



Wyoming Game and Fish Department

Conserving Wildlife, Serving People

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July 13, 2026

WER 6312.05a

United State Forest Service

Caribou-Targhee National Forest

Teton Basin Ranger District

Grand Targhee Resort Master Development Projects

Final Environmental Impact Statement and Draft Record of Decision Objection

Teton County

Jay Pence

District Ranger

United States Forest Service

1405 Hollipark Dr.

Idaho Falls, ID 83401

jay.pence@usda.gov

Dear Mr. Pence,

The staff of the Wyoming Game and Fish Department (Department) has reviewed the Draft Record of Decision (ROD) and Final Environmental Impact Statement (FEIS) for the Grand Targhee Master Development Projects in Teton County. The Department is statutorily charged with managing and protecting all Wyoming wildlife (W.S. § 23-1-103). Pursuant to our mission, we offer the following comments for your consideration.

The Department has been involved with this project as a Cooperating Agency since 2020. Through the various iterations of the process, we have relied upon and valued our long-standing relationship with the United States Department of Agriculture Forest Service (Forest Service) broadly and the Caribou-Targhee National Forest (CTNF) more specifically, with a long history of successfully working together to achieve mutual goals. The Department's primary concern has been the expansion into the South Bowl area and the subsequent impacts to bighorn sheep. We have provided ample technical data and expertise to guide any expansion while minimizing impacts to this Species of Greatest Conservation Need.

Given our consistent position, the information we and other cooperators have provided over the last 6-years, the potential for significant detrimental impacts to wildlife, and the range of alternatives being considered, we are thoroughly disappointed with the CTNF's decision to pursue the most impactful alternative.

Page 4 of the ROD states: *Whether this change [actions authorized in the decision] is viewed as positive or negative is rooted in an individuals' values and their personal views on what a ski area*

should be, what level of recreation is acceptable on Forest Service lands, and what benefits or impacts will be experienced by the communities that surround the resort.

This characterization dismisses over three decades of collaborative work among the Department, CTNF, Grand Teton National Park, the Bridger-Teton National Forest, livestock operators, conservation organizations, recreation advocates, hunting groups, range and habitat managers, and other partners focused specifically on balancing science-based wildlife management with other uses in the Tetons and is a concerning oversimplification of the process which preceded the draft decision.

The Department formally objects to the draft decision outlined in the ROD supported by the Objection Points below due to the likely impacts caused by the Selected Alternative, specifically the Special Use Permit (SUP) expansion into South Bowl. The Department's objections are based on biological information, management objectives, statutory responsibilities, and years of interagency coordination.

Objection Point 1. Draft decision fails to adequately consider state wildlife management authority, legal and statutory responsibilities, and existing agreements between the State of Wyoming and the Forest Service:

The Teton bighorn sheep herd (also known as the Targhee herd) is a core, native bighorn sheep herd in Wyoming per Wyoming Statue § 11-19-604. State law requires the Wyoming Game and Fish Department to manage bighorn sheep in accordance with the Wyoming Statewide Bighorn/Domestic Sheep Interaction Working Group Plan (known as the Wyoming Plan). Per state law, the core, native bighorn sheep herds are the highest priority for bighorn sheep management in the state. As such, the Department, federal land management agencies, and non-profit conservation organizations have dedicated an outsize amount of effort, funding, and commitment to ensuring the continued persistence of the Teton bighorn sheep herd. Page 14 of the ROD describes the predicted impact of the decision on bighorn sheep as:

Loss of habitat within and in the vicinity of the project area, particularly in South Bowl and in Teton Canyon, which is likely accessed through South Bowl, has the potential to harm viability of the Teton Range Herd.

...the Selected Alternative has the potential to result in an overall decline in the population of the Teton Range Herd...

The Wyoming Game and Fish Commission (WGFC) has the statutory authority to manage wildlife populations within Wyoming. The decision recognizes the potential to harm the viability of the Teton Range Herd. The Department has consistently provided data, research, and expert opinion supporting a likely impact to the viability of the herd with expansion into South Bowl. The Selected Alternative and decision that will result in a likely reduction in the viability and population size of the Teton bighorn sheep herd and impedes the Department's and the WGFC's ability and statutory authority to manage the herd on behalf of Wyoming stakeholders, consistent with WGFC population objectives and the long-term biological integrity of a herd.

Furthermore, the Wyoming Plan is recognized in an Agreement for Shared Stewardship between the State of Wyoming and the Forest Service signed in January of 2026 (Appendix A). Bullet point 3 under the “Mutual Commitments for Shared Stewardship in Wyoming” is the following:

***We are committed to collaborative planning and management.** The State and the USDA Forest Service will continue to work cooperatively to implement and integrate Wyoming's Forest Action Plan, Wyoming's Strategic Wildlife Action Plan and Strategic Habitat Plan, the Statewide Bighorn/Domestic Sheep Interaction Working Group plan, Wyoming's Greater Sage-grouse Executive Order, the USDA Forest Service's 5-year Vegetation Management Plans, land and resource management plans, and the National Cohesive Wildland Fire Management Strategy. Parties will work to identify and map shared priorities across all lands and share proper and appropriate data and tools to implement land and resource management plans.*

The ROD and Selected Alternative not only run counter to Wyoming state law but also the shared agreements between the State of Wyoming and the Forest Service regarding management of bighorn sheep and their habitats.

Objection Point 2. Decision is inconsistent with the Forest Plan: The decision is not consistent with the intent of the 1997 Revised Targhee National Forest Plan (Forest Plan). Page III-56 of the Forest Plan specifies the following Wildlife Goals:

- *Maintain or improve big game winter range.*
- *Coordinate with Grand Teton National Park and the Wyoming Game and Fish Department in the management of the bighorn sheep population and habitat.*
- *Provide for recreational activity while maintaining the integrity of crucial wildlife habitats.*
- *Work with the Intermountain Research Station to establish a research project to study the effects of recreation on bighorn sheep in the Teton Range subsection.*

As stated previously, the Project Design Criteria (PDC) and minimization measures included in the FEIS and ROD plus the removal of 31 acres of the South Bowl expansion do not meaningfully mitigate impacts to bighorn sheep. Given the lack of effective mitigation and the impacts identified on page 14 of the ROD, expansion into South Bowl is inconsistent with the Forest Plan's Wildlife Goals by authorizing development in intact, crucial habitat for bighorn sheep and greatly reducing the integrity of crucial wildlife habitats.

Objection Point 3. The analysis presented Section 3.13 of the FEIS does not adequately support the decision and the decision does not follow Forest Service Policy for sensitive species.

Bighorn sheep are a sensitive species on the CTNF. Per the Forest Service Manual 2600, Section 2670.22, for sensitive species, the Forest Service must:

...maintain viable populations of all native and desired nonnative wildlife, fish, and plant species in habitats distributed throughout their geographic range on National Forest System lands.

Viable populations, defined on page 12 of the Forest Service Manual 2600 Chapter 2670, are:

A population that has the estimated numbers and distribution of reproductive individuals to ensure the continued existence of the species throughout its existing range (or range required to meet recovery for listed species) within the planning area.

As stated on page 14 of the ROD, viability of the Teton bighorn sheep has the potential to be harmed with the Selected Alternative. It is the CTNF's responsibility to maintain the habitat required for the State managed viable Teton population to persist. If the herd declines as a result of the Selected Alternative, the FEIS and ROD do not include any analysis, assessment, or biological justification for how population viability for bighorn sheep is expected to be maintained within the planning area, as per the definition above, and as is required for a sensitive species.

The ROD and FEIS justify what the Department has consistently expressed to be a likely decline of bighorn sheep and the likely reduced population viability of the Teton bighorn sheep herd due to the existence of two other bighorn sheep herds on the CTNF in Idaho. However, the future persistence of these other two bighorn sheep herds is highly uncertain. The two herds in Idaho are both reintroduced, have relatively low numbers, one has not been surveyed for over 5 years so its current status is uncertain, are isolated from surrounding herds, and are infected with pneumonia pathogens (including *Mycoplasma ovipneumoniae*) that are affecting their herd health and long-term survival (H. Miyasaki pers. Comm). For these reasons, it is unclear if these herds will persist over the long term and therefore, it is not biologically appropriate to rely on these herds to meet bighorn sheep population viability requirements on habitat managed by the CTNF.

Teton bighorn sheep herd is native and *Mycoplasma ovipneumoniae* has never been documented in the herd, even after multiple years of disease sampling. Native bighorn sheep herds are rare and therefore have irreplaceable genetics that are important for the species as a whole (Cassirer et al. 2026). According to Cassirer et al. 2026, "preventing additional loss of genetic variation in bighorn sheep that have undergone thousands of years of local adaptation is important for conservation and management into the future." The Teton bighorn sheep herd is genetically distinct from other neighboring, native bighorn sheep herds (S. Dewey, pers. Comm), elevating their genetic importance.

The Forest Service Manual 2600 Section 2670.32 also states that Policy for sensitive species includes:

- 1) *Assist states in achieving their goals for conservation of endemic species...*
- 3) *Avoid or minimize impacts to species whose viability has been identified as a concern.*
- 4) *Analyze, if impacts cannot be avoided, the significance of potential adverse effects on the population or its habitat within the area of concern and on the species as a whole. (The line officer, with project approval authority, makes the decision to allow or disallow impact, but the decision must not result in loss of species viability....)*

5) Establish management objectives in cooperation with the states when projects on National Forest System lands may have a significant effect on sensitive species population numbers or distributions...

In addition to the concerns over viability of the bighorn sheep, the Department, as a cooperating agency, has provided a large amount of technical data and expertise on bighorn sheep in this herd as well as expressed substantial concerns about impacts to bighorn sheep from the proposed SUP expansion throughout development of the EIS. Some key technical data have not been included accurately in the Biological Evaluation (BE) and FEIS (see Objection Point 4) for this sensitive species. Moving forward with the decision would result in a violation of point 5 above.

Objection Point 4. The Forest Service did not accurately incorporate technical data provided by Wyoming Game and Fish Department as a Cooperating Agency into the FEIS and did not accurately integrate the results of their own studies into the Affected Environment and Environmental Consequences assessment.

The FEIS still contains inaccurate information stating that there are five bighorn sheep herds on the CTNF, as there are only three (FEIS page 294). The Department provided the following information on page 4 of WER 6312.05:

For bighorn sheep, the DEIS and BE use outdated information from 2016 and 2017 to describe other bighorn sheep herds on CTNF. The BE states that there are 5 bighorn sheep herds on CTNF (South Lemhi, South Beaverhead, and Lionhead (2 herds) in Idaho and Targhee Herd in Wyoming) and that there are a total of approximately 300 sheep (BE; page 19). However, according to the most recent Idaho Department of Fish and Game Bighorn Sheep Management Plan (May 2022) the population estimates have changed in the last 8-9 years. The Lionhead Herd is made up of two game management units, however, this area is not consistently occupied by sheep and a few individuals only occur on a transient/foraging basis from a neighboring herd in Montana (IDF&G 2022; H. Miyasaki pers. comm.). The BE appears to include this herd and a population estimate of 105 sheep as part of its population viability analysis for the Targhee Planning Area, however this herd entirely resides in Montana outside of CTNF and it should not be included. The BE describes population numbers for the South Lemhi Herd as 41 and the South Beaverhead Herd as 36, however, the more recent counts from IDF&G (2022) are 110 and 17, respectively. Furthermore, the BE considers the entire Targhee Herd as residing on CTNF when referencing impacts at the Targhee Planning Area scale. Many sheep from the Targhee herd primarily reside in Grand Teton National Park, which is not within the Targhee Planning Area. Therefore, the Targhee Planning Area has 3 bighorn sheep herds and realistically fewer than 200 sheep (South Lemhi Herd, 110; South Beaverhead Herd, 17; and Targhee Herd, approximately 50 on CTNF) versus the 300 stated in the BE.

We recognize and appreciate the attempt to better explain the bighorn sheep herds considered in the FEIS on pages 294-295:

It should also be noted that the Lionhead herd primarily resides in Montana and consists of transient individuals, which may not contribute to population dynamics within the CTNF.

The Department reaffirms our position that the Lionhead Herd should be removed from consideration, thus limiting focus of potential project-related impact to three herds with fewer than 200 sheep in the Planning Area.

On page 3 of WER 6312.05, the Department provided more recent results from a fecal DNA study conducted by Grand Teton National Park that annual population estimates for the Teton bighorn sheep population ranged from 118-132 sheep during the study. The FEIS (pg. 294) and BE (pg. 22) still contain outdated and inaccurate preliminary results that have since been modified with improved methods in the study. The preliminary results were shared in a newspaper article but the accurate numbers are reported in a forthcoming journal publication (Butler et al. *in review*, Wildlife Society Bulletin). We again acknowledge the attempts to update population estimates but the attempt falls short of fully integrating the population estimates we previously provided, which further calls into question the lack of consideration of impacts to bighorn sheep with the Selected Alternative.

The FEIS states that the camera study conducted by an environmental consulting firm failed to detect bighorn sheep in South Bowl during winter, suggesting that bighorn sheep do not use the area in the winter. The consultants that conducted the camera study in South Bowl acknowledge significant limitations, specifically including uncertainty in sheep detections due to terrain, camera placement and field view, snow depths, and camera deployment failures. As such, the results do not definitively demonstrate lack of bighorn sheep use of South Bowl in winter (FEIS pg. 292).

Suggested Remedy to the Department's Objections

The only effective remedy to the Department's Objection Points is to avoid SUP expansion and the subsequent development into South Bowl.

Thank you for the opportunity to comment. If you have any questions or concerns, please contact me at (307) 777-4501.

Sincerely,



Angi Bruce
Director
Wyoming Game and Fish Department
5400 Bishop Blvd.
Cheyenne, WY 82006

AB/jd/rc

cc: Chris Wichmann, Wyoming Department of Agriculture



AGREEMENT FOR SHARED STEWARDSHIP

Between

THE STATE OF WYOMING

And the

**UNITED STATES DEPARTMENT OF AGRICULTURE
FOREST SERVICE**

This updated Agreement for Shared Stewardship is hereby made and entered into by the State of Wyoming, and the United States Department of Agriculture Forest Service to work towards shared interests and the national framework of Shared Stewardship.

Introduction

In 2020, Governor Mark Gordon and then Secretary Sonny Perdue crafted and enacted the first iteration of this Agreement for Shared Stewardship (Agreement). Since the original Agreement was completed, multiple beneficial projects have been implemented across the state of Wyoming. Areas in which this Agreement could be improved have been identified, creating a need for updating the existing Agreement. This new Agreement, and all addendum hereby incorporated by reference, shall serve as the new Agreement between the State of Wyoming (State) and the United States Department of Agriculture Forest Service (USDA Forest Service) and is effective upon final signature.

The State and the USDA Forest Service share mutual goals and commitments to advance Shared Stewardship in Wyoming. All parties in this Agreement commit to existing partnerships, programs, and initiatives. This document outlines the commitment of both the State and the USDA Forest Service, working in close partnership and good faith, to improve forests and grasslands across Wyoming.

This Agreement is not an authorizing tool; the parties will rely on all available authorities, including, but not limited to, the Good Neighbor Authority, applicable Farm Bill Authorities, and the Cooperative Forestry Assistance Act, to implement priority projects.

The National Vision and Framework of Shared Stewardship

The USDA Forest Service initiative for cross-boundary land management is described in the 2018 document *Toward Shared Stewardship Across Landscapes: An Outcome-Based Investment Strategy*.

This strategy addresses challenges faced by federal, state, and private managers of forests and rangelands, including catastrophic wildfires, invasive species, degraded watersheds, insects and disease. Many of these challenges are not new but have changed in urgency, severity, frequency, or scale in recent years. Ecosystems and associated forest and grassland health, wildfire, watersheds, habitat, forage, and other resources are not strictly confined or defined by administrative boundaries, which make the concept and practice of Shared Stewardship vital to addressing these issues in a meaningful way.

Through Shared Stewardship, the State and the USDA Forest Service will work collaboratively to determine priorities, implement projects, share resources, and work towards identification of the highest need for protection or restoration within surrounding communities, watersheds, and priority areas across all lands. This approach addresses short term needs, long-term desired outcomes, and furthers multiple-use, sustained yield concepts. This outcome-based strategy has three primary elements:

1. Strategize on a statewide level. The State and USDA Forest Service will work together to achieve desired cross-boundary outcomes by combining mutual skills and resources. The State will lead in bringing stakeholders together to discuss strategies, issues, and priorities. Existing or newly developed statewide strategies will provide guidance for coordinating activities across jurisdictional boundaries, where appropriate.
2. Implement meaningful projects in the right places, at the appropriate scale. The State and the USDA Forest Service will utilize mapping and decision-making tools to identify the highest priority areas for projects to occur and work together to determine the appropriate scale for implementation.
3. Use all available tools to promote proactive management. The State and the USDA Forest Service will use all available authorities and tools to achieve desired outcomes and work towards implementation of strategies.

Mutual Commitments for Shared Stewardship in Wyoming

The State and the USDA Forest Service developed the following mutual commitments for Shared Stewardship in Wyoming:

1. ***We are committed to joint planning and resource sharing, especially in overlapping decision space, for immediate and ongoing work across the landscape.*** The State and the USDA Forest Service will work together to determine where and how to use available legal authorities and management tools, share financial resources, and leverage resources to the greatest extent possible to accomplish work across jurisdictional boundaries. We jointly commit to building, maintaining and expanding our collective relationships with communities, counties, tribal organizations, collaborative groups, community groups, conservation groups, and other stakeholders; to plan and act in a coordinated manner. We commit to work with all our partners to identify shared outcomes for cross-boundary work and utilize Good Neighbor Authority to the extent practicable. As of 2025, three state agencies (Office of State Land and Investment: State Forestry Division, Wyoming Department of Agriculture, and Wyoming Game and Fish Department) have used Master Agreements under the Good Neighbor Authority to accomplish needed work; these existing Master Agreements continue in accordance with their terms.

2. ***We are committed to continuing existing successful partnerships and programs.*** Wyoming and the USDA Forest Service have a long history of working cooperatively across landscapes through both state and federal programs. These long-standing partnerships and programs provide a foundation from which Shared Stewardship in Wyoming can be advanced. Current partnerships and programs include, but are not limited to: Forest Legacy, Health and Stewardship, Urban & Community Forestry, State Fire Assistance, Interagency Cooperative Fire Management and Response, Sage Grouse Implementation Team, Governor's Invasive Species Initiative, Bighorn National Forest Steering Committee, and the Programmatic Agreement on Compliance with the National Historic Preservation Act on USDA Forest Service lands in Wyoming. The State and the USDA Forest Service agree to collaboratively work in these partnerships and programs and identify and leverage other potential partnerships, initiatives, and programs in the future.
3. ***We are committed to collaborative planning and management.*** The State and the USDA Forest Service will work cooperatively to implement and integrate Wyoming's Forest Action Plan, Wyoming's Strategic Wildlife Action Plan and Strategic Habitat Plan, the Statewide Bighorn/Domestic Sheep Interaction Working Group plan, Wyoming's Greater Sage-grouse Executive Order, the USDA Forest Service's 5-year Vegetation Management Plans, land and resource management plans, and the National Cohesive Wildland Fire Management Strategy. Parties will identify and map shared priorities across all lands and share proper and appropriate data and tools to implement land and resource management plans.

Modifications, Periodic Review and Termination of Agreement

The State and the USDA Forest Service will communicate on a regular basis to implement items outlined in this Shared Stewardship Agreement. The parties mutually agree to periodically review and make appropriate adjustments to this Agreement every four years, or as needs are identified, until the Agreement terminates in accordance with applicable law, regulation and policy. This Agreement is intended to be a "living document", to last no longer than 10-years. This Agreement will terminate 10-years from the date of the last signature.

General Terms and Conditions

1. Nothing in this Agreement affects the federal government's USDA Forest Service's government-to-government and trust relationship with Tribes or affects the USDA Forest Service's ability to exercise its authority under or ability to comply with federal law.
2. The State and the USDA Forest Service will evaluate the use of separate instruments to implement management activities associated with forest lands.
3. This Agreement in no way restricts the State and the USDA Forest Service from participating in similar activities with other entities.
4. This Agreement creates no right, benefit, or trust responsibility, substantive or procedural, enforceable by law or equity. The State and the USDA Forest Service shall manage their respective resources and activities in a separate, coordinated mutually beneficial manner to meet the purposes of this Agreement. Nothing in this Agreement authorizes the State and the USDA Forest Service to obligate or transfer anything of value.
5. Specific, prospective projects or activities that involve the transfer of funds, services, property, and/or anything of value to a party requires the execution of separate agreements and are contingent upon numerous factors, including, as applicable, but not limited to:

availability of appropriated funds and other resources; cooperator availability of funds and other resources; administrative and legal requirements (including agency authorization by statute); etc.

6. Nothing in this Agreement is intended to alter, limit, or expand the agencies' statutory and regulatory authority.

Authorized Representatives

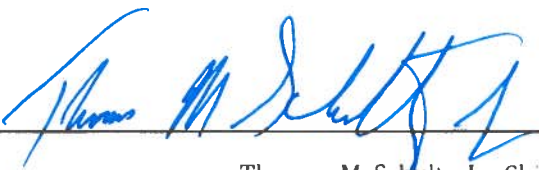
By signing below, each party certifies that the individuals listed are authorized to act in their respective areas for matters related to the Shared Stewardship Agreement.

In Witness whereof, the parties hereto have executed this Agreement as of the last date written below.

State of Wyoming

Date: 16 January 2026  _____
Mark Gordon, Governor of Wyoming

US Department of Agriculture

Date: 21 January 2026  _____
Thomas M. Schultz, Jr., Chief, USDA Forest Service

ADDENDUM 1

Increasing Responsible Forest Management in Wyoming

This addendum to the agreement for Shared Stewardship is directed at bolstering Wyoming's forest products industry and timber management. The addendum relates to those agencies of the State that closely manage or cooperate in the management of Wyoming's timber resources.

Introduction

Wyoming's forests and grasslands are an essential part of the state's identity and heritage, spanning millions of acres across rugged mountains, rolling foothills, and river valleys. From the lodgepole pine forests of the Medicine Bow and Shoshone to the mixed conifers of the Black Hills and Bighorns, these lands provide not only rich wildlife habitat and clean headwaters but also irreplaceable spaces for hunting, fishing, grazing, timber production, and recreation.

For generations, Wyoming citizens depended on and cherished forests as "working lands", supporting local economies and rural communities through forestry, livestock grazing, wood products, energy development, tourism, recreation, wildlife habitat, fishing and hunting access, and outdoor traditions. The stewardship of these diverse landscapes is inseparable from the Wyoming way of life, underscoring a commitment to manage forests with a focus on sustainability, access, resilience, and shared benefit for all who live in or visit the state.

These lands include all or portions of eight National Forests and one National Grassland, which together represent the backbone of Wyoming's forested landscapes:

Bighorn National Forest	Black Hills National Forest
Bridger-Teton National Forest	Caribou-Targhee National Forest
Medicine Bow-Routt National Forest	Thunder-Basin National Grassland
Shoshone National Forest	Ashley National Forest
Uinta-Wasatch-Cache National Forest	

Shared Vision for Increasing Active Forest Management

The State and the USDA Forest Service share a commitment to secure America's timber independence, revitalize rural economies, and protect Wyoming communities from catastrophic wildfire while recognizing the mutual benefits of a coordinated, landscape-scale approach to forest restoration and management. This includes the implementation of current and future national and state direction, including, but not limited to, the Forest Service National Active Forest Management Strategy, Executive Order 14225 - Immediate Expansion of American Timber Production, Secretarial Memo 1078-006 - Increasing Timber Production and Designating an Emergency Situation on National Forest System Lands, and Wyoming Executive Order 2025-04 - Increase of Active Forest Management in Wyoming.

Through existing authorities and the agreement for Shared Stewardship, the State and the USDA Forest Service will:

1. Expand sustainable domestic timber production by striving to jointly establish timber harvest goals by developing annual and 5-year work plans associated with those goals.
2. Streamline project delivery through the use of available tools and authorities that facilitate active forest management, including the implementation of new and expanded NEPA categorical exclusions and emergency authorities.
3. Leverage state-federal partnerships to address capacity constraints, enabling proper management of all lands and forest resources.
4. Enhance wildfire resilience, improve forest health, and enhance wildlife habitat by increasing the pace and scale of thinning, timber salvage, fuels reduction projects, and habitat restoration projects.

Timber-specific Objectives of Addendum 1

In many areas, timber-specific projects are in drastic need of implementation. This Addendum has identified three main areas of emphasis.

1. Wood Recovery and Utilization
 - a. Sustainable Timber Harvest: Increase wood product recovery from fuels-reduction and restoration projects, particularly an outlet for small-diameter wood.
 - b. Rapid Post-Wildfire Response and wood utilization: Co-develop and implement protocols for swift deployment of response teams and resources following wildfires
 - c. Market Development: Support local industry, milling, and bioenergy initiatives.
2. Collaborative Prioritization and Planning
 - a. Joint Identification of Priority Landscapes: use risk assessments, spatial data, and stakeholder input to annually identify and plan projects in high-priority areas for fuels reduction, restoration, and timber recovery.
 - b. Create Interagency Implementation Teams: In instances where resource sharing or agency expertise are not captured by other agreements or mechanisms, create interagency teams to address specific forest issues and maintain effective and efficient management of Wyoming forests.
 - i. These interagency implementation teams are to include other federal and state agencies, local government, and other partners.
 - c. Pilot Programs: pilot a new active management strategy within two National Forests in Wyoming, focused on increasing sustainable timber production while improving overall forest health and resilience. These landscapes will be strategically selected to demonstrate how the State's capacity, contracting efficiency, and local expertise can accelerate project implementation at a meaningful landscape scale.
 - i. The pilot projects will emphasize the efficiencies of the Wyoming Good Neighbor Authority on federal forested lands through streamlined planning, workforce integration, and expanded use of state contracting tools. Lessons learned through these pilot projects will inform future large-scale planning

efforts across Wyoming National Forests and provide a framework for integrating state-led implementation under the Shared Stewardship model.

3. **Monitoring and Adaptive Management**

- a. For monitoring purposes, the State and USDA Forest Service will create a combined tracking system for acres treated, wood recovered, and restoration outcomes.
- b. Based on progress, results, and stakeholder feedback, the State and USDA Forest Service will apply adaptive management strategies to adjust priorities and projects as necessary.

Other Shared Stewardship Opportunities

Through existing authorities and the agreement for Shared Stewardship, the State and the USDA Forest Service will identify opportunities to jointly manage other resources on Forest Service administered lands, including but not limited to:

1. Enhancing and providing sustainable wildlife habitat,
2. Supporting tourism and recreation opportunities,
3. Preserving and increasing grazing opportunities and Animal Unit Months (AUMs) statewide,
4. Exploring new opportunities to partner in energy development,
5. Engaging in collaborative planning.

The Parties affirm their commitment to collaborative decision-making, transparency, and a science-based, outcome-driven approach.

Commitment, Funding, and Review

To the extent consistent with existing authorities and available appropriations, the State and the USDA Forest Service agree to allocate staff, funding, and technical resources to jointly identify projects or other actions derived from the provisions of this Addendum. This Addendum will be reviewed annually and may be amended as new science or conditions warrant.



The past is prologue: contemporary and historical genetic variation in a bighorn sheep metapopulation

E. Frances Cassirer^{1,2} · Soraia Barbosa^{1,2,5} · Kimberly R. Andrews² · Nathan Borg^{3,6} · Jennifer R. Adams² · Hollie Miyasaki⁴ · Michael S. Mitchell³ · Lisette P. Waits²

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Abstract

Bighorn sheep (*Ovis canadensis*) experienced widespread population declines and extirpations during the late 19th and early 20th centuries, and recovery has been limited in scope and magnitude. We explored the molecular legacy of this history by comparing genetic diversity and structure in a native Rocky Mountain bighorn sheep (*O. c. canadensis*) metapopulation in central Idaho to genetic variation in samples collected from the same area up to 138 years earlier and to mitochondrial DNA haplotypes in bighorn sheep populations across western North America. The contemporary Idaho metapopulation was structured into 6 genetic groups with varying levels of admixture that largely corresponded with 5 population management units as defined by the distribution of bighorn sheep and suitable habitat. Nuclear DNA microsatellite diversity (expected heterozygosity H_e) was higher in historical samples from a private collection dated between 1879 and 1985 from the Lower Salmon (H_e 0.756) and Middle Fork Salmon populations (H_e 0.735) than in contemporary samples (Lower Salmon H_e 0.677, Middle Fork H_e 0.720). The Lower Salmon historical samples also had higher mitochondrial DNA (mtDNA) haplotype diversity (H_d 0.972), and more private microsatellite alleles (11) than contemporary samples from Lower Salmon (H_d 0.792, 0 private alleles). Thirteen Idaho mtDNA haplotypes were assigned to a haplogroup containing desert (*O. c. nelsoni*, *O. c. mexicana*, *O. c. weemsi*) and Sierra Nevada (*O. c. sierrae*) bighorn sheep lineages, consistent with gene flow between Rocky Mountain and desert sheep subspecies. This haplogroup contained 35% of the Idaho samples collected between 1879 and 1985, and only a single contemporary sample (0.01%). Our analyses show that a history of population declines, fragmentation, and lack of recovery is reflected in a loss of genetic diversity and connectivity in the Idaho native bighorn sheep metapopulation and a reduction in gene flow between bighorn sheep subspecies.

Keywords Connectivity · Genetic diversity · John Carrey · Mitochondrial DNA · Microsatellites · Wildlife disease

E. Frances Cassirer and Soraia Barbosa contributed equally to this work.

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Introduction

Over the past 12,000 years (the Holocene), wild animals, especially large mammals and birds, have experienced periods of declines and extinctions on most continents, including North America, often coincident with human dispersals and colonization (Barnosky et al. 2004; Roycroft et al. 2021; Smith et al. 2021). A relatively recent and well-documented example of this is bighorn sheep (*Ovis canadensis*), previously an abundant and widely distributed mammal native to western North America (Seton 1927; Buechner 1960). Starting in the late 19th century, populations declined and were extirpated across their range in the United States primarily due to introduction of diseases from domestic sheep (*Ovis aries*) and goats (*Capra aegragrus hircus*), unregulated hunting, and competition for forage with livestock associated with American westward expansion and settlement (Buechner 1960; Whiting et al. 2023). In the state of Idaho, archaeological and paleontological evidence, along with early written accounts indicate that bighorn sheep were widespread and common for millennia, coexisting with indigenous people who relied on wild sheep for practical, cultural, and ceremonial purposes (Russell 1921; Shutler and Shutler 1963; Pavesik 1971; Butler 1978). By the early 20th century, Idaho bighorn sheep distribution was reduced to the Salmon River and its tributaries in the central part of the state, restricted to areas that were relatively inaccessible to humans and livestock within the traditional lands of the Shoshone-Bannock and Nez Perce tribes (Smith 1954; Buechner 1960). Declines continued through the 1960's in the remnant, fragmented Salmon River populations, largely attributed to degraded habitat conditions on winter ranges, disease, poor lamb recruitment, and ongoing hunting pressure (Morgan 1971).

Habitat protections, changes in livestock grazing including a decline in the domestic sheep industry (summarized in Thorne et al. 2021), and additional restrictions on hunter harvest (Hickey 1978) allowed for some recovery in the 1970's and 1980's (Hickey 1982; Ballard 1991), but outbreaks of respiratory disease and associated high rates of mortality continued to occur in native Idaho bighorn sheep populations into the 1990's, and disease-induced mortality is still an obstacle to recovery (Akenson and Akenson 1992; Scott 1996; IDFG 2022). Although bighorn sheep have been reestablished elsewhere in the state through translocations into vacant ancestral ranges, the surviving native populations contain over half of Idaho's wild sheep and are an irreplaceable genetic and ecological resource (IDFG 2022).

Reflecting scientific and public interest in bighorn sheep and the management actions implemented for their restoration, previous studies have evaluated contemporary genetic diversity and structure (Ramey 1995; Buchalski et al. 2015;

Malaney et al. 2015; Rodríguez-Rodríguez et al. 2015; Epps et al. 2018, 2024; Deakin et al. 2020; Stowell et al. 2020; Barbosa et al. 2021), explored the genetic effects of translocations (Whittaker et al. 2004; Miller et al. 2012; Olson et al. 2012; Malaney et al. 2015; Gille et al. 2019; Jahner et al. 2019; Flesch et al. 2020; Barbosa et al. 2021), and natural recolonizations (Epps et al. 2010), evaluated climate vulnerability (Creech et al. 2020), identified major barriers to gene flow (Epps et al. 2005, 2018) and examined phylogeographic structure and systematics (Wehausen and Ramey 2000; Buchalski et al. 2015; Santos et al. 2021; Wright et al. 2024; Jahner et al. 2025). However, there have been few opportunities for comparing contemporary and historical levels of genetic structure and diversity in native bighorn sheep populations, and there have been no comprehensive genetic analyses of indigenous bighorn sheep in Idaho.

Genetic material obtained from museum specimens and private collections has shown great promise as a source of historical data that has been used for many purposes, including investigating changes in genetic diversity and gene flow over time. (Miller and Waits 2003; Casas-Marce et al. 2012; Card et al. 2021; Davis and Knapp 2024). In this study we describe contemporary (2000–2017) genetic variation of native sheep (*O. c. canadensis*) in Idaho in comparison to other modern-day populations in North America and in the context of genetic information obtained from the horns of bighorn rams from the Salmon River dated between 1879 and 1985 from the private collection of John Carrey (b.1914 – d.2002), an Idaho rancher, guide, and author (Carrey and Conley 1977;1978; Carrey et al. 1979). We use these analyses to (1) evaluate contemporary genetic diversity and structure among Idaho native sheep population management units (PMUs), and (2) explore changes in genetic variation following a period of population declines and fragmentation.

Materials and methods

Study area

We obtained biological samples collected from native bighorn sheep in interconnected populations (the metapopulation) in the Salmon River watershed, identified as five population management units (PMUs) by the Idaho Department of Fish and Game (IDFG) with a minimum combined abundance of approximately 2,400 sheep (IDFG 2022; Table S1). Connectivity within the metapopulation was inferred prior to this study based on the availability of continuous suitable habitat as determined by maximum entropy models of sheep occurrence (Maxent 3.4.1; Phillips et al. 2006; Phillips and Dudík 2008; Phillips et al. 2017) and lack of significant barriers to movement among PMUs (IDFG

2022). Other evidence supporting connectivity included a wave of pneumonia outbreaks that spread across the metapopulation in the 1980's and early 1990's. The outbreak was associated retrospectively with a unique strain of the genetically variable bacterium *Mycoplasma ovipneumoniae* (Manlove et al. 2019) that originated in domestic sheep and was presumably transmitted by movements of bighorn sheep across populations (Scott 1996; IDFG 2022), likely following contact between the two species on domestic sheep grazing areas (e.g. Smith 1954, p. 53, Cassirer et al. 2017; Besser et al. 2021).

The geographic ranges delineated by IDFG PMUs represent areas periodically or regularly used by groups of bighorn sheep in similar habitats with similar management priorities. This study focuses on the Middle Main Salmon (Middle Main), East Fork Salmon (East Fork), Middle Fork Salmon (Middle Fork), Lower Panther – Main Salmon (Lower Panther), and Lower Salmon PMUs which are located in a relatively remote area of approximately 7,400 sq km of potential bighorn sheep habitat, mostly on public lands including portions of the Frank Church - River of

No Return, Boulders, White Clouds, Jerry Peak, and Gospel Hump Wilderness Areas (Fig. 1, IDFG 2022). We also included two samples obtained from horns and skulls discovered in formerly occupied habitats that no longer contain resident bighorn sheep populations: one in the Pioneers PMU and another collected at Lone Pine Mountain between the East Fork PMU and the adjacent reintroduced Lost River Range PMU (Fig. 1; Table 1).

Translocations have been widely used in efforts to restore bighorn sheep in Idaho and elsewhere throughout their range, however, there has only been one translocation of sheep into the native Salmon River metapopulation. This occurred in 1984, when 16 bighorn sheep from

the reintroduced Lostine, Oregon population (established in 1971 with sheep from Banff, Alberta) were released into the Lower Panther PMU. Three of the Idaho PMUs in this study were used to re-establish and supplement bighorn sheep populations in and outside Idaho. Between 1969 and 1992, a total of 247 bighorn sheep were translocated out of the Middle Main (104 sheep), Lower Panther (130 sheep), and East Fork PMUs (13 sheep, IDFG 2022). This includes

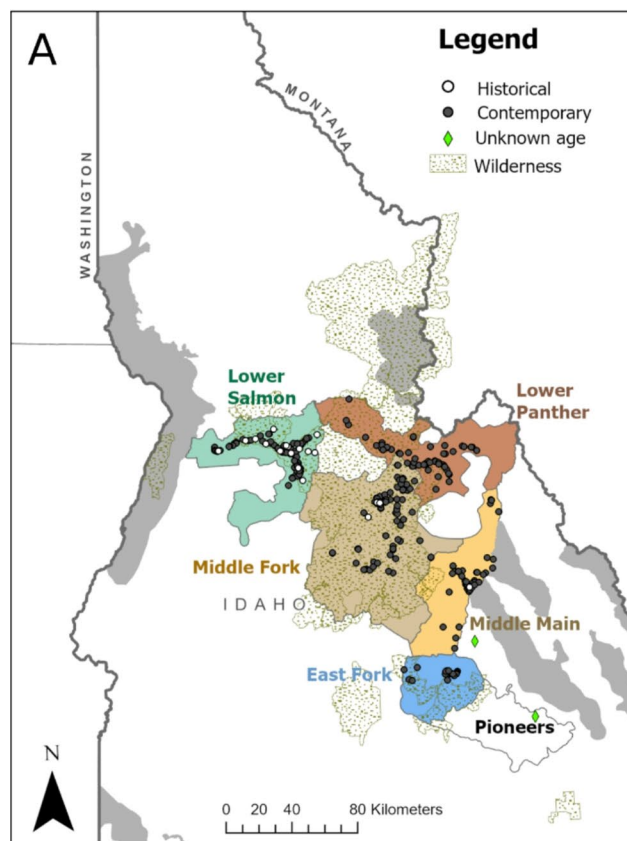


Fig. 1 Distribution of contemporary and historical samples from Idaho native bighorn sheep and photos of representative skulls in the John Carrey collection. (A) Sample collection locations superimposed on the distribution of bighorn sheep in Idaho. Colored and labeled polygons represent native bighorn sheep population management units



(PMUs) and reintroduced PMUs are shaded gray. Historical samples include the John Carrey collection and samples collected in the Middle Main population in 1989. (B) Examples of specimens from the John Carrey collection included in this study

Table 1 Number and sources of DNA samples collected in five population management units (PMUs) of native Bighorn sheep in Idaho, and the number of those samples used for mitochondrial (mtDNA) and microsatellite (usat) analyses

PMU	Sample type					Sex			Marker type	
	Total	Blood/Serum	Fecal	Horn	Bone	Female	Male	Unknown	mtDNA	usat
<i>Contemporary samples(2000–2017)</i>										
Lower Salmon (LS)	117	55	39	23		58	57	2	44	113
Middle Fork (MF)	94	8	26	60		28	66		44	93
Middle Main (MM)	55	20	11	24		19	36		26	55
Lower Panther (LP)	57	18	18	21		24	31	2	29	57
East Fork (EF)	34	25	6	3		21	12	1	8	34
<i>Historical samples(1989)</i>										
Middle Main (MM-H)	34	34				6	5	23	27	33
<i>Historical samples Carrey collection(1879–1985)</i>										
Lower Salmon (LS-H)	27			23	4		27		26	23
Middle Fork (MF-H)	5			4	1		5		5	5
<i>Unknown time period</i>										
Lone Mountain	2			2			2			1
Pioneers	1				1		1			1
Total	425	160	100	160	6	151	236	38	209	415

translocation of seven sheep from the Middle Main population into the adjacent Lost River Mountain Range in 1969 to re-establish a population in vacant habitat. This release was supplemented with sheep from Banff, Alberta (24) and Whiskey Basin, Wyoming (17) in the 1970's, and 62 bighorn sheep from the Sun River, Montana population in 2005 (IDFG 2022). Radio-telemetry data and movements of marked sheep indicate that there is mixing (and therefore potentially gene flow) between the reintroduced Lost River Range population and the native Middle Main sheep on a portion of their winter range (IDFG, unpubl. data).

Sampling

We collected fecal samples from free-ranging sheep, both males and females, and we obtained shavings from the keratin sheath of horns obtained from males harvested by hunters or found dead of natural causes. We also collected blood via jugular venipuncture during captures conducted by net-gunning from a helicopter or ground darting with chemical immobilization agents following Idaho Department of Fish and Game animal care and safety protocols ("Contemporary" samples, Table 1 and S2, Fig. 1). We extracted DNA from 33 archived serum samples obtained during captures in the Middle Main PMU in 1989, prior to the most recent documented pneumonia outbreak in this population (Scott 1996), and from horn shavings obtained from rams from the Lower Salmon and Middle Fork PMUs collected by John Carrey ("Historical samples", Table 1; Fig. 1). At one time the Carrey collection contained over 100 bighorn sheep skulls from the Salmon River, but the current collection, located at the Jack O'Connor Hunting Heritage and Education Center in Lewiston, Idaho (Barker 2015), contains

35 heads and horn sheaths dating back to 1879 based on inscriptions on the skulls (Fig. 1). We received samples from 34 skulls or horns from the collection. The 32 samples we were able to genotype (mitochondrial DNA $n=31$, nuclear DNA $n=28$) were from specimens dated between 1879 and 1985 ($n=12$) or were undated ($n=20$).

Based on geographic location information recorded for the skulls and horns, we were able to identify PMUs for all specimens and specific collection locations for 28 (Table S3, Fig. 1). Samples from horns and a skull of unknown age discovered outside the current distribution of bighorn sheep in 2007 on Lone Pine Peak ($n=1$) and 2009 at the head of Navarro Canyon in the Pioneers PMU ($n=1$) were also included in principal component analyses of nuclear DNA and structure analyses. Hereafter these two samples are referred to as "samples of unknown age" (Table S3).

DNA extraction and amplification

DNA was extracted from fecal samples using the Fast QIAamp DNA Stool Mini Kit (Qiagen, Inc.), and from whole blood, serum, and horn shavings samples using the DNeasy Blood and Tissue Kit (Qiagen, Inc.). Fecal and horn shavings samples were extracted in a laboratory dedicated to low quality DNA samples. One negative control was included in each extraction to monitor for contamination of reagents.

We amplified the mitochondrial control region for all samples (Table 1) using three sets of primers (Fig. S1): the primers L15712 5'–3' (AAC CTC CCT AAG ACT CAA GG) and BETH 5'–3' (ATG GCC CTG AAG AAA GAA CC) (Ramey 1995) amplified one fragment with around 600 base pairs (bp) for blood and serum samples, and we

designed two nested primer sets, OCan_F1-2 (CAY ACC CAT ACA AGA AAA GCA CAC) and BHInt_R (CTT TAT GTY CCA TGT ACG AAC) and OCan_F3 (CAY YAA AGT ACA TGG GAC AT) and BETH, to split the 600 bp fragment into two smaller fragments (~300 bp) for use with more degraded samples (Fig. S1). The PCR reactions per sample contained 0.1 µl of AmpliTaq Gold™ (5 units/µl, Thermo Fisher Scientific, Lafayette, Colorado), 1.5 µl of MgCl₂ (25 mM), 1.5 µl of buffer (10X), 0.6 µl of dNTPs (10mM), 1.5 µl of each primer (2 µM), 1.5 µl of DNA extract in a 15 µl reaction volume, where the remaining volume was water. The thermocycler profile for all fragments was an initial denaturation step of 94 °C for 10 min followed by 55 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 40 s. We purified the PCR products by mixing 5 µl DNA with 2 µl Exosap and then incubating at 37 °C for 15 min, 80 °C for 15 min, and 4 °C for 3 min. All samples were sequenced using the Big Dye Terminator v3.1 Cycle Sequencing Kit (Perkin Elmer) with the upstream primer and run on an Applied Biosystems 3130xl Genetic Analyzer following the manufacturer's protocols and analyzed with the software using Sequencer 3.0 (Gene Codes Corporation, Inc.) and Geneious v8.1.9 (Kearse et al. 2012). In Geneious, we aligned sequences using the ClustalW function (Thompson et al. 1994), and trimmed all reads to 297 bp, which was the number of bases with overlap across all sequences.

We amplified a total of 15 microsatellite loci in two multiplex PCR reactions for each sample (Borg 2014; Barbosa et al. 2021). Eleven loci are expected to be adaptively neutral due to their position in the genome, whereas four are putatively under selection because they are located within (or close to) genes associated with immune function (*BL4*, *MMP9*, *MHC 1*, *TCRB*; Table S4). Sex for fecal samples was determined by PCR-amplification and fragment length analysis in triplicate using the SEY47 and SEY48 primers which amplify of a portion of the bovine amelogenin locus on the X and Y chromosomes following the protocol of Ennis and Gallagher (1994). Sex was known for contemporary blood samples and for horn shaving samples. All PCRs were run with negative controls to test for reagent contamination. PCR products were run on an Applied Biosystems 3130xl Genetic Analyzer and scored using GeneMapper v3.7 (Applied Biosystems, Inc).

Each multiplex microsatellite PCR was performed twice per sample, and samples with less than 50% amplification success were discarded from the dataset. At least one additional PCR was performed for each multiplex in fecal and horn samples; heterozygote genotypes were accepted after each allele was observed in at least two independent PCRs, and homozygote genotypes were accepted after the genotype was observed in at least three independent PCRs. Samples were discarded from the dataset if a consensus genotype

was not obtained for at least 13 loci after five PCRs per multiplex (Taberlet et al. 1996; Waits and Paetkau 2005).

To determine whether our dataset included more than one sample obtained from the same individual ("replicate samples"), we first calculated the probability that siblings would have identical genotypes at the loci tested for each herd (PIDsibs, Waits et al. 2001) with GENALEX v6.5 (Peakall and Smouse 2006). We calculated PIDsibs for 11 loci because we allowed missing data for up to two loci per individual, and therefore every pair of individuals had at least 11 of the same loci genotyped in both individuals. We then used GENALEX to identify samples in the full dataset that had identical microsatellite genotypes, and we used field data to evaluate whether these samples could originate from the same individual. PIDsibs ranged from 9.6×10^{-5} to 2.4×10^{-4} for 11 loci across PMUs, indicating that matching genotypes were highly likely to originate from samples collected from the same individual. We removed duplicate genotypes and final sample sizes for unique individuals are provided in Table 1. Unless otherwise noted, we conducted all subsequent analyses for PMUs with ≥ 5 samples separating out contemporary and historical samples, and we did not include the two samples of unknown age.

Mitochondrial genetic diversity

We obtained 116 sequences for the bighorn sheep mitochondrial DNA control region from the National Center for Biotechnology Information (NCBI) GenBank accessed in 2021 (Table S5) and aligned them with mitochondrial sequences obtained in this study using Geneious v8.1.9 (Kearse et al. 2012). We refer to these sequences as the 'North American' dataset (Appendix C1). We also aligned the sequences generated in this study independently, which hereafter referred to as the 'Idaho' dataset (Appendix C2).

We built haplotype networks using Popart v1.7 (Leigh and Bryant 2015) by calculating a median joining network for the combined North American and Idaho datasets. We used DNAsp v5.10 (Librado and Rozas 2009) to estimate the number of haplotypes (HT), haplotype diversity (Hd), number of segregating sites (S) and nucleotide diversity (π) in the Idaho dataset. We calculated two summary statistics of population demography to ascertain if there were signs of deviations from a neutral model of constant population size, such as recent population expansion or contraction: Tajima's D (Tajima 1989) and Fu's F_s (Fu 1997). We estimated significance for the summary statistics through coalescent simulations of Theta with 1,000 replicates and a 95% confidence interval. We calculated all parameters separately for contemporary and historical samples in the Lower Salmon, Middle Fork, and Middle Main PMUs, and we also compared historical samples from the Lower Salmon and Middle

Fork in the Carrey collection to contemporary samples from the Lower Salmon and Middle Fork PMUs. We then tested for significant differences between nucleotide and haplotype diversity across PMUs using the *genetic_diversity_diffs* R script (Alexander et al. 2016).

Nuclear genetic diversity and population structure

We evaluated deviations from Hardy-Weinberg equilibrium (HWE) for each locus in each PMU with ≥ 5 samples using a chi-square goodness-of-fit statistic in the *PopGenReport* R package (Adamack and Gruber 2014). We considered loci to deviate from HWE if the chi-square statistic was significant ($p < 0.05$) in at least 50% of the PMUs examined. We examined genetic diversity at all loci and at neutral and putatively adaptive loci separately for all PMUs with ≥ 5 samples by calculating observed heterozygosity (H_o) and expected heterozygosity (H_e) using the function *basic.stats*, and allelic richness (A_R) using the function *allelic.richness* from the *hierfstat* R package (Goudet 2005). For each PMU we calculated the number of private alleles (alleles not found in any other PMU) using *PopGenReport* R package (Adamack and Gruber 2014). We tested for significant differences in allelic richness, and number of private alleles among PMUs and across time periods using a permutation test (two-sided, 9999 permutations) implemented in *fstat* v2.9.3.2 (Goudet 2002). We tested for significant differences between H_o and H_e within each PMU and for differences in H_e between PMUs using the *t.test* function from the *stats* base R package (RCoreTeam 2018). To investigate population genetic structure across all loci, we used a non-model based approach using principal components analysis (PCA) for all samples and all loci using the *dudi.pca* function from the *ade4* R package (Dray and Dufour 2007). Missing data was imputed as the mean within each PMU. We also ran PCA analyses on contemporary samples from males and females separately. We performed a discriminant analysis of principal components (DAPC) for each dataset, using the *dapc* function from the *adegenet* R package (Jombart and Ahmed 2011). DAPC was performed using pre-defined clusters (PMUs) based on sampling locations. Because group membership was specified a priori, no clustering inference (e.g. K-means or BIC analysis) was conducted. We conducted both PCA and DAPC analyses as the latter maximizes the separation between groups, while the former searches for the largest total variance, and may fail to find population structure if there is high intrapopulation variation (Jombart et al. 2010). We also used a model-based approach to determine population structure using only loci in HWE. We conducted Bayesian clustering analyses using STRUCTURE 2.3.4 (Pritchard et al. 2000) in R using the *ParallelStructure* R package (Besnier and Glover 2013),

using the admixture and correlated allele frequency models, with 1×10^5 burn-in steps and 9×10^5 subsequent steps. We varied K from 1 to 10, where K is the number of populations defined a priori, and ran 5 independent replicates for each K . For plotting and visualization, we used the *pophelper* R package (Francis 2017). We conducted STRUCTURE analyses with and without including the historical samples and samples of unknown age and comparing contemporary samples from males and females.

To evaluate population differentiation, we calculated the pairwise F_{ST} (fixation index) for total, neutral, and adaptive loci between each pair of PMUs using the function *genet.dist* using the Weir and Cockerham (1984) method, and estimated significance using the function *boot.ppfst*, both from the *hierfstat* R package, evaluating statistical significance for a 95% confidence interval with 1,000 bootstraps. To evaluate sex biased dispersal, we computed pairwise F_{ST} between contemporary females and males separately for each PMU, using all loci, and evaluated statistical significance as before. We used the FSTAT v2.9.3.2 “Biased dispersal” software package (Goudet 2002) to compute contemporary genetic divergence (F_{ST}), inbreeding coefficient (F_{IS}) and Relatedness (R) of females and males across the five PMUs. We tested for significant differences between sexes using 10,000 randomizations.

Finally, we performed an Analysis of Molecular Variance (AMOVA) to quantify the proportion of genetic variation in mitochondrial and nuclear DNA explained by differences between contemporary and historical samples between and within PMUs, as well as among contemporary PMUs by sex. For the 297 bp region of mitochondrial DNA, we used the *amova* function from the *ade4* R package (Dray and Dufour 2007) and for 15 microsatellite loci we used the *poppr.amova* function from the *poppr* R package (Kamvar et al. 2014). We estimated significance using the *randtest* function from the *ade4* R package with 999 permutations.

Historical and contemporary effective population sizes

We investigated demographic changes in mitochondrial DNA over time with Bayesian Skyline Plot (BSP) analyses using BEAST v2.4.6 (Bouckaert et al. 2014). We ran 5 replicates of Markov Chain Monte Carlo (MCMC) chains for 100,000,000 iterations each (with 1,000,000 burn-in), sampling every 10,000 steps. We evaluated run convergence through effective sampling size (ESS) scores with Tracer v1.5 (Rambaut and Drummond 2015). We used a strict molecular clock model, with a mutation rate of 6.1×10^{-6} and variance between 4.2×10^{-6} and 7.9×10^{-6} (Buchalski et al. 2016), and the Hasegawa-Kishino-Yano (HKY) nucleotide substitution model, considering a gamma value of 4

and allowing the estimation of the proportion of invariant sites. We then used the combined runs resampled to 10,000 iterations to perform BSP analyses for each PMU with ≥ 30 samples, including both contemporary and historical samples. Year of sampling was input for each sample with the exception of the Carrey collection samples which were all assigned an average year, as no collection date was available for most of them.

We used the software BOTTLENECK v1.2.02 to test nuclear data for bottlenecks in both historical and contemporary PMUs with ≥ 10 samples, as recommended by the authors (Piry et al. 1999). We used two methods to estimate bottlenecks: the stepwise mutation model (SMM) and the two-phase model (TPM) with a ratio of 95% of mutations conforming to a stepwise mutation model and 5% as multi-step. We determined significance using the Wilcoxon signed-rank test (one tail), which is more appropriate when analyzing < 20 loci (Piry et al. 1999). We estimated effective population size (N_e) with NeEstimator v2 (Do et al. 2014), using the Linkage Disequilibrium (LD) method for contemporary samples in each PMU. We considered a Lowest Allele Frequency value of 0.02 for all estimators following the recommendations of Waples and Do (2010).

Results

Mitochondrial genetic diversity and structure

By combining mitochondrial DNA control region sequence data from NCBI GenBank with our mitochondrial DNA sequences we obtained a 265 bp alignment for 325 samples from North America: 209 samples from this study and 116 samples from other investigations in the western United States, Canada, and Mexico that were assigned to seven subspecies in the NCBI metadata (Table S5, Fig. S1). This North American dataset showed two distinct haplogroups (Fig. 2). One group represented most *O. c. canadensis* and all *O. c. californiana* samples and included most of the Idaho samples (labeled as haplogroup “A” in Fig. 2). The other group (labeled as haplogroup “B” in Fig. 2) contained desert (*O. c. nelsoni*, *O. c. mexicana*, *O. c. weemsi*) and Sierra bighorn sheep (*O. c. sierrae*) lineages as well as one Wyoming and one Idaho contemporary *O. c. canadensis* sample, and 12 of the historical samples from this study. Three historical Idaho samples in haplogroup B shared haplotypes with samples from desert sheep (*O. c. nelsoni*) and one historical Idaho haplotype matched the *O. c. canadensis*

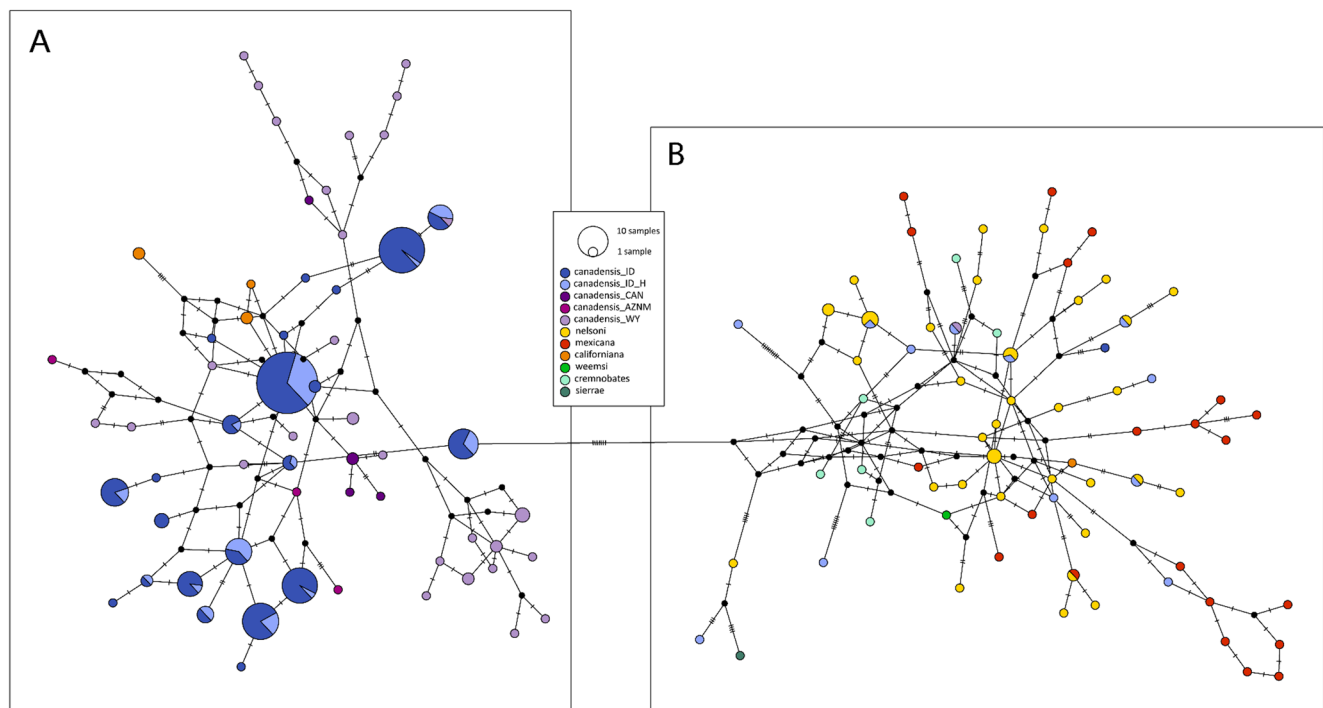


Fig. 2 Bighorn sheep range-wide median joining haplotype network of 265 base pairs of the mitochondrial control region from 209 sequences generated from native Idaho bighorn sheep (Table 1) and 116 sequences obtained from NCBI GenBank (Table S5). These data included samples from *O. c. canadensis* (253 sequences), *O. c. nelsoni* (39 sequences), *O. c. mexicana* (21 sequences), *O. c. californiana* (6 sequences), *O. c. weemsi* (1 sequence), *O. c. cremonobates* (6 sequences) and *O. c. sierrae* (1 sequence). Each circle represents a unique haplotype, and size is

proportional to the number of samples with a given haplotype. Colors represent subspecies and, for *O. c. canadensis*, geographic origin as indicated in the legend: Idaho (ID), Arizona/New Mexico (AZ/NM) and Wyoming (WY), USA, and Alberta (CAN). For Idaho samples, we further distinguished between contemporary (dark blue) and historical (light blue, ID_H) samples. The number of mutations between haplotypes is represented by black strokes, and black circles represent inferred unsampled haplotypes. A and B represent two haplogroups

sample from Wyoming in this haplogroup. Thirty-seven of 130 haplotypes in the North American dataset were represented in the Idaho dataset, and 27 of those (73%) were exclusive to Idaho (Fig. 2). Nearly all Idaho contemporary samples, most of the Middle Main and all the Middle Fork historical samples were in haplogroup A (Fig. 3). Idaho samples in haplogroup B included historical samples from Lower Salmon, a single historical Middle Main sample, and a contemporary sample from Lower Panther (Fig. 3).

The historical Carrey collection samples from Lower Salmon and Middle Fork had the highest number of haplotypes and haplotype diversity. We found 12 private haplotypes in the 28 Carrey collection samples: 10 in 23 samples from the

Lower Salmon and 2 in the 5 samples from the Middle Fork, whereas we found 10 private haplotypes in 352 contemporary samples (Table 2). Haplotype diversity was significantly higher in contemporary samples from the Middle Fork than in contemporary samples from Lower Panther or Middle Main, which had the lowest haplotype diversity (Table 2 and S6). No significant deviations from neutrality were detected in any dataset, except for the Lower Salmon historical samples, which had a significantly negative F_S value, a signal of population expansion (Table 2). The AMOVA analysis showed significant differentiation in mtDNA variance between PMUs within contemporary and historical time points but not between historical and contemporary samples (Table S7).

Fig. 3 Idaho bighorn sheep mitochondrial DNA control region haplotype network for a 297 bp fragment of 209 samples from five PMUs: Lower Salmon (green), Lower Panther (red), Middle Fork (brown), Middle Main (yellow), and East Fork (blue). Light and dark shades of green, yellow and brown represent historical and contemporary samples of Lower Salmon, Middle Fork and Middle Main, respectively. Circles represent haplotypes, and size is proportional to the number of sequences with a given haplotype, varying from 1 to 53). The number of mutations between haplotypes is represented by black strokes, and black circles represent inferred unsampled haplotypes

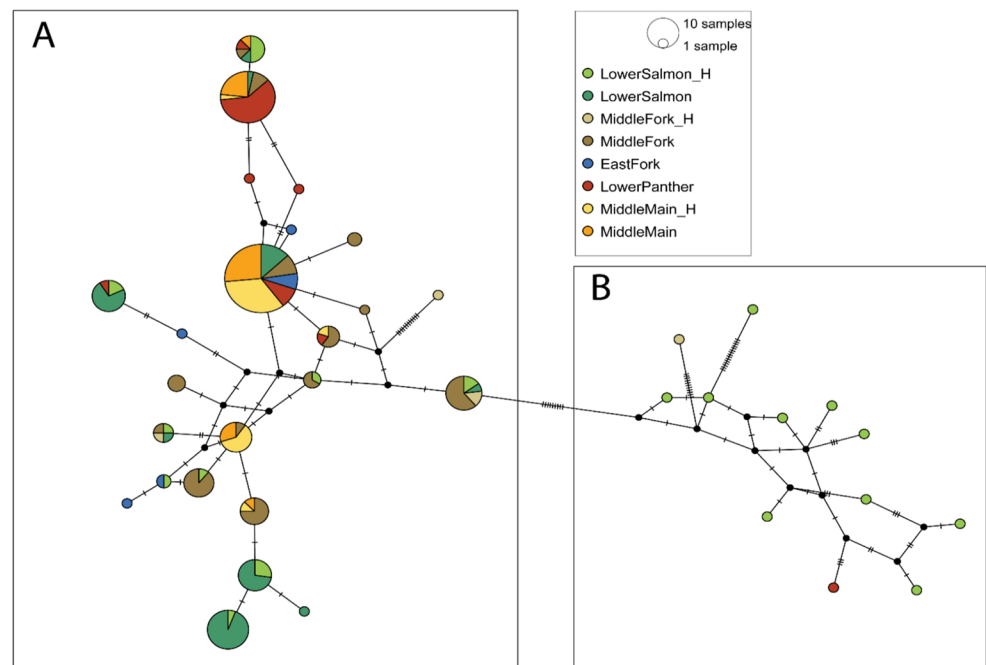


Table 2 Genetic diversity of the mitochondrial DNA control region (297 base pairs) in 209 bighorn sheep sampled across native Idaho Bighorn sheep populations in contemporary (2000–2017) and historical (1914–1989) time periods. We report number of haplotypes (HT) and private haplotypes (PH), haplotype diversity (Hd), number of segregating sites (S), nucleotide diversity (π), as well as tajima's D (D) and fu's F_S (Fs) neutrality tests. Numbers in parentheses represent standard deviation and summary F statistic values in bold are significant ($p < 0.05$)

PMU	<i>n</i>	HT (PH)	Hd	S	π	D	Fs
<i>Contemporary samples</i>							
Lower Salmon	44	9 (1)	0.792 (0.037)	17	0.013 (0.001)	0.258	1.476
Middle Fork	44	13 (3)	0.903 (0.020)	15	0.012 (0.001)	0.184	-1.815
Middle Main	26	5 (0)	0.646 (0.076)	7	0.008 (0.001)	1.016	1.749
Lower Panther	29	8 (3)	0.599 (0.097)	26	0.011 (0.004)	-1.672	0.571
East Fork	8	5 (3)	0.786 (0.151)	9	0.001 (0.002)	-0.413	-0.164
<i>Historical samples</i>							
Middle Main 1989	27	5 (0)	0.521 (0.096)	9	0.005 (0.001)	-0.946	0.579
Lower Salmon (Carrey collection)	26	20 (10)	0.972 (0.021)	43	0.035 (0.003)	0.131	-4.710
Middle Fork (Carrey collection)	5	4 (2)	0.900 (0.161)	32	0.043 (0.012)	-0.565	2.185
<i>Merged samples</i>							
Lower Salmon & Middle Fork	88	17 (4)	0.912 (0.012)	19	0.015 (0.001)	0.553	-1.347
Carrey Collection	31	21 (12)	0.936 (0.019)	49	0.035 (0.003)	-0.196	-3.686

Nuclear genetic diversity

The Idaho microsatellite dataset included 352 contemporary individuals, 61 historical individuals, and the two individuals of unknown age (Table 1 and S2). The average number of loci successfully genotyped across samples was 14.9 (99.3% of loci) for blood samples, 14.9 (99.3%) for horn samples, 14.8 (98.7%) for fecal samples, 14.8 (98.7%) for the 1989 Middle Main serum samples, 14.8 (98.7%) for the Carrey collection samples, and 14 (93.3%) for the two samples of unknown age.

We identified a total of 117 alleles across all microsatellite loci: 7–11 ($\bar{x}=8.25$) per adaptive locus and 4–13 per neutral locus ($\bar{x}=7.64$, Table S8). One neutral microsatellite locus deviated from HWE in three of the five contemporary PMUs (locus HH47, $p=0.000-0.029$), and this locus was removed from subsequent analyses. Five additional neutral loci deviated in just one PMU. Three of the four adaptive loci deviated from HWE in contemporary samples from at least one PMU: BL4 in Middle Fork ($p=0.000$) and East Fork ($p=0.014$), MMP9 in East Fork ($p=0.000$), and TCRB in Middle Fork ($p=0.028$). One neutral locus (MAF209, $p=0.006$) and no adaptive loci deviated from HWE in the historical Middle Main samples. Three neutral loci (AE129, $p=0.025$; FCB266, $p=0.038$; MAF209, $p=0.010$) and two adaptive loci (BL4, $p=0.000$; MMP9, $p=0.011$) deviated from HWE in historical Lower Salmon samples which is consistent with the finding of a significant difference between observed and expected heterozygosity (H_o and H_e) for all loci combined (Table 3).

Ninety-five alleles (81%) across all microsatellite loci were detected in both contemporary and historical samples. Twelve loci (all four adaptive and eight neutral) had at least one allele that was not detected in either contemporary or historical samples (Table S8, Figure S2). Historical samples from the Lower Salmon had more private microsatellite alleles than any contemporary or historical PMU at both neutral and adaptive loci, despite having the smallest sample size of any group other than the historical Middle Fork PMU (Table 3). The historical samples from the Lower Salmon and Middle Fork (Carrey collection) had nine private alleles across four neutral loci and three private alleles across three of the four adaptive loci (BL4, MMP9, TCRB), significantly more than any contemporary PMU ($p<0.001$, Table S9).

The Middle Fork was the only contemporary PMU to have a private allele at an adaptive locus, with one private allele at MHCI.

The historical Middle Main samples had no private alleles (Table 3 and S9, Fig. S2). The Lower Salmon and East Fork contemporary PMUs had the lowest allelic richness for all loci (3.79 and 3.34 respectively). Allelic richness was lower

Table 3 Contemporary and historical genetic diversity across native Idaho bighorn sheep populations at a total of 15 microsatellite loci including 11 neutral and 4 adaptive loci. H_o/H_e pairs in bold are significantly different at $p<0.05$. We report observed heterozygosity (H_o), expected heterozygosity (H_e), allelic richness (A_R), number of private alleles (PA), and the number of loci that deviated from Hardy Weinberg equilibrium (HWE) in each PMU

PMU	ance from Hardy-Weinberg equilibrium (HWE) in each PMU															
	Total						Neutral				Adaptive					
	n	H _o	H _e	A _R	PA	HWE	H _o	H _e	A _R	P	HWE	H _o	H _e	A _R	PA	HWE
<i>Contemporary</i>																
Lower Salmon	113	0.633	0.677	3.79	0	2	0.637	0.682	3.85	0	2	0.682	0.624	3.62	0	0
Middle Fork	93	0.663	0.720	4.12	3	6	0.665	0.710	4.07	2	4	0.657	0.747	4.28	1	2
Middle Main	55	0.675	0.697	3.94	1	2	0.695	0.710	4.06	1	2	0.618	0.660	3.64	0	2
Lower Panther	57	0.687	0.695	3.91	0	1	0.690	0.710	4.01	0	1	0.677	0.655	3.63	0	0
East Fork	34	0.619	0.645	3.34	0	2	0.624	0.635	3.33	0	0	0.603	0.673	3.37	0	2
<i>Historical</i>																
Middle Main (1989)	33	0.649	0.684	3.72	0	1	0.676	0.700	3.88	0	0	0.576	0.641	3.29	0	1
Lower Salmon (Carrey collection)	23	0.611	0.756	4.42	11	6	0.612	0.756	4.42	9	4	0.605	0.756	4.44	2	2
Middle Fork (Carrey collection)	5	0.600	0.735	4.27	1	0	0.564	0.739	4.27	0	0	0.700	0.725	4.25	1	0
<i>Merged samples</i>																
Lower Salmon & Middle Fork	206	0.645	0.714	5.51	3	8	0.646	0.711	5.75	2	6	0.643	0.722	6.18	1	2
Carrey collection	28	0.620	0.741	6.26	12	6	0.631	0.747	6.67	9	5	0.590	0.724	7.46	3	1

in the East Fork than in the Middle Fork and Middle Main PMUs ($p \leq 0.07$, Table 3 and S10).

Although the differences were not significant, expected heterozygosity (H_e) was higher in historical than in contemporary samples from the Lower Salmon and the Middle Fork. Both measures of diversity (H_e , A_r) were similar in contemporary and historical samples for Middle Main (Table 3, S10 and S11).

Nuclear DNA population structure

The PCA and DAPC analyses identified a low level of structure among PMUs (Figs. 4 and S3). The first and second principal components explained 11.17% of genetic variance in the PCA analysis of population structure using all Idaho samples, and contemporary and historical genetic samples overlapped (Fig. 4A). In the DAPC analysis, we found a slight differentiation between East Fork and Middle Main samples, and between contemporary and historical Middle Main samples on the first two axes (Fig. 4B). The Lower Salmon and East Fork samples were differentiated on axes one and three (Fig. 4C). The Pioneers sample of unknown age clustered with contemporary Lower Salmon/Lower Panther/Middle Fork, and the Lone Pine Mountain sample of unknown age clustered with contemporary Middle Fork/Middle Main/East Fork. More variance was explained by the first two principal components in samples from females (14.07%, Fig. S3C) than males, with more pronounced differentiation of Middle Main and East Fork samples (Fig. S3D). Genetic variance among PMUs for males appeared to be limited to the first axis (6.51%, Fig. S3E and F).

In the Bayesian clustering analysis of 14 microsatellite loci in contemporary samples, the likelihood probability for genetic clusters $\Pr(X|K)$ increased from $K=1$ through $K=7$

groups, with highest rate of change in likelihood (Evanno method) at $K=2$ and a smaller secondary peak at $K=6$. At $K=2$, Lower Salmon and Lower Panther separated from Middle Fork, Middle Main, and East Fork, although there was evidence for admixture between neighboring PMUs. At $K=3$, the three main groupings included (1) Lower Salmon, (2) Lower Panther/Middle Fork/Middle Main and (3) East Fork, although again the results showed evidence of admixture between neighboring PMUs. Middle Main became distinct at $K=4$. At $K=5$, some samples from the South Fork Salmon River split from the main Salmon in the Lower Salmon PMU. At $K=6$, the Middle Fork and Lower Panther PMUs became distinct from each other. Although the likelihood curve peaked at $K=7$, clustering patterns at $K=7$ and up were very similar to those at $K=6$, with all 5 PMUs distinct from each other, and the Lower Salmon PMU subdivided into two genetic clusters (Figs. 5A, S4A, S4B).

Bayesian clustering analyses incorporating historical samples and samples of unknown age showed an increase in ($\Pr(X|K)$) from $K=1$ through $K=3$ groups, and structure was highly variable across runs for $K=4$ and $K=5$. The most supported K values were $K=2$ for the Evanno method and $K=4$ for the Likelihood method (Figs. S4C and S4D). The contemporary clustering patterns did not change with the inclusion of historical samples (Fig. 6). The historical samples from both Lower Salmon and Middle Fork showed significantly greater genetic similarity to contemporary Middle Fork than to contemporary Lower Salmon samples (Fig. 6, Table S11).

The 1989 Middle Main samples were genetically similar to the contemporary Middle Main samples, and the Lone Pine Mountain sample of unknown age was genetically similar to contemporary East Fork samples. In contrast, the Pioneers sample of unknown age was genetically

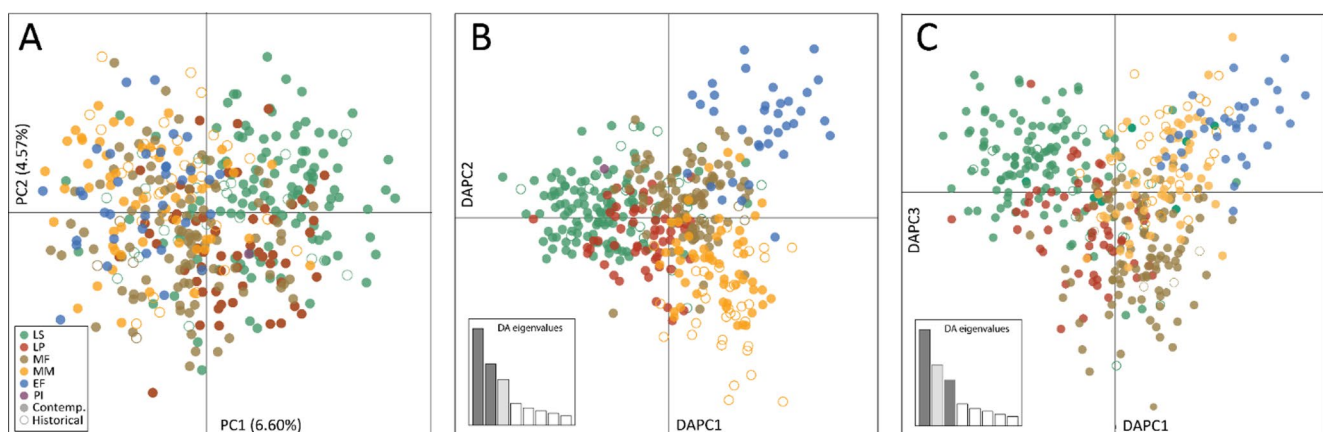


Fig. 4 Principal Components Analysis (PCA) and Discriminant Analysis of Principal Components (DAPC) for Idaho native bighorn sheep using 14 microsatellite loci. **A**. The first two axes in the PCA, the proportion of variance is explained in parentheses. **B** and **C**. The first three axes of DAPCs as represented by the bars shaded dark gray in the

histograms. Full and open circles represent contemporary and historical samples respectively ($n=413$) and colors represent PMUs where samples were obtained: Lower Salmon (LS, green), Lower Panther (LP, dark red), Middle Fork (MF, brown), Middle Main (MM, orange), East Fork (EF, blue) and Pioneers (PI, purple)

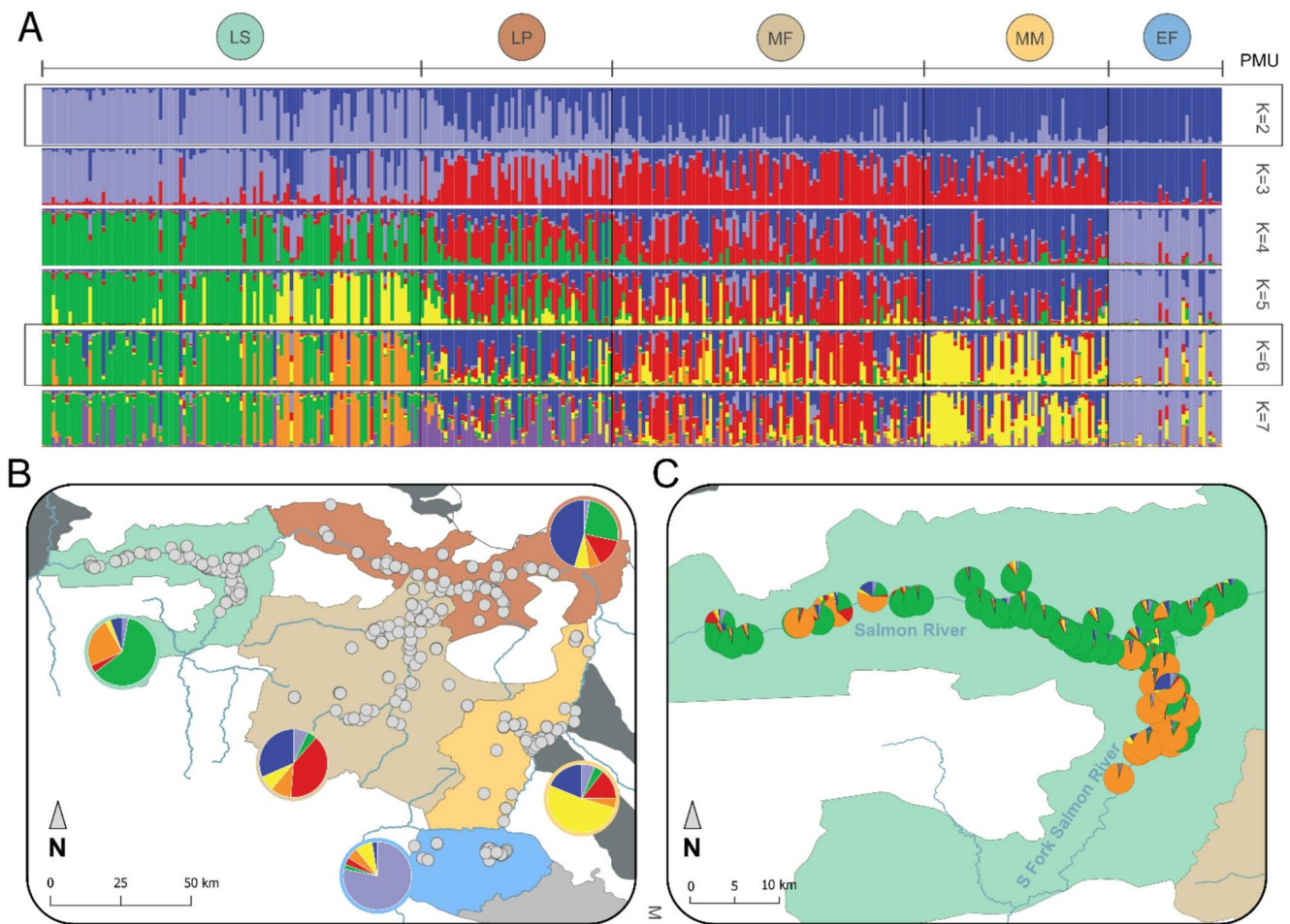


Fig. 5 Bayesian genetic population structure of the contemporary native bighorn sheep metapopulation in Idaho using 14 microsatellite loci in Hardy-Weinberg equilibrium for seven K values (number of inferred populations). **(A)** Assignment of individuals ($n=352$) is represented by vertical lines divided into colored segments that indicate the estimated probability of the individual belonging to the specific inferred population. Samples are plotted in ascending chronological order within each population. The best supported K s as inferred from the Evanno and likelihood methods are outlined at $K=2$ and 6 respectively. Top labels indicate the Population Management Unit (PMU) where samples were collected: Lower Salmon (LS), Lower Panther

(LP), Middle Fork (MF), Middle Main (MM), and East Fork (EF). **(B)** Spatial distribution of individual samples and their assignment proportions at $K=6$ shown as pie charts superimposed on PMUs colored as in top labels in 5 A. Most samples were collected along the Salmon River and tributaries represented on the map by blue lines. **(C)** Close-up of assignments of contemporary samples collected in the Lower Salmon PMU. All samples along the main Salmon River were collected on the north side of the river. Most assignments colored orange in pie charts and the structure plot at $K=6$ occur in a cluster of samples along the south side (South Fork) of the Salmon River on the right edge of the map

more similar to contemporary Lower Salmon, Lower Panther, and Middle Fork samples than to the neighboring East Fork. Structure results for females (Fig. S5) were similar to structure results including contemporary samples from both sexes (Fig. S5A) up to $K=3$, which was inferred as the best supported K using the Evanno method (Fig. S4E and S4F), while for males (Fig. S5) the East Fork PMU was not as distinct, and the best supported K was 2 (Fig. S4G and S4H).

Genetic differentiation (pairwise F_{ST} values) ranged from 0 to 0.122 for neutral microsatellite loci and were significant across all pairs of PMUs. Pairwise F_{ST} values for adaptive loci ranged from -0.011 to 0.121 and were significant across all comparisons ($p<0.001$) except for the historical

Middle Fork samples, which were not significantly different from any group likely due to small sample size ($n=5$, Table 4 and S11). The pairwise F_{ST} values in Lower Salmon and Middle Fork and Lower Salmon and Middle Main historical samples were lower than in contemporary samples (historical 0.032, contemporary 0.041), but F_{ST} values were significantly higher in historical samples from the Middle Main and Middle Fork PMUs than in contemporary samples (Middle Fork and Middle Main F_{ST} 0.075 historical, 0.028 contemporary, $p<0.001$, Table S11).

Pairwise F_{ST} values for all microsatellite loci combined showed significant differences between sexes among PMUs and between PMUs within sexes. Although F_{ST} values

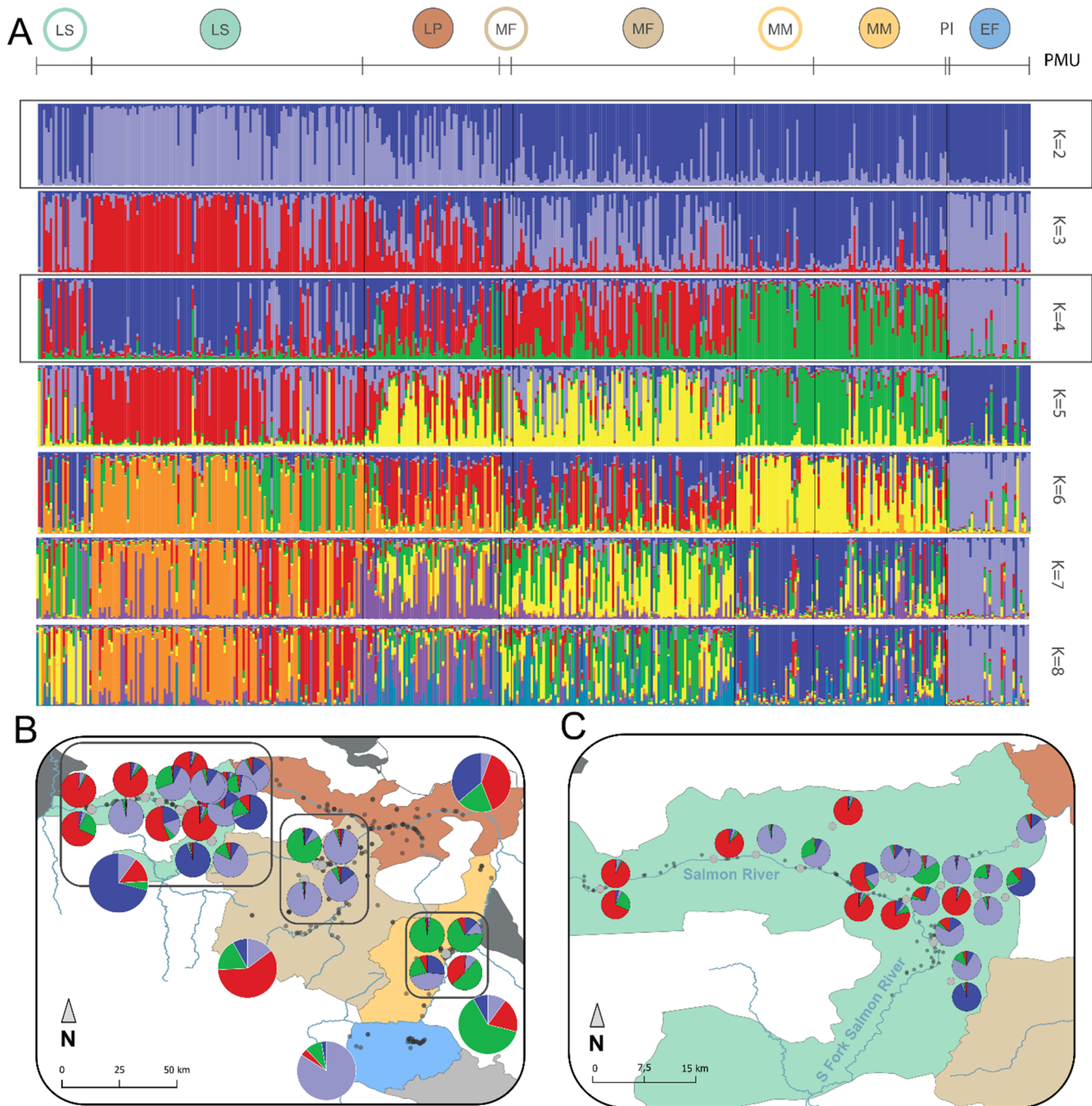


Fig. 6 Bayesian population genetic structure for Idaho native bighorn sheep in contemporary and historical time periods using 14 microsatellite loci in Hardy-Weinberg equilibrium, and 413 samples for eight K values. Each vertical line represents an individual divided into segments colored by their assignment to one of the K populations inferred. Samples are represented in chronological ascending order within each population. The most supported K s as inferred from the Evanno and likelihood methods respectively are outlined at $K=2$ and $K=4$, respectively. Top labels represent population boundaries, with which are sep-

arated into historical (H) and modern sampling periods within PMUs. PMUs are labeled as follows: Lower Salmon (LS, LS-H), Lower Panther (LP), Middle Fork (MF, MF-H), Middle Main (MM), East Fork (EF) and Pioneers (PI). **B.** Spatial distribution of individual samples and their assignment proportions at $K=4$ shown as pie charts superimposed on PMUs colored as in top labels in 5 A. Most samples were collected along the Salmon River and tributaries represented on the map by blue lines. **C.** Close-up of assignments of contemporary and historical samples collected in the Lower Salmon PMU

Table 4 Pairwise F_{ST} values across PMUs for 10 neutral microsatellite loci (below diagonal) and 4 adaptive loci (above diagonal) in contemporary and historical samples from Idaho native bighorn sheep populations. Bold values above and below the diagonal are significantly different from zero ($p < 0.001$)

PMU	LS	LP	MF	MM	EF	MM-H	LS-H	MF-H
<i>Contemporary</i>								
Lower Salmon (LS)		0.020	0.046	0.065	0.092	0.074	0.018	0.030
Lower Panther (LP)	0.027		0.033	0.030	0.087	0.038	0.020	0.020
Middle Fork (MF)	0.039	0.022		0.036	0.051	0.059	0.004	0.012
Middle Main (MM)	0.057	0.041	0.025		0.083	0.022	0.053	0.049
East Fork (EF)	0.093	0.093	0.057	0.054		0.111	0.041	0.054
<i>Historical</i>								
MM 1989 (MM-H)	0.050	0.050	0.034	0.010	0.079		0.055	0.062
LS Carrey (LS-H)	0.020	0.025	0.020	0.030	0.062	0.037		−0.011
MF Carrey (MF-H)	0.122	0.080	0.046	0.050	0.097	0.079	0.047	

across PMUs were higher for females (0.056) than males (0.041), the differences were not significant ($p = 0.215$), and there was no difference in F_{ST} between sexes within PMU (Table S12). Inbreeding (F_{IS} coefficient) was significantly higher ($p = 0.002$) in males (0.075) than in females (0.017).

The AMOVA analysis of microsatellite alleles for both sexes combined showed significant ($p < 0.01$) genetic differentiation (4.6%) among all 5 PMUs within sampling period (contemporary and historical), between samples within PMU (6.2%), and among samples (89.8%). Females showed greater genetic differentiation among PMUs (5.6%) than males (4.2%) and variation between samples within PMU was significant for males (7.3%) but not for females (1.7%). Samples from the Lower Salmon, Middle Fork, and Middle Main PMUs differed between time periods (2.3%, Table S7).

Demographic trends in effective population sizes and genetic bottlenecks

We detected a decline in effective female population size (N_e females) around 200 years before present in a mtDNA bottleneck analysis of all samples combined across the metapopulation (Fig. S6A). A similar decline was observed in combined historical and contemporary samples from Lower Salmon (Fig. S6B), a more recent and smaller decline was detected in the Middle Fork samples (Fig. S6C), and no decline was detected in the Middle Main (Fig. S6D). We detected a significant bottleneck in contemporary nuclear microsatellite data from the Middle Fork ($p = 0.009$) and the historical samples from Middle Main ($p = 0.036$) and marginally significant declines and bottlenecks ($p = 0.047$, two-phase model) in contemporary samples from Lower Salmon and Lower Panther (Table S13).

There was low precision in estimates of contemporary adult (male and female) effective population size (N_e) based on microsatellite data, especially for Lower Panther

(estimate of 209, range 113–873, Table S14). The Lower Salmon and Middle Main had similar estimates for N_e (64, range 54–77 and 71, range 54–100 respectively), the Middle Fork N_e was higher (141, range 106–203) and the East Fork was lower (27, range 20–42). The ratio of effective to actual (census) adult population size (N_e/N) ranged from 0.18 in the Lower Salmon and Middle Fork populations to 0.35 in the Middle Main, and 0.44 and 0.48 in the East Fork and Lower Panther samples respectively (Table S14).

Discussion

We identified six genetic groups with differing levels of diversity and gene flow in the native Salmon River bighorn sheep metapopulation in Idaho. The genetic structure results generally supported the previous geographic designation of sheep population management units (PMUs) within an interconnected metapopulation, which were defined based on population surveys and movements of radio-collared sheep. The Middle Fork, Lower Panther, and Middle Main PMUs, centrally located in the heart of the metapopulation, have the highest levels of connectivity in structure analyses, although all PMUs show significant genetic differentiation.

We found that gene flow, genetic diversity, and effective female population sizes have decreased significantly over the past century, and we detected genetic bottlenecks in the metapopulation, consistent with a history of population declines and fragmentation. Declines are less apparent in levels of heterozygosity than in the frequency of rare alleles, particularly at neutral loci, likely reflecting the greater sensitivity of allelic diversity to population declines and genetic bottlenecks (Allendorf 1986; Leberg 1992; Allendorf et al. 2024).

The East Fork population shows the greatest isolation and differentiation in Bayesian clustering and DAPC analyses. Survey and radio telemetry data indicate that the East

Fork has been small and relatively isolated at least since the 1960's (Morgan 1971; IDFG 2022). This demographic history aligns with the comparatively low allelic richness, small contemporary effective and census population sizes, and genetic distinctiveness of the East Fork in analyses of both contemporary and historical data (Table 3; Figs. 5 and 6), all risk factors for further declines in genetic diversity (Frankham et al. 2014; Allendorf et al. 2024).

The Lower Salmon PMU on the west end of the metapopulation contains two genetically distinct but admixed groups. Some sheep on the south side of the Salmon River (South Fork of the Salmon River) are genetically more similar to sheep in the Middle Fork PMU (Fig. 5), providing evidence for historical and/or contemporary connectivity between these two PMUs. On the north side of the Salmon River most sheep are assigned to a genetic group that is most common in the Lower Salmon, likely due to random loss of alleles (genetic drift) associated with small population size and low levels of connectivity. The geographic distribution of the two genetically distinct groups suggests that the Salmon River is a permeable barrier to gene flow, consistent with previously described movements of marked sheep (Borg et al. 2017).

The signal of population expansion (negative F_u 's F_S) detected in historical samples (Table 2) suggests that the Lower Salmon PMU may have been increasing prior to the period of the historical Carrey collection samples (Ramos-Onsins and Rozas 2002). Sheep on both sides of the Salmon River were probably originally well-connected with bighorn sheep populations to the west along the Salmon River and along the Snake River in Hells Canyon that were extirpated in the early 1900's (Smith 1954). Previous high levels of connectivity to multiple populations, and an admixture event with desert sheep consistent with mtDNA haplotype networks described in this study, may have contributed to the signal of historical population growth. Today, this PMU has relatively low allelic richness and is one of the most isolated, with population structure analyses showing genetic differentiation between the contemporary Lower Salmon and the rest of the metapopulation and differentiation between contemporary and historical samples from Lower Salmon (Figs. 5 and 6, and Table S11).

An unanticipated result of this investigation was the detection of evidence for historical gene flow with desert sheep in mitochondrial DNA. Contemporary mtDNA haplotypes from desert and Rocky Mountain bighorn sheep form separate clades (Malaney et al. 2015; Buchalski et al. 2016), but in this study, 13 Idaho haplotypes (one contemporary and 12 historical) were assigned to a haplogroup containing desert and Sierra Nevada lineages, as was one Rocky Mountain sheep from Wyoming. Furthermore, three of the Idaho historical samples in this haplogroup shared identical

mtDNA haplotypes with desert sheep. In a previous study, historical bighorn sheep skulls from the Salmon River metapopulation were found to exhibit morphological intergradation with desert sheep (Wehausen and Ramey 2000). A recent paper also reported that a 1902 sample from historical desert sheep range in Texas clustered with the Rocky Mountain mtDNA haplogroup (Wright et al. 2024). A reconstruction of bighorn sheep evolutionary history using high-throughput DNA sequencing data (Jahner et al. 2025) detected a north-south geographic split between genetic lineages of *O. c. canadensis* that the authors suggested might be attributed to historical gene flow with desert sheep in the southern Rocky Mountain populations, including the Lower Salmon PMU. Combined, these results provide multiple lines of evidence for connectivity between desert (*O. c. nelsoni*) and Rocky Mountain bighorn sheep in Idaho and other regions prior to population extirpations in both subspecies in the late 19th and early 20th centuries.

While we found support for declines in genetic diversity and bottlenecks between 1879 and 2017 in the Lower Salmon and Middle Fork PMUs, the Middle Main PMU showed stable to increasing mitochondrial haplotype and microsatellite diversity between 1989 and 2017. This may indicate that the downward trajectory in genetic diversity has stabilized over the last 35 years. However, this result could be confounded by admixture consistent with known movements of radio-collared sheep between Middle Main and the adjacent reintroduced Lost River Range population (source populations Middle Main, Wyoming, Alberta, and Montana), IDFG unpubl. data. Gene flow from the Lost River Range population may also be associated with differentiation of the Middle Main from the adjacent Lower Panther and Middle Fork PMUs and separation between contemporary and historical samples in the DAPC analysis (Figs. 4 and 5).

The Salmon River bighorn sheep metapopulation inhabits its rugged terrain including the Frank Church - River of No Return Wilderness which is part of the largest designated wilderness area in the United States outside Alaska. Extensive bighorn sheep habitat in this region is somewhat protected from many anthropogenic threats faced by other bighorn sheep populations. Based on habitat availability, it is estimated that the current range occupied by the metapopulation could conservatively support five times the number of sheep it does now (IDFG 2022). However, the pathogen *Mycoplasma ovipneumoniae*, originally introduced from domestic sheep and subsequently spread by bighorn sheep (Kamath et al. 2019) has persisted in the metapopulation for decades. This bacterium can be highly lethal to lambs, and low juvenile survival is regarded as the primary factor currently limiting recovery in the Salmon River metapopulation (IDFG 2022).

By reducing host abundance, infectious diseases can fragment populations causing loss of genetic diversity, even when there is suitable habitat connecting them (McKnight et al. 2017). Low ratios of effective population size to census population size (N_e/N), an indicator of the extent of genetic variation expected in a population, in the Middle Fork and Lower Salmon PMUs (0.18, Table S14) may reflect poor lamb recruitment. This ratio is expected to be lower in populations with high variance in breeding success among individuals, as well as populations with overall low fecundity or offspring survival (Hedrick 2005; Waples et al. 2013; Waples 2024). The effective population size is also a measure of the predicted rate of loss of genetic diversity per generation due to genetic drift and can be strongly affected by migration (Hoban et al. 2022) which could explain the high variance in the estimate for the Lower Panther PMU.

Consistent with previous investigations, we found no indication of directional selection at adaptive loci associated with genes involved in immune function, for example for increased disease resistance (Boyce et al. 1997; Gutierrez-Espeleta et al. 2001; Worley et al. 2006). Although the number of private alleles in adaptive microsatellite loci declined over time, heterozygosity was generally maintained and was similar to neutral heterozygosity (Table 3).

This study provided a rare opportunity to directly compare historical and contemporary genetic diversity in a wildlife metapopulation. However, drawbacks of this investigation included limited availability of historical specimens and difficulty obtaining usable sequences from degraded and fragmented DNA in historical horn and bone samples (Raxworthy and Smith 2021). Mitochondrial and nuclear DNA microsatellites were successfully genotyped in 31 and 28 of 34 samples in the Carrey collection (89% and 80% respectively) and 3 of 9 field samples we received of unknown age (33%). In addition, we had no control over sampling strategy or metadata management, therefore all historical samples in the Carrey collection were from males, and dates and locations for some historical samples were vague or unavailable. This work also focused on mtDNA haplotypes and a small number of microsatellite loci, while genomic methods (i.e. RADSeq, whole genome sequencing) would have provided many thousands of single nucleotide polymorphism (SNP) loci (Jahner et al. 2019; Flesch et al. 2020; Jahner et al. 2025). These factors limited the amount of detail we could extract from the data and the inferences we could make. Our results may underestimate actual differences between PMUs and historical and contemporary time periods. Of necessity, we were conservative in our interpretation and addressed data and statistical power limitations by relying on multiple analyses and lines of evidence to support the results and conclusions.

Future direction

Genetic diversity contributes to fitness and survival of individuals, populations, and species, and is declining globally (Leigh et al. 2019; Shaw et al. 2025). While a significant amount of genetic diversity is retained in the Idaho native bighorn sheep metapopulation, there are indications of potential for further declines, especially in more isolated populations. Preventing additional loss of genetic variation in bighorn sheep that have undergone thousands of years of local adaptation is important for conservation and management into the future. Reducing the impacts of disease and protecting populations from new infections probably has the most potential for recovering the metapopulation to numbers that generate self-sustaining levels of gene flow and genetic diversity in the long term. Spatial structure is natural in North American wild sheep populations, even at northern latitudes relatively unaffected by anthropogenic disturbances (Roffler et al. 2014; Deakin et al. 2020). Gene flow among these healthy northern populations has been detected at 80 to 100 km, distances well within the range for naturally restoring and maintaining linkages among native Idaho populations (Fig. 1).

The historical connection of Rocky Mountain and desert bighorn sheep populations identified in this study contributes to an understanding of the distribution of bighorn sheep subspecies prior to widespread extirpations and may inform contemporary management and restoration programs, especially in peripheral ranges where bighorn sheep have been extirpated. In Idaho, Rocky Mountain bighorn sheep from other states and provinces have been translocated to mountain ranges and river canyons to the east and west of native populations and mixing with native sheep will likely increase over time. Assessing genetic similarity and phylogeographic lineage in any future translocations in the vicinity of native sheep populations would increase the likelihood that translocated animals are compatible with local gene pools (Hoban et al. 2016), and conducting genetic assessments preceding and following translocations would be informative for evaluating effects on genetic diversity and gene flow. Periodic genetic and population monitoring and finer scale analyses incorporating genomic data, such as SNPs, which provide a higher level of detail on neutral and adaptive variation and are more sensitive to changes in genetic diversity than microsatellites would also be beneficial for tracking contemporary trends in genetic diversity and gene flow (Epps et al. 2018; Leroy et al. 2018; Jahner et al. 2019; Flesch et al. 2020; Deakin and Coltman 2024; Shaw et al. 2025).

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Author contributions All authors contributed to study conception and design. Data collection was conducted and/or coordinated by NB and HM. Laboratory work and data analyses were conducted by SB, KRA, JRA, and NB under the supervision of LPW. SB, EFC, and KRA prepared figures and tables. SB and EFC wrote the first draft of the manuscript. All authors contributed to manuscript revisions and approved the final version.

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Data availability Mitochondrial DNA sequences PX897752-PX897957 will be available in NCBI GenBank upon publication.

Declarations

Competing interests The authors declare no competing interests.

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continue as revised or amended until repealed or nullified pursuant to law.

(b) Rules and regulations necessary to administer this article shall be promulgated jointly by the game and fish commission, the board of agriculture and the livestock board. The game and fish commission, the board of agriculture and the livestock board may jointly consider recommendations for changes to the plan and may revise or amend the plan through the rulemaking process pursuant to the Wyoming Administrative Procedure Act.

(c) The goal of the Wyoming bighorn/domestic sheep plan shall be to maintain the health of bighorn sheep populations while sustaining an economically viable domestic sheep population.

(d) The most current version of the Wyoming bighorn/domestic sheep plan shall be published on the website of the game and fish commission.

(e) In conformance with the Wyoming bighorn/domestic sheep plan the game and fish department may relocate or remove bighorn sheep to another area of the state if a federal judicial action or agency decision would require elimination of domestic sheep grazing in any area or herd unit designated in the Wyoming bighorn/domestic sheep plan as a nonemphasis herd. The game and fish department shall be reimbursed for the costs of relocation or removal of sheep under this subsection from funds available in the wildlife/livestock disease research partnership account.

11-19-605. Wyoming bighorn/domestic sheep relocation and removal; legislative findings; reimbursement; attorney general action.

(a) The legislature finds and declares that it is the state's policy to vigorously defend its interests in maintaining and enhancing viable livestock grazing operations on public lands in conjunction with the conservation and maintenance of healthy bighorn sheep populations in the state of Wyoming. These two (2) policies are mutually compatible as demonstrated since the adoption of the collaboratively developed Wyoming bighorn/domestic sheep plan in 2004, which was codified into law under W.S. 11-19-604 in 2015. The legislature further finds and declares that:

(i) Reintroduction of bighorn sheep and management action to protect existing populations of bighorn sheep on federal public lands has been effectively accomplished in conformance with the Wyoming bighorn/domestic sheep plan;

(ii) It is the policy of the state of Wyoming to accept any risk of contact between bighorn sheep and livestock in the vicinity of any bighorn sheep transplant or relocation and to hold livestock producers harmless in the event such contact occurs;

(iii) All wildlife in the state of Wyoming is the property of the state, and it is the policy of the state to provide an adequate and flexible system for control, propagation, management, protection and regulation of all Wyoming wildlife;

(iv) Any removal of bighorn sheep from the Sweetwater Rocks herd unit under this act shall not be attributable to domestic livestock grazing on federal bureau of land management administered lands. Rather, the removal of bighorn sheep shall be directly attributable to:

(A) Onerous federal regulation that unduly impedes the state of Wyoming's ability to manage wildlife and domestic livestock grazing in conformance with the Wyoming bighorn/domestic sheep plan;

(B) Third-party action designed to use bighorn sheep as a means of eliminating domestic livestock grazing on bureau of land management administered lands within or in the vicinity of the Sweetwater Rocks herd unit.

(v) The provisions of this section shall be enforced by the state.

(b) In conformance with the Wyoming bighorn/domestic sheep plan in W.S. 11-19-604 and pursuant to W.S. 23-1-103, the game and fish department shall relocate or remove all bighorn sheep from the Sweetwater Rocks herd unit if any federal judicial action or federal agency action requires or indicates it may require the following:

(i) The elimination, reduction or suspension of domestic livestock grazing or trailing in the Sweetwater Rocks herd unit; or

(B) Has made his permanent home in Wyoming;

(C) Is not residing in Wyoming for a special or temporary purpose; and

(D) Has abandoned his domicile in all other states, territories or countries.

(xvi) "Livestock" means horses, mules and asses, rabbits, llamas, cattle, swine, sheep, goats, poultry, or other animal generally used for food or in the production of food or fiber, and guard animals actively engaged in the protection of livestock. Bison are considered livestock unless otherwise designated by the Wyoming livestock board and the commission;

(xvii) "Home of record" means the place recorded, on military form DD 214, as the home of the individual at the time he enlisted, was commissioned or initially ordered to active duty in the military. The home of record may be changed only if there has been a break in service of one (1) full day;

(xviii) "Electronic licensing" means a system for the issuance of licenses, stamps and tags as an alternative to issuing original paper licenses, stamps and tags. An electronic licensing system is a system in which the license, stamp or tag, or authorization therefor, is received through a point of sale terminal or through a computer.

23-1-103. Ownership of wildlife; purpose of provisions.

For the purpose of this act, all wildlife in Wyoming is the property of the state, including shed antlers or horns located on state or public lands. It is the purpose of this act and the policy of the state to provide an adequate and flexible system for control, propagation, management, protection and regulation of all Wyoming wildlife. There shall be no private ownership of live animals classified in this act as big or trophy game animals or of any wolf or wolf hybrid.

23-1-104. Federal game preserves also state preserves.

All federal game preserves and sanctuaries now existing, or hereafter created, are state game animal, bird and fish preserves for the purposes of this act.

23-1-105. Migratory bird refuge in Seedskaadee area.



WYOMING GAME AND FISH DEPARTMENT

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October 12, 2020

WER 6312.03
U.S. Forest Service
Grand Targhee Resort
2018 Master Development Plan Projects
Teton County

Mel Bolling
c/o Jay Pence
Teton Basin District Ranger
U.S. Forest Service
P.O. Box 777
Driggs, ID 83422
Jay.pence@usda.gov

Dear Mr. Bolling,

The staff of the Wyoming Game and Fish Department (Department) has reviewed the 2018 Master Development Plan Projects located in Teton County. We offer the following comments for your consideration.

Thank you for the opportunity to provide comments during the scoping process for the Grand Targhee Master Development Plan Projects. The Department and Caribou-Targhee National Forest (CTNF) have a long history of working collaboratively on wildlife and habitat issues on the Teton Basin Ranger District, and we appreciate your partnership in these endeavors. The 1997 Revised Targhee National Forest Plan contains specific language in the Teton Range Subsection regarding coordination between CTNF and the Department “in the management of the bighorn sheep population and habitat” (pg. 111-56). In this spirit of coordination, we respectfully request cooperating agency status during development of the Environmental Impact Statement (EIS) for this project.

We have reviewed the scoping letter and associated projects outlined in the 2018 Grand Targhee Master Plan and offer the following comments for your consideration.

General Comments

The proposal includes projects within the existing Grand Targhee Special Use Permit Boundary (SUP), as well as two proposed SUP expansion areas: Mono Trees (~600 acres) and South Bowl (~600 acres). The proposed projects within the existing SUP area include new ski lifts, lift replacements and upgrades, lift realignments, new lighting, glading, terrain grading, road

rehabilitation, increased snowmaking, a new restaurant at the summit of Fred's Mountain, a new restaurant/bar/restrooms facility at the top of Sacajawea lift, approximately 29 miles of new mountain biking and hiking trails, additional Nordic ski trails, several new yurts, a zipline, and an aerial adventure course. We recognize the emerging needs for ski resorts to diversify their activity offerings and enhance outdoor experiences for visitors. Although these proposed projects within the existing SUP boundary will likely have some negative impacts to wildlife that will add to those already resulting from the existing development, we recognize the Forest Plan Management Prescription for this area as 4.2 Special Use Recreation Site for developed recreation. Therefore, we do not have comments or concerns related to these projects within the existing SUP boundary.

The Department is primarily concerned about how the two proposed SUP expansion areas will impact currently intact wildlife habitat, especially the South Bowl expansion into Teton Canyon. It would be helpful for the forthcoming EIS to describe in more detail the specific purpose and need for expansion into the Mono Trees and South Bowl areas in order to weigh the benefit of an expansion against the potential adverse impacts to wildlife and wildlife habitat. We also recommend the EIS include alternatives and corresponding analysis that 1) restrict proposed projects to within the existing SUP boundary without any expansion areas, and 2) restrict proposed projects to within the existing SUP boundary and only the Mono Trees Expansion Area. Lastly, the 1997 Revised Targhee Forest Plan shows Teton Canyon within the 3.2(b) – Semi-Primitive Motorized management prescription (pg. 111-120) instead of the 2.1.2 Visual Quality Maintenance management prescription referenced in the scoping letter. Therefore, it is unclear within which management prescription area the proposed SUP expansions would occur.

Bighorn Sheep

Background of the Targhee Bighorn Sheep Herd

The Department's main concern regarding this proposal is the expansion of the SUP boundary into the South Bowl area (Figure 1) and the associated impacts to bighorn sheep winter habitat, summer habitat, and movement path to a natural mineral lick in Teton Canyon. Here, we provide background describing the importance of the Targhee Bighorn Sheep Herd and the interagency efforts that have occurred over the past several decades to conserve this herd. The Targhee Bighorn Sheep Herd (also known as the Teton Bighorn Sheep Herd) is a small, isolated population that lives in the Teton Mountain Range and uses habitat within the CTNF, Bridger-Teton National Forest (BTNF), and Grand Teton National Park (GTNP). Historically, the majority of bighorn sheep in this population spent the summer at high elevations and moved to low elevation winter ranges (Whitfield 1983). However, due to a multitude of factors these seasonal movements disappeared by about 1950. Since then, the population has been non-migratory and spends the summer *and* winter at high elevations in the Teton Range. The herd persists on small areas of wind-blown winter habitat where food is scarce and energetic demands are high due to cold temperatures and surrounding deep snow. Additionally, mortality due to avalanches can be relatively high during some winters. The herd is currently estimated to be approximately 125 sheep

and appears to be stable, although very small. Over the past 40 years, aerial surveys have documented between 40-100 sheep in the herd (Wyoming Game and Fish Department Job Completion Reports, 1980-2019).

The Targhee Herd is important within the State of Wyoming because it was classified as a core, native herd in the Wyoming Statewide Bighorn/Domestic Sheep Interaction Working Group Plan (2004), and Wyoming Statute § 11-19-604. It is the smallest and most isolated of the four core, native herds in Wyoming. The herd has received a significant amount of attention, primarily through efforts to protect the herd from interaction with domestic sheep through willing-seller/willing-buyer allotment negotiations and subsequent allotment closures by the CTNF, resulting in the removal of all domestic sheep grazing in the Teton Range. The South Bowl SUP Expansion Area is within the former Table Rock – Mill Creek Sheep and Goat Allotment.

Interagency Coordination Efforts

Since the early 1980s, there has been concern about the future persistence of this herd due to its small size and limited winter habitat. Throughout the 1980s and early 1990s, Department biologists documented concerns in annual Job Completion Reports about the herd. In the early 1990s, the Teton Range Bighorn Sheep Working Group was formed and included representatives from the CTNF, BTNF, GTNP, the Department, and several other local bighorn sheep experts. This group has been active for the past three decades and has successfully worked together to conserve this herd through interagency research, monitoring, habitat improvement projects, public education, and other efforts. Over one million dollars in non-governmental funding has been put toward various conservation projects for the herd, in addition to significant government agency funding and staff time that has been dedicated to carrying out these efforts.

In March 2019, the Teton Range Bighorn Sheep Working Group convened a panel of scientists from around the western United States with expertise in the ecology, demographics, genetics, habitat requirements, nutrition, and management of bighorn sheep and epidemiology of bighorn sheep diseases, such as pneumonia. The working group asked this expert panel to review the existing research, state of knowledge, and management strategies for the Targhee Herd and identify critical data gaps, recommend strategies to improve population resilience, and prioritize management actions with the working group (Teton Bighorn Sheep Working Group, 2020). Three recommendations from the expert panel that directly apply to this scoping proposal are 1) prioritize protection of the small areas of remaining winter habitat for the Targhee Herd; 2) expand winter habitat through restoration projects using prescribed fire and/or managing natural wildfires, where appropriate; and 3) work with the community to limit human disturbance to bighorn sheep during the winter.

Over the past two years, the working group has focused its attention on undertaking a community-based collaborative process to find solutions to balance winter recreation and Targhee bighorn sheep habitat needs. Recent research showed that backcountry winter recreation was displacing

Targhee bighorn sheep from important winter habitat (Courtemanch 2014). Over \$50,000 from the Community Foundation of Jackson Hole, Grand Teton Association, Bridger-Teton National Forest, Wyoming Wild Sheep Foundation, Winter Wildlands Alliance, Teton Backcountry Alliance, and the Department has been dedicated to this community collaborative effort. The working group conducted over 50 one-on-one conversations with key stakeholders and held three collaborative public meetings for which over 120 people attended. Participants included frontcountry and backcountry skiers, guiding companies, recreation advocacy organizations, conservation organizations, County Commissioners, Jackson Hole Mountain Resort representatives, hunters, local conservationists, and other interested members of the public. Through this process, the community drafted a long list of recommended solutions for the working group to consider and present to CTNF, BTNF, GTNP, and Department decision-makers for potential implementation. This community process is still continuing and we expect that final recommendations will be made during winter 2020-2021.

Winter Habitat in Teton Canyon

Bighorn sheep winter habitat occurs throughout the north side of Teton Canyon, including the proposed South Bowl SUP expansion area. Historical winter habitat, occurs below and to the west of the South Bowl (Whitfield, 1983) (Figure 2). Based on GPS-collar data from 25 bighorn sheep ewes in the Targhee Herd and a resource selection function completed by Courtemanch (2014), Teton Canyon and the South Bowl contain the two highest tiers of winter habitat classification (Figure 3). Areas in Teton Canyon that are mapped as second highest quality winter habitat (shown in orange in attached figures) would shift to higher quality if the amount of trees and shrubs are reduced. The Department's bighorn sheep seasonal range maps have not yet been updated with this new information.

Expansion of recreation into the South Bowl SUP area would lead to new and increased levels of disturbance, resulting in a direct loss of bighorn sheep winter habitat, which is already limited. In addition, we are concerned about impacts to adjacent winter habitat areas. It is reasonable to expect that visitor out-of-bounds skiing would increase around the proposed South Bowl and Mono Trees SUP expansion areas, leading to indirect bighorn sheep habitat loss through human activity disturbance (Courtemanch 2014). The South Bowl expansion area would allow for relatively easy access to backcountry areas to the east along the divide between North Fork of Teton Canyon and South Leigh Creek to the GTNP boundary. We are also concerned that backcountry skiing activity would increase in the Apostles Cliffs below the Mono Trees expansion area, which is where the natural mineral lick is located. The current scoping proposal does not detail whether there would be any new gates allowing public access outside of the resort and how this would or would not be managed. We encourage the Forest Service to include an analysis of the impacts on wildlife, including bighorn sheep, from new backcountry access points and increased numbers of recreationists in areas with previously low use. The proposal also mentions the need for avalanche control in the South Bowl, which would introduce significant noise into Teton Canyon. We suggest

that the expected levels and frequency of noise are disclosed and analyzed for their potential effects on wildlife.

In addition to current winter habitat, several low and mid elevation canyons on CTNF are known to be historical winter range for this herd, including Moose Creek, Fox Creek, Darby Creek, and lower Teton Canyon (Whitfield 1983). From 1970-2000, there was little documentation of bighorn sheep using these areas due to high numbers of domestic sheep and vegetation succession from lack of fire (Wyoming Game and Fish Department, 1988; Wyoming Game and Fish Department, 1990). However, after domestic sheep allotments were closed in the late 1990s and early 2000s, we documented a significant shift by bighorn sheep back into many of the former allotments, including historical winter ranges in Fox Creek and Darby Creek. Bighorn sheep have been documented using Teton Canyon in the summer months in recent years, however less winter use has been documented. We suspect that bighorn sheep have not recolonized historical winter ranges in Teton Canyon due to the advanced vegetation succession present in the canyon (i.e., high shrub and tree densities due to lack of fire). However, there has been sporadic use in the canyon, especially by rams, which has been documented on a GTNP remote camera in the Apostles Cliffs between 2017 and 2020, as well as one verified observation by the Department in early April 2017 of a ram in lower Teton Canyon. There is also an unverified public report of a ram in the South Bowl in February 2018. The lack of data of bighorn sheep use in Teton Canyon, especially during the winter, could also be a result of very few rams being collared ($n=2$) during research efforts from 2008-present.

In order to restore historical winter range areas in Teton Canyon, the Department has worked collaboratively with CTNF to plan and design the Teton Canyon Hazardous Fuels Reduction Project (decision signed June 2018), which will include prescribed fire treatments to restore approximately 840 acres of bighorn sheep habitat (Figure 4). We expect that bighorn sheep will expand into this area and start using it immediately since some animals already visit the area throughout the year. This project is a rare opportunity to restore historical low elevation bighorn sheep habitat in the Tetons. The majority of sheep habitat occurs within designated Wilderness or within GTNP, which are areas where targeted habitat treatments are not possible. This project could also result in an excellent scenario for public viewing of bighorn sheep. Historical bighorn sheep habitat in lower Teton Canyon is visible from the Teton Canyon Road and winter groomed trail, as well as the Reunion Flats Campground. Approximately, 279 acres of the proposed prescribed burn are within the South Bowl SUP expansion area and the rest are below or directly west of the South Bowl. If the South Bowl SUP expansion area is approved, it will impact the current opportunity to restore historical bighorn sheep winter habitat in Teton Canyon.

Summer Habitat in Teton Canyon

Bighorn sheep summer habitat is present in Teton Canyon in larger quantities than winter habitat (Figure 5). Summer habitat was mapped using an RSF based on 25 GPS-collared ewes (Courtemanch 2014, Courtemanch et al. 2017) (Figure 5). Summer use by bighorn sheep has also

been documented, including a GPS-collared ewe that visited the area in the summers of 2008 and 2009 with a lamb at heel both years (Courtemanch 2014) (Figure 5). In addition to this collared ewe, there have been public reports of mixed ewe/lamb groups in the South Bowl, as well as one Department observation, which show that nursery groups use this area. Ram groups have also been observed throughout the north side of Teton Canyon, including the South Bowl and Apostles Cliffs (Figure 5). There has been a remote camera established at the natural mineral lick from 2017 – present, which documented at least 13 unique adult rams (based on distinct horn morphology) using the area in 2018. This is roughly 30% of the total estimated rams in the Targhee Herd.

Movement to Natural Mineral Lick in Teton Canyon

A natural mineral lick occurs down canyon from the South Bowl SUP expansion area in the Apostle Cliffs. Mineral licks are localized habitat features that are relatively rare on the landscape and important to the health of mountain ungulates (Holl & Bleich 1987, Ayotte 2005, Mincher et al. 2008). High levels of human use or disturbance along movement paths to limited point resources (e.g., watering holes or mineral licks) can prevent animals from visiting (Leslie & Douglas 1980, Keller & Bender 2007). There are a small number of known mineral lick sites that receive consistent visitation by bighorn sheep in the Teton Range (Courtemanch 2014, GTNP unpublished data). It is not known whether bighorn sheep that use the Teton Canyon lick site also use other licks. Therefore, impeding bighorn sheep access to the Teton Canyon mineral lick could cause health impacts to those individuals. Since approximately 30% of rams in the Targhee Herd appear to be using the Teton Canyon lick, as well as nursery groups, it is likely an important source of minerals for this population.

The GPS-collared ewe that visited this lick in 2008 and 2009 moved through the proposed South Bowl SUP expansion area to get there (Figure 6, Figure 7). Based on the configuration of sheep habitat in Teton Canyon, it is reasonable to assume that most or all of the sheep move through the South Bowl to get to and from the lick. The area below the proposed South Bowl SUP expansion and on the south side of Teton Canyon is not suitable bighorn sheep habitat, and therefore sheep are unlikely to adopt a new path to access the mineral lick. The Department is concerned that development within the proposed South Bowl SUP expansion area would prevent bighorn sheep from accessing the mineral lick. Even though not proposed at this time, we are concerned the proposed development in the South Bowl would increase the possibility of summer activities being permitted in the future. Even if summer recreation activity does not occur in the South Bowl SUP expansion area, the infrastructure from winter skiing (i.e., buildings, ski lifts, roads, etc.) could deter bighorn sheep from moving through this area. As a similar comparison, bighorn sheep summer habitat exists within the Jackson Hole Mountain Resort boundary, but there have never been documented observations of sheep moving through the area.

Mel Bolling
October 12, 2020
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Moose

Moose utilize habitats in Teton Canyon year-round, and Department Wildlife Observation System (WOS) records indicate this area is used by moose in the winter (Figure 8). There are no records of moose in the proposed South Bowl or Mono Trees SUP expansion areas; however, these areas would provide easier access for out-of-bounds skiing and could potentially increase disturbance to moose during the winter. We recommend the EIS include an analysis of expected levels of out-of-bounds skiing, if and how Grand Targhee may manage access to out-of-bounds use, and how this activity may impact moose.

Thank you for the opportunity to provide comments. We look forward to continued participation in the development of the EIS for this project. If you have any questions, please contact Doug McWhirter, Jackson Region Wildlife Management Coordinator, at 307-733-2321.

Sincerely,

A handwritten signature in black ink, appearing to read "Amanda Losch". The signature is fluid and cursive, with the first name "Amanda" being more prominent than the last name "Losch".

Amanda Losch
Habitat Protection Supervisor

AL/mf/ct

cc: U.S. Fish and Wildlife Service
Doug McWhirter, Wyoming Game and Fish Department
Aly Courtemanch, Wyoming Game and Fish Department
Joe Budd, Office of Governor Gordon
Chris Wichmann, Wyoming Department of Agriculture

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Figure 1. View of the north side of Teton Canyon from the Table Mountain trail. The black line represents the approximate area of the proposed South Bowl Special Use Permit Expansion Area.

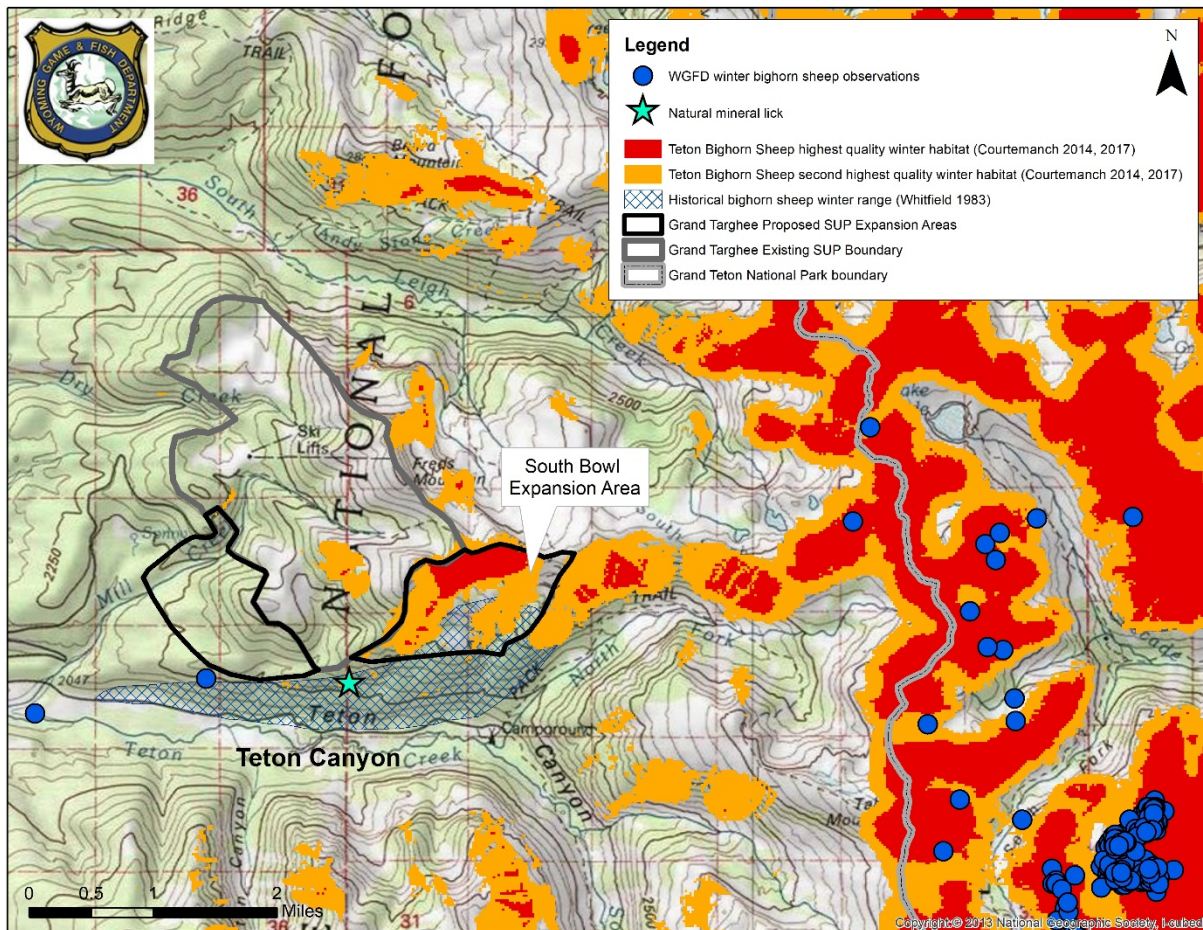


Figure 2. Targhee bighorn sheep winter habitat and winter observations in the greater Teton Canyon area. Targhee bighorn sheep winter habitat (highest quality (red) and second highest quality (orange) from Courtemanch 2014 and Courtemanch et al. 2017); winter bighorn sheep locations from Wyoming Game and Fish Department Wildlife Observation Database and GPS-collared sheep (blue dots); Teton Canyon natural mineral lick (star); historical bighorn sheep winter range (hashed blue) (Whitfield 1983); current Grand Targhee Special Use Permit area (grey line), and proposed special use permit expansion areas (black lines).

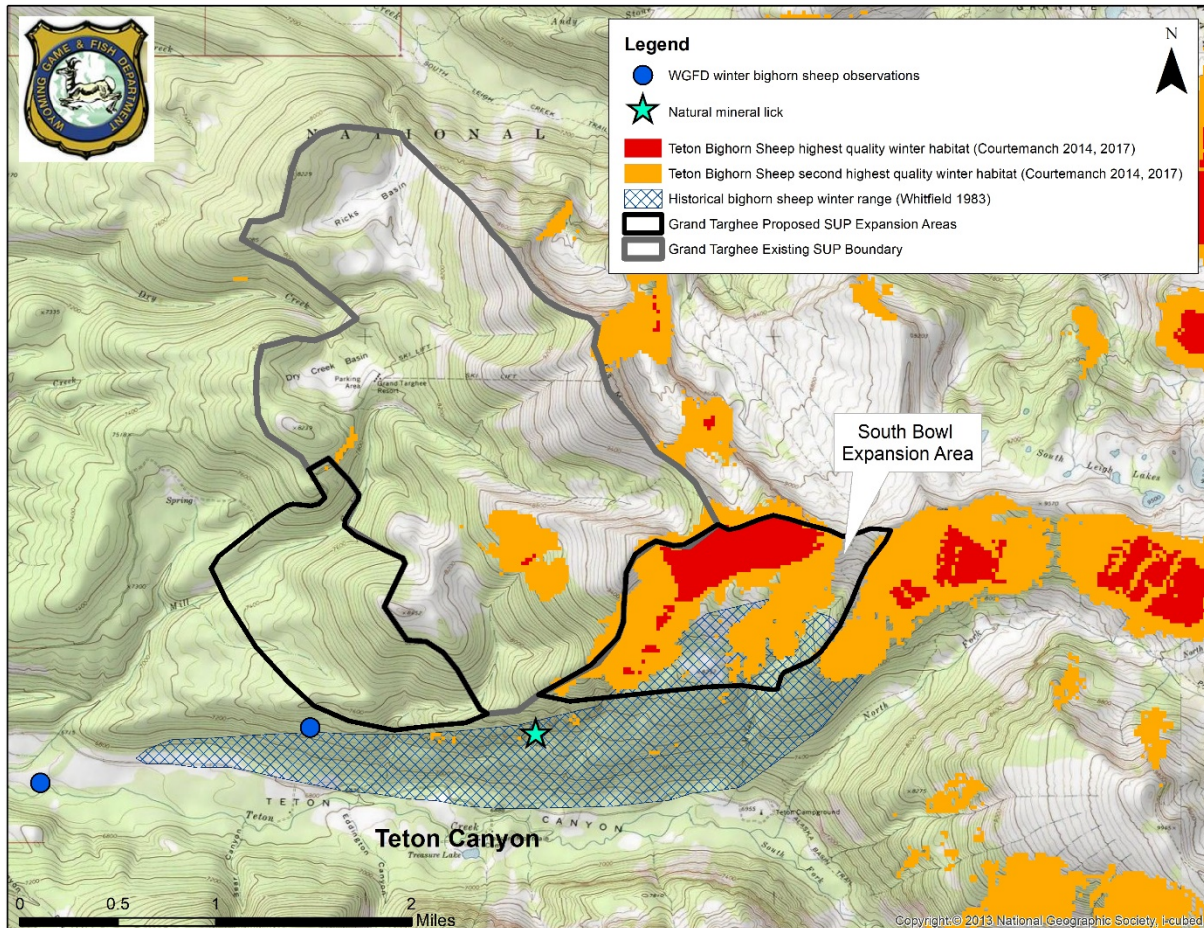


Figure 3. Targhee bighorn sheep winter habitat and winter observations in the vicinity of the proposed project. Targhee bighorn sheep winter habitat (highest quality (red) and second highest quality (orange) from Courtemanch 2014 and Courtemanch et al. 2017); winter bighorn sheep locations from Wyoming Game and Fish Department Wildlife Observation Database (blue dots); Teton Canyon natural mineral lick (star); historical bighorn sheep winter range (hashed blue) (Whitfield 1983); current Grand Targhee Special Use Permit area (grey line); and proposed special use permit expansion areas (black lines).

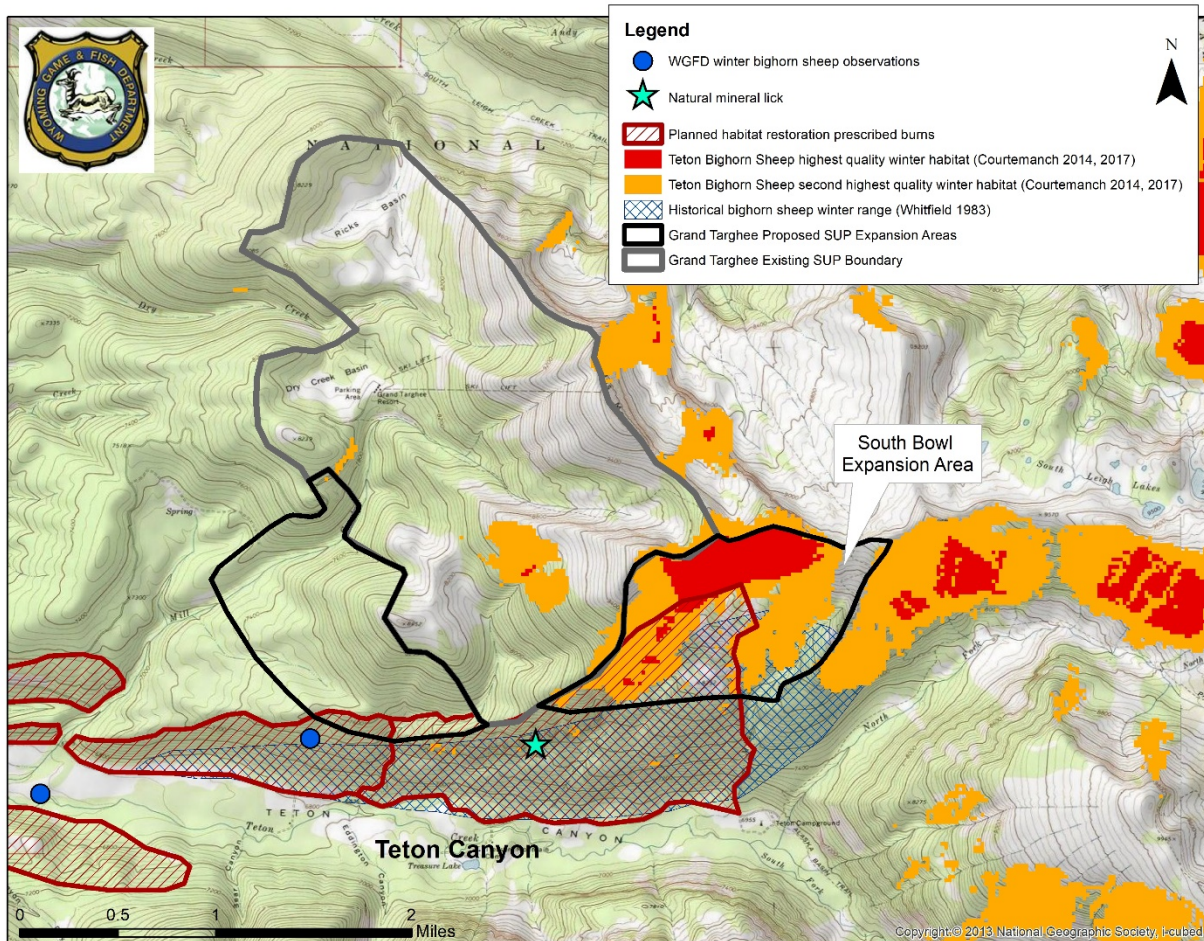


Figure 4. Targhee bighorn sheep winter habitat and planned Teton Canyon Hazardous Fuels Reduction Project prescribed burn areas that would restore bighorn sheep habitat. Targhee bighorn sheep winter habitat (highest quality (red) and second highest quality (orange) from Courtemanch 2014 and Courtemanch et al. 2017); winter bighorn sheep locations from Wyoming Game and Fish Department Wildlife Observation Database (blue dots); Teton Canyon natural mineral lick (star); historical bighorn sheep winter range (hashed blue) (Whitfield 1983); planned prescribed burn areas (hashed red); current Grand Targhee Special Use Permit area (grey line); and proposed special use permit expansion areas (black lines).

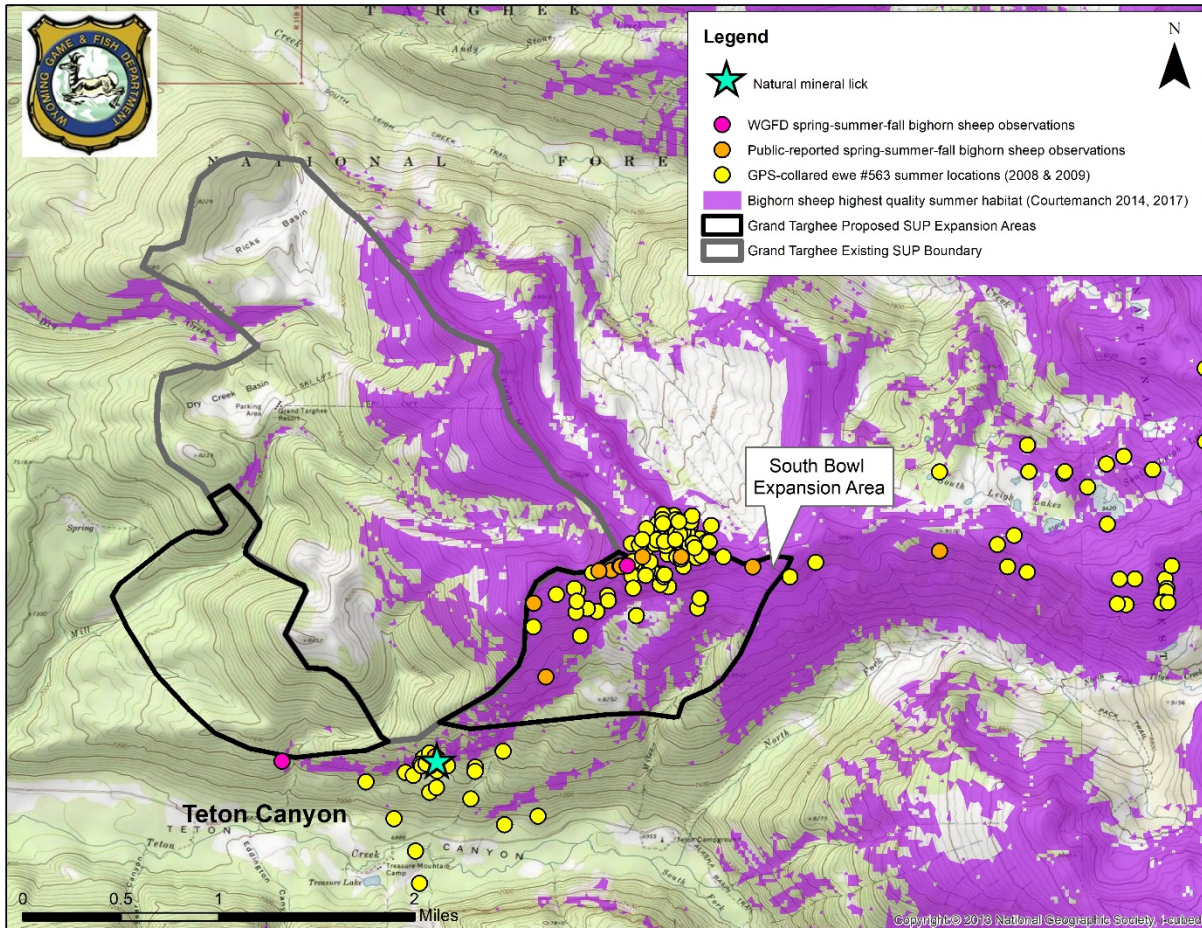


Figure 5. Targhee bighorn sheep summer habitat and summer observations in the vicinity of the proposed project. Targhee bighorn sheep summer habitat (purple) (from Courtemanch 2014 and Courtemanch et al. 2017); Wyoming Game and Fish Department summer bighorn sheep observations (pink dots); public-reported summer bighorn sheep observations (orange dots); GPS-collared ewe #563 movements (yellow dots); current Grand Targhee Special Use Permit area (grey line); and proposed special use permit expansion areas (black lines).

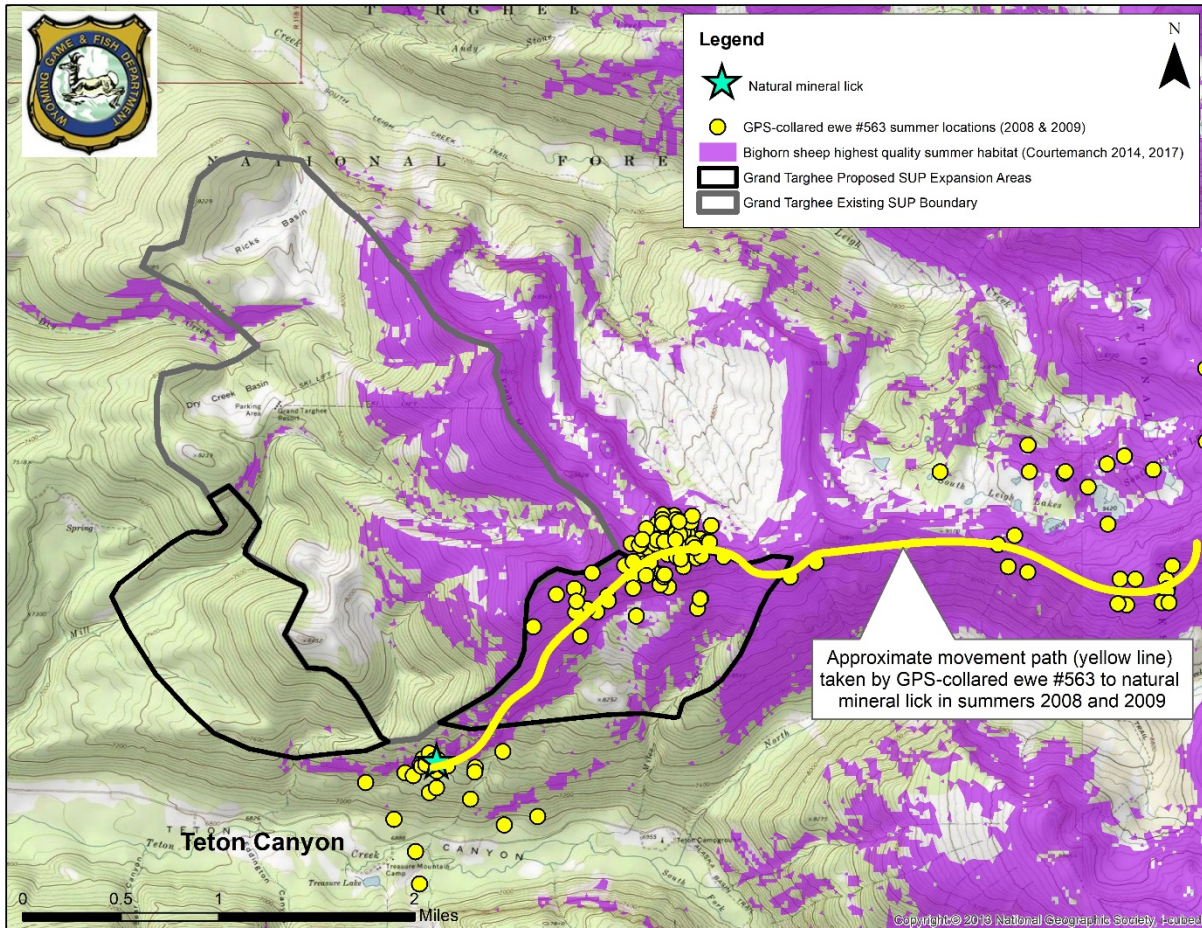


Figure 6. Targhee bighorn sheep summer habitat and approximate movement path of GPS-collared ewe to access Teton Canyon mineral lick. Targhee bighorn sheep summer habitat (purple) (from Courtemanch 2014 and Courtemanch et al. 2017); GPS-collared ewe #563 locations in summers 2008 and 2009 (yellow dots); approximate movement path to access mineral lick (yellow line); current Grand Targhee Special Use Permit boundary (grey line); and proposed special use permit expansion areas (black lines).

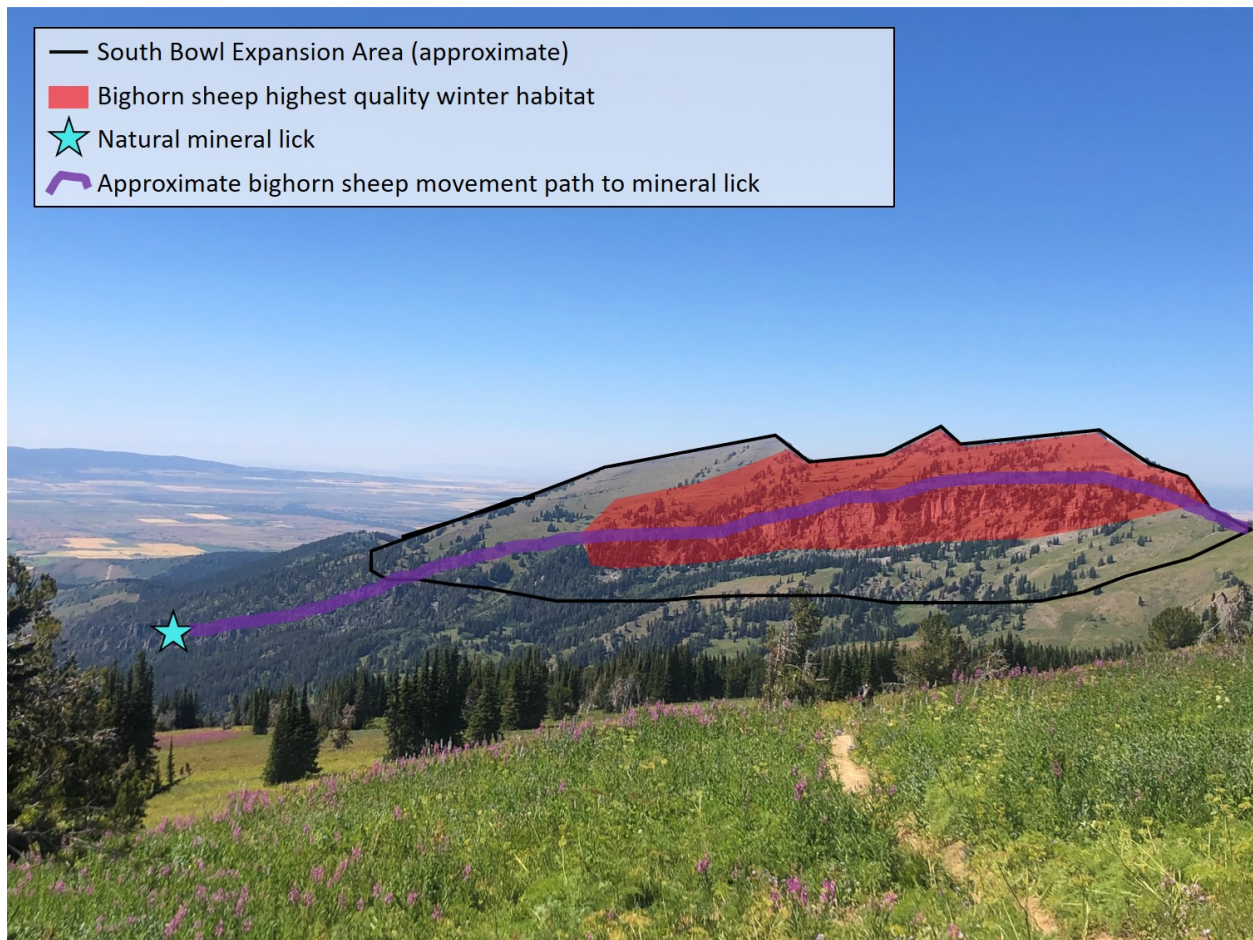


Figure 7. View of proposed South Bowl Special Use Permit expansion area (within black line) from Table Mountain Trail with Teton Canyon mineral lick (star); approximate bighorn sheep movement path to lick shown (purple line); and bighorn sheep highest quality winter habitat area (red).

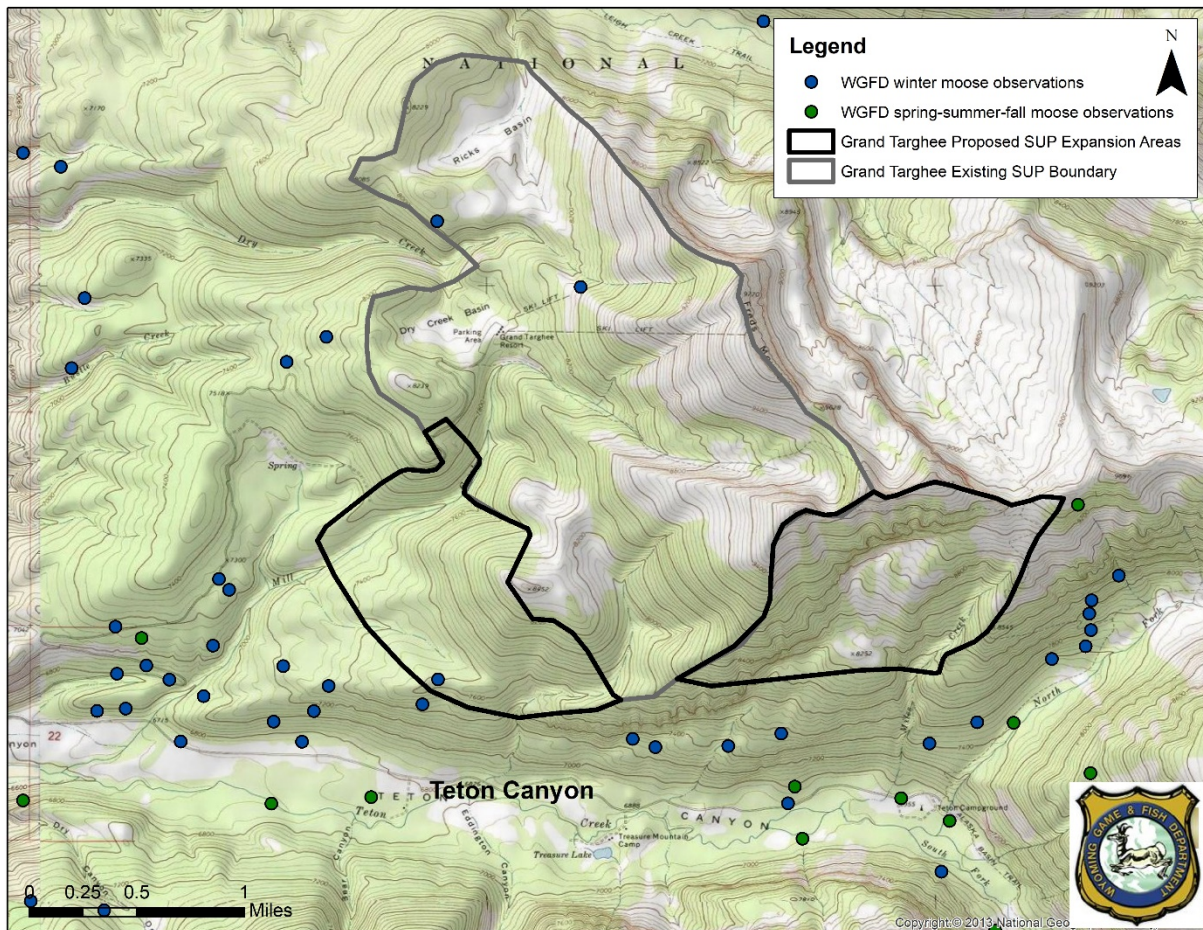


Figure 8. Moose winter (blue) and summer (green) observations in Teton Canyon and surrounding area from the Wyoming Game and Fish Department Wildlife Observation Database (1988-present). Current Grand Targhee Special Use Permit boundary (grey line) and proposed special use permit expansion areas (black lines).



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June 20, 2025

WER 6312.05

United States Department of Agriculture

United States Forest Service

Grand Targhee 2018 Master Development Plan DEIS

Teton County

Jay Pence

District Ranger

United States Forest Service

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Idaho Falls, ID 83401

jay.pence@usda.gov

Dear Mr. Pence,

The staff of the Wyoming Game and Fish Department (Department) has reviewed the proposed Grand Targhee 2018 Master Development Plan Draft Environmental Impact Statement (DEIS) and supporting documents. The Department is statutorily charged with managing and protecting all Wyoming wildlife (W.S. 23-1-103). Pursuant to our mission, we offer the following comments for your consideration.

The Department has been involved with the proposed project since requesting cooperating agency status in 2020. We appreciate the opportunity for involvement past, present, and future to ensure impacts to wildlife and wildlife habitat are avoided and minimized to the degree possible. The Department's long-standing relationship with the Caribou-Targhee National Forest (CTNF) and our ability to successfully work together to achieve the goals of the CTNF while minimizing impacts to wildlife.

Since our initial engagement, the Department's primary concern has been the impacts of expansion into the South Bowl area specifically on bighorn sheep habitat. Our comments during scoping and on the Biological Evaluation (BE) provided ample information on the fragility of the Targhee bighorn sheep herd and the potential for impacts with the expansion into the South Bowl. We appreciate the updates made to the BE that accurately reflect the Department's position and the CTNF's efforts to integrate data into the decision-making process. The Department made it clear in our initial engagement that we do not have comments or concerns related to any expanded use within the existing Special Use Permit area. Our focus remains on the proposed expansion areas.

Hunting Access – The Grand Targhee permit area and surrounding areas provide hunting opportunity, which is used primarily by deer, elk, and bear hunters. It is imperative that hunting access remain unhindered with whatever alternative is chosen moving forward.

Bighorn Sheep – A major concern remains the South Bowl proposed expansion's impact on the Targhee Bighorn Sheep Herd (also known as the Teton Range Herd), a small, isolated, non-migratory population of approximately 100 sheep. This herd, classified as a core, native herd in Wyoming, relies on limited wind-blown winter habitat at high elevations. However, the herd also utilizes mid-elevation habitats during winter periods with less snow and late winter/spring, which are found in Teton Canyon. This is the smallest of the four native herds in Wyoming and is disease free, primarily as a result of ample interagency efforts focused on minimizing exposure to domestic sheep interactions, removing overlapping mountain goats, and engaging in research, monitoring, and habitat improvement. The Teton Range Bighorn Sheep Working Group (TRBSWG), which is made up of representatives from the Department, National Park Service, U.S. Forest Service, and other local bighorn sheep experts, convened an expert panel in 2019 comprised of other bighorn sheep experts from around the western United States to review the status of the Targhee Bighorn Sheep Herd. As the BE states, this expert panel emphasized that prioritizing protection of remaining winter habitat, removing mountain goats, expanding habitat through restoration, and limiting human disturbance were paramount for the future sustainability of this herd (TRBSWG, 2020). These recommendations reinforce the Department's stance on the proposed Grand Targhee expansion into South Bowl.

Collaborative efforts and extensive public engagement by the TRBSWG have focused on balancing winter recreation with bighorn sheep habitat needs. Research clearly shows that winter recreation displaces bighorn sheep from crucial winter habitat (Kolek 2024, Courtemanch 2014), which is accurately acknowledged in the DEIS and BE. This research indicated that backcountry skiing activity does not appear to create a barrier to bighorn sheep movement through those areas, however, we expect that ski resort expansion, including chairlifts, constant human activity during the daytime, nighttime grooming operations, avalanche control noise, road activity, etc. would most likely prevent bighorn sheep from moving through this area. As a result, the Department is concerned that expanded ski resort development in South Bowl, would lead to unsustainable direct and indirect loss of the already limited winter habitat with impacts overflowing to adjacent areas and also creating a barrier to bighorn sheep movement farther down Teton Canyon to access a mineral lick and other occupied year-round habitat. From 2020-2021, the TRBSWG worked diligently with the backcountry skiing community to craft solutions and compromises to meet bighorn sheep habitat needs and winter recreation desires. These efforts culminated in a report which included recommendations for balancing bighorn sheep habitat and backcountry skiing in Teton Canyon (TRBSWG 2021). The recommendations included a winter closure of the South Bowl area and Apostles cliffs but retained two designated backcountry skiing routes through the area. The Department continues to stand by this recommendation which balances bighorn sheep habitat protection with maintaining backcountry skiing access in Teton Canyon.

The DEIS and BE provide population data from Department aerial surveys and a fecal DNA study conducted by the National Park Service (NPS), however there are important data updates from the past few years that should be included. The DEIS and BE state that the herd size is approximately

125 sheep. However a severe winter in 2022/2023 impacted the herd and numbers are now approximately 100 sheep. The Department conducted aerial surveys in February 2023 and February 2025 which counted 71 sheep and 80 sheep, respectively (WGFD 2023, WGFD *in prep*). The herd declined from an observed 104 sheep in 2022 to 71 sheep in 2023 over the severe winter (32% decline). The neighboring Jackson Bighorn Sheep Herd also underwent a similar population decline of approximately 30% during the 2022/2023 severe winter (WGFD 2023).

The BE also includes preliminary results from an NPS fecal DNA study to estimate the herd size. The BE accurately states that the preliminary results in 2022 estimated the herd size to be approximately 178 sheep. However, errors in the genotyping methodology were subsequently discovered and after they were corrected, the annual herd sizes were estimated to be the following: summer 2019 (122 +/- 26 (SE)), summer 2020 (121 +/- 7 (SE)) summer 2021 (118 +/- 12 (SE)), and summer 2022 (132 (+/- 6 (SE)) (NPS, *unpublished data*). The average estimated population size during the study was 123 sheep, therefore very close to our approximation of 125 sheep before the severe winter. Unfortunately, the study ended before the severe winter of 2022/2023. However, these data have helped determine the relative accuracy of the Department's annual aerial surveys. Winter aerial surveys during the same time periods detected 82% (February 2020), 74% (February 2021), and 88% (February 2022) of sheep compared to the fecal DNA population estimates before the severe winter. Therefore, on average the Department's aerial surveys are detecting approximately 81% of the sheep in the herd, which is within the range of previous research on bighorn sheep detection probability with aerial surveys (Bodie et al. 1995, Blum et al. 2024, Ruhl et al. 2025). The most recent survey in February 2025 counted 80 sheep, therefore using the 81% correction, our current population estimate is 99 sheep.

This herd is vulnerable to impacts from periodic, severe winters that occur in the Teton Range. Therefore, conserving what remains of their limited winter habitat is vital to their survival. Maintaining movement paths for sheep to access mid-elevation habitats such as in Teton Canyon is also vitally important in the winter and spring when sheep are at their lowest body condition and at their highest risk of mortality. In several places in the DEIS and BE, it is mentioned that there are 54 acres of modeled high quality bighorn sheep habitat in South Bowl, which would be impacted by expansion. This is true, however, there are also larger areas of occupied habitat and a mineral lick located down drainage in Teton Canyon that have well-documented, year-round sheep use and would be indirectly impacted by threatening the bighorn sheep movement path through South Bowl. This is taken into account when the BE estimates that 1,270 acres that are currently occupied by the Targhee Bighorn Sheep Herd (WGFD 2019) would be directly or indirectly impacted by the South Bowl expansion (pg. 31). Although this is only 0.8% of the herd's occupied range, it includes important winter and spring habitat with well-documented sheep use as well as contains a mineral lick. If access to the mineral lick is severed, alternative access routes are unlikely given the unsuitable habitat to the south. We agree with the BE where it states, "the small size and isolated nature of the Teton Range bighorn sheep population means that access to suitable habitat during difficult winter months, as well as during the summer fat gain, is vital to ensure that the population can persist" (pg. 23) and "the proposed South Bowl expansion combined with the general trend of increasing recreation activity throughout the range of the Teton bighorn sheep herd has the potential to result in a cumulative loss of habitat significant enough to potentially threaten population viability of the herd" (pg. 31).

While bighorn sheep have been well-documented using Teton Canyon for year-round habitat, significant vegetation succession has decreased the quality of habitat in the lower part of the canyon near the Apostles Cliffs. The Department, in collaboration with CTNF, has planned, funded, and begun implementing habitat improvement efforts as part of the Teton Canyon Hazardous Fuels Reduction Project. This project includes prescribed fire and mechanical treatments to reduce fuels and improve big game habitat, much of which is within or adjacent to the proposed South Bowl expansion. This habitat restoration effort is a rare opportunity given the prevalence of Wilderness Area and other special management areas where such treatments are not possible, however it would be jeopardized by the South Bowl expansion. We agree with the BE where it states “the proposed expansion under Alternatives 2 and 4...would significantly reduce or even completely nullify these habitat improvements for bighorn sheep” (pg. 30).

The DEIS describes how each alternative would impact population viability of Region 4 sensitive species within the “Targhee Planning Area”. For example, on pages 306-307 in the DEIS, “...degradation of habitat in South Bowl and Teton Canyon due to the proposed development, combined with projected increases in recreation activity throughout the range of the Teton bighorn sheep herd, has the potential to substantially reduce access to adequate nutrition and protective habitat. As a result, this alternative has the potential to result in an overall decline in the population of the Teton or Targhee Herd. Although the Proposed Action would impact the Teton Range bighorn sheep, across the overall Targhee Planning Area (which contains multiple herds), the alternative *May Impact Individuals or Their Habitat but would Not Likely Contribute to a Trend Toward Federal Listing or Cause a Loss of Population Viability*”. It is our understanding through discussions with CTNF staff the “Targhee Planning Area” is the CTNF although it is not explicitly defined in the BE or the DEIS.

For bighorn sheep, the DEIS and BE use outdated information from 2016 and 2017 to describe other bighorn sheep herds on CTNF. The BE states that there are 5 bighorn sheep herds on CTNF (South Lemhi, South Beaverhead, and Lionhead (2 herds) in Idaho and Targhee Herd in Wyoming) and that there are a total of approximately 300 sheep (BE; page 19). However, according to the most recent Idaho Department of Fish and Game Bighorn Sheep Management Plan (May 2022) the population estimates have changed in the last 8-9 years. The Lionhead Herd is made up of two game management units, however, this area is not consistently occupied by sheep and a few individuals only occur on a transient/foraging basis from a neighboring herd in Montana (IDF&G 2022; H. Miyasaki *pers. comm.*). The BE appears to include this herd and a population estimate of 105 sheep as part of its population viability analysis for the Targhee Planning Area, however this herd entirely resides in Montana outside of CTNF and it should not be included. The BE describes population numbers for the South Lemhi Herd as 41 and the South Beaverhead Herd as 36, however, the more recent counts from IDF&G (2022) are 110 and 17, respectively. Furthermore, the BE considers the entire Targhee Herd as residing on CTNF when referencing impacts at the Targhee Planning Area scale. Many sheep from the Targhee herd primarily reside in Grand Teton National Park, which is not within the Targhee Planning Area. Therefore, the Targhee Planning Area has 3 bighorn sheep herds and realistically fewer than 200 sheep (South Lemhi Herd, 110; South Beaverhead Herd, 17; and Targhee Herd, approximately 50 on CTNF) versus the 300 stated in the BE.

In addition, it is important to note that there is no connectivity between the herds in the Targhee Planning Area. The Targhee Herd is one of the few native bighorn sheep herds in the western United States that has never been extirpated, reintroduced, or augmented via translocation. The herd is genetically unique due to this history and is genetically distinct from surrounding herds in Wyoming and Idaho, making it additionally valuable to the species as a whole (Kardos et al. 2010, TRBSWG 2020). The Department disagrees with the determination that expanding into South Bowl would not impact the population viability of bighorn sheep in the Targhee Planning Area. The cumulative impacts portion of the BE rightfully identified the potential for cumulative impacts, which includes South Bowl expansion, to threaten the population viability of the Targhee herd. Given the significant contribution of the Targhee herd to the overall population of bighorn sheep within the Targhee Planning Area and the isolated nature of sheep in the Targhee Planning Area, loss of Targhee sheep population viability equates to loss of population viability of sheep in the Targhee Planning Area.

The southern edge of the proposed Mono Trees expansion area does not appear to follow any topographical features. It includes a small portion of south-facing slopes in Teton Canyon above and to the west of the Apostles Cliffs. It is unclear why this area is included and we request that the proposed boundary be adjusted to follow the topographic ridgeline, generally matching the northern edge of the Teton Canyon Hazardous Fuels Treatment areas and also avoiding WGFD mule deer crucial winter range (BE; Figure 17). As proposed, this small portion of the Mono Trees expansion area would also impact bighorn sheep by allowing development and activity directly above bighorn sheep occupied habitat in the Apostles Cliffs and into known foraging areas west of the cliffs (WGFD observation of 6 bighorn rams in this area on May 1, 2025). In addition, if the Mono Trees expansion area is approved, we request that CTNF prohibit Grand Targhee from conducting avalanche control activities within their permit boundary that purposely initiate avalanches which run outside of the permit boundary (which has become current practice in South Bowl). Initiating avalanches along the south side of the proposed Mono Trees expansion area could cause direct mortality to bighorn sheep, mule deer, elk, moose, and other wildlife in Teton Canyon outside of the permit boundary.

Overall, the proposed expansion to South Bowl will be detrimental to the long-term persistence of the Targhee Bighorn Sheep Herd. The Department recommends avoiding expansion into South Bowl to minimize additional and unnecessary threats and promote long-term persistence of bighorn sheep in the Teton Range.

Wolverines – The Department's second major concern with the proposed expansion is the potential for impacts to wolverines. In Wyoming, wolverines are a federally protected species and Tier II Species of Greatest Conservation Need due primarily to low population size, unknown population trajectory, and habitat loss due to climate change and human development. Wolverines have been documented in the area around Grand Targhee and, as mentioned in the Biological Assessment (BA), there have been a number of research and monitoring efforts in the Tetons. The research efforts have included collection of telemetry data and observations in our Wildlife Observation System database, which we present in Appendix A. The Department is concerned the loss of habitat provided in the BA does not accurately represent the subsequent impacts to

wolverine given the low densities in which they persist and the importance of all currently suitable habitat near the project area. The results of a DNA analysis in 2023 confirmed a minimum population size of 11 individuals in Wyoming (Pilgrim and Schwartz 2023). A loss of any one individual is, thus, significant. The potential for impact on future population stability is larger if the individual impacted is a breeding female.

The three primary research efforts that have occurred near Grand Targhee Resort were from papers cited in the BA, specifically Copeland et al. (2007) and Heinemeyer et al. (2019), and from an additional report and paper (Inman et al. 2013). The report is provided in Appendix B. The Inman et al. (2013) effort resulted in predicted maternal habitat, which includes the South Bowl and Mono Trees expansion areas (Appendix A). In addition, six collared wolverines' home ranges tracked for the Inman et al. (2013) study overlap Grand Targhee and the proposed expansion areas, of which four were females. Similarly, Heinemeyer et al. (2019) predicted female wolverine habitat, which includes much of Teton Canyon and overlaps a significant portion of the proposed South Bowl and Mono Trees expansion areas. It should also be noted that female wolverines have smaller home ranges than males, approximately 303 km² (Inman et al. 2013), which alters the percentage of the home range removed in the BA and should be considered in future drafts of the EIS. The tracking data, regularity of wolverine observations and wolverine sign make clear that the greater Grand Targhee area has been used by multiple generations of wolverines in the past and would likely continue to support wolverine into the future. The tracking data also suggest avoidance of the current resort boundary, a behavior that would likely extend to the expansion areas if developed.

Denning habitat is referenced in the BE and DEIS and the CTNF has a wolverine denning habitat predictive model, which was used in the assessment to quantify potential impact of the proposed activities. The BA also references a suspected den site discovered approximately 0.5 mile east of the proposed South Bowl expansion area. Wolverines require deep, persistent snowpack and undisturbed terrain for successful reproduction, as females create both natal dens and maternal dens, often several per reproductive year, in snow caves or rocky crevices where young can safely develop. The construction of ski runs, lifts, and associated infrastructure would eliminate these essential microhabitat features, while the ongoing human activity and avalanche control measures would create persistent disturbance that could prevent successful breeding or direct mortality. We agree with the determination in the BA (page 58) that expansion to South Bowl in particular may affect, likely to adversely affect individual wolverines. As mentioned earlier in our comments, the loss of one individual would negatively impact the wolverine population in the Teton Range specifically and Wyoming.

Beyond the immediate footprint of development, the expansion would fragment the broader landscape connectivity that wolverines require to maintain viable populations. Maintaining genetic diversity is essential to regional wolverine populations, which is only accomplished through maintaining functional habitat including forest cover and lack of human disturbance (Day et al. 2024). These wide-ranging carnivores need extensive territory to find adequate prey and mates, often traveling hundreds of miles across mountainous terrain. The increased human presence, noise, and infrastructure associated with expanded ski area operations would create barriers to wolverine movement and potentially isolate populations on either side of the development. Given

wolverines' already precarious status and their extreme sensitivity to habitat fragmentation, we are concerned that the loss of South Bowl and Mono Trees would negatively impact the long-term persistence of wolverines in the region.

In addition to concerns over habitat loss, fragmentation, and increased human disturbance, the Department requests clarification on the wolverine-specific Conservation Measure in the BA. Measure 20 under Wildlife and Fish Project Design Criteria references buffers being placed around active den sites if discovered during construction and operation. The Department requests additional detail on how dens would be located—whether opportunistically or through systematic methods—and on the proposed buffer sizes. Effective protective buffers would likely need to be substantial, and we question the practicality of implementing them successfully.

Forest Raptors – The Department agrees with the assessment that the Mono Trees expansion will affect forest-nesting hawks and owls given the detections of various SGCN raptors. We continue to recommend that the survey effort conducted to date be fully justified, as the data are now five years old and are being used to inform decisions on alternative selection and impact analysis. We recommend the following:

- Update survey effort in the South Bowl and Mono Trees expansion areas.
- Assess differences between two survey periods for changes and update EIS and supporting documents to accurately reflect current impact potential.
- If expansion into South Bowl or Mono Trees occurs, conduct additional clearance surveys and apply protections as described to all documented raptor nests.

The Department supports and appreciates the Best Management Practices integrated into the project development if expansions occur.

Prevent Establishment and Spread of Noxious Weeds and Invasive Annual Grasses – The Department appreciates the focus on preventing the establishment and spread of noxious weeds and invasive annual grasses (IAGs). Noxious weeds and IAGs can cause significant harm to the ecosystem when introduced. Ground-disturbing activities can create an environment that facilitates establishment by unwanted plants. They significantly reduce the quality of wildlife habitat and their presence increases the probability of catastrophic wildfire. The potential economic impacts to the State of Wyoming are severe, and once these species become established, eradication is difficult and costly. Prevention of establishment remains the best way to keep Wyoming's habitats free of noxious weeds and IAGs.

The Noxious Weed Risk Assessment (Risk Assessment) is overall sufficient and should decrease the probability of noxious weed and IAGs becoming problematic. The Department recommends in addition to the commitments outlined in the Risk Assessment, that trails be surveyed every year for consistency with other locations in the Early Detection and Rapid Response approach outlined under criteria number 9(c) in section 2. Noxious Weeds and IAGs can establish and spread quickly and the potential for that to occur on trails is equal to that in the other areas surveyed annually.

Jay Pence
June 20, 2025
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Thank you for the opportunity to comment. If you have any questions or concerns please contact Ross Crandall, Habitat Protection Biologist, at (307) 367-5615.

Sincerely,



Doug Brimeyer
Deputy Director

DB/rc

cc: U.S. Fish and Wildlife Service
Chris Wichmann, Wyoming Department of Agriculture

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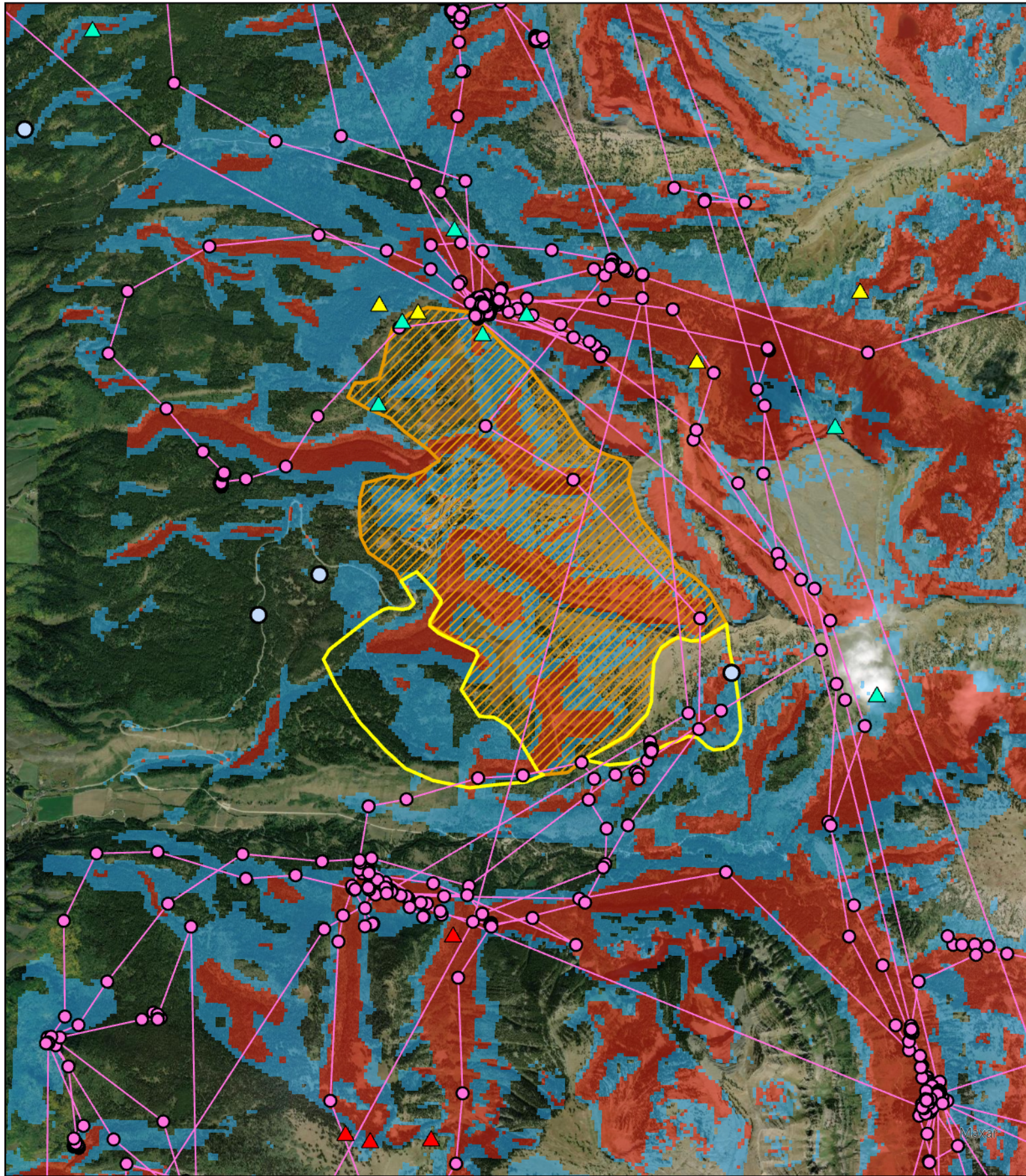
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Appendix A. Maps of wolverine habitat, home range estimates, observations, and collar locations relative to the proposed actions.



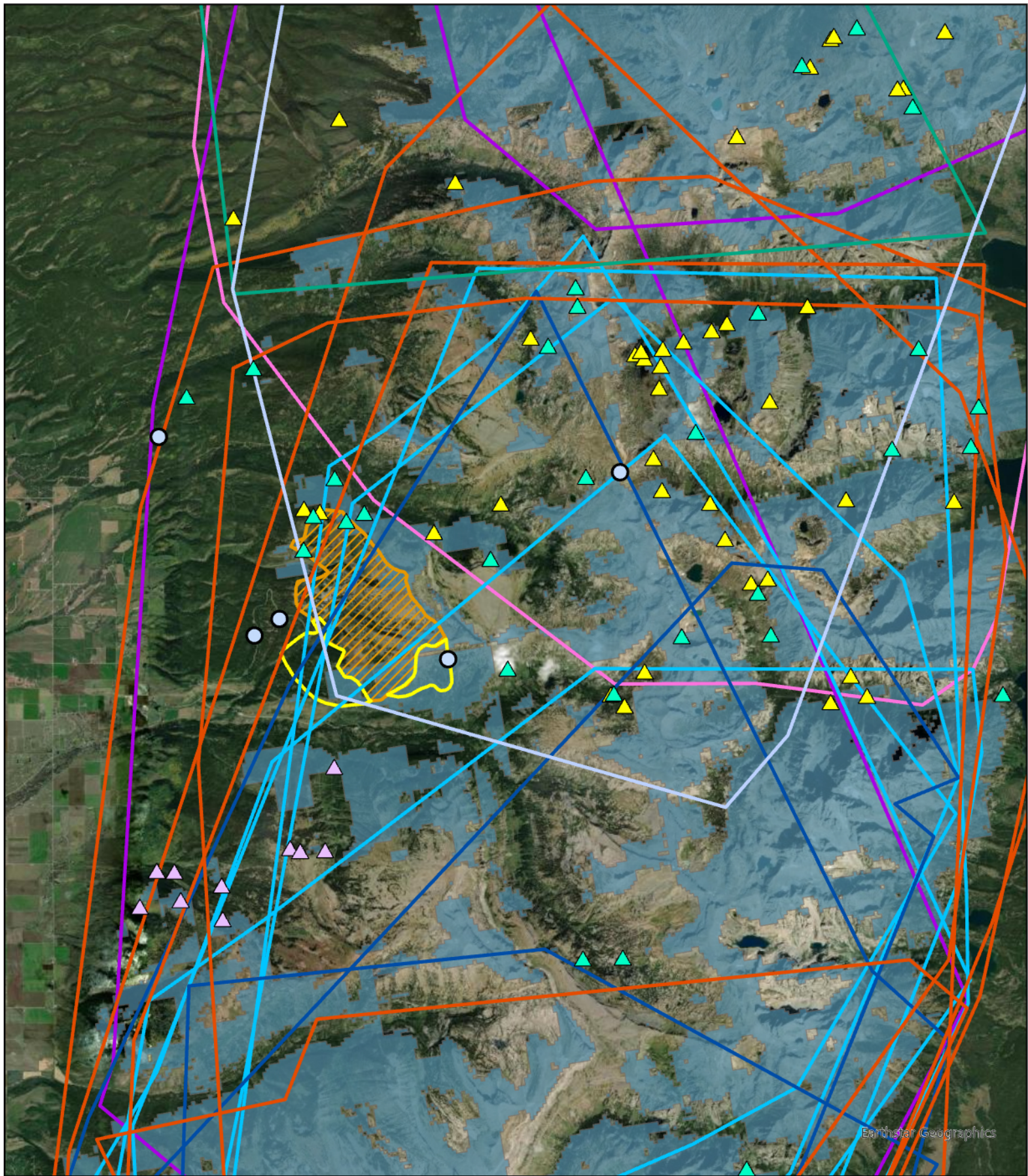
Legend

- | | | | |
|---|---|--|---|
| <p>● GPS-tagged wolverine movements (n=1) (2014-2015) (K. Heinemeyer)</p> <p>○ WGFD WOS confirmed wolverine records (2009-2025)</p> | <p>VHF-tagged wolverines (n=3) relocations, 1998-2000 (J. Copeland)</p> <p>▲ F402</p> <p>▲ F468</p> <p>▲ M399</p> | <p>Female wolverines predicted potential habitat (K. Heinemeyer et al. 2019)</p> <p>■ Moderate</p> <p>■ High</p> | <p>▨ Grand Targhee current boundary</p> <p>▭ Grand Targhee proposed expansion areas</p> |
|---|---|--|---|

0 0.5 1 Miles



Map produced by Wyoming Game and Fish Department, June 2025, with data from J. Copeland, K. Heinemeyer, and WGFD



Legend

- WGFD WOS confirmed wolverine records (2009-2025)
- Predicted maternal wolverine habitat (Inman et al. 2013)
- △ VHF-tagged wolverines (n=3) relocations, 1998-2000 (J. Copeland)
 - △ F402
 - △ F468
 - △ M399
- Wolverines annual 100% minimum convex polygons (n=7) (2001-2006) (Inman et al. 2013)
 - F401
 - F402
 - F404
 - F405
 - M301

- M304
- M561
- ▨ Grand Targhee current boundary
- Grand Targhee proposed expansion areas

0 1.5 3 Miles



Map produced by Wyoming Game and Fish Department, June 2025, with data from B. Inman, J. Copeland, and WGFD

Appendix B. Wolverine genetics report confirming a minimum population size of 11 individuals in Wyoming.



REPORT



Project: DNA Analysis of Wolverine (*Gulo gulo*) Survey Samples Submitted by Wyoming Department of Game and Fish 2021-2022; Individual and Sex ID

Date Issued: August 18, 2023

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REPORT



We tested 39 non-invasively collected samples identified as being from wolverine for individual and sex identification. We also tested DNA obtained from hair provided from a female captured wolverine (WY152305) from collaring efforts. These samples were analyzed using a panel of microsatellite loci and a sexing locus used previously in wolverine. Twenty-two of the 39 samples had sufficient DNA to produce an individual genotype (56%; Table 1). In addition, four samples had more than two alleles at multiple loci indicating more than one individual wolverine (“mixed individual”) and one sample had alleles both from wolverine and marten (“mixed with marten”). We obtained quality DNA from female WY152305 for analysis. Ten individuals were identified from the non-invasive survey samples (Table 1). Data from these 11 individuals as well as WY152305 were compared to the four wolverines identified from 2016 and 2017 multi-state wolverine survey samples, as well as other regional wolverines. The 10 individuals identified from non-invasive samples (six females and four males) and female WY152305 are all new individuals to the DNA database (Table 2).

Table 1. DNA individual and sex identification results from wolverine identified from samples submitted from WYGF 2021-2022 wolverine surveys.

Sample ID	Cell	Study Area	Lat	Long	Date Collected	Shipment	DNA Species ID	DNA Individual ID	DNA Sex ID	Recapture
C116.2021.12.08.V1.B2	116	Huckleberry Ridge	44.10373	-110.61491	12/8/2021	1	Wolverine	poor DNA	poor DNA	
C033.2021.12.06.V1.B3	33	Boulder Creek	43.15917	-109.90971	12/6/2021	1	Wolverine	WY22_Gulo-F1	Female	No
C032.2021.12.02.V1.B3	32	Kilgore Creek	43.08338	-110.53865	12/2/2021	1	Wolverine	poor DNA	poor DNA	
C161.2021.12.05.v1.B1	161	Blackwater Creek	44.38130	-109.76380	12/5/2021	2	Wolverine	poor DNA	poor DNA	
C161.2022.01.11.v2.B1	161	Blackwater Creek	44.38130	-109.76380	1/11/2022	2	Wolverine	poor DNA	poor DNA	
C161.2022.01.11.v2.B2	161	Blackwater Creek	44.38130	-109.76380	1/11/2022	2	Wolverine	poor DNA	poor DNA	
C087.2021.12.09.v1.B1	87	Triple East Fork	43.76470	-109.30214	12/9/2021	2	Wolverine	poor DNA	poor DNA	
C087.2021.12.09.v1.B3	87	Triple East Fork	43.76470	-109.30214	12/9/2021	2	Wolverine	WY22_Gulo-M2	Male	No
C087.2021.12.09.v1.B4	87	Triple East Fork	43.76470	-109.30214	12/9/2021	2	Wolverine	WY22_Gulo-M2	Male	No
C267.2022.01.12.v2.B1	267	Sheepherder Lake	44.96702	-109.51216	1/12/2022	2	Wolverine	WY22_Gulo-F3	Female	No
C267.2022.01.12.v2.B3	267	Sheepherder Lake	44.96702	-109.51216	1/12/2022	2	Wolverine	WY22_Gulo-F3	Female	No
C267.2022.01.12.v2.B4	267	Sheepherder Lake	44.96702	-109.51216	1/12/2022	2	Wolverine	WY22_Gulo-F3	Female	No
C116.2022.01.20.v2.B1	116	Huckleberry Ridge	44.10373	-110.61491	1/20/2022	3	Wolverine	multiple individuals		
C116.2022.01.20.v2.B2	116	Huckleberry Ridge	44.10373	-110.61491	1/20/2022	3	Wolverine	multiple individuals		
C116.2022.01.20.v2.B3	116	Huckleberry Ridge	44.10373	-110.61491	1/20/2022	3	Wolverine	multiple individuals		
C116.2022.01.20.v2.B4	116	Huckleberry Ridge	44.10373	-110.61491	1/20/2022	3	Wolverine	multiple individuals		
C043.2022.01.19.v2.B1	43	Slide Creek	43.28251	-109.80036	1/19/2022	3	Wolverine	WY22_Gulo-M4	Male	No
C043.2022.01.19.v2.B3	43	Slide Creek	43.28251	-109.80036	1/19/2022	3	Wolverine	poor DNA	poor DNA	
C085.2022.02.03.Scot1	85	Five Pockets	43.76525	-109.66595	2/3/2022	4	Wolverine	poor DNA	poor DNA	
C085.2022.02.03.Scot2	85	Five Pockets	43.76141	-109.66586	2/3/2022	4	Wolverine	WY22_Gulo-F5	Female	No
C033.2022.02.16.v3.B1	33	Boulder Creek	43.15917	-109.90971	2/16/2022	5	Wolverine	WY22_Gulo-M4	Male	No



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C116.2022.02.22.v3.B1	116	Huckleberry Ridge	44.10373	-110.61491	2/22/2022	5	Wolverine	poor DNA	poor DNA	
C043.2022.02.17.v3.B1	43	Slide Creek	43.28251	-109.80036	2/17/2022	5	Wolverine	WY22_Gulo-M4	Male	No
C043.2022.02.17.v3.B3	43	Slide Creek	43.28251	-109.80036	2/17/2022	5	Wolverine	WY22_Gulo-M4	Male	No
C161.2022.02.15.v3.B1	161	Blackwater Creek	44.38130	-109.76380	2/15/2022	6	Wolverine	WY22_Gulo-F6	Female	No
C161.2022.02.15.v3.B3	161	Blackwater Creek	44.38130	-109.76380	2/15/2022	6	Wolverine	WY22_Gulo-F6	Female	No
C101.2022.03.03.v3.B1	101	Divide Lake	43.93361	-110.24067	3/3/2022	6	Wolverine	poor DNA	poor DNA	
C101.2022.03.03.v3.B4	101	Divide Lake	43.93361	-110.24067	3/3/2022	6	Wolverine	WY22_Gulo-M7	Male	No
C245.2022.04.06.pull.B1	245	Pilot Creek	44.94605	-109.90605	4/6/2022	7	Wolverine	WY22_Gulo-M8	Male	No
C245.2022.04.06.pull.B3	245	Pilot Creek	44.94605	-109.90605	4/6/2022	7	Wolverine	mixed with marten		
C161.2022.04.07.pull.B1	161	Blackwater Creek	44.38130	-109.76380	4/7/2022	7	Wolverine	WY22_Gulo-F6	Female	No
C161.2022.04.07.pull.B3	161	Blackwater Creek	44.38130	-109.76380	4/7/2022	7	Wolverine	WY22_Gulo-F6	Female	No
C085.2022.04.15.pull.B1	85	5 Pockets	43.80013	-109.70362	4/15/2022	8	Wolverine	WY22_Gulo-F9	Female	No
C085.2022.04.15.pull.B2	85	5 Pockets	43.80013	-109.70362	4/15/2022	8	Wolverine	WY22_Gulo-F9	Female	No
C116.2022.04.07.v5.B1	116	Huckleberry Ridge	44.10373	-110.61491	4/7/2022	8	Wolverine	WY22_Gulo-F10	Female	No
C116.2022.04.07.v5.B3	116	Huckleberry Ridge	44.10373	-110.61491	4/7/2022	8	Wolverine	WY22_Gulo-F10	Female	No
C116.2022.04.07.v5.B4	116	Huckleberry Ridge	44.10373	-110.61491	4/7/2022	8	Wolverine	poor DNA	poor DNA	
C033.2022.03.18.SCAT1	33	Boulder Creek	43.16381	-109.90874	3/18/2022	8	Wolverine	WY22_Gulo-M4	Male	No
C033.2022.03.18.SCAT2	33	Boulder Creek	43.15917	-109.90971	3/18/2022	8	Wolverine	poor DNA	poor DNA	

Table 2. DNA individual and sex identification results from a female wolverine capture by WYGF 2023.

Sample Type	Lab-ID	Location	Lat	Long	Date Collected	Collector	Sex	DNA Individual ID	Recapture
Hair from Capture	WY-152305	Boulder Basin	44.11879	-109.5674	3/11/2023	Heather O'Brien	Female	WY-152305	No

Please let us know if you have any questions; we look forward to working with you in the future.