for the 20 years after reaching a prevalence of 1 percent, which may not occur for several more years.

Our third assumption was that both the female elk harvest rate and the elk calf survival rate would change depending on the elk population size in the herd unit. The CWD model resulted

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in higher elk recruitment rates (as indexed by the number of elk calves per adult female) than what has been observed in the JHU. From 2000 to 2021 the proportion of adult female elk with calves (calf:cow) averaged 0.22 (minimum=0.18 and maximum=0.29), whereas our model without the effects of CWD and a stable elk population had a calf:cow ratio of approximately 0.4 (minimum 0.25; maximum 0.5). This difference in elk recruitment may be due to observational biases in classification surveys or other discrepancies between modeled and actual elk vital rates in the JHU. Our modeled calf:cow ratio increased to 0.5 as the elk population declined due to CWD; this is similar to the calf:cow ratios in the Northern Bighorn Herd Unit of Wyoming when that population was growing rapidly from 2005 to 2015 (Wyoming Game and Fish Department, written commun., 2005–15). Due to the high calf:cow ratios, the CWD model predicted that the elk population could remain stable even when CWD prevalence reached 20 percent, whereas Galloway and others (2021) predicted that the NER elk would begin to decline when CWD prevalence reached 7 percent using a model with a constant low elk recruitment rate.

There are several other factors, in addition to supplemental feeding and CWD, likely to affect elk during the next 20 years in the JHU and that we did not include in our analyses. Climate change may increase the frequency and intensity of summer droughts, thus reducing the quality of summer forage (Rickbeil and others, 2019) and reducing snowpack in winter (Hostetler and others 2021), which may reduce the duration of supplemental feeding (Cross and others, 2007). In addition, our modeling approach did not account for the effect of predators on CWD (Miller and others, 2008; Wild and others, 2011; Brandell and others, 2022) or evolutionary changes to either elk (Monello and others, 2017) or CWD prions (Velásquez and others, 2020). Uncertainties remain on all these issues that were beyond what could be addressed in this report. Future work could assess the value of reducing these uncertainties (for example, Maxwell and others, 2015).

Summary

Modeling results for 20 years indicated a short- versus long-term tradeoff between the continue feeding and no feeding alternatives for elk in the National Elk Refuge and Jackson Elk Herd Unit. Continuing to supplementally feed elk at the National Elk Refuge was predicted to result in a chronic wasting disease (CWD) prevalence of 35 percent and a coincident decline in the elk population of 54 percent on average by year 20 of the model. The cessation of elk supplemental feeding was predicted to result in early declines in elk populations during the first 5-10 years but more stable elk populations thereafter coincident with a lower CWD prevalence than the continue feeding alternative. The no feeding alternative for the National Elk Refuge still resulted in a CWD prevalence of, on average, 24 percent due, in part, to supplemental feeding on other feedgrounds in the Jackson Elk Herd Unit. Given the predicted decline in the elk population, elk harvest was also predicted to decline by approximately 75 percent

across all management alternatives. The model predicted that by year 20, CWD-induced deaths in winter would be approximately equal to the number of elk harvested.

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Appendix B1. Additional Model Details

Elk harvest and vital rates in the chronic wasting disease (CWD) model were modified from Cook and others (2023) to match the observed data more closely in the Jackson Elk Herd Unit (JHU; table B1.1).

Annual calf survival rates were assumed to be a nonlinear function of elk population size relative to the carrying capacity (K_{HU}) of the herd unit (fig. B1.1). In addition, calf and adult elk survival rates in unfed subpopulations were stochastically reduced in 25 percent of the 20 model years due to severe winters (fig B1.2). The additional severe winter mortality in figure B1.2 was extrapolated from Hobbs and others (2003). To apply the function in figure B1.2 to the Fall Creek Elk Herd Unit (FCHU), elk population size was converted to population density based on the amount of elk winter habitat in the herd unit (JHU=837 km², FCHU=499km²; fig. B1.1; table 4 of Cook and others 2023; Wyoming Game and Fish Department, 2021a).

Table B1.1. Elk vital and harvest rate estimates used in the elk chronic wasting disease model.

[Parameter notation relates to the model code in Cross and Cook (2024) and the model developed by Cook and others (2023). SD, standard deviation; ϕ , phi; γ , gamma; h, harvest]

Vital rate	Notation	Mean	Parametric SD ¹	Process SD ²
Maximum calf survival	ϕ_1	0.6	0.103	0.0385
Juvenile survival ^{3,4}	ϕ_{2-3}	0.88	0.0085	0.0042
Adult male survival ^{3,4}	ϕ_4	0.95	0.017	0.0034
Adult female survival ^{3,4}	ϕ_5	0.93	0.0085	0.0034
Calf reproduction ^{3,4}	γ_1	0	0	0
Yearling female reproduction ⁵	γ_3	0.25	0.033	0.035
Adult female reproduction ⁵	γ_5	0.82	0.033	0.035
Harvest mortality calf ⁶	h_1	0.06	0.007	0.005
Harvest mortality yearling male ⁶	h_2	0.01	0.007	0.005
Harvest mortality yearling female ⁶	h_3	0.07	0.007	0.005
Harvest mortality adult female ⁶	h_5	0.07	0.007	0.005
Harvest mortality adult male ⁶	h_4	0.08	0.007	0.005

¹Parameteric variation created different mean values across simulations.

²Process variation resulted in parameter variation between years within a simulation.

³Data were approximated from Galloway and others (2021).

⁴Data were approximated from Raithel and others (2007).

⁵Data were approximated from Cotterill and others (2018).

⁶Data were approximated from the Jackson Elk Herd Unit from 1993 to 2020 (Wyoming Game and Fish Department, 2021b, and references therein).

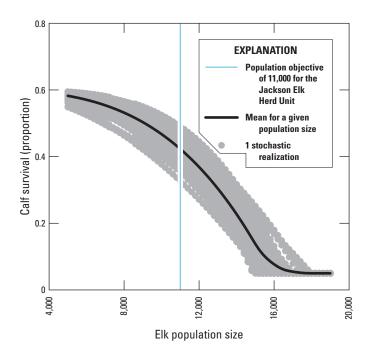


Figure B1.1. Line graph showing the assumed annual calf survival as a function of the Jackson Elk Herd Unit (JHU) population size (table 4 of Cook and others, 2023; Wyoming Game and Fish Department, 2021a).

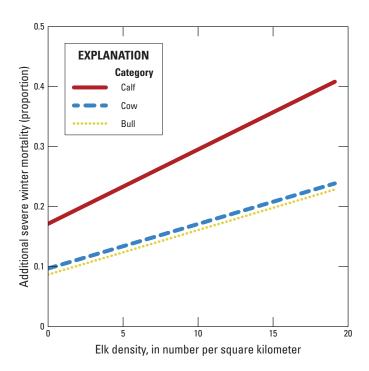


Figure B1.2. Line graph showing the modeled effects of severe winter on the mortality of elk in different age and sex classes beyond natural and hunting mortality as a function of elk population size in the Jackson Elk Herd Unit. These relationships were derived from Hobbs and others (2003).

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Appendix B2. Expert Elicitation

We elicited parameter estimates from a panel of eight experts for how Cervus elaphus canadensis (elk) would move to other subpopulations if the National Elk Refuge (NER) discontinued winter feeding. The initial elicitation focused on parameters of interest under two conditions. One condition represented the expectations of experts for elk transitions in the years immediately preceding elk feedground management action. The second condition was focused on longer term dynamics of elk habitat selection and were presented as a separate set of questions. In total, we included 12 questions focused on parameter values, relationships, and estimates that were unknown but necessary to estimate elk movement and resource selection under different alternatives for the Environmental Impact Statement on the NER. Because the differences between the immediate transition and longer term (in other words, equilibrium) set were minor, we included only the estimates from the immediate transition in our modeling work. We report only the raw and fitted distributions for questions that were used in this chapter.

Elk Spatial Transitions Without National Elk Refuge Feeding

For each of the questions about elk redistribution during immediate transition from feeding, assume an average snowfall year in duration of season and sustained snow depths. Also, assume that elk that are the focus of these questions may have learned behavioral responses to feeding that were acquired under normal feeding operations. This includes the annual return of individuals to the NER with an expectation that supplemental food will be provisioned when forage becomes scarce.

Assuming the NER no longer provisions food to elk on the Refuge, the specific questions were:

- What proportion of the NER feedground elk will hold on native winter range in the same year that the NER does not provision supplemental feed? (Fig. B2.1*A*; questions 1, 2, 3, 4, and 5 are linked together such that central and (or) best guess estimates should sum to approximately 1.)
 - 1a. Of the NER elk that do not transition to State feedgrounds, what proportion will hold on native winter range in the NER when the Refuge does not provision supplemental feed? (Questions 1a and 1b are linked so that central estimates should sum to 1.)
 - 1b. Of the NER elk that do not transition to State feedgrounds, what proportion will transition to private lands conflict areas and winter range off the Refuge when the NER does not provision supplemental feed? (Questions 1a and 1b are linked so that central estimates should sum to 1.)
- 2. What proportion of the NER feedground elk will relocate to Gros Ventre feedgrounds (Patrol Cabin and Fish Creek) in the same year that the NER does not provision supplemental

feed? (Fig. B2.1*B*; questions 1, 2, 3, 4, and 5 are linked together such that central and (or) best guess estimates should sum to approximately 1.)

- 3. What proportion of the NER feedground elk will relocate to South Park feedground in the same year that the NER does not provision supplemental feed? (Fig. B2.1*C*; questions 1, 2, 3, 4, and 5 are linked together such that central and (or) best guess estimates should sum to approximately 1.)
- 4. What proportion of the NER feedground elk will relocate to Horse Creek feedground in the same year that the NER does not provision supplemental feed? (Fig. B2.1*D*; questions 1, 2, 3, 4, and 5 are linked together such that central and (or) best guess estimates should sum to approximately 1.)
- 5. What proportion of the NER feedground elk will relocate to Camp Creek feedground in the same year that the NER does not provision supplemental feed? (Fig. B2.1*E*; questions 1, 2, 3, 4, and 5 are linked together such that central and (or) best guess estimates should sum to approximately 1.)

Expert Panel Responses

The results of each expert's answers to the questions above are shown in figures B2.1 and B2.2. (Expert 6 did not respond to questions 1a and 1b.) The four-point estimates were an expert's low, high, and best estimates of a parameter and their confidence that the actual value would fall within the low and high values. The individual expert estimates were aggregated to provide the prediction in figure B2. Distributions were then aggregated by fitting a single Dirichlet distribution, which ensured that the sum of each estimated beta distribution included the upper limit of one for the proportional data we elicited (Conroy and Peterson, 2013).

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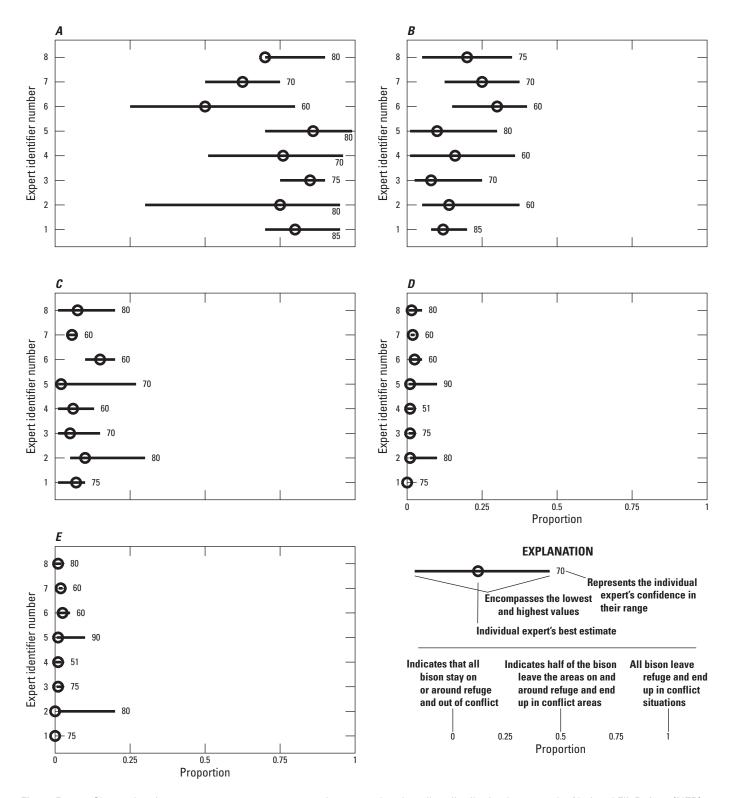


Figure B2.1. Charts showing raw expert responses to questions 1–5 related to elk redistribution between the National Elk Refuge (NER) and other feedgrounds. *A*, results of question 1, *B*, results of question 2, *C*, results of question 3, *D*, results of question 4, and, *E*, results of question 5.

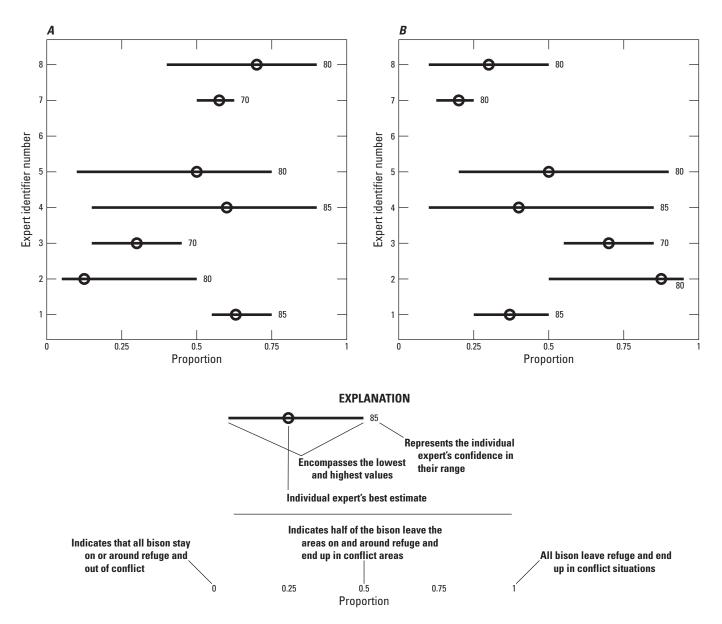


Figure B2.2. Chart showing raw expert panel responses to questions 1a and 1b related to elk redistribution between National Elk Refuge (NER) and conflict areas: *A*, results of question 1a: Of the NER elk that do not transition to State feedgrounds, what proportion will hold on native winter range in the NER when the refuge does not provision supplemental feed?; *B*, results of question 1b: Of the NER elk that do not transition to State feedgrounds, what proportion will transition to private lands conflict areas and winter range off the refuge when the NER does not provision supplemental feed?

Evaluating Elk Distribution and Conflict Under Proposed Management Alternatives at the National Elk Refuge in Jackson, Wyoming

By Gavin G. Cotterill, Paul C. Cross, Eric K. Cole, Jonathan D. Cook, Margaret C. McEachran, and Tabitha A. Graves

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Conversion Factors

U.S. customary units to International System of Units

Multiply	Ву	To obtain
	Length	
foot (ft)	0.3048	meter (m)
nternational System of Units to U.S. custo	mary units	
Multiply	Ву	To obtain
	Length	
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
meter (m)	1.094	yard (yd)
	Area	
square kilometer (km ²)	247.1	acre
square kilometer (km ²)	0.3861	square mile (mi ²)

Datums

Vertical coordinate information is referenced to the North American Vertical Datum of 1988 (NAVD 88).

Horizontal coordinate information is referenced to the North American Datum of 1983 (NAD 83).

Supplemental Information

Elk global positioning system (GPS) collar data from the National Park Service, U.S. Fish and Wildlife Service, and Wyoming Game and Fish Department come from sources as cited. At the time of writing, not all reports from these agencies were available online; for elk GPS collar data from nonpublic documents, contact the respective agency. Likewise, not all vegetation type data from the U.S. Fish and Wildlife Services and U.S. Department of Agriculture Forest Service were available online; for vegetation type data from nonpublic documents, contact the respective agency.

Abbreviations

CWD	chronic wasting disease
FWS	U.S. Fish and Wildlife Service
GIS	geographic information system
GPS	global positioning system
GVTA	Gros Ventre Transition Area
JHU	Jackson Elk Herd Unit
NER	National Elk Refuge
NFCHU	Northern Fall Creek Elk Herd Unit
NWRTA	Native Winter Range Transition Area
RSF	resource selection function
SDM	structured decision-making
WGFD	Wyoming Game and Fish Department
WSMET	Wildlife Subject Matter Expert Team

Evaluating Elk Distribution and Conflict Under Proposed Management Alternatives at the National Elk Refuge in Jackson, Wyoming

By Gavin G. Cotterill,¹ Paul C. Cross,¹ Eric K. Cole,² Jonathan D. Cook,¹ Margaret C. McEachran,¹ and Tabitha A. Graves¹

Abstract

We evaluated measurable attributes describing the current and future distribution of Cervus elaphus canadensis (elk) across a region surrounding Jackson, Wyoming, for five feedground management alternatives proposed by the U.S. Fish and Wildlife Service as a revision to the 2007 "Bison and Elk Management Plan" of the National Elk Refuge. A resource selection function evaluated measurable attributes of interest to managers, including elk use of private property and sensitive habitat types at monthly timesteps and varying winter conditions. The study area boundaries were created through an expert elicitation process and consist of the Jackson Elk Herd Unit, Grand Teton National Park, the National Elk Refuge, and the northern third of the Fall Creek Elk Herd Unit. For each of the five alternatives, we distributed monthly elk numbers calculated in a concurrent analysis that simulated chronic wasting disease dynamics in this system for 20 years. Measurable attributes representing potential elk use of (1) private property, (2) cattle properties as an index of Brucella *abortus* risk, and sensitive habitats consisting of (3) *Populus* tremuloides Michx. (quaking aspen), (4) Populus angustifolia E. James (narrowleaf cottonwood), and (5) Salix L. (willow) in core winter use areas all closely followed the declines of elk abundance projected by the elk chronic wasting disease model. After 20 years, the continue feeding alternative ranked most favorably in terms of limiting elk days on private property and reducing brucellosis risk from elk to cattle because this alternative concentrated elk on the National Elk Refuge and resulted in the lowest elk population sizes. However, other management alternatives, including increase harvest and reduce feeding, tended to limit elk use of sensitive quaking aspen, narrowleaf cottonwood, and willow habitats during winter (December-April).

Introduction

This analysis provides scientific support for the U.S. Fish and Wildlife Service (FWS) regarding management decisions at the National Elk Refuge (NER) in Jackson, Wyoming. The NER has fed most of the Jackson elk herd for part of the winter for more than a century. Cervus elaphus canadensis (Erxleben, 1777; elk) abundance has changed over time, but the average number fed at the NER each winter during 2017-22 was approximately 7,500 elk, 70 percent of the Jackson elk herd (Wyoming Game and Fish Department [WGFD], 2022b). Previous research has shown that winter feeding operations create large, dense aggregations of animals that facilitate the transmission of multiple pathogens, including Brucella abortus (which causes brucellosis; Cross and others, 2007), Psoroptes spp. (scabies species; Samuel and others, 1991), and Pasteurella multocida (which causes pasteurellosis; Franson and Smith, 1988). Chronic wasting disease (CWD), which is always fatal to hosts, affects ungulates (including elk, Alces alces [Linnaeus, 1758; moose], and deer) and can lead to population declines (Edmunds and others, 2016). In 2020, the first CWD-positive elk was detected in Grand Teton National Park. In Wind Cave National Park, CWD has reached prevalence as high as 18-29 percent in elk (Sargeant and others, 2021). Chronic wasting disease is spread directly through animal-to-animal contact and indirectly through environmental exposure to prions, the malformed PrP proteins that are the infectious agent of CWD (Miller and others, 2004). Prions can persist for years, if not decades in the environment. Accordingly, CWD could have a larger effect on the Jackson elk herd than that observed in other populations because feeding at the NER greatly increases elk contact rates and elk densities (Galloway and others, 2017; Janousek and others, 2021).

The FWS is writing an environmental impact statement and revising its Bison and Elk Management Plan (U.S. Fish and Wildlife Service and National Park Service, 2007) in consideration of the disease risk to the herd. A structured decision-making (SDM) process, facilitated by the U.S. Geological Survey, provides scientific support for this revision (this volume, chap. A, Cook and others, 2025). Briefly, the management alternatives under consideration include (1) continue feeding, (2) immediate cessation of feeding

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(hereafter referred to as no feeding), (3) increase elk harvest for a 5-year period to reduce the NER winter elk population to 5,000 animals, followed by feed cessation (hereafter referred to as increase harvest), (4) attempt to lower the number of elk to 5,000 by reducing the feed provisioned to elk at the NER for a 5-year period, followed by feed cessation (hereafter referred to as reduce feeding), and (5) continue feeding until CWD prevalence in the Jackson elk herd is estimated to be 3 percent, followed by feed cessation (hereafter referred).

This analysis predicted future elk space-use (the areas that elk will occupy) during a 20-year period in the vicinity of Jackson, Wyoming, under the proposed alternatives. The overall approach closely followed previous research in the Bridger-Teton National Forest (Cook and others, 2023), wherein a resource selection function (RSF) was fit to elk global positioning system (GPS) collar data. The RSFs were used to estimate the per capita probability of use across the study area for various population segments of elk at monthly timesteps (Cotterill and Graves, 2024). Elk abundance estimates were derived from a dynamic population and disease simulation model (hereafter, elk CWD model) under the management alternatives (this volume, chap. B, Cross and others, 2025) and projected across the study area using the RSFs. The elk CWD model, in conjunction with the RSFs, formed the basis for the calculation of what we refer to as our measurable attributes, the metrics of interest to decision-makers defined during the SDM process (this volume, chap. A, Cook and others, 2025).

Most of the future alternatives under consideration included novel conditions for which scant or no relevant elk GPS collar data exist. For example, winter feeding operations at the NER have never been experimentally discontinued to allow researchers to observe elk behavior and population dynamics in the absence of feeding. However, decades of research in this study area provided insights into the potential future behavior of elk under the no feeding alternative. Relevant situations included (1) a mild winter with substantial forage resources during which no feeding occurred at the NER, (2) attempts to reduce the duration of feeding by initiating feeding later in the season and ending feeding earlier in the season, and (3) one occasion where underestimating the number of elk in the NER caused elk to be fed reduced rations (Janousek and others, 2021; FWS, 2019). We used a formal expert-elicitation process to collate these insights to parameterize the elk space-use models. Expert judgment is a quantitative expression of an expert's belief, based on relevant system knowledge, and when elicited by a formal process designed to minimize cognitive biases, can result in reliable predictions when empirical information is impossible or infeasible to collect (Adams-Hosking and others, 2016; Martin and others, 2012; O'Hagan and others, 2006; Runge and others, 2011; Speirs-Bridge and others, 2010). The resulting models integrated the expert-provided information from the Wildlife Subject Matter Expert Team (WSMET; this volume, chap. A, Cook and others, 2025) with elk collar data such that model predictions closely matched expected outcomes from the expert elicitation process.

The analysis area under consideration was delineated by the WSMET and consists of two contiguous regions, the Jackson Elk Herd Unit (JHU) and the Northern Fall Creek Elk Herd Unit (NFCHU). Refer to appendix C1 for a map of the analysis area (fig. C1.2). The JHU matches the Jackson Elk Herd Unit as designated by the Wyoming Game and Fish Department and generally extends north from State Highway 22 and Jackson to encompass Grand Teton National Park, the National Elk Refuge, and other lands up to the southern Yellowstone National Park boundary and east to the Continental Divide (WGFD, 2022a). The NFCHU is the northern third of the Fall Creek Elk Herd Unit (WGFD designation; WGFD, 2022a; refer to this volume, chap. A, fig. A1 in Cook and others, 2025). The WSMET included the NFCHU to consider potential effects from elk movements under alternatives with reduced feeding. Public entities, including the U.S. Department of Agriculture Forest Service, the National Park Service, the FWS, and the State of Wyoming, manage much of the analysis area. However, in addition to the NER, other low-elevation areas that ungulates use in winter tend to be private property, mostly developed for agricultural or residential purposes. Of immediate concern was the potential conflict resulting from negative effects elk could have on private property, livestock, and sensitive vegetation communities if the NER were to cease winter feeding operations. The measurable attributes evaluating these negative effects consisted of the estimated elk use of private property, the Brucella abortus transmission risk from elk to cattle on private property, and elk use of core Populus tremuloides Michx. (quaking aspen), Populus angustifolia E. James (narrowleaf cottonwood), and Salix L. (willow) sensitive vegetation communities.

Methods

The NER has never experimentally discontinued feeding, and therefore, we could not fit models to the full suite of conditions that characterized the management alternatives. Yet, a primary goal of this work was to make quantitative predictions of elk redistribution if the NER ceases feeding elk in winter. To bridge this knowledge gap, a hybrid approach of fitting a resource selection function to data was used where possible, and then predictions were adjusted under the alternatives based on information about current and future elk movements from the expert-elicitation process.

An RSF was first estimated based on a use-availability design (Johnson and others, 2006), which measures where an animal has been compared to where an animal could have been. This RSF predicted space-use patterns that closely matched recent conditions and expert knowledge using data for two elk subpopulations: (1) elk fed during winter and (2) elk not fed in winter. To match the structure of the elk CWD model, monthly probability of use was predicted based on elk GPS collar locations. Fed and unfed population segments were pooled for May through November because the WSMET believed summer range selection patterns were not significantly different for these population segments. Winter was defined as December through April, and we further differentiated between average and severe winters. Severe winters were characterized as winters during which snowfall patterns concentrated more elk on feedgrounds (locations where wildlife agencies feed elk in winter), the NER had to provision larger amounts of feed to elk, and winter elk calf mortality exceeded 5 percent even with additional feed. These criteria were met in approximately 25 percent of recent observed years (this volume, chap. B, Cross and others, 2025). These combinations of variables created 27 monthly elk location datasets, consisting of 7 summer month (May-November) datasets and 20 winter month datasets (December-April). Each of the 5 winter months had fed and unfed population segments and both average and severe winter conditions (5[months]×2[fed, unfed]×2[average, severe winter]=20 datasets). The RSFs were fit to each dataset of elk locations separately to produce 27 predictive maps, each representing the study area as a grid of 1,020 by 1,020-meter (m) cells with values corresponding to the broad-scale RSFs' per capita probability of use. Thus, the values of the cells in a predictive map sum to one. We estimated the number of elk in each cell by multiplying the number of elk from the elk CWD model (this volume, chap. B, Cross and others, 2025) by the matching predictive map. To express monthly elk use in daily figures, we calculated elk days by multiplying the number of elk estimated to use a given area by the number of days in each month. For alternatives that included feed cessation at the NER, we developed a set of rules for modifying the predictive maps once feeding stopped to match the elk CWD model assumptions and expert judgment (this volume, chap. B, Cross and others, 2025).

The overarching goal of the analysis was to calculate how elk distribution changes influenced measurable attributes, indicating issues of concern to managers. The measurable attributes, identified during the SDM process, can be used to evaluate the performance of the alternatives against one another. Most attributes reflected concerns at the scale of the study area. The reduce feeding alternative included a provision that elk exclosures (fenced areas that exclude elk) be built in the NER to protect sensitive areas—vegetation communities, including quaking aspen, narrowleaf cottonwood, and willow-during winter. The NER is significantly smaller than the full study area, and the proposed exclosures were small relative to the resolution of the broad-scale RSF across the full study area. To evaluate the local effects of exclosures on the quaking aspen, narrowleaf cottonwood, and willow species in the NER, a second (fine-scale) RSF was estimated at a 30 by 30 m resolution for the NER during winter. The broad-scale RSF projected the numbers of elk in the NER, and the fine-scale RSF distributed the numbers of elk across the NER.

Implementation of the Alternatives

The effects of the feedground management alternatives were accounted for through three avenues: (1) alternatives changed elk-population sizes for categories representing herd units and fed or unfed elk status, as detailed in "Predictions of elk and chronic wasting disease dynamics on the National Elk Refuge and surrounding areas in Jackson, Wyoming—Chapter B of National Elk Refuge Feedground Management Alternatives" (this volume, Cross and others, 2025), (2) when feeding stopped on the NER, some elk from the NER moved to the Gros Ventre River drainage north and east of the NER or to non-feedground areas based on expert elicitation results, and (3) for the reduce feeding alternative, predicted elk space-use that fell within the boundaries of proposed elk exclosures in the NER was subtracted when calculating sensitive area measurable attributes.

The elk CWD model accounted for elk redistribution in the absence of feeding by transitioning elk to other herd units or changing their status from fed to unfed. Based on the expert-elicitation process, the elk CWD model assumes that roughly 50 percent of previously fed elk become unfed elk that still used the NER extensively. The remainder of the previously fed elk either became unfed elk that overwinter on native winter range-land away from the feedgrounds-or moved to other State feedgrounds in the Jackson or Fall Creek Elk Herd Units and became fed elk there (roughly in equal proportion; this volume, chap. B, Cross and others, 2025). Additionally, the elk CWD model used random draws in each year of every simulation to determine whether the winter was characterized as severe or average. The combination of population segment, winter condition, and time of year dictated which of the 27 predictive maps (corresponding to the datasets) was used to distribute elk numbers across the study area.

We assumed that our RSFs did not change during the 20 years of simulations for non-winter months and for unfed elk during winter. However, during the winter months of December through April, predicted fed elk space-use was adjusted to match expert-elicited predictions and the elk CWD model assumptions for broad-scale movements in the absence of feeding (this volume, chap. B, Cross and others, 2025).

Lastly, predicted elk space-use falling within proposed elk exclosures on the NER was subtracted from the calculations pertaining to sensitive vegetation community effects under the reduce feeding alternative. Predicted elk use inside the exclosures was not removed from the NER, but we assumed that these elk did not affect sensitive areas outside the exclosures.

Measurable Attributes

A total of five measurable attributes were determined for each of the management alternatives: (1) the number of elk days on private property, (2) the risk of Brucella abortus transmission from elk to cattle, expressed as the number of Brucella-caused elk abortions on private properties in the region where cattle could overwinter and (3-5) the number of elk days on sensitive vegetation communities during winter. The cumulative number of elk days on sensitive vegetation communities was further divided to capture specific effects on (3) quaking aspen, (4) narrowleaf cottonwood, and (5) willow species vegetation communities. Each of the sensitive vegetation calculations was restricted to winter months and to the portion of the study area that was defined as highly used wintering elk habitat based on expert judgment (refer to app. C1). Under the reduce feeding alternative, which included building the proposed elk exclosures, the elk days in sensitive vegetation communities (measurable attributes 3–5) were recalculated across the NER using the fine-scale NER winter RSF. Predicted elk space-use falling within proposed exclosures was subtracted from the total. This approach assumed that exclosures were designed to avoid displacing elk onto unprotected sensitive

quaking aspen, narrowleaf cottonwood, or willow vegetation communities within the NER. The elk CWD model performed 100 simulations for each alternative. The elk spatial measurable attributes were calculated for each simulation and the summarized distributions of these results are presented in this chapter.

Publicly available private property data were obtained from Teton County (Teton County, Wyoming, 2023) and included the winter cattle properties contributing to the brucellosis risk measurable attribute. Winter cattle properties were defined through personal communication with WGFD personnel. Sensitive areas (quaking aspen, narrowleaf cottonwood, and willow vegetation communities) were defined based on vegetation types included in map layers from Grand Teton National Park (Cogan and others, 2005), the NER (FWS, written commun., 2023), Teton County (Cogan and Johnson, 2013), and Bridger-Teton National Forest (Forest Service, written commun., 2023). These sensitive vegetation layers were verified, and the assessment scales were identified using input from the National Park Service, FWS, and WGFD staff.

Brucella abortus is transmitted among hosts through direct contact with the products of *Brucella*-induced abortions. Elk primarily abort during the spring (Cross and others, 2015). To estimate brucellosis risk from elk to cattle, we used the same methods as in Cook and others (2023): the predicted number of *Brucella*-caused abortions in elk on properties used for overwintering cattle was calculated by multiplying the number of female elk on the identified cattle properties in each month by the monthly brucellosis abortion hazard for elk (Cross and others, 2015), assuming a constant pregnancy rate of 80 percent in sexually mature females and an average brucellosis seroprevalence (the percentage of sampled elk with detectable antibodies) of 30 percent.

Elk Global Positioning System (GPS) Data

The elk GPS collar data within the study area were provided by the FWS, Grand Teton National Park, and WGFD (FWS, written commun., 2024; National Park Service, written commun., 2024; WGFD, written commun., 2024). Observations from GPS were collected between 2006–23 with most individuals being collared at the NER in winter months between 2016–22. The total number of observations exceeded 2.2 million (table C1).

Broad-Scale Resource Selection Function

State Highway 22 likely creates a partial barrier to elk movement between the two regions of our study area (the Jackson and Fall Creek Elk Herd Units). Elk rarely crossed this highway in the GPS dataset; however, there were limited data available for elk in the Fall Creek Elk Herd Unit, and the WSMET agreed that more elk are likely to move across this boundary if the NER stops feeding. The elk CWD model accounted for this movement between regions (this volume, chap. B, Cross and others, 2025). The spatial models in this chapter subsequently used the projected number of elk in each region in all simulations of the alternatives from Cross and others (this volume, chap. B, 2025) and assumed Table C1.The number of adult female Cervus elaphus canadensis(Erxleben, 1777; elk) and the number of elk-years with globalpositioning system (GPS) locations from 2006 to 2023 data inJackson, Wyoming, that contributed to estimating habitat selectionacross spatial and seasonal categories in our models.

[An elk-year is defined as any time that an individual elk had a working GPS collar during the corresponding seasons, regardless of whether the full period was observed. Retention of data in the models estimating habitat selection was not conditional on being observed for full monthly or seasonal periods. Winters are defined as December through April, summers are May through November. Severe winters were characterized as winters during which snowfall patterns concentrated more elk on feedgrounds, the National Elk Refuge had to provision larger amounts of feed to elk, and winter elk calf mortality exceeded 5 percent even with additional feed. Winters not meeting these criteria were defined as average. NA, not applicable]

Season	Severity	Number of female elk	Number of elk-years
F	all Creek Elk Her	d Unit	
Summer elk	NA	24	47
Winter-fed elk	Average	17	20
Winter-fed elk	Severe	4	4
Winter-unfed elk	Average	3	3
Winter-unfed elk	Severe	4	4
	Jackson Elk Herc	l Unit	
Summer elk	NA	236	650
Winter-fed elk	Average	183	325
Winter-fed elk	Severe	204	241
Winter-unfed elk	Average	31	48
Winter-unfed elk	Severe	23	23

that elk remained within those herd units. The habitat covariates used by Cook and others (2023) from Maloney and others (2020) were also used in this study, namely the annual integrated Normalized Difference Vegetation Index, elevation, density of roads within a 2.5 kilometers (km) buffer of the location, maximum snow water equivalent, and the percentage of forest and percentage of native herbaceous cover within a 2.5 km buffer of the location (Cross and others, 2023; Maloney, 2020). Other habitat covariates included the distance to feedgrounds, calculated as the distance from the centroids of the four feeding areas on the NER and State feedgrounds in the JHU and NFCHU. With feedback from the WSMET, two continuous variables for aspect were added, where northness was the cosine-transformed radians and eastness was the sine-transformed radians. Other variables added based on WSMET feedback included the location's distance to water (Dewitz and U.S. Geological Survey, 2021; Yan and others, 2019); distance to grass and distance to barren ground (Dewitz and U.S. Geological Survey, 2021); distance to agriculture (Forest Service, written commun., 2023; Cook, 2005; Teton County, Wyoming, 2023); and average minimum January temperature (Thornton and others, 2022). For fed elk in winter months, covariates included a binary feedground raster map for the NER; all raster maps were created at or resampled to a 1,020-m resolution (Cotterill and

Graves, 2024). This resolution required fewer modifications to the original GIS data, was computationally practical, and was deemed appropriately precise considering multiple sources of uncertainty in the elk CWD model and our spatial analysis.

Elk habitat selection coefficients, β , were estimated by employing a use-availability design and logistic regression. For each cell, *l*, we computed the resource selection probability function (Johnson and others, 2006), *w*, as the following equation:

$$w_{ljk} = \exp(\beta_{0jk} + x_{1ljk}\beta_{1ljk} + \dots + x_{nljk}\beta_{nljk}),$$

where

x is a vector of mean values of each environmental variable within each cell,

j is the month, and

k is an indicator variable for fed (*k*=1) or unfed elk (*k*=2).

Equation C1 estimated the per capita probability of use in each cell, $U(x_i)$, as the following equation:

$$U(x_{ljk}) = w(x_{ljk}) / \sum w(x_{ljk}), \qquad (C1)$$

and equation C2 estimated the number of elk, n, in each cell as the following equation:

$$n_{ljkt} = N_{jkt} U(x_{ljk}), \tag{C2}$$

where

 N_{ikt}

For measurable attributes associated with the number of elk days in a particular location, the number of elk estimated in each cell was multiplied by the number of days in the month.

Because the NFCHU region had limited data (from as few as three elk; table C1), we assumed elk in both regions respond similarly to habitat and supplemental feed availability and estimated habitat selection coefficients using data combined across the regions. Each monthly elk GPS dataset contributing to these models was randomly thinned to 6,072 locations, the smallest number of locations in any dataset, because the number of GPS locations varied greatly across datasets, and the total number of cells in the study area was only 6,000 at the 1,020-m resolution. Standardizing the sample size across datasets provided comparable estimates across models in terms of effect magnitude, because the ratio of used-to-available points influences model intercepts. Next, within each region, the per capita probability of elk space-use map was estimated using equation C3:

$$U(x_{ljkR}) = w(x_{ljkR}) / \sum w(x_{ljkR}), \qquad (C3)$$

where

R refers to the region either the JHU or NFCHU.

One of the covariates in *x*, the binary raster map of the NER only exists in the JHU, but we reasoned that the three State feedgrounds in the NFCHU hold a similar level of attraction for fed elk during winter. Therefore, in the per capita probability of elk use calculations for winter-fed elk in the NFCHU, the NER covariate was replaced with a binary raster map representing South Park, Horse Creek, and Camp Creek feedgrounds. Further information supporting this assumption can be found in appendix C2.

Defining available habitat for RSF studies is fraught even under ideal circumstances (Northrup and others, 2013; Warton and Shepherd, 2010), but frequently employed methods include defining availability according to seasonal elk space-use based on home-range or kernel-density estimator methods (Manly and others, 2002). In our case, the GPS dataset likely does not include a representative sample of unfed elk in the system, particularly when divided into monthly timesteps and differing levels of winter severity. As a result, following those conventions could omit habitats occupied by segments of the elk population in our study area, a factor that was considered when the expert elicitation process defined the study area (this volume, chap. A, Cook and others, 2025). Another common convention in use-availability RSF designs is to sample availability at 10 times the number of used locations (Lowrey and others, 2021), but this convention is inadequate when the resolution of the considered areas is coarse (in other words, areas have fewer cells to sample). Most of these concerns are motivated by ensuring accurate estimation of specific habitat selection coefficients and reducing bias from autocorrelated habitat features (Northrup and others, 2013), some of which can be improved through even sampling (for example, a census) of the landscape to represent the full availability of habitats (Benson, 2013). In this analysis, no inference is based on individual selection coefficients, nor is there an inference to habitat selection of elk outside of our study system. The primary goal of the RSF was to predict elk space-use that closely matched observed elk selection patterns and expert judgment in the study area or in segments of the elk population where no comparable observational data existed. To fully represent the available conditions, one available point per cell was sampled in the study area (number of cells in the study area and number of available locations used in the model [n]=6,000).

Experts predicted that once the NER stops feeding elk, NER fed-elk will (1) move to State feedgrounds in the Gros Ventre River drainage, (2) become unfed-elk, or (3) move to the NFCHU. The elk CWD model moves elk to separate population segments to match the proportions of elk that experts identified as likely to transition to each segment (refer to this volume, chap. B, Cross and others, 2025). No further adjustments to the RSF were needed to accommodate the transition of NER elk to the NFCHU because this area had separate predictive maps. To implement the remaining changes for elk-space use predictions, we adjusted the probability of elk use in the NER and two transition areas. The following are cells identified to include in transition areas: (1) areas in the Gros Ventre River drainage surrounding State feedgrounds predicted to be used by fed elk and (2) other winter range areas away from feedgrounds predicted to be used by unfed elk (Native Winter Range Transition Area; NWRTA). The Gros Ventre Transition Area (GVTA) consisted of cells with greater than 0.0001 per capita

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probability of use for fed elk in February in the Gros Ventre River drainage and comprised 82.2 square km. The NWRTA consisted of cells with greater than 0.0001 per capita probability of use for unfed elk in February. The NWRTA included areas in the Gros Ventre River drainage farther from feedgrounds, private property in the area around Jackson, Wyoming, and other areas near the NER (encompassing 131 square km), excluding the GVTA and NER (app. C3). The RSF initially overestimated elk space-use in the GVTA and underestimated NER elk space-use compared to the elk CWD model. Because of these over and underestimations, a portion of GVTA elk was moved to the NER during winter months. Then, under the alternatives where feeding on the NER was discontinued, portions of predicted fed elk space-use in the NER were transitioned to the GVTA or NWRTA in accordance with expert judgment and the elk CWD model once feeding stopped (fig. C1). As feeding stoppage varied by alternative, this transition was made at various time points according to the alternative: (1) under the no feeding alternative, the NER elk transitioned to the GVTA or NWRTA in the first year; (2) under the increase harvest and reduce feeding alternatives, the elk transitioned at the beginning of the sixth year; (3) under the disease threshold alternative, the elk transitioned at the beginning of the third year because this year was when most elk CWD model simulations predicted that the 3 percent prevalence threshold of CWD in the Jackson elk herd was met. The proportions of fed elk being assigned onto or away from the NER during winter did not change according to winter severity. However, the average and severe winter RSFs made different predictions for the initial distributions of elk in the winter months before the relocation.

Fine-Scale National Elk Refuge Winter Resource Selection Function

To evaluate the measurable attributes pertaining to elk use of sensitive areas in the NER, including evaluating the effects of proposed elk exclosures under the reduce feeding alternative, winter elk space-use in the NER was modeled at a fine-scale resolution (30-m cells). We followed the same use-availability design described in the "Broad-Scale Resource Selection Function" section, fitting models only to data falling within the NER boundary between December and April (the winter months). Fitting models to these data excluded most of the unfed elk data previously used in the broad-scale RSF. However, during the unprecedentedly mild winter of 2017–18, feeding was never initiated in the NER. Therefore, in fitting this RSF, the unfed elk datasets were augmented with the GPS observations collected on any elk in the NER that winter. This augmentation precluded the possibility of modeling differences in elk space-use according to winter severity because of inadequate data. The fine-scale NER RSF featured fewer covariates than the broad-scale study area RSF. The unfed-elk RSF model included continuous aspect variables (northness and eastness), distance to grass, elevation, and slope at 30-m resolution (National Aeronautics and Space Administration Jet Propulsion Laboratory [NASA JPL], 2013). The fed-elk model included all covariates of the unfed-elk model and a distance to feeding area covariate, which was calculated using the four designated

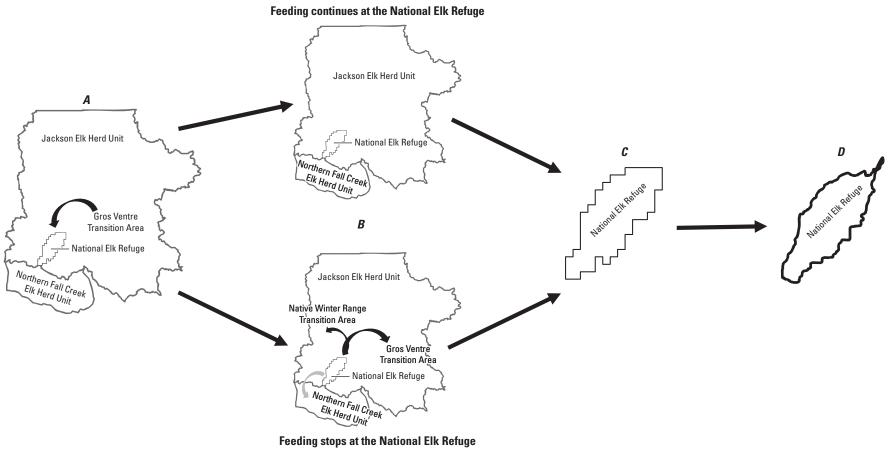
feeding areas in the NER. The number of used locations was randomly thinned to equal the dataset with the least number of observations (n=8,018), and 1 available point was sampled per cell (n=112,988). As with the broad-scale RSF, monthly per capita predicted elk use maps were generated for fed and unfed elk (5 months×2 population segments=10 maps).

Calculating the measurable attributes for the NER in winter was a multistep process based on the 100 simulations of abundances by population segment output by the elk CWD model (this volume, chap. B, Cross and others, 2025). First, the broad-scale RSF, in conjunction with abundances from the elk CWD model, was used to predict the number of fed and unfed elk in the NER at every winter monthly timestep in the simulations. Next, the numbers of elk in the NER were projected according to the selection coefficients of the fine-scale RSF (fig. C1). Finally, the per capita probability of elk use was calculated using equation C1, where the NER boundary defined the area available. Under the reduce feeding alternative, zero elk days were assumed to fall within elk exclosure boundaries.

Results

The broad-scale RSF predicted more fed elk in the NER and State feedgrounds in midwinter compared to December and April when more animals are moving toward or away from feedgrounds in the JHU (fig. C2) and NFCHU (fig. C3) portions of the study area. Predicted elk space-use of the NER by fed and unfed Jackson elk closely matched the GPS locations (fig. C4). Predicted elk using the NER, State feedgrounds located in the Gros Ventre River drainage, and native winter range closely matched numbers from the elk CWD model during the 20 years of simulations across alternatives (figs. C5, C3.2, C3.3). Information about the summer RSF predictions can be found in appendix C4 (figs. C4.1, C4.2).

During the 20 years of simulations, the number of elk days on private property and sensitive vegetation communities reflected the changes in abundance projected in chapter B (this volume, Cross and others, 2025). However, the relative performance of alternatives varied among measurable attributes. The continue feeding alternative produced median estimates with the fewest cumulative elk days on private property and the least brucellosis risk from elk to cattle, although the interquartile ranges from 100 simulations overlapped across most alternatives, especially the increase harvest and reduce feeding alternatives (fig. C6). The no feeding and disease threshold alternatives produced the highest median estimates for these two measurable attributes. In terms of elk days in sensitive vegetation communities, the continue feeding alternative ranked well for narrowleaf cottonwood and willow when calculated with the broad-scale RSF but poorly for quaking aspen (fig. C7). The four alternatives that featured feeding cessation on the NER projected less impact on quaking aspen, narrowleaf cottonwood, and willow in the NER than the continue feeding alternative. Following feed cessation, the fine-scale winter RSF for the NER predicted lower elk densities in the National Elk Refuge. Further information can be found in appendix C5 (fig. C5.1).



Data from Cotterill and Graves, 2024

Figure C1. Flowcharts of the modifications to predicted fed-*Cervus elaphus canadensis* (Erxleben, 1777; elk) distributions during the winter months (December through April) and how winter elk space-use was projected across the National Elk Refuge (NER) in Jackson, Wyoming. *A*, a portion of fed elk was moved from the cells encompassing Gros Ventre Transition Area (GVTA) to the NER. *B*, under the continue feeding alternative, no further changes were made, but under other alternatives and years where the NER did not feed elk, fed elk predicted to be in the NER by the resource selection function (RSF) were relocated to the GVTA and non-feedground cells (Native Winter Range Transition Area, NWRTA). The elk chronic wasting disease model also moved a portion of those elk to the Northern Fall Creek Elk Herd Unit (NFCHU). *C*, the adjusted predictive maps from the broad-scale RSF in *B* estimated the number of elk in the NER in the winter months. *D*, the estimated numbers of elk in the NER from *C* were reprojected across a 30-meter resolution NER winter RSF to calculate the effects of elk on sensitive vegetation communities in the NER.

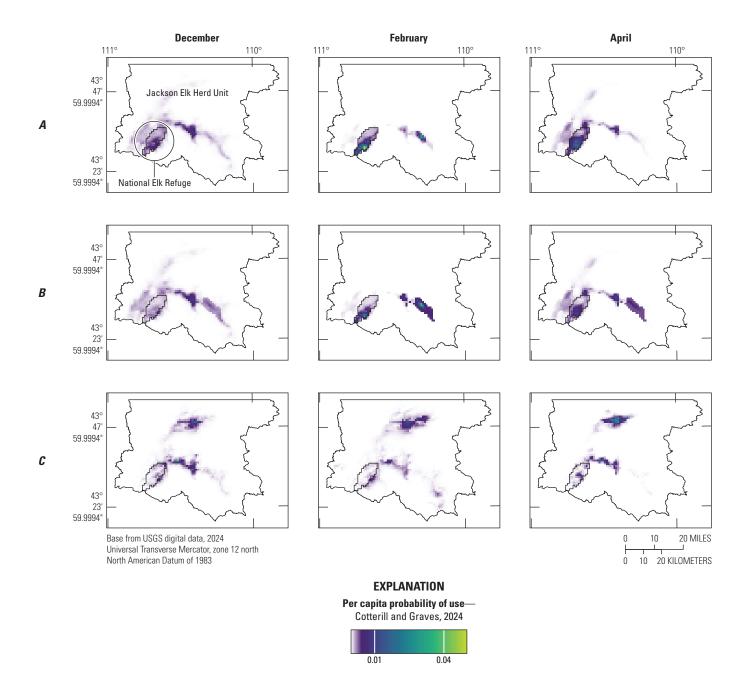


Figure C2. Maps showing the predicted monthly per capita probability of use within the Jackson Elk Herd Unit region of the study area for 3 months during average winter (December–April) conditions for, *A*, fed *Cervus elaphus canadensis* (Erxleben, 1777; elk) when feeding occurs on the National Elk Refuge (NER); *B*, fed elk when feeding on the NER is halted; and, *C*, unfed elk. The northern portion of the Jackson Elk Herd Unit had nearly zero predicted elk space-use during these months and is not shown.

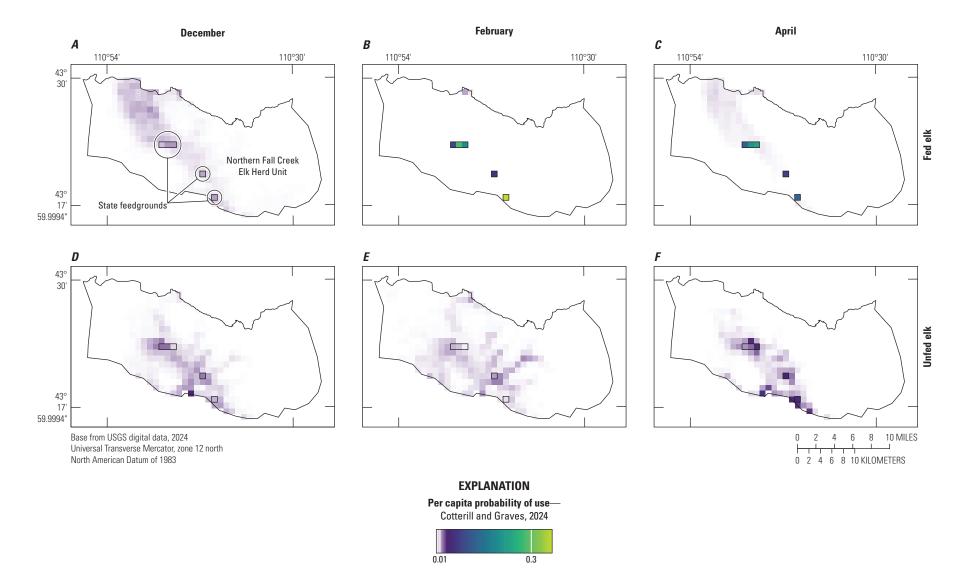


Figure C3. Maps showing the predicted monthly per capita probability of use for fed and unfed Northern Fall Creek Elk Herd Unit *Cervus elaphus canadensis* (Erxleben, 1777; elk) within the study area for 3 months during average winter conditions. *A*, fed elk in December. *B*, fed elk in February. *C*, fed elk in April. *D*, unfed elk in December. *E*, unfed elk in February. *F*, unfed elk in April.

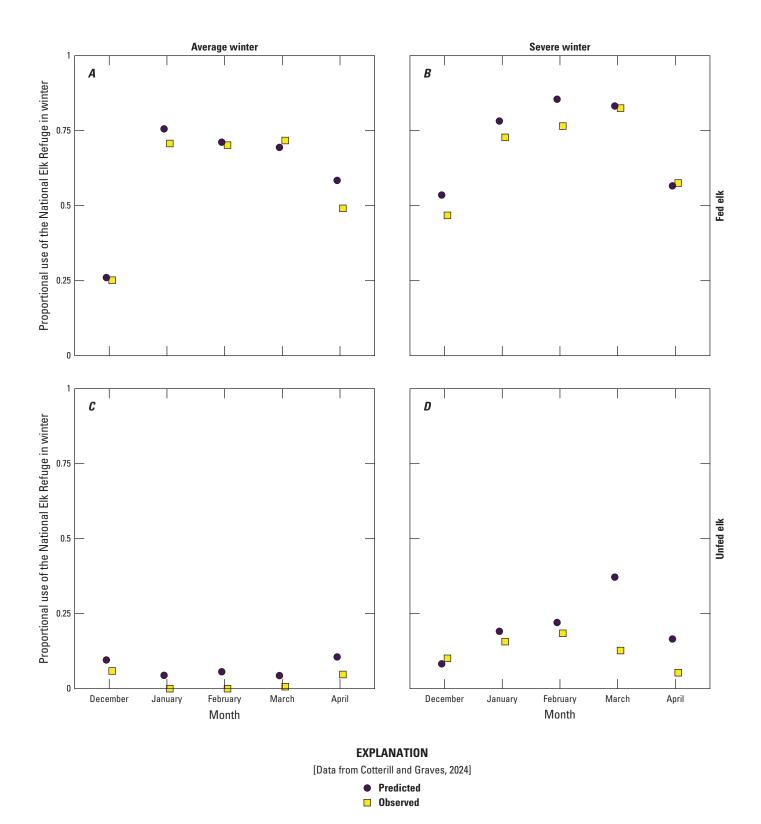


Figure C4. Symbol graphs showing the proportional use of the National Elk Refuge (NER) in Jackson, Wyoming, by Jackson Elk Herd Unit *Cervus elaphus canadensis* (Erxleben, 1777; elk) during winter months (December through April) under average winter conditions for, *A*, fed elk and, *C*, unfed elk, and under severe winter conditions for, *B*, fed elk and, *D*, unfed elk. The predicted use was calculated from the resource selection function (after reassignment of elk from the Gros Ventre Transition Area to the National Elk Refuge), and the observed use was calculated using global positioning system (GPS) collar data.

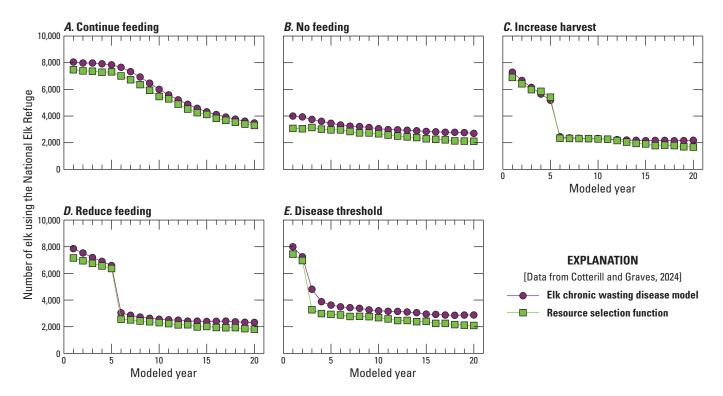


Figure C5. Line graphs comparing the predicted number of *Cervus elaphus canadensis* (Erxleben, 1777; elk) using the National Elk Refuge (NER) in Jackson, Wyoming, in February, during 20 modeled years under the following feedground management alternatives: *A*, continue feeding, *B*, no feeding, *C*, increase harvest, *D*, reduce feeding, and, *E*, disease threshold. Elk chronic wasting disease model (Elk CWD model) values represent the mean values from 100 simulations. The resource selection function (RSF) predicts the average numbers of all elk in the NER.

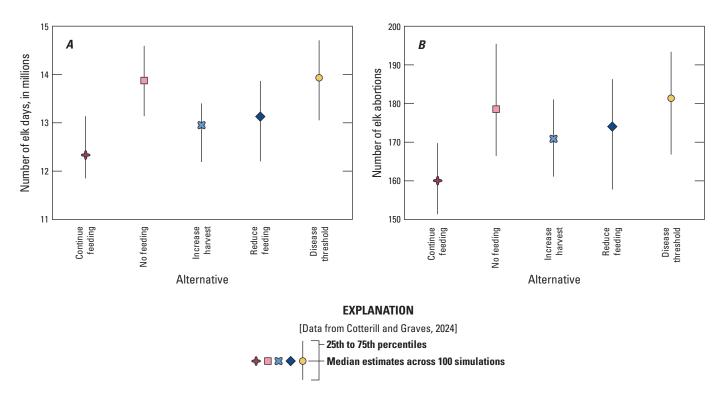


Figure C6. Error bar charts showing the cumulative sums for, *A*, the predicted number of *Cervus elaphus canadensis* (Erxleben, 1777; elk) days on private properties, and, *B*, the predicted number of abortions on winter cattle properties at the end of the 20-year simulations for five feedground management alternatives based on the broad-scale resource selection function (RSF).

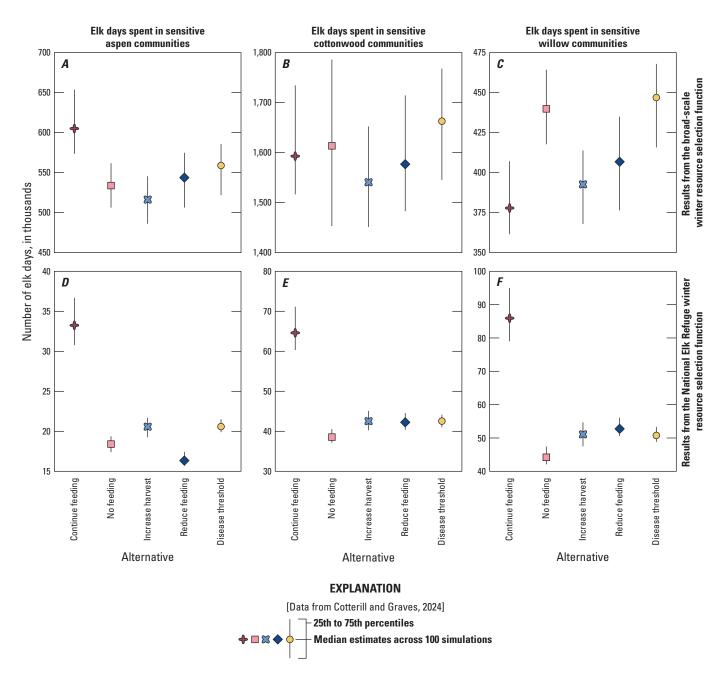
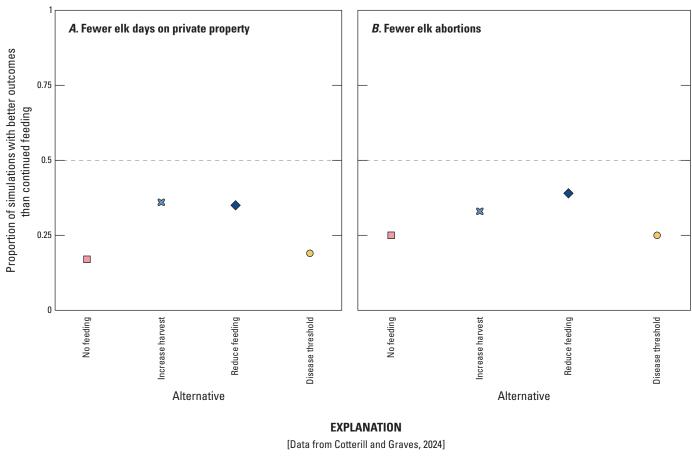


Figure C7. Error bar charts showing the cumulative sums for the number of *Cervus elaphus canadensis* (Erxleben, 1777; elk) days in sensitive vegetation communities at the end of the 20-year simulations for five feedground management alternatives for the winter (December–April) using the broad-scale resource selection functions (RSF) for the full study area (on communities of, *A, Populus tremuloides* Michx. [quaking aspen], *B, Populus angustifolia* E. James [narrowleaf cottonwood], and, *C, Salix* L. [willow]) and the fine-scale RSF for the National Elk Refuge (NER) in Jackson, Wyoming (on communities of, *D*, quaking aspen, *E*, narrowleaf cottonwood, and, *F*, willow). The reduce feeding alternative includes a provision for building additional elk exclosures in the NER, which would primarily benefit quaking aspen.

There was substantial variation in the projected measurable attributes throughout the 100 simulations of each alternative. In terms of limiting the cumulative year-round elk space-use of private property, the continue feeding alternative ranked highest in 64–83 percent of simulations across the other alternatives, although the increase harvest and reduce feeding alternatives out-performed the continue feeding alternative in 36 and 35 percent of simulations, respectively (fig. C8). Similarly, although the continue feeding

alternative ranked highest in limiting brucellosis transmission risk from elk to cattle (expressed as the number of *Brucella*-caused abortions on private properties used for overwintering cattle), some of the alternatives outperformed the continue feeding alternative in a substantial proportion of simulations, including the reduce feeding alternative (better in 39 percent of simulations), the increase harvest alternative (33 percent), and even the no feeding alternative (25 percent; fig. C8).



--- Performance equal to continue feeding alternative

Figure C8. Plots showing the proportion of 100 simulations in which the other feedground management alternatives were projected to yield better outcomes than the continue feeding alternative in Jackson, Wyoming, for, *A*, the predicted number of *Cervus elaphus canadensis* (Erxleben, 1777; elk) days on private property, and, *B*, the predicted number of *Brucella*-caused elk abortions on winter cattle properties. Higher values indicate better outcomes.

When summed through the end of the first five years of implementation, the increase harvest and reduce feeding alternatives (the alternatives that reduce NER elk abundance) outperformed the continue feeding alternative in terms of private property use by elk and were similar to continue feeding in terms of brucellosis risk (refer to app. C6 for more information).

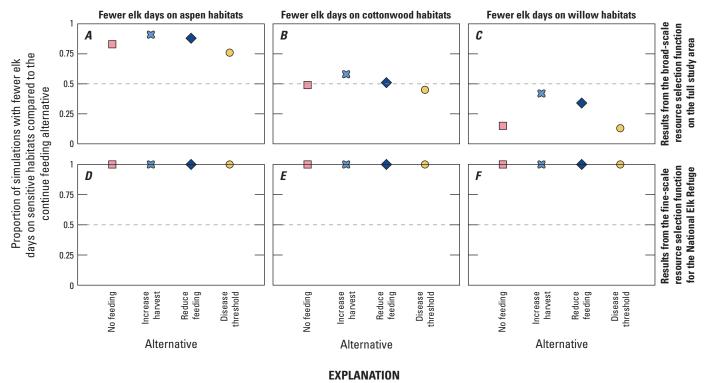
In the matter of elk negatively affecting sensitive vegetation communities in winter, the continue feeding alternative frequently performed worst (fig. C9). Across core quaking aspen, narrowleaf cottonwood, and willow areas, the increase harvest alternative outperformed the continue feeding alternative in 98, 52, and 42 percent of simulations, respectively, across the full study area. Within the NER boundary, the continue feeding alternative performance was the worst in nearly all cases. The 5-year rankings of the sensitive area measurable attributes supported all other alternatives compared to continue feeding, particularly for the NER (refer to fig. C6.2).

Lastly, we summarized the mean annual sums of these measurable attributes in the first and last years of the simulations to provide some additional context (table C2).

There was substantial variation among the 100 simulations when viewed at any given timestep across each alternative. However, an overall pattern was clear: measurable attributes associated with elk space-use decreased in time across all alternatives because of the projected declines in elk abundance from Cross and others (this volume, chap. B, 2025).

Summary

Cervus elaphus canadensis (Erxleben, 1777; elk) abundance was projected to decline during the 20-year period across the alternatives, including the continue feeding alternative. Depending on the alternative, most abundance changes resulted from disease effects, management actions taken to reduce feeding or elk abundance directly, or a combination of those factors (this volume, chap. A, Cook and others, 2025). The measurable attributes reflected human-elk conflicts on private property, including prospective elk-to-cattle brucellosis spillover risk and effects on sensitive vegetation communities in winter (December–April). These effects



[Data from Cotterill and Graves, 2024]

-- Performance equal to continue feeding alternative

Figure C9. Plots showing the proportion of 100 simulations in which the other feedground management alternatives were projected to yield better outcomes than the continued feeding alternative for *Cervus elaphus canadensis* (Erxleben, 1777; elk) days on sensitive vegetation communities in winter (December–April) using the broad-scale resource selection function (RSF) for the full study area (elk days on communities of, *A, Populus tremuloides* Michx. [quaking aspen], *B, Populus angustifolia* E. James [narrowleaf cottonwood], and, *C, Salix* L. [willow]), and the fine-scale RSF for the National Elk Refuge (NER), Jackson, Wyoming, only (elk days on communities of, *D*, quaking aspen, *E*, narrowleaf cottonwood, and, *F*, willow). Higher values indicate better outcomes.

Table C2. The mean sums and standard deviations of the five measurable attributes throughout the full study area in Jackson, Wyoming, in the first (year 1) and last (year 20) years of 100 simulations across the five feedground management alternatives.

["Number of abortions" are given in absolute values. All of the other metrics are reported in thousands of *Cervus elaphus canadensis* (Erxleben, 1777; elk) days. Sensitive vegetation communities consist of communities of *Populus tremuloides* Michx. (quaking aspen), *Populus angustifolia* E. James (narrowleaf cottonwood), and *Salix* L. (willow). The standard deviation is shown in parentheses after the mean sum for each metric. A higher standard deviation indicates greater variation across simulations, while a lower standard deviation indicates more similarity across simulations]

Feedground management alternative	Number of elk days on private property	Number of abortions	Number of elk days on sensitive aspen habitats	Number of elk days on sensitive cottonwood habitats	Number of elk days on sensitive willow habitats
			Year 1		
Continue feeding	849 (43)	11 (1)	42 (4)	111 (11)	26 (2)
No feeding	963 (65)	13 (1)	35 (3)	122 (13)	29 (3)
Increase harvest	839 (48)	11 (1)	40 (4)	108 (11)	25 (2)
Reduce feeding	852 (49)	11(1)	43 (5)	113 (11)	27 (3)
Disease threshold	846 (48)	11 (1)	42 (4)	110 (11)	26 (3)
			Year 20		
Continue feeding	390 (82)	5 (1)	19 (6)	48 (15)	12 (3)
No feeding	491 (102)	7 (1)	20 (4)	52 (16)	16 (3)
Increase harvest	458 (108)	6 (2)	18 (5)	47 (14)	15 (4)
Reduce feeding	458 (104)	6(1)	18 (5)	48 (14)	15 (4)
Disease threshold	506 (105)	7 (2)	21 (4)	54 (16)	17 (4)

were projected to decrease when abundance declined, and in general, the magnitude of these effects in year 20 was roughly half of what was estimated in year 1. However, the exact numbers depend on the alternative. On average, the continue feeding alternative predicted the smallest elk population at the end of year 20 because of the high chronic wasting disease (CWD) mortality (this volume, chap. B, Cross and others, 2025). Continue feeding is also predicted to concentrate more elk at the National Elk Refuge (NER) compared to other alternatives, and the NER contained a relatively large proportion of core Populus tremuloides Michx. (quaking aspen) areas. As a result, continue feeding is projected to result in fewer elk days on private property and reduced brucellosis spillover risk to cattle, but more elk days on quaking aspen areas across the full study area and more elk days on sensitive vegetation communities in the NER. Although the continue feeding alternative had the lowest projection for cumulative risk of brucellosis transmission from elk to cattle, fully contextualizing this risk is difficult without putting the risk into economic terms, which required information that was unavailable at the time of this study; estimates of the cost of brucellosis spillover events to cattle producers in the Jackson Elk Herd Unit have not been documented. We predict differences among the alternatives of about 19-20 elk abortions on cattle properties over the full 20-year simulation period. However, brucellosis risk decreased over time under all alternatives (by roughly half) because elk numbers decreased. A constant seroprevalence rate was assumed, but if elk densities decrease as elk abundance decreases, then brucellosis seroprevalence may also be expected to decline. The total number of predicted elk abortions on winter cattle properties across the alternatives may be less than or nearly equal to historical elk abortion numbers, which did not result in reported cattle Brucella infections in the Jackson Elk Herd Unit.

A fraction of the Jackson elk herd migrates beyond the extent of the study area as defined in this analysis, typically onto adjacent public lands including Yellowstone National Park. Between May and November, 7-12 percent of the global positioning system (GPS) locations in our dataset fell outside the study area. These areas are beyond the authority of the cooperating agencies that contributed to the structured decision-making process, and for the purposes of calculating the measurable attributes in this analysis, only the number of elk days on private properties was likely affected by this decision. Whereas the number of elk days on private property was calculated across all months of the year, other attributes were limited to winter months. Calculation of the sensitive vegetation community measurable attributes was also spatially constrained to core elk winter range. By restricting the summer range, the summer use of private property inside the Jackson Elk Herd Unit was potentially overestimated, although this effect could be similar across alternatives. Thus, although the absolute numbers would change if the study area expanded, this change should not affect the relative ranking of the alternatives against one another.

The GPS data used in this modeling effort were originally collected for a variety of purposes and included mostly female elk captured on feedgrounds. Thus, incorporating expert knowledge was important in developing an appropriate and useful resource selection function (RSF), wherein the numbers of elk predicted in important areas generally match expert knowledge. We accommodated shifts in forage resources using monthly predictions, but forage may decline quickly in some areas where large numbers of elk transition, particularly in low forage years, potentially yielding subsequent movements. Although small areas in these monthly RSFs differ from known use patterns, these differences are consistent across alternatives and should minimally affect rankings across alternatives.

We incorporated as much model complexity as was allowable given our dataset. One limitation was the paucity of unfed-elk collar data, which is not surprising in a region where approximately 90 percent of the elk are fed during the winter (Wyoming Game and Fish Department [WGFD], 2022b) but also makes it challenging to predict what will happen without any feeding. Another limitation was the lack of feedback among models that approximated space-use and elk numbers. The elk CWD model informed our space-use models, but the results from the space-use models did not inform the elk CWD model. If the NER stops feeding elk and Bison bison (Linnaeus, 1758; bison) in winter, some redistribution of animals is expected. The details of that redistribution likely depend on factors not considered in the RSF, including the fidelity of individuals to seasonal ranges and shifting predator densities. For instance, an implicit assumption of habitat selection modeling is that future elk space-use will look like past elk space-use. Yet, the proportion of long-distance migrants in the Jackson elk herd decreased by approximately 40 percent over the 34-year period ending in 2012 (Cole and others, 2015). If this trend continues, we may be underestimating elk use of private properties across the 20-year simulations, and it is unclear how the feedground management alternatives may impact this declining trend in migration.

This chapter presents results based on all available GPS data from 287 female elk from 2006–23. From those GPS data, resource selection functions were estimated for fed and unfed elk across different management alternatives under severe and average winters at a 1,020-meter resolution on a monthly basis over 20 years (27 different predictive maps). We also did this on a 30-meter basis for NER-specific measurable attributes. Formal expert elicitation was used for those aspects that were not predictable given the available data and merged those with quantitative models while accounting for uncertainties. Finally, we summarized the results according to five measurable attributes representing the objectives of the NER. While there are areas for future improvement, these maps provide the best available information to decision-makers on this difficult management decision.

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Appendix C1. Core Elk Winter Areas Defined by the Expert Panel

We convened a panel of eight experts with specialized expertise in *Cervus elaphus canadensis* (Erxleben, 1777; elk) behavior and movement dynamics within the region. The panel included 5 staff members from the Wyoming Game and Fish Department, 1 staff member from the U.S. Fish and Wildlife Service, and 2 staff members from the National Park Service. The panel experts participated in a mapping exercise that defined core elk wintering habitats within the study area for National Elk Refuge (NER) elk when food was not provided. These core areas could include winter range on public lands and conflict private land areas (private lands where conflict could arise between owners and elk). Specifically, the experts responded to the following two verbatim questions about elk transitions to different areas immediately after feeding stops on the NER:

- Of the elk that transition off [the] NER and onto a mix of conflict private land areas and winter range, we are interested to know what the "core area" of use is. We define core area as the area where 50 percent of the elk that transition off [the NER] will go (not to include State feedgrounds).
- 2. How confident are you that the polygon includes the core areas used by elk and excludes areas that are not used in years where feed is not provisioned?

We asked the panel to assume an average snowfall year with regard to the duration of the season and sustained snow depths. We also asked the panel to assume that elk may have learned behavioral responses to feeding from the normal feeding operations. Behaviors included the annual return of individuals to the NER with an expectation that supplemental food would be provisioned when forage becomes scarce. Question 1 was completed in Microsoft PowerPoint, and their raw estimates are shown in figure C1.1.

Polygons provided by individuals were merged in ArcGIS Pro (fig. C1.2) to generate a minimum convex polygon that included all areas demarcated by each respondent. This polygon represents the maximum area where experts thought 50 percent of winter elk would be located after feed cessation, which reduced the spatial extent under consideration when calculating the sensitive area measurable attributes (fig. C1.2).

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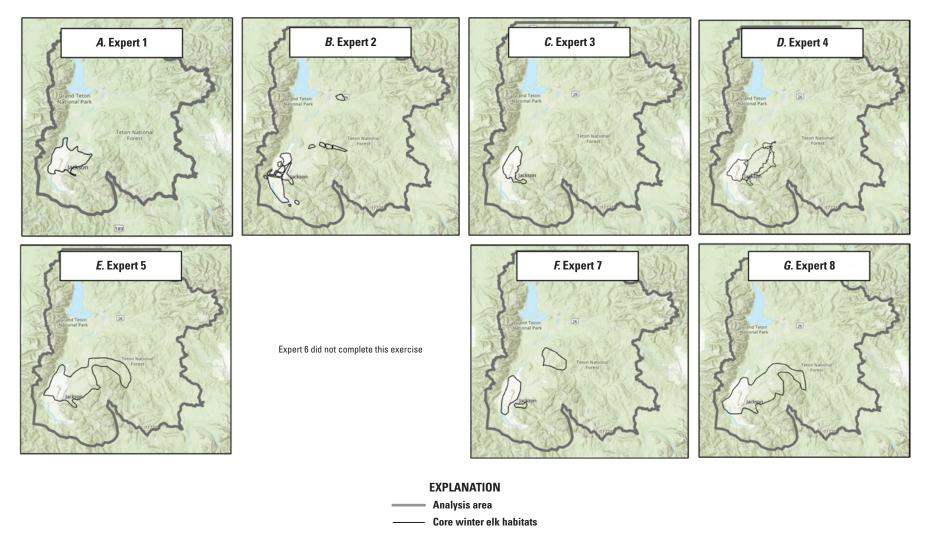


Figure C1.1. Maps showing the raw polygons drawn by experts depicting core winter *Cervus elaphus canadensis* (Erxleben, 1777; elk) habitats in the study area in Jackson, Wyoming, under no-feeding conditions (excluding a response from Expert 6, who did not complete the exercise).

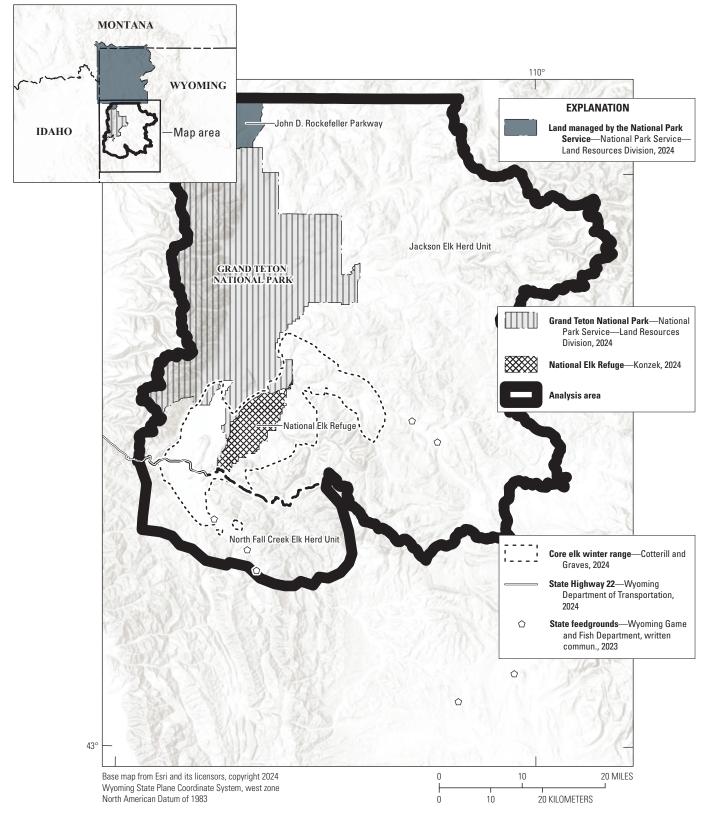


Figure C1.2. A map of the full study area that consists of two regions divided by State Highway 22: the Jackson Elk Herd Unit to the north and the Northern Fall Creek Elk Herd Unit to the south. The National Elk Refuge and State feedgrounds are shown in addition to the core *Cervus elaphus canadensis* (Erxleben, 1777; elk) winter range identified by experts as the core elk winter habitat.

Appendix C2. Predicted Elk Use of Winter Feedgrounds in the Northern Fall Creek Elk Herd Unit

A limited number of collars have been deployed for the Northern Fall Creek Elk Herd Unit (NFCHU), so location data from both the NFCHU and Jackson Elk Herd Units (JHU) were used to model habitat selection. Few Cervus elaphus canadensis (Erxleben, 1777; elk) crossed State Highway 22 (the boundary of the Jackson and Fall Creek Elk Herd Units) in the global positioning system (GPS) data spanning 2006–23, and the resource selection model does not account for this apparent barrier effect. To address this movement, we used expert elicitation to estimate how many elk would cross the highway to the NFCHU. These movements were incorporated as changes in abundance in the elk chronic wasting disease model described in Cross and others (this volume, chap. B, 2025). Thus, the population model resulted in separate abundance predictions for each herd unit. Although we estimated selection across the full study area using data from both JHU and NFCHU, we applied the abundance predictions to predict elk use for each region. The predicted probability of use map of each region was scaled to sum to 1. In doing so, we reasoned that State feedgrounds in the NFCHU were functionally similar to the National Elk Refuge (NER) in the Jackson Elk Herd Unit, and the selection coefficient for the NER in the Jackson Elk Herd Unit could be used to inform selection for the State feedgrounds. We then compared the predicted versus observed proportional winter elk space-use of the NFCHU feedgrounds (fig. C2.1).

Although some monthly predictions had larger differences (January in average winters, December and April in severe winters), the cumulative use by elk over the full winter (December–April) was similar.

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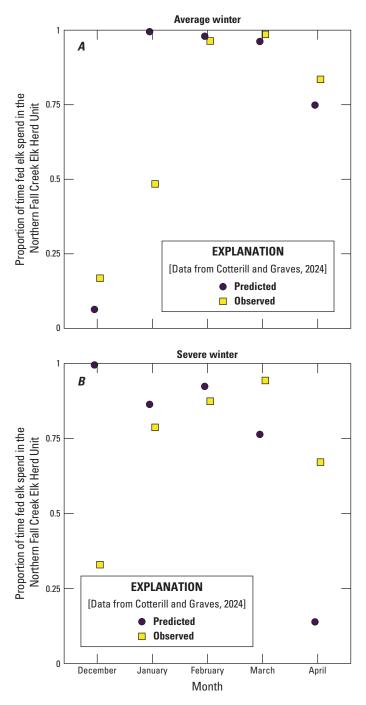


Figure C2.1. Symbol graphs showing the predicted and observed proportional use by fed *Cervus elaphus canadensis* (Erxleben, 1777; elk) for three State feedgrounds in the Northern Fall Creek Elk Herd Unit (NFCHU) during, *A*, average winters, and, *B*, severe winters. Winters are defined as December through April. Predicted values were the proportion of the NFCHU resource selection function probability of use occurring on feedgrounds, and observed values were the proportion of global positioning system (GPS) observations occurring on feedgrounds.

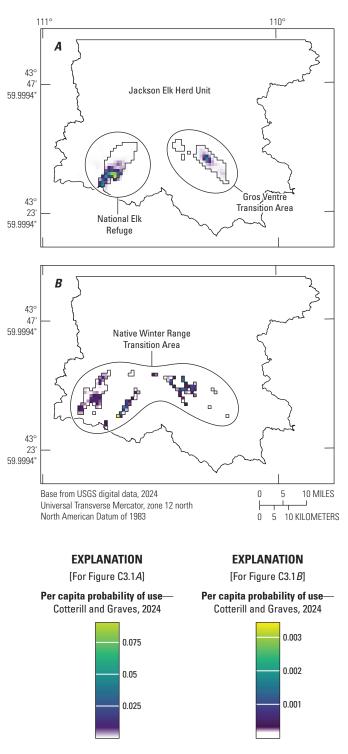
Appendix C3. Adjusted Use Predictions for Jackson Elk Attending State Feedgrounds in the Gros Ventre River Drainage or in the Native Winter Range

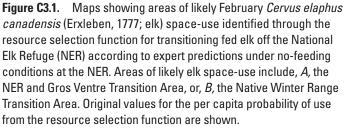
To align predictions of *Cervus elaphus canadensis* (Erxleben, 1777; elk) space-use under no-feeding winter conditions at the National Elk Refuge (NER) with expert opinion when no feeding occurs on NER, areas of important fed elk use were first identified from the resource selection function in the transition areas because these were not explicitly described by the experts initially. To identify the Gros Ventre Transition Area (GVTA; fig. C3.1), the February severe winter conditions map of predicted per capita elk use in the Gros Ventre River drainage was used because that map shows when and where elk are most spatially constrained while attending the State feedgrounds located in the Gros Ventre River drainage. The GVTA was classified as cells where predicted per capita use exceeded 0.0001 (equivalent to use by 1 elk in 10,000). This approach identified 79 cells, equal to 82.2 square kilometers, at the 1,020-meter resolution of the broad-scale resource selection function (RSF). Similarly, to identify the Native Winter Range Transition Area (NWRTA), we classified cells used by fed elk near, but outside of, the NER and the GVTA. The NWRTA cells also used average winter conditions, when elk use is less constrained spatially and includes a larger proportion of private property where conflict is possible. Using the same 0.0001 per capita predicted elk space-use threshold for classification, 126 cells (area=131.1 square kilometers) were identified as the NWRTA. Then, we adjusted the per capita probability of use maps such that RSF predictions matched the elk chronic wasting disease (CWD) model and (expert predictions) for the different population segments at monthly timesteps. The fed elk RSFs initially overpredicted GVTA use and underpredicted NER use. For each feedground management alternative, 30 percent of the total predicted use falling in the GVTA was transitioned to NER. Then, for alternatives where NER feeding ceased, portions of the predicted fed-elk use falling inside the NER were transitioned to the GVTA and NWRTA. Under the no feeding alternative, elk transitioned from the NER to the GVTA and NWRTA in the first winter of simulations. Under the reduce feeding and increase harvest alternatives, elk transitions started in the sixth year. Under the disease threshold alternative, elk transitions occurred in the third year, when most simulations predicted that 3 percent CWD prevalence would be met. To adjust the per capita use maps and thus transition elk, the per capita probability of use was proportionally subtracted across all cells in the NER and evenly added to all cells in the transition areas. Based on the best match to the expert opinion and results of those opinions embedded in the elk CWD model, 45 percent of NER elk use was assigned to the GVTA, and 5 percent of the remaining NER use was assigned to the NWRTA. These relative percentages are provided for clarity and reproducibility. However, they should not be directly interpreted as percentages of the herd transitioning away from NER. For that percentage, we refer to Cross and others (this volume, chap. B, 2025) and the expert predictions. Here, our adjustments to the map closely match the elk CWD model assumptions (figs. C3.2 and C3.3). Although the NWRTA was used to relocate fed NER elk to probable areas of use under the no-feeding

alternative, to compare our spatial predictions to elk CWD model predictions for the unfed segment of the Jackson elk herd, we summarized all elk in the study area outside of the NER and GVTA, not only elk within the NWRTA (fig. C3.3).

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- Cotterill, G.G., and Graves, T.A., 2024, Supporting code for— Evaluating elk distribution and conflict under proposed management alternatives at the National Elk Refuge in Jackson, Wyoming: U.S. Geological Survey software release, at https://doi.org/10.5066/P14FF6E6.
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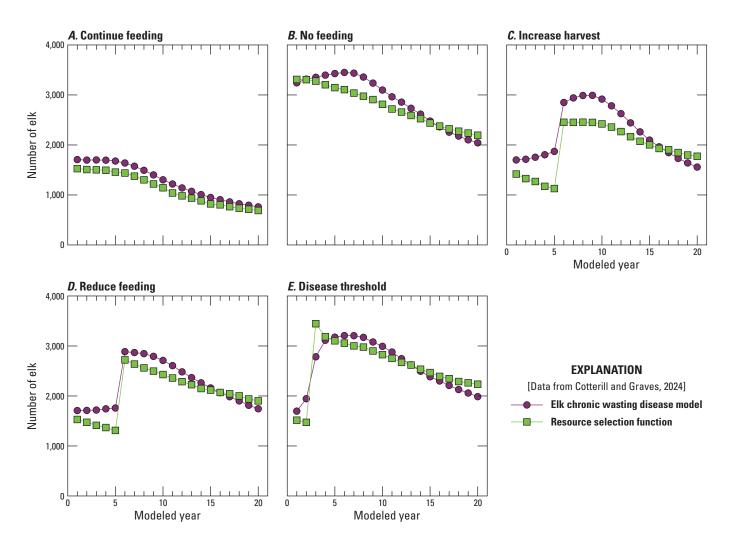


Figure C3.2. Line graphs comparing the numbers of *Cervus elaphus canadensis* (Erxleben, 1777; elk) using the State feedgrounds in the Gros Ventre River drainage in February during 20 modeled years under the following feedground management alternatives: *A*, continue feeding, *B*, no feeding, *C*, increase harvest, *D*, reduce feeding, and, *E*, disease threshold. The disease simulation model for elk chronic wasting disease (CWD) predicts the average February numbers for Gros Ventre elk (a population segment of the Jackson elk herd in Cross and others [this volume, chap. B, 2025]) across all simulations. The resource selection function (RSF) numbers predict the average February numbers of elk inside the Gros Ventre Transition Area. Average February numbers are calculated from 100 simulations for each year, but figure C3.2 also shows 20 years of predictions for each alternative.

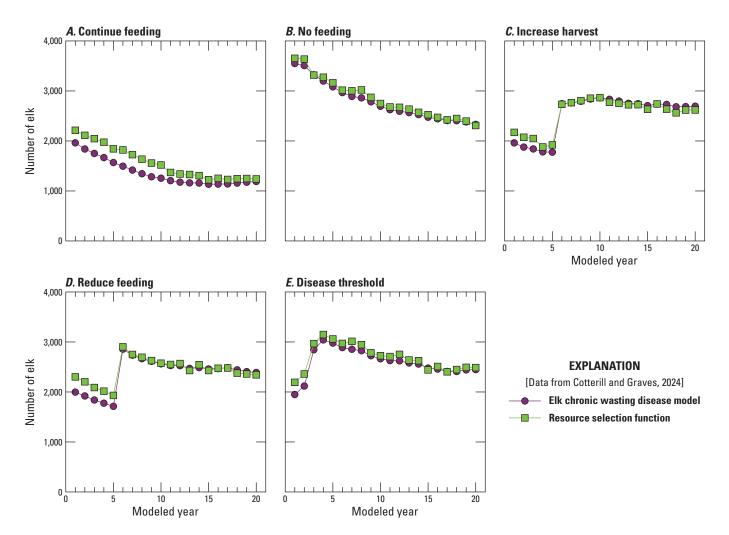


Figure C3.3. Line graphs comparing the predicted numbers of *Cervus elaphus canadensis* (Erxleben, 1777; elk) inside the Jackson Elk Herd Unit using all areas outside of the National Elk Refuge (NER) and the Gros Ventre Transition Area (GVTA) in February across 20 modeled years under the following feedground management alternatives: *A*, continue feeding, *B*, no feeding, *C*, increase harvest, *D*, reduce feeding, and, *E*, disease threshold. The disease simulation model for elk chronic wasting disease (CWD) predicts the average February numbers for the unfed portion of the Jackson elk herd across all simulations, and the resource selection function (RSF) numbers predict the average February numbers of Jackson Elk Herd Unit elk outside of the NER and the GVTA. Average February numbers are calculated from 100 simulations for each year, but figure C3.3 also shows 20 years of predictions for each alternative.

Appendix C4. Elk Summer Predictive Maps from the Broad-Scale Resource Selection Function

Summer predictive *Cervus elaphus canadensis* (Erxleben, 1777; elk) use maps were modeled without any adjustments (fig. C4.1). We verified that the relative predicted versus observed elk use of high- and low-elevation areas was similar (fig. C4.2). We defined high-elevation areas as those at or above 2,400 meters (7,874 feet); anything below 2,400 meters (7,874 feet) was defined as low elevation. For reference, the town of Jackson, Wyoming, is at approximately 1,901 meters (6,237 feet).

Reference Cited

Cotterill, G.G., and Graves, T.A., 2024, Supporting code for— Evaluating elk distribution and conflict under proposed management alternatives at the National Elk Refuge in Jackson, Wyoming: U.S. Geological Survey software release, at https://doi.org/10.5066/P14FF6E6.

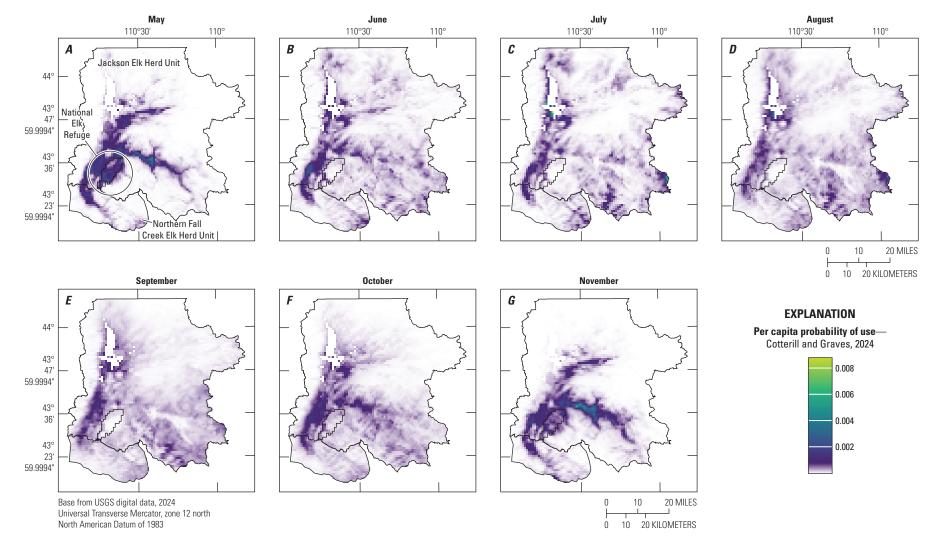


Figure C4.1. Maps showing the per capita probability of use by *Cervus elaphus canadensis* (Erxleben, 1777; elk) in the study area during summer months (May–November). The study area comprises two regions divided by State Highway 22. These regions are the Jackson Elk Herd Unit to the north and the Northern Fall Creek Elk Herd Unit to the south.

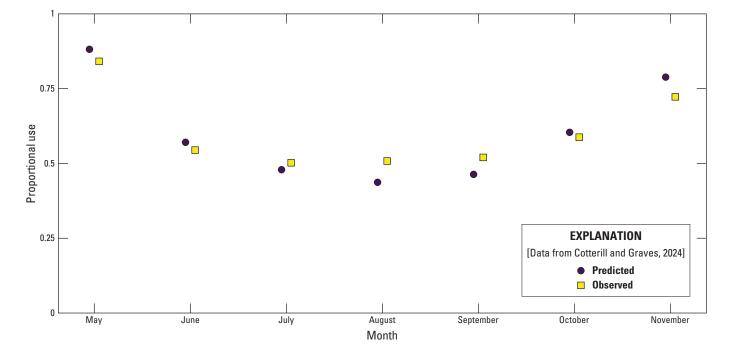


Figure C4.2. Symbol graph showing the proportions of *Cervus elaphus canadensis* (Erxleben, 1777; elk) using areas below 2,400 meters (7,874 feet) in elevation across the study area between May and November. The predicted proportions are calculated from the broad-scale resource selection function (RSF), and the observed proportions are calculated from the elk global positioning system collar data.

Appendix C5. Elk Predictive Maps from the National Elk Refuge Winter Resource Selection Function

The fine-scale winter resource selection function for the National Elk Refuge (NER) predicted lower *Cervus elaphus canadensis* (Erxleben, 1777; elk) densities on the NER following feed cessation under the other feedground management alternatives compared to the continue feeding alternative (fig C5.1).

Reference Cited

Cotterill, G.G., and Graves, T.A., 2024, Supporting code for— Evaluating elk distribution and conflict under proposed management alternatives at the National Elk Refuge in Jackson, Wyoming: U.S. Geological Survey software release, at https://doi.org/10.5066/P14FF6E6.

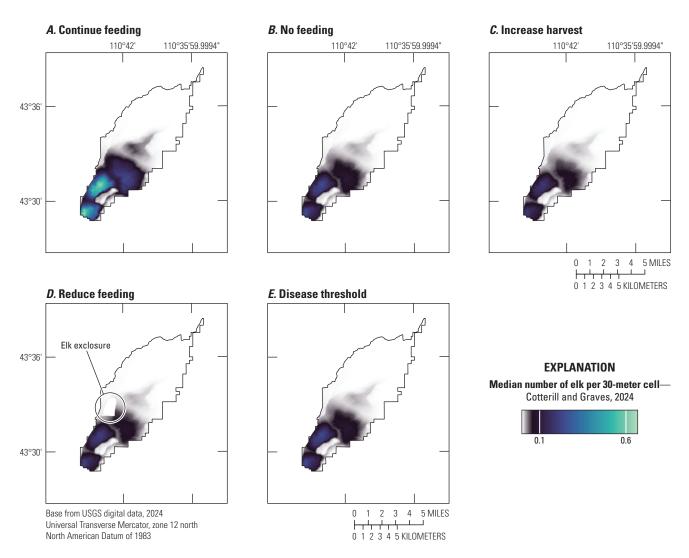


Figure C5.1. Maps showing the median number of *Cervus elaphus canadensis* (Erxleben, 1777; elk) predicted per 30-meter cell on the National Elk Refuge in February of the sixth simulation year (the first year after feed-cessation under the increase harvest and reduce feeding alternatives) for the following feedground management alternatives: *A*, continue feeding, *B*, no feeding, *C*, increase harvest, *D*, reduce feeding, and, *E*, disease threshold. The reduce feeding alternative also included proposed elk exclosures.

Appendix C6. Near-Term Rankings (5 years) of Measurable Attributes

The 5-year rankings closely follow (1) the *Cervus elaphus canadensis* (Erxleben, 1777; elk) chronic wasting disease model's projections of Jackson Elk Herd Unit abundance in the first 5 years, (2) the assumptions made regarding elk transitioning to other areas after the National Elk Refuge feed cessation, and (3) the prediction under the disease threshold alternative that 3 percent chronic wasting disease prevalence is rapidly exceeded. As a result, the alternatives predict 1,000–2,000 fewer Jackson Elk Herd Unit elk per year in the first 5 years after implementing other feedground management alternatives compared to the continue feeding alternative (figs. C6.1, C6.2).

Reference Cited

Cotterill, G.G., and Graves, T.A., 2024, Supporting code for-Evaluating elk distribution and conflict under proposed management alternatives at the National Elk Refuge in Jackson, Wyoming: U.S. Geological Survey software release, at https://doi.org/10.5066/P14FF6E6.

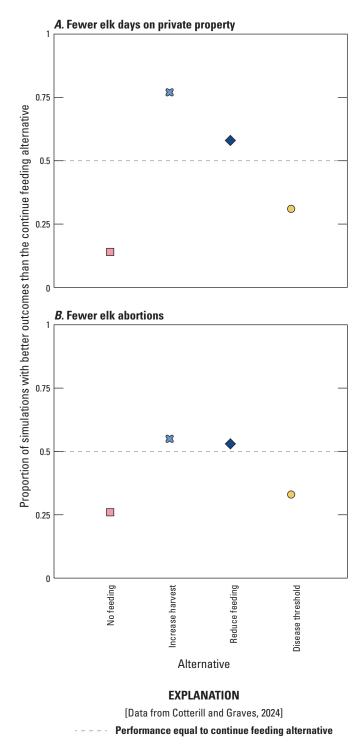
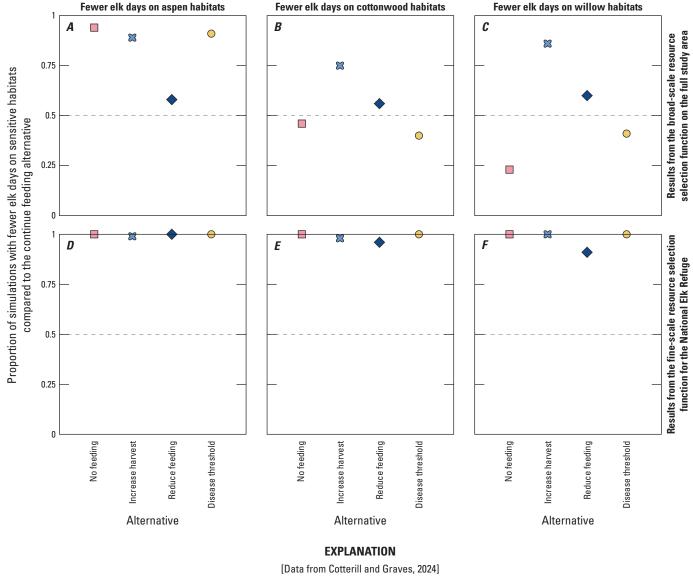


Figure C6.1. Plots showing the proportion of 100 simulations in which the other feedground management alternatives were projected to yield better outcomes compared to the continue feeding alternative in terms of, *A*, the projected number of *Cervus elaphus canadensis* (Erxleben, 1777; elk) days on private property and, *B*, the brucellosis risk to cattle during the first 5 years following implementation of the feedground management alternatives. Higher values indicate better outcomes.



---- Performance equal to continue feeding alternative

Figure C6.2. Plots showing the proportion of 100 simulations in which the other feedground management alternatives were projected to yield better outcomes compared to the continue feeding alternative in terms of *Cervus elaphus canadensis* (Erxleben, 1777; elk) affecting sensitive vegetation communities December–April using, *A*, the broad-scale resource selection function (RSF) for the full study area (elk days on communities of, *A, Populus tremuloides* Michx. [quaking aspen]; *B, Populus angustifolia* E. James [narrowleaf cottonwood]; and, *C, Salix* L. [willow]) and the fine-scale RSF for the National Elk Refuge (NER) in Jackson, Wyoming, only (elk days on communities of, *D,* quaking aspen, *E*, narrowleaf cottonwood, and, *F*, willow). These projections are for the first 5 years following implementation of the feedground management alternatives. Higher values indicate better outcomes.

Bison Population Dynamics, Harvest, and Human Conflict Potential Under Feedground Management Alternatives at the National Elk Refuge in Jackson, Wyoming

By Jonathan D. Cook, Margaret C. McEachran, Gavin G. Cotterill, and Eric K. Cole

Chapter D of Decision Analysis in Support of the National Elk Refuge Bison and Elk Management Plan

Edited by Jonathan D. Cook and Paul C. Cross

Ecosystems Mission Area—Biological Threats & Invasive Species Research Program

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Abbreviations

CWD	chronic wasting disease
FWS	U.S. Fish and Wildlife Service
GTNP	Grand Teton National Park
NPS	National Park Service
NER	National Elk Refuge
WGFD	Wyoming Game and Fish Department
WSMET	wildlife subject matter expert team

Bison Population Dynamics, Harvest, and Human Conflict Potential Under Feedground Management Alternatives at the National Elk Refuge in Jackson, Wyoming

By Jonathan D. Cook¹, Margaret C. McEachran¹, Gavin G. Cotterill¹, and Eric K. Cole²

Abstract

Bison bison (Linnaeus, 1758; American bison) were once abundant across North America but declined due to overharvesting in the late 1800s. The reintroduced population in and around Jackson, Wyoming has averaged 485 individuals between 2018-2023 and is the subject of a planning process to inform management strategies that will guide the U.S. Fish and Wildlife's next "Bison and Elk Management Plan" for the National Elk Refuge. This small population may benefit from historical winter-feeding operations on the National Elk Refuge because those operations may increase overwinter survival and limit human-bison conflicts, which are the number of individual bison that engage in nuisance, damaging, or otherwise aggressive behaviors with humans and livestock, that may lead to culling and other sources of mortality (for example, vehicle collisions). To inform the next "Bison and Elk Management Plan," the U.S. Geological Survey used a population model to evaluate five management alternatives for bison and Cervus elaphus canadensis (Erxleben, 1777; elk) feedground operations that included continuing the elk and bison feeding program, immediately stopping the feeding program, and three other alternatives that would phase out the feeding program after a period of time. The results indicate that the bison population would be expected to decline over the next 20 years under all alternatives that stop feeding bison on the refuge. Further, this decline would lead to an associated reduction in bison harvest opportunities for resident, nonresident, and Tribal hunters. Finally, human-bison conflicts would also be expected to increase under the no feeding alternatives because bison may venture onto private lands in greater numbers if feed is not provisioned during winter months. In combination, these results suggest that feeding may lead to better outcomes for bison over the next 20 years; however, these effects may be traded off against other downsides of the feedground program, such as increased rates of animal-to-animal contact on feedgrounds that can lead to disease transmission.

Introduction

Bison bison (Linnaeus, 1758; American bison) were once abundant and widespread across large extents of North America (Jones and others, 2020). The population that inhabited areas in and around Yellowstone National Park (fig. D1) was nearly extirpated by the mid-1880s and was lost from Jackson Hole, Wyoming. Bison were subsequently reintroduced into the Jackson region when 20 individuals were relocated from Yellowstone to an enclosure at Jackson Hole Wildlife Park in 1948 (U.S. Fish and Wildlife Service [FWS], 2019). The enclosed bison were supplemented with other bison from Theodore Roosevelt National Park after the discovery of brucellosis led to culling of the original herd. Then, in 1968 11 adults and 4-5 calves escaped and began ranging freely throughout the region, including seasonal movements to habitats on Grand Teton National Park (GTNP), the National Elk Refuge (NER), and other surrounding public and private lands. The escaped bison founded a free-ranging herd that initially remained at low abundance (less than 40 individuals). However, following the discovery of supplemental food provisioned to Cervus elaphus canadensis (Erxleben, 1777; elk) on the NER, the population grew by 10-14 percent annually starting in the 1980s (FWS and National Park Service [NPS], 2007). Winter counts in 2007 estimated a population high of 1,059 individuals; a more recent mid-winter count in 2023 estimated 514 individuals (WGFD, 2023).

While the larger population size has conveyed certain advantages to the Jackson bison herd, it has also led to some negative aspects related to human-bison conflicts and overgrazing on sensitive habitats. For example, larger bison populations are more resilient to random events and genetic effects, including bottlenecks (drastic population reduction) and drift (random gene variant fluctuations) that are a concern for bison in this population because of their low genetic diversity (Hartway and others, 2020). Larger populations likewise increase opportunities for wildlife viewing and photography, harvest by resident and nonresident Wyoming hunters, and Tribal ceremonial and subsistence take. However, this larger bison population has damaged native grasslands and other habitats from overgrazing, competed with elk for critical resources, elevated disease transmission risk from bison to domestic livestock, and increased costs to natural

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²U.S. Fish and Wildlife Service.

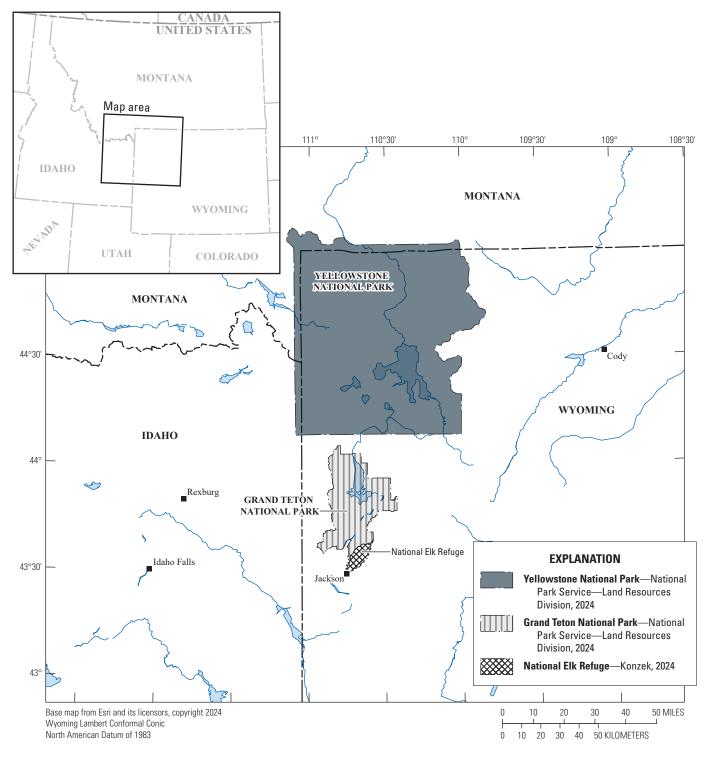


Figure D1. Map showing the boundaries of Yellowstone National Park, Grand Teton National Park, and the National Elk Refuge—the areas used by bison in the Greater Yellowstone Ecosystem, Wyoming.

resource agencies associated with bison management. Thus, successful bison management may require balancing the positive aspects of larger populations while limiting the effects of overabundance on sensitive habitats and human-bison conflicts.

Managing bison and associated conflicts falls under the authority of land management agencies, FWS, NPS, and state agencies tasked with managing wildlife and livestock, including the Wyoming Game and Fish Department (WGFD) and the Wyoming Livestock Board. Under their management authority, FWS is evaluating a range of management alternatives for bison and elk on the NER as part of their next "Bison and Elk Management Plan." Currently, FWS provisions supplemental food to bison and elk during winter months to increase individual survival and reduce the potential for bison-elk and human-bison conflicts (FWS, 2019). The feeding program mainly operates between January and April of each year, depending on forage production and availability, and is guided by the "Step-Down Bison and Elk Management Plan" (FWS, 2019), which intends to reduce the reliance of bison and elk on winter feeding.

The alternatives under consideration for the next "Bison and Elk Management Plan" for the NER could alter feedground operations and replace the existing management (FWS and NPS, 2007) and step-down (FWS, 2019) plans. The alternatives were developed by FWS to evaluate changes to elk winter feeding in response to a recent detection of chronic wasting disease (CWD) in elk and concern that CWD could spread faster in elk in feedground settings (Cook and others, 2023). While bison are not susceptible to CWD, changes to winter feeding activities could change bison abundance, bison harvest, and the location and number of human-bison conflicts. This report details the development of a sex- and age-structured matrix model that uses empirical data and expert judgment to evaluate a set of proposed management alternatives and provide numeric estimates for objectives associated with bison abundance, bison harvest, and human-bison conflict potential over time and after 20 years of implementation (Cook and others, 2025b, this volume, chap. D). The results will inform an Environmental Impact Statement and assist managers in selecting an alternative that best meets management priorities and mandates on the NER.

Methods

We adapted an existing sex- and age-structured matrix model that was previously used to model other ungulate population dynamics and used it to evaluate alternatives in support of the NER "Bison and Elk Management Plan" (Cross and Almberg, 2019; Cook and others, 2023; Cross and others, 2023). The work to adapt the model proceeded in close collaboration with a wildlife subject matter expert team (WSMET) of 13 individuals with expertise in bison ecology and wildlife management principles. The team helped describe the expected changes to bison space use and population dynamics, the potential response of management agencies to bison populations, and also provided data that were then developed into quantitative relationships. To inform parameter values, published literature and expert elicitation were used to estimate vital (population change) rates, harvest statistics, and other parameters. For expert elicitation, we used a modified Delphi and IDEA ("Investigate, Discuss, Estimate, Aggregate") protocol with six science expert panelists who hold specialized knowledge about the parameters of interest (Hanea and others 2017); this group (herein referred to as 'experts', 'expert panel', or 'expert panelist(s)') was considered separate from the WSMET but did include five common members.

To initiate the model, historical bison herd counts and simulated bison population performance were incorporated with relevant sources of structural and parametric uncertainty identified by a scientific expert panel. For each alternative, we ran 1,000 projections while randomly sampling from the parametric uncertainty defined by the distribution for each parameter in each simulation. We then used the model to predict abundance, harvest, and winter movement dynamics of bison on and off the NER and under the management alternatives. In the following sections, we describe our methods, including the model structure, incorporation of alternatives, parameter estimation methods, and initial conditions.

Model Structure

The matrix model included five distinct sex and age classes chosen to represent demographic groupings that experience different vital and harvest rates within the Jackson bison herd. Those classes included (1) calves (0–1 years old) of both sexes, (2) male yearlings (1–2 years old), (3) female yearlings, (4) adult (more than 2 years old) males, and (5) adult females. The maximum age that an individual could reach was 15 years of age, and we assumed that reproduction began at age 2. The model transitioned those sex and age classes through monthly time steps and important life history events, including births in the spring, harvest in the fall, and monthly natural survival.

In addition to these monthly transitions, we included the following three dynamics that affect population performance: (1) calf mortality as a function of winter feeding and winter conditions, (2) mortality for all sex and age classes in human-bison conflict situations (for example, bison vehicle collisions, bison on cattle lands), and (3) an adaptive harvest rate-setting process as a function of the overall population size during February counts.

For calf mortality in severe winters and under unfed conditions, we allowed for increased mortality from January to April. The increased mortality was a result of a lack of available forage and increased expenditure of fat reserves during times of high snowpack. The reduction in survival was only applied to the calf class based on conversations with the WSMET and only in a proportion of modeled years (oral commun., 2024). We assumed that each year had a 0.25 probability of being severe enough to cause excess calf mortality.

The other source of mortality, human-bison conflict, also occurred in winter months. To determine how many bison would experience conflict and mortality in the winter, we randomly

assigned individual bison to one of the three following segments: (1) NER feedground, (2) native winter range, and (3) conflict bison population segments. The NER feedground bison were bison individuals that overwinter on NER, whereas the native winter range and conflict bison population segments overwinter off of NER either in areas with low conflict potential (native winter range segment), or in areas with high conflict potential (conflict segment). The conflict bison were expected to have increased use of private lands where negative interactions with local residents, livestock, and vehicles would occur, thus, we assumed that this segment was subjected to a higher monthly mortality rate. We determined the proportion of bison in each segment based on expert judgment and historical winter counts of bison on the NER and winter range. The feedground segment represented those individuals that overwinter on the NER (January-April in the model) in an average year and received most of their daily caloric intake by consuming provisioned food resources. The winter range segment consisted of individuals who did not overwinter on the NER feedgrounds but instead spent winter months on native winter ranges, including the northern and eastern areas of the GTNP (WSMET, oral commun., 2024). The final group, conflict bison, was assumed to either be at a low number when feedgrounds were operational or at a high number when feedground operations ceased (WSMET, oral commun., 2024). Under these unfed conditions, we assumed that the proportion of bison that used the NER (and expected to be fed) would split onto private lands if food were not provisioned. Further, we assumed that conflicts would be higher under severe winter conditions. Additional details on calf and conflict mortality are in the "Incorporating Alternatives" section.

For adaptive harvest, we allowed harvest rates of each sex and age class to be set annually according to the relationship between the February count and the Jackson bison herd objective of 500 total animals. The WGFD manages ungulates in Wyoming according to population objectives (\pm 20 percent), which consider available habitat, sustainable harvest opportunities, human-wildlife conflict, disease, and other factors. Population objectives are recommended by WGFD wildlife managers using biological and social considerations, undergo a public input process, and are decided by the Wyoming Game and Fish Commission (WGFD, 2024). The WGFD conducts population surveys annually and sets annual hunting seasons based on those surveys. The functional relationship of the adaptive harvest within the model, therefore, allowed for higher annual harvest rates in years when bison populations were large relative to the objective and lower rates when populations were small relative to the objective. If populations fell 20 percent below the objective (for example, February counts below 400 individuals), then the harvest rate was set to 0.01 to approximate only the continuation of Tribal harvests during those years. In the past, five bison per year have been harvested by the Shoshone-Bannock Tribes of Eastern Idaho, but recently, the Eastern Shoshone Tribe of the Wind River Reservation has also participated. We calibrated the relationship between the harvest and the objective based on historical data from the WGFD (unpub. data, 2024; calibrated data shown in app. D1).

Incorporating Alternatives

The specific set of management alternatives considered here was described by FWS and included these five options (for full details, including the connection with elk population size, please refer to Cook and others, 2025a, this volume, chap. A):

- 1. *Continue feeding.*—The NER will continue to provision food to bison and elk during winter months based on forage availability and number of conflicts.
- 2. *No feeding.*—The NER will immediately stop provisioning food to bison and elk during winter months.
- 3. *Increased elk harvest, then stop feeding.*—The NER will continue to provision food to bison and elk during winter months for the next 5 years, during which time the NER will work with the WGFD to increase elk harvest and attempt to reduce elk population size to 5,000.
- 4. *Reduce feeding, then stop feeding altogether.*—The NER will provision a reduced ration to elk during winter months for the next 5 years to reduce the elk population size to 5,000 prior to feedground closures. Exclosures will be designed to protect aspen stands in the south region of the NER and for willow and cottonwood north of the NER.
- 5. Feeding phaseout after 3 percent chronic wasting disease (CWD) prevalence.—The NER will continue to provision food to bison and elk during winter months until CWD sampling reveals 3 percent prevalence in the Jackson elk herd, at which point all feeding activities will cease on the NER. The timing of the 3 percent trigger (for example, years of feeding until this 3 percent disease threshold was reached) was informed based on estimates from Cross and others (2025, this volume, chap. B).

The performance metrics, or the measures that were used to evaluate the performance of each alternative on bison, were (1) the population size of bison in year 20, (2) the cumulative number of bison harvested across 20 years, and (3) the cumulative number of bison involved in human-bison conflict across 20 years. The FWS selected the 20-year projection period to match the typical plan implementation period before revisions are considered.

To project each of the alternatives, the model was altered to include the anticipated management strategy changes. For the continue feeding alternative, the basic structure of the population model was used, using historical data to split a single herd into two segments between the NER feedground and winter range segment during winter months. The adaptive harvest was also included to approximate the continue feeding harvest rate-setting process. The study assumed that under all alternatives the NER feedground and winter range segments experienced the same birth and natural mortality rates regardless of winter year type (that is, no excess mortality in severe winters during the years when feeding occurs on the NER). We expected that, under continue feeding, bison would locate supplemental food or other sources of forage even in severe winters because of the small population size in the Jackson region. Further, while harvest rates are likely different between NER and winter range segments, we only allowed for a single adaptive harvest rate to affect the entire population because of data limitations and challenges in including additional model complexities.

The proportion of bison in each population segment for a given year was estimated by fitting a beta distribution to the proportion of the bison population observed on the NER feedground in February from 2014–23 (table D1). The proportion of winter range bison was taken as one minus the proportion of bison counted on the feedground (table D1). In addition to the NER feedground and winter range segments, a low probability (0.015) of bison from either segment coming into human conflict each year was included after being approximated from Wyoming Department of Transportation, written commun., 2023). This estimate is likely higher in reality because it does not include data collected in the GTNP. Further, the GTNP works to reduce human-bison conflicts by actively moving bison off of roadways during winter months.

Table D1. Bison population counts, proportion fed, and harvest totals from 2014 through 2023 in the Jackson, Wyoming region.

[Counts include bison on and off the NER feedground, summed total of the raw counts conducted in February, adjusted counts that account for the imperfect sightability of bison in unfed settings, the percent of bison on feed, and total harvest. — data were not yet available]

Year	Fed counts	Unfed counts	Raw counts	Adjusted counts	Percent on feed	Total harvest
2014	778	8	786	786	96.9	299
2015	677	14	691	691	97.5	206
2016	618	48	666	668	92.9	274
2017	504	42	546	548	92.3	70
2018	0	567	567	567	0.0	91
2019	155	329	484	495	32.0	92
2020	306	182	488	494	62.7	109
2021	144	299	443	454	32.5	91
2022	382	84	466	469	82.0	130
2023	360	72	432	434	83.3	

The four other alternatives that included variations on feed cessation on the NER were incorporated by adapting the model to include their respective mechanisms of change associated with winter habitat use changes of unfed elk and conflict potential. The adaptations were essentially the same across alternatives and primarily varied according to the timing of implementation. Under the no feeding alternative, model adaptations were triggered immediately (in other words, all modeled years), whereas under the increased harvest and reduced feeding alternatives, the changes occurred starting at the 5-year mark or after the disease threshold was met under the disease threshold alternative (in other words, 3 percent CWD prevalence detected in elk; Cross and others 2025, this volume, chap. B). Once feeding stopped (under no feeding, disease threshold, increased harvest, and reduced feeding alternatives), the changes to the model included the following conditions:

- A larger proportion of the bison population transitioned to conflict situations during unfed winter months. This conflict population segment came from the proportion of bison that transitioned to the NER feedgrounds but were then not provisioned any food. On average, in the first year after the feedground program ended and in an average winter, 21 percent (95-percent prediction interval, 4 to 50 percent) of bison that returned to the NER for winter food provisions were expected to transition to conflict situations, whereas 79 percent of those bison would avoid conflict. The previously described winter range segment remained in place as part of the four no feeding alternatives.
- 2. We estimated that more previously fed bison would transition to conflict situations during severe winter conditions. In contrast to the percentage of conflict bison in the first year of no feeding in an average winter (21 percent, on average), the aggregate estimate for conflict bison in severe winters was 48 percent (95-percent prediction interval, 19 to 79 percent). We defined severe winters in a manner consistent with Cotterill and others (2025, this volume, chap. C) and thus treated it as a random variable with an annual probability of occurrence of 25 percent.
- 3. Conflict bison had lower overwinter survival compared to bison that stayed on the NER and winter range. We estimated the reduction in survival using expert judgment (app. D2) and expected mortality to occur from various sources, including bison vehicle collisions and culling on private lands.
- 4. In addition to increases in the proportion of bison that experienced conflict, the WSMET (oral commun., 2024) expressed uncertainty about how human-bison conflict may play out over time, especially under a prolonged lack of supplemental feeding on the NER and given any other changes that occur to mitigate acute bison conflicts (for example, private landowners erect fencing to protect haystacks). As a result, we worked with the WSMET to develop two competing hypotheses. The first was that the proportion of the bison population that ends up in conflict remains the same year after year, and the second was that the proportion of bison that end up in conflict changes over time. We used expert judgment to elicit weights on each hypothesis as well as the trend in the second. More details on the hypotheses and elicitation can be found in appendixes D2 and D3.

Parameter Estimation

Limited information is available for the Jackson bison herd to estimate vital and harvest rates under the management alternatives. For survival rates, we used data from Yellowstone

D6 Bison Population Dynamics, Harvest, and Human Conflict Potential at the National Elk Refuge in Jackson, Wyoming

bison, including information published in annual bison status reports that estimate mean survival and year-to-year variation (Geremia and others, 2019). We used Geremia and others (2019) estimates from 2000-19 for adult female, adult male, and calf annual survival (table D2). Calf annual survival estimates were then applied to our yearling age class as well (ages 1-2 years old; table D2). We further reduced calf survival in severe winters by first performing a repeated and random Bernoulli draw $\{0,1\}$ in each simulation year that functioned as an indicator of winter severity, where 0 indicated average winter survival and 1 indicated a severe winter. The annual probability of a severe winter was set to 0.25 based on the NER data and Cross and others (2025, this volume, chap. B). Then, based on whether it was a severe winter, either the baseline survival was applied as described above or monthly calf survival was 95 percent of baseline winter survival to approximate calf mortality during harsh winters. The reduced survival was derived by reviewing research on ungulate response to severe winter conditions (e.g., mule deer survival during the 2016-17 and 2018-19 severe winters was reduced from 0.9 to 0.65-0.7; LaSharr and others, 2023) and adjusting those effects relative to expectations about bison.

Table D2.Vital rates of bison in the Greater Yellowstone Ecosystem,including herds in Yellowstone National Park and the Jackson,Wyoming region.

[SD=standard deviation]

Demographic	Mean	Parametric SD				
Survival rates ¹ ,	Survival rates ¹ , annual					
Calf	0.90	0.04				
Yearling	0.90	0.04				
Adult female	0.95	0.01				
Adult male	0.95	0.03				
Reproduction rate	s², annual					
Calf and yearling	0.00	0.00				
Adult female	0.71	0.13				
Harvest mortality rates ³ , annual						
Maximum calf	0.01	0.01				
Maximum yearling male	0.18	0.07				
Maximum yearling female	0.18	0.07				
Maximum adult female	0.20	0.07				
Maximum adult male	0.48	0.07				

¹Approximated from Geremia and others, 2019.

²Approximated from Cain and others, 1997; 1998; 1999; 2000; 2001; 2002; 2004.

³Approximated from WGFD, unpub. data, 2024.

For birth rates, we used annual progress reports from a multi-year bison study (1997–2004) in the GTNP that focused on the reproduction and demography effects of brucellosis infection (Cain and others, 1997; 2004). The reports include annual data on collared and aged female bison, including pregnancy checks and

monitoring for births. In other herds, brucellosis seropositivity, a bacterial infection, has been shown to reduce bison birth rates (Fuller and others, 2007). In this study, all pregnancy and birth rate data, from both seropositive and seronegative bison, were used to estimate the overall adult female reproduction rate because of the uncertainty in how brucellosis trends might change over time under the alternatives (table D2). Finally, based on WGFD harvest data (WGFD, unpub. data, 2024), harvest rates were estimated, and then a sex and age class-specific maximum harvest rate was calculated by dividing the total annual harvest by the total February counts of the NER and native winter range bison (table D2). Maximum harvest rates informed our estimates for annual harvest as a function of population size (app. D1).

Winter bison distribution was informed by winter counts from 2018–23 (table D1). Bison have been counted at the NER and on the winter range since the 1940s. Prior to 2018, the majority overwintered on and around the NER. More recently, the proportion using feedgrounds has decreased (NPS, written commun., 2023). Therefore, we used 2018-23 data to assign bison to the NER feedgrounds and winter range. Under the no feeding alternatives, the individual four-point estimates (that is, low, high, central estimate, as well as a measure of uncertainty) from each science expert panel was used to generate random aggregate distributions that further split the NER bison into those that are expected to stay on the refuge and those that transition to conflict (app. D2). The aggregate distributions were generated by first fitting a distribution that matched the support of the parameter of interest (for example, beta distribution for vital rate parameters) to the quantiles provided by the experts. Then each distribution was aggregated using the Vincent average method (Howerton and others, 2023).

Initial Conditions

Starting values for the population size in models were randomly selected at the start of each simulation using data from 2018-23 and adjusted for imperfect detection of winter range bison (table D1). Our adjusted counts assumed that sightability was perfect on the NER but was biased low for counts of bison on winter ranges. Hess (2002) estimated bison count error during ground and aerial surveys in summer and winter. The probability of detection estimates ranged from 0.919 (95-percent confidence interval, 0.819 to 0.955) during winter aerial counts when bison were distributed in smaller groups in denser cover to a probability of detection of 0.975 (95-percent confidence interval, 0.959 to 0.983) during summer ground counts while bison were in larger groups but still distributed across the landscape in ways that challenged observation. Based on conversations with WSMET (oral commun., 2024) and given the landscape conditions in the region, we assumed that sightability was high and used the higher sightability estimate of 0.975. We further assumed that bison counts for fed bison occurred without error because of the smaller and denser population of the NER bison compared to Hess (2002). Thus, we fit the Hess (2002) sightability estimates to a beta distribution and assumed the true count of bison from the February counts to be given by equation D1:

$$p^{sight} \sim beta(180.35, 10.36)$$

$$N_t^{Total} = N_t^{FG} + \frac{N_t^{WR}}{p^{sight}},$$
 (D1)

where

- p^{sight} is the sightability estimate for animals on the winter range that may be observed imperfectly;
- N_t^{FG} is the February population count for bison on the NER feedground;
- N_t^{WR} is the February population count for winter range bison;
- N_t^{Total} is the sightability-adjusted estimate for the total bison population size.

In addition to accounting for observational error, we also treated the starting population size as a random variable to account for interannual variability in count data. Overall, bison counts have had a declining trend over recent years with 786 individuals counted in 2014 but 432 in 2023 (table D1). To avoid sampling from this declining trend, we used a subset of annual count data (2019–23) and randomly drew from these counts to initialize each model projection (modeled year, *y*, where *y*=0 for the initial population size).

Results

The Jackson bison herd was projected to remain stable under the continue feeding alternative with a final median population size of 541 individuals in year 20 (table D3). Under the no feeding, disease threshold, increased elk harvest, and reduced feeding alternatives, we projected smaller population sizes of 469, 470, 472, and 473 individuals, respectively. Thus, the difference between the continue feeding and alternatives that called for the cessation of feeding was 13 percent smaller population sizes at year 20 (table D3). In terms of population projections over

Table D3.Median population size in year 20, median cumulative
harvest over 20 years, and median cumulative number of conflict
bison over 20 years under the 5 alternatives in the Jackson,
Wyoming region.

[SD, standard deviation]

Alternatives	Population size	SD	Harvest	SD	Conflict bison	SD
Continue feeding	541	57	1,879	198	143	16
No feeding	469	65	1,292	247	1,077	474
Disease threshold	470	67	1,387	248	905	482
Increased harvest	472	70	1,496	245	756	473
Reduced feeding	473	65	1,508	234	756	441

time for the no feeding, disease threshold, increased harvest, and reduced feeding alternatives, we projected a gradual decrease in populations starting in the years immediately following any change in feeding operations on the NER (fig. D2).

For harvest projections, the 20-year cumulative number of bison harvested was 1,879 under the continue feeding alternative and between 371 to 587 fewer animals than in the other four alternatives that stopped feeding. The no feeding alternative resulted in 1,292 bison harvested over the next 20 years, compared to 1,387 under the disease threshold, 1,496 under increased harvest, and 1,508 under reduced feeding alternatives. On an annual basis, these resulted in an average of 95 harvested bison in the first year and 93 harvested in year 20 under continue feeding management. For the rest of the alternatives that call for the cessation of feeding, there was a declining trend in average annual harvest. Under no feeding, the average annual harvest was 94 in year 1 and 56 in year 20; increased harvest alternative had an average harvest of 97 in year 1 and 59 in year 20; reduced feeding had averages of 97 in year 1 and 60 in year 20; and, finally, the disease threshold averaged 97 in year 1 and 57 in year 20 (fig. D3).

For the projections of the number of conflict bison, experts generally agreed that bison behavior would change over time in response to feed cessation. This study incorporated the two hypotheses about these temporal trends in conflict. The first hypothesis, that there was no trend in bison conflicts over time (for example, bison do not learn new behaviors that might lead to increased or decreased conflict), had an overall average belief weight of 0.19, whereas the other hypothesis, that bison conflict would either increase or decrease over time, had an overall average belief weight of 0.81. These results indicate that the expert panel believed it to be approximately 4 times more likely that bison conflict dynamics will change over time (app. D3). However, despite this general agreement, there was less agreement about the direction of that change (for example, whether conflicts would increase or decrease over time). One out of five experts believed that conflict would increase over time, but four out of five believed that conflict would decrease over time. As a result, we developed a mixed distribution that drew from either an increasing (one-fifth of the weight) or decreasing (four-fifths of the weight) proportion of the NER bison population as ending up in conflict situations.

Overall, after incorporating the structural uncertainty about future human-bison conflicts and parametric uncertainty about the proportion of bison that will redistribute into areas of conflict, we found that the continue feeding alternative had the lowest median number of conflict bison (143 cumulative across 20 years; fig. D4*A*; table D3) and the no feeding alternative had the highest number of conflict bison (1,077 cumulative across 20 years; fig. D4*B*; table D3). The other three alternatives had intermediate values of conflict bison with 756 increased harvest, 756 reduced feeding, and 905 disease threshold (fig. D4*C*, *D*, and *E*; table D3). In general, incorporating the two hypotheses surrounding changes in human-bison conflict over time led to a high degree of uncertainty around these median values, and a declining trend in conflict once feeding on the NER was stopped.

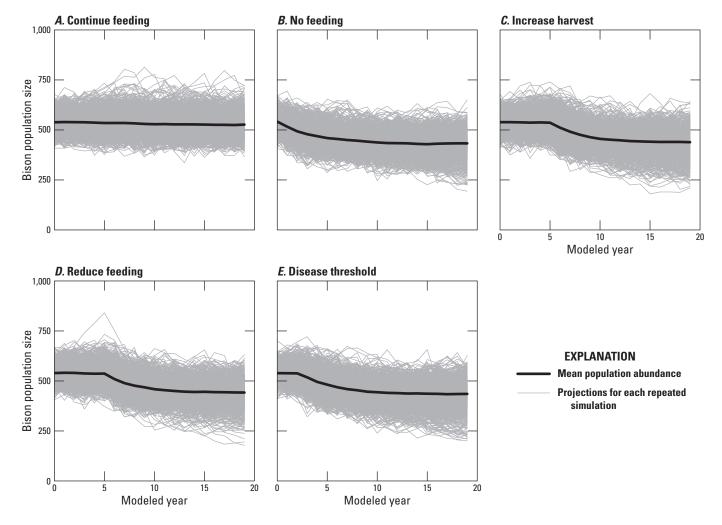


Figure D2. Graphs showing the projected bison population size in the Jackson, Wyoming region over time under the five alternatives: *A*, continue feeding, *B*, no feeding, *C*, increase harvest, *D*, reduce feeding, and, *E*, disease threshold.

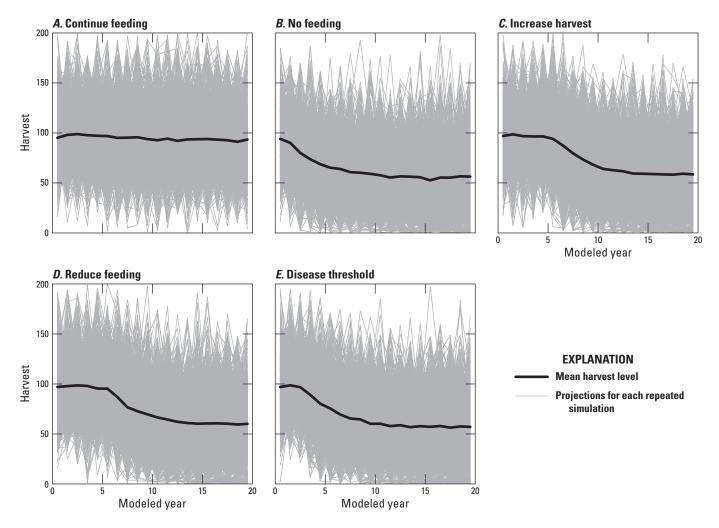


Figure D3. Graphs showing the projected bison harvest in the Jackson, Wyoming region over time under the five alternatives: *A*, continue feeding, *B*, no feeding, *C*, increase harvest, *D*, reduce feeding, and, *E*, disease threshold.

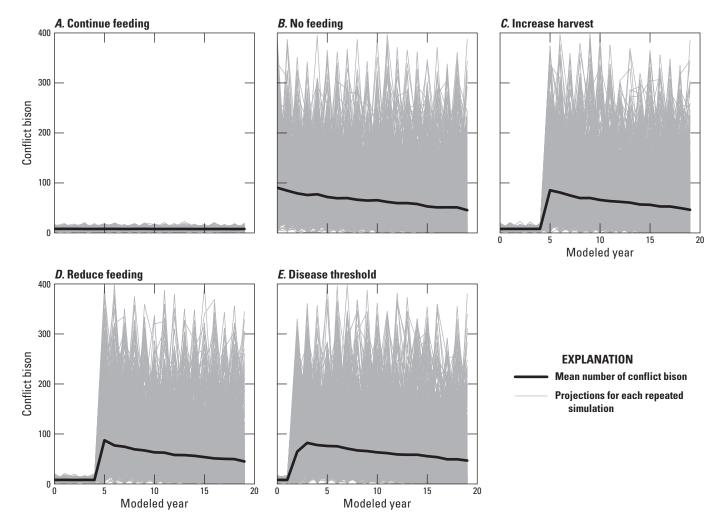


Figure D4. Graphs showing the projected human-bison conflicts in the Jackson, Wyoming region over time under the five alternatives: *A*, continue feeding, *B*, no feeding, *C*, increase harvest, *D*, reduce feeding, and, *E*, disease threshold.

Across the three metrics (bison abundance, harvest, and conflicts), the continue feeding alternative performed the best in the near-term (3–5 years) as well as in the long-term (20 years; fig. D5). However, the other four alternatives ranked comparably at year 20, with a reduced number of bison and harvest, as well as a higher but declining conflict potential compared to continue feeding. Nevertheless, how those changes occurred over time was slightly variable and depended on when feedground operations were ceased. For example, under the no feeding alternative, the decline in bison abundance and harvest and the increase in conflict started to happen in the first year, whereas, under the phaseout alternatives (reduced ration and aggressive harvest), this decline did not begin until year 5. The disease trigger alternative was intermediate in the performance of all metrics and depended on detecting CWD within elk before feeding is stopped.

Summary

This study projected the consequences of five potential management alternatives on three indicators for the Jackson, Wyoming, *Bison bison* (Linnaeus, 1758; American bison) herd over the next 20 years. The alternatives included one that maintained the National Elk Refuge feedground program and four others that stopped feeding over different time spans; the performance metrics used to evaluate the alternatives included bison abundance in year 20, as well as the cumulative harvest and number of conflict bison over that same period. In terms of performance, the continue feeding alternative was estimated to perform the best across all

three metrics. For abundance, continuing the feedground program resulted in a stable population over time; the 20-year estimate of 541 individuals was 68–72 individuals larger than the four alternatives that stop feeding activities on the National Elk Refuge. Similarly, this study found that continuing to feed bison led to higher harvest and fewer conflicts when compared against the alternatives that stop overwinter feeding.

Several assumptions were made in this modeling work that affected the overall results. First, we assumed that the Wyoming Game and Fish Department would continue to manage the Jackson bison herd in relation to the existing population objective of 500 individuals. This assumption had a strong effect on abundance and harvest projections. For example, under the continue feeding management alternative, the adaptive harvest rate setting process limited the potential growth of the bison herd by increasing harvest within years with higher population sizes and over the 20-year projections. On an annual basis, this led to an average of approximately 95 bison being harvested in each year in our continue feeding projections compared to an average of 97 harvested annually between 2018-23 (WGFD, unpub. data, 2024). While the comparisons between observed and simulated results match well for the continue feeding alternative, no comparable data are available to make these comparisons under the four alternatives that stop feeding on National Elk Refuge.

In contrast to the continue feeding alternative and the stable population of around 500 bison under this alternative, the four alternatives that stop feeding resulted in reductions in average population size and annual harvest. This was primarily a result of an increase in human-bison conflict and the associated reduction in survival that is expected by experts in conflict situations. The

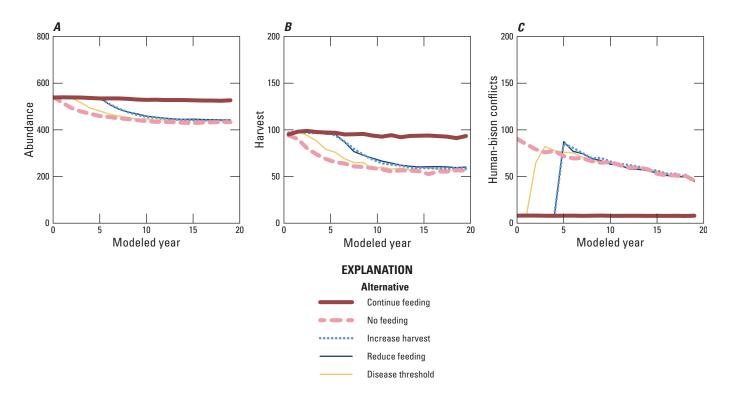


Figure D5. Graphs showing the projected effects of the alternative on the performance metrics over time under the five alternatives: *A*, abundance, *B*, harvest, and, *C*, human-bison conflicts.

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expert panel, which informed the transition of bison to conflict without feeding and the associated survival of conflict bison, estimated that survival would be reduced by between 3–25 percent, depending on the sex and age of the individual (table D1, app. D2). This reduction dramatically reduces the available bison harvest, particularly as the population approaches 400 individuals and the adaptive harvest relationship in the simulation model reduces the harvest rate closer to zero under these conditions.

This study assumed that fed and unfed bison have experienced, and will continue to experience, vital rates similar to the much larger bison population that inhabits Yellowstone National Park and surrounding areas. Most of the vital rate information, except for birth rates, drawn from the Yellowstone herd, was used to make assumptions about the productivity of the Jackson herd, should the National Elk Refuge select an alternative that required the cessation of feeding. Further, we assumed that there would be excess mortality in 25 percent of years that lowered the monthly survival of calves in severe winters. Lastly, we assumed the success rate of bison hunters to remain the same over time; however, if bison no longer return to areas where they are currently vulnerable to harvest, it is conceivable that bison harvest dynamics change over the next 20 years in ways that are unpredictable. In total, none of these assumptions can be tested prior to a management decision on the feedground program; however, the results for the continue feeding alternative tend to align well with observations of the Jackson herd over the past six February counts in terms of harvest and overall abundance.

We assumed that there is no relationship between bison density and brucellosis seropositivity. Brucellosis seropositivity affects the birth rates of bison (for example, higher rates of brucellosis result in lower birth rates) and thus, any changes to disease dynamics may affect the productivity of this herd and the resulting estimates of population size, harvest, and conflict potential. Furthermore, we assumed no relationship between elk and bison, and the potential for predators to switch prey in future scenarios in which elk numbers decline.

Finally, our projections indicate that the continuation of the feedground program has the potential to lead to more bison and harvest, as well as fewer conflicts when compared to the no feeding, disease threshold, reduced feeding, and increased elk harvest alternatives. However, the continue threat of elevated transmission of bison and elk diseases makes decisions on whether and how to feed these herds a difficult one.

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Appendix D1. Adaptive Harvest

Annual bison harvest is regulated to ensure a stable population size over time (table D1.1). Within our model, we incorporated a submodel that defined an adaptive relationship between annual harvest rate and February population size to ensure that the simulated population was not driven more than 20 percent below the population objective as a result of harvest. The submodel that we used to approximate this adaptive process was given by equation D1.1:

$$h_{a,y} = \left(hmax_{a,s}\left(1 - c\left(\frac{Objective}{N_{y}^{Total}}\right)^{\delta}\right)\right), \quad (D1.1)$$

where

 $h_{a,y}$ is the harvest rate by age (a) and model year (y);

- N_y^{Total} is the total February population size from the current simulation year (y);
- *Objective* is the population objective (500) for the Jackson bison herd;
 - *c* is the proportion reduction when population was at carrying capacity;
 - δ controls the shape of the density-dependence; and,
 - $hmax_{a,s}$ is the maximum harvest rate by age class (a) and sex (s).

We assumed that the proportion reduction, c, and shape parameter, δ , were the same as values used in Cook and others (2023) and approximated the relationship between harvest and population size (fig. D1.1)

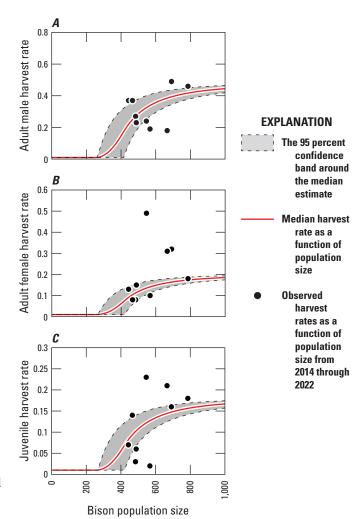
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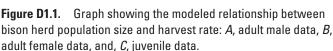
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Table D1.1.Number of active hunting licenses in Wyoming andtotal bison harvest for juveniles, males, and females from years2013 through 2022. Data from Tribal harvest not included.

[Each hunter can only harvest one bison per license. Data are from the Wyoming Game and Fish Department (2022)]

Year	Total active licenses	Juvenile harvest	Male harvest	Female harvest	Total harvest
2014	321	32	111	156	299
2015	288	36	47	123	206
2016	281	37	69	168	274
2017	111	2	46	22	70
2018	182	2	73	16	91
2019	146	5	50	37	92
2020	161	7	72	30	109
2021	139	11	59	21	91
2022	141	16	68	46	130





Appendix D2. Expert Elicitation

We elicited experts on parameters using seven questions that were focused on unknown parameter values, relationships, or estimates, that were necessary to estimate bison population dynamics under different alternatives for the "Environmental Impact Statement" on bison and elk management on the National Elk Refuge (NER). These parameters and their uncertainty were elicited using a series of structured techniques that minimize bias and maximize the accuracy of estimates derived from the experts (Morgan, 2014; Sutherland and Burgman, 2015). Specifically, we used a four-point elicitation method to estimate a distribution that represented each expert's knowledge (Speirs-Bridge and others, 2010) as well as a modified Delphi process that maximized the ability of the group to share privileged knowledge with one another in a way that might help improve individual and group-aggregate estimates (Hanea and others, 2017).

Uncertainty About Bison Vital Rates and Redistribution

The expert panel's responses to Question 1—"Under current feeding operations, some bison spend at least part of the winter months overwintering on the NER in most years. In an average winter, what proportion of bison that overwinter on the NER would relocate to high conflict locations if the NER stopped provisioning supplemental feed?"—can be found in figure D2.1.

The expert panel responses to Question 2—"Under current feeding operations, some bison spend at least part of the winter months overwintering on the NER in most years. In a severe winter, what proportion of bison that overwinter on the NER would relocate to high conflict locations if the NER stopped provisioning supplemental feed?"—can be found in figure D2.2.

The expert panel responses to Question 3—"Assume that there were 100 human-bison conflicts in the first year after the NER stopped provisioning food, how many bison would you expect to be in conflict situations in year 20 after the NER stopped feeding (that is, no feeding for the past 20 years)?"—can be found in figure D2.3. The panel was instructed to assume that years 1 and 20 were exactly the same in terms of winter conditions, habitat and landscape composition and configuration, and management response to bison movements. And to also assume that the overall population of bison remains the same, including the movements between the NER and other seasonal ranges (fig. D2.3).

The expert panel responses to Question 4—"For bison groups that overwinter on areas of high conflict potential, how many adult female bison would survive out of 100 annually?"—can be found in figure D2.4. The panel was instructed to assume that, on average, 95 out of 100 adult female bison survive annually in feedground areas and other locations of low human-bison conflict potential.

The expert panel responses to Question 5—"For bison groups that overwinter on areas of high conflict potential, how many juvenile female bison would survive out of 100, annually?"—can be found in figure D2.5. The panel was instructed to assume that, on average, 95 out of 100 juvenile female bison survive annually in feedground areas and other locations of low human-bison conflict potential.

The expert panel responses to Question 6— "For bison groups that overwinter on areas of high conflict potential, how many adult male bison would survive out of 100, annually?"—can be found in figure D2.6. The panel was instructed to assume that, on average, 95 out of 100 adult male bison survive annually in feedground areas and other locations of low human-bison conflict potential.

The expert panel responses to Question 7—"For bison groups that overwinter on areas of high conflict potential, how many juvenile male bison would survive out of 100, annually?"— can be found in figure D2.7. The panel was instructed to assume that, on average, 95 out of 100 juvenile male bison survive annually in feedground areas and other locations of low human-bison conflict potential.

The expert panel responses to Question 8— For bison groups that overwinter on areas of high conflict potential, how many bison calves would survive out of 100, annually?—can be found in figure D2.8. The panel was instructed to assume that, on average, 90 out of 100 bison calves survive annually in feedground areas and other locations of low human-bison conflict potential.

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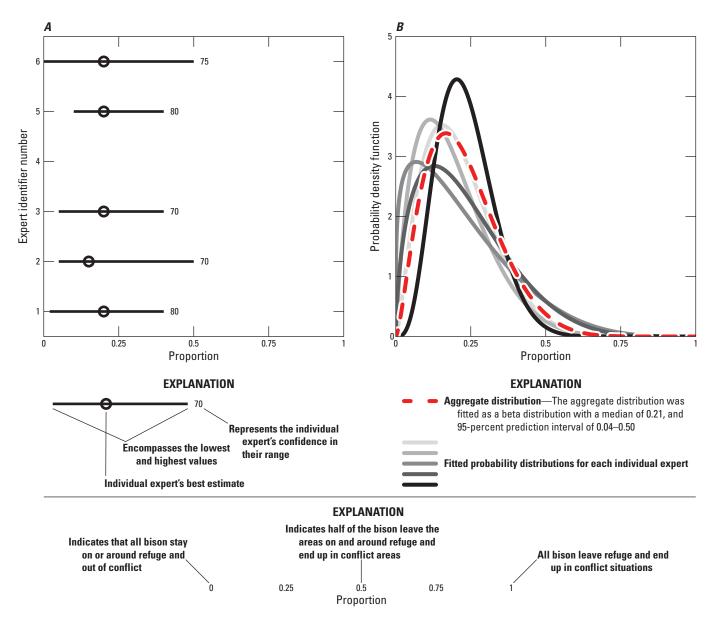


Figure D2.1. Graphs showing, *A*, the raw, four-point estimates of each of the five experts, and, *B*, the fitted probability distributions for each individual expert and the aggregate distribution for Question 1.

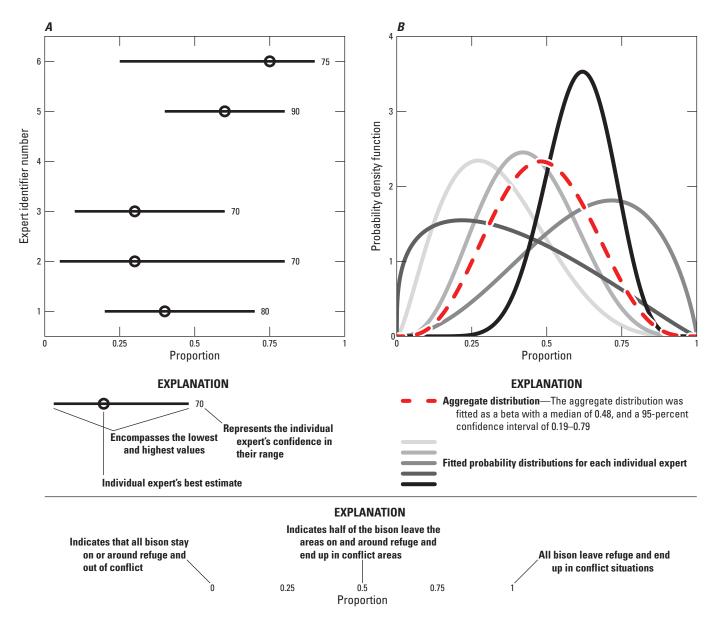


Figure D2.2. Graphs showing, *A*, the raw, four-point estimates of each of the five experts, and, *B*, the fitted probability distributions for each individual expert and the aggregate distribution for Question 2.

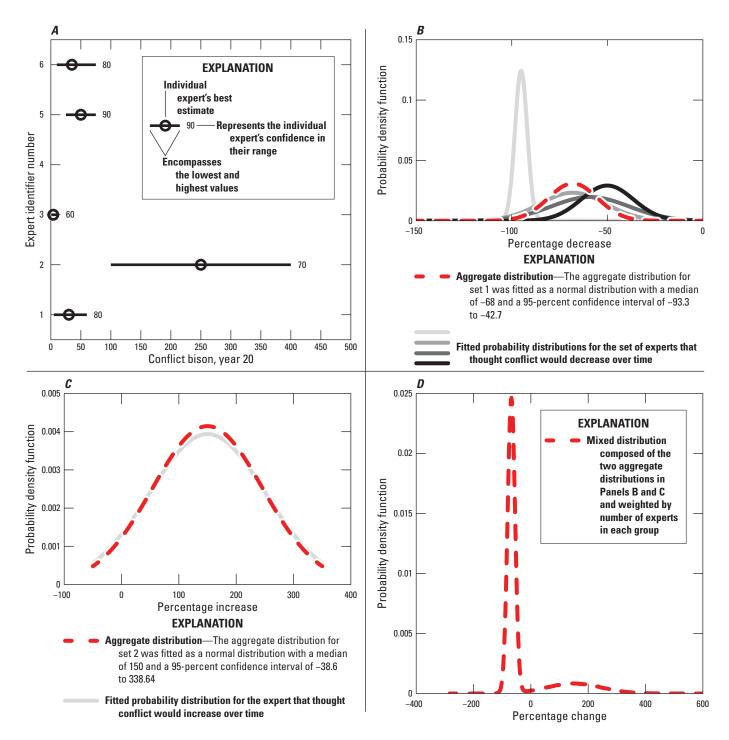


Figure D2.3. Graphs showing, *A*, the raw, four-point estimates of each of the five experts. One set of experts (n=4) estimated that conflict would decrease over time. Another expert (n=1) estimated that conflict would increase over time; *B*, the fitted probability distributions for the set of experts that thought conflict would decrease over time and their aggregate distribution; *C*, the fitted probability distributions for the expert that thought conflict would increase over time and their aggregate distribution; *and*, *D*, the mixed distribution that includes expert set 1 and set 2. Expert 4 participated in other questions about the distribution and survival of bison but did not complete the question about belief in the two hypotheses.

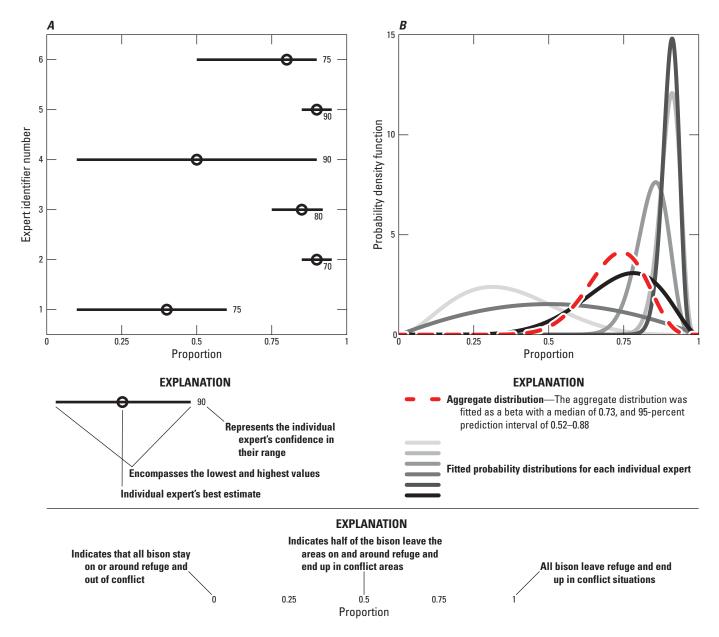


Figure D2.4. Graphs showing, *A*, the raw, four-point estimates of each of the six experts, and, *B*, the fitted probability distributions for each individual expert and the aggregate distribution for Question 4.

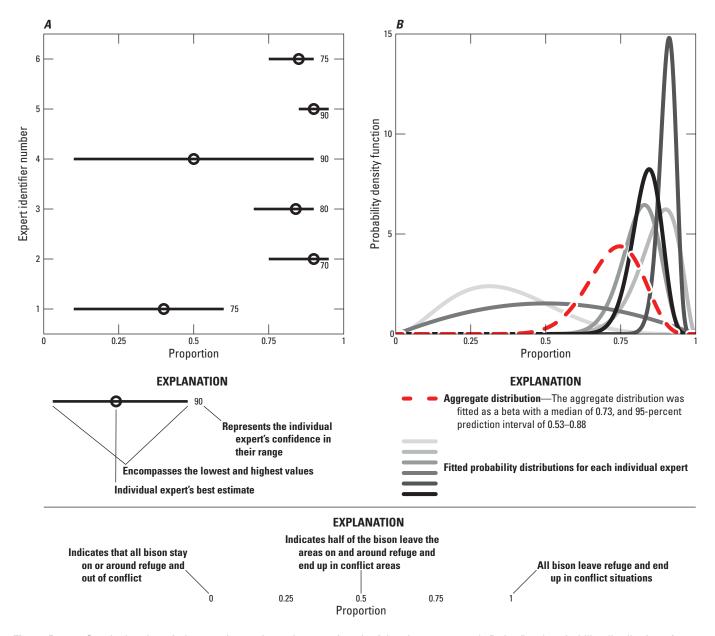


Figure D2.5. Graph showing, *A*, the raw, four-point estimates of each of the six experts, and, *B*, the fitted probability distributions for each individual expert and the aggregate distribution for Question 5.

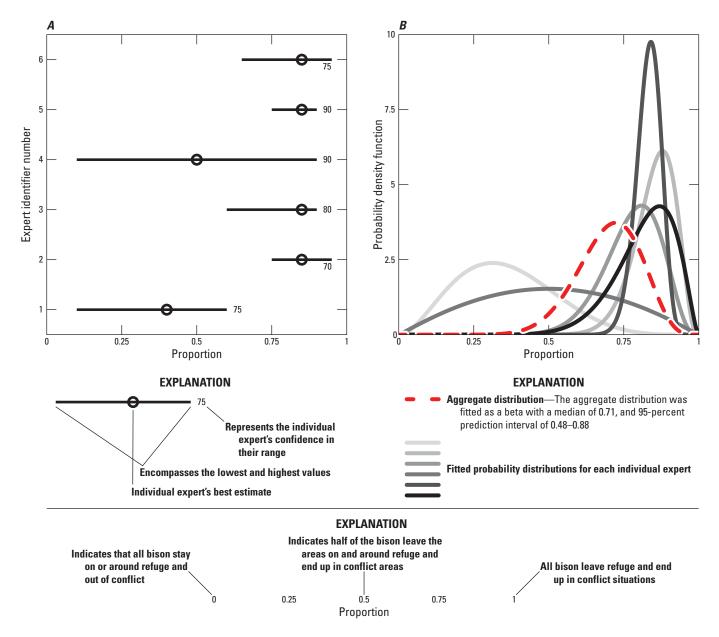


Figure D2.6. Graphs showing, *A*, the raw, four-point estimates of each of the six experts, and, *B*, the fitted probability distributions for each individual expert and the aggregate distribution for Question 6.

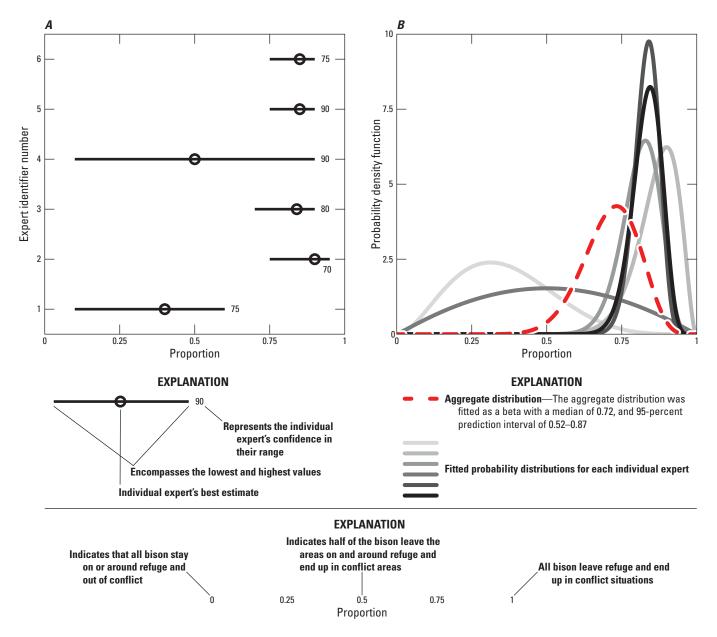


Figure D2.7. Graphs showing, *A*, the raw, four-point estimates of each of the six experts, and, *B*, the fitted probability distributions for each individual expert and the aggregate distribution for Question 7.

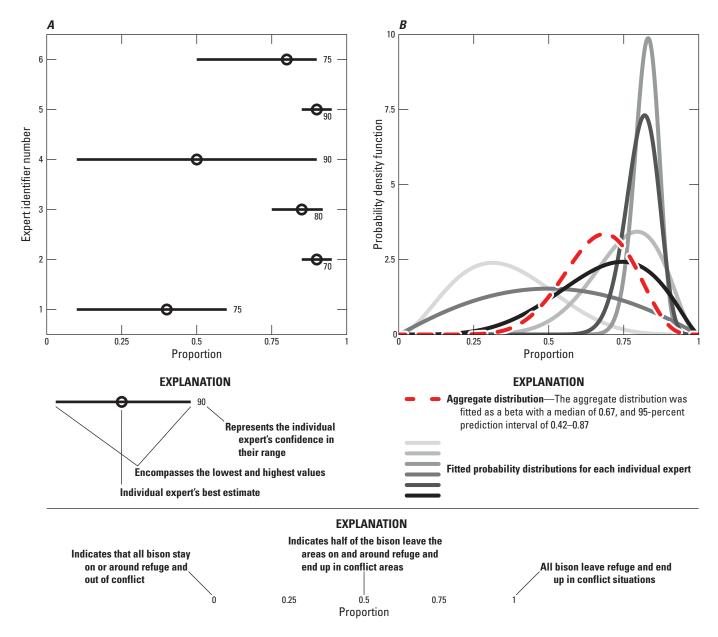


Figure D2.8. Graphs showing, *A*, the raw, four-point estimates of each of the six experts, and, *B*, the fitted probability distributions for each individual expert and the aggregate distribution for Question 8.

Appendix D3. Incorporating Structural Uncertainty in Human-bison Conflict Potential

Human-bison conflict as a result of changing feedground management, changes to landscape and environmental conditions (for example, winter severity patterns), and the potential response of wildlife management agencies to those conflicts is uncertain in the near- and long-term. Based on conversations with the expert panel and these sources of uncertainty, we considered the following two principal hypotheses in the number of human-bison conflicts over time (table D3.1):

- Hypothesis 1. Human-bison conflict will remain relatively stable over time such that the proportion of bison that transition from winter range habitat on and around the National Elk Refuge to conflict situations will remain the same over time (fig. D3.1); and,
- Hypothesis 2. Human-bison conflict will have an increasing or decreasing trend over time as a result of a multitude of potential mechanisms, including actions by agencies or the public that prevent conflict better over time, or from learned behaviors of bison that lead to avoidance of these areas (fig. D3.1).

We informed the weight on each of the two hypotheses (stable and increasing or decreasing conflict potential) using the expert panel. We asked each expert to provide their belief, on a 0-1 scale, that human-bison conflict would reduce or increase over time. We then took the mean of those estimates and used it for the weight on hypothesis 2, and 1 minus the mean value as the weight for hypothesis 1. Table D3.1 includes the response of each expert panelist and the mean value used in the population projections.

Table D3.1. Expert belief in hypotheses 1 and 2.

[Hypothesis 1 is that human-bison conflict will remain relatively stable over time such that the proportion of bison that transition from winter range habitat on and around the National Elk Refuge to conflict situations will remain the same over time. Hypothesis 2 is that human-bison conflict will have an increasing or decreasing trend over time as a result of a multitude of potential mechanisms, including actions by agencies or the public that prevent conflict better over time or from learned behaviors of bison that lead to avoidance of these areas. Expert 4 participated in other questions about the distribution and survival of bison but did not complete the question about belief in the two hypotheses. —, no response]

Expert number	Belief in hypothesis 1	Belief in hypothesis 2	
1	0.15	0.85	
2	0.25	0.75	
3	0.25	0.75	
4			
5	0.30	0.70	
6	0.00	1.00	

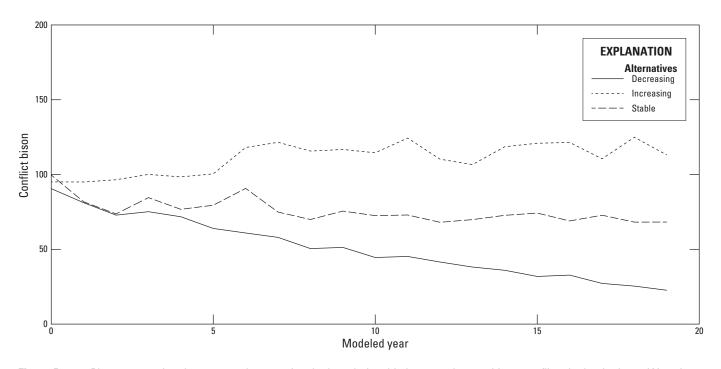


Figure D3.1. Plot representing the structural uncertainty in the relationship between human-bison conflicts in the Jackson, Wyoming region and the underlying hypotheses for how conflict might change over time.

Estimating the Social and Economic Consequences of Proposed Management Alternatives at the National Elk Refuge in Jackson, Wyoming

By Margaret C. McEachran, Andrew Don Carlos, Gavin G. Cotterill, Eric K. Cole, Jonathan D. Cook

Chapter E of Decision Analysis in Support of the National Elk Refuge Bison and Elk Management Plan

Edited by Jonathan D. Cook and Paul C. Cross

Ecosystems Mission Area—Biological Threats & Invasive Species Research Program

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Abbreviations

>	greater than
<	less than
CWD	chronic wasting disease
FWS	U.S. Fish and Wildlife Service
JHU	Jackson Elk Herd Unit
NER	National Elk Refuge
WGFD	Wyoming Game and Fish Department

Estimating the Social and Economic Consequences of Proposed Management Alternatives at the National Elk Refuge in Jackson, Wyoming

By Margaret C. McEachran¹, Andrew Don Carlos², Gavin G. Cotterill¹, Eric K. Cole², Jonathan D. Cook¹

Abstract

The National Elk Refuge (Refuge) is managed by the U.S. Fish and Wildlife Service and includes habitats for bison and elk. Bison and elk provide opportunities for wildlife-related recreation and contribute to the tourism industry in and around Jackson, Wyoming. Over the last century, the Refuge has provisioned supplemental feed to elk and, more recently, bison during winter months to ensure adequate forage and prevent starvation and conflict with private landowners. However, supplemental feeding artificially aggregates animals and can increase rates of disease transmission and localized damage to sensitive habitats near the feeding areas. This report presents analyses and results to support two of the nine management objectives in the next "Bison and Elk Management Plan," with a particular focus on the social and economic consequences of five management alternatives considered in this study. The alternatives are to continue feeding bison and elk during winter months on the Refuge, stop feeding after CWD is measured at 3 percent prevalence or above in the Jackson elk herd, stop feeding immediately, reduce feeding for five years and then stop feeding, and increase elk harvest for five years and then stop feeding. These alternatives are anticipated to alter bison and elk population and space-use dynamics, with corresponding effects on wildlife-related recreation and tourism, including the number of visitors and sleigh-ride participants on the Refuge, and hunters and outfitters within the Jackson Elk Herd Unit. The performance of each of this study's alternatives was variable, resulting in overlap in the performance of alternatives on the select objectives over the next 20 years. Generally, visitation-related objectives performed better under the continue feeding alternative, whereas hunting-related objectives performed better under the increase harvest alternative. The results presented here may assist U.S. Fish and Wildlife Service decision makers in balancing social and economic benefits identified in the decision-making process for the "Bison and Elk Management Plan" with other objectives evaluated in this report.

Introduction

The National Elk Refuge (NER or Refuge) spans 24,700 acres in northwestern Wyoming and is a part of the larger Greater Yellowstone Ecosystem that includes the Yellowstone National Park, Grand Teton National Park, and several national forests across Wyoming, Montana, and Idaho (fig. E1). The Refuge provides important seasonal habitats for many species including Cervus canadensis nelsoni (Erxleben, 1777; Rocky Mountain elk), bison bison (Linnaeus, 1758; bison), Canis lupus (Linnaeus, 1758; grey wolves), and Ovis canadensis (Shaw, 1804; bighorn sheep). Drawn by opportunities to view wildlife and scenery, participate in outdoor recreation, and visit rich cultural and historical sites, the Refuge receives several hundred thousand visitors annually (Dietsch and others, 2020). In addition, the Refuge offers visitors a place to hunt, fish, and ride horse-drawn sleighs to view the elk herd during winter (Dietsch and others, 2020). The management of the NER is administered by the U.S. Fish and Wildlife Service (FWS), and its primary purpose is to protect habitat for elk and other big game species. However, the Refuge has sought to provide opportunities for wildlife-dependent recreation and environmental education for the public and to prevent human-wildlife conflict (National Wildlife Refuge System Improvement Act of 1997-Public Law 105-57, 111 Stat. 1252).

Lower elevation areas surrounding Jackson, Wyoming (fig. E1) have historically provided important overwintering habitat for many wildlife species, including elk. The NER was established in 1912 to ensure access to adequate elk winter range and reduce elk consuming feed or crops intended for domestic livestock when natural winter forage was insufficient. To supplement limited natural winter forage, the local citizens began feeding Jackson elk during winter months in 1910–1911, and, once established, the NER began conducting these efforts (FWS and NPS, 2007); the Refuge also began feeding bison in 1980 when a small free-ranging herd discovered the feedgrounds (Boyce, 1989). This supplemental feeding results in dense aggregations of elk and bison on the Refuge, providing opportunities to view higher numbers relative to unfed settings elsewhere in the Jackson region.

Across the country, over 500 Refuges in the National Wildlife Refuge System generate \$3 billion annually and support 40,000 jobs, illustrating the substantial economic and social contributions

¹U.S. Geological Survey.

²U.S. Fish and Wildlife Service.

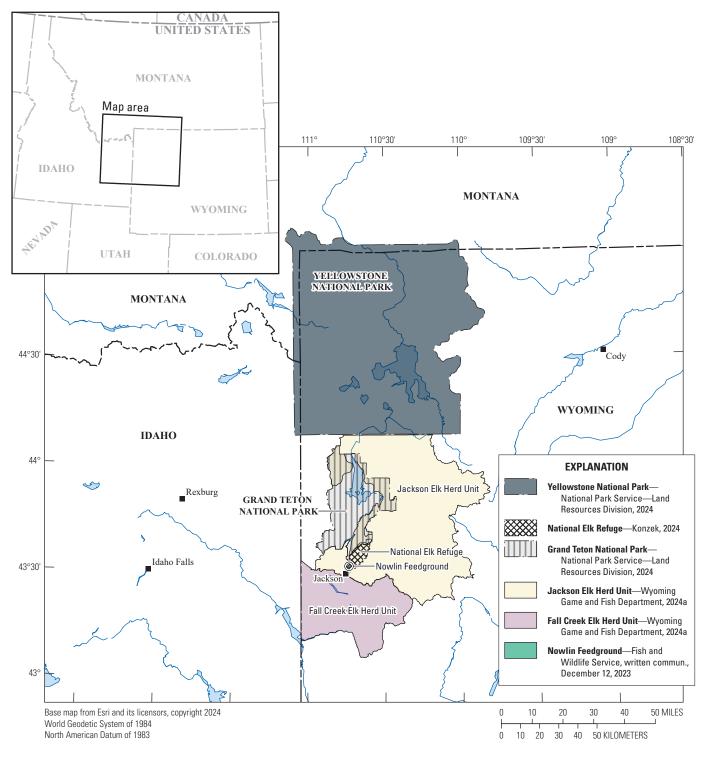


Figure E1. Map showing the location of the National Elk Refuge, Grand Teton National Park, Yellowstone National Park, Jackson Elk Herd Unit, Fall Creek Herd Unit, and Nowlin Feedground within the study area.

that Refuges make (Caudill and Carver, 2019). For the NER, wildlife-related recreation and tourism provide notable economic benefits to the Jackson region. The most recent systematic visitor survey found that many visitors come to the Refuge for unique opportunities to view large numbers of elk up close when elk are being fed during the winter months. This highlights the effect that feeding activities have on tourism in the area (Dietsch and others, 2020) and suggests that changes to bison and elk feeding may affect tourism.

Several thousand hunters also visit the region to purchase harvest tags and pursue elk in the Jackson Elk Herd Unit (JHU), bringing additional economic benefits (Koontz and Loomis, 2005). Finally, hunting outfitters operate businesses and receive economic revenue based on opportunities to guide clients in the pursuit and harvest of elk.

In addition to local recreational and economic benefits, supplemental feeding has been used to reduce elk and bison use of agricultural or other private properties when winter forage is scarce. Wintertime provisioning of supplemental feed is typically triggered when winter sampling of available forage biomass at index sites, selected to represent sites preferred by elk in the south end of NER, indicates that forage availability has fallen below 300 pounds per acre (U.S. Fish and Wildlife Service, 2019). Together with the Wyoming Game and Fish Department (WGFD) wildlife hazing actions designed to actively and non-lethally move elk away from problem areas (U.S. Fish and Wildlife Service, 2019), the provisioning of supplemental feed on the NER effectively minimizes elk and bison use of private lands, thereby minimizing the risk of human-wildlife conflict in the Jackson region. Human-wildlife conflicts include the depredation of agricultural products, damage to structures and livestock by wildlife, and transmission of infectious diseases from wildlife to livestock.

Supplemental feeding also has negative consequences for the social and economic aspects of the system. The dense aggregations of elk on the NER during winter months degrade vulnerable plant communities and increase the likelihood of transmission of several infectious diseases, including diseases with significant economic implications, such as brucellosis and chronic wasting disease (CWD). Brucellosis is a bacterial disease that affects elk, bison, and cattle and is transmitted when a susceptible individual contacts a fetus aborted from an infectious individual (National Academy of Sciences, Engineering, and Medicine, 2020). Brucellosis can lead to substantial costs for cattle producers because of requirements for testing, quarantine, and culling of infected herds if the disease is detected to prevent future spread and risk of human infection (Boroff and others, 2016). Chronic wasting disease is a progressive, neurodegenerative disease of cervids caused by an infectious prion, which persists in prion-contaminated environments and may cause population declines in densely aggregated winter populations using feedgrounds (Galloway and others, 2021; Cook and others, 2023). Chronic wasting disease was first detected in the Jackson elk herd in 2020. Although no further positive elk have been detected despite mandatory testing of all harvested elk on the Refuge, the disease is expected to increase in prevalence which could

have significant consequences for Jackson elk populations as well as the social and economic benefits associated with them (Cross and others, 2025, this volume, chap. B).

The FWS is currently creating an Environmental Impact Statement to revise its bison and elk management plan and to determine how to manage these populations in balance with the social, ecological, economic, and cultural features of the Greater Yellowstone Ecosystem landscape. The FWS is using a structured decision-making process to identify the fundamental objectives for this decision, including several related to the social and economic benefits that elk and bison provide to the area (Cook and others, 2025a, this volume, chap. A). A subset of those objectives is the focus of the analyses and reporting of this chapter, including Fundamental Objective 5—Maintain and enhance multiple use opportunities and public enjoyment; and Fundamental Objective 8—Maximize local economic benefits associated with bison and elk presence on the NER and surrounding lands.

To achieve their objectives, FWS is considering at least five alternatives that may affect the social and economic benefits associated with elk and bison in the NER and surrounding areas (Cook and others, 2025a, this volume, chap. A). Under a continue feeding alternative, the NER will continue to provision food to bison and elk during winter months based on forage availability and any human-wildlife conflicts. Under a no feeding alternative, the NER will immediately stop provisioning food to bison and elk during winter months. Under an increase harvest alternative, the NER will continue to provision food to bison and elk during winter months at current feeding rates for the next 5 years and then stop feeding. During this 5-year phaseout, the NER will work with the WGFD to increase elk harvest quotas for Hunt Area 77 (the NER, fig. E1) to reduce the elk population prior to feeding cessation. Under a reduce feeding alternative, the NER will continue to provision food to bison and elk consistently during winter months over the next 5 years but will reduce the daily amount of food that is provided to elk. The goal will be to reduce rations such that the total number of elk wintering on the NER will decline to 5,000 animals; then, after 5 years, feeding will stop completely. Finally, under a disease threshold alternative, the NER will continue feeding operations until CWD reaches 3 percent prevalence in the Jackson elk herd, at which point all feeding activities will cease on the NER.

The analyses presented herein provide decision makers with evidence for the potential effects of these management alternatives on the economic and social performance metrics, including visitation to the NER and visit- and hunting-related spending in the Jackson region. In this report, 20 model years marks the progress after implementation.

Methods

The U.S. Geological Survey developed three models to analyze the effects of the alternatives on visitation, visit- and hunting-related spending. The first model estimated the NER

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visitation, which we used to project visitor spending and sleigh ride participation; the second model estimated revenue from elk harvest tag sales; and the third estimated other hunting-related revenue for outfitters under changing elk and bison populations.

Modeling Visitation to the NER

Tourism in the Jackson region was expected to fluctuate as a function of several factors including national-scale socioeconomic trends, weather conditions, and wildlife presence (Loomis and Caughlan, 2004). This study's analysis only considered winter visitation (December–April) because that is when elk are concentrated on the Refuge, when feeding occurs, and when most visitors come to the NER, historically.

To predict the changes in the NER visits under each alternative, we worked with technical experts from FWS, National Park Service, and WGFD to model historical visitation to the NER using 2005–23 data. At the time of publication, NER visitation data were not publicly available from FWS. We first developed a set of predictors that could affect visitation patterns at the NER based on expert guidance and a study by Loomis and Caughlan (2004). The predictors included: annual U.S. population estimate (U.S. Census Bureau, 2024), annual per capita income for U.S. residents (U.S. Census Bureau, 2024), monthly consumer price index (Federal Reserve Bank of St. Louis, 2024), monthly vehicle counts at the Moose, Wyoming entrance of Grand Teton National Park (National Park Service, written commun., 2024), monthly average temperature (degrees Fahrenheit), monthly precipitation total (inches) from the Jackson area weather station (Abatzoglou and Hegewisch, undated), and weekly counts of elk and bison on the NER that were summed into monthly counts (FWS, written commun., 2024). Indicator variables for month and year to account for any general short- and long-term trends in visitation that could not be explained by the variables previously listed were also considered.

Initial examination of the variables revealed strong correlations among consumer price index, Grand Teton National Park visitor counts, U.S. population, income per capita, and the variable for year. We retained only the year variable and considered it an index for all variables that trended positively with visitation over time. Further, monthly bison counts were excluded at this stage because of recent changes in bison herd dynamics that have resulted in a smaller population size and less wintertime use of the NER with no observable effect on the NER visitation. All predictor variables were centered and scaled to a mean of 0 and standard deviation of 1 using their historical mean and standard deviation prior to model fitting.

For model fitting and parameter estimation, we fit an initial model of monthly NER visitor center counts as a negative binomial response variable regressed on the remaining variables using a Bayesian approach (elk monthly counts, average monthly temperature, average monthly precipitation, year, and month variables). No evidence that average monthly temperature or precipitation affects the NER visitation was found and therefore these variables were excluded. We then fit a final model using monthly NER elk counts, year and month variables. This model was used to predict winter *visits* to the NER in each month, *i*, with a mean, μ , and dispersion parameter θ given by equation 1:

$$visits_i \sim NegBin(u_i, \theta) \tag{1}$$

$$\log(\mu_i) = \beta_0 + \beta_1 month lyelk + \beta_2 month Dec + \beta_3 month Jan + \beta_4 month Feb + \beta_5 month Mar + \beta_6 year.$$

We used uninformative priors distributed as *Normal(0, 100)* for the slope terms, and *Normal(10, 100)* for the intercept. We ran 3 Markov chain Monte Carlo simulations (Gelman and Rubin, 1992) with 50,000 iterations, a thinning rate of 2, and a burn-in of 25,000 to generate posterior distributions for each model parameter, β . We assessed convergence using the Gelman-Rubin statistic (Gelman and Rubin, 1992) and model fit using a Bayesian posterior predictive check to estimate a Bayesian *p*-value (Gelman and Tuerlinckx, 2000). All statistical analyses were performed in R (version 4.3.1) and the r2jags package (R Core Team, 2018; Su and Yajima, 2024).

To predict future NER winter visitation under each alternative, we sampled from the posterior distribution for each variable of the fitted model and multiplied it by the corresponding simulated elk count, and temporal variable (month and year). The posteriors of the fitted coefficients were used to represent parametric uncertainty in the effect that each predictor had on future NER visitation. The results from chapters B and C provided 100 estimates of elk counts at monthly timesteps for 20 years under each alternative (Cotterill and others, 2025, this volume, chap. C; Cross and others, 2025, this volume, chap. B). The other predictors were time variables (month, year) that did not change across alternatives.

Predicting Visitor Spending

Changes in visitor spending were calculated using the projected number of visitors from the previous model in conjunction with NER visitor spending data collected during December 2018 and March 2019 (Dietsch and others, 2020). These data report differences in spending by residency status (local was defined as residing within 50 miles of the Refuge and nonlocal residents

defined as holding residence greater than 50 miles from the Refuge) and trip purpose (primary purpose, equal purpose to other local attractions, and incidental purpose includes trips to the NER that were unplanned). These data were also expected to be representative of winter season NER visitors and spending patterns that may be affected by the alternatives. For the visitor-related spending calculations, only data from nonlocal residents (respondents who lived >50 miles away from the Refuge) were included because of limited data for local residents (<50 miles from the Refuge). Local residents represented only 20 percent of survey respondents, were inconsistent in reporting their Refuge-related spending, and did not typically report a number of days associated with each trip. Additionally, local residents were assumed to continue spending money in the local area under all alternatives whereas nonlocal resident spending may be sensitive to any changes caused by the alternatives.

In accordance with guidance prescribed by the Office of Management and Budget (2023) and an assumption that benefits of consumer spending in the near term are more valuable than those that are received farther into the future, future spending values were adjusted using a nominal discount rate of 4.7 percent annually. This nominal discount rate adjusts for declining present value for monetary benefits that are received many years into the future.

Predicting Sleigh Ride Participation

Private concessionaires offer sleigh rides that provide winter NER visitors the opportunity to experience the Refuge and get close to large groups of elk (Loomis and Caughlan, 2004). Given the possibility that feeding changes could affect sleigh ride participation and operations, the historical relationship between sleigh ride participation and weekly elk counts on the Nowlin feeding area where sleigh rides occur were assessed. We used Pearson's correlation coefficient and a generalized linear model with a negative binomial response variable fit to historical sleigh ride data using the glm.nb() function from the MASS package (Venables and Ripley, 2002). At the time of publication, NER sleigh ride data were not publicly available from FWS.

Hunting and Hunter-associated Spending

The changes to future elk populations and associated effects to elk harvest tag sales and hunting-related spending were evaluated under each alternative. In chapter B, Cross and others (2025, this volume) predicted the number of harvested elk in each age and sex class and under each of the five alternatives. Those data were then used to estimate the total number of harvest tags that could be sold annually (n_{tags}) by WGFD under each alternative given by equation 2:

$$n_{tags} = \sum_{c=1}^{4} \frac{n_{huntedc}}{1 - p_{notused} - p_{notfilled}}$$
(2)

ntagsis the number of elk tags that WGFD could
sell annually,nhunted_cis the number of harvested elk in each
demographic class, c, (juveniles, females,
yearling males or adult males) annually,pnotusedis the mean proportion of tags that are
purchased but not used by hunters, andpnotfilledis the mean proportion of tags that are
purchased, the hunter went afield, but did
not successfully harvest an animal.

The study assumed that hunters who purchased a tag but did not hunt (*pnotused*) contributed to WGFD tag sale revenue but not to local economic revenue, while hunters who went afield contributed to economic revenue regardless of whether they successfully filled the tag (harvested an animal). Average tag use and hunter success rates were derived using 2017–21 harvest data from the JHU (WGFD, 2024b). The total WGFD tag revenue was then calculated by multiplying the number of tags of each type by the corresponding cost per tag (WGFD, 2024b) to account for differences in cost of each tag type. A discount rate of 4.7 percent was applied to elk harvest tag sale revenue.

Hunting on the NER (WGFD Hunt Area 77) is unique in that hunters with unfilled tags for other hunt areas may use the tag on the NER. Given this uncertainty, our results are an approximation of future revenues because we assumed that a decrease in the number of elk that were available to harvest (estimated as total harvested elk in Cross and others, 2025, this volume, chap. B) resulted in an exact proportionate decrease in the number of elk tag sales, elk hunting trips, and elk hunting-related spending for each alternative and did not account for the possibility that hunters may still purchase tags and related goods elsewhere. We also only included elk harvest that occurs in the JHU under the alternatives and did not consider any elk that transitioned to the Fall Creek Herd Unit under the no feeding alternatives. For additional detail see Cross and others (2025, this volume, chap. B) for information regarding elk transition dynamics under the alternatives.

To estimate the total hunting trips and hunting-related spending, we used hunter-spending estimates from Koontz and Loomis (2005) and adjusted for an annual inflation of 2.8 percent between 2001 and 2024. Hunter characteristics were assumed to be consistent over time (for example, spending by residency) and used recent WGFD data to estimate the proportion of resident hunters and hunter success rates. We calculated annual hunting trip-related spending, *totalspend*, using average values from Koontz and Loomis (2005) and given by equation 3:

$$totalspend = \sum_{r=1}^{2} nhunter s_r \times tspen d_r \times tyea r_r \quad (3)$$

where

nhunters

is number of hunters by residency status, r (Wyoming resident or non-Wyoming resident),

E6 Social and Economic Consequences of Management Alternatives at the National Elk Refuge

tspend	is per-trip spending by hunter residency, and
tyear	is number of trips per year by hunter residency.
	residency.

Wyoming residents were further subdivided and a weighted average of local and nonlocal residency status was calculated based on data from Koontz and Loomis (2005). Finally, the total spending values were multiplied by a discount rate of 4.7 percent.

Outfitter Revenues

To estimate how changes in hunting could affect outfitter revenues, the proportion of hunted elk in JHU harvested by outfitter-guided clients was estimated using historical data (Wyoming State Board of Outfitters and Professional Guides, 2024). Predictions of future permitted outfitters and clients served were then estimated by applying these proportions to the predicted number of harvested elk under each alternative from Cross and others (2025, this volume, chap. B). McWhirter and others (2022) estimated the average cost of a guided elk hunt to be \$5,000, so we multiplied this value by the respective number of guided clients (regardless of whether they successfully harvested an elk) that were predicted under each alternative to predict future effects on outfitter revenue under each alternative and applied a discount rate of 4.7 percent.

Results

Predicted Changes in Nonhunting Visitors and Visitor-related Spending Under Each Alternative

The fitted model of historical NER winter visits as a function of monthly elk and temporal variables was consistent with observed data (posterior predictive check value=0.62) and each parameter successfully converged (Rhat<1.1; table E1). The effect of historical monthly elk counts on NER winter visitation was weakly positive (mean, 0.03; 95 percent credible interval, -0.05 to 0.10) and 74 percent of the posterior distribution was greater than zero. The median effect size corresponded to an average of 2.5 additional visitors for every 100 additional elk on the NER. When carrying the fitted model and its posteriors forward to project differences in predicted NER winter visits, minimal differences were found among the alternatives; although, a high degree of uncertainty was found within each alternative (fig. E2). Note that in the negative binomial model, where the predictors were centered and scaled prior to fitting, the parameter estimates represent one standard deviation change in the predictor variable as a result of a change in the log of NER visits.

The average 20-year cumulative estimate for NER winter visitors was slightly higher under the continue feeding alternative compared to the other alternatives (table E2); however, there

Table E1.Predictor variables of negative binomial model ofhistorical winter visits to the National Elk Refuge in Jackson,Wyoming, parameter symbology, and fitted parameter estimates.

[The estimates were used to predict future visits under each of the proposed management alternatives and using predictions of future elk counts from Cross and others (2025, this volume, chap. B) and Cotterill and others (2025, this volume, chap. C). %, percent; CI, credible interval]

Variable	Parameter	Mean estimate (95% CI)
intercept	β_0	8.98 (8.80–9.15)
monthlyElk	β_{I}	0.03 (-0.05-0.10)
monthDec	β_2	0.83 (0.60-1.05)
monthJan	β_3	0.75 (0.51-0.98)
monthFeb	eta_4	0.93 (0.67-1.20)
monthMar	β_5	0.90 (0.63-1.18)
year	β_6	0.15 (0.07-0.24)

Table E2.Cumulative predicted nonhunting winter season visitorsand net present value-adjusted nonhunting visitor spending duringwinter months (December–April) on the National Elk Refuge inJackson, Wyoming, predicted under each alternative.

[Note that these totals do not reflect the spending of local residents that live within 50 miles of the Refuge because of small sample size and inconsistencies in their reporting of local National Elk Refuge-related spending. \$, U.S. dollar; SD, standard deviation]

Alternative		cumulative sitors, in sands	Predicted cumulative spending, in millions (\$)	
	Mean	SD	Mean	SD
Continue feeding	3,375	791.7	2,978	698.6
No feeding	3,271	774.4	2,886	683.3
Increase harvest	3,296	763.0	2,908	673.3
Reduce feeding	3,288	755.1	2,901	666.3
Disease threshold	3,286	752.9	2,889	664.3

was large within-alternative variation and substantial overlap of performance estimates for all alternatives. Predicted visitor spending under each alternative maintained this pattern, with nonhunting NER visitor spending predicted to be slightly higher on average under the continue feeding alternative compared the other alternatives, but with a large range of within-alternative variation (table E2).

Predicted Changes in Sleigh Ride Participants Under Each Alternative

A slight positive correlation was revealed between historical elk counts on the Nowlin feeding area and the number of sleigh ride participants (Pearson's correlation coefficient=0.38). The elk-only model showed a small effect of Nowlin feedground

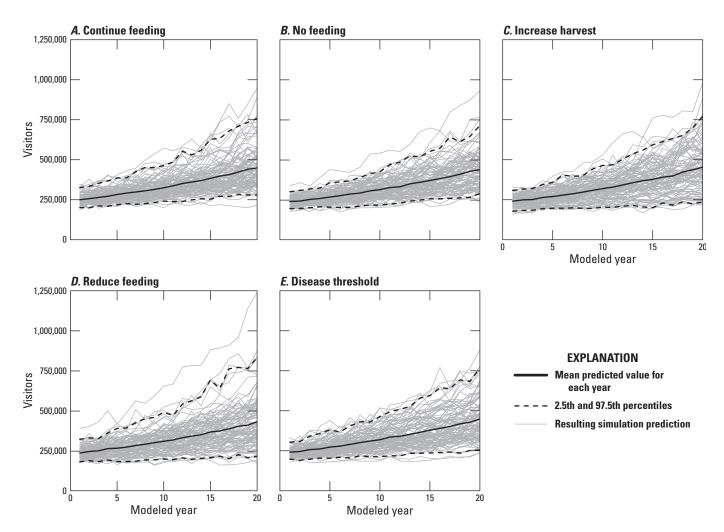


Figure E2. Graph showing annual predicted visitors to the National Elk Refuge in Jackson, Wyoming, during winter months under each alternative. *A*, continue feeding, *B*, no feeding, *C*, increase harvest, *D*, reduce feeding, and, *E*, disease threshold.

elk counts on sleigh ridership (4.23×10^{-05} , p > 0.05). This small effect corresponded to a one-unit change in elk counted on the feedground resulting in a 0.16-unit change in expected number of sleigh ride participants. As a result, based on an evaluation of historical data, we concluded that sleigh ride participation did not differ substantially across alternatives.

Predicted Changes in Hunting Visitors and Hunting-related Spending Under Each Alternative

The number of harvested elk varied through time and according to the alternative (Cross and others, 2025, this volume, chap. B). The harvest generally decreased as elk population projections fell below the JHU population objective of 11,000 elk (WGFD sets population objectives for each elk herd unit according to their estimates of a sustainable population); the decline in harvest was included in Cross and others (2025, this volume, chap. B) as an assumed response by WGFD to declining elk abundance under the alternatives. Because we assumed proportionate spending by resident and nonresident Wyoming hunters remained the same as historical data, the increase harvest alternative resulted in hunting rates and hunting-related revenues that were initially much higher than the other alternatives but dropped rapidly after the initial period of intensive elk harvest. When considering these changes over time, the increase harvest alternative had higher predicted tag revenues (Mean=\$6.60 million, SD=\$574,000) and hunter-related spending (Mean=\$101.29 million, SD=\$9.56 million), but had substantial overlap in the estimated ranges of the alternatives (table E3; fig. E3).

Predicted Changes in Outfitter Revenues Under Each Alternative

In the last five years, an average of 19.5 outfitters (SD=3) guided an average of 17 clients (SD=17.5) each per year. Annually, elk harvested by outfitter-guided clients averaged 218 elk (SD=71 elk), which accounted for 21 percent of the annual total elk harvested in the JHU (SD=3.7 percent).
 Table E3.
 Twenty-year predictions of the cumulative revenues

 from elk tag sales and the total predicted spending by elk hunters
 in the Jackson Elk Herd Unit of Wyoming under each alternative.

[\$, dollar; SD, standard deviation]

Alternative	Cumulative tag revenue, in thousands (\$)		Cumulative spending by hunters, in thousands (\$)	
	Mean	SD	Mean	SD
Continue feeding	5,472	640	88,539	12,214
No feeding	5,004	770	76,140	14,836
Increase harvest	6,604	574	101,294	9,558
Reduce feeding	4,765	758	73,023	14,145
Disease threshold	5,248	717	81,988	14,254

For every elk harvested in JHU annually, outfitters guided an average of 0.35 clients (including those who did not successfully harvest an elk).

Projecting these proportions over 20 modeled years, the increase hunting alternative had the highest predicted number of clients with an average estimate of 3,758 clients served over the next 20 years and a cumulative outfitter revenue of \$14.5 million. The next highest performing alternative was the continue feeding alternative with an average of 3,480 clients and \$12.6 million in revenue, followed by the disease threshold alternative with an average of 3,319 clients and \$11.7 million in revenue (fig. E4). The lowest cumulative number of clients and revenues were predicted under the reduce feeding alternative with 2,879 clients and \$10.4 million in revenue over the next 20 years.

Summary

After evaluating the effects of the five management alternatives under consideration for bison and elk management on National Elk Refuge (NER or Refuge) on social and economic dimensions of concern, this study found minor to moderate differences in the performance of the alternatives on the cumulative number of NER winter visitors, cumulative revenue from elk hunting license sales, cumulative local economic revenues resulting from hunting and nonhunting visitors, and revenues for outfitters guiding in the Jackson Elk Herd Unit. In general, large variation within predicted estimates of elk populations, harvested animals, and visitation resulted in substantial overlap in the estimates of performance of the alternatives for each performance metric. Although we predicted the highest number of NER visitors under the continue feeding alternative, we found that monthly elk counts explained less than 1 percent of the variation in historical NER winter visitation. However, the results of Cross and others (2025, this volume, chap. B), Cotterill and others (2025, this volume, chap. C), and

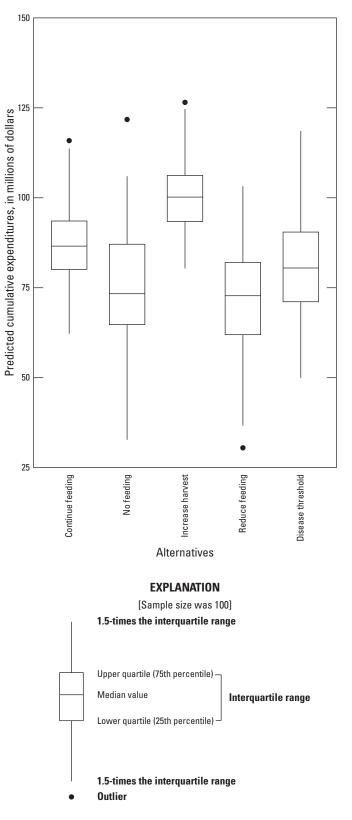
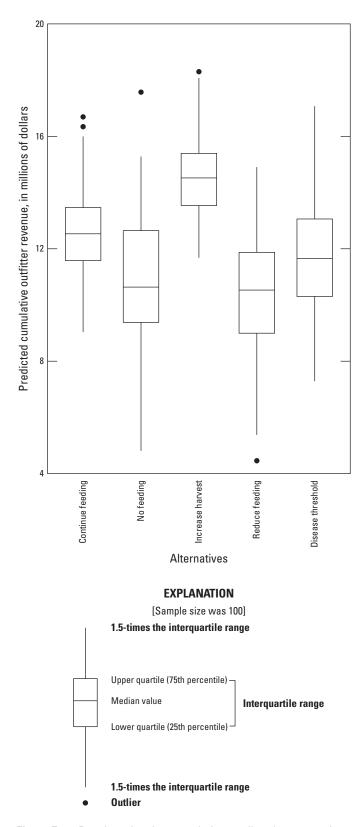
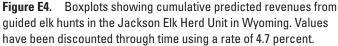


Figure E3. Boxplots showing cumulative predicted spending by elk hunters in the Jackson Elk Herd Unit in Wyoming over 20 model years. Values have been discounted through time using a rate of 4.7 percent.





Summary E9

Cook and others (2025b, this volume, chap. D) predict substantial declines in elk and bison numbers on NER in winter months so the number of NER visitors and associated revenues could change in unexpected ways that are not fully captured by these analyses. The increase harvest alternative performed better on the hunting-related performance metrics on average, including Wyoming Game and Fish Department (WGFD) revenue from elk harvest tag sales, regional revenue from hunting-related spending, and outfitter-revenue, but there was large within-alternative variation.

Some of the estimates presented here are conditioned on strong assumptions about future outcomes. For example, we assumed that any changes in the number of Refuge visitors in winter months resulted in a direct and proportional change in non-hunting visitor spending; however, it is possible that this connection is not as direct. Instead, there is a possibility that non-hunting expenditures do not change in direct proportion to future trends in elk and Refuge visitation, especially given that 87% of Refuge visitors reported that the Refuge was not the only reason to visit the Jackson, Wyoming region (Dietsch and others, 2020). We further assume that future relationships between wildlife populations and visitation, hunting, and related spending can be approximated by relationships of the past. However, if management alternatives drive large changes in elk and bison numbers on the Refuge as indicated in Cross and others (2025, this volume, chap. B), Cotterill and others (2025, this volume, chap. C), and Cook and others (2025b, this volume, chap. D), the relationships might also change. Any effect of elk starvation and CWD-related mortalities that result from changes to NER feeding may negatively affect visitation and hunting in ways not predicted because of public reactions to seeing animals in poor condition.

We assumed that CWD would not affect hunter participation in the region. Previous studies of hunting patterns following CWD emergence have predicted hunting participation declines as CWD prevalence increases (for example, Needham and others, 2006). However, effects on participation vary by state, species pursued, and hunters' emotional response to CWD (Schroeder and others, 2021). Other studies have shown that these declines reverse and hunting returns to normal levels even as CWD prevalence increases (for example, Holland and others, 2020). Therefore, we assumed that hunter participation would remain constant despite predicted increases in CWD throughout the 20-year evaluation period.

Finally, the benefits predicted under the increase harvest alternative may be challenging to implement and thus may affect the revenues generated by outfitters in the region. The harvest regulation changes that would lead to the higher harvest that is predicted in the increase harvest alternative fall primarily under the authority of WGFD. As a result, actions that fall outside of the FWS decision process supported by these analyses would be required to implement this alternative.

Despite the limitations of this study, the findings remain informative for making decisions about elk and bison management of NER. The assumptions were guided by local and regional experts and apply equally across alternatives and thus could be expected to affect each alternative in similar ways. As a result, differences among alternatives may represent good approximations of their relative performance. For this reason, the analyses presented here may assist decision makers in assessing the relative performance of each alternative concerning the anticipated effects on the social and economic benefits that elk and bison provide to the region.

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