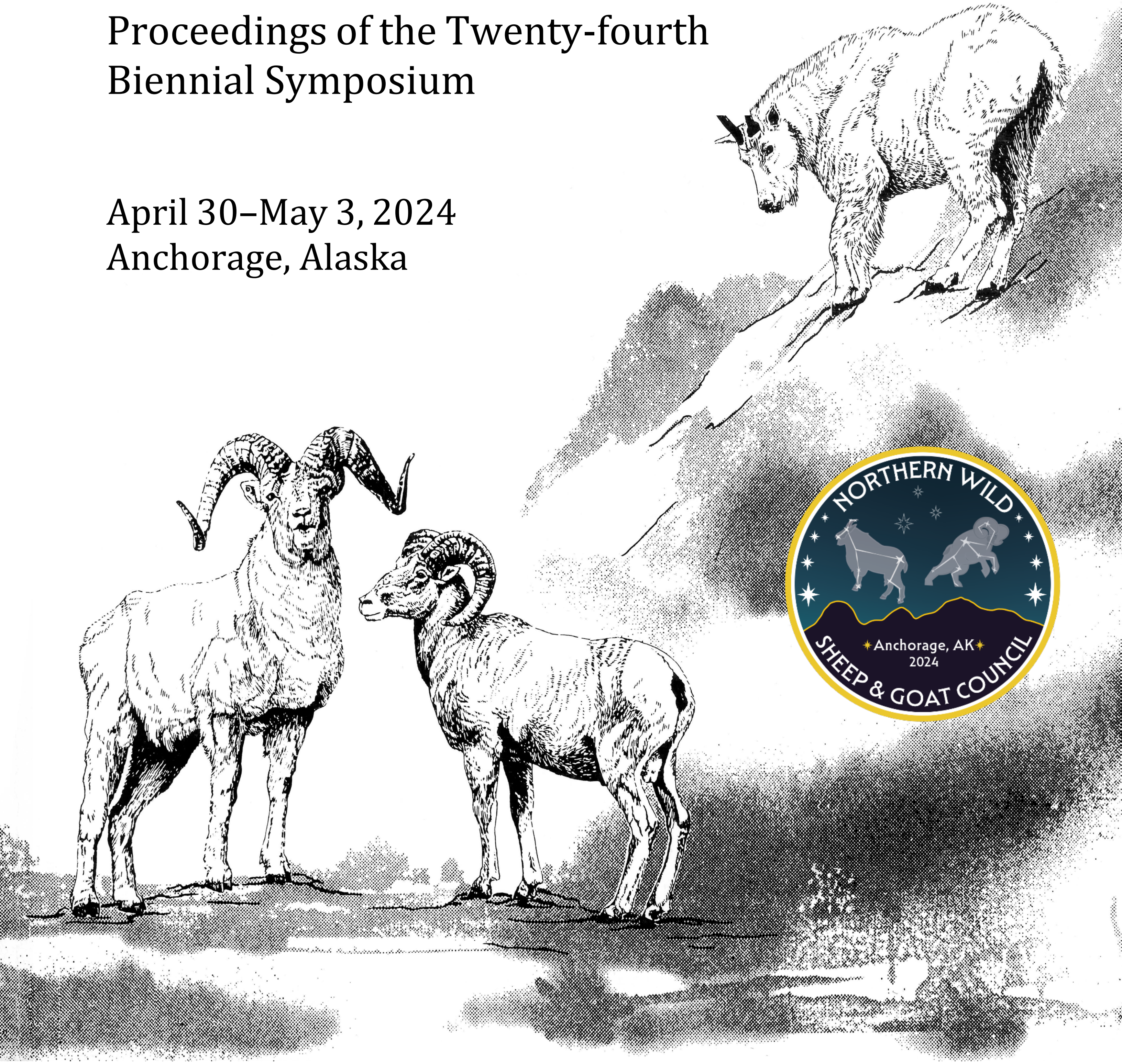
Northern Wild Sheep and Goat Council

Proceedings of the Twenty-fourth Biennial Symposium

April 30–May 3, 2024
Anchorage, Alaska



Northern Wild Sheep and Goat Council

PROCEEDINGS OF THE 24TH BIENNIAL SYMPOSIUM

APRIL 30–MAY 2, 2024
ANCHORAGE, ALASKA

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For Hard Copies contact:
Northern Wild Sheep and Goat Council
c/o Kevin Hurley, NWSGC Executive Director
412 Pronghorn Trail Bozeman, MT 59718 USA
(406) 404-8750
khurley@wildsheepfoundation.org

The Northern Wild Sheep and Goat Council is a non-profit professional organization developed in 1978 from the Northern Wild Sheep Council. Proceedings may also be downloaded from the NWSGC website. *www.nwsgc.org*

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Northern Wild Sheep and Goat Council

We would like to thank our many sponsors for their generous contributions and support for this symposium!

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NORTHERN WILD SHEEP AND GOAT COUNCIL SYMPOSIA

Date	Symposium	Location	Symposium Coordinator/Chair	Proceedings Editor(s)	NWSGC Executive Director
May 26–28, 1970	NWSC 1	Williams Lake, BC	Harold Mitchell		
April 14–15, 1971	NAWSC 1	Fort Collins, CO	Eugene Decker/Wayne Sandfort	Eugene Decker	
April 11–13, 1972	NWSC 2	Hinton, AB	E.G. Scheffler		
April 23–25, 1974	NWSC 3	Great Falls, MT	Kerry Constan/James Mitchell		
Feb. 10–12, 1976	NWSC 4	Jackson, WY	E. Tom Thorne		
April 2–4, 1978	NWSGC 1	Penticton, BC	Daryll Hebert/M. Nation	Daryll Hebert/Michael Nation	
April 23–25, 1980	NWSGC 2	Salmon, ID	Bill Hickey		
March 17–19, 1982	NWSGC 3	Fort Collins, CO	Gene Schoonveld	James Bailey/Gene Schooneveld	
Apr. 30–May 3, 1984	NWSGC 4	Whitehorse, YK	Manfred Hoefs	Manfred Hoefs	Wayne Heimer
April 14–17, 1986	NWSGC 5	Missoula, MT	Jerry Brown	Gayle Joslin	Wayne Heimer
April 11–15, 1988	NWSGC 6	Banff, AB	Bill Wishart	Bill Samuel	Wayne Heimer
May 14–18, 1990	NWSGC 7	Clarkston, WA	Lloyd Oldenburg	James Bailey	Wayne Heimer
Apr. 27–May 1, 1992	NWSGC 8	Cody, WY	Kevin Hurley	John Emmerich/Bill Hepworth	Wayne Heimer
May 2–6, 1994	NWSGC 9	Cranbrook, BC	Anna Fontana	Margo Pybus/Bill Wishart	Kevin Hurley
Apr. 30–May 3, 1996	NWSGC 10	Silverthorne, CO	Dale Reed	Kevin Hurley/Dale Reed/Nancy Wild (compilers)	Kevin Hurley
April 16–20, 1998	NWSGC 11	Whitefish, MT	John McCarthy	John McCarthy/Richard Harris/Fay Moore (compilers)	Kevin Hurley
May 31–June 4, 2000	NWSGC 12	Whitehorse, YK	Jean Carey	Jean Carey	Kevin Hurley
April 23–27, 2002	NWSGC 13	Rapid City, SD	Ted Benzon	Gary Brundige	Kevin Hurley
May 15–22, 2004	NWSGC 14	Coastal Alaska	Wayne Heimer	Wayne Heimer/Dale Toweill/Kevin Hurley	Kevin Hurley
April 2–6, 2006	NWSGC 15	Kananaskis, AB	Jon Jorgenson	Margo Pybus/Bill Wishart	Kevin Hurley
April 27–May 1, 2008	NWSGC 16	Midway, UT	Anis Aoude	Tom Smith	Kevin Hurley
June 7–11, 2010	NWSGC 17	Hood River, OR	Craig Foster	Vern Bleich	Kevin Hurley
March 12–15, 2012	NWSGC 18	Kamloops, BC	Steve Gordon/Steve Wilson/ Mari Wood	Steve Wilson/Mari Wood	Kevin Hurley

Northern Wild Sheep and Goat Council

NORTHERN WILD SHEEP AND GOAT COUNCIL SYMPOSIA (Cont'd)

Date	Symposium	Location	Symposium Coordinator/Chair	Proceedings Editor(s)	NWSGC Executive Director
June 2–5, 2014	NWSGC 19	Fort Collins, CO	Janet George	Bruce Watkins, Ricki Watkins	Kevin Hurley
May 9–12, 2016	NWSGC 20	Moscow, ID Pullman, WA	Hollie Miyasaki/Rich Harris/ David Smith	Rich Harris	Kevin Hurley
May 21–24, 2018	NWSGC 21	Whitefish, MT	Brent Lonner/Bruce Sterling/ Caryn Dearing	Justin Gude	Kevin Hurley
November 3–5, 2020	NWSGC 22	Alberta (virtual)	Beth MacCallum	Kathreen Ruckstuhl	Kevin Hurley
April 4–7, 2022	NWSGC 23	Jackson, WY	Doug McWhirter	Doug McWhirter/Aly Courtemanch/Peach Van Wick	Kevin Hurley
April 29–May 2, 2024	NWSGC 24	Anchorage, AK	Todd Rinaldi	Todd Rinaldi	Kevin Hurley

Northern Wild Sheep and Goat Council

GUIDELINES OF THE NORTHERN WILD SHEEP AND GOAT COUNCIL

The purpose of the Northern Wild Sheep and Goat Council is to foster wise management and conservation of northern wild sheep and goat populations and their habitats.

This purpose will be achieved by:

1) Providing for timely exchange of research and management information;
2) Promoting high standards in research and management; and
3) Providing professional advice on issues involving wild sheep and goat conservation and management.

I. The membership shall include professional research and management biologists and others active in the conservation of wild sheep and goats. Membership in the Council will be achieved either by registering at, or purchasing proceedings of, the biennial conference. Only members may vote at the biennial meeting.

II. The affairs of the Council will be conducted by an Executive Committee consisting of: three elected members from Canada; three elected members from the United States; one ad hoc member from the state, province, or territory hosting the biennial meeting; and the past chairperson of the Executive Committee. The Executive Committee elects its chairperson.

III. Members of the Council will be nominated and elected to the executive committee at the biennial meeting. Executive Committee members, excluding the ad hoc member, will serve for four years, with alternating election of two persons and one person of each country, respectively. The ad hoc member will only serve for two years.

The biennial meeting of members of the Council shall include a symposium and business meeting. The location of the biennial meeting shall rotate among the members' provinces, territories and states. Members in the host state, province or territory will plan, publicize and conduct the symposium and meeting; will handle its financial matters; and will prepare and distribute the proceedings of the symposium.

The symposium may include presentations, panel discussions, poster sessions, and field trips related to research and management of wild sheep, mountain goats, and related species. Should any member's proposal for presenting a paper at the symposium be rejected by members of the host province, territory or state, the rejected member may appeal to the Council's executive committee. Subsequently, the committee will make its recommendations to the members of the host state, territory or province, for a final decision.

The symposium proceedings shall be numbered with 1978 being No. 1, 1980 being No. 2, etc. The members in the province, territory or state hosting the biennial meeting shall select the editor(s) of the proceedings. Responsibility for quality of the proceedings shall rest with the editor(s). The editors shall strive for uniformity of manuscript style and printing, both within and among proceedings. The proceedings shall include edited papers from presentations, panel discussions or posters given at the symposium. Full papers will be emphasized in the proceedings. The editor will set a deadline for submission of manuscripts.

Members of the host province, territory, or state shall distribute copies of the proceedings to members and other purchasers. In addition, funds will be solicited for distributing a copy to each major wildlife library within the Council's states, provinces, and territories.

IV. Resolutions on issues involving conservation and management of wild sheep and goats will be received by the chairperson of the Executive Committee before the biennial meeting. The Executive Committee will review all resolutions and present them with recommendations at the business meeting. Resolutions will be adopted by a plurality vote. The Executive Committee may also adopt resolutions on behalf of the Council between biennial meetings.

V. Changes in these guidelines may be accomplished by plurality vote at the biennial meeting.

Northern Wild Sheep and Goat Council

FOREWORD

The papers and abstracts included in these proceedings were presented during the 24th Biennial Symposium of the Northern Wild Sheep and Goat Council, held April 30–May 3, 2024, in Anchorage, Alaska, at the Hotel Captain Cook. The theme was "***Recovering Populations in a Changing Environment***". The myriad challenges faced by mountain sheep and mountain goats in Alaska and other northern jurisdictions were skillfully addressed by our keynote speakers, technical presenters, and panelists. To our more than 40 speakers, panelists, and poster presenters, thank you each for sharing your experiences, your data, your perspectives, and your recommendations for enhancing the status and management of mountain sheep and mountain goats in Alaska and beyond.

Special thanks to Chair Todd Rinaldi of the Alaska Department of Fish and Game (ADF&G) for leading a dedicated Alaska Symposium Planning Group, largely composed of current and former ADF&G personnel, supplemented by volunteers from the University of Alaska, the National Park Service, and the Alaska Chapter of the Wild Sheep Foundation. Thanks to all the Alaska Planning Group members who put so much effort into organizing a timely, focused agenda, with a diverse spectrum of speakers and technical experts. Logistically and topically, the field trips were not only enjoyable but also allowed many attendees the chance to experience some of Alaska's magic landscapes and wildlife, some for the first time. We also thank Denali National Park for hosting a post-symposium field trip providing attendees with an opportunity to experience this iconic region.

Thanks to Manny Eicholz of ADF&G for handling a complicated registration process and the fiscal components of such a large gathering. Thanks to Heidi Hatcher and Roy Churchwell of ADF&G for managing the abstract submission process and arranging the final symposium agenda. Appreciation also to session moderators who worked skillfully to keep the presenters and sessions on time!

Heartfelt thanks are extended to the sponsors who helped make this symposium happen! Please take note of all the symposium sponsors displayed on page ii of these Proceedings. We simply could not hold these biennial symposia without the strong support of many diverse, dedicated individuals, organizations, agencies, and supporters of mountain sheep and mountain goat conservation.

These Proceedings were edited by Todd Rinaldi. Peer-reviewers included Julie Cunningham, Rich Harris, and Roy Churchwell. Suggested editorial comments were provided to each senior author; senior authors had opportunity(ies) to accept or reject suggested edits, prior to submission of their final manuscripts. Formatted page proofs were forwarded to respective senior authors prior to inclusion into the final proceedings. Final content, particularly verification of literature citations, is the responsibility of the authors.

While NWSGC strives for professional, scientific presentations at our symposia, followed up with quality manuscripts for our proceedings, NWSGC Guidelines do not rigidly specify format, minimum data requirements, or thresholds of statistical analysis for subsequently included manuscripts. Thus, NWSGC Proceedings may contain manuscripts that are more opinion-based than data- or fact-based; critical evaluation of information presented in these proceedings is the responsibility of subsequent readers.

Kevin Hurley
NWSGC (volunteer) Executive Director
March 16, 2026

IN MEMORIAM

Dr. James A. Bailey

May 14, 1934—May 30, 2023

Jim Bailey passed away at this home in Montana on May 30, 2023.
A longtime contributor, advocate, and lifelong member of the Northern Wild Sheep and Goat Council, Dr. Bailey served as instructor in wildlife management at the University of Montana, 1968-69, and landed an instructorship at Colorado State University in 1969. At Colorado State, he taught Principles of Wildlife Management, Wildlife Nutrition, Big Game Management, and Population Dynamics, among other courses. He was senior editor, assembling the book, Readings in Wildlife Conservation for The Wildlife Society in 1974, and published Principles of Wildlife Management with John Wiley & Sons in 1984.

Dr. Bailey mentored several graduate students at Colorado State, concentrating research on wild ungulates, especially bighorn sheep and mountain goats. He retired from Colorado State as a full professor in 1990.
He was a member of the Colorado and New Mexico chapters of The Wildlife Society, the Gallatin Wildlife Association, a Life Member of the Rocky Mountain Bighorn Society, the Desert Bighorn Council and the Northern Wild Sheep and Goat Council.

Jim's last great act for wildlife conservation was his tireless advocacy for wild bison. Dr. Bailey's consistent and impassioned message to his fellow wildlifers was "We can do better". Thank you, Dr. Bailey, for issuing this worthwhile challenge.

James Russell Allen

June 13, 1952—June 13, 2023

James "Jim" Russell Allen passed away peacefully on June 13, 2023.
James began his advanced wildlife education at Vermilion (Lakeland) College earning a Fish and Wildlife Technician Diploma and ended many years later with a Master's Degree in Environmental Sciences from the University of Alberta. He worked for 43 years as a wildlife biologist and wildlife manager for the Alberta government at Red Deer, Drumheller, Rocky Mountain House, Edson, Edmonton and ended his career back in Rocky Mountain House where he retired.

He served as Head of Game Management and Priority Species Section for the Alberta government. He was a long-term member of the Northern Wild Sheep and Goat Council as well as The Wildlife Society, serving on the board of directors for both the Canadian Section and the Alberta Chapter, also serving a term as President of the Alberta Chapter. He also worked with many non-government wildlife organizations like the Alberta Trapper's Association, Alberta Fish & Game Association, the Wild Sheep Foundation, Alberta Professional Outfitters Association, and many others. James was an avid hunter and fisherman and especially loved horse trips to the mountains and primitive weapons hunts.

Kevin Hurley and many NWSGC folks knew and worked with Jim Allen for many years, on a variety of ungulate management issues and strategies. Most notably, Jim volunteered to be on the WAFWA Wild Sheep Working Group's initial effort in 2007 to develop the first iteration of WAFWA's 'Recommendations for Domestic Sheep and Goat Management in Wild Sheep Habitat"; this document was revised in 2010, again in 2012, and is undergoing update/revision again in 2024. "Jim was a very capable biologist, a solid resource to turn to for practical advice, and he was a good man. The wild sheep and goat world misses a guy like Jim Allen."

Northern Wild Sheep and Goat Council

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Northern Wild Sheep & Goat Council
Anchorage, AK
2024

DISEASE ECOLOGY

Evaluation of Long-Term Patterns of Mycoplasma Ovipneumoniae Carriage in Bighorn Sheep and the Implications for Test and Remove Protocols

BRITTANY L. WAGLER, *University of Wyoming, Laramie, WY, 82071, USA; bwagler@uwyo.edu*
RACHEL A. SMILEY, *University of Wyoming, Laramie, WY, 82071, USA*
JACK N. GAVIN, *University of Wyoming, Laramie, WY, 82071, USA*
TONY W. MONG, *Wyoming Game and Fish Department, Cody, WY, 82001, USA*
COREY CLASS, *Wyoming Game and Fish Department, Cody, WY, 82001, USA*
ALYSON B. COURTEMANCH, *Wyoming Game and Fish Department, Jackson, WY, 82006, USA*
DOUG MCWHIRTER, *Wyoming Game and Fish Department, Jackson, WY, 82006, USA*
CHEYENNE STWEART, *Wyoming Game and Fish Department, Jackson, WY, 82006, USA*
DARYL LUTZ, *Wyoming Game and Fish Department, Lander, WY, 82520, USA*
ZACH GREGORY, *Wyoming Game and Fish Department, Lander, WY, 82520, USA*
PATRICK HNILICKA, *U.S. Fish and Wildlife Service, Lander, WY, 82520, USA*
ARTHUR LAWSON, *Shoshone and Arapahoe Fish and Game Department, Fort Washakie, WY, 82514, USA*
DEAN CLAUSE, *Wyoming Game and Fish Department, Pinedale, WY, 82941, USA*
BRANDON M. SCURLOCK, *Wyoming Game and Fish Department, Pinedale, WY, 82941, USA*
RUSTY C. KAISER, *U.S. Forest Service, Pinedale, WY, 82941, USA*
WILLIAM H. EDWARDS, *Wyoming Game and Fish Department, Laramie, WY, 82071, USA*
JESSICA E. JENNINGS-GAINES, *Wyoming Game and Fish Department, Laramie, WY, 82071, USA*
JENNIFER L. MALMBERG, *University of Wyoming, Laramie, WY, 82071, USA*
KEVIN L. MONTEITH, University of Wyoming, Laramie, WY, 82071, USA

ABSTRACT: New management strategies for bighorn sheep (*Ovis canadensis*) have eradicated or lowered the prevalence of *Mycoplasma ovipneumoniae* (Mo) in some populations suffering from pneumonia, which subsequently increased recruitment of young. Though test and removal may be a promising tool to mitigate disease, the long-term patterns of Mo carriage and what variables affect the ability to identify chronically infected individuals remain unknown. Further, the criteria for removal and seasonal timing of testing vary across agencies and populations, which could influence the success of test and removals. Using 4 populations of bighorn sheep in Northwest Wyoming, we evaluated long-term patterns of Mo carriage and how age and the season of testing influences the probability of testing positive for Mo, remaining positive, and detecting chronic carriers. The probability of testing positive for Mo was higher for both younger and older animals compared with mid-aged animals. Further, animals were more likely to test positive for Mo in March than in December. Given the higher probability of testing positive in March, animals were more likely to be identified as chronic carriers if testing only occurred in March. Using 1 positive test as removal criteria increased the percentage of animals removed and increased the percentage of removals that were not chronic carriers compared with criteria using 2 positive tests. Timing and repetition of testing affects the probability of identifying chronic carriers and thus, this work will assist in creating targeted test and remove protocols to match specific population needs and management objectives.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24:1–2; 2024

KEYWORDS: bighorn sheep (*Ovis canadensis*), chronic carriers, disease carriage, intermittent carrier*, Mycoplasma ovipneumoniae*, pneumonia, test and cull, Wyoming. pneumonia, respiratory disease, selective culling, wildlife disease.

Optimizing Mycoplasma Ovipneumoniae "Test and Remove" Management to Restore Bighorn Sheep Populations in Idaho, Oregon, and Washington

FRANCES CASSIRER, *Idaho Dept. of Fish and Game, Lewiston, ID, 83501, USA; frances.cassirer@idfg.idaho.gov*
JANA ASHLING, *Idaho Dept. of Fish and Game, Lewiston, ID, 83501, USA*
HOLLIE MIYASAKI, *Idaho Dept. of Fish and Game, Idaho Falls, ID, 83401, USA*
WILLIAM MOORE, *Washington Dept. of Fish and Wildlife, Ellensburg, WA, 98926, USA*
DENNIS NEWMAN, *Idaho Dept. of Fish and Game, Salmon, ID, 83467, USA*
SCOTT D. PECKHAM, *Peckham Engineering, Wasilla, AK, 99654, USA*
BRIAN RATLIFF, *Oregon Dept. of Fish and Wildlife, Baker City, OR, 97814, USA*
ERIN WAMPOLE, *Washington Dept. of Fish and Wildlife, Ellensburg, WA, 98926, USA*
BRENT WOLF, *Oregon Dept. of Fish and Wildlife, Enterprise, OR, 97828, USA*

ABSTRACT: Management of respiratory disease is an important component of recovering and maintaining resilient wild sheep populations. The pathogen *Mycoplasma ovipneumoniae* is the agent responsible for initiating most pneumonia outbreaks in wild sheep and persistence of this bacterium can have long-term negative effects on recruitment and population recovery. We initiated a multi-jurisdictional adaptive management project in 2020 to investigate and improve selective removal methods for clearing *M. ovipneumoniae* from 7 populations in Idaho, Oregon, and Washington ranging in size from less than 100 to over 500 sheep. We conducted over 600 captures in these populations, collected health samples, and deployed GPS and VHF collars. Here we report on the history of disease, current *M. ovipneumoniae* infection and exposure prevalence, strain-typing, demographics, mortality investigations, and management actions taken to date. We describe how we are leveraging the range in population sizes, ecology, and health characteristics to identify factors that might be associated with the effectiveness of "test and remove" management for improving health of wild sheep populations.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24:3; 2024

KEYWORDS: bighorn sheep, chronic carriers, disease management, Idaho, infection prevalence, GPS, multi-state collaboration, *Mycoplasma ovipneumoniae*, Oregon, test and remove, Washington.

Using Social Grouping and Population Substructure to Improve Test and Remove Management of Bighorn Sheep

SCOTT D. PECKHAM, *Peckham Engineering, Wasilla, AK, 99654; scott.peckham78@gmail.com*
FRANCES CASSIRER, *Idaho Dept. of Fish and Game, Lewiston, ID, 83501, USA*
HOLLIE MIYASAKI, *Idaho Dept. of Fish and Game, Idaho Falls, ID, 83401, USA*
WILLIAM MOORE, *Washington Dept. of Fish and Wildlife, Ellensburg, WA, 98926, USA*
BRIAN RATLIFF, *Oregon Dept. of Fish and Wildlife, Baker City, OR, 97814, USA*
ERIN WAMPOLE, *Washington Dept. of Fish and Wildlife, Ellensburg, WA, 98926, USA*

ABSTRACT: Bighorn sheep (*Ovis canadensis*) have been widely impacted by *Mycoplasma ovipneumoniae* (*Movi*) and associated polymicrobial pneumonia, causing all-age die-offs, limiting lamb recruitment, and often resulting in long-term population declines or even local extirpations. Due to *Movi's* ability to persist in populations for decades, management options to restore infected bighorn sheep herds have been extremely limited. Recently, the "test and remove" strategy has been successfully employed mostly in small free-ranging bighorn herds in the U.S. and Canada. However, test and remove requires extensive capture and handling of bighorn over multiple years and its applicability and efficacy in larger herds has received less attention. Building on previous success, a collaborative project was initiated in late 2020 to apply test and remove management in seven populations in Idaho, Oregon, and Washington in effort to restore populations, assess factors that may impact the efficacy of test and remove, and apply an adaptive management strategy to facilitate clearance of *Movi.* Here we analyze social behavior of more than 300 GPS-collared females within populations and report preliminary results in the context of *Movi* infection and exposure. Populations ranged from approximately 60 to 550 in size and were both native and reintroduced. Population substructure was identified by modeling the overlap of home range between each individual female within a population as a directed social network and applying a hierarchical clustering method to estimate social groups. Study populations ranged from no substructure (one social group) to nine. Health testing results differed among populations and observed prevalence of *Movi* infection in adults ranged from 0–25%. We explored differences in infection and exposure within populations to determine whether we could focus on specific subpopulations with higher rates of infection or exposure in larger populations to help improve future capture efforts and facilitate clearance of *Movi*. We found that focusing on subpopulations with higher antibody prevalence or lower lamb survival increased the likelihood of detecting *Movi* carriers.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24:4; 2024

KEYWORDS: bighorn sheep (*Ovis canadensis*), fitness, gene flow, metapopulation connectivity, *Mycoplasma ovipneumoniae*, Oregon, pathogen transmission, metapopulation, "test and remove", Washington.

Exploring the Geneflow-Disease Trade-off within Bighorn Sheep Metapopulations

LAUREN E. RICCI, *Utah State University, Logan, UT, 84322, USA*; lauren.ricci@usu.edu
MIKE COX, *Nevada Department of Wildlife, Reno, NV, 89511, USA*
KEZIA R. MANLOVE, *Utah State University, Logan, UT, 84322, USA*

ABSTRACT: Metapopulation connectivity is generally thought to increase population growth due to the beneficial effects of gene-flow on fitness. However, when disease is present in a system, the connectivity that leads to gene-flow can also facilitate disease transmission, potentially muting connectivity's predicted benefits for population growth. To explore trade-offs between gene-flow and pathogen transmission in real-world bighorn sheep (*Ovis canadensis*) metapopulations, we incorporated temporally dynamic movement and connectivity rates into a model of metapopulation growth, gene- flow, and pathogen transmission dynamics. We parameterized simulations with movement and connectivity parameters specific to 3 environmentally distinct ecoregions inhabited by bighorn sheep within the State of Nevada. The timing and duration of mating season, and the resulting seasonal connectivity structure, varied between ecoregions due to differing environmental constraints. This led to different outcomes to the disease-gene-flow trade-off depending on the timing and intensity of connectivity. These findings highlight the need for detailed, system-specific analyses of movement and connectivity when considering optimal management in the face of competing pathogen and gene-flow mediated risks.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24:5; 2024

KEYWORDS: bighorn sheep (*Ovis canadensis*), connectivity rates, disease, fitness, gene flow, metapopulation growth, pathogen transmission.

Rocky Mountain Bighorn Sheep Microbiome and Associations with Host Health and Disease States

PATRICIA C. BREWSTER, *Department of Microbiology and Cell Biology, Montana State University, Bozeman MT, 59717, USA; Working Dogs for Conservation, Missoula MT, 59802, USA; patriciabrewster@montana.edu*

MICHELE LOVARA, *Department of Natural Resource Management, South Dakota State University, Brookings SD, 57007, USA; Working Dogs for Conservation, Missoula, MT, 59802, USA*

TODD NORDEEN, *Nebraska Game and Parks Commission, Alliance, NE, 69301, USA*

JEFF TILLERY, *Department of Natural Resource Management, South Dakota State University, Brookings, SD, 57007, USA*

SEAN RYDER, *Department of Natural Resource Management, South Dakota State University, Brookings, SD, 57007, USA*

KATHERYN P. HUYVAERT, *Department of Veterinary Microbiology and Pathology, Washington State University, Pullman, WA*

WILLIAM SEVERUD, *Department of Natural Resource Management, South Dakota State University, Brookings, SD, 57007, USA*

ABSTRACT: The microbiome of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) is relatively understudied yet has significant implications for disease management given recent population declines linked to respiratory disease caused by *Mycoplasma ovipneumoniae*. The microbiome consists of a diverse array of bacteria, protozoa, viruses, and fungi in a delicate balance of pathogenic and symbiotic organisms that contribute to maintaining host homeostasis and regulating the immune system. Metrics of the diversity of the microbiome are thought to reflect health where less diverse microbial communities are associated with dysbiosis and disease. In this project, we will investigate associations between metrics of microbiome diversity (e.g., taxon richness among and between individuals and herds) and *M. ovipneumoniae* infection status. Free-ranging Rocky Mountain bighorn sheep from herds in western Nebraska and The Badlands of South Dakota will be captured and nasal, oral, and fecal samples will be collected. We will also collect information on individual sex, age, and weight. *M. ovipneumoniae* status will be determined by real-time PCR. Lastly, we will employ PacBio sequencing methods to characterize the microbiome diversity at different taxonomic levels, from family to species. We anticipate that bighorn sheep that are RT-PCR positive for *M. ovipneumoniae* will have lower microbial diversity in their microbiomes than RT-PCR-negative individuals.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24:6; 2024

KEYWORDS: biome diversity, disease state, microbiome, *Mycoplasma ovipneumoniae*, Nebraska, PacBio sequencing, polymerase chain reaction (PCR), Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*), South Dakota.

Johne's Disease in a Rocky Mountain Bighorn Sheep in Southeastern Wyoming, USA

SAMANTHA E. ALLEN, *Wyoming Game and Fish Department, Laramie, WY, 82070, USA*
JACQUELINE P. KURZ, *Wyoming State Veterinary Laboratory, Laramie, WY, 82070, USA*
TEAL CUFAUDE, *Wyoming Game and Fish Department, Saratoga, WY, 82331, USA*
HALLY KILLION, *Wyoming State Veterinary Laboratory, Laramie, WY, 82070, USA*
JESSICA JENNINGS-GAINES, *Wyoming Game and Fish Department, Laramie, WY, 82070, USA*
PEACH VAN WICK, *Wyoming Game and Fish Department, Wheatland, WY, 82070, USA; peach.vanwick@wyo.gov*
KERRY SONDGEROTH, *Wyoming State Veterinary Laboratory, Laramie, WY, 82070, USA*

ABSTRACT: Infectious disease threats to Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) can be a limiting factor to population growth. One of these infectious diseases, *Mycobacterium avium* subspecies *paratuberculosis* (MAP; Johne's disease), is a chronic, bacterial enteric disease primarily of domestic ruminants that causes progressive wasting and, in some species, diarrhea, and is ultimately invariably fatal. It has been documented in North American wild ruminants (bighorn sheep, mountain goat, elk, deer) since 1979; however, the prevalence and implications of this disease in free-ranging populations is unknown. In May 2021, an adult female bighorn sheep carcass was retrieved from southeastern Wyoming. Postmortem gross and histologic examination was performed at the Wyoming State Veterinary Laboratory. Lesions consistent with MAP infection were identified and included emaciation, evidence of diarrhea, and inflammation of the abdominal lymph nodes, liver, and a segment of the small intestines. Large numbers of bacteria consistent with MAP were detected within the affected segment of intestine, and the presence of fecal MAP was confirmed by polymerase chain reaction (PCR) assay. A subsequent investigation was initiated to ascertain population-level prevalence. Fecal samples were collected from the field from the same herd unit as the MAP-positive bighorn sheep carcass. All fecal samples collected (n = 73) tested negative for MAP by PCR. This baseline work suggests that while uncommon, MAP can occur in free-ranging bighorn sheep in Wyoming and represents the need to consider all disease risks threatening bighorn sheep, encourages and guides future surveillance and diagnostics, and reinforces the importance of separation of wildlife and domestic animals.

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KEYWORDS: disease, domestic animal, Johne's disease, *Mycobacterium avium paratuberculosis* (MAP), polymerase chain reaction (PCR), Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*), ruminant, Wyoming, Wyoming State Veterinary Laboratory.

A Real Pain in the Butt: Gastrointestinal Parasites Impact Horn Growth of Rocky Mountain Bighorn Sheep

TANISHA C. HENRY, *Department of Biological Sciences, University of Calgary, Calgary, AB, T2N 1N4, CA; tanisha.henry@ucalgary.ca*
PETER NEUHAUS, *Department of Biological Sciences, University of Calgary, Calgary, AB, T2N 1N4, CA*
KATHREEN E. RUCKSTUHL, *Department of Biological Sciences, University of Calgary, Calgary, AB, T2N 1N4, CA*

ABSTRACT: Sexual selection often leads to exaggerated secondary selected traits, such as large horns in bighorn rams (*Ovis canadensis*), which confer the bearer fitness benefits. These traits are the product of female mate choice and male-male competition for limited mating opportunities. Elaborate traits are expensive to develop and maintain, and thus an honest signal indicating the quality of an individual to potential mates and competitors. Bighorn rams establish a dominance hierarchy before the mating season, and monopolize breeding with 1 female at a time, leading to a high skew in the reproductive success of dominant males. Morphological traits such as body mass and horn length, in addition to age and social experience, are predictors of reproductive success in males. Disease limits bighorn male horn growth: however, there is a paucity of research on how parasites impact the growth of sexually selected traits in ungulates. We investigated the extent to which 6 gastrointestinal parasites as well as lungworms influence the annual horn growth of bighorn sheep. We include the number of parasite eggs shed in feces as well as the overall parasite richness for each male. We found that across age classes parasite species richness is negatively correlated with annual horn growth, while the effect of infection intensity varies with both age class and parasite species. These findings have implications for wildlife disease monitoring as well as bighorn sheep conservation initiatives.

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KEYWORDS: bighorn sheep (*Ovis canadensis*), gastrointestinal parasites, horn growth, horn morphology, lungworm, ram, sexual selection, ungulate.

Bacterial Strain Typing in a Population of Bighorn Sheep Experiencing Polymicrobial Lamb Pneumonia

KAREN A. FOX, *Colorado Parks and Wildlife, Wildlife Health Program, Fort Collins, CO, 80526, USA; karen.fox@state.co.us*
CHRISTOPHER A.W. MACGLOVER, *Department of Veterinary Sciences, University of Wyoming, Laramie, WY, 82070, USA*
ALLEN E. VITT, *Colorado Parks and Wildlife, Terrestrial Biologist, Pueblo, Colorado, USA 81007*

ABSTRACT: We recently developed an assay for multilocus sequence typing of bighorn sheep respiratory pathogens using multiplex polymerase chain reaction (PCR), amplicon sequencing, and a custom bioinformatics pipeline. The assay specifically assesses *Mannheimia haemolytica*, *Bibersteinia trehalosi*, *Pasteurella multocida*, and *Mycoplasma ovipneumoniae*, as well as providing a broad analysis of bacterial composition through a 16S rRNA analysis. We used this assay to analyze 30 post-mortem tissue samples, acquired over 14 years, from a population of bighorn sheep in southeastern Colorado (RBS 9). Chronic respiratory disease and lamb mortality in this herd prompted removal of a sub-herd in 2013, but the population was considered stable from 2013–2022 despite the persistence of respiratory pathogens in the adult population. During the summers of 2022 and 2023, we observed heavy lamb mortality in 1 sub-herd due to polymicrobial bronchopneumonia. We pursued bacterial strain typing to help understand what changed in the population that might explain the re-appearance of lamb pneumonia. Lung tissues from the lambs with pneumonia were predominated by a single strain each of *M. ovipneumoniae*, *B. trehalosi*, and *P. multocida*. Prior to 2022, in the absence of observable lamb pneumonia, multiple strains of *M. ovipneumoniae* and *P. multocida* were circulating in the bighorn population. The strains of *M. ovipneumoniae* and *P. multocida* identified in the lamb pneumonia cases were present in the population since at least 2016 and 2010 respectively. Only 1 strain of *B. trehalosi* was detected in the bighorn population prior to the observation of lamb pneumonia, while a different *B. trehalosi* strain was found in the dead lambs. The introduction of a novel *B. trehalosi* strain was the most significant microbial change in the population that we identified associated with the observation of lamb pneumonia in 2022/2023. Continued strain typing work will provide context for further interpretations.

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KEYWORDS: *Bibersteinia trehalosi*, bioinformatics, bighorn sheep, Colorado, *Mannheimia haemolytica*, multilocus sequence typing, *Mycoplasma ovipneumoniae*, *Pasteurella multocida*, pathogen, polymerase chain reaction (PCR), polymicrobial lamb pneumonia.

Advancing Diagnostic Precision through MALDI-TOF and Whole Genome Sequencing

CHRISTOPHER A.W. MACGLOVER, *Department of Veterinary Sciences, University of Wyoming, Laramie, WY, 82070, USA; cmacglov@uwyo.edu*
JESSICA JENNINGS-GAINES, *Wildlife Health Laboratory, Wyoming Game and Fish Department, Laramie, WY, 82070, USA*
HALLY KILLION, *Wyoming State Veterinary Laboratory, Laramie, WY, 82070, USA*
KERRY S. SONDGEROTH, *Department of Veterinary Sciences, University of Wyoming, Laramie, WY, 82070, USA*

ABSTRACT: We performed a comprehensive retrospective study to discern the diagnostic capabilities of MALDI-TOF mass spectrometry to strain-type bacterial pathogens implicated in bighorn sheep respiratory disease. This investigation sought to elucidate the etiology of acute die-off events by examining 81 *Mannheimia* spp. isolates through advanced MALDI-TOF strain typing functions and validated with whole genome sequencing. Analysis of *Mannheimia* spp. isolates, including *Mannheimia haemolytica*, *M. glucosida*, *M. ruminalis*, and *M. varigena*, revealed substantial misidentification when solely utilizing the standard manufacturer MALDI-TOF database, particularly concerning *Mannheimia glucosida*, which was frequently misidentified as *Mannheimia haemolytica*. However, the addition of type-strain profiles to the standard MALDI-TOF database corrected the inaccuracies, demonstrating the critical role of a comprehensive reference database, now available for routine bacterial identification at the Wyoming State Veterinary Laboratory. After correctly classifying the isolates using whole genome sequencing, Mannheimia haemolytica was only isolated in bighorn sheep during acute all-age die-offs (1993 Shell Canyon, WY; 2008 Rattlesnake Butte, CO; 2020–2021 Laramie Peak, WY; 2022–2023 Devil's Canyon, WY). The study also identified a novel *Mannheimia* species frequently present in asymptomatic bighorn sheep. These findings underscore the limitations of the current manufacturers MALDI-TOF databases in accurately diagnosing pathogenic agents, emphasizing the need for updated and expanded databases to support more accurate species identification obtained from bighorn sheep. Presently, it is recommended to use sequencing, either whole genome or MLST phylogenetics, for accurate differentiation of *Mannheimia* species, but we have shown that it can be used to inform MALDI-TOF for more robust bacterial identification with the ultimate goal of informing and optimizing management and conservation strategies.

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KEYWORDS: bacterial pathogens, bighorn sheep, Colorado, MALDI-TOF mass spectrometry, *Mannheimia haemolytica*, *Mannheimia glucosida*, *Mannheimia ruminalis*, *Mannheimia varigena*, strain typing, Wyoming.

Bighorn Sheep Paranasal Sinus Tumors: Uncovering Changes within a Respiratory Environment

STEVEN E. EDMONDS, *Washington State University, Pullman, WA, 99164, USA; steven.edmonds@wsu.edu*
KAREN A. FOX, *Colorado Parks and Wildlife Health Lab, Fort Collins, CO, 80526, USA*
KATHRYN P. HUYVAERT, *Washington State University, Pullman WA, 99164, USA*

ABSTRACT: Paranasal sinus tumors (PNSTs) are an understudied disease in bighorn sheep (*Ovis canadensis*) that confounds research on bighorn sheep respiratory disease. PNSTs are characterized as circumferential, diffuse thickenings of the nasal passages or cranial sinuses. These masses can cause a partial or complete obstruction to air flow with potential impacts on physiology, blood oxygenation, or susceptibility to infectious diseases. The disease progression is unknown and its contribution to mortality is currently unattainable. Therefore, this project aims to deepen the understanding of PNSTs by better understanding the microbial environment associated with the presence of PNSTs. Results from a pilot study are presented here comparing microbial 16S gene sequence data among 9 Colorado bighorn sheep split into 3 different groups: i) with established sinus tumors; ii) with normal sinus tissue from PNST-positive herds; and iii) with normal tissue from PNST-negative herds. The aim of this pilot study is to identify associations between metrics of microbial diversity and the presence of PNSTs. Preliminary results suggest an association between the presence of grade II PNSTs and reduced alpha diversity (i.e., species diversity) of upper respiratory microbes. Reduced microbial diversity can occur because of an infection, immunosuppression, or disruption of anatomical and cellular function. All these factors are or may be related to PNSTs. Next steps include understanding how microbial diversity changes with PNST progression and investigating associations with other disease-associated microbes such as *Mycoplasma ovipneumoniae*.

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KEYWORDS: bighorn sheep (*Ovis canadensis*), Colorado, disease, gene sequencing, *Mycoplasma ovipneumoniae*, microbes, Paranasal sinus tumors (PNSTs), microbes.

MOVEMENT ECOLOGY

Movements of Bighorn Rams in Extant Populations

IAN F. GAZELEY, *University of Alberta, Edmonton, AB, T6G 2R3, Canada; gazeley@ualberta.ca*
MARK S. BOYCE, *University of Alberta, Edmonton, AB, T6G 2R3, Canada*

ABSTRACT: Transmission of pathogens from domesticated animals presents a substantial risk to native sheep species. Populations of wild sheep are at high risk from the bacterium *Mycoplasma ovipneumoniae* (*M. ovi*) which occurs at high rates in domestic caprids (30–70% of herds). The mountainous areas of southwest Alberta, Canada are home to significant extant populations of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) that have experienced historic and recent livestock disease outbreaks. To assess disease transmission risks, and predict disease spread among populations, the University of Alberta, Government of Alberta, Parks Canada and multiple NGOs initiated a cooperative project to provide a thorough understanding of movement behaviour, habitat selection, and metapopulation connectivity in the region. A total of 70 bighorn rams (age 1.5–9.5, median 4.5) were net-gun captured (n=61) or chemically immobilized (n=9) and fitted with GPS collars in 2022 and 2023. Early analyses of data from collars and remote cameras collected between April 2022 and October 2023 showed variable migration patterns, occasional dispersal, and highly variable rut and foray behaviours among individuals and herds. Daily movement varied in summer (mean 3.55 km/day, 2.03–5.57) and winter (3.14 km/day, 1.07–5.67), with total seasonal cumulative distances of 753.5 km (434.7–1,010.0) and 452.1 km (176.7–697.9), respectively. Local convex hull estimates (K=25) of annual home range averaged 69.6 km2 (10.3–242.7). Two rams were tracked before and during an *M. ovi* outbreak until death, allowing comparison with non-diseased ram movements. Additional analyses on forays, dispersal and habitat selection will be presented.

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KEYWORDS: Alberta, dispersal, extant populations, habitat selection, home range, migration, *Mycoplasma ovipneumoniae*, ram, Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*).

Exploratory and Resident Movements of Translocated Rocky Mountain Goats in Oregon

ANDREW J. WALCH, *Oregon Department of Fish and Wildlife, Bend, OR, 97702, USA; andrew.J.walch@odfw.oregon.gov*
COREY HEATH, *Oregon Department of Fish and Wildlife, Bend, OR, 97702, USA*
SETH HARJU, *Heron Ecological, Kingston, ID, 83839, USA*
JESSICA CLARK, *Oregon Department of Fish and Wildlife, Bend, OR, 97702, USA*
DON WHITTAKER, *Oregon Department of Fish and Wildlife, Salem, OR, 97302, USA*

ABSTRACT: Rocky Mountain goats (*Oreamnos americanus*) are native to the Central Oregon Cascades, and historically existed in small, isolated populations until their extirpation in the early- to mid-nineteenth century. The Oregon Department of Fish and Wildlife (ODFW), in partnership with the Confederated Tribes of the Warm Springs Reservation of Oregon (CTWSRO) began restoration efforts with 3 separate translocation events in 2010, 2012, and 2016. These translocations resulted in a robust goat population. We used movement metrics from animals collared during releases to identify range establishment periods for the population. Results will inform and improve effectiveness of further translocation and genetic supplementation efforts of Rocky Mountain goats in other suitable habitats in the Cascade mountain range of Oregon.

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KEYWORDS: Cascade Mountain range, Confederated Tribes of the Warm Springs Reservation, genetic supplementation, Oregon Department of Fish and Wildlife, Rocky Mountain goats (*Oreamnos americanus*), restoration, translocation.

Diverse Migration Patterns and Seasonal Habitat Use of Stone's Sheep (*Ovis dalli stonei*)

GRACE E. ENNS, *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada; WSP Canada, Calgary, AB, T6G 2R3, CA;* genns@ualberta.ca
BILL JEX, *Fish and Wildlife Branch, British Columbia Ministry of Forests, Smithers BC, V0J 3W0, CA*
MARK S. BOYCE, *Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2R3, CA*

ABSTRACT: We describe temporal and spatial patterns of space-use and migrations by 16 GPS-collared Stone's sheep (*Ovis dalli stonei*) from 9 bands in the Cassiar Mountains of northern British Columbia, Canada. Our objectives were to identify timing of spring and fall migrations, characterize summer and winter ranges, map migration routes and stopover sites, and document altitudinal change across seasons. Our last objective was to assess individual migration strategies based on patterns of geographic migration, altitudinal migration, or residency. Median start and end dates of the spring and fall migrations were 12 and 17 Jun (range: 20 May to 5 Aug), and 30 Aug and 22 Sep (range: 21 Aug to 7 Jan), respectively. Individuals showed high fidelity to winter ranges over the limited duration of the study. Winter and summer ranges of most individuals (n = 15) occurred at moderate to high elevations that varied < 150 m between seasonal ranges. The median distance traveled along geographic migration routes was 16.3 km (range: 7.6–47.4 km). During the spring migration, most geographic migrants (n = 8) used at least 1 stopover site (median = 1.5, range: 0–4), while almost all migrants (n = 11) used stopover sites more frequently in the fall (median=2.5, range: 0–6). We found collared females exhibited 4 different migration strategies which mostly varied across bands. Migration strategies included long-distance geographic migrants (n= 5), short-distance geographic migrants (n = 5), vacillating migrants (n = 2), and abbreviated altitudinal migrants (n = 4). We conclude that female Stone's sheep in the Cassiar Mountains displayed a diverse assemblage of seasonal habitat use and migratory behaviors. By delineating seasonal ranges, migration routes and stopover sites, we identify areas of priority to help inform land-use planning in the region and conservation of native migrations of Stone's sheep.

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KEYWORDS: British Columbia, Cassiar Mountains, migrant, migration strategy, seasonal habitat use, Stone's sheep (*Ovis dalli stonei*), temporal and spatial use pattern.

Identifying Mineral Lick Locations from Movement Data

IAN F. GAZELEY, *University of Alberta, Edmonton, AB, T6G 2R3, Canada; gazeley@ualberta.ca*
WENHAO YIN, *University of Alberta, Edmonton, AB, T6G 2R3, Canada*
MARK S. BOYCE, *University of Alberta, Edmonton, AB, T6G 2R3, Canada*

ABSTRACT: The spatial distribution of mountain ungulates is driven by trade-offs between inter- and intraspecific competition for resources, predation risk, and access to mates. Mineral licks are important landscape elements that are known to influence the movements of ungulate species and are used regularly during spring and summer months. While there is no definitive consensus on why animals utilize mineral licks, there is no doubt that they are frequently and repeatedly visited by alpine ungulates during spring and summer. The temporal and spatial concentration of ungulate activity at mineral licks suggests that they may play a role in pathogen transmission. The mountains and foothills of southwest Alberta, Canada are home to a large population of bighorn sheep that have experienced historic disease outbreaks associated with exposure to domestic livestock. Using temporally explicit spatial data from GPS-collared bighorn sheep (n=67), representing 89 summer seasons, we identified patterns of movement associated with the use of known mineral licks to predict locations of previously unknown lick sites. The resulting model allows prioritisation of site investigations for the identification of high probability mineral lick locations used by bighorn sheep. Identifying the location of these important landscape features will help us understand disease transmission risk and design effective outbreak response plans, as well as assist in species management in multi-use landscapes.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24: 15; 2024

KEYWORDS: Alberta, bighorn sheep, competition, domestic livestock, GPS, mineral lick, movement pattern, ungulate.

PREDATION AND HARVEST

Exploring How the Environment Shapes Predator-Prey Dynamics in the Sierra Nevada

ELIZABETH A. SIEMION, *Utah State University, Logan, UT. 84322, USA; California Dept. of Fish & Wildlife, Bishop, 93514, CA USA; liz.siemion@usu.edu*
YASAMAN N. SHAKERI, *University of Wyoming, Laramie, WY, 82071, USA*
THOMAS R. STEPHENSON, *California Dept. of Fish & Wildlife, Bishop, CA, 93514, USA*
KEZIA R. MANLOVE, *Utah State University, Logan, UT, 84322, USA*

ABSTRACT: Environmental variation shapes prey selection, predation risk, and predator-prey dynamics. For example, seasonal conditions drive predator-prey dynamics by affecting the spatial arrangement of predator and prey populations, leading to changes in prey selection by predators and predation risk for prey. As such, understanding how predator-prey dynamics change under different environmental conditions has important implications for managing predator and prey species. The Sierra Nevada climate is characterized by predictable seasonal changes that drive the spatial redistributions of mule deer (Odocoileus hemionus) and subsequent mountain lion (*Puma concolor*) movement. For the federally endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; Sierra bighorn), increased proximity to mule deer during winter is associated with elevated mountain lion predation on low- elevation winter range. We developed a Bayesian hierarchical discrete choice model that identifies prey species at mountain lion kill sites using investigated kill site characteristics and mountain lion GPS data between 2018 and 2023. Ultimately, we will use this model to determine how environmental conditions drive Sierra bighorn predation risk and predator-prey dynamics in a multi-prey system. Climate change may change the frequency and intensity of low-elevation winter range use by Sierra bighorn, affecting the extent to which mountain lions limit Sierra bighorn populations. The relationship between the environment and mountain lion prey selection will provide insight for predicting predation dynamics on Sierra bighorn under environmental change and for selecting management strategies that reduce predation risk on Sierra bighorn.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24:16; 2024

KEYWORDS: Bayesian hierarchical discrete choice model, mountain lion (*Puma concolor*), mule deer (*Odocoileus hemionus*), Nevada bighorn sheep (*Ovis canadensis sierrae*), predator risk, Sierra bighorn, Sierra Nevada.

Maximizing Utility of Compulsory Registration for Harvest-Based Monitoring of Bighorn Sheep in Alberta

NILS ANDERSON, *Hunting and Fishing Branch, Government of Alberta, Edmonton, Alberta, T5K 0G5, CA; Nils.Anderson@gov.ab.ca*
GRANT CHAPMAN, *Hunting and Fishing Branch, Government of Alberta, Edmonton, Alberta, T5K 0G5, CA*

ABSTRACT: Alberta has conducted compulsory registration of bighorn rams since 1985, collecting long term data that are essential to species management. Since 2017, additional morphological measurements have been taken from the horns of harvested rams to better describe the relationship between age and horn curl class. This relationship is critical for a variety of management-related functions, including:

1) Comparison of growth rate across geographic areas and time periods
2) Simulation of outcomes across alternative harvest strategies (e.g. minimum curl restrictions)
3) Estimation of realized harvest rate
4) Monitoring population trend through time (and back into the past)

Although often used in fisheries management, harvest-based population assessments are less common in wildlife management. This method relies on the harvest sample being representative of the population age structure (i.e. non-selective harvest within the legal-size class), as well as the harvest rate being uniform across the area of interest, and consistent over the time period of interest. This alternative approach can support estimation of realized harvest rates (as well as population size and structure), reducing reliance on more expensive aerial inventory methods.

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KEYWORDS: age class, Alberta, bighorn sheep (*Ovis canadensis*), harvest rate, harvest-based population assessment, horn morphology, ram.

Peer Pressure as an Effective Tool for Reducing Harvest of Female Mountain Goats

STEPHEN W. BETHUNE, *Alaska Dept. of Fish & Game, Sitka, AK, 99835, USA; stephen.bethune@alaska.gov*

ABSTRACT: Wildlife managers across North America recognize the importance of minimizing harvest of female mountain goats (*Oreamnos Americanus*) to maintain sustainable hunting opportunities. Low reproductive rates put goat populations at risk of overharvest when even relatively few females are harvested. Minimal sexual dimorphism makes male only harvest strategies impractical. Managers have employed various techniques to reduce female harvest including educational requirements and penalizing individual hunters (disqualified from future hunts) when they harvest a nanny. A point system with a maximum harvest of 6 points (billy = 1 point, nanny = 2 points) per 100 goats observed during aerial surveys is used to manage most Alaskan goat hunts. This point system was initiated on Baranof Island in Southeast Alaska with the 2006 season. The point system had no impact on high female harvest (>40%). Declining populations resulting from three consecutive deep snow winters (2006–2009) and continued high female harvest prompted managers to devise a new strategy of collective punishment referred to as "one and done". Beginning in 2011, Baranof Island was divided into nine hunt zones with a corresponding quota based on recent surveys. But instead of a point system, a hunt zone is closed by emergency order after the first female is harvested, regardless of the remaining quota. In 2017, Baranof Island was further divided into 34 zones, allowing for greater opportunity if one of the new smaller hunt areas is closed. This strategy has created collective peer pressure within the local goat hunting community to target males, which maintains opportunity for other hunters. Since "one and done" began in 2011, female harvest has declined to 18% of the overall harvest compared to 41% in the 15 seasons preceding this strategy and has been the most effective management tool for reducing female mountain goat harvest in Alaska to date.

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KEYWORDS: Alaska, Baranof Island, mountain goat (*Oreamnos Americanus*), harvest strategy, hunter education, nanny, one and done, peer pressure.

The Potential for Rapid Evolution in Response to Exploitation-Induced Selection

MICHAEL B. MORRISSEY, *School of Biology, University of St. Andrews, UK KY16 9ST; michael.morrissey@st-andrews.ac.uk*
RENÉ MALENFANT, *Department of Biology, University of New Brunswick, Fredericton, NB, E3B 5A3, Canada*
FANIE PELLETIER, *Département de Biologie, Université de Sherbrooke, QC, J1K 2R1, Canada*
DAVE COLTMAN, *Department of Biology, Western University, ON, N6G 2V4, Canada*
MARCO FESTA-BIANCHET, *Département de Biologie, Université de Sherbrooke, QC, J1K 2R1, Canada; m.festa@usherbrooke.ca*

ABSTRACT: The phenomenon of substantial and sustained evolutionary response to strong directional selection is well established in evolutionary theory and empirical studies. However, recent conceptual papers and modelling studies aimed at the question in bighorn sheep (*Ovis canadensis*) come to the opposite conclusion, suggesting that the scope for response to strong selection of highly heritable traits such as horn size is minimal. Here we address a series of errors in the most recent such paper (Coulson et al.'s 2018, in *The Journal of Wildlife Management* 82: 46–56), all of which predispose the model to predict a minimal response to selection. We explain the nature of the errors, re-run all analyses with and without errors, and provide additional results showing how established evolutionary principles govern evolutionary changes in mountain sheep horn size. Once the errors are corrected, the model in Coulson et al. (2018) predicts an evolutionary change in horn length of bighorn sheep very similar to published empirical estimates for the Ram Mountain population in Alberta: approximately 2.5 cm over 2–3 generations of intensive selective harvest.

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KEYWORDS: Alberta, bighorn sheep (*Ovis canadensis*), evolution, selection, Ram Mountain, quantitative genetics, *The Journal of Wildlife Management,* trophy hunting.

INTRODUCTION

A surprising controversy attends the suggestion that persistent directional selection on a heritable trait, enforced by morphologically defined criteria for legal harvest, may cause evolutionary change in mountain sheep horns (Boyce and Krausman 2018). While it is widely accepted that harvest-induced selection based on body size or other physical traits can cause rapid evolutionary change in other species, for example in elephants (Campbell-Staton et al., 2021) and fish (Heino et al. 2015), strong reluctance exists to accept that morphologically defined criteria for legal harvest may have similar effects in bighorn sheep (*Ovis canadensis*; Heimer 2004, Heimer and Lee 2004, Traill et al., 2014, Boyce and Krausman 2018, Heffelfinger 2018, Coulson et al., 2018). Quantitative genetic methods applied to empirical data have reported an evolutionary component to changes in horn size in the individual-based, pedigreed, long-term study of bighorn sheep at Ram Mountain, Alberta (Festa-Bianchet et al. 2019) while the population was hunted (Coltman et al. 2003, Pigeon et al. 2016). Modelling studies, however, have claimed either that sustained evolutionary responses to sustained directional selection should not occur (Traill et al. 2014), or that the rate of evolutionary change reported for the Ram Mountain population is implausible (Coulson et al 2018).

The genetic basis of the evolutionary response of a population to directional artificial selection on a specific trait is well established in theory (Falconer 1992, Walsh and Lynch 2018), and corroborated experimentally (Clayton et al. 1957, Robertson 1966; Hill and Caballero 1992; Pélabon et al. 2021). The breeder's equation is highly instructive, providing the per-generation rate of evolutionary change in the of a trait, $\Delta z\bar{z}$, as (1) $\Delta z\bar{z} = h^2 SS$, where h^2 is the heritability (Wright 1921), proportion of phenotypic variation in a population that is due to heritable genetically based differences among individuals, and

SS is the selection differential, the difference in mean phenotype between breeding individuals and population mean phenotype, unweighted by fitness (Lush 1937, Robertson 1966, Price 1970). Heritability can be very high, often exceeding 50% of total phenotypic variance (i.e., $h^2 > 0.5$) for morphological traits (Hill 2010), even in free-ranging wild populations (Postma 2014), and is substantial for bighorn sheep horn morphology (Coltman et al. 2003, 2005, Wilson et al. 2005, Pigeon et al. 2016). Under artificial selection, the selection differential SS , may be very strong. Although responses to artificial selection are often somewhat less than predicted by the breeder's equation (Hill and Caballero 1992, Pélabon et al 2021), the equation generally makes robust predictions of the magnitude of the selection response for directional selection on specific traits. It is therefore surprising that many authors focusing on the potential for responses to artificial selection in wild sheep argue that substantial response to selection is unlikely. For example, Heffelfinger (2018) argues that many processes in nature, such as plasticity, maternal effects and environmental variability, will severely limit or oppose the response to selection. Although many ecological processes play out simultaneously, and interact, with evolutionary processes, all of ecology is not stacked in opposition to evolution. Kardos et al. (2018) provided a response to Heffelfinger's (2018) flawed perspective.

Similarly, a modelling paper by Traill et al. (2014) purported to show that very strong selection leads to only a minimal change in phenotype and no sustained response. To the contrary, a substantial body of theory indicates that sustained evolutionary responses are to be expected, and artificial selection has elicited sustained genetic responses in a diversity of species. Subsequent work by Janeiro et al. (2017; see also Hedrick et al 2014) demonstrated the error: Traill et al. (2014) use a notion of inheritance based on the regression of offspring trait values at one year of age or earlier on the value of traits in their fathers at the time of conception. Clearly, if genes act throughout development to influence values of traits in adults, genetic variation will have little or no manifest effects in offspring at recruitment, even if they inherit genes from their fathers that will affect their phenotype when they reach their fathers' ages (Janeiro et al. 2017). The biometric relations among kin will reflect inheritance only if traits are measured at equivalent ontogenetic stages has been recognised and been standard practice for some time (Galton 1886, 1888). More specifically, Janeiro et al. (2017) showed that the cross-age parent–offspring regression used in the Traill et al. (2014) model, despite vociferous claims (Coulson 2012) of its generality, did not subsume established theory of inheritance, and instead was guaranteed to always find no measurable evolution, no matter the true evolutionary dynamics of a trait.

Coulson et al. (2018) claimed that sustained responses to directional selection will occur, but that rates reported from the Ram Mountain population (Coltman et al. 2003, Pigeon et al. 2016) were orders of magnitude greater than is theoretically possible. Here, we re-run Coulson et al.'s (2018) simulation models and obtain results consistent with estimated rates based on quantitative-genetic analyses of Ram Mountain data (Coltman et al. 2003, Pigeon et al. 2016). We identify 5 features of the analysis and interpretations given in Coulson et al. (2018) that diverge markedly from the authors' stated intention of applying a model based on established quantitative genetic assumptions. We also clarify changes in the literature that have appeared since the publication of Coulson et al.'s (2018) paper.

Distinguishing genetic and environmental contributions to trends in phenotype

After adjusting to age 4, the horns of mature bighorn sheep males on Ram Mountain, Alberta, Canada, declined in length by ~20 cm between 1972 and 2002 (approximately 5 generations; Coltman et al. 2003, Pigeon et al. 2016). After about 1985, environmental conditions deteriorated, partly through density-dependent effects (Jorgenson et al. 1998). Until 1996, the population was subjected to intense selection by trophy hunters: although only ~2.4 rams on average were harvested each year, this represented ~40% of males with legal-sized horns, most of which were taken before they reached peak reproductive age (Jorgenson et al. 1998, Coltman et al. 2003). Prior to the study by Coltman et al. (2003), the observed decline in horn size of adult males was thought to be primarily due to environmental effects; the possibility that unintentional artificial selection contributed to smaller horns was untested. Using linear mixed-effect models, Coltman et al. (2003), found: (1) a decline in horn length of 2–4-year-old males over time, which was significant even after accounting for age and resource availability (β = 0.35 cm/year, $P < 0.001$); (2) substantial heritability in horn length of 2–4-year-old males (h^2 =

0.69 after accounting for age and resource availability); and (3) a small but significant proportion of the change in horn length from 1972–2002 attributable to a change in breeding values, a measure of individuals' heritable genetic merit (β = -0.075 cm/year, $P < 0.001$). The slope of the overall phenotypic trend, and that of the proportion attributable to genetic change (i.e., evolution) were clearly and separately reported in Coltman et al. (2003). The genetic contribution to the overall change was approximately 2.25 cm of the total 20 cm decline in horn length over the 30-year study period. Contrary to statements in Coulson et al. (2018), Coltman et al. (2003) did not argue, based on high heritability, that the phenotypic trend was primarily genetic.

The results of Coltman et al. (2003) attracted some controversy (Traill et al., 2014). Like other applications of the animal model of the time (e.g., Réale et al., 2003), Coltman et al. (2003) did not include year as an effect in the estimation of breeding values. Year should have been included to eliminate any bias in the estimate of changes in breeding value over time, as is now common practice following Postma (2006) and Hadfield et al. (2010). Including year in the estimation of breeding values indirectly accounts for unmodelled features of the environment that may lead to change in mean phenotype. Coltman et al.'s (2003) model, however, included a key variable, mean yearling ewe mass each year, which integrated the effects of population density (Festa-Bianchet et al. 2003). Inclusion of annual mean yearling ewe mass in the analysis of ram horn length had 2 important consequences. First, it likely captured much of the effect of density on horn size, minimising the risk that changing density could generate a spurious trend in breeding values. Second, since the index of density had a strong trend during the period analysed in Coltman et al. (2003), it indirectly captured the effects of other unmeasured environmental variables that may have been changing as well, and that normally would be accounted for by including an effect of year of measurement. A subsequent analysis by Pigeon et al. (2016) using the improved methods suggested by Postma (2006) and Hadfield et al. (2010) and including year as a covariate confirmed the general pattern identified by Coltman et al. (2003). Pigeon et al. (2016) found that breeding values declined by ~2.5 cm over approximately 2–3 generations during the period of intensive hunting, and that the decline stopped when the intense trophy hunt was stopped. Finally, Pigeon et al. (2016) estimated that the probability that the observed change in the genetic component of male horn length was attributable solely to genetic drift (as opposed to a response to selection) was <10%).

What factors determine the rate of evolutionary change?

The breeder's equation, and other expressions for how different aspects of selection and genetic variation relate to one another in a range of circumstances (Robertson 1966, 1969; Lande 1979, 1980, Lande and Arnold 1983; Morrissey 2014; 2015) provide us with some understanding of what factors influence the rate of evolutionary change. Two general conclusions flow from the breeder's equation (Eq. 1): i) for a given strength of selection, higher heritability will generate faster responses to selection, and ii) for a given heritability, larger selection differentials will generate faster evolution. Therefore, the amount of phenotypic variation in a population constrains the possible strength of selection, because the mean of selected parents cannot differ much from the overall mean if the trait has little variation in the population. The more variation, the greater potential for selection to act.

Coulson et al. (2018) used 70 cm as an initial value for the mean horn length for four-year-old rams (from empirical data reported by Jorgenson et al. 1998). However, they used arbitrary values for initial additive genetic variance (σ^2_{AA}) of 3 cm^2 and for total phenotypic variance (σ^2_{zz}) of 5 cm^2. For bighorn sheep, these parameters were estimated by Pigeon et al. (2016) as approximately σ^2_{AA} = 17.9 cm^2 and σ^2_{zz} = 45.0 cm^2. Earlier estimates in Coltman et al. (2005; σ^2_{AA} = 12.0 cm^2 and σ^2_{zz} = 30.6 cm^2) were also much larger than those used by Coulson et al. (2018). Thus, the best empirically supported estimate of heritability of horn length in 4-year-old bighorn rams is $h^2 = \frac{\sigma^2_{AA}}{\sigma^2_{zz}} = \frac{17.9}{45.0} \approx 0.4$ (Pigeon et al. 2016). In contrast, the initial heritability used in Coulson et al.'s models was $h^2 = \frac{\sigma^2_{AA}}{\sigma^2_{zz}} = \frac{3}{5} = 0.6$; thus, while the values for σ^2_{AA} and σ^2_{zz} are of a very different magnitude than published values for bighorn sheep horn length, the corresponding heritability value is at the higher end of the range of available estimates of h^2 , both for bighorn sheep horn size, and more generally for morphological traits in wild populations (Postma 2014). Does this make the genetic parameters in Coulson et al.'s (2018) model generous in assessing the potential for rapid evolution of horn size in bighorn sheep? That depends not only on heritability, but also on how the value of σ_z^2 influences the selection differential.

The selection scheme in Coulson et al.'s (2018) model allowed all below-average individuals to survive, whereas above-average individuals were culled with probability α ranging from 25 to 100%. This scheme can be viewed as an elaboration on truncation selection, which has well-known properties (reviewed in chapters 14 and 16 of Walsh and Lynch 2018). The Coulson et al. (2018) selection model can be described as follows: a fraction α of the population is subjected to negative truncation selection at the mean (some above-average individuals are culled, and the next generation is sired by the remaining individuals) and a fraction $1-\alpha$ is not subjected to selection. This formulation leads to a straightforward analytical expression for the relationship between α and the selection differential,

(2a) $$S = \sqrt{\frac{2}{\pi}}\,\sigma_z \frac{\alpha}{\alpha-2},$$

where σ_z is the square root of the phenotypic variance, or the phenotypic standard deviation. When $\alpha = 1$, all males with phenotype greater than the mean are culled (a scheme known as truncation selection at the mean), and the selection differential is

(2b) $$S = -\sqrt{\frac{2}{\pi}}\,\sigma_z .$$

The derivation of Eq. 2a,b follows from noting that the distribution after selection must follow a χ distribution with one degree of freedom (equal to a half-normal distribution; Eq. 2b) or a mixture of a χ and a Gaussian distribution (i.e., χ for a component α of the population, and Gaussian for a component $1-\alpha$; Eq. 2a). In the sex-limited model constructed here, this selection differential pertains to the selected sex, not to the entire adult population. Sex-limited selection is easily accommodated by existing evolutionary quantitative genetic theory (e.g., Lande 1982).

Focusing on the most intense selection scenario, Coulson et al.'s (2018) model gives a selection differential of $S = -\sqrt{\frac{2}{\pi}}\sigma_z = -\sqrt{\frac{2}{\pi}}\sqrt{5} = -1.78\text{cm}$. In contrast, exactly the same selection scheme applied using published estimates of the variance components yields $S = -\sqrt{\frac{2}{\pi}}\sigma_z = -\sqrt{\frac{2}{\pi}}\sqrt{45.0} = -5.35\text{cm}$. Thus, by using the arbitrary value of 5 for phenotypic variance, rather than the empirically estimated value of 45, Coulson et al. (2018) relegate the magnitude of selection, for any given culling scheme, to approximately one third of the value that would be relevant to bighorn sheep. It is unclear, given their intention to compare their model to bighorn sheep, for example by plotting their modelled evolutionary trajectories, and a purported evolutionary trajectory for horn length from Coltman et al. (2003) on the same graph, why Coulson et al. (2018) used the reported mean for the trait in question, but not the other critically important parameters of the trait's phenotypic distribution, especially a value of phenotypic variance with a reasonable order of magnitude. The differences in the selection differential and evolutionary prediction based on the breeder's equation between the estimated variance components and those used by Coulson et al. (2018) are substantial. This is demonstrated in Figure 1, by comparing part (a) (Coulson et al.'s 2018 variance components) with parts (c) and (e), which use available estimates of the additive genetic and total phenotypic variances for horn length of young adult males. Applying Coulson et al.'s (2018) model but changing it only by using published estimates of variance components makes it even more consistent with the estimated evolutionary change in horn length at Ram Mountain (Figure 1 c, e). This difference is driven more by the total phenotypic variance than the heritability; using the somewhat lower heritability empirically estimated for bighorn sheep horn length with reasonable values for the phenotypic variance also results in substantially greater selection (Figure 2a) and per generation evolutionary change of a trait under sex-limited selection (Figure 2b).

What evolutionary responses should be expected from exploitation-induced selection in natural populations?

Coulson et al. (2018) simulated a range of selection strengths, the strongest being when all individuals with phenotypes above the mean are culled. That selection scheme generates a within-generation change in mean phenotype of approximately 0.8 phenotypic standard deviations (for a Gaussian trait; this can be obtained from Eq. 2; see also Bulmer 1976, Walsh and Lynch 2018). This change is stronger than typically observed strengths of natural selection (Kingsolver et al. 2001, Morrissey 2016) but is comparable to experimental

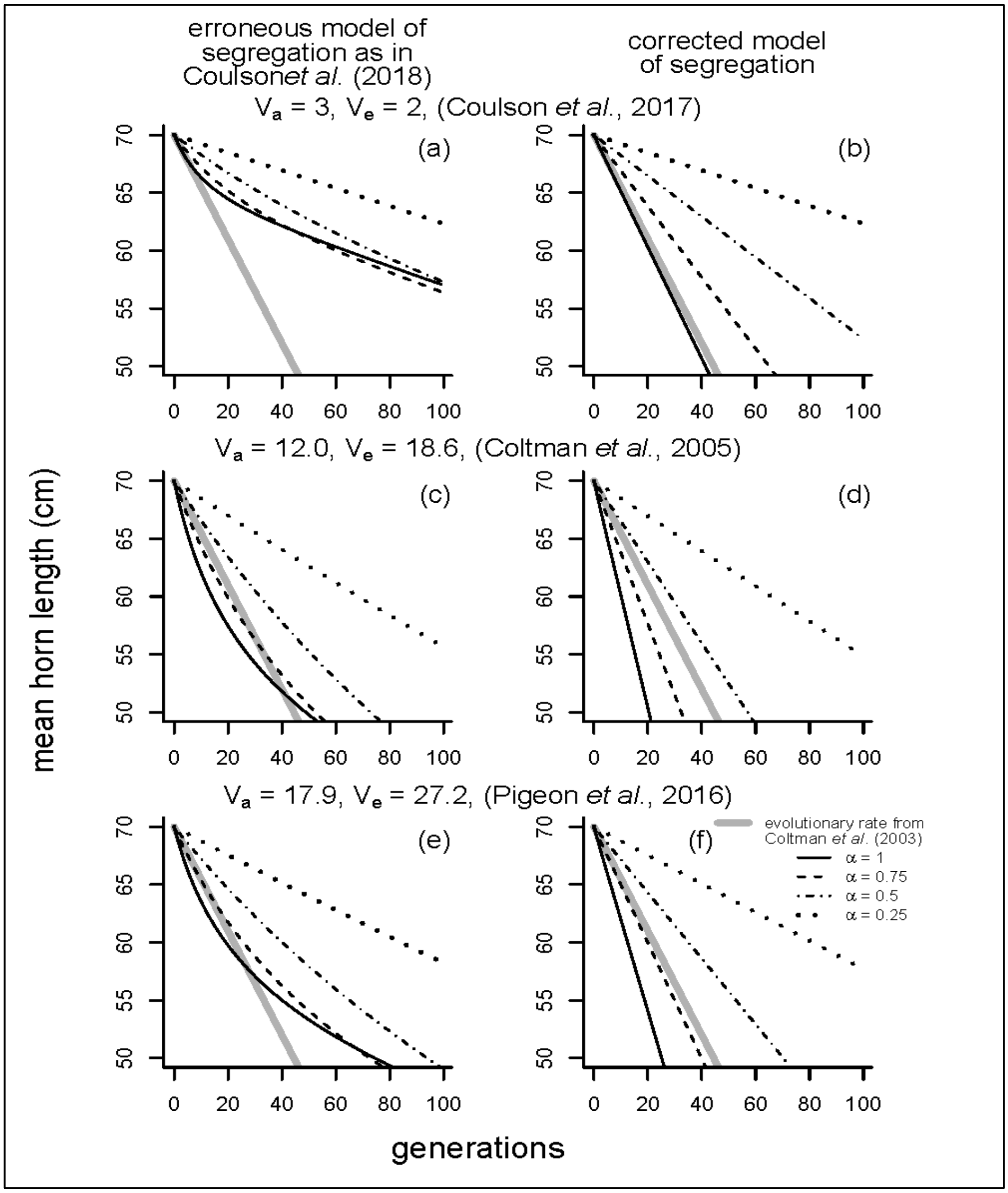

Figure 1. The genetic (evolutionary) trend in breeding values of bighorn sheep horn length reported in Coltman et al. (2003) in relation to the models in Coulson et al. (2018). In the left column, results from the Coulson et al. (2018) model are reproduced and plotted in relation to the inferred evolutionary trend in mean breeding value as estimated by Coltman et al. (2003). Coulson et al. (2018) erroneously related their results to the phenotypic trend. In the right column, Coulson et al.'s (2018) models are corrected for an error that conflated effects of selection on the linkage equilibrium component of the genetic variance with reductions in the genic variance and related to the same previous evolutionary inference. The culling parameter, α, is the probability of harvest of males with horns longer than the average (initially, 70 cm). At α = 1, all these above-average individuals are removed. The reference line (thick dashed grey) here represents the evolutionary inference reported in Coltman et al. (2003); Coulson et al. (2018) depict the much steeper phenotypic trend that was partly affected by environmentally-induced phenotypic changes, mostly acting via density changes in the Ram Mountain population, which is very much steeper but an incorrect representation of the evolutionary inference reported in Coltman et al. (2003).

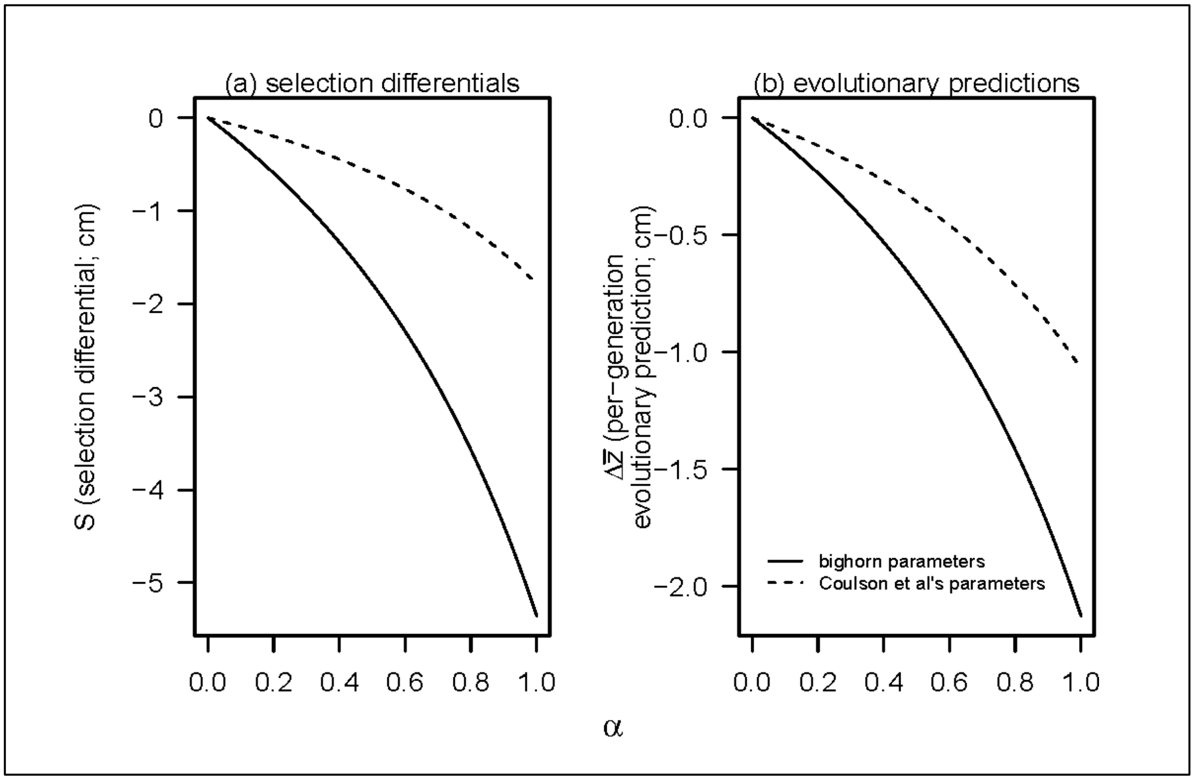

Figure 2. The strength of selection (a), and predictions of the initial per-generation evolutionary rate (b), using Coulson et al.'s (2018) selection scheme. The culling parameter α is the probability of harvest of males with above-average trait values.

artificial selection studies or agricultural breeding programs. For example, in a study specifically focused on the potential for responses to anthropogenic selection, Uusi-Heikkilä et al. (2015) applied truncation selection where the 75% of individuals with the largest trait values were culled. For a given phenotypic variance, this selection is 60% stronger than the most intense selection considered by Coulson et al. (2018).

Helpfully, when an appropriate phenotypic variance is used, the range of culling parameter values used in Coulson et al. (2018) is relevant to selection caused by quota-free trophy hunting of bighorn sheep, as currently practiced in most of Alberta, Canada. For the years in which trophy hunting occurred at Ram Mountain, we calculated the mean horn length at age 4 of all individuals and of rams that were not shot. Horn measurements were collected throughout the summer from rams caught in a corral trap (Jorgenson et al.1998). Because most trophy hunting mortality occurs between ages 4 and 7, and the peak reproduction for males is mostly after this age period (Coltman et al. 2002; Martin et al. 2016), the difference in these mean phenotypes approximates the hunting-induced selection differential for horn size at age 4. Males that were not shot had horns on average 2 cm shorter than all males together, or one-third of a phenotypic standard deviation. Coulson et al.'s (2018) culling scheme, with $\sigma_z = \sqrt{45}$ and $\alpha = \frac{1}{2}$ returns a selection differential of about 1.8 cm, using Eq. 2a.

Combined with a heritability (h^2 , see eq. 1) of approximately 0.4 (Pigeon et al. 2016), this sex-limited selection should generate evolutionary change of about 0.4 cm per generation ($\Delta \bar{z} = \frac{1}{2} h^2 S = \frac{1}{2} \cdot 0.4 \cdot 2\ cm = 0.4\ cm$). Thus, using a value for phenotypic variance empirically estimated for bighorn sheep, the general evolutionary quantitative genetic framework used by workers in the bighorn sheep and similar systems makes evolutionary predictions of similar magnitude to those predicted by the model published by Coulson et al. (2018), at least in the first few generations. Over the longer term an additional issue about how the segregational variance is handled becomes important. This matter will be considered later. We first examine another erroneous aspect of Coulson et al. (2018) about the detectability of change.

How large a change in mean phenotype is detectable? Coulson et al. (2018) draw lines on their figures representing a change from the initial mean phenotype of 1.96 standard deviations of phenotype, and they suggest that this represents the limit of detectability of changes in mean phenotype. However, uncertainty of any statistic (in this instance, the sample mean) is related to natural variability as well as to sample size. It is thus not related to the standard deviation, but rather to the standard error. Differences in mean phenotype of at least 1.96 standard errors, not standard deviations, are detectable (in the sense of a one-sample, two-tailed test of significance at the 0.05 threshold for the *p*-value, which seems to be Coulson et al.'s 2018 intention, though it is unstated). With sample sizes relevant to bighorn sheep, or many studies of natural populations with 100 or more observations, 1.96 standard errors and 1.96 standard deviations differ by approximately a factor of 10. Moreover, the 1.96 standard error limit of detectability applies to a test for the difference of a mean of a single sample to a hypothesized null value. The question at hand relates to detecting a change in a quantity over time, which depends on additional factors, such as a regression model's residual variance and the variance of the predictor variable. It is not clear why Coulson et al. (2018) expect that the detectability limit relevant to a one-sample two-tailed test would apply to the methods actually used to decompose phenotypic changes in natural populations into their genetic and environmental components. Nonetheless, armed with an understanding of the distinction between biological and statistical variation (standard deviation vs. standard error), it will often be possible to characterise ecologically relevant changes in phenotype; by calling on mixed-model methods, inferences of its genetic components are possible as well.

Coulson et al.'s (2018) figures 1–3 included lines depicting their understanding of the limit of detectability of an evolutionary change, but it does not occur at the stated value of $70 - 1.96\sqrt{5}$ cm of horn length, as would be expected given their stated parameter values. Inspection of their code (available at *https://github.com/tncoulson/JWM-Coulson-et-2017*) reveals that the line plotted uses a phenotypic variance of 13 cm^2 rather than 5 cm^2 as otherwise used in their models. Why the authors used larger, yet still arbitrary, values of the phenotypic variance to generate their figure is unclear.

How large a change in a trait is important?
In bighorn sheep at Ram Mountain, a part of the change in mean phenotype for horn morphology was attributable to evolution (Coltman et al. 2003, Pigeon et al*.,* 2016). The effects of other factors, such as density, were much larger (Douhard et al., 2017). That does not render evolutionary change unimportant.

Over all, but the shortest time scales, no one factor will be the overwhelming driver of most characteristics of populations that may be of ecological, social, cultural, recreational or economic significance. It is disconcerting to see suggestions to managers to dismiss one source of change if it is not the sole driver of an important property of a population. The estimated evolutionary change in horn length breeding value at Ram Mountain between 1975 and 1996 was about 2.5 cm (Pigeon et al. 2016). That is at the low end of the range of changes in age-adjusted average horn length observed in heavily harvested populations of bighorn sheep (Festa-Bianchet et al. 2014) and Stone sheep (*Ovis dalli stonei*; Douhard et al. 2016) over longer periods. A few centimetres of horn growth make the difference between a ram that is legal to harvest and one that is not (see Figure 1 in Pelletier et al. (2012) and Festa-Bianchet et al. 2014) and could therefore be very relevant to both ram survival and management. Additionally, evolutionary change differs from other effects on traits in an important way: it is not immediately reversible. The timescales required to reverse any undesirable evolutionary effects of exploitation under future management scenarios are likely much longer than the timescales on which the effects of management actions on density or forage availability, for example, could be expected to occur.

What do Coulson et al.'s (2018) models say about whether intense trophy hunting may have important evolutionary consequences? Coulson et al.'s (2018) interpretation is that the potential is very small. However, this conclusion is obtained by comparing their model results to the *phenotypic*, not evolutionary, trajectory for bighorn sheep horn size at Ram Mountain, which experienced a rapid decline for a variety of reasons as discussed. It is unclear how a primarily ecologically based decline in horn size in a given population should be the measure by which the magnitude of evolution should be judged.

A useful way of making rates of evolutionary change comparable across species or traits is to express evolutionary change in units of standard deviations of phenotype (Haldane 1949, Huxley 1942). If we reproduce results of Coulson et al.'s (2018) model outputs, but express them in units of standard deviations, we get a very different impression (Figures 3a, 3b). Coulson et al.'s (2018) strongest selection scenarios can change mean phenotype by as much as one phenotypic standard deviation in 5 years, given the reasonable value of heritability that they employ. Even their weakest selection scenario can induce a change so large that the mean phenotype is outside the original phenotypic range (i.e., cumulative evolution of ~2 standard deviations) over 100 generations. To illustrate the magnitude of these changes expressed in standard deviations, Figure 3c shows the shift in the distribution of phenotype over 20 generations.

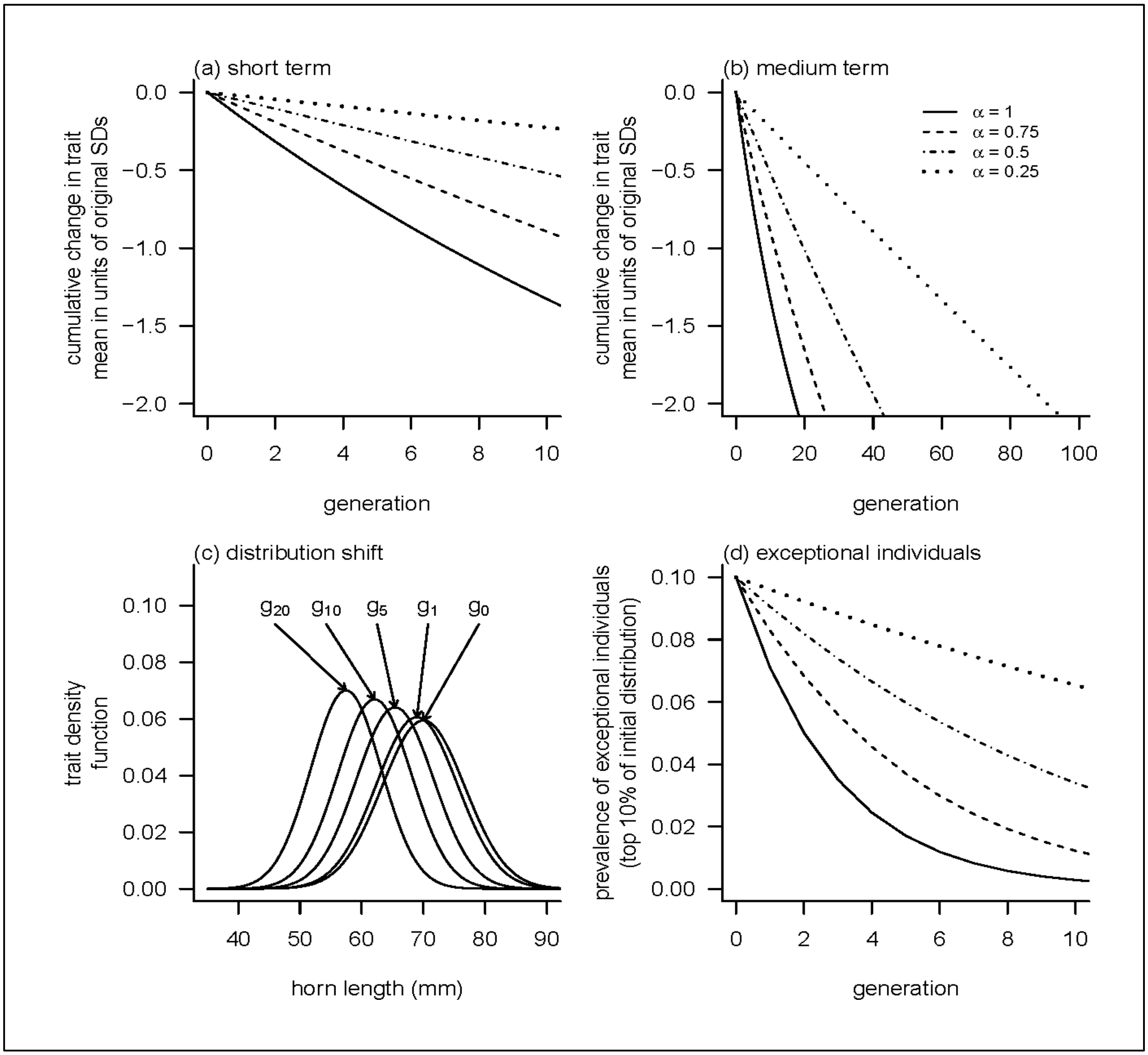

Figure 3. Depictions of Coulson et al.'s (2018) model results in phenotypic standard deviations, to allow comparison across species and traits. These results use published estimates of variance components for young adult male bighorn sheep horn length instead of Coulson et al.'s (2018) arbitrary values, and a correct model of segregation. Equivalent plots using Coulson et al.'s (2018) variance components and erroneous model of segregation are in Figures S1 and S2. Panels (a) and (b) re-plot results from Figure 1b, over short (<10 generation) and medium (<100 generation) time scales; the latter (b) is the x-axis time scale used in Coulson et al. (2018). Panel (c) is an additional depiction of the change in standard deviations, showing the changes in the full distribution of a normal trait. 'g' refers to the number of generations of selective harvest. Panel (d) represents evolutionary change as the decrease in the prevalence of individuals with exceptional trait values, defined as those in the top 10% of the initial distribution of the trait.

In the context of the potential evolutionary consequences of intense trophy hunting, we can construct an even more directly informative representation of the magnitude of the evolutionary changes predicted by the Coulson et al. (2018) models. Imagine that to enter the record book, a trophy must have horns in the top 10% of the range currently expressed in its population. With Coulson et al.'s (2018) selection scenarios, at what rate would evolutionary change reduce the prevalence of record-book animals from the initial frequency of 10%? The answer, derived from Coulson et al.'s (2018) models, is presented in Figure 3d. The strongest selection scenario essentially eliminates trophy animals in about five generations. Even the weakest selection (25% harvest of trophy males) considered by Coulson et al. (2018) generates a reduction in the prevalence of record book animals by over a third in 6–7 generations. These are timescales very relevant to wildlife management: 6 generations of bighorn sheep is about the time elapsed since the 4/5-curl minimum legal size was established in Alberta in 1968.

Results in Figure 3 are plotted based on Coulson et al.'s (2018) model but using published variance component estimates and the corrected model of segregation (see below; the model iterated to generate Figure 1e, f). Using Coulson et al.'s (2018) arbitrary variance components (Figure S1) actually generates even more rapid evolution in terms of phenotypic standard deviations, because evolutionary change in standard deviations is more dependent on heritability than on genetic variance. Model results using both the arbitrary variance components and Coulson et al.'s (2018) erroneous model of segregation also generate substantial evolutionary change (see below and Figure S2). This model, praised by Boyce and Krausman (2018) for suggesting that rapid evolution is unlikely, actually predicts *faster* evolution of small horns (in units of phenotypic standard deviations) than what has been reported empirically over much of the range of selection intensity that it considered.

Segregation, genic vs. genetic variance, and the potential for sustained evolutionary responses to harvest-induced selection

In Coulson et al.'s (2018) models, the response to selection is attenuated over time. Indeed, in the absence of mutation or gene flow, selection will ultimately erode genetic variation. When genetic variation is gone, the response to selection must stop. Unfortunately, the behaviour of Coulson et al.'s (2018) models arises from a simple mistake. This section will correct that mistake and explore what is known about potential evolutionary responses to sustained strong directional selection, such as that induced by intense phenotype-based exploitation. After considering the issue from first principles, we examine the nature of this additional error in Coulson et al.'s (2018) model.

The effect of selection influence genetic variance: principles

If many loci contribute variation to a continuous trait, then the response to selection in a single generation will result from very small changes in allele frequencies at many loci. Because non-trivial evolutionary change can result from very small allele frequency changes at each of many individual loci, selection of quantitative traits has modest effects on the genetic variance in the short term, allowing sustained and rapid evolutionary change. These are basic properties of the 'infinitesimal model' of variation in quantitative traits (Bulmer 1980).

In the long term, selection changes allele frequencies. In the very long term, in the absence of migration or mutation, selection will erode genetic variation, attenuating the response to selection. In the short term, however, selection causes linkage disequilibrium. Directional and stabilizing selection both cause alleles with positive and negative effects on selected traits to become associated in gametes (and thus individuals), reducing the genetic variance (Felsenstein 1965; Bulmer 1971, 1974).

How genetic variance is influenced by both selection and recombination is most transparently handled by the Bulmer equation (Bulmer 1971):

(3) $$\Delta d = -\frac{d}{2} + \frac{h^4}{2}\delta(\sigma_z^2)$$

where d is the contribution of linkage disequilibrium to the additive genetic variance; as such, $\sigma_A^2 = \sigma_a^2 + d$, where σ_a^2 is the linkage equilibrium value of the additive genetic variance, or the genic variance. Δd is thus the change in the disequilibrium contribution to σ_A^2 from one generation to the next. h^4 is the square of the heritability, and $\delta(\sigma_z^2)$ is the within-generation change in phenotypic variance caused by selection. The first term on the right-hand side of (Eq. 3) reflects the partial deterioration of previously accumulated linkage disequilibrium contributions to the additive genetic variance, assuming a large genome such that most loci are unlinked. The second term represents the new linkage disequilibrium contribution to d generated by selection in the current generation. Recombination is powerful: in a scenario involving many loci spread throughout the genome, recombination by itself restores half of the accumulated effect of linkage disequilibrium on σ_A^2 to the linkage equilibrium value (i.e., the genic variance) each generation. In contrast, the contribution of selection to changing σ_A^2 is modest, as it depends on half the squared heritability. Since heritability varies between zero and one, half its square is typically a small value.

The equations for the dynamics of the mean (the breeder's equation; Eq. 1) and variance (the Bulmer equation; Eq. 3) can be coupled to make evolutionary predictions, as we do below. First, however, we use Eq. 3 for a closer look at the short-term effects of selection on genetic variance.

Under truncation selection at the mean, the strongest selection scenario in Coulson et al.'s (2018) paper, the change in the variance takes a particularly simple form (derivable from more general expressions given in Bulmer 1976): the proportional reduction in the phenotypic variance is related to the square of the selection intensity $\bar{\imath}$, as

(4) $$\frac{\sigma_z^{*2}}{\sigma_z^2} = (1 - \bar{\imath}^2),$$

where $\bar{\imath} = \frac{S}{\sigma_z}$ and σ_z^{*2} is the phenotypic variance after selection. Consequently,

(5) $$\delta(\sigma_z^2) = \sigma_z^{*2} - \sigma_z^2 = -\sigma_z^2 \bar{\imath}^2 .$$

These are fairly general equations. In the specific scenario of truncation selection on a sex-limited trait, or any male-specific selection, there are no within-generation changes in the mean and variance in females. We will therefore proceed with the sex-limited version of equations (1) and (5), which if S represents selection in one sex are

(6a) $$\Delta\bar{z} = \frac{1}{2} h^2 S.$$

(6b) $$\delta(\sigma_z^2) = -\frac{1}{2}\sigma_z^2 \bar{\imath}^2 = -\frac{1}{2} S^2.$$

We can now iterate the evolutionary trajectory, but we will first take a more analytical look at the behaviour of the genetic variance under the consistent directional selection of truncation selection at the mean.

Bulmer (1976) showed that the equilibrium value of the disequilibrium contribution to the genetic variance, $\hat{d}$, is given by $\hat{d} = \delta(\sigma_z^2)\hat{h}^4$ where $\delta(\sigma_z^2)$ is the reduction phenotypic variance, and $\hat{h}^4$ is the square of the heritability, both at their equilibrium values. The implications of this formula are not intuitive, because both terms on the right-hand side are themselves functions of $\hat{d}$. Its basic message, however, is quite straightforward. Because the equilibrium heritability is a number between 0 and 1, its square is typically a modest value. Consequently, even under sustained selection, the disequilibrium contribution will reach a modest maximum equilibrium value. To achieve a result more specific to the modified truncation selection model considered here, and one given entirely in terms of equilibrium parameter values, we need only substitute (eq. 2b) and (eq. 6b) into the Bulmer equation (eq. 3) and solve for the equilibrium values, where $\Delta d = 0$ (Bulmer 1974). The equilibrium value of d, i.e., $\hat{d}$, and writing the environmental variance as σ_e^2, is

(7) $$\hat{d} = \frac{-(2+\pi)\sigma_a^2 - \pi\sigma_e^2 + \sqrt{4(1+\pi)\sigma_a^4 + \left(2\sigma_a^2 + \pi(\sigma_a^2 + \sigma_e^2)\right)^2}}{2+2\pi}.$$

Being a solution to a quadratic equation, (7) is complex. General solutions in terms of equilibrium values are necessarily of this form, see equations 16.13a and 16.13d in Walsh and Lynch (2018).

The effect of selection on the genetic variance: models of artificial selection in bighorn sheep

The general theory of short-term effects of selection on the genetic variance can be evaluated for the instructive case where we assume that estimated variance components in bighorn sheep are the linkage equilibrium values. They are not—they have, of course, been influenced by past processes including selection—but this will give us an idea of the likely magnitude of $\hat{d}$ under Coulson et al.'s (2018) most intensive selection scheme (100% harvest of above-average males). For the variance components given by Pigeon et al. (2016), $\sigma_a^2 = 17.9$ and $\sigma_e^2 = 27.1$, $\hat{d} = -1.89$. This represents approximately a 10% reduction in the genetic variance; in terms of the phenotypic standard deviation, it is a reduction in variability of approximately 2%. It is well known that the Bulmer effect is typically modest, even for strong selection (e.g., Turelli and Barton 1994). An illustration of equation (7) is a graphical depiction of the effects of linkage disequilibrium at equilibrium, for a range of heritabilities. Figure 4 shows this for heritabilities between 0 and 1, using the observed phenotypic variance of horn length in young adult male bighorn sheep: the effects of even strong truncation selection

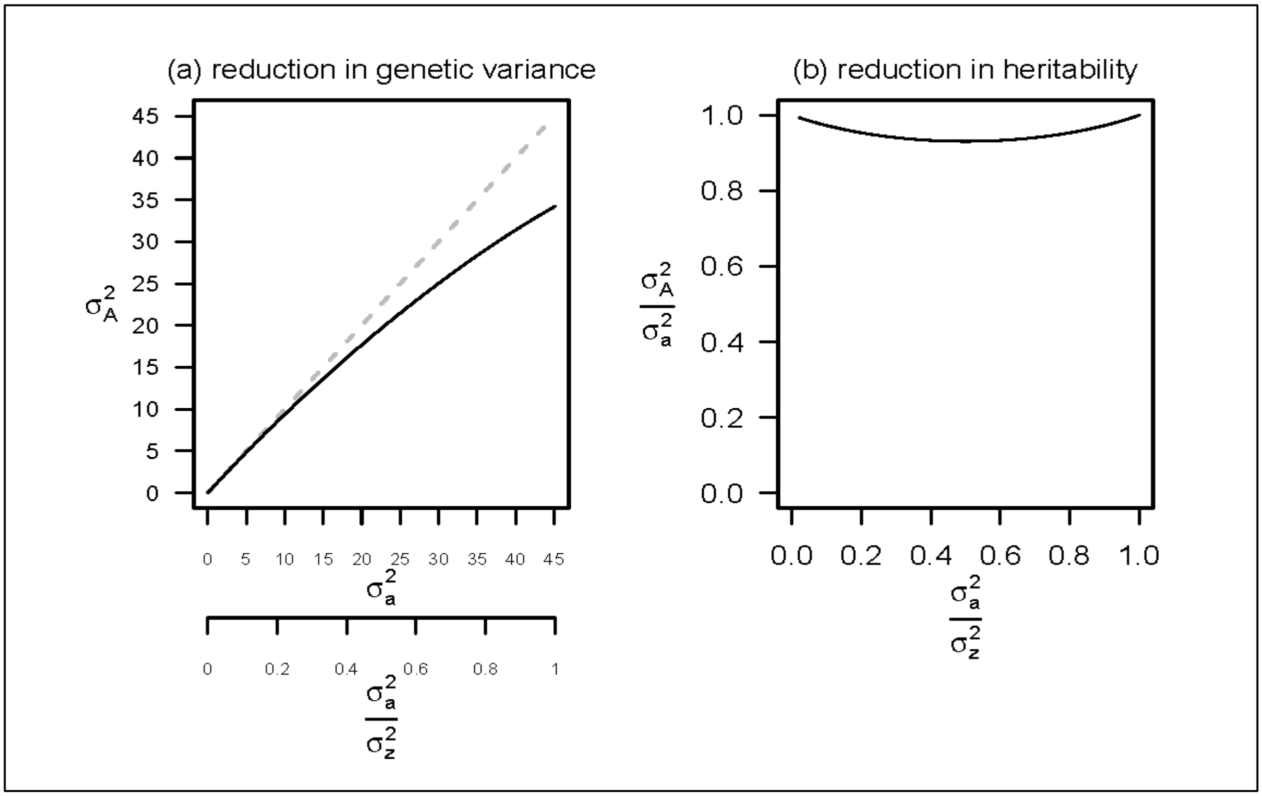

Figure 4. The effect of selection on additive genetic variance ($\sigma\sigma_A^2$; panel a) and heritability (h^2 or $\frac{\sigma\sigma_A^2}{\sigma\sigma_Z^2}$; panel b). The dashed line in (a) represents equality of the genic and additive genetic variance, which would occur in the absence of selection-induced linkage disequilibrium. Both $\sigma\sigma_A^2$ and h^2 are depicted for ranges of the linkage equilibrium value of heritability between zero and one. The phenotypic variance is set at $\sigma\sigma_Z^2$ = 45.0 cm^2, the observed value for young adult horn length in bighorn sheep males.

such as culling all above-average individuals, on the genetic variance are quite modest. The feature of Coulson et al.'s (2018) results that intense selection through trophy hunting will rapidly erode genetic variance in horn size is thus contrary to theory.

How does sustained selection change both the mean and variance of a trait?

Established theory (eight decades for the breeder's equation, four for the Bulmer equation) suggests that the genetic variance for a polygenic trait under sustained directional selection should be only fractionally reduced at equilibrium, while Coulson et al.'s (2018) model rapidly eliminates genetic variation. In addition to theory, much empirical evidence supports the notion that genetic variation can persist for directionally selected traits over many generations, allowing very large and sustained responses to selection. Classic artificial selection studies of quantitative traits with sustained responses include, for example, abdominal bristle number in *Drosophila spp.* (Yoo 1980) and oil content in maize (Dudley 2007), and striking examples of rapid and sustained response to artificial selection in livestock are well known, for example, the well-documented and dramatic increases in growth and feed efficiency in broiler chickens (Zuidhof et al., 2014).

Coulson et al. (2018) intended their model to be based on standard statistical mechanics for inheritance of a continuous trait under the infinitesimal model (Bulmer 1980). However, the implementation contains yet another error. The segregational variance (the variance of differences between individuals' breeding values and the means of their parents' breeding values) is half the value of the additive genetic variance at linkage equilibrium (i.e., the genic variance), not the value including linkage equilibrium at a given time. The consequence of this new error is a mistaken erosion of genetic variation over time, which does not correspond to any known process in population genetics. The error does, however, make it appear more likely that selection through trophy hunting will be inconsequential. Coulson et al. (2018) did in fact apply the correct infinitesimal model of quantitative genetic variation (i.e., where the segregational variance is half of the genic variance), but relegated the associated results to a supplement, presenting the erroneous results that generate less cumulative evolutionary changes in the main document. The difference between iterating the coupled breeder's and Bulmer equations as opposed to Coulson et al.'s (2018) erroneous models is given in the contrast between the columns of Figure 1.

Of course, selection will change allele frequencies in a way that must ultimately erode genetic variation. The joint breeder's and Bulmer equations do not account for this allele frequency change. They only account for the effects of selection on the genetic variance via the generation of non-random association of alleles across loci. To explore the possibility that Coulson et al.'s (2018) model represents a reasonable rate of erosion of genetic variance, we ran individual-based simulations using their selection scenario. We used a demo-genetic scenario close to the infinitesimal model and with little drift (1,000 loci all with equal effects and initially balanced allele frequencies) and a population size of 1,000 males and 1,000 females. We also used a scenario involving fewer loci of larger effects (100 loci, also with equal effects and initially balanced allele frequencies) and a more realistic population size for many managed populations (100 males and 100 females). Both scenarios are much better modelled by the standard mechanics provided by the breeder's and Bulmer equations, in the short and medium terms (Figure 5a–c).

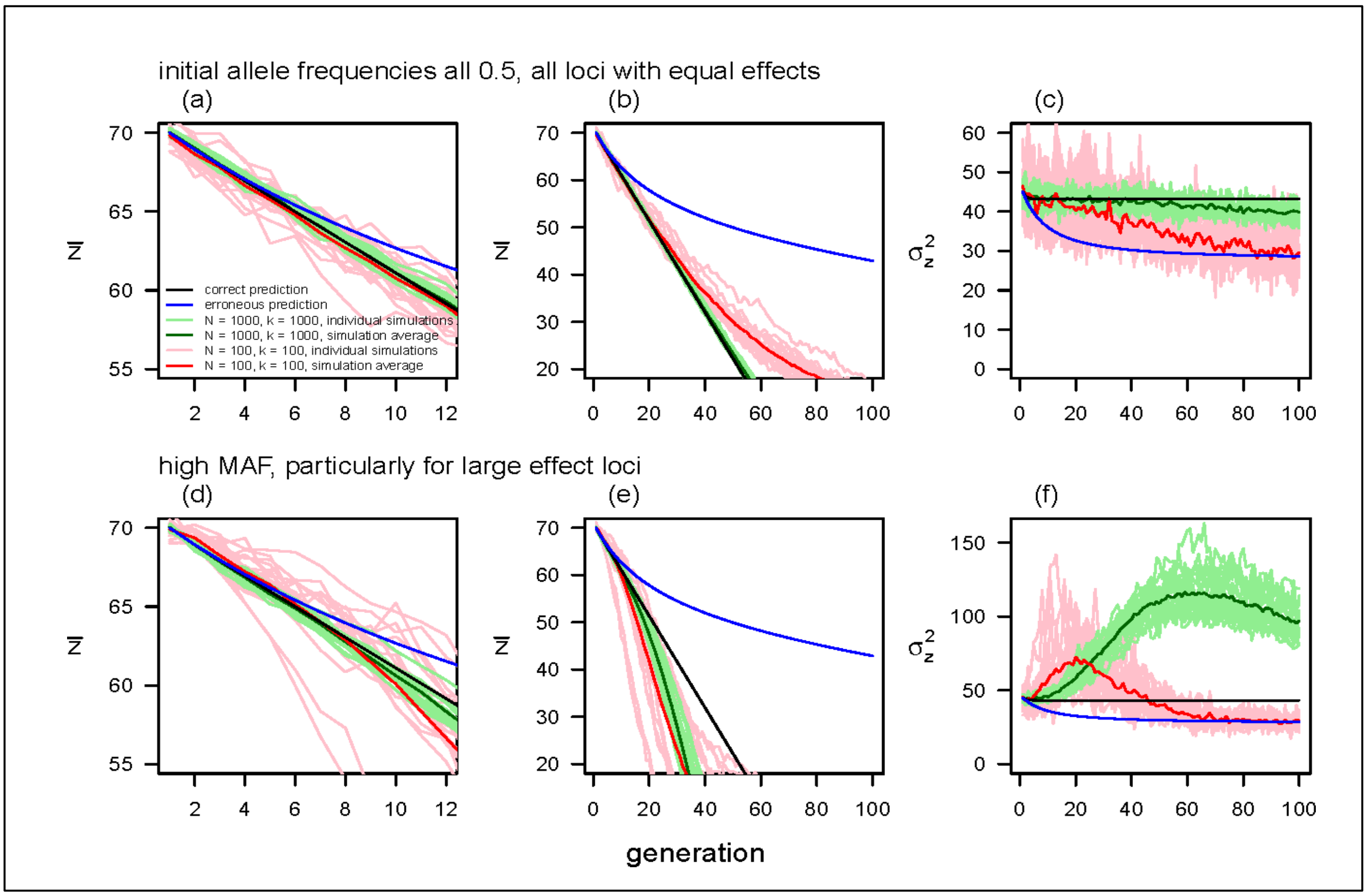

Figure 5. Comparison of established quantitative genetic models with numerical simulations of evolutionary responses to selection of polygenic characters. Initial conditions reflect estimates of the population mean value for horn size in 4-year-old bighorn rams (approx. 70 cm), the additive genetic variance (σ_{A}^{2} = 17.9 cm^2) and the phenotypic variance (σ_{z}^{2} = 45.0 cm^2). In simulations in panels (a–c), *k* = 100 or 1000 loci are simulated with equal initial allele frequencies. In panels (d–f), the same numbers of loci are considered, but their frequencies and allelic effects are simulated from more natural distributions: loci with lower minor allele frequency are more common, and most loci with large effects have low minor allele frequencies. Panels (a) vs (b) and (d) vs (e) depict the same results, but with axes adjusted to focus on short-term (a, d) and longer-term (b, e) change. These figures, except for the blue lines, use the phenotypic and additive genetic variances estimated for bighorn sheep; equivalent plots with the arbitrary (smaller) variance components used by Coulson et al. (2018) are in Figure S.

With few loci and a small population size, and without any immigration or mutation, genetic variation is typically eroded within the time frame represented in Coulson et al.'s (2018) figures (see our Figure 5c); however, the cumulative evolution that occurs before genetic variation is eroded is much greater: despite this latest error, the model predicts evolution similar to that reported for bighorn sheep at Ram Mountain (Pigeon et al. 2016).

How does the effect of selection on genetic variance depend on genetic architecture?

Although selection will erode genetic variation in the long term, that erosion will not necessarily be immediate. In the simulations considered up to this point (Figure 5a-c), the initial conditions have allele frequencies of 0.5 for each of the alternate alleles. For any allelic substitution effects, this allele frequency generates the maximum possible genetic variance. Consequently, genetic variance can only be eroded. In reality, most polymorphisms will have much lower minor allele frequencies (MAF), and furthermore, it is likely that for any ecologically important trait that has experienced past selection, the polymorphic loci with the largest allelic substitution effects will be those with low MAF (Wright 1937, Park 2011). We therefore conducted a second set of simulations, where high and low initial allele frequencies were most common, and loci with these high and low initial frequencies had some of the largest effects, in terms of substitution of one allele for the other, on the trait. Figure S4 shows an example of the resulting joint distribution of allele frequencies and allelic substitution effects.

When an allele is rare, it contributes very little genetic variance to a trait, even if it has a large effect on phenotype relative to the other alleles at the same locus. If that allele is selected against, its elimination results in very little change in the genetic variance. However, when a rare allele is positively selected and its frequency increases, its contribution to genetic variance can increase substantially. Consequently, while directional selection will eventually erode genetic variation, in the medium term, selection can substantially increase the genic and genetic variances (Bürger and Lynch 1995; Bürger 2000). This is illustrated in the simulations using a range of allele frequencies and distributions of effects on phenotype (Figure 2d–f). Selection can cause substantial increases in genetic variance, accelerating the response to selection over ecologically relevant periods of time. Thus, the erroneous model of segregation in Coulson et al. (2018) does not necessarily coincide with any probable departures from any model of selection such as the breeder's equation, with or without Bulmer's mechanics for fine details of transient changes in the genetic variance of quantitative traits.

We reproduced all analyses depicted in Figure 5 using Coulson et al.'s (2018) values of $\sigma_A^2 = 3$ and $\sigma_z^2 = 5$. Although these values correspond to a somewhat higher heritability, Coulson et al.'s (2018) selection scheme leads to less evolutionary change due to the lower phenotypic variance (Figure S3). Coulson et al.'s (2018) parameters, using the observed mean of 70 cm, and arbitrary values of σ_A^2 and σ_z^2 result in evolutionary rates of about half those generated using the published estimates.

The present findings considering recently published works

In 2017, after a clearly marked 'version of record' of Coulson et al.'s (2018) had appeared online, and while an earlier version of the present article was under review at *The Journal of Wildlife Management*, the version of record of Coulson et al.'s (2018) article was changed extensively, without alerting readers of these changes. Additionally, in 2019, *The Journal of Wildlife Management* published materials that would appear to pre-empt and contradict conclusions of the present article, re-drawing, but deleting key components, of figures from the present article in a correspondence (Boyce et al. 2019) that was ostensibly published to respond to other matters (Festa-Bianchet 2019).

One of the substantive changes relative to the original version of record of Coulson et al., (2018) was the addition of statements to key figure captions in Coulson et al. (2018; modified version of record) to the effect that the evolutionary rates from model results were not intended to be instructive about evolution of horn size in bighorn sheep. These assertions are surprising. The clearly stated conclusions of Coulson et al. (2018; both the original version of record and the modified version) are that their models disprove the plausibility of rates of evolution inferred for horn size of Ram Mountain bighorn sheep (Coltman et al. 2003, Pigeon et al. 2016). Additionally, the statements added to figure captions asserting that comparisons were not intended to be made in relation to bighorn sheep are contradicted by the very fact that the figures plotted the phenotypic change in horn size in Ram Mountain bighorn sheep as the sole comparison to the Coulson et al. (2018) model results.

A second substantive change was the inclusion of a paragraph in the discussion of Coulson et al. (2018; modified version of record). The new paragraph states that Coltman et al. (2003) concluded that most of the observed phenotypic change in horn length at Ram Mountain was due to evolution, because heritability of horn length is relatively high. In fact, Coltman et al. (2003) categorically did not conclude that most of the phenotypic change was genetically based. We have already explained this point, but we repeat it here considering the changes to Coulson et al. (2018): Coltman et al. (2003) reported an estimated phenotypic decline of 3.5 mm per year, and the inference of the genetic contribution to that decline was 0.75 mm per year. Furthermore, the inference of the rate of genetically based (i.e., evolutionary) change was in no way based on a notion that high heritability means that phenotypic change can be assumed to equate to genetic change; rather, the estimate was based on a model-based estimate of the genetic trend.

Boyce et al. (2019) responded to various points raised by Festa-Bianchet (2019) in relation to the special section on wild sheep management (The Journal of Wildlife Management, volume 82, issue1). The point that Coulson et al.'s (2018) arbitrarily small phenotypic variance results in a distorted picture of the potential for evolution was *not* included in Festa-Bianchet's (2019) communication. It was addressed in an earlier version of the present article, which was in review at The Journal of Wildlife Management at the time, but was ultimately not published there. Nonetheless, Boyce et al. (2019) included an apparent response about the phenotypic variance.

Boyce et al. (2019) contend that a larger value of the phenotypic variance would not lead to appreciably more rapid evolution than Coulson et al. (2018) reported. In support of this contention, Boyce et al. (2019) present the results depicted in figure 1e of the present article. However, Boyce et al. (2019) only plot the lowest culling rate (25%; recall that Coulson et al. (2018) considered culling rates up to 100% for males with above average horn size). Furthermore, while Coulson et al. (2018) plotted their results with a y-axis range from 50-70 cm of horn length (a scale we retain for ease of comparison), the plot in Boyce et al. (2019) uses a range from 0-70 cm. While their figure consequently gives the impression of a shallow slope, the full results (Fig 1e of the present paper) show that a faithful reproduction of Coulson et al.'s (2018) results with an appropriate phenotypic variance indeed greatly changes the scope for evolutionary change. Why Boyce et al. (2019) presented material that has the appearance of negating results of ours that were in review at the time at the same journal is not clear.

CONCLUSION

Coulson et al.'s (2018) conclusion that estimated rates of evolution in response to trophy hunting in the Ram Mountain population are orders of magnitude greater than is theoretically possible rests on a series of errors. Foremost, they portray research on Ram Mountain as assigning the entire phenotypic change as genetically based. Multiple papers quantified both genetic and non-genetic sources of variation and trends in ecologically important traits in bighorn sheep, including horn size (e.g., Coltman et al. 2003, 2005, Wilson et al. 2005, Pigeon et al. 2016). Taken together with other mistakes, including an erroneous model of segregation, confusion of standard deviation with standard error, and the peculiar mixture of some parameter values from bighorn sheep, such as the population mean and phenotypic trend, but not others (esp., variance components), are puzzling.

We submit that Coulson et al.'s (2018) claim, that the magnitude of evolutionary change in response to exploitation is theoretically implausible, is deeply flawed. By correcting key errors made by Coulson et al. (2018), we have shown a clear congruence of theory and data. We note that all these errors support the claim that hunting-induced evolutionary change in mountain sheep horns is irrelevant to management. We welcome further work motivated to better understand these trends, and to help guide future management decisions. It is important that work continues to refine our theoretical and empirical understanding of evolution as a consequence of exploitation.

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NUTRITION AND DEMOGRAPHY

Nutritional Paradoxes in Wild Sheep, Goats, and Other Northern Ungulates

KRISTIN DENRYTER, *Alaska Department of Fish and Game, Palmer, AK, 99645, USA; kristin.denryter@alaska.gov*
KATHERINE L. PARKER, *University of Northern British Columbia, Prince George, BC, V2N 4Z9 CA*
ROBERT G. WHITE, *Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, 99775, USA*

ABSTRACT: Nutritional paradoxes, in which a conclusion about nutritional ecology seems absurd or self-contradictory but upon deeper investigation is well supported, abound for northern ungulates. The presence of nutritional paradoxes challenges management and conservation efforts to understand their complexities and nuances. To disentangle their intricacies, we evaluate nutritional paradoxes through the lens of behavioral, physiological, and life-history adaptations in northern ungulates. We scoured decades of work on nutrition and foraging ecology of northern ungulates and identified several paradoxical questions including: 1) How do ungulates obtain fats, which are essential for all animals, from plant-based diets that have essentially no fat? 2) How do ungulates achieve adequate energy and protein intake when peaks in energy and protein in forage are phenologically mismatched? 3) How do ungulates balance the cost of mineral acquisition with the cost of acquiring adequate macronutrients (e.g., carbohydrates, fats, protein)? 4) How do ungulates meet energy and protein requirements when dietary concentrations are below requirements? 5) How do individuals persist when nutrition is limiting (e.g., to meet requirements for production, growth, and survival during periods of starvation)? 6) How do populations persist when nutrition is limiting? We illustrate each of these paradoxical questions with empirical or modeled examples in wild sheep, goats, and other northern ungulates to demonstrate that the self-contradictory nature of the nutritional paradox is "solved" by the individual through behavioral and physiological adaptations, often resulting in life-history effects, which resolve the contradiction. Understanding how northern ungulates "make a living" despite these paradoxes has been a challenge for biologists because they contradict some assumed and adopted biological "laws" and hypotheses.

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KEYWORDS: body fat, forage maturation hypothesis, forage quality, functional response, Green World Hypothesis, match-mismatch, northern ungulate, trophic mismatch.

Female Dall's Sheep Summer Nutrition in the Chugach Mountains, Alaska

LUKE METHERELL, *Alaska Department of Fish and Game, Anchorage, AK, 99518, USA; luke.metherell@alaska.gov*
TOM LOHUIS, *Alaska Department of Fish and Game, Anchorage, AK, 99518, USA*
TODD BRINKMAN, *University of Alaska Fairbanks, Fairbanks, AK, 99775, USA*
LARA HORSTMANN, *University of Alaska Fairbanks, Fairbanks, AK, 99775, USA*

ABSTRACT: As part of recent research efforts by the Alaska Department of Fish and Game (ADF&G) to identify issues related to current population declines in Alaskan Dall's sheep (*Ovis dalli dalli*), we conducted a summer nutrition study on a subpopulation of female Dall's sheep (ewes) in the Chugach Mountains of Southcentral Alaska. Over the summers of 2016, 2017, and 2018, we assessed ewe diet compositions and identified forage types through video observation of foraging ewes. During this time, we collected forage and fecal samples to evaluate ewe forage quality [crude protein (%), gross energy (kcal/g), and apparent digestibility (Da)] and identify forage types (deciduous shrubs, evergreen shrubs, forbs, graminoids, lichen, and mushrooms). We found that ewe diet composition varied from one summer to the next as well as from early to late summer. Forage crude protein also varied intra-annually and inter-annually between all years, while gross energy varied within seasons. Nutrition studies like ours will help establish carrying capacities and identify critical habitat of the Dall's sheep within Alaska as current dynamic changes continue to occur in these alpine ecosystems.

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KEYWORDS: Alaska Department of Fish and Game, carrying capacity, crude protein, Chugach Mountains, Dall's sheep (*Ovis dalli dalli*), ewe, nutrition, forage ecology, Southcentral Alaska.

The Role of Nutrition and Disease on Lamb Survival

RACHEL A. SMILEY, *University of Wyoming, Laramie, WY, 82071, USA; rachel.smiley@state.co.us*
BRITTANY L. WAGLER, *University of Wyoming, Laramie, WY, 82071, USA*
JACK N. GAVIN, *University of Wyoming, Laramie, WY, 82071, USA*
ALYSON B. COURTEMANCH, *Wyoming Game and Fish Department, Jackson, WY, 83001, USA*
macglove MCWHIRTER, *Wyoming Game and Fish Department, Jackson, WY, 83001, USA*
DARYL LUTZ, *Wyoming Game and Fish Department, Lander, WY, 82520, USA*
ZACH GREGORY, *Wyoming Game and Fish Department, Lander, WY, 82520, USA*
PATRICK HNILICKA, *U.S. Fish and Wildlife Service, Lander, WY, 82520, USA*
ARTHUR LAWSON, *Shoshone and Arapahoe Fish and Game Department, Fort Washakie, WY, 82514, USA*
DEAN CLAUSE, *Wyoming Game and Fish Department, Pinedale, WY, 82601, USA*

ABSTRACT: Juveniles are often the most susceptible demographic to disease, and mothers have a critical influence on the survival of their offspring. Maternal influence on offspring survival can occur through many pathways, including transmission of pathogens, energetic allocation to growth and survival, and behavioral care. One of the greatest conundrums in the conservation of bighorn sheep (*Ovis canadensis*) is why populations dealing with similar suites pneumonia-associated pathogens vary in their ability to recover from outbreaks. To date, the focus on the role of pathogens has overshadowed an understanding of how maternal state and care contribute to recruitment—and ultimately recovery. Using a 5-year dataset of maternal characteristics (pathogens, nutritional condition, immune function), lamb characteristics, pathogen presence and lamb survival in 2 populations of bighorn sheep in Northwest Wyoming, we investigated the relative influence of pathogens and maternal resource allocation on lamb survival. Over the first 6 months of life, the mother's nutritional condition, which reflects the amount of stored energy, was the most influential factor to the survival of her lamb; mothers with more fat reserves have greater probability of raising lambs than mothers with less fat. Energetic resources are first prioritized for the maintenance and survival of the mother; as she gets burdened with increasing energetic demands (i.e., from carrying pathogens, immune function, and reproduction), costs are passed on to her lamb, ultimately coming at the cost of lamb survival. The fundamental role that maternal condition plays on survival of offspring becomes increasingly important in the context of disease.

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KEYWORDS: Bighorn sheep (*Ovis canadensis*), disease, lamb survival, maternal condition, nutrition, pathogens.

Extreme Environmental Events and Transient Dynamics Shape Multiple Population Trajectories in Sierra Nevada Bighorn Sheep

THOMAS R. STEPHENSON, *California Department of Fish and Wildlife, Bishop, CA, 93514, USA; tom.stephenson@wildlife.ca.gov*
ROBERT C. KLINGER, *U.S. Geological Survey, Western Ecological Research Center, Bishop, CA, 93514, USA*

ABSTRACT: We modeled spatio-temporal dynamics of endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) within the context of hierarchical complexity. A long-standing paradigm is that population dynamics of large mammal herbivores (≥ 10 kg) are characterized by low variation in adult survival and high variation in recruitment. However, some tenets on which this paradigm is based (asymptotic dynamics) may be unrealistic for many species, especially those inhabiting highly variable environments that exist in relatively small subpopulations. Based on modeling of a 22-year dataset of 14 bighorn subpopulations across 5,000 km^2, we have found: (1) extreme events produce transient dynamics in adult survival and recruitment that shape population trajectories for many years; (2) subpopulations can exhibit responses that vary in magnitude and direction to annual environmental conditions; and (3) the taxa is meaningfully characterized by variability in levels and timing of trajectories within subpopulations rather than a mean "trend" or population growth rate across subpopulations. We anticipate that the capability to quantify responses to extreme snow years and years of high predation which this dataset has given us will be broadly applicable to wild sheep with disjunct populations inhabiting highly variable environments. As has been reported elsewhere, we observed a portfolio of migratory behaviors and patterns of habitat selection amongst Sierra bighorn. We observed cascading effects of migratory diversity on demography. We recognize that, once lost, some migratory patterns are more difficult to reestablish than others. Nevertheless, metapopulation persistence may benefit from restoring populations where high-quality seasonal ranges require complex migratory behavior (e.g., longer distances through less preferred habitat). A diverse portfolio of migratory behaviors and occupied landscapes is essential for maximizing the representation, redundancy, and resiliency that are at the core of species restoration. A changing climate presents challenges and opportunities for the restoration of wild sheep populations.

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KEYWORDS: asymptotic dynamics, environmental events, migratory behavior, metapopulation, population trajectory, recruitment, Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), transient dynamics, restoration.

Rates And Causes of Ewe and Ram Mortality in the Chugach, Talkeetna, and North Wrangell Mountains, Alaska, 2009–2022

TOM LOHUIS, *Alaska Department of Fish and Game, Anchorage, AK, 99518, USA; thomas.lohuis@alaska.gov*
KYLE SMITH, *Alaska Department of Fish and Game, Anchorage, AK, 99518, USA*
CHRIS BROCKMAN, *Alaska Department of Fish and Game, Palmer, AK, 99645, USA*
HEIDI HATCHER, *Alaska Department of Fish and Game, Glennallen, AK, 99588, USA*
JEFF WELLS, *Alaska Department of Fish and Game, Tok, AK, 99780, USA*

ABSTRACT: Mortality curves for Dall's sheep have been published by multiple researchers. In general, mortality rates are low but nonzero for sheep ages 2–8. During recent winters, however, overwinter mortality rates in radio collared animals in some mountain ranges in Alaska were much greater than reported previously. In winter 2019–2020, 34% of all radio collared sheep in the Talkeetna mountains, and 10% of those in the Chugach died from a variety of causes including avalanches, predation, disease, falls, and malnutrition. During the winter of 2020–2021, 19% of the Talkeetna mountains study population and 6% of those in the Chugach died from similar causes. In winter 2021–2022, collared animals in the Talkeetnas experienced a 29% mortality rate, with 20% mortality in collared animals in the Chugach mountains. We will review rates and causes of mortality in radio collared rams and ewes in the Chugach, Wrangell, and Talkeetna mountains between 2009–2022. In most winters, overall adult mortality rates were between 5–12%. Accelerated mortality rates nearly triple those levels in recent years have contributed to population declines.

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KEYWORDS: Alaska, Chugach mountains, Dall's sheep (*Ovis dalli dalli*), ewe, mortality, ram, radio collar, Talkeetna mountains, winter.

HUMAN-WILDLIFE CONFLICTS AND BIGHORN RECOVERY

Bighorn Sheep Recovery, Collapse and Rescue on the Navajo Nation

NIKE J. GOODSON, *Stevens Wildlife Consulting, 15300 Horse Creek Road, Bozeman, MT, 59401, USA;* stevenswildlife@earthlink.net
DAVID R. STEVENS, *Stevens Wildlife Consulting, 15300 Horse Creek Road, Bozeman, MT, 59401, USA*
JEFFREY COLE, *Navajo Nation Department of Fish and Wildlife, Window Rock, AZ, 86515, USA*
JESSICA L. FORT, *Navajo Nation Department of Fish and Wildlife, Window Rock, AZ, 86515, USA*

ABSTRACT: In 1997 there were 31 desert bighorn sheep (*Ovis canadensis nelsoni*) in a single herd on the Navajo Nation. We identified cattle grazing and river-based recreation as limiting factors and reduced impacts of both during 1997 through 2000. During the next 13 years transplants initiated 2 new herds and the total population on the Navajo Nation increased to over 500 bighorn sheep. Lamb production and survival were consistently high from 2000 through 2013. In 2014 lamb survival declined precipitously in the Lower San Juan Canyon herd. In 2016 lamb survival declined steeply in the nearby Upper San Juan Canyon herd. Bighorn sheep tested positive for *Mycoplasma ovipneumonia*e (M. ovipneumoniae) in the Lower San Juan Canyon herd in 2015 and in all 3 herds on the Navajo Nation in 2018 and 2020. Poor lamb survival continued in both the Upper and Lower San Juan Canyon herds through 2021. During winter 2021-2022 we conducted a test and remove operation in the most severely impacted herd in the Lower San Juan Canyon. We also captured and tested ewes in the Upper San Juan Canyon. Surveys in fall of 2022 indicated increased lamb survival in both the Lower and Upper San Juan Canyon herds.

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KEYWORDS: desert bighorn sheep (*Ovis canadensis nelsoni*), lamb survival, *Mycoplasma ovipneumoniae*, Navajo Nation, San Juan Canyon herd, test and remove.

INTRODUCTION

From the beginning of field studies of bighorn sheep in North America populations have been subject to devastating declines separated by periods of population increase and range expansion (Smith 1954). Evidence indicates that *Mycoplasma ovipneumoniae* has been the dominant cause of declines in bighorn sheep populations in North America (Besser et al. 2012). The desert bighorn sheep herds on the Navajo Nation provide examples of healthy expanding herds where introduction of *M. ovipneumoniae* resulted in suddenly increased mortality of juveniles and long-term declines in recruitment. After over a decade of population increase, the initiation of 2 new herds on the Navajo Nation and an over 10-fold increase in the abundance of desert bighorn on the Navajo Nation, *M. ovipneumoniae* was introduced into one desert bighorn herd in the Lower San Juan Canyon. The infection was transmitted to the nearby Upper San Juan Canyon herd within 2 years. The population trajectory of both herds changed abruptly from increasing to declining. Lamb recruitment dropped to near zero and continued low. In the past wildlife management agencies responsible for bighorn sheep populations that were suffering long-term declines due to pneumonia had few options. Usually, bighorn sheep herds recovered without intervention; however, clearing *M. ovipneumoniae* from a herd can take decades and recovery is not assured (George et al. 2009). However, recently managers have been successful in clearing bighorn sheep herds of *M. ovipneumoniae* through capturing ewes, testing them for *M. ovipneumoniae* and removing those that test positive (Cassirer and Besser 2025). We attempted to arrest the decline in the Lower Canyon desert bighorn herd by capturing surviving ewes, testing them for *M. ovipneumoniae* and removing those that tested positive from the herd. We monitored fall lamb survival to determine success.

STUDY AREA

The study area was located in the San Juan River Canyon and Glen Canyon in southeastern Utah (Figure 1). The San Juan River formed the north boundary of the Navajo Nation within the ranges of the San Juan Canyon herds. In Glen Canyon the high water mark of Lake Powell was the Navajo Nation boundary. The Upper Canyon bighorn sheep range encompassed 113 km2 and included 30 km of the river canyon and a valley that extended about 4 kilometers south from the river. The Lower San Juan Canyon bighorn range was separated from the Upper Canyon by about 3 km of unsuitable terrain, a highway and the village of Mexican Hat. It encompassed 170 km^2 and included 55 km of river canyon. The Glen Canyon bighorn sheep range included 42 km of Lake Powell shoreline and encompassed 450 km2. Elevations ranged from 1128 m at Lake Powell to 1600 m on the rim above the Lower Canyon.

Bighorn sheep were native to both the San Juan River Canyon and to Glen Canyon. Populations in the Lower San Juan Canyon (below Mexican Hat) and in Glen Canyon were extirpated prior to 1970. The original native herd inhabited the San Juan River Canyon from Comb Ridge to the Mexican Hat Rock. At the initiation of our study in 1997 the bighorn sheep ranged nearly exclusively (with the exception of less than 10 observations of rams) on the Navajo Nation (south) side of the San Juan River. Later the Utah Department of Natural Resources transplanted bighorn sheep into locations north of the San Juan River and north of the San Juan Arm of Lake Powell on land managed by the Bureau of Land Management (BLM).

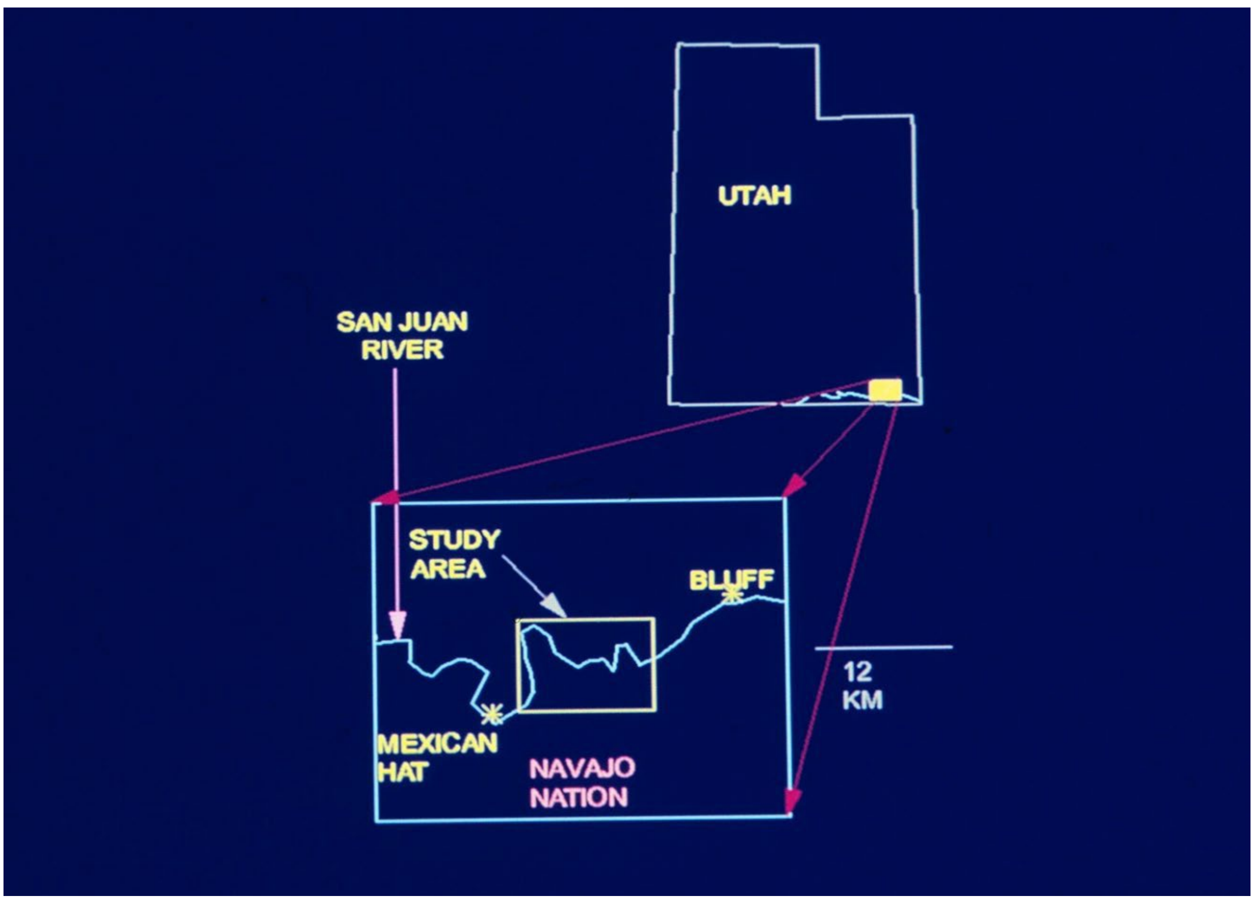

Figure 1. Location of the original, native herd in the Upper San Juan River Canyon in southeastern Utah.

Bighorn sheep were native to both the San Juan River Canyon and to Glen Canyon. Populations in the Lower San Juan Canyon (below Mexican Hat) and in Glen Canyon were extirpated prior to 1970. The original native herd inhabited the San Juan River Canyon from Comb Ridge to the Mexican Hat Rock. At the initiation of our study in 1997 the bighorn sheep ranged nearly exclusively (except for less than 10 observations of rams) on the Navajo Nation (south) side of the San Juan River. Later the Utah Department of Natural Resources transplanted bighorn sheep into locations north of the San Juan River and north of the San Juan Arm of Lake Powell on land managed by the Bureau of Land Management (BLM).

METHODS

At the initiation of the study in November 1996, 16 of 31 bighorn sheep in the Upper Canyon population were captured, ear tagged and fitted with VHF transmitters. Additional bighorn sheep in the Upper Canyon were collared and fitted with VHF transmitters in 1997, 2002, 2005, and 2011. In 2018 21 bighorn sheep were captured in the Upper Canyon. Nineteen were fitted with VHF and Iridium GPS transmitters and 2 with VHF only transmitters. Bighorn sheep carrying VHF transmitters were visually located on average once per week yearlong during 1997 and 1998. During 1999–2021, intensive fieldwork was conducted during spring (April through June) and for 2 months during fall (September through early December). We visually located radio collared bighorn sheep in the Upper Canyon herd or estimated their locations by triangulation 2–4 times per month during field periods 1999–2021. We programmed Iridium GPS units to return two locations per day 12 hours apart and to download location data twice per week. VHF and GPS collars were programmed to transmit a mortality signal if bighorn did not move for 6 hours.

We fitted 13 (11 ewes and 2 rams) of 24 bighorn sheep transplanted from the Upper San Juan Canyon herd to initiate the Lower Canyon in October 2003 with VHF transmitters. In 2010 20 bighorn sheep were transplanted to the Lower Canyon from the Upper Canyon in a supplemental transplant to expand herd range. We equipped 15 of these 20 sheep with VHF transmitters. In 2015 we captured 4 ewes and 1 ram equipped them with VHF transmitters and released them on the Lower Canyon range. We visually located or estimated by triangulation the locations of these bighorn sheep 1–2 times per month during field periods 2004-2021. In 2018 we captured 13 additional bighorn sheep and fit them with Iridium GPS transmitters and released them in the Lower Canyon.

In January 2008, 30 bighorn sheep were transplanted to Wetherill Canyon in Glen Canyon. We radio collared 20 of these transplants (17 ewes, 3 rams) with VHF transmitters. To expand their range, in 2015 we conducted a supplemental transplant of 14 bighorn sheep (12 of which, 10 ewes and 2 rams) were equipped with VHF and Iridium GPS transmitters into Mountain Sheep Canyon east of Wetherill Canyon. We located radio collared bighorn in Glen Canyon 1-2 times during spring field seasons and once during fall field seasons from 2008–2021.

For each visual observation, we recorded location, habitat use, movements, group size, sex-age composition, lactation status of ewes, association with a lamb for marked ewes, marked bighorn sheep present, and social behavior of marked and unmarked individuals. Interactions between bighorn sheep and domestic livestock, interactions between bighorn sheep and predators, and interactions between bighorn sheep and humans or humans with dogs were recorded. When we received a mortality signal, we attempted to locate the carcass and determine the cause of death. Causes of death were assigned based on observations of marked bighorn sheep prior to death and examination of the carcass and mortality site. When carcasses were found in good condition, we submitted the head and portions of the lungs to the Navajo Nation Veterinary Program for examination.

From 2010 on we collected nasal swabs and blood from all bighorn sheep captured and submitted them to the Washington Animal Disease Diagnostic Laboratory (WADDL) for PCR and Elisa testing for *M. ovipneumoniae*. We surveyed potential transplant areas on the Navajo Nation using fixed wing and helicopter aerial surveys, and boat-based surveys. Minimum population sizes were estimated by locating as many as possible of the bighorn ewes with active radio collars within a time span that precluded interchange among groups and counting them and their marked and unmarked associates. To this total we added the number of marked individuals known to be on the study area that were not observed. We estimated the number of adult rams based on the observed ratio between adult rams and ewes during the rut.

RESULTS

The original population in the Upper San Juan River Canyon in 1997 was 31 bighorn sheep. In 1997 cattle grazed virtually the entire river corridor through the bighorn range and the central area of the bighorn range. A gate to protect the bighorn range from poaching was vandalized and a ram was killed illegally. We observed bighorn displaced from the river corridor by boaters with dogs and boaters camping in areas critical to the bighorn for river access and lamb rearing. Our first recommendations were to construct barriers to protect most of the river corridor in the bighorn range from cattle grazing, negotiate an end to cattle grazing in the center of the bighorn range, repair gates to limit access and discourage poaching, eliminate dogs from accompanying boaters through the bighorn range and close overnight camping in critical areas used by bighorn for access to the river and lamb rearing (Goodson et al. 1999). Barriers were erected in the canyon to prevent cattle access to approximately 80% of the river corridor through bighorn range. An agreement was reached with Navajo grazing authorities to eliminate cattle grazing in the central area of the bighorn range. We were fortunate that there were no valid Navajo Nation grazing permits within the river corridor in the bighorn range. Two areas of the river corridor where we observed ewes with young lambs accessing the river to drink and which were used disproportionately by ewes rearing lambs were closed to overnight camping administratively by the Navajo Nation to protect the bighorn from disturbance (Goodson et al. 1999). The BLM managed recreation on the San Juan River and incorporated information on the closures in the information they provided to permit applicants. BLM river rangers met river runners at the launch sites to check permits and patrolled the river enforcing regulations. Based on our concerns the BLM eliminated dogs from accompanying boaters through the Upper Canyon bighorn range making the river and riparian vegetation more accessible for the bighorn. The Navajo Department of Fish and Wildlife facilitated repair and fortification of the 2 gates controlling access into the bighorn range.

The herd grew from a pre-lambing minimum of 31 in March to a fall estimate of 37 in 1997. In 1998 the herd grew to a minimum of 45, in 1999 to a minimum of 56, in 2000 to at least 61, in 2001 to minimum of 65, in 2003 to at least 85. Excellent mean annual survival of adult ewes during 1997-2001 (0.97, 90% CL 0.93, 1.00) was important to population growth. Mean annual survival of adult rams was lower 0.86 (90% CL 0.75, 0.97). Survival of lambs from birth through fall declined from 0.80, 90% CL 0.67, 0.93 (1997-1998) to 52%, 90% CL 0.40, 0.64 (2000, 2001) (Goodson et al. 2002). By 2002 the herd had grown to sufficient size to enable us to consider expanding bighorn sheep presence on the Navajo Nation through establishment of a second herd. We also recommended limited permit hunting of mature rams beginning in 2001.

In 2001 a single ram permit was sold by the Navajo Department of Fish and Wildlife through the Foundation for Wild Sheep. Over the next decade hunting was expanded to three tags for trophy rams through auctions and fourth permit was assigned through a lottery for tribal members.

Bighorn sheep transplants and movements

We began surveys in the San Juan Canyon below Mexican Hat (Lower San Juan Canyon) to assess its suitability as a transplant location in 2002. The Lower San Juan Canyon was a continuation of the Upper San Juan Canyon with similar vegetation and topography. The Lower Canyon was approximately twice the length of the Upper Canyon but had more limited side canyons. We found records of bighorn in the Goosenecks of the Lower Canyon from as recently as the mid-1960's (Wilson 1968) but no sign of current occupancy by bighorn sheep. Suitable bighorn sheep habitat in the Lower San Juan Canyon was separated by only 3 km of unsuitable terrain, a highway (US 163), and a small town, Mexican Hat, Utah from the Upper San Juan Canyon range.

In fall 2003 24 bighorn sheep were captured in the Upper Canyon and released in the Lower Canyon. The release site was 40 river miles (40 km straight line) from the range of the source herd in the Upper Canyon. Captured bighorn were trucked to the canyon rim and slung by helicopter about 1 km into the canyon. The new herd increased to a minimum count of 90 bighorn sheep in 2010. In December 2010 we transplanted 14 bighorn sheep from the Upper Canyon to the Lower Canyon to expand the new herd's range down canyon and reduce density in the Upper Canyon range. These bighorn were released 60 river miles and 50 straight line kilometers from the source herd range. Bighorn in the Lower Canyon were counted during 2-4 river trips each year. Our highest count of bighorn sheep from the river was 59 in 2008, 50 in 2010, 107 in 2011, and 137 in 2012. Weather conditions influenced counts with higher counts achieved in hot, dry conditions when bighorn concentrated near the river. We estimated the Lower Canyon herd to include at least 150 bighorn sheep in 2013.

In 2005 we began the search for another release site. We conducted aerial and boat-based surveys of the San Juan Arm and south (Navajo) side of Lake Powell. We selected Wetherill Canyon as a transplant site due to its extensive habitat, distance from domestic sheep grazing and access to water. In January of 2008 we transplanted 30 bighorn sheep from the Upper San Juan Canyon to near the mouth of Wetherill Canyon in Glen Canyon. The release site was 120 km from the range of the source herd. We trucked the bighorn sheep in crates to the end of the closest road on the west side of Navajo Mountain. From there the bighorn were slung by helicopter about 20 km to the release site near the mouth of Wetherill Canyon.

In January 2015 we made a second transplant of bighorn sheep from the Upper San Juan Canyon herd to Glen Canyon. Fourteen bighorn sheep were released at the mouth of Mountain Sheep Canyon east of Wetherill Canyon to extend the range of the transplant herd and reduce density on the Upper San Juan Canyon herd range. From 1997 to 2013 desert bighorn sheep populations on the Navajo Nation grew from 31 bighorn in a single herd to over 500 bighorn sheep in three herds (Figure 2).

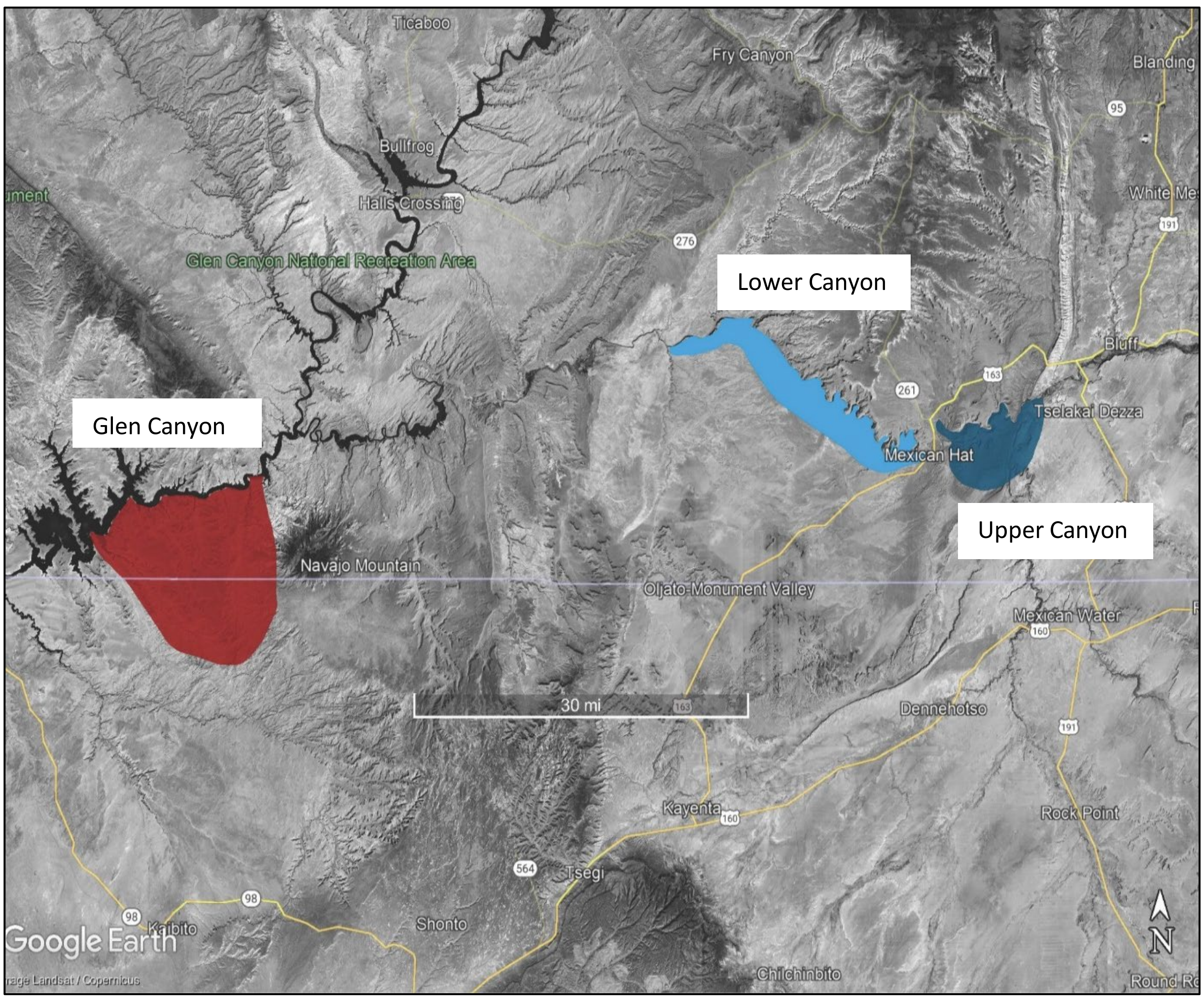

Figure 2. Locations of desert bighorn herds on the Navajo Nation.

In 2008 the Utah Department of Wildlife Resources (UDWR) released 30 bighorn sheep into John's Canyon across the San Juan River from the Lower Canyon herd. The initial release was followed by supplemental releases into John's Canyon in 2013 (16 bighorn sheep) and 2014 (6 bighorn sheep). In 2013 the UDWR released 49 bighorn at Nokai Dome on the San Juan Arm of Lake Powell about 50 km from the Glen Canyon herd and about 40 km from the Lower Canyon herd (pers. comm. Jace Taylor, UDWR, April 18, 2019) (Figure 3). The John's Canyon herd range was about 40–55 km south of ranges of the Red, White and Dark Canyon herds that had suffered die offs in the 1980s and had not recovered (pers. comm. Jace Taylor UDWR April 18, 2019) (Figure 3).

We radio tracked and observed bighorn rams crossing the San Juan River to the north (BLM) side and returning to the Navajo (south) side in both the Upper and Lower Canyon ranges. The UDWR (Annette Rouge pers. comm. April 17, 2015, pers. comm. Dustin Mitchell, UDWR, April 29, 2019) recorded radio collared rams moved from the transplanted herd in John's Canyon north to the range of the Red Canyon herd and returned to John's Canyon. GPS locations from bighorn sheep we released at Mountain Sheep Canyon in Glen Canyon showed at least two rams and two ewes crossed Lake Powell to the north shore at the Kaiparowitz plateau and returned to Mountain Sheep Canyon. At least 2 other radio collared rams travelled south to a domestic sheep flock on Navajo Canyon about 40 km from the area used regularly by radio collared ewes of the Glen Canyon herd. We also received a report of two rams crossing US highway 163 moving from the Upper to the Lower San Juan Canyon near Mexican Hat, Utah (pers. comm. Rick Boretti, BLM, October 2012) (Figure 4).

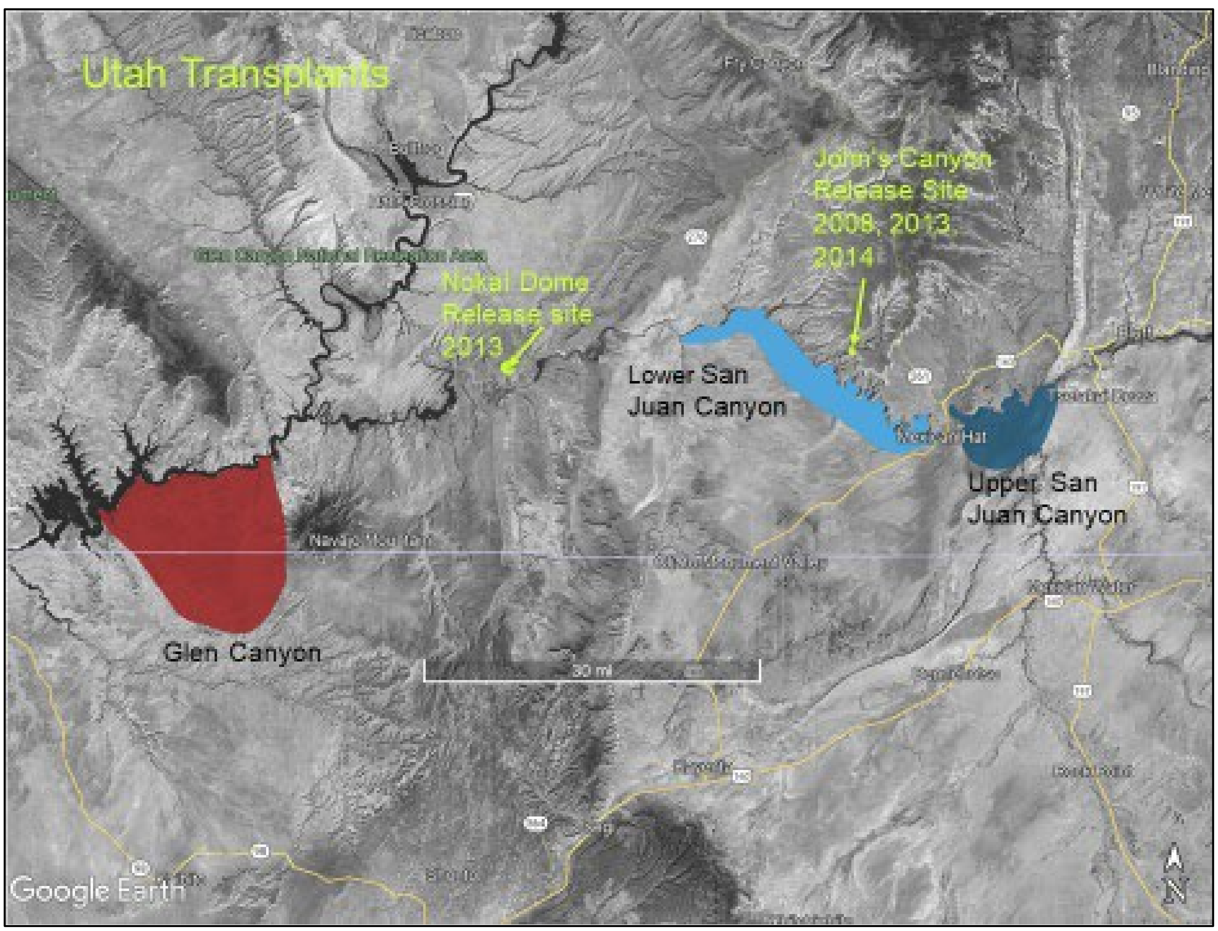

Figure 3. Utah Department of Wildlife Resources transplants of desert bighorn sheep near the Navajo Nation.

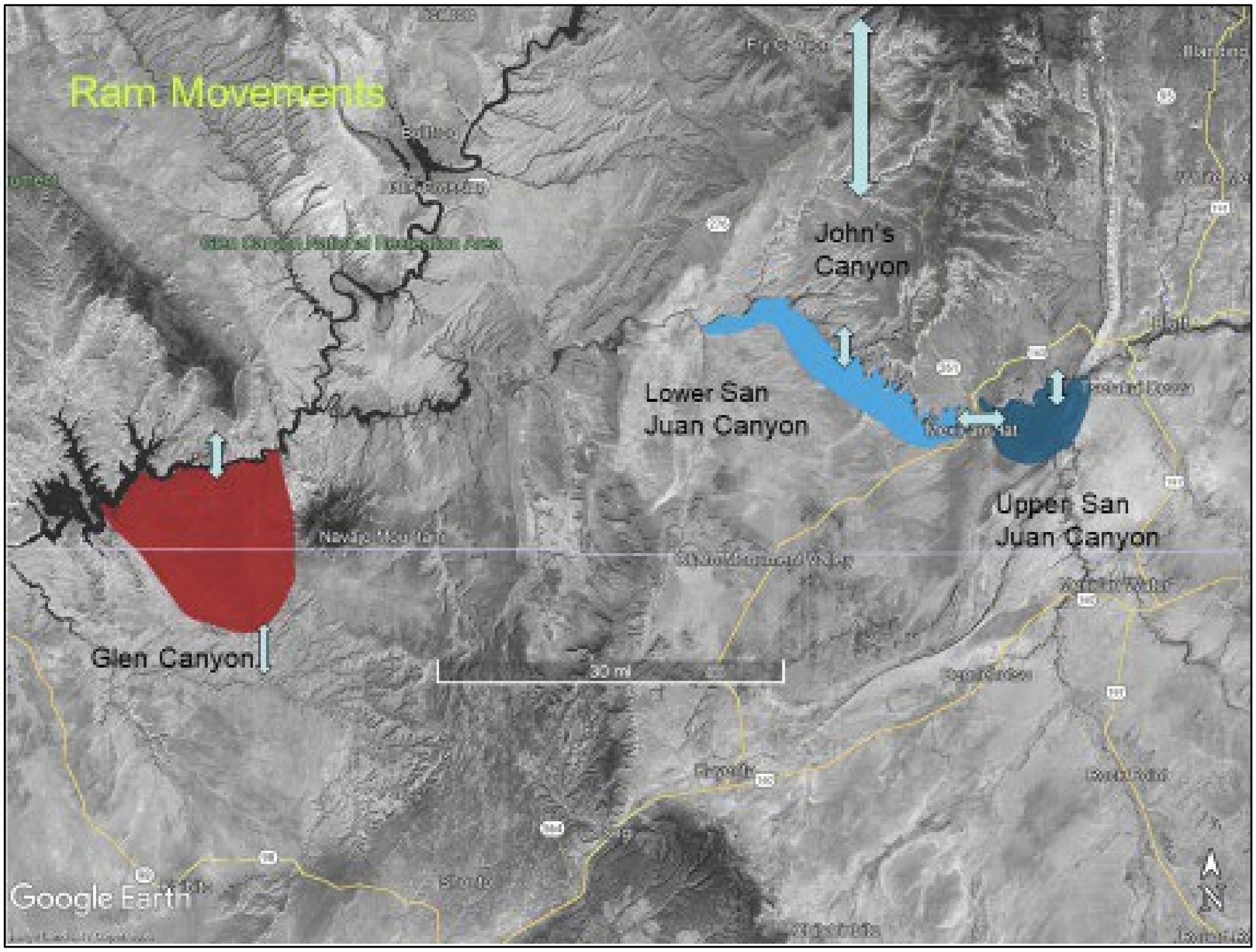

Figure 4. Ram forays outside core ranges 2000–2014.

Population declines and disease testing

In the Lower Canyon lamb:ewe ratios in October ranged from 0.7 to 1.0 during 2004-2013. In October 2014 we observed 20 ewes and 0 lambs. In the Upper Canyon fall lamb:ewe ratios were consistently over 50 percent from 1997 through 2015. Typical ratios were observed in December 2014 (0.78) and December 2015 (0.62). In 2016 we observed 29 ewes in December and 4 lambs (lamb:ewe ratio 0.24). In December 2017 we observed 38 ewes and no lambs. In the Glen Canyon the lamb:ewe ratio in October before Movi infection (2015–2017) averaged 0.62. After infection (2019–2020) the average fall lamb:ewe ratio declined to 0.39.

All bighorn sheep captured in the Upper Canyon in 2010 (N=20) tested negative for *M. ovipneumoniae*. After the decline in lamb survival observed in 2014 we captured 5 bighorn in the Lower Canyon and tested them for *M. ovipneumoniae*. All 5 were positive for Movi by both Elisa and PCR indicating exposure and active infections. In 2015 we captured and tested 16 bighorn sheep from the Upper Canyon and all were negative for Movi on PCR and Elisa. In 2018 M. ovipneumoniae was detected using PCR in all three herds (Upper Canyon N=18, Lower Canyon N=13, Glen Canyon N=8). The proportion of bighorn testing positive were Lower Canyon (0.92), Glen Canyon (0.38) and Upper Canyon (0.20). In 2020 bighorn captured in all three herds tested positive for Movi using PCR (Lower Canyon, N=10, 50% detected, Upper Canyon, N= 29, 28% detected, Glen Canyon, N=50, 6% detected (Figure 5).

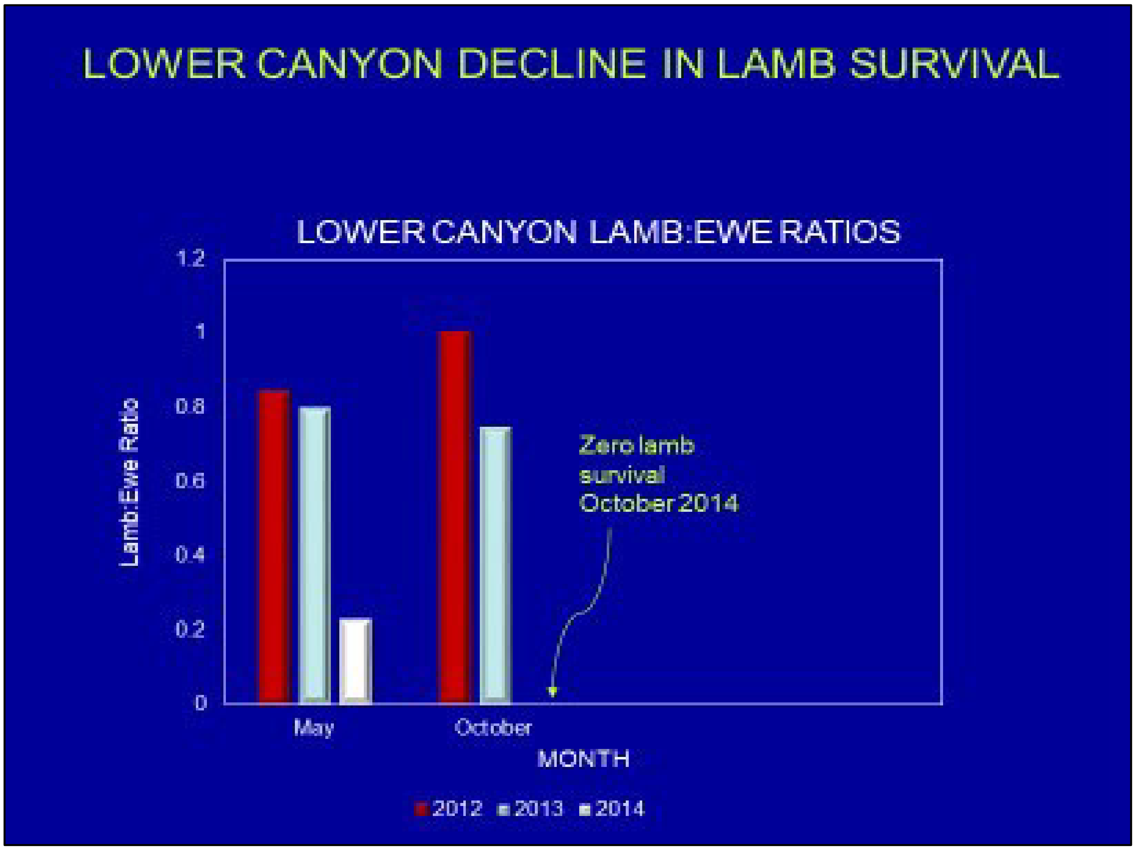

Figure 5. Lower Canyon spring and fall lamb:ewe ratios 2012–2014.

In the Lower Canyon population estimates declined from 174 in 2012 (minimum count 137) to 46 (minimum count 33) in 2020. In the Upper Canyon population estimates declined from 320 (minimum count 189) in 2016 to 100 (minimum count 63) in 2020. We estimated the Glen Canyon herd remained stable at about 300 bighorn sheep from 2017-2020 based on stable minimum counts in Wetherill and Mountain Sheep Canyons (2015, 93; 2016, 88; 2018, 74; 2019 95; 2020, 91) and lamb recruitment (fall lamb:ewe ratios 2015, 0.64; 2016, 0.67; 2017, 0.54; 2019, 0.52; 2020, 0.26).

Strain-typing, based on 4 loci, was conducted by WADDL on samples provided in 2018 and 2020. Strain 1 was shared between the Upper and Lower San Juan Canyon and Nokai Dome (a Utah transplant herd across the San Juan Arm of Lake Powell and over 30 km distant from both the Lower Canyon and Glen Canyon herds). This confirmed that at least one strain (Strain 1) was transmitted from the Lower to the Upper Canyon and indicated the same strain crossed the San Juan River. Strain 2 was identified in Glen Canyon and was shared with the Kaiparowits herd on the other side of Lake Powell indicating that this strain crossed Lake Powell. Strains 3 and 4 were identified in the Lower and Upper Canyon herds and did not match any other strains. Earlier trees provided by WADDL based on the same data using IGS found a match between the Lower Canyon and John's Canyon herds and indicated Strain 4 in the Upper San Juan Canyon was identical with Strain 1 shared with the Nokai Dome and the Lower Canyon herds (Figure 6).

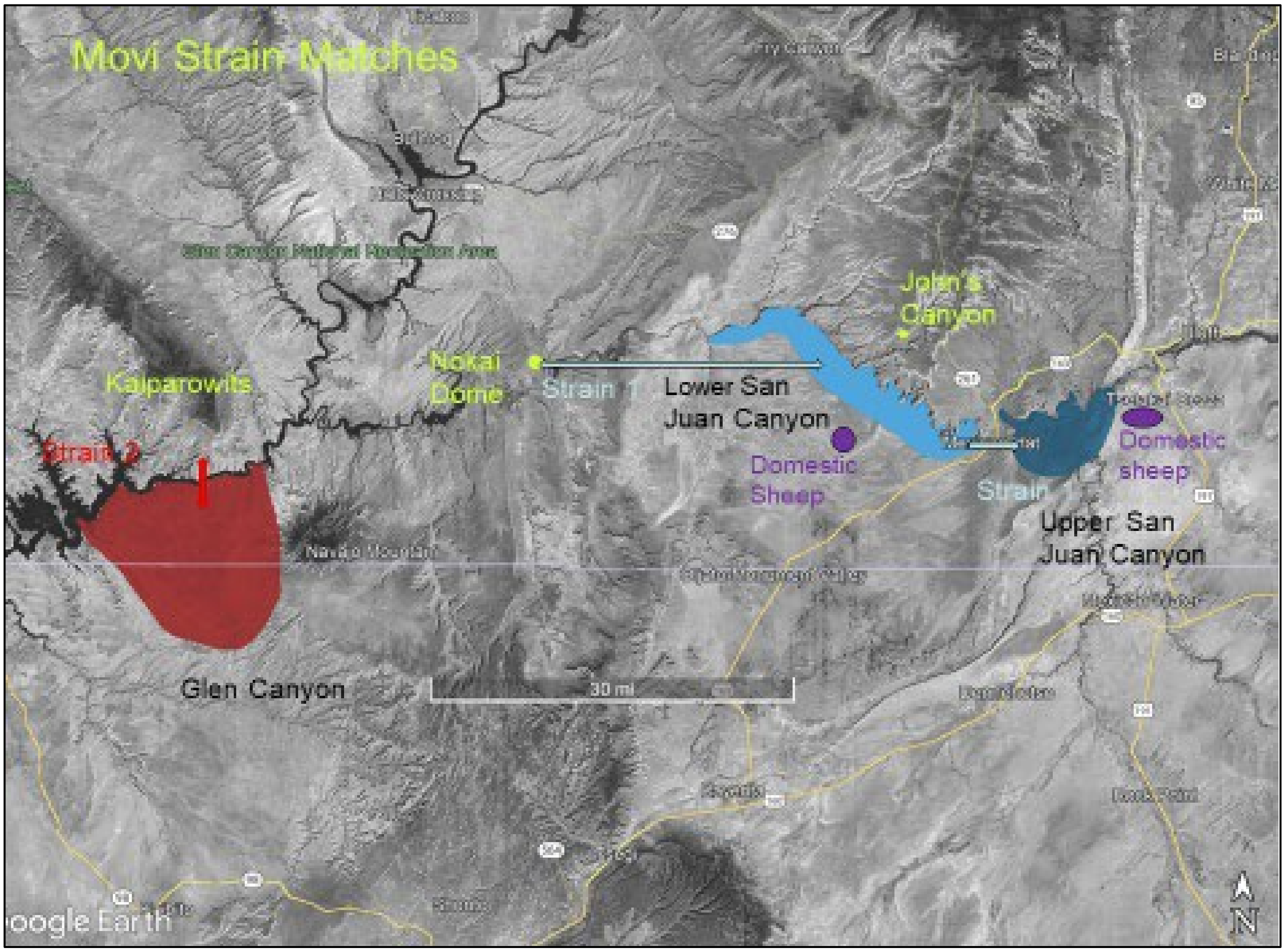

Figure 6. Strain matches among bighorn sheep herds on the Navajo Nation and nearby bighorn sheep herds in Utah.

Local domestic sheep flocks were tested for *M. ovipneumoniae* in 2012 (all domestic sheep in 3 flocks containing 14, 24, and 50 sheep, respectively). Over half (54%) of the domestic sheep were positive for *M. ovipneumoniae* using PCR. Samples from domestic sheep were strain tested by WADDL in 2021 and no matches were found between strains identified in bighorn sheep tested in 2018 or 2020 and strains identified in local domestic sheep flocks.

Navajo domestic sheep flocks are typically grazed near homesteads. Flocks often include goats and sheep and are usually accompanied by dogs. Navajo sheep ranchers usually pen their flocks at night. These precautions are needed to protect flocks from feral dogs which are common on the Navajo Nation and coyotes. They may also serve to reduce the risk of close contact between bighorn sheep and domestic sheep. We also received one unverified report that bighorn

M. ovipneumoniae. Three helicopter capture operations were required to capture all surviving ewes

rams observed close to Navajo domestic sheep were shot because of a Navajo belief that the bighorn ram would transmit disease to their flock.

A domestic sheep flock grazed within 1.5 km of the Upper Canyon bighorn range from 1997-2021. No domestic sheep flocks grazed within 4 km of the Lower Canyon herd range from 2002–2021. However, strain testing and timing of lamb mortality indicate that the Lower Canyon was infected with *M. ovipneumoniae* before the Upper Canyon and transmitted at least one strain to the Upper San Juan Canyon herd. All captured Upper Canyon bighorn (N=16) tested negative for *M. ovipneumoniae* in 2015, after Lower Canyon ewes lost their entire 2014 lamb crop and all 5 bighorn captured in the Lower Canyon in 2015 tested positive for *M. ovipneumoniae*.

In 2021–2022 we conducted a capture, test and remove operation to clear the Lower Canyon herd of in the Lower San Juan Canyon. Bighorn hid under ledges after the first hour of capture and capture success declined. A total of 13 bighorn ewes were captured, 8 ewes tested positive for *M. ovipneumoniae* and 5 ewes tested negative. All ewes testing positive were removed from the population during a fourth helicopter operation.

In October 2022 for the first time since 2013 ewes in the Lower Canyon raised healthy lambs. The 5 surviving ewes were observed with 3 lambs in October, a lamb:ewe ratio of 0.60. Ewes in the Upper Canyon (N=20) were captured and tested for *M. ovipneumoniae*, (5 positive, 25%), however, none was removed. In December of 2022 we observed 5 healthy lambs and a total of 23 ewes in the Upper Canyon. The fall lamb:ewe ratio in the Upper Canyon (0.22) was the highest observed since 2016.

DISCUSSION

Chronic or acute pneumonia in bighorn sheep related to infection with *M. ovipneumoniae* has been implicated in many bighorn sheep declines and die-offs. It has caused increased adult mortality and severe and persistent declines in lamb survival (Besser et al 2012). Infections of M. ovipneumoniae typically cause all-age die-offs followed by low lamb survival. This pattern is caused by differential immune competency in adult and juvenile bighorn sheep. Adult bighorn sheep have stronger immune systems than lambs. Some ewes that survive the initial die-off clear the infection. Other ewes survive but are not able to clear the infection and continue to shed bacteria. It is these carrier ewes that maintain the disease in the population. Lambs receive passive immunity from their mothers through suckling. However this protection is short lived. Lambs typically develop pneumonia between 2 weeks and 2 months of age and most succumb before they reach 3 months of age. Persistent pneumonia in lambs had caused long term declines in bighorn sheep populations and led to extirpation of some herds (Besser et al. 2012, Besser et. al. 2021). Infection with *M. ovipneumoniae* was associated with near zero lamb survival in the Lower San Juan Canyon herd from 2014 through 2021 and with poor lamb survival in the Upper San Juan Canyon herd from 2016–2021.

The likely sources of *M. ovipneumoniae* infection in the Lower Canyon were bighorn sheep that the UDWR transplanted across the river from the Lower Canyon into John's Canyon in 2008. At least 2 rams from the John's Canyon herd moved north and contacted bighorn of the Red Canyon herd (Annette Roug, UDWR, pers. comm. April 17, 2015; pers. comm. Dustin Mitchell, UDWR, April 29, 2019). The Red Canyon herd and nearby White Canyon and Dark Canyon herds underwent pneumonia die-offs in the 1980's and 1990's following an introduction of domestic sheep into the range of the Dark Canyon herd. None of these herds have recovered. They remain at a population level less than half of pre-die-off abundance (pers. comm. Jace Taylor, UDWR, April 18, 2019, personal communication Dustin Mitchell, UDWR, April 29, 2019). Bighorn rams crossed the San Juan River in the Lower Canyon and move between the Lower and Upper Canyons. It is likely that rams moving across the river infected the Lower Canyon herd in 2013-2014. In 2015-2016 1 or more rams likely moved from the Lower Canyon to the Upper Canyon infecting the Upper Canyon herd with *M. ovipneumoniae*. Strain matches confirmed that the Lower Canyon and Upper Canyon herds share at least one strain of *M. ovipneumoniae* and that the same strain is present across the San Juan River in Utah bighorn sheep herds. The John's Canyon and Nokai Dome herds in Utah that share Movi strains with the Navajo San Juan Canyon herds have experienced low lamb survival similar to the Lower and Upper San Juan Canyon herds (personal communication Jace Taylor, UDWR, April 18, 2019).

Infection with *M. ovipneumoniae* was confirmed in the Glen Canyon herd in 2018. Strain testing indicated that bighorn sheep from Glen Canyon crossed Lake Powell and were infected by bighorn sheep on the Kaiparowitz plateau that use the opposite shore of Lake Powell. Movements of GPS equipped bighorn confirmed that both ewes and rams crossed Lake Powell near the mouth of Mountain Sheep Canyon where Lake Powell is at least 0.8 km wide and returned to Mountain Sheep Canyon. Thus Glen Canyon bighorn were infected with a different strain of *M. ovipneumoniae* that our data indicated had less severe impacts on survival of lambs and adults.

Recent publications have documented successful efforts to recover bighorn herds infected with M. ovipneumoniae (Garwood et al. 2020, Besser et al. 2021, Cassirer and Besser 2025, Weyand et al. 2025). In the past wildlife management agencies responsible for bighorn sheep populations that were suffering long-term declines due to pneumonia had few options to deal with the situation. Usually bighorn sheep herds recover without intervention; however, clearing *M. ovipneumoniae* from a herd can take decades and recovery is not assured (George 2009). Use of improved disease testing has provided better information on the course of the disease and suggested alternative management. Results of research on *M. ovipneumoniae* epidemiology in the Hells Canyon metapopulation of Rocky Mountain bighorn sheep suggested testing of bighorn sheep to identify carrier ewes could be useful in management (Cassirer et al. 2020). Two types of tests are commonly used: blood tests that determined antibodies (Elisa) in blood that indicate prior exposure to the disease and PCR tests on nasal swabs that indicate bighorn that are shedding bacteria in their nasal passages. The PCR test permits identification of bighorn sheep that continue to shed bacteria maintaining Movi in the population and causing persistent lamb mortality (Cassirer et al. 2020).

Weyand et al. (2018, 2025) presented results from experiments in which bighorn ewes that tested positive for *M. ovipneumoniae* on PCR were removed from groups of captive bighorn ewes and from free-ranging herds. Lambs survived in pens with no carrier ewes and in free-ranging herds where carrier ewes were removed. All lambs died in pens including carrier and non-carrier ewes. It was not necessary to cull rams. Rams join ewes during the rut when lambs are about 6 months old and lamb immune systems have matured so that most survive a *M. ovipneumoniae* challenge. Removal of carrier ewes succeeded in increasing lamb survival in penned studies and in free-ranging bighorn sheep herds in Hells Canyon, Montana and South Dakota (Cassirer et al. 2017, Garwood et al. 2020, Besser et al. 2021, Cassirer and Besser 2025, Weyand et al. 2025). Lamb survival rebounded in the Lower Canyon herd following removal of ewes that tested positive for *M. ovipneumoniae* providing preliminary evidence for population recovery.

MANAGEMENT IMPLICATIONS

When transplanting into or near ranges occupied by other bighorn sheep consider transplanting only ewes. Our first transplant to Glen Canyon in 2008 was into unoccupied bighorn range and none of the transplanted bighorn with radio collars moved large distances or swam Lake Powell.

We recommend multiple years of capture and testing to determine whether ewes carry *M. ovipneumoniae* consistently and removing only ewes that test positive at least twice for *M. ovipneumoniae* in 2 different years. Capturing testing and removing in one year may result in removing ewes that are not consistent carriers. We received different result for 2 nasal swabs collected from the same ewe during a single capture. We recommend testing 2 nasal swabs per ewe for *M. ovipneumoniae* using PCR, considering only ewes that test positive on both swabs as positive for *M. ovipneumoniae*, and removing only ewes that test positive on both swabs for at least 2 years. An objective of capturing 60–80 percent of ewes each year and capturing and testing over several years would provide more reliable results and result in fewer ewes removed. Monitor fall lamb survival to determine success. A fall lamb:ewe ratio of greater than 50 percent would indicate a recovering herd.

We recommend intensive field monitoring on bighorn sheep ranges with high levels of recreation and/or livestock use to determine conflicts and develop mitigation strategies. In our study field monitoring determined areas where erection of barriers would eliminate cattle from extensive areas of river canyon and identified areas critical to bighorn for access to water and riparian vegetation.

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Holding On: Forty Years of Bighorn Sheep Habitat Mitigation Along Koocanusa Reservoir in Northwest Montana

ETHAN S. LULA, *Montana Fish, Wildlife and Parks, MT, 59873, USA; ethan.lula@mt.gov*
CHRIS HAMMOND, *Montana Fish, Wildlife and Parks, MT, 59873, USA*
LAUREN MICHELSON, *USDA Forest Service, MT, 59804, USA*
TY SMUCKER, *Montana Fish, Wildlife and Parks, MT, 59873, USA*

ABSTRACT: In 1972, the Libby Dam, in northwest Montana, was completed, resulting in the flooding of 175 kilometers of the Kootenai River and the formation of the transboundary Lake Koocanusa. Having historically occupied the eastern slopes of the Kootenai River Valley, the native Ural-Tweed population of bighorn sheep (*Ovis canadensis*), lost approximately 1,761 ha of low-elevation winter and spring habitat during inundation. In 1984, a joint agreement between the Bonneville Power Association (BPA), Montana Fish, Wildlife and Parks (MFWP), and the Unites States Forest Service (USFS) was initiated with the purpose of improving the remaining habitat to ensure the persistence of the Ural-Tweed population. Since then, the USFS has treated and retreated approximately 11,330 ha of forest with various silvicultural prescriptions and prescribed fire. Despite this effort, the Ural-Tweed population declined from an estimated 150–200 animals in 1990, to a contemporary estimate of less than 40. In 2018, GPS data from 2 collared females indicated that seasonal use of historic range had greatly been reduced, prompting FWP and the USFS to begin evaluating the effects of past treatments and the factors limiting population growth. Included as part of a 2022 statewide adaptive management research project, efforts have been directed towards capturing bighorn sheep within the Ural-Tweed population for demographic and space use monitoring concurrent with ongoing habitat treatments. Results of this work will be used to focus habitat treatments, improve population monitoring, and revise the collaborative mitigation strategy along Lake Koocanusa.

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KEYWORDS: adaptive management, bighorn sheep (*Ovis canadensis*), habitat mitigation, habitat treatment, Kootenai River, Lake Koocanusa, Montana, Ural-Tweed.

Toward Resolving the Domestic/Wild Sheep Grazing Issue on Public Lands: A Suggested Paradigm Shift in Government Policy

RICHARD B. HARRIS, *Washington Department of Fish and Wildlife (retired), Charlo, MT 59824, USA; rharris@montana.com*

ABSTRACT: The conflict between the interests of wild and domestic sheep on public lands arising from risk of pathogen spillover has embroiled public agencies in the U.S., frequently invoking lawsuits and interest-based legislation. I review the long and frustrating history of efforts to protect bighorn sheep from contact with commercially-raised domestic sheep in central Washington State, USA. I suggest that such seemingly intractable conflicts result from outdated public policy that fails to acknowledge the legitimate interests both of wildlife advocates and of those livestock producers who have premised their business model on access to public land. A useful analogy is the response by public agencies to attitudinal changes toward large predators. For decades, public policy favored eradication of wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and mountain lions (*Puma concolor*), allowing livestock producers in the western U.S. to set up their operations with modest risk of depredation. As public views evolved and resource agencies changed course these predators began a comeback, albeit with attendant costs to producers. However, public policy did not expect producers to shoulder the entire burden. Instead, governments acknowledged the altered landscape by instituting programs to assist producers in minimizing conflicts, and to compensate them monetarily when losses occurred. Similarly, sheep grazing on public land began well before wide recognition of their ability to transmit pathogens (primarily *Mycoplasma ovipneumoniae*) to their wild cousins. Public support of bighorns on public lands, along with awareness of the conflict with domestics, has since increased. However, unlike the analogous policy toward large predators, publicly funded programs in the U.S. that could facilitate moving domestics well away from wild sheep (or retiring grazing allotments entirely) have not been instituted. Thus, wild sheep advocates and domestic producers are faced with a zero-sum situation, in which one side must absorb considerable losses for the other to achieve its goals. Unsurprisingly, both sides dig in, solicit outside support, and decisions are informed more on the basis of political power than on comprehensive and fair public policy. I suggest public funding should reflect both the public's uncontested support for wildlife on public lands as well as fairness for producers for whom the rules have changed and could provide the needed catalyst to transcend the current impasse.

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KEYWORDS: bighorn sheep (*Ovis canadensis*), compensation, disease, domestic sheep, fairness, governance, policy, U.S. Forest Service, Washington State.

There are no villains in this story. This discussion paper is not about individual people; rather it is about systems of governance. My contention is that good and honorable people have acted rationally given the prevailing incentives created by existing laws, regulations, and institutions. But those laws, regulations, and institutions—which I collectively term "governance"—have failed to successfully transform public desires for wild bighorn sheep (*Ovis canadensis*) on one hand, and for fairness and consistency on the other hand, into policy that would direct on-the-ground decisions and actions. The result has been dead bighorn sheep, reduced bighorn populations, polarized debate, defensiveness, science denialism, lawsuits, and general frustration in every direction.

In this discussion paper, I briefly review the history of attempts to protect bighorn herds in central Washington State, USA from pneumonia-causing pathogens transmitted by commercially-raised domestic sheep (*Ovis aries*) that legally graze on public lands (Appendix A). Following that, I consider how governance has framed the incentives that produced the standoff. First though, a caveat: to my knowledge, we lack definitive—at least of the sort that would stand up in a court of law—that the diseases documented in the bighorn herds at issue were caused via contact with commercially-raised domestic sheep. To the possible objection that my premise (i.e., that commercially-grazed domestic sheep pose a threat to the wellbeing of certain bighorn herds) is too speculative to merit this level of discussion, I would offer 2 responses: First, circumstantial evidence clearly implicates domestic herds as the cause of at least some disease events in central Washington (Bernatowicz et al. 2016, Appendix B). Second, even if *Mycoplasma ovipneumoniae* in wild bighorns had other origins, we know from well-documented events elsewhere (Cassirer et al, 2017, Manlove et al. 2019, Besser et al. 2021) the risk to bighorns from commercial herds was, and remains, substantial.

1. Brief overview of governance relevant to protecting bighorns in Washington from pneumonia (see Appendix A)

Bighorn sheep were extirpated from Washington by the early 20th century (Johnson 1983, 1996), in contrast to other jurisdictions in western North America, which although experiencing marked declines in bighorns from historic numbers nonetheless retained remnant populations (Buechner 1960). Documentation of the causes for the extirpation is scant, but it is likely that pneumonia-causing pathogens transmitted from formerly abundant domestic sheep (Oliphant 1948, Galbraith and Anderson 1991) were a substantial contributor to the factors of overhunting and habitat loss that are frequently invoked for historic bighorn declines (Johnson 1983, Cassirer et al 2017). Thus, extant bighorn sheep populations in Washington have all come about through translocation which began in 1957, with sheep sourced primarily from British Columbia and Montana. Whether by design or serendipity, the geographic distribution of bighorns in Washington by the early 21st century closely resembled our best estimates of their historic range (Figure 1), albeit with increased insularity and reduced connectedness among core habitats (Lyman 2009, WDFW 2015).

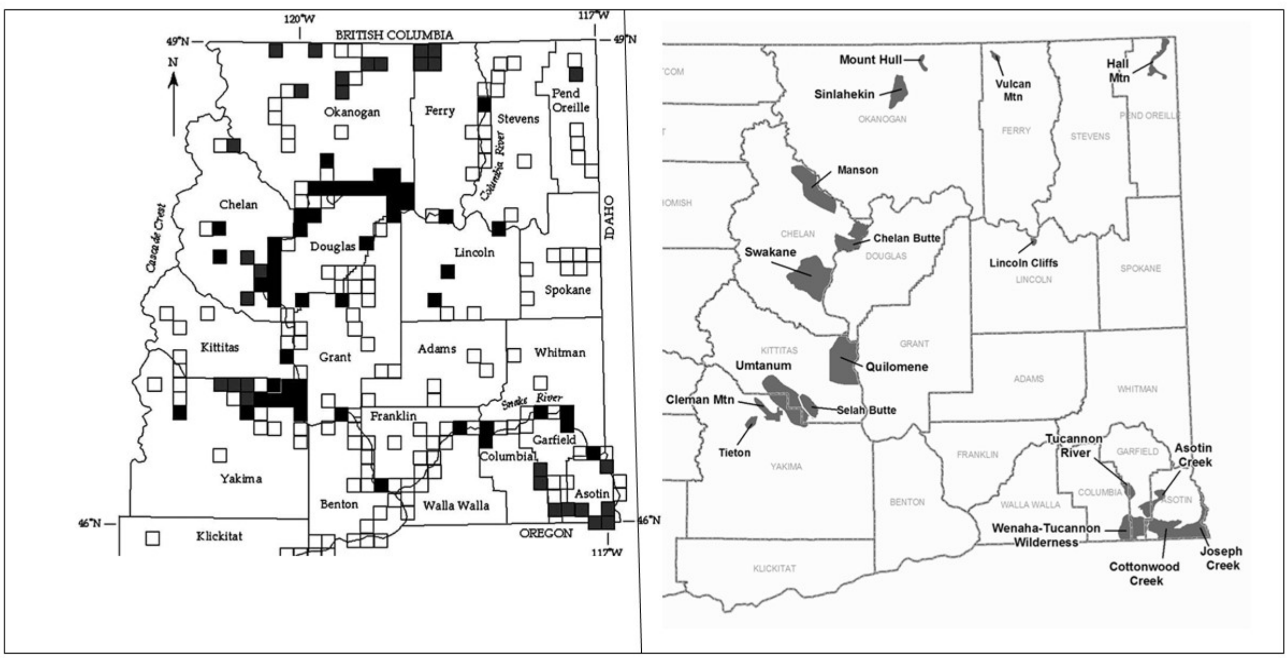

Figure 1. Maps showing approximate locations of bighorn sheep (*Ovis canadensis*) herds in Washington State, USA as of 2013 (right-hand panel), and townships sampled for palaeozoological remains by Lyman et al. (2009) (boxes) with the subset of those townships in which bighorns were either reported, or remains of bighorns were identified (prior to European settlement) indicated by filled-in boxes (left-hand panel). Note substantial correspondence between the two geographic distributions. Left-hand panel adapted from Lyman et al. (2009). County boundaries are shown in both panels for reference.

As is common in western U.S. states, large-scale commercial sheep farming in Washington declined in importance and scale during the 20th century (National Research Council 2008, Rousso 2020), with a notable exception being a large operation based southeast of Yakima that began in 1920. That family-run operation had as many as 12,000 sheep, although by 2017 had been reduced to less than half that number, but had always premised its business model on access to public lands for grazing during summer. Thus, by the time bighorns were returned to many historic habitats by the Washington Department of Fish and Wildlife (Johnson 1996), domestic sheep were already a seasonal presence on the landscape (Figure 2). Further, the owners/managers of sheep operations were well known and respected in the community and enjoyed a reputation of being both responsible and responsive to public and agency concerns.

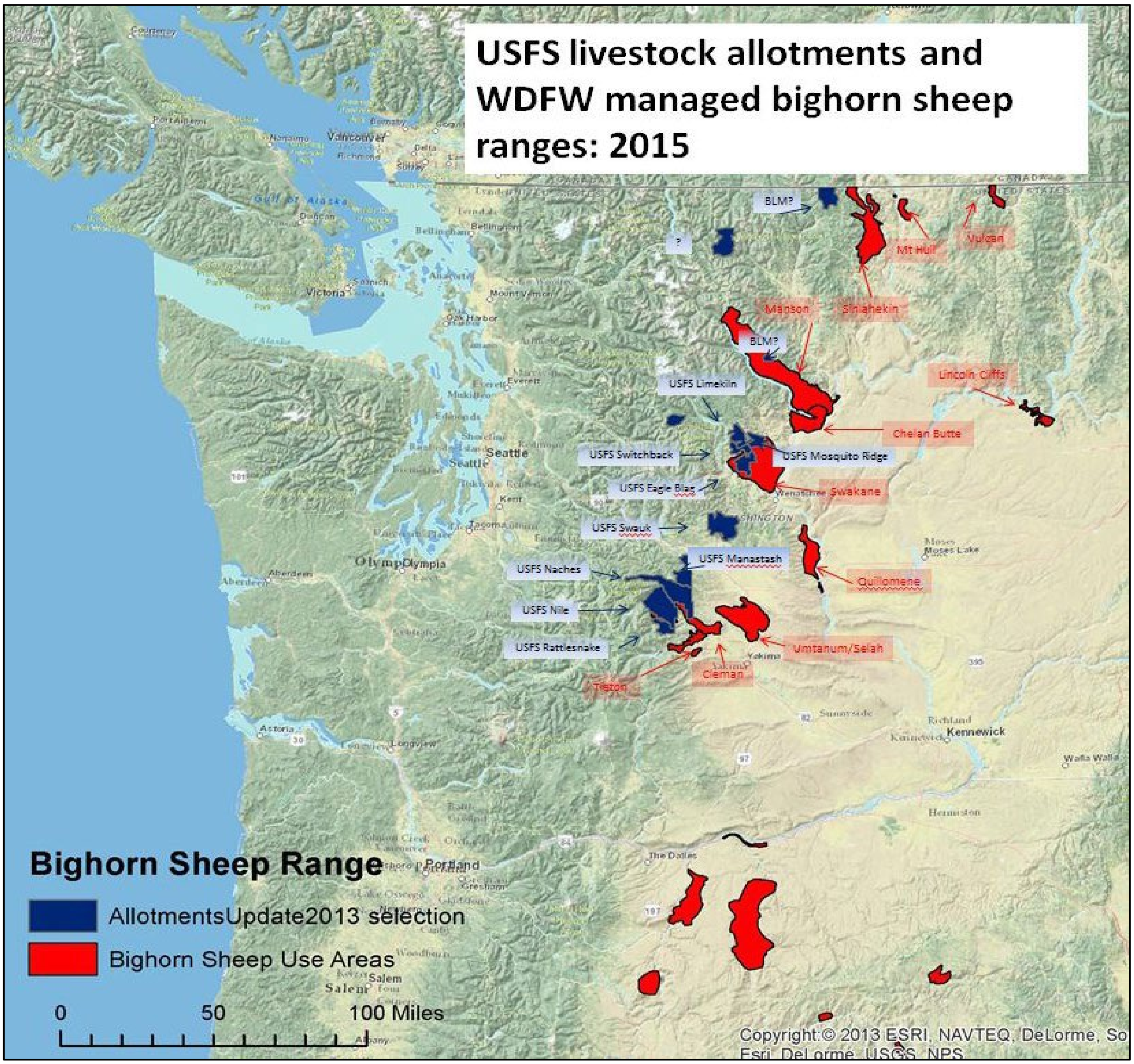

Figure 2. Map showing approximate locations of bighorn sheep (*Ovis canadensis*) herds in Washington State, USA as of 2013 (red polygons) and domestic sheep allotments on the Okanogan-Wenatchee National Forest and legally occupied by commercially-raised animals seasonally (blue polygons). Also shown are bighorn herd ranges in Oregon, not discussed in this paper.

From the outset, both wildlife managers at the Washington Department of Fish and Wildlife (WDFW) and land managers with the Okanogan-Wenatchee National Forest (OWNF) were aware that conflicts might arise between the newly repatriated bighorns and commercially-raised domestic sheep, primarily in the form of pathogen transmission (Foreyt and Jessup 1982, Wehausen et al. 2011). Until the late 20th century, neither the details of pneumonia nor the extent of movements by either wild or domestic sheep that could lead to pathogen transmission were fully appreciated. However, by 1998, with the reintroduction of bighorns in the Tieton River area near Naches, WA, a memorandum of understating (MOU) between the 2 agencies (WNF 1998) acknowledged that pathogen transmission from domestics could occur, and that spatial separation was desirable. Useful as this recognition was, the wording in this MOU maintained a somewhat detached tone regarding pathogen transmission, noting only that bighorns had previously been extirpated "for various reasons", relegating to WDFW the responsibility for evaluating "risks associated with bighorn sheep found mixed in with domestic sheep" and recommending "practices to prevent contact and potential transmission of diseases between wild and domestic sheep". However, the MOU tasked the OWNF not only with notifying WDFW when bighorns were known to enter a domestic allotment or when domestics were observed outside allotment boundaries, but also with taking "immediate action to remove those [domestic] animals" (Appendix A).

The following year, a similar agreement specific to the newly reintroduced Swakane and Manson bighorn sheep herds was signed by both agencies (WNF 1999).This second MOU went slightly further in articulating that "bighorned [sic] sheep and domestic sheep are incompatible due to disease transmission and cannot be allowed to interact" and required the Forest Service to keep domestic sheep "…outside agreed upon bighorn sheep management areas as a buffer for disease". However, the MOU acknowledged that domestic allotments existed within the bighorn management area and deferred until an unspecific future date resolution of that conflict.

Despite these MOUs and the increasing recognition generally of disease dynamics in sheep, grazing of domestic sheep continued under fundamentally unchanged policies during the early 2000s. If disease events occurred among bighorns, they were minor or at least failed to elicit substantial concern or controversy, perhaps because the bighorn herds remained small (albeit were growing both in abundance and distribution, Wampole 2023). Shortly after 2000 however, most bighorn herds managed by WDFW in the Cascade foothills began increasing markedly, as did the risk of pathogen transmission.

What had simmered as a hypothetical concern first came to a boil in November 2009 when pneumonia was first documented in the Umtanum/Selah bighorn herd, resulting in considerable mortality and (fruitless, if well-intended) agency-implemented culling of diseased bighorns (Bernatowicz et al. 2016). Although the source of infection was never identified—and indeed this herd was among the furthest from active domestic allotments—the risks to bighorns from domestics were highlighted by the occurrence of this herd collapse, which was similar to those that had occurred hundreds of miles away in the Hells Canyon Area for years (Cassirer et al. 2013), but which the Cascade foothill herds had not heretofore experienced.

About 2 years later, documents produced by the OWNF suggested that it might be taking the risks to bighorns from nearby domestic sheep increasingly seriously. In June 2011, it published a proposed action in preparation for updating its outdated forest plan, in which it hypothesized that its future course of action would be to "provide temporal or spatial separation between bighorn sheep and domestic sheep to reduce the risk of potential disease spread." In August 2011, a memo from the United States Forest Service (USFS 2011b) Deputy Chief in Washington, DC to all Regional Foresters spoke specifically and directly to the need to assess bighorn sheep viability "where management objectives include maintenance or enhancement of bighorn sheep populations". By March of 2012 the OWNF had completed a draft viability assessment of bighorns, but it was never finalized or formalized.

A second outbreak of pneumonia among bighorns on the OWNF in April 2013 appeared to elicit increased expressions of concern (if not actual regulatory actions) by the USFS (Appendix A). This time it was the previously thriving Tieton Herd that was affected, and the strain of *M. ovipneumoniae* involved was particularly virulent, killing about 90% of the herd within only a few weeks. Of relevance is that the Cleman Mountain herd was located directly adjacent to the Tieton Herd, and, despite documented movements between the two herds in the recent past, had yet to become infected. Thus, to protect the Cleman Herd from this evidently quite lethal strain, WDFW removed the few surviving Tieton animals (Bernatowicz et al. 2016).

In the wake of the dramatic collapse of the Tieton herd, the OWNF organized several presentations and discussions focused on the evident conflict between domestic and wild sheep from May 2013 to March 2016, some of which the public was invited to attend, others designed primarily as opportunities for agency staff to share views. During this time, a report that OWNF had contracted was finalized detailing the findings of the agency-sanctioned model quantifying the risk of contact between domestics legally grazing on allotments and each bighorn herd (Lyons et al. 2016). This report confirmed that most bighorn herds with ranges near or on the OWNF were at considerable risk. At almost the same time, however, the OWNF issued new ten-year grazing permits for domestic sheep on the existing allotments without formal review, new analyses, or public announcements.

During regularly scheduled meetings with regional USFS staff, WDFW biologists and leadership evinced increasing frustration with the lack of substantive actions by OWNF staff to prevent recurrences of the 2 disease outbreaks (Appendix A). Independently, groups representing the sheep industry (or the lessees themselves) produced letters to the agencies (as well as newspaper editorials) casting doubt on the notion that permitted domestic sheep might have had a role in the disease outbreaks, and even questioning the validity of the science that formed the understanding of the bacteria and the risk it posed to bighorns when in close proximity to domestic sheep.

In June 2016, the OWNF held an open meeting in Ellensburg, Washington, at which agency and Yakama Tribal staff (as well as academic researchers) updated the public on the science and the management issues, and where the OWNF announced that a formal reassessment of the sheep grazing allotments would soon commence. However, any plans the OWNF may have had to assess the allotments directly (as had been suggested in Ellensburg) were subsequently shelved in favor of a reevaluation of the allotments within the context of the Forest Plan. This alternative process was not initiated until May 2019, almost 3 years after the public meeting, and 2 months after pneumonia associated with *M. ovipneumoniae* had been diagnosed in yet another Cascade foothill herd (Mt. Hull). The first interagency, multidisciplinary team meeting associated with this new process occurred in September 2019, but progress on the analyses and writing of the associated document was slow.

In October 2020, dead rams and *M. ovipneumoniae* were found in a fourth bighorn herd (the aforementioned Cleman, which WDFW had earlier gone to great lengths to protect), and 12 additional bighorns were prophylactically removed from yet a fifth herd (Quilomene) after a domestic sheep belonging to the commercial operator (and later confirmed to harbor *M. ovipneumoniae*) was euthanized following a comingling event (Wampole 2023). In short, while the OWNF moved formal analyses forward at a snail's pace, it continued to permit commercial sheep grazing in the high-risk allotments at a time when pathogen transmission and disease events continued to occur. If the costs and benefits of permitting commercial sheep grazing were integrated into OWNF's decision-making, the externalities associated with them (i.e., costs to the public's interest in healthy bighorn populations) were evidently passed on to others.

In November 2020, a pair of wildlife advocacy groups sued the OWNF over its repeated failure to address the disease transmission issue, asking that the court enjoin the agency from authorizing domestic sheep grazing until analyses demonstrating compliance with its own laws and policies was complete. In June 2022, the judge ruled that because the OWNF was engaged in its environmental review, the plaintiffs had nothing to challenge and thus ruled against them. After appealing to the 9th Circuit Court, the plaintiffs and the OWNF agreed to a settlement on June 12, 2023 (Ninth Circuit 2023) that required the agency to complete its analysis and publish a decision by December 31, 2027. It also stipulated that should the ultimate decision require closing of any allotments, a 2-year prior notice to the lessee would be required. Thus, the 2022 settlement agreement resulted in the OWNF doing essentially what it had committed to doing 11 years earlier, albeit with a 5-year timeline followed by a 2-year delay, and this time presumably enforceable by a federal court.

In summary, beginning at least as early as 1998, it was clear to OWNF managers that bighorns would, at best, be detrimentally affected, and at worst be unable to establish self-sustaining populations if domestic sheep were permitted to graze within reasonable proximity. But it evidently required not only repeated (and ofttimes redundant) internal analyses and formal processes but also a lawsuit to bring the situation to a point where allotment closures may (and not "shall") take effect in early 2030. That said, nothing in this long history provides grounds for concluding that the USFS acted dishonorably, much less illegally, at any point. The methodical pace at which OWFN moved created a positive feedback loop, inducing yet further delays as staff—and critically, decision-makers such as District Rangers and Forest Supervisors—retired or moved to other positions, seemingly resetting the clock (or at least introducing a continual series of learning curves) for new staff.

Still, it is difficult for a dispassionate observer to conclude that bureaucratic processes alone kept the agency from acting more decisively to ensure adequate separation of domestic from bighorn sheep. It seems plausible that reasonable solutions would not have required 35-plus years of consideration, during which 2 herds suffered major outbreaks and 3 others became infected (but fortunately escaped relatively unscathed), had governance been clearer in pointing out a way to satisfy the seemingly conflicting mandates faced by the OWNF.

I believe that something else in the system was acting to prevent resolution of the problem in a fair and equitable way. Some other factor, unaddressed by laws or regulations and beyond the reach of the judicial system, was getting in the way of protecting bighorns while treating the legally permitted and well-respected private business fairly. My thesis is that the operating laws and regulations had, perhaps inadvertently, set up the problem as a classic zero-sum game, in which for one side to achieve its objectives the opposing side would be forced to absorb a total loss. In short, the solution to protecting the bighorns from pneumonia transmitted by domestic sheep, which was clearly the public interest, was to discontinue domestic sheep allotments that had any reasonable chance to pose a risk. But that solution would force the operator to radically alter their business model with no help or compensation whatsoever from the public that stood to benefit from that decision. Conversely, the way to assure that the livestock owner could remain in business was to retain the status quo, but that solution would put the public's bighorn sheep at continual risk because of the likelihood of additional disease outbreaks. What was missing was fairness, and a mechanism to assure that the true costs of a desired outcome (disease-free bighorn sheep in this case) would be borne by those who sought it.

2. How governance has approached two similar issues

In this section, I briefly examine 2 areas of U.S. public policy in which attempts have been made to provide a benefit that has been clearly articulated as being in the public interest, while treating with fairness and compassion private interests that are adversely affected: natural resource policy toward large carnivores, and acquisition of private property through eminent domain. Neither provide exact templates for the sheep issue but are worthy of consideration both for the general approach they have adopted, and because they have been largely successful.

2a. Large carnivores in the western U.S.

In the 19th century, and through most of the 20th, public policy, as practiced by natural resource management agencies at both federal and state levels, held that wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and mountain lions (*Puma concolor*) —large carnivores hereafter—were undesirable and should be eliminated (Leopold et al. 1963, Kellert et al. 1996, Schwartz et al. 2003). This was rather successfully accomplished, and the extirpation of large carnivores eased the way for private individuals and companies to apply to public land management agencies for permits to graze their livestock on public lands. There were, of course, restrictions and conditions, and the issue of predation was not completely absent, but at least livestock grazers in the west didn't have to deal with large carnivores.

By the late 20th century, public policy toward large carnivores had generally, if not universally, changed. By this point in time, large carnivores were seen (again, formally via policy, if not necessarily by livestock interests) as an integral part of ecosystems, and in parts of the west where people are suitably scarce, their recovery and persistence supported (Leopold et al. 1963, Kellert and Westervelt 1983, George et al. 2016). That said, public lands agencies acknowledged that large carnivores sometimes killed livestock otherwise legally grazing on public lands, or caused indirect, sublethal losses (e.g., Hoag et al. 2011, Ramler et al. 2014). In a sense, policy recognized that we had changed the rules applied to these law-abiding livestock grazers in the middle of the game. Whereas livestock operators began and expanded their businesses under one set of assumptions (large carnivore-free public lands), they were now (and without their personal consent) facing a different set of public priorities.

There could have been 2 alternative public policy positions taken to the new reality. On one extreme, policy could have said, in essence, "*Oops, we hadn't realized that bringing back large carnivores was going to cause economic hardship to otherwise law-abiding business people, so never mind, roll back the clock, we're changing our mind and no longer support large carnivore recovery, at least where livestock on public land might be affected*". The other extreme could have been to say "*Sorry Mr. Rancher, but times have changed. Tough luck, you've gotta' like it or lump it. It's a new world out there, we have a more comprehensive view of nature and better science than we used to and if that's to your economic detriment, too bad*". But from a comprehensive public policy perspective, a better position – and the one most agencies have implicitly adopted – was to say "*Yes, the world has changed, yes, we continue to support large carnivore recovery, but no, livestock businesses shouldn't be asked to shoulder the entire burden created by this new reality. Instead, public agencies are going to help livestock operators adjust, help protect their livestock, and pay reasonable compensation when losses occur, because this wasn't the situation they'd earlier signed up for."* The help given to livestock interests would not be complete or perfect, and they had no doubt must absorb some losses. But at least this policy approach recognized both the changing values of the majority (favoring restoration of large carnivores), while also acknowledging the responsibility of that majority to livestock interests that would be disproportionately burdened by those changes.

A few examples illustrate the way public agencies have stepped up to help livestock interests in western U.S. states without abandoning support, generally, for large carnivores. In Montana, where all three large carnivores are now reasonably common in mountainous areas close to private ranches, the state wildlife agency has invested considerable resources in supporting regionally-based staff whose job is to minimize carnivore-livestock conflicts. As of early 2024, Montana Fish, Wildlife and Parks (MFWP 2024a) employed 12 full-time field staff focused on conflicts with bears (albeit not all in areas with heavy livestock presence), as well as a statewide education specialist for whom preventing conflicts with bears was a high priority. When state legislation in Montana restricted the geography on which these staff could work, the U.S. Fish and Wildlife Service hired federal staff to augment the state technicians. Even the U.S. Department of Agriculture's Wildlife Services, which already (and more typically) became involved only when lethal removal of an offending wild animal was required, hired staff focused on nonlethal conflict prevention. Montana Fish, Wildlife, and Parks employed an additional 5 full-time field staff focused on reducing conflicts with wolves, in addition to a statewide carnivore coordinator (MFWP 2024b). These staff worked with ranchers (as well as smaller-scale, artisanal livestock producers) to minimize the chance that their operations would attract large carnivores, to help protect livestock when carnivores were close–by, and when prevention efforts failed, to move, or when necessary, remove depredating carnivores. Similar programs existed in the states of Wyoming, Idaho, and Washington.

When preventing depredation fails, Montana has, since 2007, publicly funded a separate program, administered under the aegis of its Department of Livestock, which compensates livestock owners for verified losses to wolves, grizzly bears, and mountain lions the fair market value of the animals lost (Montana Department of Livestock, 2024). In doing so, Montana is hardly unique. As of 2021, almost all western U.S. states and Canadian provinces with emerging populations of large carnivores had initiated some variant of a livestock damage and loss compensation system (Table 1; Nyhus et al. 2003, 2005; Muhly and Musiani 2009; Dickman et al. 2011; Lee et al. 2016), with most funds coming from public sources.

Now, let us go back and apply this rough template to the way public policy in the U.S. has approached bighorn sheep. In the 19th century, large bands of domestic sheep were grazed—

Table 1. Summary of livestock compensation programs in North America including grizzlies, wolves, and/or lions. Adapted from Morrison (2012) and Morehouse et al. (2018) and supplemented where possible with updated information.

Jurisdiction	Predators considered (W = wolves, GB = grizzlies, L =lions)	Livestock considered: C = cattle, S = sheep, G = goats, H = horses, 0 = other	Value of confirmed kills paid (FMV= fair market value)	Probable losses of livestock compensated	Injuries to livestock compensated	Missing animals compensated	Preventive measures required	Funding F = federal; S = state/province, H = hunters; P = private group
Alberta	W, GB, L + black bear, eagle	C,S,G,O	FMV	Yes, FMV* 0.5 if within 90 days and 10 km of confirmed loss	Yes, for veterinary expenses	?	No	F: 48%; H: 52%
Arizona/New Mexico	Mexican wolf	C (others at discretion of Council)	Calf: $750, Yrlg: $1K; Cow: $,1.2K; Bull $2K	Yes = 50% of confirmed	Yes	?		F:100%
British Columbia	W, L + coyote (some sources indicate GB)	C	FMV* 0.8 (Calves< 4 mos: $300(Cdn): older claves 75% FMV; bulls, dairy cattle) up to $2K.	No	No	No	Yes	F: 60%; S: 40%
Colorado	L + black bear	?		?	?	?	Yes[1]	F, S, H
Idaho	W	C,S,+dogs	FMV, possible multiplier on case-by-case basis	Yes: FMV if funds available	Yes	Yes, case-by-case	Yes (50% match)	F: 100%
Idaho[1]	GB[4]	C,S,G	FMV -- $1,000 deductible	unclear	uncle	No	Unclear	H: 100%
Manitoba	W, L + black bear, coyote, fox	C,S	90% FMV up to $2K	Yes: 50% FMV	Yes	No	Yes	F:60%, S:40%
Michigan	W, L + coyote	C,O	FMV	?	?	Depends	No	S: 100%
Minnesota	W	?	FMV up to $2K	No	Yes	No	?	S: 100%
Montana	W, GB, L	C,S,G,H,O	FMV	Yes	Yes if funds available	No	No	~ F 10%, S 85%: P 5%
Ontario	W, L + others	C, others	FMV (specified in a table)	No	Yes	No	Yes	F,S
Oregon[2]	W	C,S,G,H,O	FMV	Yes	Yes	Depends[3]	Yes	F: 100%
Saskatchewan	W, L + black bear, coyote, lynx, fox, eagle	C,S G,H,O		Yes: 50% FMV	Yes: up to 80% FMV	No	Yes	F: 60%, S:40%
Yukon	B, ?	?	Determined by board	?	?	?	Yes	F, S
Washington	W	C,S,H,O	FMV if on site of < 100 acres; FMV*2 if > 100 acres	Yes, half of confirmed values	Yes	Yes	Yes, cooperative agreement with WDFW	F (wolves only); S for other species
Wisconsin	W	C,S,G,H,O	FMV	Yes; FMV	Yes	Yes, over 'normal' levels	Yes	S: 100%
Wyoming[1,2]	W, GB, L+ black bear	C,S,G,H	FMV*7 if wolf near Yellowstone; FMV*3.5 if grizzly; otherwise, FMV	unclear	Yes	Yes (via multiplier)	No	H: 100%

[1] Claimant must allow big-game hunting.
[2] Administered on county basis.
[3] See Schick 2017 for details.
[4] Applicable only after grizzly bears are delisted.

sometimes freely, sometimes with some oversight—on what were, or later became, public lands. In the early 20th century, when public land agencies became involved, grazing became more regulated but was still common. Nobody considered, because nobody really knew, that domestic sheep essentially killed bighorns. Bighorns disappeared, but nobody really noticed or knew why. Regardless, this was the regulatory world inherited by today's remaining commercial sheep operators. Similar to being in a large carnivore-free world, those that grazed near historic bighorn habitat lived in a bighorn-less world.

Values gradually changed and wildlife agencies started reintroducing bighorns to their former ranges. And before long, it became increasingly clear that domestic and wild sheep didn't mix. You simply couldn't have both in the same area, or even in close proximity to one another.

At this point, policy could have taken either of two extreme positions (similar to carnivore scenario, above). Policy could have said, essentially, "*Oops, we hadn't realized that bringing back bighorns was going to cause a conflict with existing domestic sheep grazing practices and potentially cause economic hardship to otherwise law-abiding business people. So never mind, roll back the clock, we're changing our mind and no longer support bighorn sheep recovery, at least where that might affect domestic sheep grazing on public land*". Alternatively, the other extreme could have said, essentially, "*Sorry Mr. Sheep Rancher but times have changed. Tough luck, you've gotta like it or lump it. It's a new world out there, we have a more comprehensive view of nature and better science than we used to, if that's to your economic detriment, too bad*".

But at this point, the analogy between public policy approaches toward large carnivores and bighorns breaks down, because no comprehensive and fair public policy position has been institutionalized that would recognize both the newer social/ecological values (bighorns, in this case) as well as the value of compensating those who played fairly by rules (that had been changed on them). Instead, public policy *writ large* has stopped, effectively handing off this unresolved conflict to individual, local levels to somehow work out. Either domestic sheep are permitted to continue grazing near bighorns (with attendant costs to the public interest), or sheep allotments are discontinued (regardless of the impacts to the livestock operator). We should not be surprised to find that dealing with the conflict on any given local scale has been fraught, because policy failed to provide a mechanism to formally legitimize the interests and values of both sides. Instead, local level contests have been left to resolve conflicts either in an "I win, you lose" way, or by some sort of compromise.

In short, it makes little sense to expect fair or ethical resolution to this kind of conflict when done only at a local level, lacking the larger policy framework, similar to what we have (imperfectly) worked out for large carnivores. We need the public at large to recognize both values and help by providing resources to allow a fair resolution.

2b. Eminent domain as practiced in the U.S.

Most of the general public probably harbor negative views of government's use of its power of eminent domain, imagining the courageous owner of a historic, if dilapidated, shack fighting off the powerful and despotic government coveting that land for a new highway overpass. But although abuses have doubtless occurred, it is useful to recall that the reason eminent domain exists in U.S. law is because it advances a public good. There are instances in which the public's interest in a commonly-supported project simply must outweigh the interests of a private individual or corporation, no matter how noble or Quixotic their opposition may appear. But equally important are the 2 Constitutional caveats to use of eminent domain: first, that it can be exercised only when doing so clearly advances a public good, and second, that it must be accompanied by just compensation.

However, even granting that cancellation of a grazing lease on public land is not the same as a legal "taking" (see Raymond 1997), only the first of the 2 elements are provided for by existing law and regulation when it comes to the bighorn pathogen issue. The U.S. Forest Service clearly has the legal authority to revoke, or at least to not renew, a livestock allotment when environmental concerns justify doing so. But it has neither authority nor funds to compensate an operator who is thereby financially disadvantaged.

One reasonable alternative policy to that suggested by the eminent domain analogy is for privately-funded organizations to fill the void, by offering to purchase leases otherwise owned by a livestock operator. This has been implemented, in some cases with great success, by organizations such as the Wild Sheep Foundation (WSF) and the National Wildlife Federation (NWF; Fischer 2019). I see at least 3 problems with reliance on private organizations to provide the financial resources required to achieve just compensation. First, even the largest organizations may be unable to raise enough funds to make whole a grazing operation that may have to fundamentally change its business strategy (or liquidate completely). Second, any arrangements among private parties remain voluntary. While that is ideally a virtue, it leaves the prospective funder at a disadvantage in promoting the public good if the grazing operator simply declines to participate, because there is no legal stick to accompany the financial carrot. Finally, and most fundamentally, it entrusts to privately–funded organizations what ought to be a legitimate function of government, i.e., providing for habitats in reasonable abundance for a publicly-valued wildlife species on public land. Wildlife advocacy groups such as WSF and NWF deserve the public's enduring gratitude for stepping up, but it trades one type of injustice for another if one special interest (typically, although not entirely, bighorn sheep hunters) is required to bear the burden of compensating another special interest (commercial sheep grazing operators) so that the public at large can benefit.

3. A suggested paradigm shift

Are there alternatives that honor the desire of residents of states harboring native bighorn populations to have thriving populations of bighorn sheep where habitat conditions allow but still provide justice for businesses that might be asked to bear burden seen as unfair? I think there are, but they will require financial resources, probably at the statewide level. The approach providing the most risk reduction to bighorns is clearly to prohibit domestic sheep grazing on any public lands associated with a non-negligible risk of contact. But this would entail an economic loss to operators, perhaps to the point of requiring them to change their business model entirely. As a matter of public policy, it seems unjust to insist that they alone bear this cost. If purchasing allotments (or entire herds) is the only effective solution, which seems clear is the case in central Washington, it seems appropriate for the citizens of Washington to bear that cost. Although expensive if viewed from the perspective of an individual landowner or business operator, a one-time, special allocation that would provide the necessary funds would be minor if communalized across Washington's almost 8 million people.

An operator might still argue that they have been hurt even if made financially whole: they may wish to continue their business because it is their tradition, not simply because it is a way to make a living. But as with large carnivores, society should not lose sight of greater values to avoid any and all inconvenience to those disadvantaged. Monetary compensation for a killed calf may be viewed as a poor substitute for the live calf, but livestock operators can reasonably expect fairness, not necessarily special accommodation. Providing for financial compensation to the private party harmed would allow the government agency to forthrightly address the public interest in bighorns that is implicit in law and regulation, while simultaneously achieving the public's expectation of fairness.

4. Management Implications

Neither of the templates I have offered that might undergird a paradigm shift to public policy regarding risk to bighorns on public lands are perfect models, ready for direct application. In the case of large carnivore depredation on livestock, the risks at issue are to the domestic animals whereas for sheep, the risks are to the wild ones. As well, policies to ameliorate the risks to livestock from carnivores, whether preventative or compensatory, are largely intended to allow for some measure of coexistence between the two (or perhaps put more precisely, temporal/spatial segregation on a small scale). In contrast, substantial evidence has accumulated that effective separation between the 2 types of sheep on a spatial scale that recognizes the likelihood of forays and mutual attraction remains the sole approach to assuring that risk to bighorns is acceptably low (Schommer and Woolever 2008, Whiting et al. 2023). Coexistence between domestic and wild bighorns while preventing transmission of potentially lethal pathogens is a meaningful concept only if such coexistence is to be interpreted on a large spatial scale, where domestic sheep are zoned as allowable where bighorn populations are absent or undesired, and are proscribed in and around those regions where bighorn populations have persisted or been restored.

The concept of eminent domain is also an imperfect analogue for allotments permitted to private entities on public land. Acknowledging that some still disagree with this interpretation, settled case law has held that livestock allotments on public lands in the U.S. are not considered private property, but rather are privileges accorded when the public interest allows (36 CFR § 222.3(b); Public Lands Council v. Babbitt, 2000). Here, a useful concept was elucidated by the U. S. Supreme Court in United States v. Fuller ((1973): "*The constitutional requirement of just compensation derives as much content from the basic equitable principles of fairness…as it does from technical concepts of property law."* (for a similar perspective, see Raymond 1997) Thus, in arguing that substantial consideration be afforded to private interests that would be greatly harmed by eliminating a grazing permit, I am expressly not making an argument that permit revocation would constitute a legal taking.

Despite these important ways in which these 2 public policy examples differ from the sheep pathogen issue, they both embody fundamental principles that seem applicable. First, they clearly support the supremacy of the public good, as expressed in law, regulation, and more informally by opinion surveys, even where private interests are harmed. But importantly, they also acknowledge the "basic equitable principles of fairness" so baked into human nature, by accepting that the costs associated with that public good should be shouldered by the public, and not by the private interest that is thereby harmed. No doubt, many livestock owners would prefer to operate on public lands with no large carnivores at all than on lands where these predators are accepted and valued (despite assistance being provided to cope with them). I would not argue that livestock owners happily accept the public's relatively new support of large carnivores as long as they benefit from technical and financial support; many no doubt remain resentful. Similarly, a private party whose property is subjected to an eminent domain acquisition may well retain a sense of grievance toward the government despite receiving fair compensation. My argument supporting financial support of dispossessed domestic sheep operators is not premised on making everybody happy. Rather, it is premised on the value of the government doing as well as possible by all competing interests.

The notion that some government entity should step up to provide financial compensation for commercial sheep operators where necessary is not one that can easily (or perhaps even legally) be promoted by staff at wildlife agencies. However, that does not preclude non-governmental entities, or even legislators themselves, from proposing solutions along these lines. A precedent (in fundamental concept if not in detail) was provided by the state of Washington in 1989 (and again via revision in 2023) when the governor signed HB 1460 that created the Trust Land Transfer (TLT) program. This program provides a funding mechanism for transferring state trust lands of high ecological value (but that are otherwise mandated to generate revenue for trust beneficiaries) to protected status (RCW 79.17.300, WDNR 2024). The program requires a formal appraisal of any land parcel subject to transfer and includes oversight to ensure objectivity and fairness. Because the TLT program is specific to State Trust Lands and the need in the bighorn case is for funding that would safeguard wildlife from otherwise lawful economic activity, it does not provide a precise template. However, it plausibly paves the way for mobilizing public funds where high priority conservation actions are otherwise poorly accommodated by existing legal structures.

At the federal level, the Multi-Use Conflict Reduction Act (2005) introduced in the 109th Congress would, had it been adopted, have compensated holders of leases for relinquishing permits in ecologically sensitive areas. Among the rationales it cited for compensating ranchers were that doing so would "help recapitalize an ailing sector of rural America, by providing economic options to permittees and lessees...and allowing them to restructure their ranch operations, start new businesses, or retire with security". Following along similar lines could facilitate federal land managers in narrowing the gap between public and private interests, a gap that has seemingly frustrated attempts to protect bighorn sheep from pathogens.

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APPENDIX A: Partial timeline of agency actions related to protecting bighorns in central Washington State, USA: 1988–2024.

1. December 1988. The (then) Washington Department of Wildlife and the Pacific Northwest Region of the USDA Forest Service sign a memorandum of understanding clarifying the roles and responsibilities of both agencies in "protecting, perpetuating, and managing" fish and wildlife on US Forest Service lands, and providing for close cooperation between both agencies. Among other stipulations, this MOU called for annual meetings between regional USFS staff and state wildlife officials to share issues of concern (USFS 1988).
2. March 1998. A Memorandum of Understanding between the (then) Wenatchee National Forest and the Washington Department of Fish and Wildlife (WNF 1998) is finalized that clarifies roles and responsibilities for the newly restored Tieton bighorn sheep herd. The USFS agrees to require that domestic sheep be "carefully herded to keep them from straying outside the approved area for domestic sheep use, and WDFW agrees to investigate exposure and evaluate risks associated with bighorn sheep found mixed in with domestic sheep and recommend practices to prevent contact.
3. August 1998. A Memorandum of Understanding between the (then) Wenatchee National Forest and the Washington Department of Fish and Wildlife is finalized (WNF 1999) that clarifies objectives for restoring the Manson and Swakane bighorn sheep herds. Among other objectives are to "prevent interactions that transmit disease between domestic sheep and bighorn", and to "complete … a risk assessment" and to "maintain domestic sheep outside agreed upon bighorn sheep management areas as a buffer for disease" but delays resolution of allotments that are acknowledged to be within the area in question.
4. October 1998. In a memo to the (then) Wenatchee National Forest, regional and national bighorn sheep biologist Tim Schommer strongly urges the Forest to look at all opportunities to reduce contact between domestic and bighorn sheep, including converting some domestic sheep allotments to use by cattle (Schommer 1998).
5. May 2000. The Supervisor of the (then) Wenatchee National Forest signs a decision notice providing for continued domestic sheep use of 4 grazing allotments near bighorn sheep herds (WNF 2000). The decision commits the Forest to complete a habitat assessment for the Swakane Herd within a year, that grazing would only be permitted on a year-to-year basis in the southern portion of the area if the Swakane Herd was increasing within a previously defined core area, and that grazing on 3 of the allotments would be terminated if the Swakane Herd expanded outside of the area previously defined by WDFW in 1995.
6. September 2004. The (newly combined) OWNF Supervisor signs a Record of Decision (OWNF 2004) renewing 4 additional grazing allotments adjacent to the Cleman Mountain and Tieton bighorn herds, albeit with "adaptive management" that calls for rerouting some domestic sheep trailing if "*domestic sheep encounters with bighorn sheep become a problem as determined by the District Range Specialist in consultation with WDFW*".
7. May 2008. USDA RMRS-GTR 209, entitled "A review of disease related conflicts between domestic sheep and goat and bighorn sheep" is published (Schommer and Woolever 2008). It concludes that *"Pressing resource management decisions cannot wait for a complete understanding of all aspects of respiratory disease processes in bighorn sheep. In landscapes where management objectives include the maintenance or enhancement of bighorn sheep populations, the risk of potential of disease transmission between domestic sheep/goats and bighorn sheep must be addressed. The available information supports creating spatial and/or temporal separation between domestic sheep/goats and bighorn sheep as a prudent management technique to manage the risk of disease transmission.*
8. November 2009. Pneumonia is documented in the Umtanum/Selah bighorn herd; substantial mortality and culling continues through spring 2010 (Bernatowicz et al. 2016).
9. May 2010. The Confederated Tribes and Bands of the Yakama Nation writes to the Chief of the USFS, indicating that they have not been adequately represented in previous interactions, and that failure to ameliorate threats to bighorns in the area they consider to have cultural and subsistence significance would be in violation of the Treaty of 1855.

10. September 2010. OWNF Supervisor requests that WDFW nominate and authorize representatives for an interdisciplinary team to consider management and conservation of bighorn sheep on the Forest. Names are subsequently provided by the Governor of Washington.
11. June 2011. OWNF publishes a Proposed Action for Forest Plan Revision, which includes bighorn sheep as a focal species (USFS 2011a). Anticipating what a new Plan might include the document states "Management direction would be to provide temporal or spatial separation between bighorn sheep and domestic sheep to reduce the risk of potential disease spread."
12. August 2011. A memo from the Deputy Chief of the USFS to all Regional Foresters (USFS 2011b), ends with the text "Where viability assessments indicate a high likelihood of disease transmission and a resulting risk to bighorn sheep population viability across the forest, the goal of spatial and/or temporal separation between domestic sheep/goats and bighorn sheep is the most prudent action we can use to manage risk of disease transmission."
13. March 2012. The Draft Terrestrial Species Viability Assessments for the National Forests in Northeastern Washington (Gaines et al. 2012) completed. Bighorn sheep are a focal species; the risk of disease transmission from domestic sheep is considered high if > 20% of a buffered area (1 mile surrounding mapped bighorn habitat) overlaps an active allotment. Priority actions suggested to improve connectivity among bighorn habitats include "reducing the risk of disease spread."
14. April 2013. The Tieton bighorn sheep herd is decimated by virulent strain of *M. ovi.* WDFW lethally removes the few survivors (Bernatowicz et al. 2016).
15. May 2013. The OWNF convenes a round-table meeting to discuss pneumonia in both wild and domestic sheep, including top researchers, at the local district office in Naches, WA.
16. December 2013. The OWNF asks the multi-agency Tapash Collaborative to convene additional stakeholders (including Yakama Tribes, Washington Department of Natural Resources, and local offices of the U.S. Bureau of Land Management) to investigate if suitable areas for domestic sheep grazing might be found on lands beyond the OWNF. This effort quickly founders and is abandoned after it becomes clear that no other land manager can offer alternative grazing areas for the commercial herd.
17. May 2014. Regional USFS staff and WDFW statewide staff meet in Olympia. Concerns are shared about risk of disease transmission from commercially-grazed domestic sheep to bighorn sheep in the OWNF.
18. February 2015. Regional USFS staff and WDFW statewide staff meet again in Olympia. Concerns are again shared about risk of disease transmission from commercially-grazed domestic sheep to bighorn sheep in the OWNF.
19. March 2015. The WDFW director writes to USFS regional director reiterating the state's concern about disease transmission to bighorn herds in the OWNF.
20. June 2015. OWNF, USFS Region 6, and WDFW staff meet in Wenatchee to discuss plans for moving forward with minimizing the risk of disease transmission where wild bighorn herds exist, and domestic sheep allotments are of concern.
21. February 2016. Regional USFS staff and statewide WDFW staff meet in Olympia once again, bighorn issues are once again raised.
22. February 2016. The Washington Conservation Science Institute, under contract from the USFS, issues its final report entitled "Application of the Bighorn Sheep Risk of Contact Model on the Okanogan-Wenatchee National Forest" (Lyons et al. 2016). It concludes "*The Cleman Mountain and Tieton bighorn sheep herd home ranges overlap active sheep allotments and thereby might be considered a top priority for updating the NEPA* [National Environmental Policy Act] *analysis, including the qualitative information about disease transmission and herd management this Risk of Contact Tool did not address. Additionally, because the results indicated the Chelan Butte, Cleman Mountain, Swakane, Tieton and Umtanum bighorn sheep herds may be expected to experience a disease outbreak within 50 years, they would be another possible priority for updating the NEPA analysis, including the qualitative information about disease transmission and herd management this Risk of Contact Tool did not address.*
23. February 2016. OWNF, USFS Region 6, and WDFW staff meet again in Wenatchee to revisit plans for

moving forward with minimizing the risk of disease transmission where wild bighorn herds exist, and domestic sheep allotments are of concern now that the Risk of Contact final report is complete.

24. March 2016. The WDFW director writes again to USFS regional director reiterating the state's concern about disease transmission to bighorn herds in the OWNF.
25. June 2016. The OWNF Supervisor publishes an open letter committing the USFS to begin a formal NEPA process focused on domestic sheep allotments by autumn 2016.
26. August 2016. The OWNF and the Tapash Collaborative invites the public to hear presentations in Ellensburg, WA from agency staff and academic researchers regarding bighorn sheep, domestic sheep, and the risk of disease transmission. However, the public is not invited to ask questions because, it is announced, a formal EIS process to examine domestic sheep allotments would soon commence, which would provide avenues for public involvement.
27. The Consolidated Appropriations Act of 2016 passes the US Congress. The accompanying explanatory statement includes the following: "*…the Service…[shall] complete risk of contact analyses using appropriate data sources… and identify all allotments that are suitable for sheep grazing. The Service also [is] directed to identify and implement actions to resolve issues on allotments with a high risk of disease transmission, including, if agreeable to the directly affected stakeholders, the relocation of domestic sheep to allotments with a low risk, pending any site-specific environmental analysis…and to report to the Committees on implementation of these directives within 60 days of enactment of this Act.*"
28. April 2017. Regional USFS staff and statewide WDFW staff meet yet again in Olympia, bighorn issues are yet again raised.
29. July 2017. WDFW convenes a small, informal face-to-face discussion with the permittee and a few supporters, to share ideas and clear the air (Madsen 2017). Among those the permittee invited to participant was a staffer for the local, sitting member of the U.S. House of Representatives.
30. January 2018. The OWNF informs WDFW that it will be amending its forest-wide plan to update consideration of pathogen transmission to bighorns, and requests that specified WDFW staff participate in the interdisciplinary team; WDFW agrees and assigns the requested staff.
31. August 2018. The OWNF supervisor formally requests WDFW participation in preparation of the EIS needed to amend the forest plan regarding domestic grazing with the range of bighorn sheep (see above). An internal timeline calls for a record of decision in August 2020.
32. March 2019. Pneumonia associated with *M. ovipneumoniae* is diagnosed for the first time in the Mt. Hull bighorn sheep herd.
33. May 2019. The OWNF begins public scoping on a proposal to amend the Forest Plan to provide new direction for management of domestic sheep grazing within the range of bighorn sheep. Federal Register (May 17, 2019).
34. June 2019. A public meeting is held by OWNF as part of the scoping process in Cle Elum, WA.
35. September 2019. The OWFW ID team begins considering alternatives.
36. September 2020. The OWNF acknowledges that it is "several months behind schedule".
37. October 2020. *M. ovipneumoniae* is found in bighorn sheep in the (formerly uninfected) Cleman Mountain herd, following a report of deceased lambs. Separately, WDFW lethally removes 15 bighorns from the Quilomene herd after a domestic sheep that had been associating with bighorn sheep rams was euthanized and found to be infected with *M. ovipneumoniae.* Meanwhile, OWNF announces that it expects to release a draft Forest Plan and EIS that would overview policy on the sheep issue (but not analyze or recommend actions on specific allotments until later) in February 2021, with a final EIS expected in November 2021.
38. November 2020. Two advocacy groups, WildEarth Guardians and Western Watersheds, file suit against the OWNF for failing to address disease transmission to bighorns from permitted domestic sheep grazing and thus violating NEPA and/or the National Forest Management Act of 1976.
39. February 2023. The OWNF reinitiates scoping on the Environmental Impact Statement that originally began in May 2019 (OWNF 2023).
40. June 2023. On appeal to the 9th Circuit after losing the lawsuit, a settlement agreement is reached

with the plaintiffs, requiring the USFS to complete a new NEPA process to amend the Forest Plan (which it was already doing, see above), and in so doing, identify which existing grazing allotments are suitable or unsuitable for domestic sheep grazing due to risk of pathogen transmission to bighorn sheep.

41. December 2027. Final EIS and Record of Decision (ROD)—from above—are due.
42. January 2030. Date that any allotment closures identified by the ROD would take effect.

APPENDIX B

This paper makes no claim that *M. ovipneumoniae* in central Washington bighorn herds was transmitted by commercial herds of domestic sheep legally permitted on USFS lands. It would be exceedingly difficult to show that definitively, and I cannot exclude other possibilities as the source of infection. That said, the following information informs our understanding of the risk of such transmission:

1) A yearling ram domestic sheep belonging to the lessee was lethally removed from the range of the Tieton bighorn herd (during the epizootic) and tested positive for *M. ovipneumoniae.* Permission from the owner to conduct strain typing on this animal was not obtained from the lessee.
2) Substantial efforts were made by regional WDFW biologists to identify small flocks of domestic sheep and/or domestic goats in close enough proximity to the Cleman, Quilomene, Swakane, Tieton, Swakane, and Umtanum/Selah herds that could plausibly have caused infection (see also Heinse et al 2016.). No herds of domestic sheep were identified. A herd of domestic goats located on private land quite near the Tieton herd's range was tested shortly after the epizootic and found to be positive for a strain of *M. ovipneumoniae,* but the strain differed from that which infected the Tieton sheep.
3) Strain typing conducted on deceased animals following the collapse of the Tieton herd demonstrated that the infection came from a single source (all strain types were identical), and that the origin was from domestic sheep rather than from domestic goats (the strains are separate and can be distinguished using molecular methods; Besser et al. 2017, Maksimović, 2017, Kamath et al. 2019).
4) With permission from the lessee, the WDFW district biologist removed 1 domestic sheep from near the Tieton herd area in 2013 and found the carcass of another (the latter being too decomposed for pathogen testing).

Tribal Bighorn Management on the Flathead Indian Reservation

SHANNON CLAIRMONT, *Confederated Salish and Kootenai Tribes, Natural Resource Department, Flathead Reservation, MT, 59855, USA;* shannon.clairmont@cskt.org

ABSTRACT: A brief history of the Confederated Salish and Kootenai Tribes efforts to establish and manage several wild big horn sheep populations within the Flathead Indian Reservation. From the early years of reintroduction, through years of herd growth, establishing a regulated hunt and the cooperative effort by both Tribal and State Fish Wildlife and Parks Biologists to maintain a healthy population. Included in the end a quick look at the Mountain Goat population that inhabits the Mission Mountain front range on the eastern edge of the Flathead Indian Reservation, our concerns and efforts to maintain goats into the future.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24:72; 2024

KEYWORDS: bighorn sheep, Salish and Kootenai Tribes, Mission mountains, Flathead Indian Reservation, hunt management.

METHODS, TRANSLOCATIONS AND REINTRODUCTIONS, AND HABITAT USE

Evaluating Citizen Science Mountain Goat Counts Using GPS-Collared Goats in Southwest Montana

JULIE CUNNINGHAM, *Montana Fish, Wildlife and Parks, Bozeman MT, 59718, USA; juliecunningham@mt.gov*
KELLY PROFFITT, *Montana Fish, Wildlife and Parks, Bozeman MT, 59718, USA*

ABSTRACT: Accurate wildlife population counts inform sustainable harvest management. This is particularly important for mountain goats as they are challenging to count and susceptible to over-harvest. We evaluated a citizen-science ground counting method paired with 14 GPS collared animals to obtain minimum counts and population estimates for mountain goats in the Bridger Mountains, southwest Montana. During 2021–2023, the Rocky Mountain Goat Alliance and Montana Fish, Wildlife and Parks (MFWP) partnered to perform 3 ground-based surveys. Surveys occurred by strategically posting citizen volunteers at the same day and time throughout goat habitat within the mountain range. We processed survey data using an algorithm considering time, location, and group composition to eliminate duplicate observations. Treating collared animals as marked and resighted animals as recaptured, we estimated annual population sizes using Peterson (Chapman–corrected) mark-recapture estimators. Minimum mountain goat counts were 28 in 2021 (a year when smoke from wildfires impeded visibility), 93 in 2022, and 103 in 2023. Observers detected 2 of 10 collared goats (20%) in 2021, 10 of 13 collared goats (77%) in 2022 and 10 of 12 of collared goats (83%) in 2023. Peterson mark-recapture estimates of the total population in 2021, 2022, and 2023 were 102 (approximate 95% confidence interval 19-184), 119 (approximate 95% confidence interval 89–149), and 122 (approximate 95% confidence interval 96–148). High recapture rates (when smoke did not impede visibility) and similarities of ground counts with mark-recapture estimates suggested that citizen-science ground counts were a replicable and informative means to inform mountain goat management in this study area.

Biennial Symposium of the Northern Wild Sheep and Goat Council 24:73–79; 2024

KEYWORDS: Bridger Mountains, citizen science, GPS collar, ground survey, mark-recapture, Montana, mountain goat (*Oreamnos americanus),* Peterson (Chapman-corrected) mark-recapture estimator.

Obtaining accurate survey data to inform wildlife management is key for wildlife biologists (Leopold 1933, Lancia et al. 1996). Mountain goats (*Oreamnos americanus*) are notoriously difficult to count due to their remote and rugged habitats (Chadwick 1983, Rice et al. 2009) and they are also a species which can be susceptible to overharvest (Festa-Bianchet and Côté 2008). In Montana, wildlife biologists use multiple tools to obtain minimum counts from which they recommend hunting license numbers and harvest rates (DeCesare and Smith 2019). Biologists use helicopters, fixed-wing aircraft, and ground surveys during winter, early spring, mid-summer, late-summer, and fall months, sometimes with several years between surveys (DeCesare and Smith 2019).

Ground-based methods have shown promise for counting and estimating mountain goat populations in some areas where using biologists or trained citizen scientists could produce useful data (Belt and Krausman 2012, DeVoe et al. 2015, Flesh and Belt 2017). In other areas, ground counts returned lower population counts than aerial surveys but nonetheless were an economically efficient method of obtaining important information and providing community education and awareness (Reynolds et al. 2022).

Montana Fish, Wildlife and Parks (MFWP) used aerial surveillance (helicopter and fixed-wing aircraft) to count mountain goats in the Bridger Mountains from 1978 to 2016, during which time the highest count recorded was 74 goats in 2002. In 2017 and 2019, MFWP and the Rocky Mountain Goat Alliance (RMGA) conducted two citizen science ground-based surveys in the Bridger Mountains, resulting in counts of 79 and 127 mountain goats. These results suggested ground-based surveys could be an effective method for obtaining minimum mountain goat counts in the Bridger Mountains. Building from these efforts, our objective was to employ mark-recapture methods using radio-collared mountain goats (2021–2023) to provide insights regarding the effectiveness of citizen science ground-counts to estimate mountain goat sightability and population size.

STUDY AREA

The study area was Bridger Mountain Range north of Bozeman, Montana (approximately 45.90°N, -110.98°W; Figure 1). The Bridger Mountains run north to south and are approximately 40km long and 8–10km wide. The mountains are bordered by rolling forested foothills to the east and a sharp transition to grassy foothills on the western front. Elevations range from 1,800m in the foothills to 2,946m at the highest peak. Depending on elevation and aspect, forest communities can include Rocky Mountain juniper (Juniperus scopulorum), Douglas fir (Pseudotsuga menziesii), lodgepole pine (Pinus contorta), Engelmann's spruce (Picea englemanii), limber pine (Pinus flexilis), and subalpine fir (Abies lasiocarpa). Understories include a substantial non-native component with timothy grass (Phleum pratense) and sweet clover (Melilotus spp.) noted even at high elevation. Tree line is approximately 2,400m. The area is considered a dry mountain range with mean annual precipitation of 51cm (USDA 2012), and only 4 lakes, 3 of which may be ephemeral.

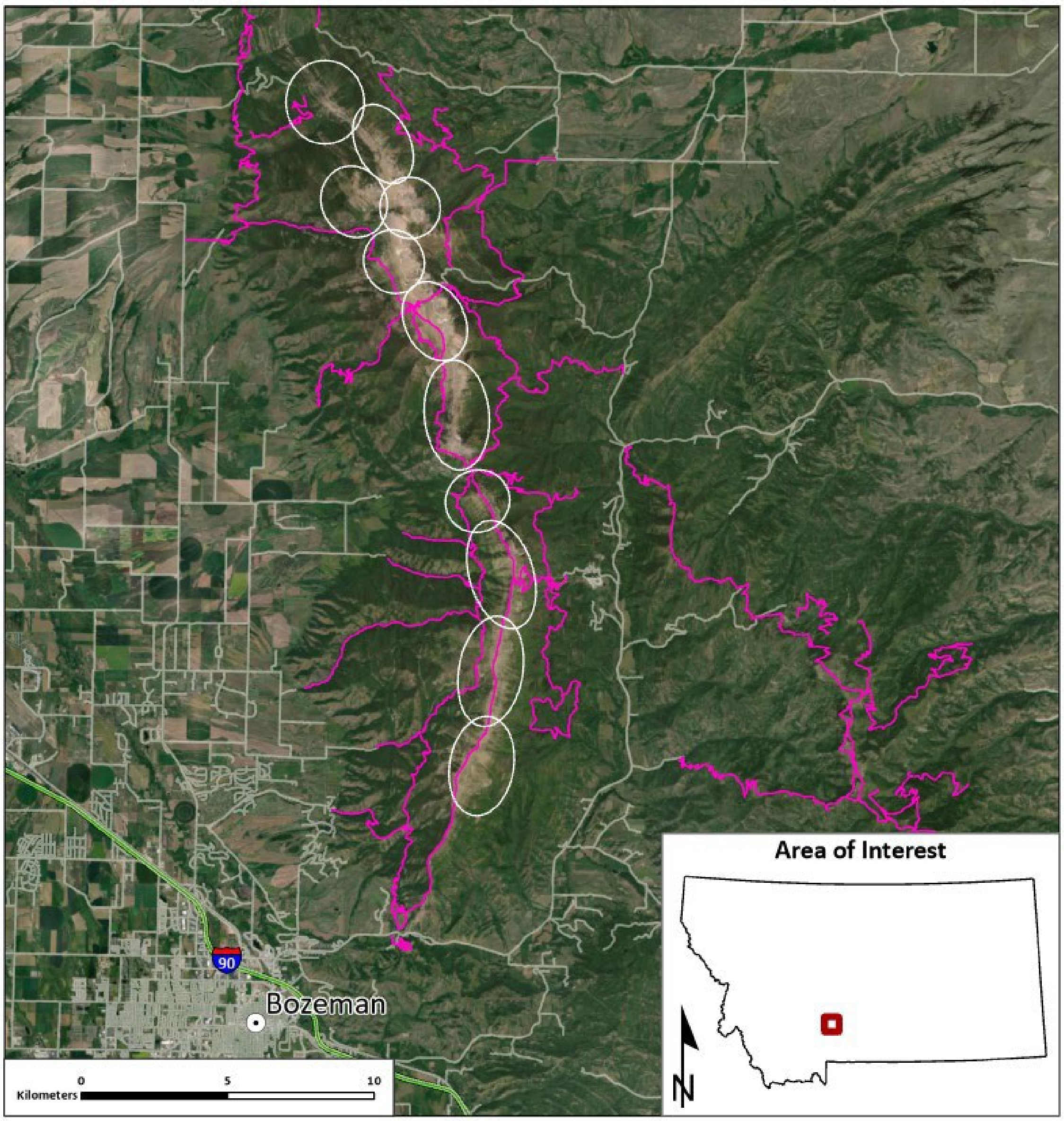

Figure 1. Bridger Mountains, southwest Montana, trails (pink) and ground survey observation areas (white ellipses).

Mountain goats were introduced to the Bridger Mountains in 1969 from a founding population of 13 individuals. Their population appears to be thriving despite significant human recreational use across their habitat (Macdonald et al. *in review*, MFWP unpublished data). A network of >190km of designated USFS trails exists in the approximately 80km^2 of known mountain goat distribution (Figure 2). Goat habitat selection models indicated mountain goats avoid tree cover in this area (Macdonald et al. *in review*). Mountain goat distribution is almost exclusively on U.S. Forest Service lands. Mountain goats are accessible to hunters and grow to trophy size, making the 5 hunting licenses issued annually among the most prized hunting opportunities in Montana. Mountain goats also provide viewing opportunities to Bozeman's burgeoning recreational community.

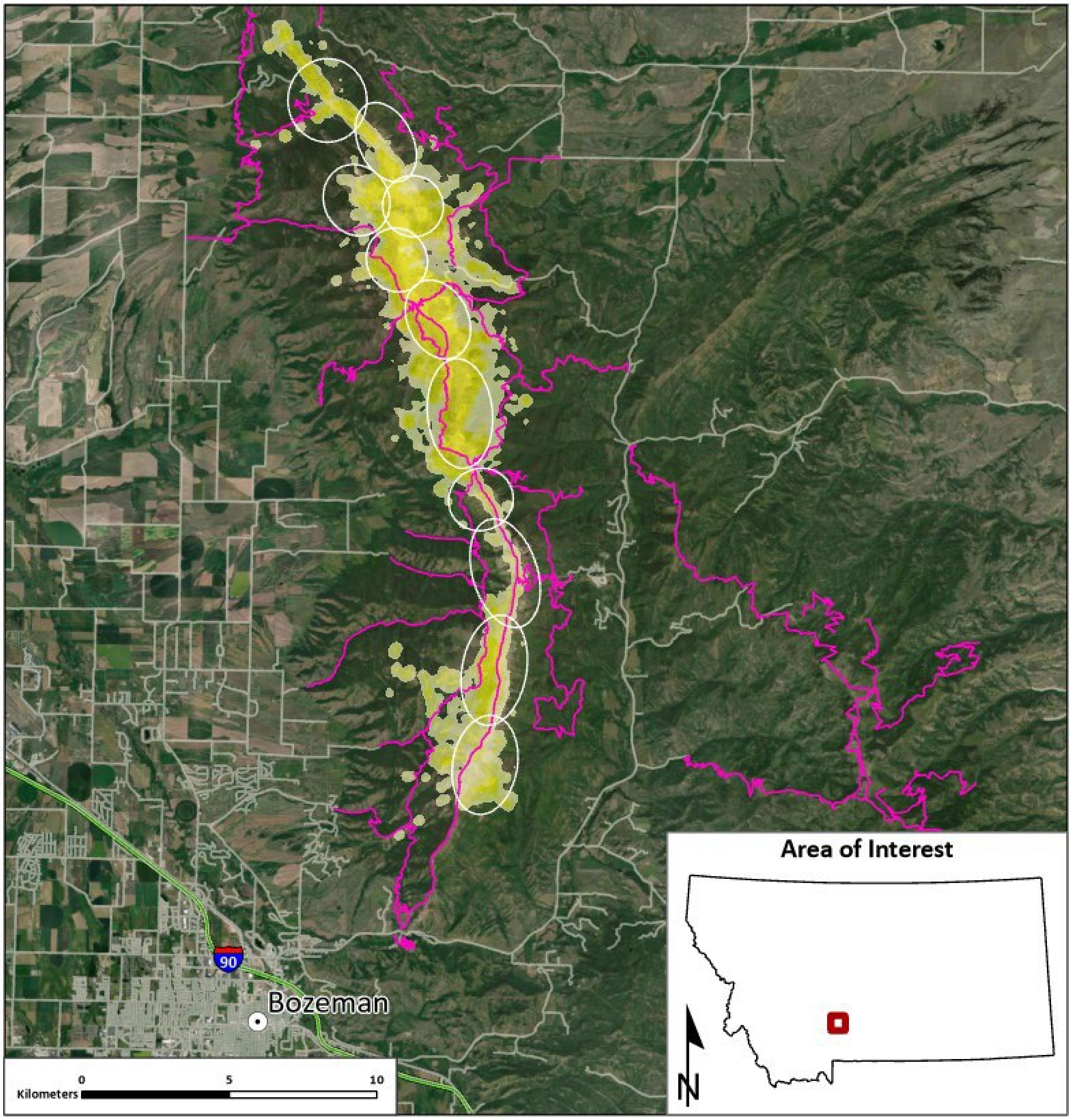

Figure 2. Bridger Mountains, southwest Montana, with mountain goat distribution (yellow) from 14 GPS-collared goats (11 females, 3 males), trails in yellow and observation areas in white.

METHODS

Ground Counting Methods

The RMGA and MFWP organized 3 citizen scientist ground counts: August 8, 2021; July 23, 2022; and July 15, 2023. We required volunteers to attend an evening training session on the Friday immediately preceding the Saturday counting day. Training sessions taught volunteers to classify goats by age and sex using a 9-minute video produced by the RMGA (*https://youtu.be/bgC-iluZieI*). Volunteers were also trained on how to collect data and assigned observation areas. We directed volunteer groups of at least 2 observers to one of 11 prespecified observation areas designated by known goat concentrations, viewsheds, and safe access (Figure 1 and Figure 2). Observation areas were approximately 4–8km^2. We directed observers to hike to up to observation points within each observation area. Observers counted all goats seen while they were in the field. By design, viewsheds from adjacent observation areas overlapped slightly, thus reducing the likelihood of missing a goat group. We ensured all volunteers had binoculars and spotting scopes to search for mountain goats. The survey window was between 4pm and 9pm on the evening of the survey. We selected this timeframe because it was a period of high mountain goat movement activity, suggesting they would be more visible than during a time when they may be bedded (Figure 3). This study design saturated known mountain goat habitat with observers within a small temporal window during a time of high goat activity and provided a snapshot of goat presence while minimizing likelihood of goat movement between viewing areas. To prevent introducing bias, we did not tell volunteers where the GPS-collared mountain goats were before or during their surveys, nor did we locate the collared goats before the surveys.

Observers recorded location of goats using topographic maps, hand-held GPS units, or phone-based applications such as onX™. We recorded the time of observations, including when they first saw the goats and when they last saw them. We recorded behavior of the goats, particularly if goats were moving and if so, in what direction. We recorded the total count, and if possible, classified the groups to males, females, and young of the year. Finally, we recorded the presence of a radio-collar on any goats in the group. In instances marked goats were observed but the collar was not detected due to distance or thick fur, we determined after the survey whether the timestamp and GPS location aligned with the groups observed and therefore whether that collared animal was likely in that group.

DATA ANALYSIS

We used ArcGIS software to map all locations within the assigned survey window of 4pm to 9pm. Based on average observed step-length (Figure 3), locations within 1,000m of one another could possibly be duplicate observations of the same individual(s). If the same team saw different groups of different composition within 1,000m of one another, these were different groups. If observed by different teams, groups of similar composition (i.e., nanny and kid groups or groups of billies) were considered duplicates. Removing duplicates and summing remaining counts yielded a total minimum count for each survey.

We downloaded GPS data to determine where goats were during the survey window. We overlaid the observers' locations and the mountain goat GPS data and notes of whether collars were observed to determine the number of collared goats that were observed (i.e., recaptured).

We estimated population size using Chapman's modification to the Lincoln-Peterson mark recapture model (Chapman 1951). Chapman's adjustment reduces bias when population sizes are small.

$$NN_{eeeeee.} = \frac{[(nn_2+1)(nn_1+1)]}{cc+1} - 1$$

Where $N_{est.}$ = the estimated population size, n_1 = the number of marked animals present, n_2 = the total number of animals seen (marked and unmarked, i.e., recaptured) and m = the number of marked animals seen. We calculated approximate 95% confidence intervals (C.I.) by multiplying the square root of the variance by 2 (Chao and Huggins 2005).

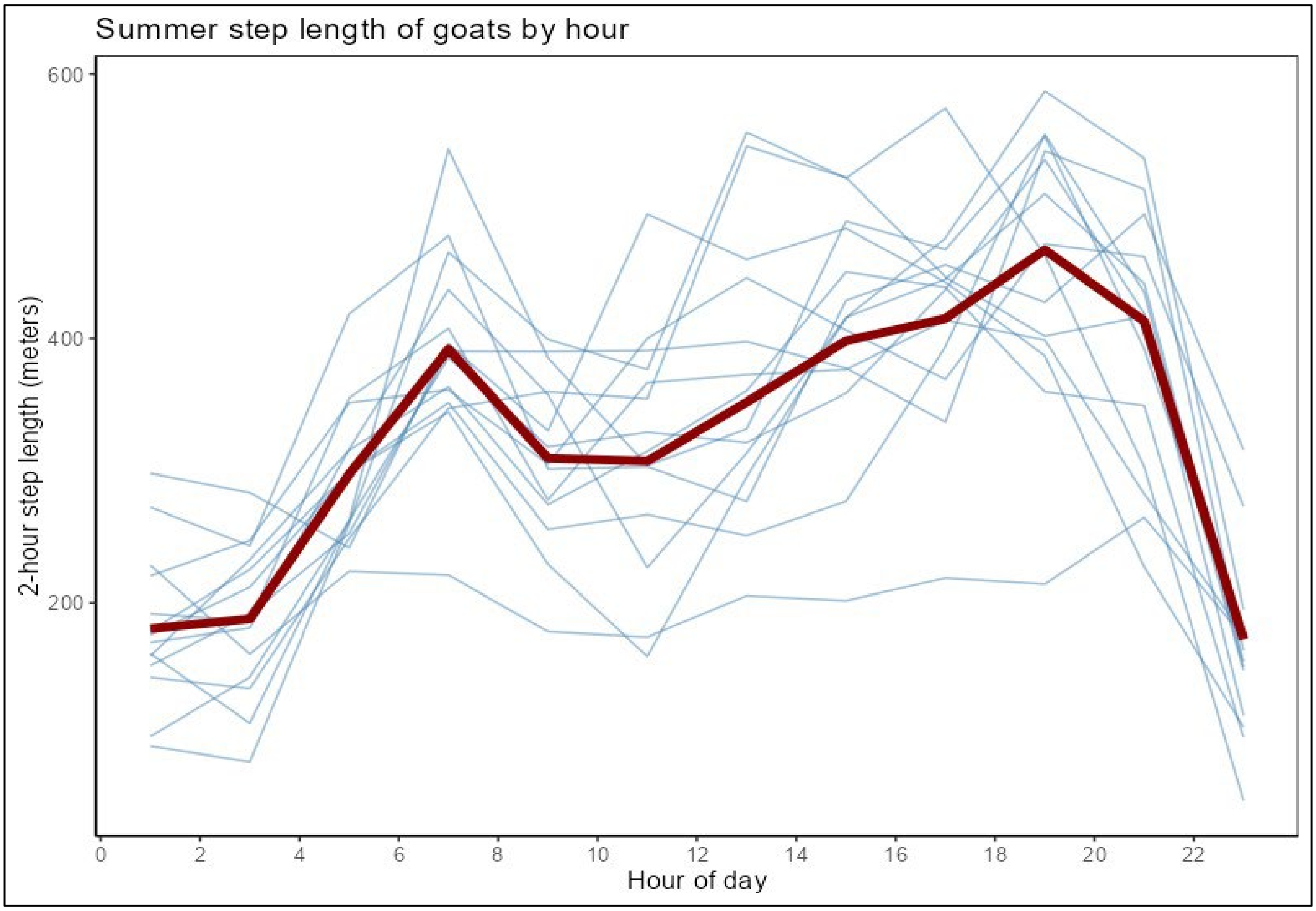

Figure 3. Step length of 14 GPS collared-goats (11 female, 3 male) during 2-hour time intervals during summer months. The surveys were implemented in the 16:00-20:00 time frame when mountain goat movement rates were highest.

RESULTS

We conducted 3 ground-based surveys: 8 August 2021, 23 July 2022, and 15 July 2023, all between 4pm and 9pm. The 2021 survey coincided with hot weather (approximately 30°C) and thick smoke which impeded visibility. The 2022 and 2023 surveys occurred under clear skies with cooler temperatures (approximately 20–25°C). In 2021, teams detected 28 mountain goats in 12 groups and observed 2 of 12 marked mountain goats (Table 1). In 2022, teams detected 93 mountain goats in 32 groups and observed 10 of 13 marked mountain goats. In 2023, teams detected 103 mountain goats in 25 groups and observed 10 of 12 marked mountain goats.

The Peterson-Chapman population estimates for 2021, 2022, and 2023 were 102 (approximate 95% C.I. 19–184), 119 (approximate 95% C.I. 89–149), and 122 (approximate 95% C.I. 96–148). Of 22 instances marked goats were observed, there were 6 instances the collars themselves were not seen, either due to distance or to the thick fur obscuring the collar visibility. Observers correctly identified the sex of the collared goats 15 of the 16 occasions when collars were observed. There was one case when a collar was seen but observers classified the goat as "unknown sex adult".

Table 1. Year of mountain goat count in Bridger Mountains, with total goats seen (after potential duplicated were removed), the number of kids, yearlings, males, females, unclassified adults, unclassified goats, number of radio collared goats seen versus the number available to be seen, and the Chapman-corrected Peterson population estimate with approximate 95% confidence interval (C.I.).

Year	Total	Kids	Yearlings	Males	Females	Unc. Ad.	Unc. All	Collared goats seen/avail.	Population estimate (+/- 95% C.I.)
2021	28	6	3	8	3	0	8	2/10	102 (19–184)
2022	93	16	8	16	28	11	14	10/13	119 (89–149)
2023	103	22	10	17	33	17	4	10/12	122 (96–148)

DISCUSSION

The 2022 and 2023 ground surveys in the Bridger Mountains resulted in a high proportion of the collared individuals detected (77–83%), sightability which is comparable to some aerial surveys (Rice et al. 2009). The 2021 survey was negatively impacted when thick smoke from western wildfires rolled in unexpectedly and reduced visibility. Furthermore, the temperature was 5–10°C hotter during the 2021 survey than the 2022 and 2023 surveys, potentially prompting mountain goats to seek thermal shelter in less-visible locations like under shady cover or in crevasses.

Ground counts may be an effective population surveillance method in a study area like the Bridger Mountains where trail densities are high facilitating easy access to goat habitat, where expected goat distribution is restricted enough for several teams to observe the area completely, and where goats are less likely to use hiding cover (DeVoe et al. 2015). In larger wilderness areas with more continuous goat habitat, or areas where goat visibility may be obscured by vegetation, researchers may need to consider using more teams of people and developing a study design to sample over space and time as described in Belt and Krausman (2012) and DeVoe et al. (2015). If wildlife managers are uncertain, comparing ground counts with aerial surveys may indicate which method(s) are preferred for that geography (Reynolds et al. 2022).

Montana Fish, Wildlife and Parks has been employing citizen-science ground counts in partnership with RMGA since 2013. These counts began in the Henry's Mountains (approximately 44.771, -111.388), an isolated mountain range approximately 120km south of the Bridger Range. Mountain goats pioneered into the Henry's Mountains and were first documented in 2010. The Henry's Mountains have similar features with the Bridger Range: mountain goat distribution generally occurs above treeline and is a small spatial area (approximately 70km^2) and goat habitat is readily accessible by trail. Five ground-based surveys run in 2013, 2018, 2020, 2022, and 2024 counted 46, 58, 77, 101, and 112 goats respectively (MFWP, unpublished data). During the 2018 survey, MFWP worked together with Idaho Fish and Game (IDFG) to collaboratively survey the area: MFWP and RMGA did a ground survey and IDFG conducted a helicopter flight survey over the same area within 2 weeks of the ground count. The ground survey returned 58 goats with 14 kids, and the IDFG helicopter survey returned 57 goats with 14 kids. The agreement between these 2 survey methods suggested similar sightability rates and that ground surveys could be an effective methodology in this mountain range as well.

Selecting and training observers is key to effective surveys. Montana Fish, Wildlife and Parks and RMGA worked together to select volunteers to assign to each observation area. Rocky Mountain Goat Alliance volunteers were often capable hunters with particular interest in mountain goats, experienced backcountry hikers with good optics and familiarity with searching for wildlife. The training session held before each count was key to ensuring volunteers accurately classified goat groups. Correct field classifications allowed for easy removal of duplicate records because total count, age, and sex classifications were similar.

MANAGEMENT IMPLICATIONS

For some agencies managing mountain goats, simple citizen science ground-based counts may be effective and replicable methods to monitor populations. Sightability rates may differ between study areas, and success of the counts could be influenced by the training and abilities of volunteers, the knowledge of mountain goat distribution and viewsheds in planning observation points, by weather conditions during the surveys, and by geospatial factors intrinsic to survey areas. Areas with high trail densities, predictable goat distributions, and high visibility (i.e., areas without dense shrub growth and where mountain goats avoid canopy cover) may increase the success of ground-based counts.

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Examining the Influence of Ecotypic Variation and Environmental Factors that Contribute to the Success of Translocated Bighorn Sheep

SEAN MCCAIN, *University of Nevada, Reno, NV, 89557, USA; seanrmccain@nevada.unr.edu*
KELLEY M. STEWART, *University of Nevada, Reno, NV, 89557, USA*
VERNON C. BLEICH, *University of Nevada, Reno, NV, 89557, USA*
BRETT P. WIEDMANN, *North Dakota Game & Fish Department, Dickinson, ND, 58601, USA*
RUSTY ROBINSON, *Utah Department of Natural Resources, Salt Lake City, UT, 84116, USA*

ABSTRACT: Bighorn sheep (*Ovis canadensis*) were extirpated from much of their historic range in the 19^{th} and 20^{th} centuries because of widespread disease. In response, translocations emerged as a valuable restoration tool to return bighorn sheep to their native range in North America, but many of these translocated populations were characterized by low recruitment, limited range expansion, and poor population performance. Some investigators have implicated a failure to consider local adaptations to environmental conditions as a factor limiting translocation success, but research examining region-specific environmental factors has been limited. Our objective is to examine the spatial and temporal differences in resource selection between male and female bighorn sheep in the Little Missouri River region of North Dakota, an area that is most appropriate for the Rocky Mountain ecotype, and Antelope Island in Utah, which is most appropriate for the desert ecotype. Historically, populations at both locations experienced poor performance because of possible ecotype mismatch, but they are now improvingafter the addition of stock from source locations that more closely align with their release sites. The addition of bighorn sheep ecotypes from source environments that more closely align with the target environment might appear to be a strong predictor of improved population trajectories. To evaluate factors that might positively influence population trajectories, we are using resource selection functions to compare selection patterns in both locations. Our results will contribute to the improvement of restoration strategies and enhance translocation success.

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KEYWORDS: Antelope Island, bighorn sheep *(Ovis canadensis)*, desert ecotype, Little Missouri River, North Dakota, resource selection, Rocky Mountain ecotype, spatial temporal distribution, translocation, Utah.

Seasonal Habitat Use of a Re-Introduced Rocky Mountain Goat Population in Oregon

JESSICA S. CLARK, *Oregon Department of Fish and Wildlife, Bend, OR, 97702, USA;*
jessica.s.clark@odfw.oregon.gov
COREY HEATH, *Oregon Department of Fish and Wildlife, Bend, OR, 97702, USA*
SETH HARJU, *Heron Ecological, Kingston, ID, 83839, USA*
ANDREW WALCH, *Oregon Department of Fish and Wildlife, Bend, OR, 97702, USA*
DON WHITTAKER, *Oregon Department of Fish and Wildlife, Salem, OR, 97702, USA*

ABSTRACT: Rocky Mountain goats (*Oreamnos americanus*) historically existed in small, isolated populations in the Central Oregon Cascades until their extirpation early in the mid-nineteenth century. The Oregon Department of Fish and Wildlife (ODFW), in partnership with the Confederated Tribes of the Warm Springs Reservation of Oregon (CTWSRO), began restoration efforts with 3 separate translocation events in 2010, 2012, and 2016. Using location data from animals radio collared during the release, we developed seasonal (summer and winter) resource selection function (RSF) models of this newly translocated population. We used mixed effects logistic regression models in a use-availability framework to estimate relative probability of use based on a variety of topographic, vegetative, environmental, and anthropogenic covariates. This analysis marks the first of its kind to explore Rocky Mountain goat habitat selection in central Oregon. Results will be used to identify basic habitat characteristics important to Rocky Mountain goats in this region, will inform climate change implications for this high-altitude species, and will help identify potential areas for future translocation projects.

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KEYWORDS: Cascades, Confederated Tribes of the Warm Springs Reservation of Oregon, habitat selection, Oregon, Oregon Department of Fish and Wildlife, Rocky Mountain goats *(Oreamnos americanus)*, resource selection function.

Navigating Uncertainty: The Adaptive Value of Low Fidelity in Desert Bighorn Sheep

IAN MONTGOMERY, *Utah Division of Wildlife Resources/Utah State University, Cedar City, UT, 84721, USA; imontgomery@utah.gov*
KEZIA MANLOVE, *Utah State University, Logan, UT, 84322, USA*

ABSTRACT: An individual's fitness is fundamentally tied to its ability to access high-quality forage and avoid predators; attributes that vary across the physical environment the individual inhabits. Individuals with better information about the area they inhabit should have greater fitness because they can move more directly among resource patches while minimizing exposure to predation risk. However, factors influencing range fidelity can fluctuate seasonally in response to changes in the environment. Individuals that live in temporally predictable environments can benefit from having high fidelity to their seasonal ranges, however, when predation risk or food availability are not predictable through time, high site fidelity may reduce fitness. Desert bighorn sheep (*Ovis canadensis nelsoni*) are synonymous with the arid desert southwest and occupy environments that are stochastic across space and time, making them an ideal species for testing hypotheses about adaptive range fidelity. We utilized GPS data from the Zion desert bighorn population in southwest Utah to (a) determine seasonal home ranges and core areas, (b) quantify site fidelity, and (c) monitor survival and cause of mortality. We then estimated time within the seasonal core area and used that value as a measure of site familiarity to examine how risk of mortality varied with familiarity across both temporal and spatial scales. We found that larger seasonal home ranges were associated with reduced seasonal mortality rates, and that seasonal mortality rates were elevated when individuals concentrated space use within smaller regions of their home ranges. Our results indicate that in temporally unstable environments, site fidelity may be a maladaptive strategy. Consequently, conservation efforts should focus on maintaining and supporting high connectivity within desert bighorn ranges to ensure that animals are able to access adequate resources while still limiting predation risk.

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KEYWORDS: connectivity, Desert bighorn sheep (*Ovis canadensis nelsoni*), fitness, GPS, home range, mortality, site fidelity, survival, Utah Zion National Park.

Surviving with Low Genomic Diversity: The Impacts of Reintroduction Management on Inbreeding and Genetic Load in Bighorn Sheep (*Ovis canadensis*)

MICHAEL R. BUCHALSKI, *Wildlife Genetics Research Unit, Wildlife Health Laboratory, California Department of Fish and Wildlife, Sacramento, CA, 95670, USA; Michael.Buchalski@wildlife.ca.gov*

SAMANTHA L. R. CAPEL, *Wildlife Genetics Research Unit, Wildlife Health Laboratory, California Department of Fish and Wildlife, Sacramento, CA, 95670, USA*

CATHERINE B. QUINN, *USDA Forest Service, National Genomics Center for Wildlife and Fish Conservation, Rocky Mountain Research Station, Missoula, MT, 59801, USA*

ABSTRACT: Bighorn sheep (*Ovis canadensis*) recovery throughout North America over the last century has been accomplished primarily through translocations from relict herds into unoccupied historical range. Yet the genomic consequences of reintroductions, including founder events, inbreeding depression, and genetic drift remain uninvestigated. This includes evaluating the risk of subsequent demographic/genetic rescue using stock from large, genetically diverse populations, as such individuals could introduce new deleterious recessive alleles. To characterize the effects of a founder event followed by complete isolation, we resequenced at 30x coverage 12 whole genomes from a 45-year-old introduced population of bighorn sheep in the Sespe Wilderness, California. This population was established from as few as 20 animals, has the lowest heterozygosity recorded for bighorn sheep, and anecdotally has shown potential phenotypic evidence of birth defects in the form of kinked tails. Yet the Sespe population has persisted at what is assumed to be near carrying capacity ($N \approx 60$) for decades. Size of runs of homozygosity suggested inbreeding was intense at the time of introduction but has been minimal in the last < 20 years. Compared to the source population (n = 12), and a genetically diverse reference population (n = 12), the Sespe individuals had a higher proportion of homozygous and fixed missense and loss-of-function mutations, which may reflect increased expression of deleterious alleles. Simulations of various augmentation scenarios are planned to evaluate extinction risk associated with introducing stock from various sized populations with differing genetic load. This study will guide future reintroductions and demographic/genetic rescue efforts for bighorn sheep throughout North America.

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KEYWORDS: bighorn sheep *(Ovis canadensis)*, California, founder events, genetic drift, genome, inbreeding, inbreeding depression, Sespe Wilderness, reintroduction, zygosity.

Non-Consumptive Effects of Hunting on Stone's Sheep Behaviour in the Spatsizi Plateau Wilderness Park, BC

JULIEN W.F. GULLO, *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada*; gullo@ualberta.ca
BILL JEX, *Fish and Wildlife Branch, British Columbia Ministry of Water, Land & Resource Stewardship, Smithers, BC, Canada*
MARK S. BOYCE, *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada*

ABSTRACT: Most of the global population of Stone's sheep (*Ovis dalli stonei*) lives within northern British Columbia, placing exceptional stewardship responsibilities in the hands of wildlife managers who manage this species for multiple values. Research has yet to focus on the non-consumptive effects (predator influence on prey trait and decision making; NCEs) of hunting on their behaviour. Because many behavioural NCEs carry potential fitness consequences, addressing this knowledge gap is necessary to develop cumulative effects management strategies of Stone's sheep populations in the future. We believe that hunting pressure, as proxied by the number of sheep hunting permits issued, will have effects on Stone's sheep behaviour, where responses will increase with increased hunting intensity. We aim to (1) identify effects of hunting activities on Stone's sheep behaviour and (2) evaluate the sensitivity of these effects to changes in hunting pressure. Using GPS telemetry data collected from sheep and hunters, remote camera-trap imaging, habitat selection modelling, and movement and group size analysis, we will compare sheep behaviour throughout seasonal changes in hunting activity. In addition, we also plan to manipulate hunting intensity during our study period by reducing authorized sheep hunting permits in our second focal year. Our research seeks to improve Stone's sheep management by adding a more comprehensive understanding of the effects of harvest regulations on wildlife behaviour and fitness and may have broader implications in reducing potentially negative non-consumptive effects of hunting on sheep populations.

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KEYWORDS: behavior, British Columbia, cumulative effects, fitness, habitat selection, harvest regulations, hunting, non-consumptive effects, Spatsizi Plateau Wilderness Park, Stone's sheep *(Ovis dalli stonei)*.

Habituated, Tolerant, or and Salt-Conditioned Mountain Goats and Human Safety

RICHARD B. HARRIS, *Montana Fish, Wildlife and Parks (retired), MT, 59620, USA; rharris@montana.com*
KURT ALUZAS, *Mt. Baker Snoqualmie National Forest, Everett, WA, 98208, USA*
LAURA BALYX, *University of British Columbia, Kelowna, BC, V1V 1V7, Canada*
JAMI BELT, *Glacier National Park, West Glacier, MT, 59936, USA*
JOEL BERGER, *Colorado State University, Fort Collins, CO, 80523, USA*
MARK BIEL, *Glacier National Park, West Glacier, MT, 59936, USA*
TONYA CHILTON-RADANDT, *Montana Fish, Wildlife and Parks, Libby, MT, 59923, USA*
STEEVE D. CÔTÉ, *Université Laval, Québec, QC, G1V 0A6, Canada*
JULIE CUNNINGHAM, *Montana Fish, Wildlife and Parks, Bozeman, MT, 59718, USA*
ADAM FORD, *University of British Columbia, Kelowna, BC, V1V 1V7, Canada*
PATTI HAPPE, *Olympic National Park (retired), WA, 98362, USA*
CHAD P. LEHMAN, *South Dakota Department of Game, Fish, and Parks, Custer, SD, 57001, USA*
KIM POOLE, *Aurora Wildlife Research, Nelson, BC, Aurora Wildlife Research, Nelson, BC, V1L 6K1, Canada*
CLIFFORD G. RICE, *Washington Department of Fish and Wildlife (retired), Olympia, WA, 98504, USA*
KIRK SAFFORD, *British Columbia Parks, Ministry of Environment and Climate Change Strategy, Penticton, BC, V8W 9M1, Canada*
WESLEY SARMENTO, *Montana Fish, Wildlife and Parks, Conrad, MT, 59425, USA*
LAURA WOLF, *Idaho Department of Fish and Game, ID, 83712, USA*

ABSTRACT: Interactions between humans and wildlife include several consumptive and non-consumptive forms. In some cases, the increased demand for wildlife viewing can precipitate new human–wildlife conflicts. Mountain goats (*Oreamnos americanus*) are native to numerous North American mountain ranges from southeastern Alaska to southwestern Montana, USA. Goat habitat typically consists of steep terrain and cold weather habitats, which has left them particularly vulnerable to climate change. Their alpine environments also make them vulnerable to disturbance by aircraft and land-based motorized human activity. We reviewed and characterized situations in which goats in close proximity to humans on foot may become a nuisance or dangerous to people. We identify how such interactions might occur, focusing on the array of intensity observed in different settings. We summarize and evaluate interventions that have been attempted and may warrant additional research. Goats that tolerate people along hiking trails, perhaps through a habituation-like process, can typically be kept at a safe distance simply by shouting, clapping hands, or vigorous gestures. Goats that have learned to associate people with a salt reward (e.g., typically urine deposited on the ground, less frequently sweat obtained directly by licking) are more likely to be successfully hazed by tossing small stones, hitting the animal in the flank or rear. Salt-conditioned goats sometimes come within touching distance of humans; we strongly advise against prodding or poking these animals with sharp objects such as trekking poles. The recreating public that ventures into goat habitat is the ultimate source of these conflicts. Education, compliance, and possibly some infrastructure improvements can lessen the potential for conflicts and provide new and safer opportunities to view goats.

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KEYWORDS: anthropogenic disturbance, climate change, habituation, mountain goats *(Oreamnos americanus)*, tolerance, salt conditioned, wildlife viewing.

Managing for Population Recovery of Mountain Goats on the Kenai Peninsula, Alaska

JASON HERREMAN, *Alaska Department of Fish and Game, Homer, Alaska, 99603, USA; jason.herreman@alaska.gov*

JOHN P. SKINNER, *Alaska Department of Fish and Game, Anchorage, Alaska, 99518, USA*

ABSTRACT: Mountain goat (*Oreamnos americanus*) management on the Kenai Peninsula, Alaska has evolved over time as our understanding of the species has improved and environmental conditions continue to change. Populations were found to decline under management strategies once deemed successful. We compared mountain goat minimum count numbers, harvest levels, population trends, and survey techniques collected and used during 1980–2008 to data collected after the implementation of a new harvest strategy (2009–2021) to determine if mountain goat minimum count numbers recovered under the new strategy and if it appropriately manages goat populations. Recent surveys indicated the Kenai Peninsula wide minimum count numbers have returned to historic levels. Recovery of minimum count numbers occurred after nannies with kids were removed from the harvest and a new management system was instituted that included a 5-year no hunting penalty for any individual that harvested a nanny. Paired surveys and a general trend in counts with respect to time of year suggest that goat surveys on the Kenai Peninsula should be conducted in the fall to maximize sightability.

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KEYWORDS: Alaska, harvest, Kenai Fjords National Park, Kenai Peninsula, management, mountain goat, *Oreamnos americanus,* population decline, recovery.

Mountain goat (*Oreamnos americanus*) hunting on the Kenai Peninsula has been popular since statehood due to the accessibility of goats from the road system and the Kenai Peninsula's proximity to the state's highest population density in the Anchorage area. Human pressures have increased as human populations continue to grow and mountain recreational activities such as heli-skiing, snowmachining, backcountry skiing, heli-snowmachining, and general heli-recreation increase. Overharvest and other anthropogenic pressures have likely contributed to population fluctuations over time (McDonough and Selinger 2008, Herreman 2022). Managers have adjusted management schemes and survey techniques to address these fluctuations, and to maintain a sustainable hunting and viewing opportunity for goats across the Kenai Peninsula. In this paper, we retrospectively analyze trends in goats and changes in harvest during different time periods to contrast different management schemes and examine potential biases of shifting survey timing.

Mountain goat management at statehood began with liberal bag limits and season dates, but by 1970 the Alaska Department of Fish and Game (ADFG) recognized that these were unsustainable and changes in management regulations ensued (ADFG 1960, 1976; Del Frate and Spraker 1994). By 1980 a draw permit system was established in conjunction with registration permits. Draw hunts were split into 35 management units based on survey areas to help distribute hunting pressure (Delfrate and Spraker 1994). Late season registration hunts were held in management units in which harvest opportunity remained after the close of the draw season. Management unit boundaries have remained relatively stable since inception.

The number of management units open to hunting has varied slightly through the years (Delfrate and Spraker 1994, McDonough and Selinger 2008, Herreman 2022), with 32 units open as of 2021 to the possibility of a hunt if management criteria are met. The number of drawing permits allocated to each management unit was originally based on the number of goats observed during surveys, accessibility of the unit, and historical success rates for each unit. Harvest rates for draw hunts were set at 5% of the observed goats in a unit and later increased to 7% (Delfrate and Spraker 1994). The Alaska Board of Game authorized a maximum of 500 draw permits to be issued for all management units combined on the Kenai Peninsula in any given year.

The management objective during the 1990s was to maintain a population of 4,000–4,500 goats, with a predominantly male harvest of greater than 66% (Delfrate and Spraker 1994). Population estimates were calculated as a range, assuming 70–90% of goats were observed during aerial minimum count surveys. The combined draw-registration hunt system was deemed successful (Delfrate and Spraker 1994) until the early 2000s, despite indications of declining populations documented in the late 1990s (Healy 2002).

Due to documented population declines from 1992 to 2000, a regulation change was instituted in 2001 prohibiting hunters from harvesting nannies with kids. With this regulation change, efforts to educate hunters about the negative population effect of harvesting nannies were increased. As populations continued to decline, new managers sought means to reverse the population trend. Beginning in 2008, the ADFG developed and implemented a new management scheme using explicit criteria to determine the number of draw and registration hunting permits issued each year by management unit (McDonough and Selinger 2008). Criteria were based on population size and trends, past harvest rates, sex composition of the harvest, the age of survey data, access, and ecotype (McDonough and Selinger 2008). Additionally, a regulatory penalty for harvesting a nanny was instituted in 2009 that prohibits any hunter that harvested a nanny from hunting mountain goats on the Kenai Peninsula for 5 years. Season length has changed little over the years with draw and registration hunts remaining open from 15 August–14 November. Harvest monitoring has continued through permit reporting since the establishment of harvest permits.

Consistent survey methods for mountain goats on the Kenai Peninsula were established in the 1980s, when summer fixed-wing surveys with pilot-observer teams became the ADFG standard. Nichols (1980) described the ideal conditions under which surveys should be conducted as overcast skies, with soft light and no turbulence. Despite Ballard's (1975) and Nichol's (1978) findings that neither temperature nor time of day were correlated to the number of goats seen, early morning and late evening flights, before hunting season, with temperatures below 60°F became the standard on the Kenai Peninsula from the 1980s to early 2000s. However, early morning and late evening flights could result in poor sun angle for observers, and pilot availability during these time windows was often a problem in recent years. Accordingly, surveyors began looking at other survey timing possibilities.

In 2011, work by Jenkins et al. showed less diurnal variation in the presence of goats in alpine survey grids during September versus July and goats being more available in September. The ideal conditions noted by Ballard (1975) and Nichols (1978), anecdotally were more common during fall and late summer than during traditional survey periods centered around the month of July. Temperatures were also cooler during the late summer and fall period than during the traditional survey period, which despite the lack of correlation found in earlier work, may have led to goats being more out in the open and visible. Additionally, if surveys are conducted late enough in the fall, leaf drop may have occurred making goats typically obscured by canopy cover more visible. This information, coupled with the variability of count data between early/midsummer and late summer/fall surveys done several years apart in the same survey area, led the ADFG to initiate paired surveys within the same year to address the question of whether shifting surveys to later in the season would provide better minimum count data.

STUDY AREA

The Kenai Peninsula lies south of Anchorage, Alaska and encompasses an area of approximately 21,748 km^2. Mountain goat habitat is found in the eastern portion of the Kenai Peninsula and was split into 32 different management units ranging in size from 100–1,363 km^2, Kenai Fjords National Park (KFNP) which includes 3 additional management units, and the Cooper Landing Closed Area (CLCA). KFNP and CLCA have been closed to goat hunting since their establishment in 1980 and 1960 respectively (Figure 1). The primary agencies responsible for land management within goat range outside of KFNP are the Chugach National Forest, Kenai National Wildlife Refuge, and Kachemak Bay State Park.

METHODS

We conducted a comparison of mountain goat minimum count numbers, harvest levels, population trends, and survey techniques collected and used prior (1980–2008, Delfrate and Spraker (1994)) to the implementation of the harvest strategy of McDonough and Selinger (2008) with data collected after the implementation of the new strategy (2009–2022) to determine if the population has stabilized under the new management strategy. All analyses were using ADFG goat harvest and survey data collected from 31

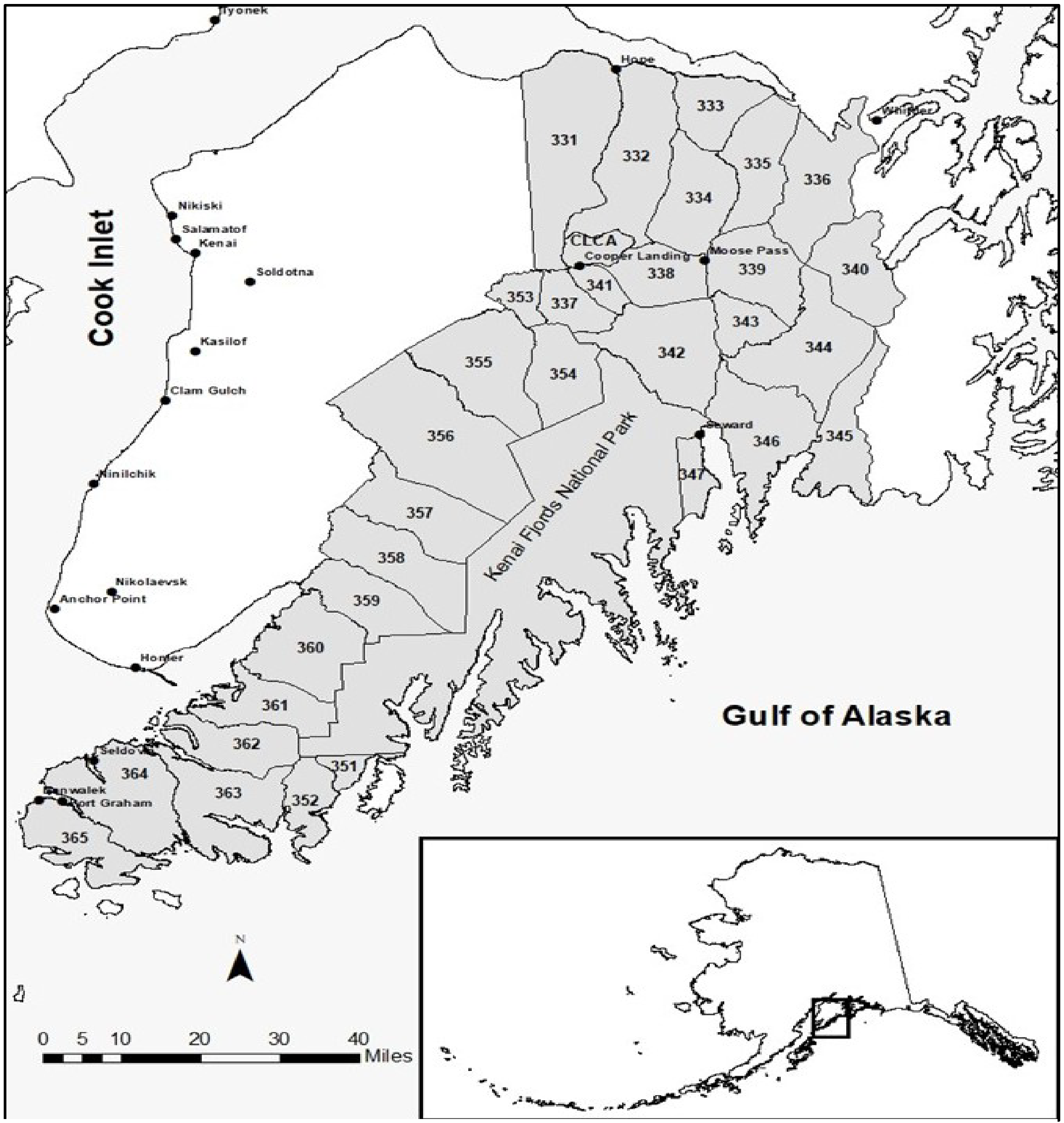

Figure 1. Kenai Peninsula, Alaska mountain goat management units 2022. Note, Kenai Fjords National Park, the Cooper Landing Closed Area (CLCA), and Unit 353 were excluded from all analyses due to a lack of harvest data.

management units (Unit 353 was excluded due to a lack of harvest data) during the period 1980 to 2022. We performed all data manipulation and statistical modeling using R statistical software (R Core Team 2023).

Surveys and effects of survey timing

Survey flight paths followed the topography of the landscape. Transects were flown along elevational contours starting at the tree/alder line working up the mountain. Each mountain face received 2–3 passes depending on the mountain height and observability. When animals were observed, pilots circled the location so that the observer could note the number and classify animals in each group. The location and movement of animals in the group were noted so that on consecutive passes animals were not recounted. By starting transects at low elevation, animals higher on the ridge were less likely to move down into the tree/alder line where they would be unobservable on consecutive passes. Goats were classified as either kids or adults (i.e., yearlings, subadults and adults combined).

Between 2011 to 2019 we opportunistically surveyed 11 management units twice in the same year. Once early in the season between July 14 and September 6 (median, August 1), and once late in the season between September 29 to October 12 (median, October 4). Pilots and observers were not the same between years due to logistical constraints, but all pilots and observers had prior mountain goat survey experience. We compared minimum counts between survey periods using generalized linear mixed (GLM) models as implemented by R-package 'glmmTMB' (Brooks et al. 2017). The response variable, minimum count, was analyzed with respect to factor variable period with 2 levels (early and late). The model included a fixed effect of period, random intercepts for each year and management unit, assumed a negative-binomial distribution of the response variable, and used a logarithmic link function.

Analysis of minimum counts

To analyze trends in total goat minimum counts, we used 459 survey records collected after June 20 of each year as raw data in generalized additive mixed (GAM) models (R-package 'mgcv'; Wood 2011), to estimate the change in minimum count (response) with respect to predictor variables year and day of year (doy) of each survey. The potential for non-linear effects from these variables were characterized using cubic regression spline functions (smooth terms) with 20 and 3 degrees of freedom, respectively. Additionally, the model included random intercept and non-linear slope effects (i.e., factor smoothers) for both doy and year for each management unit. All models used negative-binomial distributions and logarithmic link functions. Using the fitted model, we then created adjusted minimum counts for each year and management unit by using the slope (i.e. β_{doy}), of the doy effect to scale the original minimum counts by the estimated difference in expected count between October 1 and the date the survey occurred.

Analysis of changes in goat harvest

We assembled harvest data from permit reports. We then matched annual goat harvest records with adjusted minimum counts within the same management unit and year to produce 330 records that spanned years 1982 through 2021. We analyzed changes in total adult and nanny harvest rates using 2 GAM models. Each model included either total adult or nanny harvest count as response variable and year as the predictor variable coded as a cubic regression smooth term with 20 degrees of freedom. These models included adjusted minimum count as an offset term (converting the response to a rate), random intercepts and year effect factor smooths for each management unit and used a negative-binomial distribution and logarithmic link function.

Finally, using harvest data from 1982 through 2021, we analyzed the 869 records where at least one goat was killed to estimate the proportion of nanny harvest. We used a GAM model to estimate changes in harvested nannies relative to total harvested goats (response) in association with year (predictor) coded as a cubic regression smooth term with 20 degrees of freedom. This model included random intercepts and year effect factor smoothed for each management unit and used a binomial distribution and logit link function.

All models were fit using restricted maximum likelihood, and goodness-of-fit was evaluated against the random effects only (i.e., null) equivalent by likelihood ratio test. Additionally, residuals were inspected to ensure assumptions were not violated using R-package 'DHARMa' (Hartig 2022). Non-significant terms were removed stepwise based on α = 0.05 for linear terms and α = 0.01 for non-linear (i.e., GAMM smoother) terms. In GAM models, we recoded smooth terms to linear terms when they were found to have an estimated degree of freedom (edf) of nearly 1 (i.e., an indication that the response was linear). Simulations based on model posterior estimates were used to produce mean and 95% lower and upper confidence limits estimates for minimum counts, percent nanny harvest, and harvest rates across years within each of the 3 time periods of interest.

RESULTS

Survey timing

The GLM model describing the association between minimum counts and time period (late versus early) was found to have acceptable goodness-of-fit based on null likelihood ratio test ($\chi^2_{df=1}$ = 9.9, *P* = 0.002) and model residuals. Minimum counts were found to be positively associated with doy (β = 0.75, σ = 0.22, *P* = 0.001). The expected mean minimum goat count was 30 (95% confidence interval 15–61) during early season (median: August 1) and 62 (95% confidence interval: 40–102) during late season (median: October 4) surveys (Figure 2).

The model for describing trends in goat minimum counts had acceptable fit (LR: $\chi^2_{edf=28.1}$ = 49.9, *P* = 0.007) and properly distributed model residuals. Furthermore, this model explained a large amount of variance in minimum counts (deviance explained = 88.8%). Based on approximate significance for model terms, minimum counts were strongly associated with both doy ($\chi^2_{edf=1.4}$ = 8.2, *P* = 0.007) and year

($\chi^2_{edf = 7.4}$ = 80.5, P < 0.001). The effect of doy on minimum counts was found to be positive but only marginally non-linear based on edf = 1.4. We, therefore, re-fit the model including doy as a linear term to help simplify the description of this effect (β = 0.0035, σ = 0.0012, P = 0.003). We presented the non-linear and linear effects of doy in Figure 3.

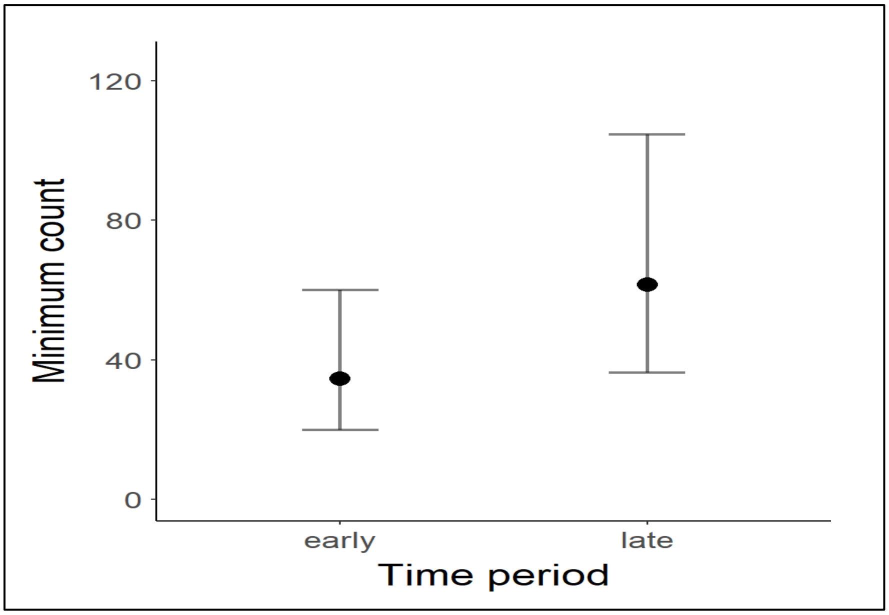

Figure 2. Mean (solid circle) and 95% confidence intervals for estimated mountain goat minimum counts during surveys conducted early (median date August 1) and late (median date October 1) in the same unit and year Kenai Peninsula, AK.

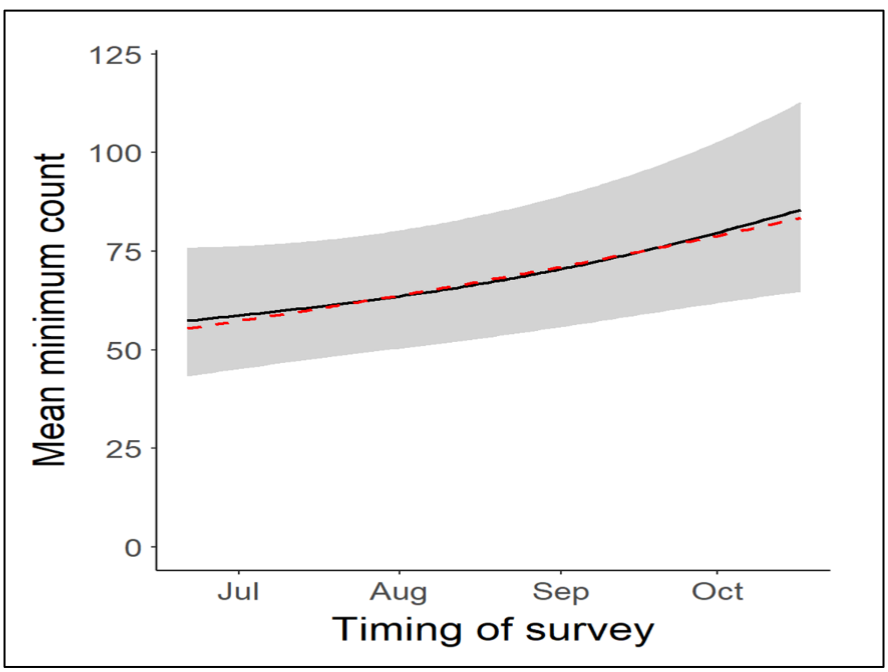

Figure 3. The estimated mean non-linear (solid curve) and linear (dashed line) effect of timing of survey (i.e., survey day of year) on mountain goat minimum counts as estimated by generalized additive mixed models. The 95% confidence limits are shown in in grey, Kenai Peninsula, AK.

Estimates for minimum count adjusted for doy of October 1 (Figure 4) showed a steep rise in counts from 1980 until 1992, a decline until 2005, and then a moderate rise until 2023, the end of the analysis period. There was considerable overlap in the confidence intervals and little trend in the adjusted minimum count estimates of 88.5 (95% confidence interval 39.2–133.7) during the period with no nanny restrictions, 72.0 (95% confidence interval 53.1–96.9) during the period with no harvest of nannies with kids, and 80.6 (95% confidence interval 58.9–118.8) during the period with a penalty for harvest of nannies with kids (Figure 5A).

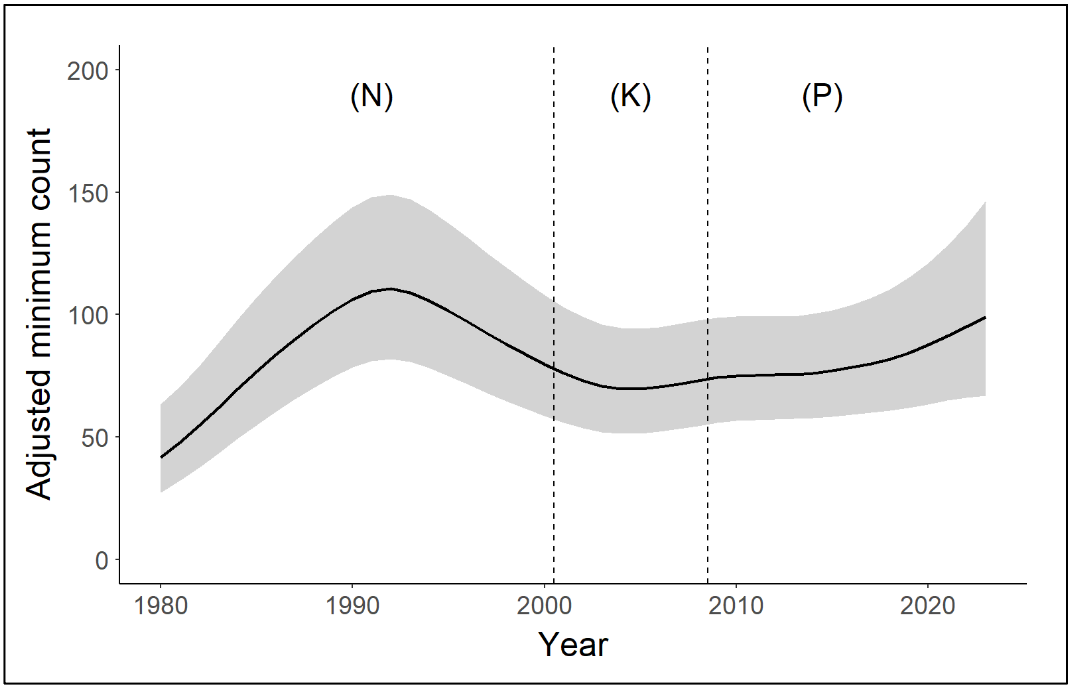

Figure 4. The estimated mean (black) and 95% confidence intervals (grey) for changes in adjusted mountain goat minimum counts over time and across 3 time periods that had no nanny harvest restrictions (N), restriction on harvest of nannies with kids (K), and a 5-y ear penalty for harvest of nannies with kids (P) Kenai Peninsula, AK. Estimates were based on the marginal generalized additive mixed model effects for year with timing of surveys of October 1.

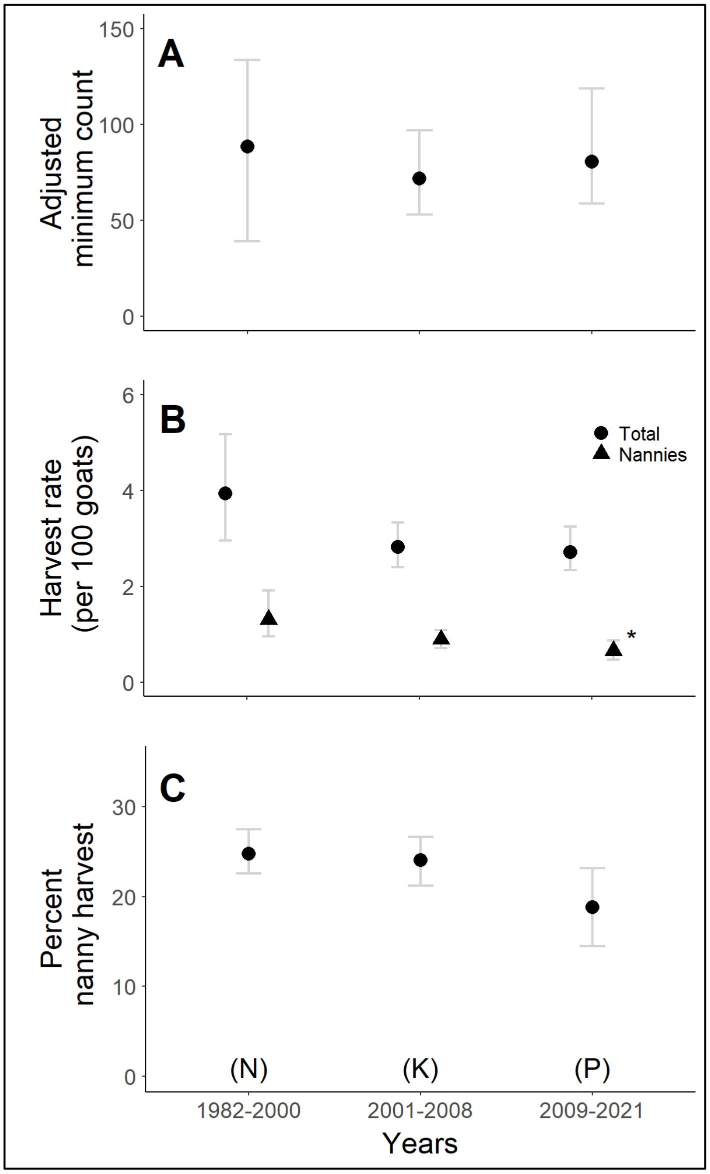

Figure 5. Estimated means (solid circles) and 95% confidence intervals (error bars) for adjusted mountain goat minimum counts (A), total and nanny harvest rates (B), and percent nanny harvest (C) across 3 time periods that had no nanny harvest restrictions (N), restriction on harvest of nannies with kids (K), and a 5-year penalty for harvest of nannies with kids (P) Kenai Peninsula, AK. All estimates were simulated using model posterior estimates for all years represented within each time period. As indicated by an asterisk (*), nanny harvest rates in the period with a 5-year penalty for harvest of nannies with kids was statistically lower than the period with no nanny harvest restrictions.

Total harvest rate had a strong, non-linear association with year ($\chi\chi^2_{eedddd = 2.7}$ = 36.1, P < 0.001) demonstrated in a moderate downward trend until flattening in 2009 (Figure 6), which coincided with implementation of the harvest strategy of McDonough and Selinger (2008). Although confidence intervals overlapped for estimates across time periods (Figure 5B), harvest rates tended to be lower during the periods with restriction on harvest of nannies with kids (mean = 2.82; 95% 95% confidence interval 2.40–3.33) and 5-year penalty for harvest of nannies with kids (mean = 2.71; 95% confidence interval 2.33–3.24) than during the period with no restrictions (mean = 3.93; 95% confidence interval 2.95–5.18).

Nanny harvest rates had a strong association with year ($\chi\chi^2_{eedddd = 1.001}$ = 31.6, P < 0.001) demonstrated in a relatively consistent and nearly linear decline over the period of analysis (Figure 6). After re-coding the year term to be linear in the model, the effect remained highly significant ($\beta\beta$ = -0.029, σ� = 0.0052, P < 0.001) and showed a 2.9% decline in nanny harvest per year over the entire period of analysis. Over the three different nanny harvest restriction periods, nanny harvest rates were 1.31 (95% confidence interval 0.96–1.91) when no restrictions were imposed, 0.89 (95% confidence interval 0.71–1.09) with restrictions on harvest with kids were applied, and 0.66 (95% confidence interval 0.47–0.87) when penalties were imposed on harvest of nannies. Based on non-overlapping confidence intervals, nanny harvest rate during the period with penalties was lower than the period with no restrictions (Figure 5B). Similar to the harvest rate models, the year effect factor smooths (random effects) did not contribute to the fit of the relative nanny harvest model ($\chi\chi^2_{dddd = 0.63}$ = 0.43, P = 0.35) and we removed it. The resulting model included year smoothed fixed-effects and random intercepts by management unit and had acceptable fit (LRT: $\chi\chi^2_{dddd = 4.82}$ = 29.6, P ≤ 0.001) and well-distributed residuals. Although this model only explained 5.6% of the deviance in relative nanny harvest, there was a strong non-linear association with year ($\chi\chi^2_{dddd = 3.74}$ = 26.1, P < 0.001). Model estimates showed that percent nanny harvest remained relatively constant until 2000 and then declined until the end of the analysis period in 2023 (Figure 7). Percent nanny harvest was 24.7% (95% confidence interval 22.6–27.5%), 24.0% (95% confidence interval 21.2–26.6%), and 18.8% (95% confidence interval 14.5–23.1%) over the three periods with differing nanny harvest restrictions (Figure 5C).

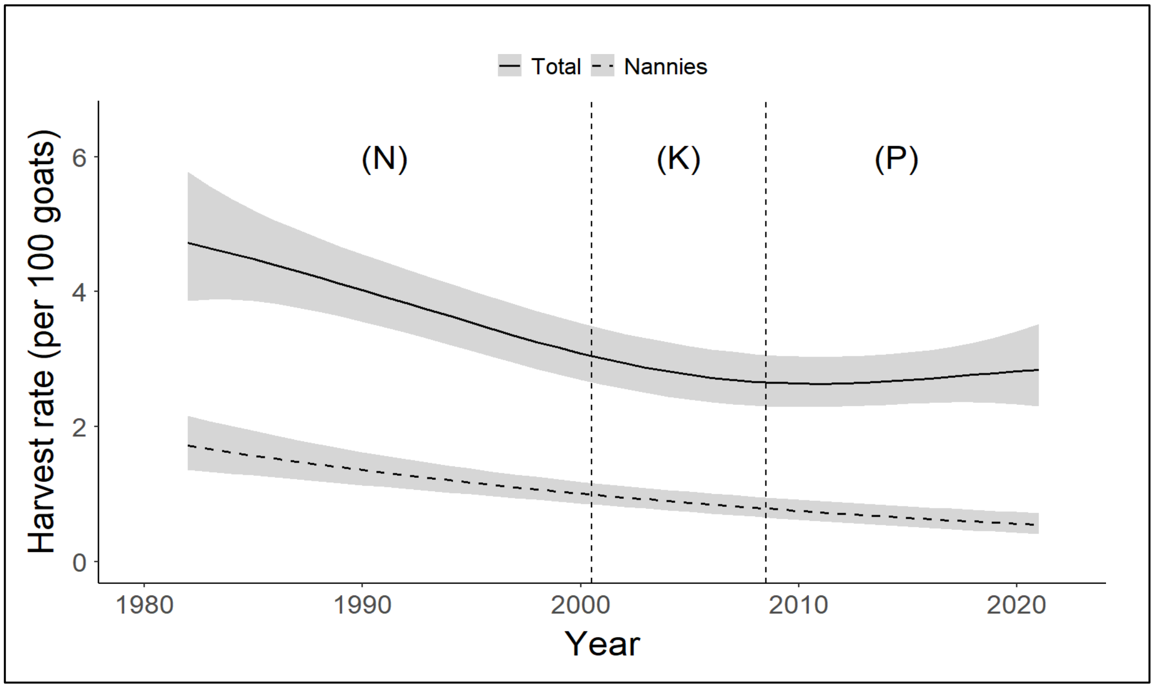

Figure 6. The estimated mean change in total mountain goat (solid) and nanny (dashed) harvest and 95% confidence intervals (grey) over time and across three time periods with no nanny harvest restrictions (N), restriction on harvest of nannies with kids.

DISCUSSION

Mountain goat minimum count numbers on the Kenai Peninsula peaked in the 1990s and then began a steady decline into the early 2000s (Figure 4). Managers needed an effective way to reverse the population trajectory. The most readily available tool that managers had to affect goat populations was through the manipulation of harvest. ADFG began incremental harvest changes to curb population decline and with the hopes of initiating population recovery. At the same time, there was a notable change in survey timing as managers attempted to maximize minimum count surveys. Although not consistent across time and survey units, past surveys tended to occur during the summer season with early morning or late evening flights whereas more recent surveys occurred in the fall during midday. Because time of day was not consistently recorded, we did not address the effect of time of day on survey results; however, we did show a positive effect of day of year on the minimum number of animals seen (Figure 2 and 3). For that reason, we adjusted minimum count levels by survey timing before comparisons were made to determine if goat numbers had improved. Adjusting the minimum count levels did not affect the overall trend in minimum count data seen before adjustments.

Management changes reducing harvest pressure (Figure 6) were not enough to stem population declines of Kenai Peninsula mountain goats. The subsequent protection of nannies with kids from harvest in 2001 appeared to slow declines (Figure 4) but only slightly reduced the percent of nanny harvest (Figure 7) and was not enough to reverse the population trajectory. Trends were not affected until the institution in 2009 of the 5-year penalty for harvesting a nanny. We hypothesize that the removal of nannies with kids from the harvest was insufficient to reverse the overall trajectory of the population due to mountain goat reproductive constraints such as late age of primiparity, small litter size, and reproductive pauses (Festa-Bianchet and Côte 2008). The addition of a penalty for harvesting a nanny and increased educational efforts on mountain goat sex identification; however, does appear to have allowed for the recovery of most goat subpopulations on the Kenai Peninsula. The harvest rate of nannies significantly declined (Figure 5B), which likely increased reproduction. The increased reproduction combined with the protection of nannies with kids led to increased recruitment. As suggested by Hamel et al. (2006), management of female harvest appears to have one of the greatest effects on the viability of mountain goat populations on

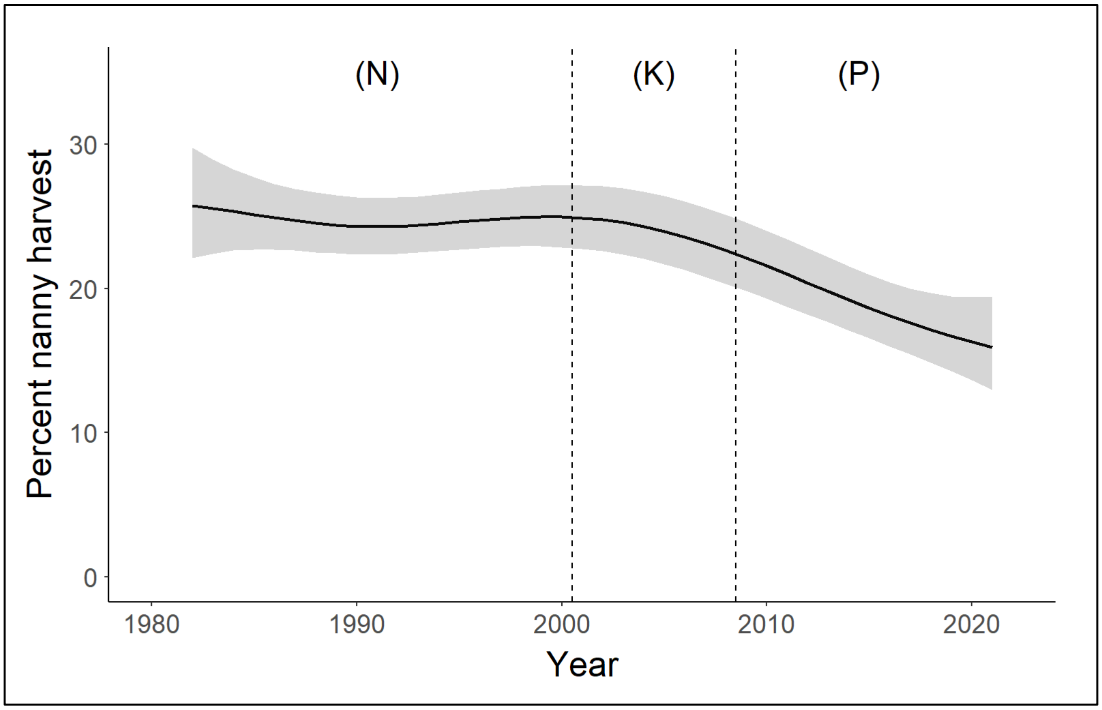

Figure 7. The estimated mean (black) and 95% confidence intervals (grey) for changes in percent of total mountain goat harvest represented by nannies across three time periods that had no nanny harvest restrictions (N), restriction on harvest of nannies with kids.

the Kenai Peninsula. Surveys beginning in 2021 indicated the mountain goat minimum count for the Kenai Peninsula had returned to near historic levels (Figure 4) and the peninsula wide harvest rate stabilized around 3% (Figure 6). Actual harvest rate varied by management unit but remained under 4% (J.K. Herreman, ADFG, Unpublished data) for all units since switching to the new management structure, which was lower than the 5–7% harvest targets set under the old management structure (Delfrate and Spraker 1994).

Although mountain goat numbers on the Kenai Peninsula recovered under the current hunt management structure, it may still be possible to improve on the system and increase harvest opportunity without detrimentally impacting goat numbers. For example, the current system relies on a limited late season hunt to maximize harvest opportunity. The late season currently overlaps with the rut, when billies are mixing more with nanny groups, which may increase the chance of sex misidentification by hunters. Access to many areas increases in difficulty during the late harvest season due to deteriorating weather conditions, increasing the chance that hunters may shoot the first available goat. Additionally, some hunters may choose to shoot a nanny to avoid the stronger taste of a rutting billy. Thus, moving the late season out of rut might further decrease female harvest and increase kid production. We recommend that managers continue to pursue avenues to improve harvest management such as restructuring management boundaries if deemed appropriate and pursing changes in season dates to further ensure sustainable nanny harvest and improve access.

Mountain goats and the biologists who manage them continue to face the unknown challenges and complications of changing environmental conditions. The effects of increasing summer and seasonal temperatures, changes in alpine plant communities, conversion of alpine habitats, increasing frequency of winter icing or rain-on-snow events, and changes in precipitation regimes (Dial et al. 2007, Ernakovich et al. 2014, Pan et. al. 2018, White et al. 2018, 2025) will all likely factor into the future changes of mountain goat population numbers. Additionally, changes in human use of mountain goat habitat as human populations increase and access to goat habitat increases will continue to add additional stressors. Managers will need to continue adapting to changing conditions to ensure the viability of mountain goats on the Kenai Peninsula and studies like this that increase the understanding of drivers of goat populations and hunter dynamics are important.

MANAGEMENT IMPLICATIONS

The manipulation of nanny take in the harvest appears to be the most important harvest factor managers can control to affect population trajectory of mountain goat populations. Effective management structures need to be flexible enough to allow managers to manipulate nanny harvest within short time frames to address population trajectory even when declines or increases are the effect of factors outside the managers control such as winter events or disease outbreaks. Standardizing surveys to the fall will maximize minimum counts and provide managers with more consistent information.

ACKNOWLEDGMENTS

We thank the many biologists, technicians, and pilots that helped collect the data used in this analysis. We are particularly grateful to N. Olson and the U.S. Fish and Wildlife Service for lending logistical support in our efforts to compare early and late minimum counts and to J. de Creeft who has piloted mountain goat surveys for ADFG for over 30 years.

ETHICS STATEMENT

This study adhered to all relevant regulations and guidelines regarding the ethics of animal welfare.

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A Comparison of Habitat and Movement Metrics Between a Hunted and Unhunted Dall's Sheep Population

BOOMER HESLEY, *University of Alaska Fairbanks, 1731 South Chandalar Drive, Fairbanks, AK, 99709, USA; cthesleyii@alaska.edu*
BRAD WENDLING, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK, 99701, USA*
GREG BREED, *University of Alaska Fairbanks, 1731 South Chandalar Drive, Fairbanks, AK, 99709, USA*

ABSTRACT: In Alaska, Dall's sheep (*Ovis dalli*) are a coveted species and predominately managed under a full-curl harvest strategy, open to residents and non-residents. Recent population declines throughout the state have heightened the concern for the long-term conservation of the species. Among those concerns are: 1) the effectiveness of the full-curl strategy during population lows, and 2) the potential impact of climate change on population dynamics. In 2023, we initiated a novel, landscape-scale, comparative study on population dynamics and demographics in largely unhunted portion of Gates of the Arctic National Park (3,200 km^2) vs. adjacent hunted state managed lands (1,290 km^2). We deployed 50 GPS collars on rams, with 25 each in a treatment (hunted) and control (unhunted) study area. Sixty ewes (30 per study area) will be GPS collared in March 2024. We hypothesize that sub-legal, subordinate, rams should replace full-curl rams in the mating system, when the older, socially dominant full-curl rams are removed. Sheep in the treatment study area will have increased movement rates, specifically during the rut and during the hunting season. These behavioral changes could interact with weather events and/or climate change to increase mortality in unexpected ways. To test our hypotheses, data will be analyzed using a dynamic parameter movement model, integrated step-selection analysis, and energetic modelling to assess differences in movement behaviors, energy expenditure, and habitats used and selected in the treatment and control areas. Understanding how hunting potentially changes the mating system dynamic and habitat selection will lead to a more nuanced understanding of how hunting pressure interacts with climate events and resource disruptions to impact Alaskan Dall's sheep populations. Results from this study will provide managers with important information to conserve sheep and fulfill their respective mission and mandates.

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KEYWORDS Alaska, Dall's sheep *(Ovis dalli)*, dynamic parameter movement model, energetics, full-curl hunt management, GPS collar, Gates of the Arctic National Park & Preserve, integrated step-selection analysis.

An Investigation of Exposure of Bighorn Sheep to the Parasite *Toxoplasma gondii* in Idaho

LAUREL K. HOSSLER, *Washington State University, Pullman, WA, 99164, USA; laurel.hossler@wsu.edu*
E. FRANCES CASSIRER, *Idaho Department of Fish and Game, Lewiston, ID, 83501, USA*
HOLLIE MIYASAKI, *Idaho Department of Fish and Game, Idaho Falls, ID, 83401, USA*
STACEY DAUWALTER, *Idaho Department of Fish and Game, Eagle, ID, 83616, USA*
KATHRYN P. HUYVAERT, *Washington State University, Pullman, WA, 99164, USA*

ABSTRACT: *Toxoplasma gondii* is a parasitic protozoan that can infect a diversity of vertebrates, including bighorn sheep. Members of the Felidae are the definitive hosts of *T. gondii* and spread the parasite by releasing oocysts into the environment via feces, infecting subsequent hosts when they ingest oocysts or infected tissue. Recent findings indicate that *T. gondii* infection in bighorn sheep can result in abortion and neonate loss. Work in other wildlife shows that T. gondii seropositivity is higher in urbanized areas and in older individuals because these factors are associated with a higher risk of exposure. We plan to evaluate the relationships among *T. gondii* antibody status, age, distance to urbanization, and bighorn sheep subspecies using data and blood samples collected from 179 adult and yearling bighorn sheep ewes from 8 populations in Idaho: 4 Rocky Mountain (*Ovis canadensis canadensis*) and 4 California (Ovis canadensis californiana). Antibodies to *T. gondii* were assayed by Indirect Fluorescent Antibody test. We detected exposure to T. gondii in a total of 18 bighorn sheep in 2 populations: the North Hells Canyon Rocky Mountain bighorn sheep population along the Snake River in northern Idaho and the Jacks Creek California bighorn sheep population in the Owyhee Canyonlands in southwestern Idaho. Within the North Hells Canyon herd, 12 of 12 ewes captured at a site near a town were seropositive whereas only 2 of 10 captured 40 miles up the Snake River were seropositive. Next steps include expanding our sample size to more deeply investigate spatial and temporal patterns of *T. gondii* exposure in wild sheep.

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KEYWORDS: California bighorn (*Ovis canadensis californiana*), ewe, Hells Canyon, Idaho, Indirect Fluorescent Antibody test, antibodies, Owyhee Canyonlands, parasite, Rocky Mountain bighorn (*Ovis canadensis canadensis*), *Toxoplasma gondii*.

Toxoplasma gondii and *Chlamydia abortus* Serosurveillance of Rocky Mountain Bighorn Sheep in Wyoming, USA

JESSICA JENNINGS-GAINES, *Wyoming Game and Fish Department, Laramie, WY, 82070, USA; jessica.jennings@wyo.gov*
BRIANNA BLUNK, *University of Pennsylvania School of Veterinary Medicine, Philadelphia, PA, 19104, USA*
KARA ROBBINS, *Wyoming Game and Fish Department, Laramie, WY, 82070, USA*
HUNTER SWILLING, *Department of Veterinary Sciences, University of Wyoming, Laramie, WY, 82070, USA*
KENNEDY HENINGER, *Department of Veterinary Sciences, University of Wyoming, Laramie, WY, 82070, USA*
ELIZABETH CASE, *Department of Veterinary Sciences, University of Wyoming, Laramie, WY, 82070, USA*
SAMANTHA ALLEN, *Wyoming Game and Fish Department, Laramie, WY, 82070, USA*

ABSTRACT: Poor lamb recruitment in Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) populations has been documented in many herds throughout parts of the western US and Canada. While respiratory pathogens definitely contribute to poor lamb recruitment, other infectious pathogens could also be playing a role. *Chlamydia abortus* and *Toxoplasma gondii* are infectious agents of domestic sheep and cattle that are known to cause abortion and stillbirth in small ruminants. While surveillance has been minimal in wildlife populations, the surveillance that has occurred did detect exposure to these pathogens in free-ranging bighorn sheep herds in the west, with *T. gondii* implicated as a causative factor in abortions and stillbirths in some free-ranging herds. Our objectives in this study were to determine seroprevalence of *C. abortus* and *T. gondii* in free-ranging bighorn sheep herds across Wyoming, USA. Serum was collected during annual bighorn sheep captures and stored at -20°C. Serum analysis was completed utilizing commercially available enzyme linked immunosorbent assays (ELISA). Antibodies to C. abortus were detected in 3 herds (Absaroka: 26.9%: 95% CI 11.9%–41.0%; Jackson: 33.3%: 95% CI: 8.4%–61.6%; Whiskey Mountain: 39.1%: 95% CI: 13.3%–61.5%), and antibodies to *T. gondii* were detected in 2 herds (Douglas Creek: 76.0%: 95% CI: 24.7%–90.6%; Ferris-Seminoe: 14.3%: 95% CI: 1.5%–42.8%). Our results suggest that these free-ranging populations were exposed to these pathogens, but it is difficult to elucidate how and when the pathogens were introduced. Continued efforts to monitor these populations, paired with submissions of any neonatal mortalities, might extend our knowledge on the significance of these pathogens, and provide some further insight into lamb recruitment.

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KEYWORDS: abortion, *Chlamydia abortus*, enzyme linked immunosorbent assays (ELISA), recruitment, Rocky Mountain bighorn sheep *(Ovis canadensis canadensis),* serosurveillance, *Toxoplasma gondii,* Wyoming.

Age Dynamics and Chronic Carriage of *Mycoplasma ovipneu*moniae Infection in Adult Domestic Sheep

KLARA J. MCKAY, *Washington State University, Pullman, WA, 99164, USA; klara.mckay@wsu.edu*
DENISE KONETCHY, *University of Idaho, Moscow, ID, 83843, USA*
LAUREN CHRISTENSEN, *University of Idaho, Moscow, ID, 83843, USA*
E. FRANCES CASSIRER, *Idaho Department of Fish and Game, Lewiston, ID, 83501, USA*
KATHRYN P. HUYVAERT, *Washington State University, Pullman, WA, 99164, USA*

ABSTRACT: Bighorn sheep (*Ovis canadensis*) populations have declined across their range due in part to pneumonia caused by *Mycoplasma ovipneumoniae*. Spillover of *M. ovipneumoniae* from domestic to wild sheep can initiate epizootics of respiratory disease. Some survivors become chronic carriers of *M. ovipneumoniae* leading to a cycle of new lamb infection and poor recruitment. Work on age dynamics in bighorn sheep shows that the youngest and oldest animals are most susceptible to infection. However, the relationships between age and chronic carriage of *M. ovipneumoniae* have not been well-explored. We seek to address this knowledge gap in domestic sheep: to what extent are age and chronic carriage related? We hypothesize a negative relationship between age and chronic carriage if carriers are more susceptible to other diseases and concomitant shorter lifespan. Alternatively, the age-carriage relationship may be positive because older animals are more likely to eventually become infected and become a chronic carrier. A third hypothesis is a non-linear relationship combining the first 2: sheep of intermediate ages are most likely to be chronic carriers. This is an ongoing study involving serial collection and testing of nasal swabs from 40 Suffolk adult domestic ewes (ages 2–11 years). Infection status is determined using real-time Polymerase Chain Reaction (PCR) and chronic carriers are classified as those with consecutive positive tests. We also consider reproductive status and travel history as factors that may contribute to infection status and chronic carriage. Understanding the dynamics of chronic carriage in domestic sheep is important for identifying individuals at higher risk of inducing spillover to bighorn sheep or in managing infection within domestic herds by removing key chronic carriers.

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KEYWORDS: bighorn sheep *(Ovis canadensis)*, chronic carrier, domestic sheep, *Mycoplasma ovipneumoniae*, pneumonia, Polymerase Chain Reaction (PCR), reproductive status, respiratory disease.

Population Dynamics of Mountain Goats in Southwestern British Columbia, Canada

CLIFFORD NIETVELT, *Ministry of Forests, Office of the Chief Forester, BC, V8W 9M1, CA; cliff.nietvelt@gov.bc.ca*
STEVE ROCHETTA, *Ministry of Water, Land, and Resource Stewardship, BC, V8M 9L6, CA; steve.rochetta@gov.bc.ca*
DARRYL REYNOLDS, *Ministry of Water, Land, and Resource Stewardship, BC, V8M 9L6, CA; darryl.reynolds@gov.bc.ca*
JOHN KELLY, *Ministry of Water, Land, and Resource Stewardship, BC, V8M 9L6, CA; john.kelly@gov.bc.ca*

ABSTRACT: With over half of the world's population of mountain goats (*Oreamnos americanus*) occurring in British Columbia, the province has a global responsibility for the conservation of this species. Mountain goats in coastal ecosystems are particularly vulnerable during the winter months, when deep snow restricts their movements and distribution, and large old forests provide crucial snow interception cover and forage. During the summer of 2015, rare catastrophic and intense wildfires occurred in the southwestern British Columbia, a coastal ecosystem, covering approximately 19,000 ha in total area. As a result of these wildfires, several legally protected mountain goat winter ranges were burned to varying degrees. Preliminary analysis indicated that ≥75% of the forest area burned 75% less likely to be occupied and contained ≥80% fewer individuals, and it directly relates to the removal of forest cover. These fires may have caused a substantial shift in the goat population, whereby goats from adjacent winter ranges may have migrated to the Meager Complex. Summer inventories of Mount Meager indicated a 138% increase in the mountain goat population in 2009 and 2016. In 2018 and 2019 we radio collared 31 mountain goats in the Mount Meager Complex. We found mortality rates for goats of both sexes extremely high. Cumulative female and male survivorship were poor, and we estimated the population to be declining at approximately 17% per year (as estimated from survivorship and recruitment data), and approximately 10% based on the inventory data. We estimated that 40% of these mortalities were a result of avalanches. Mortality rates were initially high and have since stabilized in the Meager Complex with good kid recruitment. However, mountain goat populations in an adjacent burned area have experienced declines during the same period with low kid recruitment in surveys from 2016 to 2021. Consequences of climate change on coastal mountain goat populations will be discussed.

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KEYWORDS: British Columbia, climate change, kid, mortality rate, Mount Meager Complex, mountain goats *(Oreamnos americanus)*, recruitment, survival, wildfire, winter.

Shifts in Birth Dates and Lambing Period in Dall’s Sheep: Interannual Variation or Response to Climate Change?

SONNY PARKER, *Kluane National Park and Reserve, Parks Canada, Haines Junction, YT, Y0B 1L0, CA; sony.parker@pc.gc.ca*
CARMEN WONG, *Kluane National Park and Reserve, Parks Canada, Whitehorse, YT, Y1A 3E6, CA*
JONATHAN CROMWELL, *Kluane National Park and Reserve, Parks Canada, Haines Junction, YT, Y0B 1L0, CA*

ABSTRACT: Concern about low annual lamb recruitment since 2019 at Thechàl Dhâl’ (Sheep Mountain) in Kluane National Park and Reserve in southwest Yukon, Canada, caused us to examine the temporal dynamics of lambing since the early 1970s. Survival of Dall’s sheep (*Ovis dalli*) lambs depends on ewes giving birth when environmental conditions are optimal for spring plant emergence, ease of movement, and thermoregulation. Research suggests ewes may have some control over timing of parturition in response to weather conditions leading up to lambing but less is known on the potential long- term shifts in Dall’s sheep reproductive phenology because of climate change. In spring 2023 we surveyed lambing events systematically at Thechàl Dhâl’. We compared birth dates and lambing period duration with historic estimates from 1971 and 1972 using binomial generalized linear models. We found the peak birth date was earlier by 4–5 days and the window of bulk lambing was narrower in 2023. This was indicated by significantly different regression slopes and narrower interquartile ranges (5.6 days versus 7.7 and 9.9) for 2023 data versus that in 1971 and 1972. It is not clear whether the differences we saw in 2023 truly reflect an earlier shift in reproductive phenology due to climate change or natural interannual variation. We consider our results preliminary and plan to continue more lamb surveys at Thechàl Dhâl’. If lambing is indeed occurring earlier and over shorter periods due to phenological shifts, lambs could be more vulnerable to variable spring conditions or predation.

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KEYWORDS: Canada, climate change, Dall’s sheep (*Ovis dalli*), Kluane National Park and Reserve, lambing, parturition, phenological shifts, Thechàl Dhâl’ (Sheep Mountain), Yukon.

The Role of Hunter Education, Experience, and Regulation on Mountain Goat Harvest Patterns in Alaska: Implications for Conservation and Hunter Ethics

TIMOTHY J. SPIVEY, *Alaska Dept. of Fish and Game, Anchorage, AK, 99518, USA; timothy.spivey@alaska.gov*
JEFF JEMISON[1], *Alaska Dept. of Fish and Game, Juneau, AK, 99801, USA*
KEVIN S. WHITE, *University of Alaska Southeast, Juneau, AK, 99801, USA*

ABSTRACT: Mountain goats (*Oreamnos americanus*) have relatively low survival and reproductive rates relative to other northern ungulates requiring careful management to avoid overharvest and population declines. While wildlife managers discourage female harvest, it remains legal in most jurisdictions and incorrect identification in the field often results in unintentional female (nannie) harvest. Reducing female harvest is desirable to increase population resilience and optimize hunting opportunity but knowledge is lacking on how to mitigate female harvest. We analyzed harvest (1998–2019) and follow-up hunter interview data (2008–2011) collected throughout Alaska to understand harvest patterns and inform strategies for reducing female harvest. Overall, female harvest was spatially and temporally variable with area- and year-specific proportions of female harvest ranging between 4–61%. Follow-up hunter interviews revealed that hunters who unintentionally harvested females were less experienced but did not necessarily spend less time observing animals in the field, use lower quality optics, or take longer shots. Surprisingly, of the hunters interviewed, 23% (n = 41/181) took shots longer than 300 meters with a maximum shot distance exceeding 600 meters; an observation that may have important hunter ethics and management implications. We also determined that 42% of females were harvested intentionally; a finding that suggests stricter harvest regulations are needed to meaningfully reduce female harvest, where appropriate. Hunter interview data collected during the initial 4 years (2008–2011) did not reveal an effect of educational materials, however hunter harvest data analyzed over a 12-year period (2008–2019) indicated a 7% decline in female harvest, as compared to the preceding 10-year period (1998–2007). Lastly, we examined 3 different management case studies utilizing various regulatory penalties for female harvest, each resulting in reduced female harvest. This suggests that the combination of education and regulatory incentives can promote sustainable harvest, further ensuring population viability and resilience.

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KEYWORDS: Alaska, hunter education, hunter harvest, female harvest, mountain goat (*Oreamnos americanus*), sustainable harvest, wildlife conservation.

[1] Deceased.

Space Use, Movement, and Survival of Translocated Desert Bighorn Sheep in Sonora, Mexico

DYLAN G. STEWART, *Department of Rangeland, Wildlife and Fisheries Management, Texas A&M University, College Station, TX, 77843, USA; dylan.stewart@tamu.edu*

E. ALEJANDRO LOZANO-CAVAZOS, *Departamento de Recursos Naturales Renovables, Universidad Autónoma Agraria Antonio Narro, Saltillo, CH, 25315, MX*

STEPHEN WEBB, *Texas A&M Natural Resources Institute, and Department of Rangeland, Wildlife and Fisheries Management, Texas A&M University, College Station, TX, 77843, USA*

ABSTRACT: Mountain sheep abundance across North America has declined >60% from historic times. In response, state and federal agencies have conducted >1,000 reintroduction projects, translocating >21,000 bighorn sheep. Despite these efforts, ~50% of reintroductions are considered unsuccessful, leading researchers to stress the importance of post-release monitoring on the overall success of future reintroductions. Our objectives were to quantify space use, movement, and survival of translocated Desert bighorn sheep (*Ovis canadensis mexicana*). We conducted our research in the Sierra El Alamo Mountains, ~45 km W of Caborca, in northwestern Sonora, Mexico. We captured and fitted 16 bighorn sheep (9 females, 7 male) with GPS collars, which collected 1 GPS fix every 3 hours starting in November 2023. We created monthly 95% Brownian bridge movement models (BBMM), calculated monthly distance travelled, and used the Kaplan-Meier methods to estimate survival. Monthly home range size for females was greatest in April (1,319 ha) and least in September (291 ha). Similarly, for males, home range size was greatest in February (1,533 ha) and least in October (513 ha). Cumulatively, movement was greatest from April through June (~49 km) for females and from February through April (~52 km) for males; movement was least in October and December for both sexes. Annual survival (November 2023 to November 2024) was 81% (13/16) for both sexes. Early post-monitoring data suggest the reintroduction effort was successful because annual survival was high, and reintroduced sheep joined herds with native sheep and settled into the study area quickly.

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KEYWORDS: Brownian bridge, Desert bighorn sheep (*Ovis canadensis mexicana*), GPS collar, home range, Kaplan-Meier, Mexico, Sierra El Alamo Mountains, Sonora, survival, reintroduction.

Low Lamb Recruitment and Declines in Adult Dall's Sheep: Cold Temperatures and Influence of the Snowshoe Hare Cycle

CARMEN M. WONG, *Kluane National Park and Reserve, Parks Canada, Whitehorse, YT, Y1A 3E6, CA; carmen.wong@pc.gc.ca*
ELLEN WHITMAN, *Canadian Forest Service, Edmonton, AB, T6H 3S5, CA*
SHAWN TAYLOR, *Yukon Environment, Haines Junction, YT, Y0B 1L0, CA*

ABSTRACT: Widespread extremely low lamb recruitment in Dall's sheep (*Ovis dalli*) occurred 2020 to 2022 in southwest Yukon and parts of Alaska. Declines in adults were also observed in some populations, particularly evident in 2023. Here we present these concerns and possible causes using data from aerial surveys dating back to 1977 on 4 populations of Dall's sheep. This dataset is unique not only because it is one of the longest datasets within the range of Dall's sheep but also from populations which experience little to no harvest in Kluane National Park and Reserve, southwest Yukon. Using generalized models, we found different drivers of year-to-year variation in lamb recruitment among the 4 populations. Colder falls, winters or springs and later springs were poor for lamb recruitment depending on location. The impact was amplified from apparent competition when snowshoe hare density was high, and coyote activity was also high 2 years prior. We discuss the implications of these results for Dall's sheep under future climate change in southwest Yukon.

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KEYWORDS: Alaska, climate change, Dall's sheep (*Ovis dalli*), generalized models, harvest refugia, Kluane National Park and Reserve, recruitment, snowshoe hare, weather, Yukon.

Unraveling The Complex Biogeographic and Anthropogenic History of Alaska's Mountain Goats

KIANA B. YOUNG, *Department of Environmental and Life Sciences, Trent University, Peterborough, ON, K9L 0G2, CA;* kiana.young@alaska.gov

KEVIN S. WHITE, *Program on the Environment, Department of Natural Sciences, University of Alaska Southeast, Juneau, AK, 99801, USA*

AARON B.A. SHAFER, *Department of Environmental and Life Sciences, Trent University, Peterborough, ON, K9L 0G2, CA*

ABSTRACT: Both natural and anthropogenic forces can play a substantial role in the demographic history and current structure of a wildlife population. Species with strict habitat requirements are especially susceptible to these impacts. Mountain goats (*Oreamnos americanus*) in Alaska are of particular interest in this regard due to their influence on alpine ecosystems, importance to human cultures, and their enigmatic history in some areas. Here, we used genetic tools to examine the population structure and demographic history of mountain goats in Alaska. We genotyped 816 mountain goats at 18 microsatellites, identified the number of genetically distinct subpopulations, and assessed their genetic diversity. We used Bayesian methods to investigate the demographic history relative to the known geologic and human history of Alaska, and we simulated human-mediated translocation events onto islands to address the hypothesis that Baranof Island harbored an extant population prior to an early-20th century introduction. We showed that Alaska has 4 genetically distinct subpopulations of mountain goats. The main demographic split between Southcentral and Southeast Alaska occurred following the retreat of ice after the Last Glacial Maximum. Simulations of translocation events largely aligned with the expected genetic diversity patterns of current subpopulations except for Baranof Island which showed greater diversity than the simulation, consistent with the hypothesis of an endemic population prior to the translocation. This study highlights the value of considering both natural and anthropogenic forces when assessing the biogeographic history of a species and provides new insights about the complex demographic history and biogeography of mountain goats in Alaska.

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KEYWORDS: Alaska, Baranof Island Mountain goats (*Oreamnos americanus*), Bayesian, genotyping, microsatellite, population structure, subpopulation, translocation.