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Northern Wild Sheep and Goat Council





Northern Wild Sheep and Goat Council

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Northern Wild Sheep and Goat Council Symposia

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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/M. 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
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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
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May 21-24, 2018	NWSGC 21	Whitefish, MT	Brent Lonner/Bruce Sterling/Caryn Dearing	Justin Gude	Kevin Hurley

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.

FOREWORD

The papers or abstracts included in these proceedings were presented during the 21st Biennial Symposium of the Northern Wild Sheep and Goat Council, held May 21-24, 2018 in Whitefish, Montana, USA.

Heart-felt thanks are extended to the sponsors of, and all those participating in, this highly successful 21st biennial symposium. Special thanks to Brent Lonner and Bruce Sterling (Symposium Co-Chairs) for leading the dedicated Montana organizing committee, and delivering another in a long series of first-class symposia. Caryn Dearing deserves special recognition for handling logistics, registration, and symposium minutiae. Thanks to all of the session and poster presenters for assembling and sharing relevant new science on wild sheep and goat ecology and management.

These Proceedings were edited by Justin Gude and volunteer NWSGC members prior to publication. Peer-reviewers for full papers and expanded abstracts submitted for publication in these Proceedings included Nick DeCesare, Jesse DeVoe, Tabitha Graves, Brent Lonner, Hollie Miyasaki, Bruce Sterling, Kevin White, and Don Whittaker. Suggested editorial comments were provided to each senior author; senior authors had opportunities to accept or reject suggested edits and provided an explanation of how they considered each reviewer comment prior to submission of their final manuscripts. Formatted page proofs were forwarded to respective senior authors of full papers 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 Executive Director January 30, 2019



Northern Wild Sheep and Goat Council



Table of Contents

POSTERS

Next Generation Ruggedness Indices for Modeling Escape Terrain of Desert Bighorn Sheep at Lone
Mountain, Nevada
Marcus Blum, Thomas Dilts, and Kelley Stewart1
Investigating Disease Susceptibility in Desert Bighorn Sheep
Lizabeth Bowen, Kathleen Longshore, Peregrine Wolff, Shannon Waters, A. Keith Miles, Mike Cox, and Sarah Bullock2
Cherry - Mountain Goat Monitoring in Yoho, Kootenay, and Banff National Parks of Canada Seth G. Cherry, Shelagh Wrazej, and Laura Kroesen7
Wild Sheep Ram Hunting Permit Process for Western States and Provinces Mike Cox8
Determining Population Management Unit Boundaries for Mountain Goats in Skeena Region Krystal Kriss (Dixon)9
Challenges of Predation Monitoring and Management for Sierra Nevada Bighorn Sheep Daniel J. Gammons, Thomas R. Stephenson, David W. German, Lacey Greene, and Jeffrey L. Davis10

Strategies for Helicopter Skiing Operations in the Skeena Region Len Vanderstar and Steve Gordon
The Genetic Legacy of 50 Years of Desert Bighorn Sheep Translocations in Nevada Joshua P. Jahner, Marjorie D. Matocq, Michael Cox, Peregrine Wolff, Mitchell Gritts, and Thomas L. Parchman
Observations and Recommendations During Capture of Bighorn Sheep Thomas R. Stephenson, David W. German, and Lacey Greene
When, Where, and Why Do Contacts Occur? Investigating Interactions Between Bighorn Sheep in and Around Glacier National Park
Marie I. Tosa, Tabitha A. Graves, Mark J. Biel, Daniel W. Carney, and Barb Johnston15
HARVEST & MANAGEMENT STRATEGIES Moderator - Sonja Andersen, Montana Fish, Wildlife and Parks
Selective Removal May Lead to Recovery of Ailing Bighorn Sheep Herds Tyler J. Garwood, Chadwick P. Lehman, E. Frances Cassirer, Daniel P. Walsh, Thomas E. Besser, and Jonathan A. Jenks
Age Structure of Harvested Mountain Goats as a Tool for Assessing Sustainable Harvest Karen M. Loveless, Kelly M. Proffitt, and Nicholas J. DeCesare
Monitoring of Hunted Mountain Goat Populations in West-Central Alberta: Insights Gained Over More Than Four Decades Kirby Smith, Mike Russell, Sandra Hamel, Steeve D. Côtê, Marco Festa-Bianchet, and Frédéric Dulude-de Broin
HABITAT USE, MANIPULATIONS, AND CHANGES Moderator - Pete Muennich, The Rocky Mountain Goat Alliance
The Impacts of Wildfire on Mountain Goats and Their Winter Range Habitats in a Coastal Ecosystem Clifford G. Nietvelt, Steve Rochetta, and Steve Gordon
Forage Response to Prescribed Fire in the Northern Rockies: Implications for Stone's Sheep and Elk Krista L. Sittler, Katherine L. Parker, and Michael P. Gillingham
Seasonal and Sex-Specific Variation in Space Use and Site Fidelity of Mountain Goats in Coastal Alaska Vasaman N. Shakeri and Kevin S. White

Human Visitation Limits the Utility of Protected Areas as Ecological Baselines
Mark J. Biel, Wesley Sarmento, and Joel Berger34
Characterizing the Seasonal Movements of Native and Restored Bighorn Sheep: A Case for Conserving Migratory Portfolios
Blake Lowrey, Robert A. Garrott, P. J. White, Kelly M. Proffitt, Douglas E. Mcwhirter, Kevin. L. Monteith,
Hollie Miyasaki, Ethan S. Lula, Jamin Grigg, Alyson B. Courtemanch, and Carson J. Butler35
NUTRITION & HORN SIZE Moderator - Tabitha Graves, United States Geological Survey
Northern Rocky Mountain Science Center
An Exploration of Metabolomics to Assess Physiological States in Bighorn Sheep
Robert A. Garrott, Rashelle Lambert, James Berardinelli, Jennifer Weeding, and Kelly M. Proffitt37
Assessing Dall's Sheep Horn Morphometrics as a Management Tool
Brad Wendling, Joe Want, and Chris Brockman38
Role of Harvest and Environmental Factors on Horn Size of Mountain Sheep
Tayler N. Lasharr, Ryan A. Long, James R. Heffelfinger, Vernon C. Bleich, Paul R. Krausman, R. Terry Bowyer, Justin M. Shannon, and Kevin L. Monteith39
Horn Size and Nutrition in Mountain Sheep: Can Ewe Handle the Truth?
Kevin L. Monteith, Ryan A. Long, Thomas R. Stephenson, Vernon C. Bleich, R. Terry Bowyer, and Tayler N. Lasharr41
GENETICS/GENOMICS Moderator - Mike Cox, Nevada Department of Wildlife
An Overview of Past and Present Genetic Studies of Bighorn Sheep: Reconciling Methods and
Considering Applications for Management
Clinton W. Epps and Michael Buchalski43
Genetic Evidence of Local Adaptation in Desert Bighorn Sheep Native to The Great Basin
Michael Buchalski, Clinton Epps, Walter Boyce, Marjorie Matocq, Rachel Crowhurst, Brandon Holton, Laura Thompson, Esther Rubin, and James Cain44
Does Population of Origin Affect Translocation Success in Bighorn Sheep
Frances Cassirer, Kimberly Andrews, Erin Landguth, Hollie Miyasaki, and Lisette Waits45
Evaluating Sample Size to Estimate Genomic Relatedness in Bighorn Sheep Populations
Elizabeth P. Flesch, Jay J. Rotella, Jennifer M. Thomson, Tabitha A. Graves, and Robert A. Garrott46

Using Historic Specimens to Provide Insight Into Native Bighorn Sheep Genetic Diversity and Connectivity In Idaho
Hollie Miyasaki, Kimberly Andrews, Jennifer Adams, Digpal Gour, Lisette Waits, Frances Cassirer, and Nathan Borg47
Frequently-Asked Questions About Wild Sheep Genetics and Genomics Clinton W. Epps, Lizabeth Bowen, Michael R. Buchalski, Francis Cassirer, David Coltman, Warren C. Conway, Mike Cox, Rich Harris, Joshua P. Jahner, Marjorie Matocq, Thomas L. Parchman, Caleb D. Phillips, Helen Schwantje, Zijian Sim, Lisette Waits, John D. Wehausen, and the Wild Sheep Genomics Working Group
POPULATION DYNAMICS Moderator - Justin Gude, Montana Fish, Wildlife and Parks
Dall's Sheep Population Declines in Alaska's Chugach Range May Be Related to Climate and Weather Patterns
Tom Lohuis, Kyle Smith, Luke Metherell, and Roman Dial76
Projecting the Effects of Climate Change on Mountain Goat Population Dynamics in Alaska Kevin S. White, David P. Gregovich, and Taal Levi
The Influence of Early Reproductive Success on Longevity and Late Reproductive Success in an Alpine Ungulate
Andrea Panagakis, Sandra Hamel, and Steeve D. Côté78
Ecotypic Variation in Population Dynamics of Reintroduced Bighorn Sheep Brett P. Wiedmann, Vernon C. Bleich, and Glen A. Sargeant79
Contrasting Native and Introduced Mountain Goat Populations in Montana Nicholas J. DeCesare and Bruce L. Smith80
HABITAT USE & RELATIONSHIPS Moderator - Robert Garrott, Montana State University
Habitat Selection, Movement, Disease, and Population Structure of a Re-Introduced Bighorn Sheep Population in a Canyon Environment
Tabitha A. Graves, Nate Mikle, and Emily Spencer105
Is Habitat Constraining Bighorn Sheep (<i>Ovis canadensis</i>) Distribution and Restoration? A Case Study in the Greater Yellowstone Ecosystem
Ethan S. Lula, Julie A. Cunningham, Kelly M. Proffitt, Andrea R. Litt, and Robert A. Garrott

Evaluating Success for an Intra-Mountain Range Transplant of Bighorn Sheep in Southwestern Montana Julie Cunningham, Howard Burt, Robert Garrott, Kelly Proffitt, Carson Butler, Ethan Lula, Jennifer
Ramsey, and Keri Carson107
Seasonal Use Patterns and Movements of Mountain Goats in The Mount Evans Wilderness, Colorado Lance Carpenter and Kevin Aagaard
Niche Similarities Among Introduced and Native Mountain Ungulates Blake Lowrey, Robert A. Garrott, Douglas E. Mcwhirter, P. J. White, Nicholas J. DeCesare, and Shawn T. Stewart
DISEASE SESSION 1 Moderator - Julie Cunningham, Montana Fish, Wildlife and Parks
Pneumonia in Bighorn Sheep: A Recent Review Frances Cassirer, Kezia R. Manlove, Emily S. Almberg, Pauline Kamath, Mike Cox, Peregrine Wolff, Annette Roug, Justin Shannon, Rusty Robinson, Richard B. Harris, Ben J. Gonzales, Raina K. Plowright, Peter. J. Hudson, Paul C. Cross, Andrew Dobson, and Thomas E. Besser
Fatal Pneumonia in Bighorn Sheep Lambs: The Critical Role of <i>Mycoplasma ovipneumoniae</i> Carrier Ewes Logan K. Weyand, E. Frances Cassirer, and Thomas E. Besser113
The Implications of Imperfect Detection for Establishing the Presence/Absence of Pathogens: A Web-Based Resource for Managers J. Terrill Paterson, Carson J. Butler, Jay J. Rotella, and Robert A. Garrott
Detection Error and Demographic Variability Amid Pervasive Pneumonia Pathogens in Bighorn Sheep Carson J. Butler, William H. Edwards, J. Terrill Paterson, Kelly M. Proffitt, Jessica Jennings-Gaines, Halcyon J. Killion, Mary E. Wood, Jennifer M. Ramsey, Emily S. Almberg, Sarah R. Dewey, Douglas E. Mcwhirter, Alyson B. Courtemanch, P.J. White, Jay J. Rotella, and Robert A. Garrott
DISEASE SESSION 2 Moderator - Clay Brewer, Wild Sheep Foundation
Use of Rapid Field-Based PCR Testing to Detect <i>Mycoplasma ovipneumoniae</i> Infection in Bighorn Sheep Smriti Shringi and Thomas E. Besser
Use of Intra-nasal Antibiotics as an Aid to Clearing <i>Mycoplasma ovipneumoniae</i> Carriage by Domestic Sheep Thomas E. Besser, David Casebolt, and Nicholas Hill
,

A Pilot Program to Create A Source of Domestic Sheep Free of <i>M. ovipneumoniae</i> For Cooperating	
Private Owners	
Richard B. Harris, Thomas Besser, Kelli Bush, Geraldine Glenn, Jerry Kjack, Jared Oyster, and Carla	
Schettler	119
Variation in the Annual Cost of Living of an Endangered Population of Bighorn Sheep	
Kristin A. Denryter, David German, Thomas R. Stephenson, and Kevin L. Monteith	121



Next Generation Ruggedness Indices for Modeling Escape Terrain of Desert Bighorn Sheep at Lone Mountain, Nevada

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ABSTRACT: Understanding habitat selection is critical to implementing management strategies that may benefit the population dynamics of mountain sheep. However, to ensure that resource selection functions are effective in identifying essential habitats to these mountain ungulates, the proper variables must be included in the modeling process. Delineating escape terrain has long been a primary focus of biologists trying to identify habitat that is used by females while they provision young. Several commonly used ruggedness metrics, such as vector ruggedness and arc-chord ratio, which attempt to quantify terrain ruggedness across the landscape, incorrectly identify features such as ridgetops and drainage bottoms as rugged. To alleviate these problems we have developed several new metrics. Two approaches, local vector ruggedness and standard deviation of curvature, only rely on a digital elevation model, whereas two other measures, proportion boulder/rock and the shadow index, used high-resolution aerial photography to develop a classification of these landscape features that indicate the presence of cliffs. We test the efficacy of each of these new methods at mapping rugged terrain against three commonly used ruggedness indices: vector ruggedness, arc-chord ratio, and planar to surface area ratio. Next, we compare both the old and new ruggedness indices, in combination with other variables, such as slope steepness, distance to ridgelines, and distance to drainages, to determine whether these new metrics more effectively delineate escape terrain for females with lambs. Our preliminary results suggest that these new ruggedness indices are effective at reducing confusion with ridgelines and drainages compared to the more traditional ruggedness indices, and may reduce the need for using additional variables, such as distance to ridgeline and distance to drainage bottoms to effectively delineate escape terrain. These ruggedness indices are widely applicable to any species that relies on escape terrain to avoid predators while provisioning young.

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KEYWORDS Desert bighorn sheep; *Ovis canadensis nelsoni*; habitat selection; terrain ruggedness; Nevada.





Development and Utility of a Gene Transcription Panel for Desert Bighorn Sheep (Ovis canadensis nelsoni)

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EXPANDED ABSTRACT Respiratory disease is a key factor impacting the success of the ongoing conservation and recovery of wild sheep populations (WAFWA 2017). Although the primary pathogens involved in the bighorn sheep pneumonia complex have been identified, the wide variability in herd response following infection is not well understood (Cassirer et al. 2018). The response of populations infected with *Mycoplasma ovipneumoniae* has been variable, from minimal to extensive herd mortality followed by years to decades of either poor lamb recruitment or little expression of disease and minimal impact on lamb survival (Coggins and Mathews 1992, Jorgenson et al. 1997, Cassirer et al. 2018). This variation is thought to be caused by differences in pathogen virulence, intrinsic or extrinsic factors that impact individual or herd immunity, including lungworm (*Protostrongylus* spp.) or mite (*Psoroptes ovis*) infections, malnutrition, inbreeding, harsh weather conditions, or stress associated with overcrowding (Risenhoover et al. 1988, Bailey 1990, Jones and Worley 1994, Monello et al. 2001). Although substantial management strategies have been implemented, they have been ineffective in halting the spread of the epizootic (Cassirer et al. 2018).

Traditional approaches to bighorn respiratory disease research have focused mainly on the role that pathogens play in the respiratory disease complex. The contribution of environmental variation to animal immunity and infections is largely unknown; current health evaluations and diagnostics for desert bighorn sheep provide limited information on the overall health of the animal and almost no information on the potential contributing risk-factors inherent in the habitat. This lack of diagnostic information makes it difficult to identify specific environmental conditions and stressors potentially linking variable herd responses to the spillover of such pathogens as *M. ovipneumoniae* in desert bighorn sheep (*Ovis canadensis nelsoni*) herds in Nevada.





Gene-based diagnostics such as gene transcription provide an innovative, minimally-invasive tool that improves our understanding of the health of desert bighorn sheep populations. The advantage of using gene transcript analysis in desert bighorn sheep diagnostics lies in the capacity to measure physiologic responses (acute or chronic) of an individual to environmental stressors. The earliest observable signs of health impairment are altered levels of gene transcripts, evident prior to clinical manifestation (McLoughlin et al. 2006). By concurrent evaluation of transcript levels for genes representative of multiple internal systems, it is possible to measure a physiological response of individuals as well as populations to environmental stressors like pathogens, nutritional deficiency, or contaminants. Consequently, application of quantitative gene transcript analysis technology will provide an invaluable addition to current approaches for monitoring indications of potential health impairment (McLoughlin et al. 2006). Stressor-specific analyses of gene transcription profiles can inform management actions that may mitigate stressor impacts and improve bighorn sheep recovery.

We developed real-time PCR assays for 14 genes of interest and two reference genes. These have been validated on desert bighorn sheep samples randomly selected from populations experiencing differing extrinsic and intrinsic pressures; these included the Muddy and River Mountains, Pintwater Range, and Bare Mountain populations (Figure 1). Genes of interest represent immunological and physiological systems critical to responses to stressors (inflammation, cell signaling, apoptosis, detoxification, antiviral, antibacterial, and general stress).

We analyzed gene transcription data using multivariate, nonparametric, multi-dimensional scaling analysis (NMDS) in conjunction with cluster analysis for statistical and graphical representation of individual bighorn sheep clustered by similarity in transcription and not by pre-defined groups. Statistical comparisons of individuals grouped by clusters were made using similarity profile permutation (SIMPROF) to test for significance among a priori, unstructured clusters of samples (R Development Core Team 2012). We then used principal components analysis (default stats package; R 2.8.1, R Development Core Team 2012) to determine primary genes driving cluster separation.

Individuals within a wildlife population comprise a range of physiological states. As such, clusters designated by NMDS analysis (Figure 2) included individuals across populations, indicating some similar physiologic responses. Cluster 3 comprised most sheep from the Muddy Mountains, the designated reference population (based on historic lack of M. ovipneumoniae). Thus, cluster 3 should represent animals whose physiologic responses are similar to those in the reference population; indeed, cluster 3 is comprised of sheep from all populations, a reflection of the natural occurrence of relatively "physiologically normal" individuals from the populations sampled. Cluster 1 is comprised of sheep from the River Mountains and Pintwater Range with transcript profiles representing increased (relative to other clusters) anti-viral and inflammatory responses and decreased anti-inflammatory responses. The latter has been linked with the ability of Mycobacterium to evade immune responses (Redford et al. 2011). Cluster 2 comprised sheep mostly from the Pintwater Range, with an additional two from the Muddy Mountains and one from the Bare Mountains. These sheep were characterized by high levels of heat shock protein 70 (HSP70), which has been implicated in exposure to a number of stressors (Iwama et al. 1999, Tsan and Gao 2004).





Cluster 4 comprised sheep mostly from the Pintwater Range. This cluster characterized the most divergent transcript profiles among the clusters, with multiple gene implications of physiological response to hydrocarbons or dioxin-like substances and virus.

The results of our study demonstrate that establishment of gene transcript profiles in peripheral blood samples has the potential to contribute towards an understanding of disease dynamics in desert bighorn sheep, and towards a management regime effective at mitigating the effects of *M. ovipneumoniae* by incorporating both immunological and ecological context.

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KEYWORDS *Mycoplasma ovipneumoniae*; desert bighorn sheep; *Ovis canadensis nelsoni*; gene transcription; immune function.

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Adaptive wild sheep disease management venture (DMV) strategy.

https://www.wafwa.org/committees___groups/wild_sheep_working_group/disease_m anagement_venture/

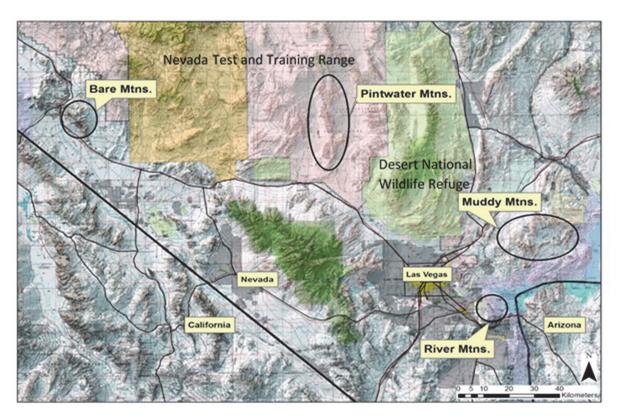


Figure 1. Map showing location of the mountain ranges, Pintwater Range, Muddy Mountains, River Mountains, and Bare Mountain Range, Nevada, where desert bighorn sheep were captured and blood samples were obtained for development of the RNA transcription panel.





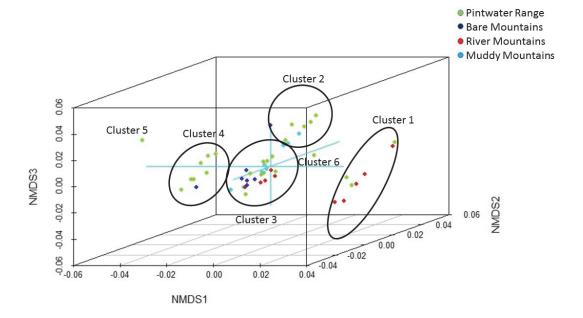


Figure 2. Multivariate, nonparametric, multi-dimensional scaling (NMDS) of gene transcription profiles of bighorn sheep sampled from four different populations (Muddy Mountains, River Mountains, Bare Mountains, Pintwater Range). Significant clusters are identified; SIMPROF, R 2.8.1, R Development Core Team 2012.

Mountain Goat Monitoring in Yoho, Kootenay, and Banff National Parks of Canada

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ABSTRACT: Protected areas, such as national parks, often contain large expanses of undisturbed wildlife habitat interspersed with human activities and infrastructure. Linear disturbances such as highways can fragment habitat while human land-use activities, recreation, and developments can displace wildlife from key resources. Determining the effects of anthropogenic influences on sensitive wildlife, such as mountain goats (*Oreamnos americanus*), is an important aspect of monitoring and managing protected landscapes for long-term sustainability. We outline key mountain goat monitoring tools used in Kootenay, Yoho, and Banff National Parks, which include remote wildlife cameras deployed at known mineral lick sites, aerial surveys, and the use of GPS tracking collars. Preliminary results are presented and discussed within the context of landscape planning and management.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:7; 2018

KEYWORDS Mountain goat; *Oreamnos americanus*; monitoring; Kootenay National Park; Yoho National Park; Banff National Park; Canada.



Wild Sheep Ram Hunting Permit Process for Western States and Provinces

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ABSTRACT: A questionnaire was completed in early 2018 by 18 of the 20 wild sheep program managers in the western U.S states and Canadian provinces on their ram hunting permit/tag process and season structure and limited hunt results. A similar review of west-wide ram harvest strategies was conducted 10 years ago. The goal of the questionnaire was to: review the demographic information collected and guidelines and criteria used in setting ram hunting permit/tag numbers; compare season structure and harvest metrics; and challenge jurisdictions to use the best available science and consider more ram hunting opportunities without sacrificing ram horn quality. Most agencies' primary objective of their aerial or ground surveys is animal composition to evaluate lamb ratios and ram age structure with 25% also wanting minimum count or detection of marked individuals for mark-resight estimate. Ten agencies classify rams based primarily on Geist's ram categories with Class IV rams as 8+ years of age, with others using a modified classification. Nine agencies use a model to estimate hunt unit population size, with 6 that correct for sightability bias on some herds, and only 1 that generates confidence intervals for their estimate. Alberta is exploring PopR Integrated modeling software. Most agencies use a guideline of the percent of the estimated population size, total rams, or mature rams to determine ram hunting permit numbers. One agency has no standard guideline. Agencies have a wide range of metrics and values for guiding ram permit numbers: 2.5 - 4% of total population - 3 (BC, CO. YK); 4.5% of all rams – 1 (CO); 7 – 10% of all rams – 6 (BC-bighorn, AZ, ND, NV, SD, NM); 10% of ¾ curl + rams – 2 (TX, MT); 15 – 25% of ¾ curl + rams - 7 (ND, CA, AB, MT, WA, AZ, NM); 20 - 30% of observed Class III & IV rams - 2 (ID, UT); 6 – 8 yr-old avg. age ram harvest previous year – WY; and 7% of previous year ram harvest 40"+ horn length – AK. The range of average ram harvest age by subspecies were: 7.8 – 9.3 for Dall/Stone; 6.5 - 7.0 for California; 6.4 - 10 for Rocky Mountain; and 6.4 - 9.0 for Deserts. Most jurisdictions have a similar hierarchical decision/approval process of: field/regional review of wild sheep data and information and suggest/submit recommendations; program lead and Bureau/Division heads provide oversight and support; wide array of stakeholder involvement; and final Board/Commission review and approval. Many agencies follow guidance provided by their wild sheep management plan. One state has a single committee that sets permit numbers with no public process. One jurisdiction is moving to a formal "Structured Decision Making" (SDM) process to better engage stakeholders, provide transparency, account for uncertainty and values/opinions, while incorporating science and following management objectives.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:8; 2018

KEYWORDS Bighorn sheep; *Ovis canadensis*; hunting; permit/tag allocation; monitoring; western North America.

Determining Population Management Unit Boundaries for Mountain Goats in Skeena Region

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ABSTRACT: Recent mountain goat (*Oreamnos americanus*) inventory work has occurred on three adjacent mountain complexes northeast of Smithers, British Columbia. This work has indicated three different population situations for each mountain: one with a potential decline, one with a potential increase, and one with relatively stable numbers. Determining if goats on these three mountain complexes are one, two or three population management units (PMU), will help ensure robust and biologically based management of mountain goats. Mountain goat PMU's have currently been derived for the Skeena region based on expert opinion along with using major watershed boundaries that may or may not serve as a barrier to animal movement throughout the majority of the Region. In Skeena south, PMU's have been left as LEH boundaries for the time being, until such time that better biological information exits. Having biologically meaningful PMU's will improve the management of goats, ensuring values such as conservation and appropriate harvest opportunities are evaluated and maintained at an appropriate scale. In this study we will use GPS collar locations and genetic data from both male and female mountain goats, on three adjacent mountain complexes, to define population structure and refine PMU's. The information will provide quality assurance that can be applied to future genetic work and further refine PMUs for the remainder of Skeena Region. The project will also assess habitat selection of collared goats and assess the currently designated ungulate winter ranges. It will also be the first collection of comprehensive baseline animal health for mountain goats in BC through live and mortality sampling.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:9; 2018

KEYWORDS Mountain goat; *Oreamnos americanus*; management units; British Columbia; GPS data; genetics; Canada.





Challenges of Predation Monitoring and Management for Sierra Nevada Bighorn Sheep

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ABSTRACT: Predation by mountain lions (*Puma concolor*) on federally endangered Sierra Nevada bighorn sheep (Ovis canadensis sierrae) has been considered an important management concern since their listing under the Endangered Species Act in 1999. However, quantifying the likelihood and impact of predation is challenging, despite predation being the leading known cause of mortality. We evaluated cause-specific survival rates from radiomarked animals but in some cases these estimates were hampered by small sample sizes, where the fate of a small number of animals can disproportionately influence calculations. An alternative is to incorporate all known deaths from predation, including uncollared animals (which comprised 13% of all known mortalities, 1999-2017), and calculate the proportion of the population killed. Unfortunately, this method is hampered by imprecise count data in some herd-years, despite many counts being near censuses. A further challenge involves monitoring lions themselves because (1) most appear not to prey on bighorn sheep (only 16 of 81 lions monitored during 1999-2017 were known to kill bighorn sheep) and (2) when predation does occur, it is episodic. Of the 4 herds that experienced the most predation in the last 19 years, "predation episodes" occurred in only 7 of 76 (9.2%) herd-years. While this lack of consistent predation may be partially attributable to predation management activities from 1999-2011, an absence of predation in herd-years from 2012-2016, when no predation management activities occurred but lions were documented to be present, indicates that this lion population has intrinsic annual variability in its impact on bighorn sheep. Thus, as predation monitoring and management is resumed, substantial effort may be expended monitoring lions that are unlikely to prey on bighorn sheep. However, inattention to predation could jeopardize achievement of recovery goals in a timely manner. For example, during the winter of 2016-17 we unexpectedly documented a significant predation episode in a herd where predation was previously thought to be unimportant. This recent episode highlighted that despite challenges and uncertainties, under certain conditions, predation of Sierra Nevada bighorn sheep by lions can clearly impede recovery efforts and continued monitoring and management is warranted.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:10-11; 2018

KEYWORDS Sierra Nevada bighorn sheep; *Ovis canadensis sierrae*; predation; mountain lions; *Puma concolor*; California.





Developing a Spatial Tool to Enable Monitoring of Aircraft Flights and Compliance with Avoidance Strategies for Helicopter Skiing Operations in the **Skeena Region**

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ABSTRACT: Guidelines to mitigate the potential disturbance and displacement effects of helicopter-skiing in areas occupied by mountain goats (Oreamnos americanus) through vertical and horizontal setback distances have been in place in British Columbia since the early 2000's. In the Skeena region, detailed mitigation strategies have been developed to ensure helicopter flight paths avoid areas occupied by mountain goats during the critical winter period. Without the ability to remotely track flight paths, assessing compliance with avoidance measures is logistically challenging in the remote mountainous terrain used by both mountain goats and the heli-skiing sector. A simple spatial tool has been created to provide immediate feedback to operators and enable performance review of individual heli-skiing operations and flight paths relative to mountain goat habitats. The tool is based on a combination of Google Earth, vertically extruded mountain goat winter range habitat polygons and Garmin Global Positioning System flight tracking. The tool enables a 3-D visual analysis of flight path performance relative to avoidance zones. An ArcGIS Visibility function also provides a more detailed assessment related to horizontal setbacks from key mountain goat winter range habitats. Continued "social licence" for the heli-skiing sector to operate on public lands and within First Nation territories hinges on maintaining public confidence that commercial back-country recreation activities do not jeopardize the sustainability of wildlife populations. This tool provides an opportunity to effectively monitor and assess operator performance and enhance public confidence that appropriate protection measures are in place and being adhered to. Formal monitoring of adherence to provincial guidelines and site-specific mitigation strategies has been enabled through application of this tool, and the results for the 2016/17 ski season for some of the six heli-skiing operations in the Skeena Region are presented.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:12; 2018

KEYWORDS Mountain goat; *Oreamnos americanus*; heli-skiing; vertical and horizontal setbacks; British Columbia; Canada.

The Genetic Legacy of 50 Years of Desert Bighorn Sheep Translocations in Nevada

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ABSTRACT: Desert bighorn sheep (*Ovis canadensis nelsoni*) are an iconic western North American species that have been heavily managed throughout their range. Once thought to be the most abundant large mammal in the state of Nevada, dramatic declines in the mid 1900's reduced population sizes and restricted the range of desert bighorn sheep primarily to southern Nevada, though a few remnant populations persisted in central Nevada. To restore central Nevadan populations, the Nevada Department of Wildlife conducted several translocations of individuals from multiple southern Nevada source populations, leading to the admixture of individuals with different genetic ancestry. Here, we used a genotyping-by-sequencing approach to generate genetic information at several thousand loci for hundreds of desert bighorn sheep individuals across the state of Nevada. We found evidence for strong population genetic structure between the source populations in southern Nevada, suggesting that substantial genetic variation still exists in the state. However, almost all central Nevadan populations have genetic signatures that strongly resemble those from their translocation source populations. Finally, one central Nevadan population was genetically distinct from all other populations and is likely the last bastion of central Nevadan genetic ancestry remaining in the state.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:13; 2018

KEYWORDS Desert bighorn sheep; *Ovis canadensis nelsoni*; genetics; translocations; Nevada.

Observations and Recommendations During Capture of Bighorn Sheep

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ABSTRACT: Bighorn sheep are captured routinely for monitoring and research, yet questions remain regarding numerous aspects of handling procedures and the effects of handling on individuals and populations. We evaluated a variety of factors that have the potential to affect the demography and behavior of bighorn following captures. We captured 653 Sierra Nevada bighorn sheep using helicopter net-gun during 2001 – 2017. Animals were restrained using hobbles and blindfolds. Captures occurred at elevations between 5,000 and 14,000 feet and most were ferried to a central location for handling. Handling times varied between 10 minutes and 2 hours. Body temperatures ranged from 99.0 to 107.70 F. Our rate of capture mortality was 2.7%. We examined the relationship among survival, vital rates (temperature, respiration and heart rate), and handling time. Movement rates and home range sizes of animals with previously deployed GPS collars were compared pre- and post-capture. We recommend continuing to hold animals with elevated temperatures to ensure adequate cooling rather than releasing hot animals. We also provide detailed recommendations for collar fitting.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:14; 2018

KEYWORDS Sierra Nevada bighorn sheep; *Ovis canadensis sierrae*; capture; net-gun; capture mortality; California.





When, Where, and Why Do Contacts Occur? Investigating Interactions Between Bighorn Sheep in and Around Glacier National Park

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ABSTRACT: Understanding mechanisms of social interactions can help address questions in evolutionary, behavioral, and infectious disease ecology. Trade-offs between costs and benefits of sociality can operate at multiple scales, and factors influencing sociality at one level are likely different from those at another level. We investigated contacts of 87 male and female bighorn sheep (Ovis canadensis) in and around Glacier National Park in Montana, USA from 2002-2011 using GPS locations. We examined relationships between contact locations, movement, and extrinsic variables (e.g., land cover, NDVI, distance to escape terrain) using a resource selection function. To assess types of contacts, we separated contacts by dyad type (male-male, femalefemale, and male-female) and examined the strengths of association for dyads with intrinsic variables (e.g., relatedness, space-use overlap, dyad type, and homophily) using a generalized linear mixed model. Finally, we identified subpopulations through contact networks using different distance criteria (25 - 100m). Most contacts occurred in March for same sex dyads and from November to January for male-female dyads. Although more contacts occurred in high quality habitat, contacts were more likely in lower quality habitat for same sex dyads. For malefemale dyads, however, contacts occurred more and were more likely in high quality habitat. Female-female dyads with high space-use overlap during the summer, moderate relatedness, and of the same age class had highest rates of association. Different contact criteria identified 3 to 4 subpopulations. Together, these results give us the power to predict where contacts are most likely to occur, which can inform disease management.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:15; 2018

KEYWORDS Bighorn sheep; *Ovis canadensis*; social interactions; contacts; Glacier National Park; Montana.





Selective Removal May Lead to Recovery of Ailing Bighorn Sheep Herds

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ABSTRACT: Bighorn sheep (Ovis canadensis), a culturally and economically valuable game species in the west, are suffering from a respiratory disease that has decimated infected populations. Biologists recently theorized that this disease is induced by the bacterium Mycoplasma ovipneumoniae (Mo) and have hypothesized that the propagation of Mo outbreaks stems from a small number of adult bighorns that chronically shed the pathogen. This induces periodic epizootics in the herd, resulting in adult mortalities, poor lamb survival, and ultimately population decline. We test this hypothesis by radio-marking and testing presence of Mo in two infected herds of bighorn sheep in the Black Hills, South Dakota, where disease histories had been developed for individual bighorns. In our experimental herd we radio-marked and tested all individuals in the population (n = 21 adults, n = 9 lambs) and removed chronic shedders based on disease histories; subsequent testing indicates Mo no longer persists in this herd. Our control herd (n = 46 adults, n = 19 lambs) still exhibits the presence of Mo and experienced 26% lamb mortality and 13% adult mortality due to pneumonia. The experimental population experienced no mortalities attributable to pneumonia. Adult survival for our control ($\hat{S} = 0.68$, SE = 0.01) did not significantly differ (Z = 1.13, P = 0.19) from our treatment ($\hat{S} = 0.83$, SE = 0.02) but may be biologically relevant. Lamb survival for our control ($\hat{S} = 0.16$, SE = 0.02) was significantly lower (Z = 4.73, P < 0.01) than our treatment ($\hat{S} = 0.87$, SE = 0.04), which suggests that the selective removal of Mo-shedding bighorns reduces pneumonia incidence and mortality in wild populations. This study has implications for wildlife managers across the west, as testing and removing chronic shedders may be more tenable than eradicating entire populations.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:16; 2018

KEYWORDS Bighorn sheep; *Ovis canadensis*; *Mycoplasma ovipneumoniae*; respiratory disease; selective removal; Black Hills; South Dakota.

Age Structure of Harvested Mountain Goats as a Metric for Assessing Sustainable Harvest

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ABSTRACT: Mountain goat (*Oreamnos americanus*) populations can be challenging to manage because of difficulties in effectively monitoring population trends and assessing demographic structure of populations. Population trends include irruptive dynamics in some introduced populations and declining trends in many native populations, resulting in wide variation in sustainable harvest rates among populations. Impacts of harvest can be difficult to detect in a timely manner, with potentially negative consequences for population management. We used a 28-year dataset of over 3,000 harvested goats to compare age at harvest from incisor cementum analysis and horn annuli across populations with varying harvest rates and population trends in southwest Montana. Horn morphology, sex ratio of harvested goats, and hunter success and effort were also compared. We found high error in horn annuli aging when compared with paired cementum aging results from the same animals, especially among young (<4 years) and older age goats (>7 years), with implications for estimation of trends in age structure. Horn length and cementum age were not correlated beyond 2 years of age; therefore, hunters were unable to select by age, and age structure of harvested goats likely reflected the population age structure. Average cementum age of harvested goats was higher among declining populations as compared to increasing populations (p<0.001) with increasing trends in age associated with declining abundance, likely due to lower recruitment in declining populations. Average ages were 4.6 for increasing populations and 6.3 for decreasing populations. Trends in the proportion of females in the harvest, hunter success and hunter effort were best explained by harvest rate, with increased harvest rate correlated with increased proportion of female harvest (p<0.001), increased hunter effort (p<0.001), and decreased hunter success (p<0.001). In the absence of increased harvest these trends may be indicators of declining goat abundance.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:17; 2018

KEYWORDS Mountain goat; *Oreamnos americanus*; harvest; age structure; demographics; population trends; Montana.



Monitoring of hunted mountain goat populations in west-central Alberta: insights gained over more than four decades.

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ABSTRACT: Mountain goat (*Oreamnos americanus*) populations were monitored in west-central Alberta from 1971 to 2017. During the initial period (1971 – 1988) most populations were subjected to an either sex harvest regime of 5% of minimum helicopter counts. Following a series of years of declining numbers, the hunting season was closed in 1988 and remained so until 2000. During this period a kid mortality study was conducted, a provincial management plan was prepared and some, but not all, herds recovered. A hunting season was re-instituted in 2000 under a more conservative harvest regime of 1-2% of observed animals with efforts to focus harvest on males only. Over the last 10 years, both hunted and unhunted herds have again declined even under a very conservative hunting season. Concurrently, poor recruitment and decreased survival of adults has resulted in a strong decline of the unhunted Caw Ridge population. These declines have coincided with harsh winters combined with higher densities of mountain goats and increasing densities of mountain lions (Puma concolor). The implication of high levels of fecal cortisol in nannies monitored at Caw Ridge (long-term study area) are also discussed.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:18; 2018

KEYWORDS Mountain goat; *Oreamnos americanus*; harvest; demographics; population trends; predation; Alberta.





The Impacts of Wildfire on Mountain Goats and Their Winter Range Habitats in a Coastal Ecosystem

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ABSTRACT: Over half of the world's population of mountain goats (*Oreamnos americanus*) occurs in British Columbia; BC has a global responsibility for the conservation of this species. Mountain goats are particularly vulnerable during the winter months, when deep snows restrict their movements and distribution, especially in wet coastal environments. During the summer of 2015, significant wildfires occurred in southwestern British Columbia covering approximately 15, 892 ha in total area. As a result of these wildfires, several legally protected mountain goat winter ranges were burned to varying degrees. There is concern that these wildfires will significantly impact the suitability of these winter ranges and negatively affect the survival of the mountain goat populations that depend on these habitats during the winter months. During February and March of 2016 and 2017, we conducted four replicate sets of helicopter surveys of 13 burned and 12 unburned winter ranges to evaluate the effects of wildfire on the local abundance of goats. Mountain goat winter ranges that were highly impacted by fire (≥75% of the forest area burned) were 75% less likely to be occupied and contained ≥80% fewer individuals. We found a positive and significant correlation between residual forest area and the number of mountain goats. This study revealed an important relationship between largescale habitat perturbations and mountain goat populations in a coastal ecosystem.

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KEY WORDS British Columbia; coastal ecosystems; habitat impacts; mountain goat; *Oreamnos americanus*; population; wildfire.

Mountain goats (*Oreamnos americanus*) are present in most of the high mountain ranges of British Columbia (Shackleton 1999). Over half of the world's population of mountain goats occur in British Columbia, and BC has a global responsibility for the conservation of this species (Côté and Festa-Bianchet 2003).

Mountain goats are a Blue listed species in British Columbia, meaning that these species have characteristics that make them particularly sensitive or vulnerable to human activities or natural events.

Mountain goats are highly sensitive to human disturbance (Festa-Bianchet and Côté 2008). Mountain goats may be



negatively affected by such disturbances such as helicopter over flights, industrial activity, and human recreation (Foster and Rahs 1983, Côté 1996, Wilson and Shackleton 2001, Hurley 2004). Mountain goats are particularly vulnerable during the winter months, when deep snows restrict their movements and distribution, especially in coastal environments (Hebert and Turnball 1977, Dailey and Hobbs 1989, Fox et al. 1989, Wilson 2005). Mountain goats in coastal ecosystems are often associated with steep slopes on southerly aspects, and often with stands of old, large coniferous trees that provide snow interception, especially after significant snow events (Hebert and Turnball 1977, Fox et al. 1989, Taylor et al. 2006, Taylor and Brunt 2007).

In British Columbia, ungulate winter ranges are recognized as important components in the survival and persistence of ungulates. The BC Forest and Range Practices Act (FRPA) provides a legal mechanism for protecting ungulate winter ranges from timber harvest and associated activities. Winter ranges are intended to provide sufficient habitat for over-winter survival of mountains goats and other ungulate species. During the summer of 2015, significant wildfires occurred in the Sea to Sky District in southwestern British Columbia covering an area of 15,892 ha. These wildfires also burned several mountain goat winter ranges.

While the effects of prescribed and wildfire are well documented with ungulate species such as white-tailed deer (*Odocoileus virginianus*) where fire can be positive (e.g., Wood 1988) and negative (e.g., Lashley et al. 2015), there little is known about the effects of wildfire on mountain goats. The British Columbia Provincial Mountain Goat Plan (Mountain

Goat Management Team 2010) has identified knowledge gaps in how mountain goats respond numerically or spatially to fire (prescribed fire or wildfire). This objective of this paper is to evaluate the impacts of wildfire on mountain goat populations in British Columbia.

STUDY AREA

Our sampling of the goat winter ranges occurred in southwestern British Columbia in two key studies areas: the Elaho River drainage (50° 08'N, 123° 31'W) and in the Upper Lillooet (50° 36'N, 123° 27'W) in the Sea to Sky Natural Resource District (Figure 1). Each area experienced significant burns due to wildfires during the summer of 2015. The Elaho burn was approximately 10,459 ha in size, while the Upper Lillooet burn was approximately 5,433 ha in extent.

The Sea to Sky Natural Resource District is approximately 1.1 million ha in size and its climatic influences are predominantly maritime, dominated by interior-cedar hemlock, coastal western hemlock, and mountain hemlock Biogeoclimatic Zones (https://www.for.gov.bc.ca/hre/becweb/).

METHODS

Data Collection

We conducted two helicopter reconnaissance flights per winter season over two years, one in February and one in March. Consistent with British Columbia's Resource Information Standards Committee (RISC) standards (RISC 2002), we conducted these flights during mid-day (1000 to 1500 hours) when goats and tracks are most readily observed. We conducted the survey approximately two days after a snowfall, allowing time for tracks to accumulate, thereby increasing the likelihood of





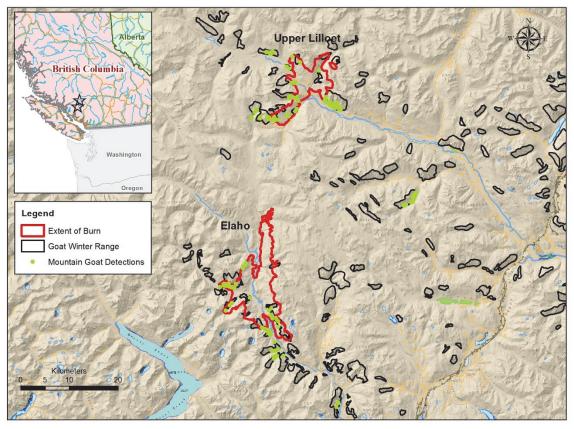


Figure 1. The two study areas, extent of the 2015 fires and mountain goat winter ranges. The green points indicate which winter ranges were sampled.

detection. An A-Star 350 helicopter was used to survey the affected goat winter ranges, with one observer in the front, and two in the rear of the helicopter. The pilot also served as a secondary observer. The observer in front served as the primary navigator, with one observer in the back as a secondary navigator using an iPad with preloaded with PDF maps and real-time GPS using Avenza Maps mobile app (http://www.avenza.com/pdf-maps).

Waypoints of mountain goats (animals or tracks) and flightpaths were recorded using a Garmin GPS 60CSx. When a set of tracks was sighted, we attempted to estimate the number of tracks observed. This was often difficult due to tree cover and / or snowmelt on warm aspects and if multiple

animals have used one location. We were confident that these tracks were from mountain goats, as these goat winter ranges did not overlap with winter ranges of black-tailed deer and moose (Alces alces), and bighorn sheep (Ovis canadensis) do not occur in this Region of British Columbia. In order not to double count the number of animals observed, tracks were only counted when goats were not directly observed in the close proximity or at all. We made efforts to locate animals, and when goats were encountered, the number of individuals were recorded and classified by age and sex (when possible), was tabulated. Mountain goats were classified as: billy (adult male), nanny (adult female), unknown adult and juvenile or kid (< 1 year



old; Festa-Bianchet and Côté 2008). For this analysis, we only examined the total number of goats. Animal welfare was paramount during surveys, and an immediate assessment of potential danger was undertaken; if an animal was determined to be in a precarious location, the helicopter moved away immediately to increase the distance from the mountain goat and reduce the potential for displacement or disturbance, which affected successful age/sex classification in some instances subsets of mountain goat winter ranges (goat winter ranges) were sampled in each of the two study areas. This subset included goat winter ranges that were burned and unburned. Unburned ranges were chosen based on their relative location to the burned areas (adjacent), and also comparable in size and characteristics to the burned ranges. In the Elaho study area, we surveyed 14 goat winter ranges, with eight goat winter ranges burned (partially or completely) and six unburned. In the Upper Lillooet study area, we surveyed 11 goat winter ranges, six burned (partially or completely) and five unburned (Figure 1). Occupancy of these winter ranges were confirmed during the establishment of these winter ranges from 1995 to 2002 (Rochetta 2002).

We calculated the forested area (ha) prior to the burn using satellite imagery in each winter range. We examined each winter range polygon visually to assess the extent of the forested area burned (in percent) and estimated the residual forested area (ha) post burn as we did not have satellite imagery to estimate the full extent of the burn.

Data Analysis

For each goat winter range in which mountain goats were observed, the total

number of animals, by age and sex (where available) was tabulated and for this analysis, all ages and sexes were pooled. Observations of mountain goat were not corrected for sightability as a correction factor has not been derived for winter surveys (Poole 2007, Rice et al. 2009). In all goat winter ranges, the numbers of tracks (fresh) were estimated, and this was especially important in goat winter ranges where few animals were sighted by many tracks were observed. In all goat winter ranges, linear density (LD) of mountain goats was calculated:

$$LD = \sum_{i} (G + T) / (\sum_{i} D$$

where G is the total number of goats sighted in winter range i, T is the number of goats estimated from tracks, and D is the distance (km) sampled in winter range i. We did not calculate goat densities because the sightability of goats in each winter range was highly variable, and the number of tracks acted as a surrogate for goat abundance (Collier et al. 2008). Mountain goat LD was calculated in each burn class category, percent of the forest cover burned: 0-25%, 25-50%, 50-75%, and 75-100%. To evaluate how LD differed between surveys in each year (e.g., February and March surveys) and between the two years, we used paired t-tests. We did this to determine of significant variability in goat abundance existed between surveys within a season (winter) and years.

We calculated the proportion of goat winter ranges occupied by goats in the winter ranges by burn class category: 0-25%, 25-50%, 50-75%, and 75-100% of the forest cover burned. For 100% occupancy, evidence of mountain goat presence (at



least one animal or one set of tracks) had to be present.

To determine the relationship between mountain goat abundance and residual (post-fire) forested area (ha), we regressed the number of goats (in winter ranges where sightability was good; however we did not corrected for sightability) in a winter range against the residual patch size of trees remaining. The residual forested area is the forest cover remaining after the fires. We did this to determine at what forest patch the numbers of goats drop off precipitously. We did not regress LD as it is a measure of relative and not true goat abundance. We also did not examine the relationship between mountain goat occupancy and residual forested area size, as this relationship is binary and does not indicate at which point mountain goat abundance begins to decline significantly.

RESULTS

We surveyed 25 individual goat winter ranges in a total of four flights in February and March 2016 and 2017 (Figure 1). Thirteen were sampled in the Elaho study area, and 11 were sampled in the Upper Lillooet study area (Figure 1). In the Elaho study area, 8 goat winter ranges were burned, and 6 were unburned. In the Upper Lillooet study area, 6 goat winter ranges were burned, and 5 goat winter ranges were unburned.

The proportion of goat winter ranges occupied by goats was substantially less in areas where ≥75% of the forested area had burned (Figure 3). Goat winter ranges in <75% of the forest covered burned were all occupied in all four surveys, whereas in goat winter ranges with ≥75% of

the forested area had burned, only 25% to 57% were occupied (Figure 3). The mean occupancy from the four surveys with \geq 75% of the forested area burned was 0.37 \pm 0.072, which is significantly less than winter ranges with <75% of the forested area burned (1.0 \pm 1.0 vs 0.37 \pm 0.072, p<0.01, t-test). However, in goat winter ranges where all of the forest cover was burned, none of these winter ranges were occupied in 2016 and in February 2017.

The LD of mountain goats was substantially less in areas where ≥75% of the forest canopy burned (Figures 2a and b). In 2016, goat winter ranges that were ≥75% burned had a LD >80% less than goat winter ranges that were <75% burned (4.8 ± $0.6 \text{ vs } 0.7 \pm 0.4 \text{ goats per km, t-tests,}$ p<0.001). Similarly, in 2017 goat winter ranges that were ≥75% burned had a LD >90% less than goat winter ranges that were <75% burned $(7.2 \pm 1.2 \text{ vs } 0.4 \pm 0.1, \text{ t-}$ tests, p<0.001). Paired t-tests indicated remarkable consistency between surveys within a season for 2016, where the LD did not differ, however in 2017, LD in the lowest percent burned class (0-25%) is significantly higher in 2017 (Figure 2b, P<0.05). The LD in burned classes from 25-100% did not differ statistically (P>0.05, t = 1.92) between surveys.

There is a significant correlation between the numbers of mountain goats (uncorrected abundance, not *LD*) on a winter range the residual forest area. All four surveys showed a positive and significant correlation between the number of mountain goats and residual forest area (Figure 4a-d). Generally residual forest area <50 ha appeared to have to least amount of goats in terms of absolute abundance (Figure 4a-d).





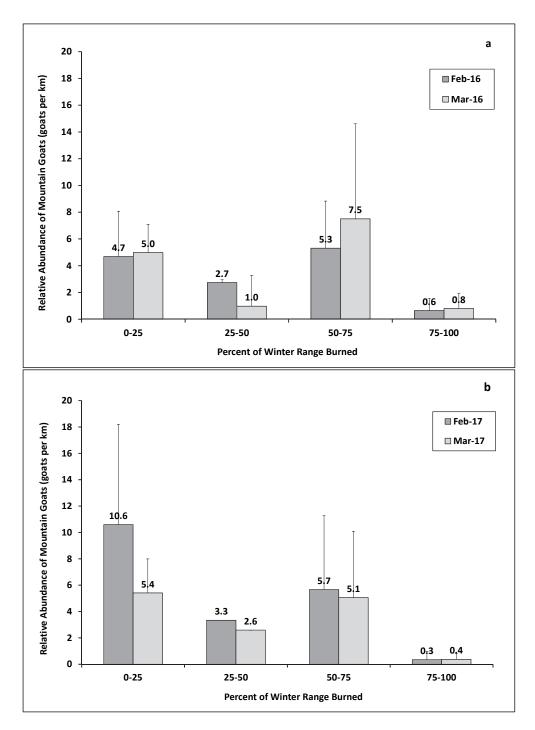


Figure 2. The relative abundance of mountain goats by burn class (percent of winter range burned ± SD) in 2016 (a) and 2017(a).





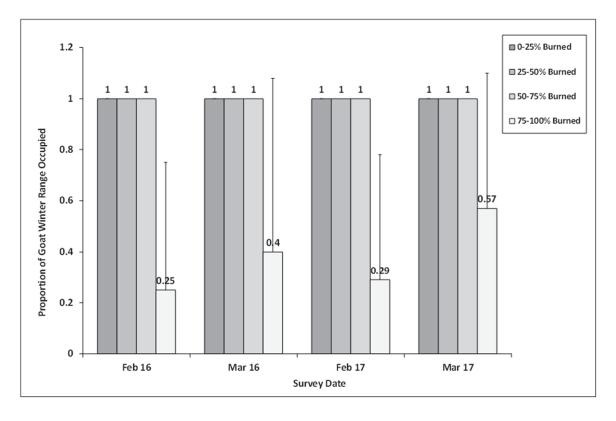


Figure 3. Proportion (± SD) of mountain goat winter ranges occupied by burn class.

DISCUSSION

The extensive fires in 2015 appear to have had a large impact on mountain goat occupancy and abundance affected winter ranges in southwestern British Columbia. Mountain goat winter ranges that were highly impacted by fire (≥75% of the forest area burned) showed 75% lower occupancy and 80% lower relative abundance. We found a positive and significant correlation between residual forest area and the number of mountain goats. Moreover, winter ranges highly impacted by fire were not occupied by goats. In some of these ranges where goats were detected, it was

just one set of tracks, and this could have been an individual travelling from one winter range to the next. This is consistent with what is known about coastal mountain goat ecology, where canopy cover is required for snow interception in coastal ecosystems with high snow accumulation on goat winter range habitats. Snow depth can also affect forage availability, as deep snow can limit available forage, and the timing and duration of snow melt also influences the ability of goats to access forage (Hebert and Turnbull 1977, Fox et al. 1989, Wilson 2005).





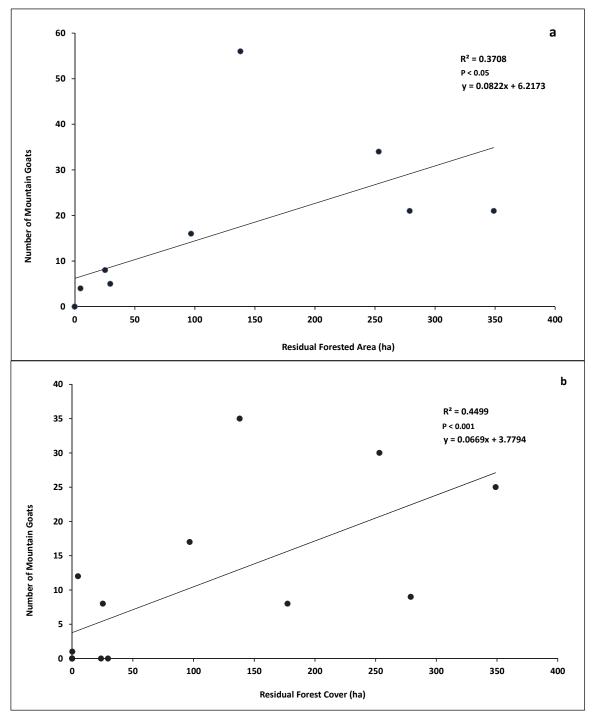


Figure 4. Correlations between the number of mountain goats and the residual forested area (ha) after the fires. Panels a-d represent the 4 survey dates, occurring in February 2016 (a), March 2016 (b), February 2017 (c), and March 2017 (d).

Mountain goats in coastal ecosystems have been shown to use more forested habitat than mountain goats in drier, interior ecosystems. Hebert and

Turnball (1977) noted that goats in coastal ecosystems in British Columbia are restricted due to excessive snow depths and use lower elevations with forest cover to





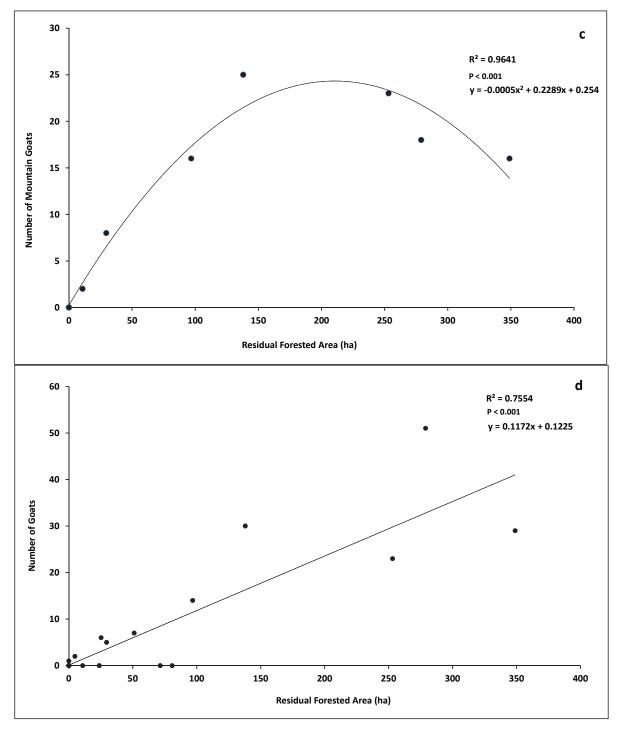


Figure 4 (continued). Correlations between the number of mountain goats and the residual forested area (ha) after the fires. Panels a-d represent the 4 survey dates, occurring in February 2016 (a), March 2016 (b), February 2017 (c), and March 2017 (d).

reduce snow depth. These authors also stated that mountain goats in coastal ecosystems are spatially more restricted and this affects group size due to harsh winter conditions (deep snows and limited cover and forage). Similarly, Fox et al. (1989) found that mountain goats in southeastern Alaska used habitats with old



growth coniferous forest in lower elevations adjacent to steep escape terrain. These authors stated that the removal of old growth forest will reduce the forage availability due to the increased snow depth. A study in southeastern Alaska by White et al. (2012) confirmed that 95% of mountain goats monitored with GPS collars wintered in low elevation forested habitats.

We found that the number of mountain goats declined significantly with a decrease in forest area size. We suspect that as forest area on goat winter ranges decreases, the ability of a winter range to have higher densities of goats will also decrease due to lack of space and suitable forage in close proximity to escape terrain (Fox et al. 1989). We found some evidence where mountain goats could have possibly moved to adjacent unburned goat winter range, based on the substantial increase in the number of goats we observed. However, since we did not have any mountain goats radio collared in these study areas before the fires and we did not sample all of the winter ranges, it is unclear whether or not goats shifted their use to different winter ranges, or these goats had perished in the fires.

MANAGEMENT IMPLICATIONS

Mountain goats are restricted in their habitat use due to their need for steep and rugged escape terrain for predator avoidance. In coastal ecosystems, goats are further restricted by their winter requirements of old growth forested areas adjacent to escape terrain for snow interception and forage. The loss of this forest cover through fire appears to have disproportional impacts to mountain goats in these ecosystems, as patch size decreases this will decrease the number of goats a winter range can support, similar to

a pattern observed for other species (e.g., Bender et al. 1998). To prevent further burning of these winter ranges, areas most susceptible to burning should be identified and if possible, apply aggressive firefighting practices to ranges that are burning.

It is unclear how mountain goats in the study areas use these burned areas during the summer months when snow is not limiting. Long-term population monitoring of these winter ranges and burned areas, combined with collaring a subset of mountain goats with GPS collars is required to evaluate seasonal habitat use and to understand the full impacts of the impacts of wildfires on mountain goat habitat use, seasonal movements, and long-term population trends.

ACKNOWLEDGMENTS

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APPENDIX 1: MOUNTAIN GOAT WINTER RANGE (GWR) SIZE (HA), FOREST AREA PRIOR TO BURN (HA), PERCENT AREA BURNED (OBSERVED), AND FOREST AREA (HA) AFTER BURN

GWR # / Site #	GWR Size (ha)	Forest Area (ha) Prior to Burn	Percent Area Burned (Observed)	Forest Area (ha) After Burn
Elaho Study Area				
Shovelnose / 07	666.0	349.0	0	349.0
30	420.9	177.4	0	177.4
31	253.6	96.2	0	96.2
26	387.3	203.6	0	203.6
58	578.4	178.8	60	71.5
57	282.1	92.7	50	46.4
41	139.9	97.5	100	0.0
56	52.5	21.4	100	0.0
39	144.1	104.4	100	0.0
25	860.5	85.2	40	51.1
40	191.9	54.1	80	10.8
66	104	80.9	0	80.9
Clendenning Park ¹	NA	NA	65	NA
Roe Creek ¹	NA	NA	0	NA
MEAN	340.1 ± 250.9	128.4 ± 87.5	44.2 ± 43.4	90.6 ± 105.3
Upper Lillooet Study Area				
ME 3	1,410.8	184.0	25	138.0
ME 2	75.5	63.2	60	25.3
ME 4	357.6	5.0	5	4.8
UL10	307.1	23.8	0	23.8
UL11	40.8	29.5	0	29.5
UL12	150.8	91.5	100	0.0
UL13	156.8	42.4	100	0.0
UL8	353.8	253.1	0	253.1
UL19	165.8	15.4	99	0.154
RA7	1,121.4	281.8	1	278.9
Petersen Crk / RY8	719.7	96.8	0	96.8
MEAN	441.8 ± 452.6	128.4 ± 87.5	35.4 ± 45.0	77.3 ± 103.3

¹Not a legally designated GWR





Forage Response to Prescribed Fire in the Northern Rockies: Implications for Stone's Sheep and Elk

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ABSTRACT: Prescribed fire is used as a management tool to enhance ungulate habitats. Since the early 1980's, up to 7,800 ha have been intentionally burned annually for this purpose in northeastern British Columbia (BC). Yet, there have been relatively few long-term studies that have quantified the effects that fire has on plant and animal communities. Two focal grazers in northern BC, Stone's sheep (Ovis dalli stonei) and elk (Cervus canadensis), are known to benefit from fires, but the length of time that burned areas remain beneficial to these species is unknown. Previous work showed that when Stone's sheep used burned areas, it was most often younger-aged areas with higher nutritional quality, but initial increases in forage quality are believed to deteriorate over time. Elk exhibited less preference for ages of burns and may be more influenced by forage quantity. The goal of this project was to characterize the attenuation of the plant and animal (Stone's sheep and elk) responses after prescribed burns implemented in 2010 in the Besa-Prophet Area of northeastern BC. We resampled permanent transects on four burned areas and four unburned (control) sites during the year of the burn, 1 year after burning, and 7 years after burning. At each site, we monitored vegetative characteristics (forage quantity and quality) and animal use (fecal pellet counts) at different elevations (high, mid and low). We sampled in early May to capture winter forage availability and in July to index maximum summer forage availability. We also quantified the potential effects of grazing by comparing forage biomass in 8 range exclosures with paired plots outside the exclosures. In the short-term (one year after burning), both ungulate species increased their use of prescribed burned areas – likely in response to increased forage digestibility and rates of forage growth; and plant diversity returned to pre-burn levels. Our findings from this last year of the project help identify effective timing for the frequency of prescribed burning in northern BC. Our management recommendations focus on enhancing positive outcomes for Stone's sheep, while mitigating any negative effects from elk (potential competition and changes in predator-prey dynamics).

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KEYWORDS Stone sheep; *Ovis dalii stonei*; elk; *Cervus elaphus*; prescribed fire; forage; British Columbia.





Seasonal and sex-specific variation in space use and site fidelity of mountain goats in coastal Alaska

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ABSTRACT: Understanding patterns of animal space use and site fidelity have important implications for conservation. For species that live in highly seasonal environments, such as mountain goats (Oreamnos americanus), space use patterns are likely to vary due to changing environmental conditions and sex-specific selection pressures. In this study, GPS location data (n = 123,481 locations) were collected from 64 radio-collared mountain goats (males, n = 36; females, n = 28) in a coastal mountain range complex near Haines, Alaska during 2010 – 2017. These data were analyzed a GIS framework using Program R (rhr and adehabitatHR packages) to derive seasonal and sex-specific fixed kernel home range estimates, and to quantify the degree of seasonal home range overlap. Overall, we determined that during the kidding season females with kids (1414±300 ha, n = 24) had smaller homes ranges than females without kids (2278±599, n = 22). Presumably this occurred due to the limited physical mobility of neonates and heightened vulnerability to predation. We also determined that females (2636±307 ha, n = 57) had larger home ranges than males (1424±155 ha, n = 74) during the summer, and males had larger home ranges (2400±155 ha, n= 67) than females (848±307 ha, n = 45) during the rut; home ranges during winter were similar in size for males (464 ± 89 ha, n=66) and females (543±100, n = 57) but substantially smaller than other times of year. Expansion of female home ranges during summer may be related to high energetic acquisition needs of reproductive females, whereas large male home ranges during the rut is likely related to seeking out mating opportunities; small winter ranges are likely due to movement constraints imposed by deep winter snows. During the summer season, we documented a high degree of site fidelity such that in 100% of cases individual animals returned to the same home range it occupied during the previous summer. During the winter 94% of males and 100% of females returned to the same home range. Within this context, we determined that males and females used large proportion of their previous winter (58%±3) and summer (79%±3) home ranges. The high degree of site fidelity highlights the importance of carefully managing such habitats for conservation.

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KEYWORDS Mountain goat; *Oreamnos americanus*; space use; site fidelity; Alaska.

Human Visitation Limits the Utility of Protected Areas as Ecological Baselines

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ABSTRACT: A key goal of protected areas is the conservation of biodiversity. Increasing visitation, however, can compromise ecological integrity. A fundamental conundrum is that if parks are to serve as our most pristine places, then we must understand how human presence alters biological interactions. Species that redistribute themselves closer to people is of growing management concern both in and out of national parks because of 1) human safety, 2) animal health, and 3) ecological consequences. Drivers of distributional change are often dissimilar but may include increased association with people for predator avoidance – the human shield hypothesis. We examine redistribution patterns with comparative, observational, and experimental approaches contrasting ecological responses of an iconic species in an USA national park - Glacier. Specifically, we focused on the role of predator avoidance and resource enhancement to test whether a cold-adapted alpine obligate, mountain goats, (Oreamnos americanus), mediate their distribution by increasing spatial overlap with humans. Individuals that enhanced mineral acquisition through access to human urine concomitantly reduced behavioral and ecological responses to grizzly bear (Ursus arctos horribilis) experiments. Goats near people also displayed reduced group sizes, vigilance, use of escape terrain, and forfeited migrations to naturally occurring minerals. Our findings re-enforce the increasing complexities of natural area management because visitation is altering ecological interactions. While protected areas offer some forms of baselines for scientists and enjoyment for millions of visitors, redistribution of species and associated ecological changes signifies that additional care will be needed in what we perceive as pristine and what is anthropogenically-altered.

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KEYWORDS Mountain goat; *Oreamnos americanus*; habituation; fear; human-mediated predation refugia; predator-prey; migratory; human-wildlife conflict.





Characterizing the Seasonal Movements of Native and Restored Bighorn Sheep: A Case for Conserving Migratory Portfolios

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ABSTRACT: Animal migrations represent the culmination of a long evolutionary history resulting in genetic, physiological, behavioral, and life-history traits that facilitate the successful interaction between individuals and biotic and abiotic factors in their environment. Once lost, attempts to restore migration generally result in diminished seasonal movements compared to historic migratory patterns. Over their broad distribution, bighorn sheep show diverse seasonal movements from resident to long-distant migrants spanning varied elevational and geographic gradients, yet much of our current understating of bighorn sheep movements stems from periodic tracking of animals instrumented with VHF collars sampled from single populations. While restoration efforts (i.e., translocations) have undoubtedly resulted in modest successes, bighorn sheep occupy only a small fraction of their former range and predominantly occur in restored populations that number fewer than 100 individuals. Although factors related to disease, competition, and habitat quality routinely inform bighorn sheep translocations, less attention has been given to seasonal movements, yet the tendency to migrate has been positively associated with translocation success. As an initial step to exploring the importance of migrations in bighorn sheep restoration, we used GPS location data to characterize the seasonal movements of over 200 female bighorn sheep across four states. Specifically, we





evaluated the presence and diversity of migratory movements between restored and native herds. We report findings from this large-scale comparative analysis spanning herds with varied demographic performance and management histories and propose stronger consideration of seasonal movements as an important component of future bighorn sheep restoration.

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KEYWORDS Bighorn sheep; individual heterogeneity; migration; *Ovis canadensis*; portfolio effects; restoration; translocation.



An Exploration of Metabolomics to Assess Physiological States in Bighorn Sheep

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ABSTRACT: Wildlife biologists have limited and relatively crude tools for assessing the health, physiology, and nutritional condition of bighorn sheep and other wild ungulates yet physiological attributes of an animal play a fundamental role in susceptibility to disease, reproduction, probability of survival, and can provide insights into the relative quality of landscapes occupied. Nuclear Magnetic Resonance spectroscopy (NMR) is an emerging technology that can identify and quantify a large suite of biological molecules (metabolites) in a blood serum sample that are products of a wide range of physiological processes. NMR-based metabolomics is being aggressively developed in the fields of human medicine and agriculture animal production in the pursuit of discovery of disease biomarkers and to detect metabolic shifts in a myriad of physiological pathways that can be bioindicators of nutritional and other environmental stresses. To explore the potential of this technology for wildlife management we collected 949 serum samples from 14 wild bighorn sheep herds in Montana and Wyoming, as well as samples from two captive research herds. These samples represented animals suspected of experiencing a range of physiological conditions including gradients in dietary intake, degree and duration of starvation, and transitions from a healthy to a disease (pneumonia) state. Sample processing and assay techniques were refined, and we successfully developed a library of 81 metabolites that can be accurately identified and quantified. We report on our analyses of these metabolic profile data to develop a 'health panel' to assess physiological states in bighorn sheep to inform restoration and management.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:37; 2018

KEYWORDS Bighorn sheep; *Ovis canadensis*; Nuclear Magnetic Resonance spectroscopy; physiology; metabolites; health; health panel; nutritional condition.





Assessing Dall's Sheep Horn Morphometrics as a Management Tool

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ABSTRACT: Dall's sheep (Ovis dalli) are a coveted big game species pursued by a relatively small but passionate group of hunters across 8 mountain ranges in Alaska. The Alaska Board of Game determines state harvest regulations and has recently been inundated with public proposals aimed at altering sheep management. Proposals are directed at reducing a perceived level of competition between resident and non-resident hunters, and to address a possible lack of legal rams available for harvest. Specifically, many hunters believe that all legal rams are harvested each year and want to increase their availability by reducing the hunting opportunities available to non-residents. Alaska hunting regulations are complex, but generally, most sheep hunting is managed under a full-curl harvest strategy. Full-curl is defined as: the tip of one horn has grown through a 360° circle described by the outer surface of the horn when viewed from the side, or both horn tips are broken, or the sheep is 8+ years old. Since 2004, successful hunters are required to seal sheep horns at Alaska Department of Fish and Game offices. In 2016, we began a study to evaluate horn morphometrics as a tool to inform management decisions. We measured and photographed ~60% of harvested rams in 2016 (474 of 783), and 2017 (483 of 798). For each horn, we quantified age, total horn length, total degree of curl, distance between consecutive annuli, and degree of curl by annulus segments. In 2016, the mean age at which rams achieved 360° curl was 8.5 years (range 5 to 12 years). In 2016, 19% of harvested rams were legally taken on criteria other than 360° of curl, while 28% of rams were harvested in the first year they became legal based on degree of curl. On the other hand, 53% of harvested rams were available for harvest during at least one previous hunting season after their horns grew through 360° curl. Our preliminary analyses indicate that hunters are only removing approximately half of all legal rams each year statewide. Using horn morphometric data to estimate ram escapement each hunting season will inform policy decisions.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:38; 2018

KEYWORDS Dall's sheep; *Ovis dalli;* horn morphometrics; hunting regulations; ram escapement; Alaska.





Role of Harvest and Environmental Factors on Horn Size of Mountain Sheep

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ABSTRACT: Harvest-induced evolution can have important implications for the sustainable management of populations world-wide; yet, the true effects of harvest remain highly debated. Even at limited temporal and spatial scales, population-level responses to harvest can occur across taxa, and include reduced size of weapons and growth rate, and early sexual maturation. Nevertheless, in most populations, the threshold of selection intensity that prompts evolutionary change is unclear. Harvest can affect patterns of weapon size in two distinct ways. First, intensive harvest can result in demographic changes, where declines in mean weapon size result from an increasing proportion of young animals harvested through time. Alternatively, selection for males with fast-growing weaponry may favor the persistence of males with slowgrowing weaponry through time and result in declines in the average size of weapons in a population despite no change in age structure. Mountain sheep (Ovis canadensis and Ovis dalli) represent an ideal system to test the effects of harvest on weapon size because harvest of mountain sheep is highly regulated throughout their range and a wealth of phenotypic data exists. Additionally, reliable age data, which is critical to test shifts in age structure of populations, is available through horn annuli of mountain sheep. We synthesized harvest records of mountain sheep throughout their range and assessed changes to age structure and horn size over 46 years. After accounting for age, temporal trends in horn size were not explained by changes to the age structure in approximately 20% of hunt areas, but instead may be associated with selective pressures or environmental conditions. Nonetheless, age-specific horn size was stable in about 80% of hunt areas, indicating harvest practices for most



populations of mountain sheep in North America have not resulted in evolutionary changes to weapon size.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:39-40; 2018

KEYWORDS Selective harvest; bighorn sheep; *Ovis canadensis*; horns; artificial evolution; harvest-induced evolution.





Horn Size and Nutrition in Mountain Sheep: Can Ewe Handle the Truth?

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ABSTRACT: Horns, antlers, and other horn-like structures are products of sexual selection, confer reproductive advantages, and are heritable and honest indicators of individual quality. In addition, horns and antlers also garner substantial societal interest that, when combined with the powerful motivation to acquire trophy animals, likely has spawned a growing "hornographic" culture fixated on males with exceptional horn-like structures. Intensive harvest of large, fast-growing males, however, may have deleterious effects on the very trait being sought, which has led to considerable controversy in the popular and scientific literature. Mountain sheep, possibly the only large ungulate in North America managed almost exclusively as a trophy species, embody this controversy because of the emphasis on managing for large males. That controversy has led to polarizing views among scientists and stakeholders as to how mountain sheep should be managed. Our goal herein was to discuss the relative contributions of the key ecological and intrinsic factors that influence horn growth, how those factors might interact with harvest strategies, and identify what determinants of horn size are most amenable to management and most effective in achieving desired outcomes. Given the hyperbole surrounding trophy management and big horns, we suggest the importance of females in the management of bighorn sheep has been largely forgotten. Females play a critically important role, not just as the reproductive segment of the population responsible for producing young, but because maternal condition can produce life-long effects on size and growth of males (via maternal effects); and additionally, abundance of females, in turn, affects nutritional limitation within populations through density-dependent feedbacks. Ultimately, we call for greater recognition of the pervasive role of the ewe—and other female ungulates—in the production of trophy males and in contributions to population performance; and accordingly, that they be better integrated into harvest and management programs.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:41-42; 2018





KEYWORDS Bighorn sheep; *Ovis canadensis*; horns; horn-like structures; nutrition; maternal condition; heritability; genetics.

An Overview of Past and Present Genetic Studies of Bighorn Sheep: Reconciling Methods and Considering Applications for Management

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ABSTRACT: Bighorn sheep have been the focus of genetic research for decades. Because of small populations sizes, natural and anthropogenic habitat fragmentation, and a long history of bottlenecks and founder effects from translocation, managing low genetic diversity has been a concern across much of the present-day range of bighorn sheep. We review past, present, and possible future directions for studies of bighorn sheep that incorporate genetic tools or address genetic management. We consider two broad and not necessarily exclusive categories of studies or approaches: those intended to use genetic signals to infer phylogeography and phylogenetic relationships, demographic history, patterns of fragmentation and connectivity, or population size, and those intended to examine the consequences of genetic variation within populations, such as inbreeding, effects of genetic diversity on fitness, local adaptation, response to disease, and heritability of desirable traits. We provide a brief overview of different methods and questions, describe examples from past and present research, consider which types of methods and markers are most appropriate for different situations, and discuss how these concepts have been applied to management of wild sheep populations in North America. Finally, we identify areas of uncertainty and questions that bear examination in future research.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:43; 2018

KEY WORDS Bighorn sheep; *Ovis canadensis*; DNA; genetics; phylogeography; genetic history.





Genetic Evidence of Local Adaptation in Desert Bighorn Sheep Native to the Great Basin

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ABSTRACT: Desert bighorn sheep (*Ovis canadensis nelsoni*) occupy a diversity of desert ecosystems throughout the southwestern United States. Significant climatic differences among these desert ecosystems suggests the potential for adaptation to local conditions in this taxon. We tested for signatures of local adaption using 2b-RAD reduced representation genotyping in conjunction with high resolution climate data for 30 native populations of desert bighorn sheep (291 individuals) distributed throughout much of its North American range. Population differentiation and ecological association tests on 11,303 SNPs identified outlier loci with alleles private to the Great Basin of California and Nevada. Private allele frequencies were correlated with higher elevation and lower annual mean temperature; logistic regression, P < 0.001. Outlier loci mapped to a ~ 5 Mb sequence on chromosome 8 of the domestic sheep genome (Oar v3.0) encompassing the EPH receptor A7 gene and six other undescribed protein coding genes. Our data suggest the few remaining desert bighorn herds native to the Great Basin may represent a unique ecotype and should be managed accordingly. Understanding the range of adaptive genetic variation present within desert bighorn sheep may prove instrumental in predicting how this taxon might respond to global climate change.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:44; 2018

KEYWORDS Desert bighorn sheep; *Ovis canadensis nelsoni*; genetic variation; adaptive ecotypes; SNPs; Great Basin; desert southwest.



Does Population of Origin Affect Translocation Success in Bighorn Sheep?

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ABSTRACT: Since 1922, over 21,000 wild sheep have been translocated within and among states and provinces in western North America for species restoration (Western Association of Fish and Wildlife Agencies Wild Sheep Working Group). In Idaho, bighorn sheep have been translocated since the 1960's from multiple states and provinces including Oregon, Wyoming, Montana, Alberta, British Columbia, and within Idaho. Several sources are often used to reestablish a single population to increase numbers and genetic diversity. As a result, despite small founder sizes, many of Idaho's reintroduced populations have similar or greater allelic richness than native populations. However, it is unknown whether translocated individuals from different source populations contribute equally to numbers and genetic diversity. We used 10 neutral microsatellite markers to empirically evaluate the genetic composition of restored populations in Idaho, and their sources. We then simulated the expected present-day genetic composition of the re-established populations, under the assumption that translocated individuals from each source population performed equally. By comparing the empirical genetic data with the simulation results, we evaluated whether the assumption of equal fitness across translocation sources was violated, and therefore whether certain source populations were more successful than others. This analysis could help inform decisions to increase the success of future translocations.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:45; 2018

KEYWORDS Bighorn sheep; *Ovis canadensis*; restoration; translocation; microsatellite markers; genetic diversity; source herds; fitness.





Evaluating Sample Size to Estimate Genomic Relatedness in Bighorn Sheep Populations

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ABSTRACT: Inbreeding and relationship metrics among and within populations are useful measures for genetic management of wild populations, but accuracy and precision of estimates can be influenced by the number of individual genotypes analyzed. Biologists are confronted with varied advice regarding the sample size necessary for reliable estimates when using genomic tools. We developed a simulation framework to identify the optimal sample size for three widely used metrics to enable quantification of expected variance and relative bias of estimates and a comparison of results among populations. We applied this approach to analyze empirical genomic data for 30 individuals from each of four different free-ranging Rocky Mountain bighorn sheep (Ovis canadensis canadensis) populations in Montana and Wyoming, USA, through cross-species application of an Ovine array and analysis of approximately 14,000 single nucleotide polymorphisms (SNPs) after filtering. We examined intra- and interpopulation relationships using kinship and identity by state metrics, as well as FST between populations. By evaluating our simulation results, we concluded that a sample size of 25 was adequate for assessing these metrics using the Ovine array to genotype Rocky Mountain bighorn sheep herds. However, we conclude that a universal sample size rule may not be able to sufficiently address the complexities that impact genomic kinship and inbreeding estimates. Thus, we recommend that a pilot study and sample size simulation using R code we developed that includes empirical genotypes from a subset of populations of interest would be an effective approach to ensure rigor in estimating genomic kinship and population differentiation.

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KEYWORDS Kinship; bighorn sheep; Ovis canadensis, sampling, single nucleotide polymorphism.





Using Historic Specimens to Provide Insight into Native Bighorn Sheep Genetic Diversity and Connectivity in Idaho

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ABSTRACT: Bighorn sheep (Ovis canadensis) have experienced severe population declines and population extirpations across the western US. One region where bighorn sheep were not extirpated is the Salmon River Drainage of Idaho. These native populations are a highly valuable and irreplaceable genetic and ecological resource. The goal of this study was to evaluate genetic diversity and connectivity among bighorn sheep in this region using a combination of current and historic specimens. Specifically, we addressed 4 questions 1) What are the levels of genetic diversity and population connectivity for native Idaho bighorn sheep? 2) Are Population Management Units (PMUs) genetically distinct? 3) What were historic levels of genetic diversity in native Idaho bighorn sheep? 4) How has diversity changed over time? We obtained 350 current samples from 5 PMUs, 43 historic samples (1989) from the Middle Main Salmon (MMS) and 34 historic samples (1923-1985) from Lower Salmon (LS) and Middle Fork (MF) using horn shavings from the Carrey Collection. We genotyped 15 microsatellite loci, eleven neutral and four adaptive. We observed the highest levels of genetic diversity in the historic samples from the Carrey Collection and from current samples in the core of the range. The Carrey Collection samples also had a much larger number of unique alleles (13) compared to the historic specimens from MMS (0) and current samples (3). Our connectivity and gene flow analyses indicated that PMUs were genetically distinct, but there was evidence for gene flow between PMUs. We found evidence for higher historic connectivity between the LS and MF PMUs compared to current samples from these regions. This is the first study in bighorn sheep to evaluate changes in genetic diversity over time using historic specimens and demonstrates that unique alleles and genetic diversity have been lost over time which has implications for fitness and adaptive capacity.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:47; 2018

KEYWORDS Connectivity; bighorn sheep; *Ovis canadensis*, genetic diversity; microsatellites; unique alleles.





Frequently-Asked Questions About Wild Sheep Genetics and Genomics

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WILD SHEEP GENOMICS WORKING GROUP

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ABSTRACT: Research focusing on population genetic variation has informed our understanding of North American wild sheep conservation and management for decades. New techniques, however, are emerging at an increasing rate, including genomics approaches that investigate a larger portion of the genome than was previously possible. Research has addressed questions at many scales, from assessing relationships among individuals within single populations, to broad-scale patterns of genetic variation across multiple states or provinces, to deep evolutionary relationships among species. Meanwhile, wildlife managers seek answers for management-relevant questions old and new that could be informed by appropriate analyses using traditional population genetics tools and newer genomic methodologies. Improving communication among researchers and wildlife managers responsible for wild sheep populations or other taxa across multiple jurisdictions, as well as clarifying what questions are best addressed by different genetic or genomic approaches, could facilitate collaboration and improve research. To that end, the informal Wild Sheep Genomic Working Group was established in 2018, including members from both research and management backgrounds. A "frequently-asked questions" (FAQ) document was established to facilitate conversation; questions were collated from group members and presented as part of a special session on genetics and genomics at the Northern Wild Sheep and Goat Council Symposium held in Whitefish, Montana, during May 2018. Here, we present an edited version of those questions with responses provided by the group, including a glossary of technical terms. We address methodological choices and ways to improve collaboration, provide examples of how population genetics research has informed management, and discuss genetic diversity, subspecies management, and genetics as a tool to understand disease. We note that the projects discussed and researchers contributing herein are not a comprehensive list of current genetic research on wild sheep, but we view this as a first step towards improving collaborative research to inform conservation and management of wild sheep and goats in North America.

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KEY WORDS Disease; DNA; genetics; genomics; local adaptation; microsatellites; SNPs; sequence; taxonomy.

For the last three decades, conservation and management of wild sheep in North America has drawn upon a rich body of research using population genetic approaches. Wild sheep have been attractive subjects for genetic research because of their evolutionary history, extensive history of population translocation and management, high value to the public as a game animal and iconic symbol of desert or alpine habitats, and because their small founder or current

population sizes raise concerns about the maintenance of genetic diversity. Genetic studies have better informed wild sheep conservation and management on numerous topics, including **phylogeography** (Ramey II 1995, Luikart and Allendorf 1996, Wilder et al. 2014, Malaney et al. 2015, Buchalski et al. 2016, Sim et al. 2016), population structure and connectivity (Gutierrez-Espeleta et al. 2000, Buchalski et al. 2015, Epps et al. 2018), trans-boundary movement (Flesch et al. 2010, Buchalski et



al. 2015), horn growth (Fitzsimmons et al. 1995, Miller et al. 2018), population growth (Johnson et al. 2011), reintroduction effects (Ramey II et al. 2000, Whittaker et al. 2004, Hedrick and Wehausen 2014, Malaney et al. 2015, Gille et al. *In press*, Jahner et al. *In press*), inbreeding depression and genetic rescue (Hedrick et al. 2001, Hogg et al. 2006, Miller et al. 2012, Olson et al. 2012), and most recently local adaptation (Kardos et al. 2015, Roffler et al. 2016) to name but a few. Thus, genetic research is likely to remain an integral component of wild sheep conservation and management for the foreseeable future.

Over the last decade, tools for genetic analysis have expanded rapidly, including approaches sometimes referred to as *genomics* because they address variation across a larger proportion of a research subject's **genome**. The distinction between genetics and genomics research, however, is not always clear, and may be best viewed as a continuum of research from small portions of the genome (e.g. 10-20 microsatellite loci or partial sequence of mitochondrial DNA [mtDNA] cytochrome b or control region) all the way to comparing nearly complete genome sequences of many individuals. Technological advancements for high-throughput DNA sequencing over the last decade have been transformative (Mardis 2013), resulting in extremely rapid change in data type and volume. These technologies can sequence millions of genomic fragments ("reads") for multiple individuals all at once, versus targeted sequencing of individual loci, or can sequence many targeted loci at once as in high-throughput microsatellite genotyping (De Barba et al. 2017). This means that in addition to traditional singlelocus approaches, geneticists can now sequence tens or hundreds of thousands of

loci simultaneously and at a very small cost. Further, these loci (e.g., single nucleotide polymorphisms, or SNPs) can occur throughout the genome including gene coding regions. Thus, it is now possible for geneticists to simultaneously assess genomic variation resulting from both demographic processes and natural selection.

With the rapid advancement of techniques and increasing sophistication of research questions, however, has come increased need for strengthening communication between wildlife managers and researchers, as well as improving collaborations across state, provincial, and national borders. The Western Association of Fish and Wildlife Agencies (WAFWA) Wild Sheep Working Group began to address that need in 2018 by convening an informal Wild Sheep Genomic Working Group, including members from both research and management backgrounds. The group has focused to date on North American wild sheep, including bighorn sheep (Ovis canadensis) and the thinhorn sheep (Ovis dalli), but the approach could be extended to mountain goats (*Oreamnos americanus*) given similar evolutionary, ecological, conservation, and life histories.

After a suggestion by Zijian Sim, the group decided to collect a list of genetics questions and allow group members to respond individually, providing a diversity of viewpoints, with the intent that those questions and responses could be collated and published. Questions fell into two general categories. One category included those questions that originated with geneticists and were directed to wildlife managers, asking what data gaps currently limit informed management and how genetics research can be of benefit. The other category included questions from





wildlife managers directed to geneticists regarding the various approaches to genetic research, and the appropriateness of the various methods for assisting with wild sheep conservation and management. Questions were provided by Mike Cox of Nevada Dept. of Wildlife (NDOW), based in part on a January 2018 survey of Wild Sheep Working Group representatives regarding critical data gaps for wild sheep genetics and genomics, with significant input from Rich Harris of Washington Dept. of Fish and Wildlife (WDFW) and authors of this manuscript. Questions were submitted in April-May 2018, edited, and then were presented for discussion at a genetics and genomics symposium at the Northern Wild Sheep and Goat Council meeting held in Whitefish Montana during May 2018.

Here, we present those questions and the responses gathered during and after the symposium. The questions and responses are organized into topics, including 1) methodological choices and ways to improve collaboration, 2) examples of how genetics research has informed management, 3) causes and consequences of genetic diversity, 4) management of taxonomic units below the species level, and 5) genetics as a tool to understand disease. Questions are numbered sequentially across categories and italicized; answers are numbered and attributed to the source. We note, however, that as participation was self-selected, not all projects and researchers currently working on wild sheep genetics are represented. We have included a glossary of technical terms (Appendix 1); terms included in the glossary are indicated in bold-face type at first usage.

QUESTIONS AND ANSWERS

Questions and needs relating to methods and collaborations

1) What are the various types of genotype/loci datasets each group is collecting- can we assess the possibility for comparisons in the future? Answer I (Epps): The Oregon State University (Epps) research group has collected neutral microsatellite (13-14 loci) and adaptive-linked microsatellite data (3-8 loci) for bighorn sheep across most of the range of desert bighorn sheep (O. c. nelsoni) in California (excluding Peninsular populations), desert bighorn in Utah and the Grand Canyon of Arizona, and are generating neutral and adaptive-linked microsatellite data for 'California' (O. c. canadensis, formerly O. c. californiana) bighorn populations in Oregon. These data can be compared with other microsatellite datasets using overlapping sets of loci by running reference samples in multiple labs to allow alignment (e.g., Gille et al. In press). We recommend that researchers extract a large quantity of DNA from several individuals to create such reference samples.

Previously, we have merged our datasets with data produced by John Wehausen, Kathy Longshore, and Jef Jaeger (southern Nevada) as part of Tyler Creech's dissertation work (Epps et al. 2016, Creech et al. 2017), Mike Buchalski, Walter Boyce, and other's data (Buchalski et al. 2015) for Peninsular bighorn work (in preparation), and with Daphne Gille, Mike Buchalski, Walter Boyce, Holly Ernest, and others for Arizona-wide analyses (Gille et al. *In press*). Although



the number of overlapping loci was small in the last case, we were able to align datasets to identify important patterns of **genetic structure** across Arizona. We hope to share data between Nevada/Oregon populations of 'California' bighorn with Marjorie Matocg at University of Nevada and potentially people working in Idaho. Microsatellite data seem to do a good job of addressing questions of bighorn genetic structure, gene flow, connectivity, and population history (e.g., Epps et al. 2018), although we are still determining what additional resolution Single Nucleotide Polymorphisms (SNPs) might bring.

In addition, the Epps Lab recently used a method of restriction siteassociated DNA sequencing (RADseq, Wang et al. 2012, see http://people.oregonstate.edu/~meyer e/docs/2bRAD 25Aug2016.pdf) to generate SNP genotypes for ~10,000 loci from Sierra Nevada bighorn sheep, Rocky Mountain bighorn sheep from Alberta and British Columbia, and desert bighorn sheep from throughout the majority of that subspecies' natural range for a landscape genomics study investigating local adaptation to climate, in collaboration with CDFW (Buchalski), University of Nevada (Matocg), and other partners. These SNPs provide a signal of genetic population structure consistent with previous analyses of microsatellite data (Buchalski et al. 2016) and at least one SNP locus shows strong evidence of selection (adaptive-linked), suggesting local adaptation among remnant herds of the Great Basin (Buchalski et al. In prep).

Answer II (Jahner): The University of Nevada group (Matocq, Parchman, Jahner) has collaborated with NDOW to generate genetic data from populations of California, desert, and Rocky Mountain bighorn sheep across Nevada. Our initial effort entailed generating microsatellite data (16 loci) from 347 individuals across 55 herds representing all three "subspecies" in Nevada (Malaney et al. (2015). These data showed marked genetic subdivision between 'California', desert, and Rocky Mountain bighorn in Nevada as well as clear signatures of hybridization where these lineages come into spatial proximity. More recently, we have generated genotyping-by-sequencing data for several hundred individuals (analogous to a type of restriction site-associated DNA sequencing (Peterson et al. 2012)), using the protocol found in Parchman et al. (2012), and have a new paper describing the genetic consequences of Nevadan desert bighorn sheep translocations over the past 50 years (Jahner et al. In press). This is a reduced representation method, where subsets of genomes are sampled and sequenced based on the distribution of restriction enzyme cut sites. These approaches allow direct sequencing and SNP detection in tens of or hundreds of thousands of genomic regions and can be executed with large numbers of individuals in a time and cost-effective manner to rapidly generate population genomic level data (Andrews et al. 2016). Our dataset of more than 17,000 SNPs was able to detect very fine-scale genetic differentiation among geographically proximate, remnant herds in southern



Nevada, a signal consistent with microsatellite data, as well as recovering signatures of admixture in translocated desert herds that reflect the history of translocation. Our ongoing sequencing efforts are focused on establishing a genome-wide view of hybridization among subspecies to complement our microsatellite-based studies, and to investigate whether some remnant, central Nevadan herds are relicts of a Great Basin lineage of desert bighorn sheep (we will be collaborating closely with Mike Buchalski and CDFW for this second question). The sequencing data that we generate should be fairly comparable with studies using similar library preparation methods, but will have little comparability to studies using other marker types. We have interest in trying the **Ovine SNP chip** (array) that other labs have successfully used (e.g., Miller et al. 2018) as a mechanism for generating genotypic data that could be readily transferable among any groups using this resource. Because we now have parallel microsatellite and SNP datasets for multiple individuals and herds, we can compare these measures of genetic variation to help bridge interpretation between these different data types (see next question).

Answer III (Sim & Coltman): The Coltman research group (University of Alberta) has two datasets that may be of interest:

 i) A ~10,000 SNP dataset typed on 55 individuals using the OvineHD SNP array. This dataset formed the basis of Sim et al. (2016), which investigated the phylogeographical history of

- thinhorn sheep (*Ovis dalli*). That paper helped resolve the relationship between Dall's, Stone's and Fannin sheep. Data from this paper are publicly available on the Dryad database: https://datadryad.org/resource/doi:10.5061/dryad.c87rm. Data from SNP arrays are comparable with other datasets generated from the same array.
- ii) A dataset of 153 neutral SNPs typed on ~2500 individuals covering the entire thinhorn sheep range. This dataset was used to study the range-wide population genetic structure of thinhorn sheep. The paper describing the results are in review so the data likely will not be available until the paper is published. In the meantime, we are happy to share the primer sequences should other groups be interested in genotyping their own samples and/or combining data. Our SNP discovery panel was chosen to ensure even representation from all jurisdictions so ascertainment bias should be minimal.

Answer IV (Waits): The Waits lab (University of Idaho) has multiple datasets that may be of interest, including:

- A dataset of neutral and adaptive-linked microsatellite loci for ~450 sheep in Idaho including some historic specimens, plus a mitochondrial DNA (mtDNA; control region) dataset for ~200 sheep.
- ii) A dataset of neutral and adaptive-linked microsatellite loci





for 300 sheep in Washington and the Lostine and Lookout populations of Oregon, as well as putative source populations in the Fraser/Williams Lake area of British Columbia (n=112).

iii) A SNP dataset generated by RADseq for the Lostine population (n=100, 142-523 loci) in Oregon (Andrews et al. 2018).

Answer V (Wehausen): In 1998, with Rob Ramey, we developed the first population genetic data for Sierra Nevada bighorn sheep. We used 13 microsatellite loci to assess genetic population structure of the surviving populations, initially using DNA extracted from fecal samples and tissue from skulls collected in the field, and sampled all populations of desert bighorn sheep immediately east of the southern Sierra Nevada to Death Valley to provide geographical context. We quickly learned that Sierra bighorn had a strong signature of a recent bottleneck and notably lower genetic diversity than other sampled populations; this finding was added to an early draft of the recovery plan for Sierra bighorn (USFWS 2007). The desert bighorn sheep data were later augmented with additional microsatellite loci and combined with additional data from the Death Valley region run in the Epps lab (Epps et al. 2016). In combination with other efforts, this completed the genetic sampling of essentially all bighorn sheep populations in California, allowing comparisons of genetic diversity metrics at neutral microsatellite loci.

The genetic research on Sierra bighorn began by using the San Diego

Zoo genetics lab, courtesy of Ollie Ryder, then transitioned to a private lab Ramey and Wehausen set up in Nederland CO. That was followed by the creation of another independent lab in Bishop, CA through the Sierra Nevada Bighorn Sheep Foundation, where all subsequent work has been performed by Wehausen. One project run in this lab investigated the question of potential fitness influences of the low genetic diversity of Sierra bighorn and found a statistically significant heterozygosity-fitness relationship in Sierra bighorn involving the probability of females having lambs in summer (Johnson et al. 2011). More than 50 microsatellite loci are now used, with more to be added in order to be able to determine parentage of all lambs in one small population genotyped from fecal samples for 20 years. Another graduate project is further examining the robustness of the findings of Johnson et al. (2011) using considerably more loci and data.

A large number of samples from Sierra bighorn have now been genotyped and resulting genetic data have been used as a basis for management actions to influence genetic diversity in reintroduced populations and existing populations through augmentation (genetic rescue), and to track genetic diversity of all populations to evaluate success of genetic management efforts. These data also have been used to investigate gene flow between some populations.

Another project from this lab has characterized genetic population structure and gene flow in southern Nevada immediately south and north of Las Vegas, in collaboration with Jef



Jaeger at UNLV and Kathy Longshore of USGS (see Epps answer above). Finally, a long-term project is using mtDNA to investigate the evolutionary history of North American wild sheep, in collaboration with R. Ramey and C. Epps. This began with the sequencing of control region for a large number of samples to compliment what Epps et al. (2010) and Boyce et al. (1999) had produced. After finding that the control region could not adequately address this question, this effort shifted to conserved protein coding genes. Additional sequence data and samples have been added periodically. This currently includes 4 genes (ND5, ND6, ND2, and COIII) for a total of 3,336 bp.

been used to describe wild sheep genetics: microsatellites, SNPs, others? What is the most appropriate sample material for each? What level of detail and types of questions that are best answered by each method? Are results from each method comparable? Answer I (Sim): Combining SNP datasets can be fairly straightforward in some cases, unlike for microsatellites where a bit of calibrating/standardizing work needs to be done (although as the Epps collaborations have shown, it is not impossible). Answer II (Parchman): This is especially the case if SNPs are called (i.e., determining what base pair is present at each variable site) using a high throughput SNP chip, such as the OvineHD SNP array. Genotyping-bysequencing (RADseq) data can be easily combined if they are generated with the same library preparation method

2) What past and present methods have

and if the raw sequencing data are available.

Answer III (Epps): I have started writing a review paper to explore this topic in detail. Different types of markers are typically best suited for different questions and may not be directly comparable. Wild sheep genetics have been addressed by many methods, including Restriction Fragment Length Polymorphisms (RFLPs) at mitochondrial or Major Histocompatibility Complex (MHC) genes (e.g., Ramey II 1995, Boyce et al. 1997), neutral microsatellite markers (e.g., Coltman et al. 2002, Whittaker et al. 2004, Epps et al. 2005, Miller et al. 2012), adaptive-linked microsatellite markers (e.g., Luikart et al. 2008a, Plowright et al. 2017), mitochondrial **DNA sequences** (e.g., Boyce et al. 1999, Buchalski et al. 2015), SNPs (e.g., Miller et al. 2014, Sim et al. 2016), and other approaches. In recent publications, microsatellite loci, mtDNA and nuclear sequence data, and SNPs seem to be most commonly employed. Microsatellites are still commonly used to estimate genetic structure and diversity (e.g., Epps et al. 2018), and identify individuals from non-invasive (e.g., feces or hair) samples as for population estimation or other purposes. Microsatellite loci are wellcharacterized by many labs, usually can be aligned with existing datasets by rerunning individual samples previously genotyped elsewhere and are relatively easy to amplify from non-invasive samples. Mitochondrial and other DNA sequence data may be best suited for phylogeographic or phylogenetic analyses or direct assessment of variation at genes of interest. Short



sequences (e.g., mitochondrial DNA sequences of up to ~600 bp or so) can be easily amplified from non-invasive samples, but "next generation" sequencing approaches usually require larger quantities of DNA with little contamination, as can be obtained from blood or tissue.

Modern high-throughput sequencing or genotyping approaches are capable of generating many more loci (usually SNPs) across the genome, and therefore allow finer-scaled or more accurate estimates of genetic structure, inbreeding, diversity, and heterozygosity that will be more representative of the rest of the genome than estimates from a small number of microsatellite loci (Miller et al. 2014). If sufficient marker density is achieved, SNPs generated from such approaches can be used to identify variable markers showing evidence of selection (e.g., landscape genomics) or association with different traits (e.g., a genome-wide association study [GWAS]). While microsatellites may also show evidence of selection if closely associated with genes of interest ("adaptive-linked") (e.g., Luikart et al. 2008a, Plowright et al. 2017), the greatly-increased number of loci in most SNP studies increases the chance of detecting associations, although strong genetic drift and isolation common to wild sheep and goat populations still make such studies challenging. Some methods of generating SNP datasets (e.g., RADseq) may not work well with non-invasive samples, degraded DNA, or small amounts of DNA, and thus are best suited to large amounts of clean DNA obtained from well-preserved blood or

tissue. SNP datasets can be difficult to align or compare among research groups if library preparation methods differ (but see Parchman's comment above). However, SNP assays can be designed to work with other types of material and such assays can be quite comparable across research groups (Carroll et al. 2018). Investment in the development of an assay (e.g., a SNP chip) that can consistently recover a large, shared set of target loci from a range of tissues or non-invasive samples will be important for moving forward in a coordinated way.

3) What are standards and options for long-term storage of wild sheep genetic material?
Answer 1 (Sim): Here are some options with positive (+) and negative (-)

attributes indicated:

- i) Horn core drillings (can be stored in paper envelopes)
 - (+) Highly stable over long periods of time (decades)
 - (+) Can be collected from animals whose tissue have putrefied
 - (+) Can be stored at room temperature
 - (+) Very space efficient
 - (-) DNA yield is low sufficient for genotyping/sequencing methods that include an amplification step (e.g., microsatellites) but may not be suitable for next generation library preparation methods like RADseq. Matocq notes, however, that by designing an assay that includes a DNA enrichment step, it may be



- feasible to work with such material.
- (-) Processing of horn cores for DNA extraction is messy – higher risk of contamination

ii) Frozen tissue

- (+) High DNA and RNA yield provided tissue is fresh and preserved soon after collection
- (+) Relatively stable if stored at -80° C, although storage in liquid nitrogen (-196° C) reduces degradation of RNA and DNA over time
- (+) Provides insight into gene expression (functional genomics), not just gene sequence data
- (-) Susceptible to equipment failure, power outages, flooding, etc., requires access to freezers

iii) Tissue in ethanol

- (+) High DNA yield provided tissue is fresh and preserved soon after collection
- (+) Can be stored at room temperature
- (+) Stable over long periods of time (years)
- (-) Ethanol is highly flammable –
 Safety rules of your institution may require special permits or special conditions for storage
- (-) Stability is highly dependent on the seal quality of storage container – containers with gasketed caps are required for long-term storage. Ethanol in containers with snap on caps (e.g., 1.5 mL centrifuge

- tubes) will eventually evaporate.
- (-) Tissue with high moisture content can dilute the ethanol, making it less effective.

Answer II (Waits): Blood is a valuable source of DNA not mentioned above, particularly because many samples have been collected for disease work. It should be frozen or mixed with lysis buffer for long term storage. When mixed 1:4 with lysis buffer, it can be stored at room temperature for months. Answer III (Epps): We and many other groups have made extensive use of DNA from blood and feces (e.g., Wehausen et al. 2004, Luikart et al. 2008b, Luikart et al. 2011, Driscoll et al. 2015, Epps et al. 2018), and some use of RNA from blood or tissue:

i) DNA from feces can be archived for decades in Tris-EDTA buffer at -80C; I have amplified microsatellite markers from 15-year-old samples collected and stored in this manner. Feces appear to be a stable source of DNA for amplification (PCR)-based analyses for years if pellets are kept dry and dark and in a controlled environment, but Wehausen got no DNA from 15-year-old samples stored in a very dry environment. There is apparent degradation over time, so it is best to extract and store the DNA as soon as possible (within a few years) or freeze the samples. Currently, however, we cannot easily use this type of sample for some of the SNP-





- type analyses (e.g., RADseq), although we could presumably do targeted assessments of specific SNPs thought to be associated with important genes, or as part of a large assay panel (see above). As others have shown, the relative ease of obtaining fecal samples greatly augments our sampling options and can easily be adapted to citizen science projects, as long as they are carefully overseen.
- ii) Marjorie Matocq notes that another benefit of collecting fecal samples is that we can use high-throughput sequencing methods to gain insight into diet (Pompanon et al. 2012) and the gut microbial communities maintained by these animals (Kohl 2017). We are learning more and more about the role of the microbiome in nutrient acquisition and immunity (Alberdi et al. 2016), and Marjorie suggests that our group should advocate including inventory of diet and microbiome in our screens of population parameters. Understanding how diet and gut microbiomes vary spatially and temporally should become an important element of how we inventory these populations, especially in relation to translocations and changing food availability and plant chemistry that is

- anticipated with climate change.
- iii) DNA from blood has been a mainstay of work using samples collected during live capture of bighorn sheep. Whole blood in EDTA, frozen, can yield usable DNA for sequencing or microsatellite analyses, but we have had trouble getting sufficient yield for genomics approaches from this type of sample. We have had the best results from spinning down blood tubes shortly after capture, pipetting off the "buffy coat" (white blood cells), and freezing that.
- iv) RNA can be isolated from blood or tissue but requires special buffers and handling. RNA is used for studies of gene transcription and expression.
- v) Hair is often collected at captures, can serve as a source of good-quality DNA, and can also be used in isotope or hormone analysis. Hair has been used for "next generation" analyses (Russello et al. 2015), but DNA quantity is low. Thus, we do not usually recommend relying on hair for DNA work on captured animals, given that blood or tissue samples are easy to obtain in most cases.
- vi) Captures and necropsies also present opportunities for detecting DNA of pathogens. Collection and storage



- methods vary depending on disease and material available but may include swabs of nasal or pharyngeal cavities on live animals (respiratory pathogens) or sections of lung, bone marrow, or other tissue.
- vii) Consider splitting important samples (blood, extracted DNA, etc.) into multiple subsamples that are stored in different locations, as freezer failures and loss of material do occur periodically. As Texas Tech University has opened a new long-term storage facility for bighorn sheep DNA, this would be an excellent repository for backup samples and could facilitate collaborations or follow-up studies.
- viii) Finally, make sure associated data are or can be linked to samples: age, sex, locality, source stock or population history, reproductive status, data on disease at time of capture, etc.

Answer IV (Conway, Phillips): The Natural Sciences Research Laboratory (NSRL), housed within the Museum of Texas Tech University, has installed Liquid Nitrogen (LN) freezer storage specifically for bighorn sheep samples (tissue; blood; fecal; swabs; etc.) via funds from the Wild Sheep Foundation and The Texas Bighorn Society. This storage will provide the in-perpetuity archival of a variety of bighorn sheep samples supporting the range-wide Disease Management Venture, and the genomics-based research on bighorn

- sheep in Texas and range-wide. The NSRL is a research repository with the mission to archive biological samples and their associated data for scientists throughout the world; requests for samples and associated data can be made by national and international researchers. The Genetic Resources Collection (GRC) of the NSRL to date curates approximately 375,000 tissue samples from >100,000 individual specimens distributed worldwide. Currently, the bighorn sheep LN freezer contains samples from ~200 desert bighorn sheep in Texas from the last three years of disease sampling captures. Efforts to obtain samples from Idaho have recently been completed – although curation and database development for those samples has just been initiated. Curation of additional samples from previous bighorn sheep work in Texas is also underway, through collaborations with Texas Parks and Wildlife Department biologists and staff and private landowners.
- 4) What are the pros and cons of using the domestic sheep genome versus efforts to improve the wild sheep genome: should all jurisdictions help contribute to this effort, and which genomics lab is best suited to take it on if worthwhile? Answer I (Jahner): In our genotyping-bysequencing (RADseq) dataset ('California', desert, and Rocky Mountain bighorn sheep populations in Nevada), we were able to align a higher percentage of bighorn sheep reads (relatively short DNA sequences generated by "next-generation" sequencing platforms) to the domestic sheep genome than to the Rocky Mountain bighorn sheep genome.



Recent improvements to sequencing platforms that generate longer reads (e.g., PacBio) or enable improved scaffolding (basically, arranging sequences and gaps of known length, e.g. Chicago libraries, Hi-C) have made highly contiguous genome assemblies readily attainable even when no reference genome exists (e.g., Bredeson et al. 2016, Putnam et al. 2016). The latter methods mean that near chromosomal level assemblies can be generated de novo for most non-model organisms at a fraction of the cost and time that would be have been required just a few years ago. Improved genome assemblies for wild sheep, including for each recognized taxonomic lineage, will be important resources for improving inference from reduced-representation resources (e.g. higher density SNP chips) and eventually enabling whole-genome resequencing for understanding the genetics of adaptation.

Answer II (Sim): A draft genome of a Rocky Mountain bighorn sheep is available via Josh Miller, formerly of the Coltman Lab (Miller et al. 2015). As it stands now, almost all the genetic resources including microsatellites, SNPs, and genome have originated from or are heavily dependent on domestic sheep, so I am personally in favor developing some resources directly from wild sheep. Jahner et al.'s (In press) observation that their dataset aligned better to the domestic sheep genome than the Rocky Mountain bighorn sheep genome may be related to the fact that the Rocky Mountain bighorn sheep genome was assembled via alignment to the domestic sheep genome, so everything ends up looking like the domestic sheep. This perhaps

further speaks to the need for more genetic resources generated directly using wild sheep.

How has genetics informed wild sheep management?

5) How successful have agencies been in

implementing management decisions based on genetics research? Answer I (Cox): Obviously Sim's work on redefining Stone/Dall Sheep distribution (Sim et al. 2016) has been accepted by British Columbia, Yukon, and NWT. I think other jurisdictions would make the right decisions based on peer-reviewed sound science. In 2000, I was successful in using the Wehausen and Ramey II (2000) study that showed the entire Great Basin was a single bighorn subspecies of desert bighorn to help dispell the old myth, assumed by my agency and past biologists, that there were 3 subspecies of bighorn in Nevada (desert, 'California', Rocky Mountain). We greatly encouraged broader distribution of desert bighorn sheep translocations after that time; unfortunately, many introductions of 'California' and Rocky Mountain bighorn had already occurred. Answer II (Epps): The Sierra Nevada Bighorn Sheep program (California Dept. of Fish and Wildlife) has used John Wehausen's estimates of genetic diversity at population and individual levels to guide translocation and augmentation strategies. Connectivity analyses by Creech et al. (2014) that were based on landscape genetic analyses of bighorn sheep in the Mojave (Epps et al. 2007) have been used by the National Park Service and Bureau of Land Management to guide decision

making around renewable energy sites.



Oregon Department of Fish and Wildlife used genetic studies to explore the consequences of multiple founder effects and conduct experimental translocations (Whittaker et al. 2004, Olson et al. 2012).

Answer III (Waits): Frances Cassirer and Hollie Miyasaki from Idaho Department of Game and Fish (IDGF) have been using results from genetic analyses by the Waits research group to inform a variety of management decisions. For instance, the genetic connecivity analysis has been used to inform land management decisions by the Forest Service, and genetic structure has been used by IDGF to evaluate how bighorn sheep were grouped into population management units.

Questions about genetic diversity

6) For wild sheep managers forced to manage relatively small and isolated herds, are there, or can there be constructed, guidelines that outline what is adequate genetic diversity before herd performance is compromised?

Answer I (Cox): I think that those of us who are managers would love to have some simple guidelines and metrics we can collect, measure, and take action on to maintain a certain level of genetic diversity.

Answer II (Epps): I think there is much to be done. The SNP-type datasets should be helpful as they cover more of the genome, but diversity estimates vary depending on marker choice. SNP diversity correlates but is not directly comparable with estimates from microsatellites (e.g., Miller et al. 2014), and may be sensitive to choice of SNPs. We need measures of herd and

individual performance to link to the genetic data, and need to recognize that many other non-genetic factors will affect those variables as well, which will make it challenging but not impossible to establish relationships between genetic diversity and performance. Sim (below) argues that estimates of genetic diversity from 8-20 microsatellites may give little resolution with respect to herd performance: I agree that many more loci would do a lot to increase power, but also believe we have not yet had many chances to confront estimates of genetic diversity of any type with herd performance metrics over large datasets. Luckily, I think we are now poised to do some of that. Answer III (Sim): Unfortunately, there is no one magic number that genetics can give that says, for instance, "if heterozygosity > 0.6145 then performance will not be compromised". What you want to know is the extent to which genetic diversity is correlated with some measure or proxy of herd performance or fitness (fecundity, horn size, body weight, etc.). What exactly herd performance means will ultimately, I think, be up to the manager and likely influenced by other ecological factors. Without the corresponding data for herd performance, a single measure of diversity is probably not useful unless the values are extremely low [for reference, Epps notes that microsatellite-based estimates of expected heterozygosity < 0.5 characterize isolated populations established from small numbers of founders (e.g., Hedrick and Wehausen 2014), which are sometimes associated with poor population performance (e.g., Hogg et al. 2006)]. As well, the



traditional 8-20 microsatellite approach to genotyping likely cannot measure genome wide diversity precisely enough to be useful for comparisons of genetic diversity and herd performance (although there is discussion on this topic, see above). Hopefully, with the price of sequencing coming down, assays using tens/hundreds of thousands of SNPs will provide enough genomic coverage to give precise enough measures of diversity for this kind of comparison. Beyond the cost of sequencing, the post-sequencing processing of large SNP datasets need to be worked out before widespread adoption since most current methods are not very user friendly and require very steep learning curves. The field is moving fast though so there is great hope on this front.

Answer IV (Waits): I agree and would like to emphasize Sim's point above that the key to understanding these relationships is to have large datasets of phenotypic/morphological/fitness trait data from individuals linked to the genetic data. This is a key area where managers and geneticists can work together.

7) Given that we have little choice now but to manage most wild sheep populations as islands (perhaps linked by artificial migration), and most are much smaller in size than historically the case, what is the current best wisdom regarding levels of diversity, inbreeding, drift that can be tolerated before we do a disservice to our populations, and how do we figure it out? Perhaps these animals are adapted to lower levels of heterozygosity than we would initially be comfortable with...but we have also seen tantalizing hints that small, stagnant populations

are sometimes jump-started by infusions of new genetic material, suggesting that heterozygosity or specific **alleles** matter. Given that practitioners lack the resources to conduct genuine studies on any but a fraction of our populations, how do we learn more and make better decisions?

Answer I (Cox): As with the Disease Management Venture (an ongoing effort by agencies to share data on bighorn sheep performance and disease), we need to share data on genetic diversity levels and simple herd performance metrics and compare/contrast west-wide. This would allow us to see the spectrum of values and identify "breakpoints" on which we can agree, for example, identifying minimum values or triggers that would require management action, or provide managers with some confidence that herds are doing just fine without genetic "rescues" or intervention.

Answer II (Jahner): It is worth noting that translocations have been successfully used in the past to elevate genetic diversity in bighorn sheep populations (Hogg et al. 2006, Miller et al. 2012, Olson et al. 2012), but we still have much to learn about 1) what constitutes "low" genetic diversity in bighorn sheep, and 2) how levels of genetic diversity actually affect important population demographic parameters.

Answer III (Epps): I believe that we can learn lessons from some of the truly isolated herds, such as the Sespe population in southwestern California, in which we see some physical abnormalities. In more natural arrays of populations connected by occasional





dispersal, as long as there is occasional gene flow among populations, I doubt that genetic diversity will decline to point where we would see obvious inbreeding effects. The biggest management question probably occurs in systems like Oregon, where decades of sequential founder effects have apparently created populations with lower genetic diversity, albeit interlinked in most cases by occasional gene flow. Is it worth bringing in individuals from different source populations, as was done experimentally in Oregon (Olson et al. 2012;2013)? Careful studies of individual and population performance, with and without challenges such as disease, coupled with better characterization of genetic diversity (e.g., using many more markers than is usual in previous microsatellite-based studies), are needed and in some cases are underway.

8) Should managers be placing more emphasis in maintaining unique remnant herds that may be isolated with low genetic diversity but are performing well? How do you measure, quantify, or place a value on the importance of these remnant herds maintaining their uniqueness? Answer I (Cox): We had some of these unique herds detected from the UNR Genomics Lab (Matocq, Jahner, Parchman) recently. We certainly want to maintain these remnant herds and their genetic integrity and even use them as source stock to expand this important historic remnant in more areas in Nevada. So yes, westwide, such herds need to be identified and enhanced-- as long as geneticists feel that their low diversity does not

compromise their performance and is outweighed by their unique traits that may be better suited to the local environmental conditions. Answer II (Jahner): This is a complicated problem. Translocations have the potential to quickly eliminate any signatures of local adaptation within a population through gene flow, which would result in the loss of ecologically and evolutionarily important variation. However, genetically isolated or unique populations are not necessarily locally adapted, and perhaps could benefit from augmentations. Any metric that attempts to prioritize some herds over others for maintaining their uniqueness should ideally consider genetic, morphological, and ecological information, but this further complicates this endeavor. Answer III (Harris): How do we distinguish between uniqueness owing to adaptive evolution versus genetic drift? Conserving every uniquelyidentifiable genetic variant can increase extinction risk due to demographic and

et al. (2016).

Answer IV (Epps): Harris' concern above identifies a real risk in my opinion-statistical significance does not imply biological significance. We found the distinction between drift and local adaptation to be a challenging problem in our recent landscape genomic project looking for adaptive genetic variation associated with climate variation across the range of desert bighorn sheep (Buchalski et al. in prep). Our solution was to exert stringent criteria (e.g., markers identified by multiple methods) to avoid false positives due to isolation

genetic processes: take a look at Weeks





and drift, but this field of study is still in its infancy.

Questions about subspecies management

9) How do we manage 'California' vs.
Rocky Mountain bighorn populations
(formerly considered subspecies)? Can
we describe genetics of original remnant
'California' bighorn herds in BC,
compare them to the translocated
'California' bighorn herds, and provide
guidelines to managers on maintaining
or mixing the 2 lineages and the pros
and cons?

Answer I (Cox): Helen Schwantje is providing samples to Marjorie Matocq to get genetics of the remnant BC 'California' bighorn herds to compare to the rest of our introduced herds in lower 48. We just need a few geneticists to share values from all the introduced herds and develop guidelines through series of brainstorm sessions with subset of geneticists and managers.

Answer II (Schwantje): Additional work may be required to target sample the "original herds".

Answer III (Epps): I am definitely interested in working on this question as well, and have worked with ODFW and Ph.D. student Rob Spaan and ongoing research to sample many of the 'California' herds in Oregon. We are characterizing neutral genetic markers at this stage for other questions (we are in process of genotyping hundreds of samples at 15-20 microsatellite loci), but some of these samples would be suitable for SNPs etc. We plan to share data with Matocq's group and are interested in comparing data with Waits, Miyasaki, and others working in Idaho. John Wehausen, Mike Buchalski,

Rob Ramey, and I have been working on some phylogeography/phylogenetics of bighorn sheep; this work could be expanded.

Answer IV (Jahner): I am currently working on generating a nextgeneration sequencing dataset to evaluate the degree of differentiation between populations of Rocky Mountain and 'California' bighorn sheep in Nevada. However, the only way to truly answer to this question is to do a broad, range-wide genetic study of populations across the entire range of the two putative subspecies, preferably using remnant populations that have not been heavily influenced by translocations. Additionally, a phylogenetic study including all of the named varieties of wild sheep in North America could provide complementary insights the history of differentiation. Indeed, as we pointed out in Malaney et al. (2015), the only way to address this question is by sampling across an westto-east transect in the Canadian portion of the distribution. Our high level of differentiation within Nevada between 'California' and Rocky Mountain bighorn may be the result of genetically distinct groups in the native/northern range, which could manifest on the landscape as a fairly sharp transition between distinct genetic groups. Alternatively, Nevada's sheep could simply be the result of having sampled at the western end ('California' source herds) and at the eastern end (Rocky Mountain source herds) of an otherwise broad pattern of isolation by distance. Answer V (Waits): We have also genotyped ~100 individuals from British Columbia herds with 15 microsatellite loci and have a mixture of 'California'





- and Rocky Mountain genetic groups, so I think it would be useful to discuss results with other labs.
- 10) For jurisdictions that have known hybridization occurring among wild sheep subspecies, what information should we be collecting to describe the consequences, and how should managers treat new or potential occurrences of hybridization? Answer I (Cox): Nevada and Arizona both have desert/Rocky Mountain hybrids. We are collecting muscle tissue from every ram harvested in our Nevada desert/Rocky herd. I think we need to accept certain level of hybridization-but yes, we also need to collect data to monitor its progression and any adaptations we document. We have had discussions in the past on how best to deal with hybrid herds (promote or eliminate) and no agreement was made; each situation and set of circumstances is different.

Answer II (Waits): Based on our current results, British Columbia has California/Rocky Mountain bighorn hybrids.

Answer III (Schwantje): Some of those hybrid animals may have been translocated into US herds, again emphasizing the need for targeted sampling in British Columbia. Answer IV (Matocg): This is a point that will require close communication with the hunting community. I have presented our hybridization results directly to members of Nevada Bighorns Unlimited, and they were enthralled with the biology and natural history that these genetic patterns suggest. Understanding the genomic and phenotypic consequences of hybridization should be an important

- goal for our group, in addition to nonhybrid genotype-phenotype relationships in this system. Sportsmen/women seem to be as eager as we are to learn about these relationships.
- 11) Are managers on the right track by managing as separate taxa the various 'types' of bighorn sheep we currently recognize? We seem well past the days of depending on traditional taxonomy...do quantifiable differences at the molecular level signify adaptive differences that we had best not lose, or alternatively, signify drift (or worse yet, loss of alleles associated with small population size) that we would best attempt to counteract? Geneticists may not all agree about the relative risks of these two. So, what do we know now, and what do we need to learn to better figure it out?

Answer I (Epps): We are still working this out, but I feel we are in position to give good guidance in many areas of bighorn sheep range. Our recent SNPbased landscape genomics study (Buchalski et al. in prep) and other analyses (e.g., Buchalski et al. 2016) suggest long-term separation between some regional populations of bighorn sheep, including those now considered a single subspecies (e.g., "Peninsular" and "Mojave" populations of desert bighorn). In absence of other information, I think applying the precautionary principle to future translocations is wise- use the nearest source available, and try not to mix lineages- but check with the latest research about what "lineages" are supported!

12) How do we consider the above in relation to our questions about the



importance of genetic diversity and managing for same? In other words, when might we consider mixing individuals from more distantly related groups in cases where we think genetic diversity is extremely low and locallyappropriate stock for augmentation may not be available? Answer I (Cox): This concern by managers is becoming prevalent westwide. We do need help in deciding what best alternatives we have for mixing if diversity is low but when we do not have source animals that are well adapted to a particular mountain range and its climate, topography, forage base, and other conditions.

Answer II (Epps): I recommend being very cautious before considering augmentation from distantly-related populations to increase genetic diversity. Here are some considerations for this type of situation:

- Is the population performing well? If so, I would not be quick to intervene just because genetic diversity is low.
- Is the population performing poorly due to documented problems with disease, predation, or some other external cause? Genetic factors could play a role, as for disease, but probably are not the fundemental problem and thus unlikely to be a quick fix.
- I would be particularly reluctant to intervene in a native (or "remnant") population not originating from a translocation. Bringing in animals from other ecosystems raises the possibility of outbreeding depression (i.e., disrupting suites of genes acting

- in concert due to local adaptation).
- More obvious cases for intervention would be populations that are artificially isolated by translocation history or enclosures, and when phyical anomalies are observed.
- Systems of reintroduced populations that have suffered from sequential founder effects are probably the best place to learn from experimentation, as was done in Oregon (Olson et al. 2012).

Questions about disease

13) Who is doing what to investigate wild sheep genetics that control or influence immune response to virulent pathogens or similarly measuring animal resilience, resistance, or stress indicators? Should jurisdictions be collecting and contributing samples to this research? Answer I (Bowen): USGS (Bowen) and NDOW have been measuring molecular immune response, and response to environmental stressors. Additional samples from jurisdictions with distinct questions would be excellent. Note: we are at the very beginning of this line of research (i.e., it is not a crystal ball). Answer II (Waits): We recently published a paper that addressed this to some degree (Plowright et al. 2017) and plan to follow up with a GWAS study using our SNP data for the Lostine herd of Rocky Mountain bighorn sheep in Oregon.

Answer III (Epps): With collaborators at Oregon State University, California Department of Fish and Wildlife, and the National Park Service, as part of the study of respiratory disease in desert



bighorn in the Mojave National Preserve, we have collected data on Mycoplasma ovipneumoniae infection, genetic diversity at neutral and adaptive-linked microsatellite markers, and measures of immune phenotype to examine correlations among these measures. We are collecting similar data in 'California' bighorn populations in Oregon. Analyses are ongoing but we hope to submit a manuscript on the Mojave system soon. Recently we published a paper investigating differences in immune phenotype in Peninsular and Mojave bighorn sheep (Dugovich et al. 2017), in which we found higher levels of natural antibody in blood of bighorn sheep from the Peninsular Ranges compared to the Mojave. We also observed markedly greater ability of plasma from Peninsular bighorn sheep to kill E. coli bacteria in vitro compared to plasma from bighorn sheep in the Mojave. Those differences suggest that important geographical variation in immune response can exist.

14) What do we currently know about the genetic basis for (or genetic correlations with) susceptibility to, and response if infected by, pathogens leading to chronic pneumonia? If we do not know as much as we would like (which I suspect is true), what practical actions can we take to learn more? Answer I (Cox): We need to bring together a subset of geneticists and managers that have collected a great deal data already on pathogen profiles and herd responses and see if there is a logical next horizon to explore. This may include digging deeper into the animal genetics for susceptibility and recovery and maybe even setting up an

experiment of sorts to challenge animals, if we have candidate herds that have unique genetics or traits and past responses.

Answer II (Cassirer): I think it would be important to bring some immunological expertise to the discussion to identify specific genes or loci that we should be looking at for this particular disease. As far as that goes, I think we also need to know more about pneumonia, why bighorn sheep are so susceptible and what parts of the immune system are (likely) responsible for that. Answer III (Epps): We are seeing some interesting correlations between genetic measures, immune phenotype, and disease in the Mojave system, but this is work in progress and needs to go through peer review. Answer IV (Bowen): Our group is working with transcription of immunological genes. We have a long way to go and need input from all of you.

CONCLUSIONS

This exercise was intended to improve communication and facilitate collaboration among managers and researchers. Some concensus has appeared regarding important research directions: these include resolving taxonomy among lineages of wild sheep (particularly 'California' versus Rocky Mountain bighorn), research to inform managing isolated, remnant, or genetically depauperate populations, and the need to clarify the utility of specific data types to answer different questions, for instance via parallel analyses of microsatellites and SNPs, using SNPs on non-invasive samples, or evaluating ways to merge SNP datasets generated from different labs. The discussion of ongoing



research projects has already led to the realization that there are opportunities for better data sharing and collaboration.

Beyond the questions addressed above, the Wild Sheep Genomics Working group has considered procedural questions about the way forward. In particular: what efforts or standards need to be done or met to promote collaboration and comparing of wild sheep genomics west-wide to help answer many of the questions we have in common? Is there a need to develop a broad west-wide plan of data sharing for different genetics questions, and are there any geneticists willing to take on (with funding) the meta-analyses of west-wide datasets vs. each jurisdiction doing their own work? Finally, can we create a simple inventory list of current wild sheep genetics research in order to identify opportunities for collaboration or sharing of resources?

In the discussions associated with preparing this document, interest has been expressed that we should seek funding to draft a data sharing plan to encourage range (west)-wide analyses. An introduction to this idea was presented to the Wild Sheep Working Group at the Western Association of Fish and Wildlife Agencies (WAFWA) meeting in Eugene, OR in July 2018 (Epps, Cox). Matocq proposed that investing in the generation of a high quality bighorn genome would be an important next step. That, combined with the reduced representation (SNP) datasets already being generated range-wide will provide the needed information to generate a bighornspecific SNP array that captures the specific loci needed to address the breadth of questions that interest this group. She further proposed that we seek funds to pay for 1-2 Postdoctoral Scholars that rotate among the key labs involved in the effort so that approaches and analyses are

necessarily shared and consistent across labs. Finally, establishing a database of ongoing research projects was proposed to facilitate future collaborations. We expect that the Wild Sheep Genomic Working Group will continue to seek opportunities for discussing and developing these approaches.

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APENDIX 1: GLOSSARY OF TERMS USED IN GENETIC AND GENOMIC RESEARCH ON WILD SHEEP. Definitions denoted by a superscript 1 were adapted from Waits and Epps (2015).

Admixture: interbreeding of two or more previously distinct genetic lineages.

Allele: a variant at a gene or locus.

DNA sequence: a representation of the actual sequence of nucleotides in a molecule of DNA, rather than an estimate of fragment number or size (as in microsatellites or RFLPs).

Heterozygosity: the degree of genetic variation in individuals or populations, as measured at variable sites (loci or genes). To be comparable, heterozygosity estimates should incorporate the same or at least similar types of loci.

¹Gene flow: the movement of alleles between populations, also referred to as "migration" in the context of population genetics.

¹Genetic structure: spatial variation in the frequency or identity of alleles

Genome: the complete DNA sequence of an organism.

Genome-wide association study (GWAS): A research approach that assesses variation at a large number of variable markers, e.g., SNPs, across the genomes of a large number of individuals, and then tests for association of alleles with phenotypes or traits in the sampled individuals. This approach can help identify genes or

particular alleles associated with traits such as disease risk.

¹Hybridization: interbreeding of individuals from genetically distinct populations, subspecies, or species.

Landscape genomics: a research approach that attempts to identify signals of selection on variable genetic markers while controlling for genetic differences resulting from isolation, drift, and phylogeographic history. The approach can help identify genes or variants associated with different local adaptations, but has methodological challenges.

Locus (plural, loci): a variable site in the genome, i.e., one that differs among individuals included in a particular analysis.

Major histocompatibility complex (MHC): a group of genes that codes for proteins involved with acquired immunity; those proteins help the immune system identify foreign material. More genetic variation at these genes, in theory, increases the chance that a specific threat can be recognized and neutralized by the immune system.

Microsatellite: sometimes referred to as short tandem repeats (STRs) or simple sequence repeats (SSRs), this type of marker includes repeating sequences of two to six base pairs. Mutations resulting in different numbers of repeated elements at a particular locus are common, making these markers suitable for analyses where individual-level variation is useful.

-Adaptive-linked: a locus where the frequency of alleles may be affected by selection on a nearby gene.





-¹Neutral: a locus where the frequency of alleles is not affected by selection.

¹Mitochondrial DNA (mtDNA): a circular DNA molecule found in the mitochondria of cells; mtDNA is haploid (only one copy) and generally is inherited only from the mother.

Ovine SNP chip (array): an assay designed for assessing SNP variation in domestic sheep which has been applied to wild sheep, albeit only a subset of loci are variable (Miller et al. 2011). A newer version of the array provides more variable loci (Miller et al. 2018).

Phylogeography: the study of the spatial arrangement of genealogical lineages, especially within and among conspecific populations and closely related species (Avise 2000).

Restriction fragment length polymorphism (RFLP): a type of analysis in which DNA is cut using enzymes that recognize particular short sequences and the size of the resulting fragments is visualized; variation in sequence among individuals leads to different patterns of cutting and thus different sized fragments. Rarely used anymore.

Restriction site-associated DNA sequencing (RADseq): reduced representation sequencing method that sequences a subsample of genomic regions guided by the genomic location and frequency of restriction enzymes. Individual DNA samples are labeled by attaching DNA barcodes, allowing large number of individuals to be pooled and simultaneously sequenced on individual lanes of the Illumina platform. These methods have revolutionized population genetics and made population genomic scale data readily available for virtually any organism. Genotyping By Sequencing (GBS) is another name often used for the same type of method (see Andrews et al. 2016 for a thorough review).

Single Nucleotide Polymorphism (SNP): variation at a single base pair of DNA. Methods such as RADseq or SNP arrays can identify or assess variation at thousands of variable sites across the genome. While the information content of a single SNP locus is lower than that of a single microsatellite locus, SNP loci can be efficiently assessed in much larger numbers for some types of DNA samples (Dugovich et al. 2017).



Dall's Sheep Population Declines in Alaska's Chugach Range May be Related to Climate and Weather Patterns

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ABSTRACT: Dall's sheep populations in the Chugach range in Alaska have declined 30-50% since the late 1980s. Research in two study areas was initiated in 2009 and 2012 to identify rates and causes of mortality, assess nutritional condition, screen for disease, and check pregnancy rates on adult (age 3-17) ewes. Additional objectives were to quantify rates and causes of mortality on lambs from natality to one year of age. In the absence of baseline data, the project was designed to identify primary factors influencing sheep populations in Southcentral Alaska. With 134 and 183 sheep-years of data on adult sheep in the two study populations, annual adult survival was 87% in each population. Lamb survival was 57% and 32%, respectively. While these rates are very similar to that reported in other study populations, pregnancy rates in Chugach ewes are low and variable, ranging from 18-88% in one population, and 44-96% in the other. It appears likely that weather, climate, nutrition, and habitat play a far greater role in shaping the trajectories of these populations than does predation. Using a combination of nutritional condition measures, forage quality assessment, and remote sensing, current research efforts are focused on assessing changes in habitat quantity and quality due to changing weather and climatic conditions. We will discuss data that led to the current research direction, and present preliminary results that suggest that tree and shrubline advance has reduced available habitat, and that warmer, drier weather has reduced diet quality. Together, these pieces of evidence suggest that carrying capacity has declined to support sheep populations at present levels.

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KEYWORDS Dall's sheep; *Ovis dalli;* lamb survival; population dynamics; nutrition; climate; weather.





Projecting the effects of climate change on mountain goat population dynamics in Alaska

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ABSTRACT: Climate change represents a primary threat to species persistence and biodiversity at a global scale. Cold adapted alpine species, such as mountain goats (Oreamnos americanus), are especially sensitive to climate change and can offer key "early warning signs" about deleterious effects of predicted change. Among mountain ungulates, survival, a key determinant of demographic performance, may be influenced by future climate in complex, and possibly opposing ways. Demographic data collected from 447 mountain goats in 10 coastal Alaska, USA, populations over a 37 year time span indicated that survival is highest during low snowfall winters and cool summers. However, General Circulation Models (GCMs) predict future increase in summer temperature and decline in winter snowfall. To disentangle how these opposing climate-driven effects influence mountain goat populations, we developed an age-structured population model to project mountain goat population trajectories for 10 different GCM/emissions scenarios relevant for coastal Alaska. Projected increases in summer temperature had stronger negative effects on population trajectories than the positive demographic effects of reduced winter snowfall. In 5 of the 10 GCM/RCP scenarios, the net effect of projected climate change was extinction over a 70 year time window (2015–2085); smaller initial populations were more likely to go extinct faster than larger populations. Using a resource selection modeling approach, we determined that distributional shifts to higher elevation (i.e. "thermoneutral") summer range was unlikely to be a viable behavioral adaptation strategy; due to the conical shape of mountains, summer range was expected to decline by 17–86% for 7 of the 10 GCM/RCP scenarios. Projected declines of mountain goat populations are driven by climate-linked bottom-up mechanisms and may have wide ranging implications for alpine ecosystems. These analyses elucidate how projected climate change can negatively alter population dynamics of a sentinel alpine species and provide insight into how demographic modeling can be used to assess risk to species persistence.

Biennial Symposium of the Northern Wild Sheep and Goat Council 21:77; 2018

KEYWORDS Mountain goats; *Oreamnos americanus*; alpine ecosystems; climate change; conservation; general circulation models; habitat change; population modeling; resource selection function; Alaska.



The Influence of Early Reproductive Success on Longevity and Late Reproductive Success in an Alpine Ungulate

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ABSTRACT: The life-history theories of aging predict lifetime trade-offs between early reproductive allocation and late-life survival, reproduction, or both components of fitness. Recent studies in wild populations have found evidence for these early-late life trade-offs, but rarely across multiple traits while exploring the additional effects of variation in environmental conditions and individual quality. Benefiting from longitudinal data on adult female mountain goats (Oreamnos americanus), we investigated the influence of age at first reproduction (AFR) and early reproductive success (ERS) on longevity, late reproductive success, and senescence rates, while accounting for the influence of natal environmental conditions and individual quality. Contrary to predictions, we did not find evidence for early-late life trade-offs. Instead, an earlier AFR and a greater ERS had positive but weak direct effects on late reproductive success. Natal population density, however, was the strongest determinant of all life-history traits, having a direct negative effect on female longevity, late reproductive success, AFR, and ERS. Although natal density reduced the probability of annual reproduction and annual survival during adulthood, higher allocation to reproduction in early life and poorer natal conditions did not lead to accelerated rates of senescence during adulthood. The results of this investigation provide an integrated picture of early-late life trade-offs, underscoring the importance of accounting for environmental conditions due to their potentially strong implications for population dynamics.

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KEYWORDS Mountain goats; *Oreamnos americanus*; natal population density; reproductive success; Alberta; Canada.



Ecotypic Variation in Population Dynamics of Reintroduced Bighorn Sheep

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ABSTRACT: Selection of bighorn sheep (*Ovis canadensis*) for translocation historically has been motivated by preservation of subspecific purity rather than by adaptation of source stocks to similar environments. Our objective was to estimate cause-specific, annual, and age-specific mortality of introduced bighorn sheep that originated at low elevations in southern British Columbia, Canada (BC ecotype), or in the Missouri River Breaks region of central Montana, USA (MT ecotype). In North Dakota, USA, mortality was similar and typically low for adult female bighorn sheep from MT (0.09 \pm 0.029 [SE]) and BC (0.08 \pm 0.017) during 2000-2016. Median life expectancy was 11 years for females that reached adulthood (2 yrs old); however, mortality accelerated with age and reached 86% by age 16. Mortalities resulted primarily from low rates of predation, disease, accidents, and unknown natural causes (<0.04 [upper 90% confidence limit]). Similar survival rates of female bighorn sheep from BC and MT, coupled with greater recruitment of bighorn sheep from MT, resulted in a greater projected rate of increase for the MT ecotype ($\lambda = 1.21$) than for the BC ecotype (1.02), and a more youthful age structure. These results support translocation of bighorn sheep from areas that are environmentally similar to areas that will be stocked. Potential benefits include more rapid population growth, greater resilience to and more rapid recovery from density-independent losses, an increased possibility that rapidly growing populations will expand into adjacent habitat, increased hunter opportunity, increased connectivity among herds, and a more complete restoration of ecosystem processes.

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KEYWORDS Bighorn sheep; *Ovis canadensis*; restoration; translocation source herds; ecotypic variation; population dynamics; North Dakota.





Contrasting Native and Introduced Mountain Goat Populations in Montana

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ABSTRACT Mountain goat (*Oreamnos americanus*) distributions in Montana include historic, native ranges as well as mountainous areas into which mountain goats have expanded from introductions to non-native habitat. We synthesized population survey and harvest data collected by Montana Fish, Wildlife and Parks (MFWP) during 1960-2015 and received responses from 18 MFWP biologists to a questionnaire regarding status, trends, and management of mountain goats across the state. In 2016 an estimated 3,685 mountain goats were managed by MFWP, 2,526 (69%) in introduced populations, and 1,159 (31%) in native populations. Compared with population estimates from the 1940s, numbers of mountain goats in native ranges (outside national parks) were currently 3-4 times fewer than the 4,100 native mountain goats estimated then. Responses by MFWP biologists supported this decline of native mountain goats and highlighted a current pattern of many small and isolated mountain goat populations. Furthermore, both hunting licenses issued for and annual harvests of native populations have declined nearly 10-fold from the 1960s to present. To the contrary, mountain goat numbers in introduced populations have generally increased and provided 84% of Montana's hunting opportunity in 2015. Biologists identified a wide range of management and research actions that would benefit management and conservation of mountain goats. These included: 1) evaluation of statistical power associated with various monitoring protocols, 2) continued maintenance of centralized databases, 3) design of monitoring approaches for longterm consistency, 4) potential development of a statewide species management plan, and 5) research into habitat factors, population dynamics, and causes of mortality of mountain goats.

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KEY WORDS Mountain goat, *Oreamnos americanus*, population, status, survey, trends.

Among North American ungulates, mountain goats (*Oreamnos americanus*) present many challenges for wildlife management and conservation. They live in remote and harsh environments where traditional monitoring techniques are challenging (Gonzalez-Voyer et al. 2001); they often occur in small isolated populations which are more difficult to monitor and face increased risk of

extirpation (Fagan and Holmes 2006); and they exhibit life history characteristics that make them particularly susceptible to overharvest and slow to recover from population declines (Gonzalez-Voyer et al. 2003, Hamel et al. 2006, Toweill et al. 2004, Festa-Bianchet and Côté 2008). Potentially as a result of some of these challenges, mountain goats have suffered recent population declines across much of the



southern portion of the species' native range over the past 50-70 years (Côté and Festa-Bianchet 2003, Festa-Bianchet and Côté 2008, Smith 2014). For example, mountain goat populations in British Columbia have declined by half from an estimated 100,000 in 1960 to 39,000-63,000 in 2010 (Mountain Goat Management Team 2010). Abundance of mountain goats in Washington has declined by 60 percent since 1950 (Rice and Gay 2010). Due to concerns about declines in Alberta, wildlife officials closed the entire province to mountain goat hunting in 1987; only in 2001 were conservative harvest guotas reinstated there (Hamel et al. 2006).

In Montana, the status of mountain goats is complicated. The western portion of the state supports native populations. To the east, additional populations were established by translocating mountain goats into prehistorically unoccupied habitat (Figure 1). License numbers to hunt native mountain goats have generally been reduced over the past three or four decades in response to population declines in some areas. Carlsen and Erickson (2008) concluded, "The decline in mountain goat populations is alarming and deserves investigation by [MFWP]. When goat populations decline, it appears they don't recover." Contrary to the decline of Montana's native mountain goats, substantial increases have been observed in some introduced populations (Williams 1999, Lemke 2004, Flesch et al. 2016). The transplanting of mountain goats into southwestern and central Montana began over 70 years ago. From 1941 to 2008, 495 animals were transplanted to 27 different sites, with some ranges receiving multiple introductions (Picton and Lonner 2008). Introduced herds in some locations have grown in both numbers and geographic

range, while other introductions appeared to have failed, whether immediately or after a period of time. Carlsen and Erickson (2008) reported that the statewide total mountain goat harvest has been relatively stable over the past 30 years, yet this summary may mask markedly different trends occurring among native and introduced populations.

Montana has a rich history of research into the biology, ecology, and conservation requirements of mountain goats, beginning with the work of Casebeer et al. (1950). Studies during the 1970s and '80s provided the most comprehensive biological information on Montana's native mountain goat populations (Chadwick 1973, Rideout 1974, Smith 1976, Thompson 1980, Joslin 1986). Several studies in the Crazy Mountains provided information on that introduced population's ecology and growth during the 1950s and 1960s (Lentfer 1955, Saunders 1955, Foss 1962). Changes in numbers and distributions of other introduced populations were closely monitored in recent years by MFWP (Swenson 1985, Williams 1999, Lemke 2004). Most recently, Flesch et al. (2016) described range expansion and population growth of introduced mountain goats in the Greater Yellowstone Area.

The aim of this study was to compile and synthesize mountain goat harvest and population information at a statewide scale across Montana during 1960–2015, with particular attention to comparing and contrasting dynamics of native and introduced mountain goat populations. We also developed and distributed an expert-opinion questionnaire to solicit the insights and opinions of MFWP personnel (area biologists and/or regional wildlife managers whose jurisdictions include mountain goats) regarding population



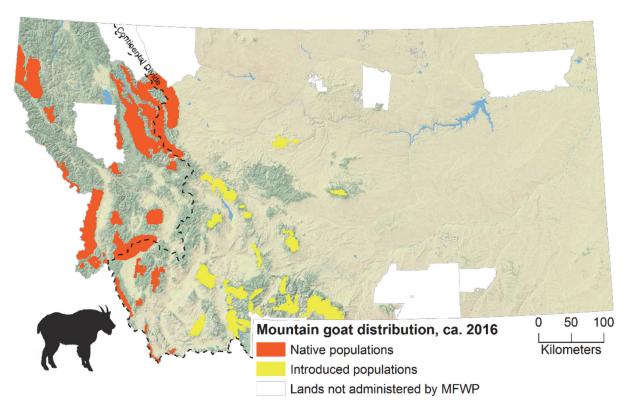


Figure 1. Distribution of extant native and introduced populations of mountain goats in Montana, 2016.

trends, limiting factors, monitoring practices, and future research and management needs. Summarized results from this survey of MFWP biologists represent the current state of knowledge about Montana's mountain goats, with potential to guide future research, monitoring, and planning efforts aimed at filling information gaps and sustaining or enhancing mountain goat populations and hunting opportunity.

STUDY AREA

Our study was in Montana, USA, during 1960–2015. Montana is 380,832 km² in area and ranges in elevation from 555–3,904 m. The western portion of the state consists predominately of a portion of the Rocky Mountains, whereas the eastern portion includes smaller island mountain ranges surrounded by large expanses of

prairie-badlands and prairie-agricultural lands mixed with timbered river drainages. January temperatures average -12° to -6°C and July temperatures average 18° to 23°C. Precipitation varies widely depending on location and elevation, with average annual precipitation ranging from 17–88 cm/year. Large mammal carnivore species sympatric with mountain goats in all or portions of the state during all or portions of the study period included mountain lions (Puma concolor), wolves (Canis lupus), black bears (Ursus americanus), grizzly bears (Ursus arctos), and wolverine (Gulo gulo). Ungulate species present on the landscape included bighorn sheep (Ovis canadensis), elk (Cervus canadensis), deer (Odocoileus spp.), and moose (Alces alces).





METHODS

Data collection

We began this project by compiling and digitizing as much historical data as we could find regarding mountain goat harvest and population monitoring. Data were retrieved from a range of sources including department-wide online databases, electronic files provided for local areas by MFWP biologists, and from paper copies of historic survey and inventory reports housed within library archives of 5 different MFWP offices. After compiling data into a single database, we sent data subsets to each area biologist for them to review and rectify with local records.

Hunter harvest. — During the early portion of the study period, 1960–1987, mountain goat harvest was monitored with a paper questionnaire mailed to all license-holders. A correction was applied to harvest estimates to account for imperfect response rates. During 1988–2004, mountain goat harvest was estimated using a mix of both phone calls and mail surveys in a continued attempt to reach all licenseholders, and since 2005 phone calls have been used exclusively. Response rates for mountain goat surveys are typically high (>90% annually), and corrections of estimates for imperfect response rates during the entire study period assumed that the relatively small proportion of nonrespondents were missing at random from the sample (Lohr 2009). Information on the sex, age, and horn measurements for harvested mountain goats was also available via a separate data stream provided by the mandatory checking of such, which was instituted in 1983 and continued to the present. In total, the compilation of mountain goat harvest data

spanned 69 hunting districts (HDs) and 56 years, for a total of 2,229 district-years of data concerning quantities of licenses issued, total numbers of mountain goats harvested, and numbers harvested according to sex.

Due to the challenge of accurately identifying the sex of mountain goats in field settings, MFWP exclusively offered either-sex licenses during this study period that allowed hunters to legally harvest either a male or female. Harvest of male mountain goats is typically the goal for both wildlife managers (e.g., to harvest animals with lower reproductive value) and for hunters (e.g., to harvest animals with larger trophy scores). To support this goal, MFWP currently offers information and videos on their website as a voluntary educational opportunity for hunters.

Population trend surveys. —Population survey data presented challenges to compile because they were not necessarily collected or summarized in a consistent manner across the state and over time. In fact, our questionnaire to MFWP biologists (described below) revealed many differences in the manner with which mountain goat population surveys were conducted, which we will describe here. Survey platforms have included a combination of rotary and fixed-wing aircraft as well as ground surveys. The timing of surveys varies widely by jurisdiction, with 25% of aerial surveys conducted during winter or early spring, 21% during mid-summer, 33% during late summer, and 21% during fall. The frequency of surveys ranged from annually (28%), to every other (19%) or every few years (19%), to "rare" (33%) among HDs. Survey results provide a minimum count and age ratios specific to various times of





year. Count data are not sightabilty-corrected population estimates but instead are treated as minimum counts for monitoring of population trend (Humbert et al. 2009). In total, we compiled >700 individual mountain goat population surveys spanning 1960–2016.

Data analysis

Hunter harvest. —We used descriptive plots and statistics to characterize trends in mountain goat hunter harvest data across the study period. These included summaries of the availability of licenses, total harvest, hunter success rates (total harvest/licenses issued), and sex ratio of harvested mountain goats. We also compared summaries of each of these statistics to assess differences in native vs. introduced populations. We used a t-test to compare the proportional harvest of females among native and introduced populations and used linear regression of this proportion over time to assess the potential for a trend during the study period.

To compare harvest data among regional populations, we grouped 69 different mountain goat HDs that have been designated during various portions of the period 1960-2015 into 28 regional "population units" (Table 1). The area and number of animals encompassed by each population unit were not consistent because we attempted to delineate populations according to biologically meaningful topographic or ecological boundaries. These groupings included 14 native population units and 14 introduced population units. We estimated the 2015 harvest rates of mountain goats by combining hunter harvest data presented here with population estimates developed

below via questionnaires to FWP area biologists (described below). Specifically, we estimated the "harvest rate" as the estimated total harvest of mountain goats in 2015 divided by the estimated population size. We estimated the "license rate" as the number of licenses issued in 2015 divided by the estimated population size of mountain goats within a given population unit. Because population estimates used in the derivation of harvest rates came from expert opinion questionnaire rather than repeatable statistical population estimation procedures, these harvest rates have important and unknown degrees of accuracy and precision.

Population trend surveys. —Population trends from aerial survey data spanning our full study period of 1960–2015 were difficult to interpret primarily because the frequency and locality of surveys were not consistent enough to meet the assumptions of an analysis of trend (Harris 1986). Thus, we focused our analysis on recent survey data collected during the 21st century (2000–2015) and identified 52 survey areas (typically HDs) with at least one survey during this period, for a total of 171 surveys.

To estimate annual population growth rates, λ , from survey count data, we used exponential growth state-space models developed by Humbert et al. (2009). These models have been shown to more rigorously measure uncertainty surrounding estimates of trend by accounting for process variance (i.e., biological variation) in annual growth rates as well as observation error that induces additional sampling noise around annual count data. Flesch et al. (2016) also used these methods in a recent analysis of mountain goat population trends from survey count data in the Greater





Table 1. Population estimates (from expert opinion), hunting licenses offered, total harvest, and estimated license rate (licenses/population size) and harvest rate (harvest/population size) of mountain goats among regional populations in Montana, 2015.

Regional population	Population estimate (Range)	Licenses	Total harvest	License rate	Harvest rate	
Cabinet	135 (125-155)	8	7	5.9%	5.2%	
Bob Marshall	360 (322-367)	13	10	3.6%	2.8%	
Mission	17 (16-18)	2	0	11.8%	0%	
Whitefish (extirpated)	0	0	0			
Anaconda it Blackfoot Flint Creek Great Burn	20 (0-40)	0	0	0%	0%	
E Blackfoot	40 (20-55)	0	0	0%	0%	
ੋ Flint Creek	25 (0-70)	0	0	0%	0%	
SGreat Burn	23 (20-25)	0	0	0%	0%	
Nest Bitterroot Eapphire	100 (80-120)	2	1	2.0%	1.0%	
ਲੂ Sapphire	10 (0-40)	0	0	0%	0%	
West Fork	30 (10-100)	0	0	0%	0%	
Beaverhead	51 (36-66)	0	0	0%	0%	
Pioneer	125 (75-150)	9	3	7.2%	2.4%	
East Front	223 (165-315)	5	4	2.2%	1.8%	
Absaroka	470 (355-538)	58	38	12.3%	8.0%	
Bridger	78 (56-98)	5	4	6.4%	5.1%	
Crazy	450 (330-550)	50	42	11.1%	9.4%	
ဋ Elkhorn	20 (9-30)	0	0	0%	0%	
Elkhorn Highland Madison	250 (140-275)	30	28	12.0%	11.2%	
ਜ਼ਿੱ Highland	10 (10-15)	0	0	0%	0%	
്റ് Madison	617 (447-760)	24	19	3.9%	3.1%	
ក្ល Sleeping Giant	0 (0-1)	0	0	0%	0%	
<u>ട്ട്</u> Snowcrest	48 (22-48)	3	3	6.3%	6.3%	
2 Tobacco Root	27 (11-44)	3	3	11.1%	11.1%	
Sleeping Giant Snowcrest Tobacco Root Big Belt	105 (81-130)	2	1	1.9%	1.0%	
Square Butte-Highwood	105 (90-135)	6	5	5.7%	4.8%	
Big Snowy	1 (1-2)	0	0	0%	0%	
Beartooth	345 (290-422)	21	12	6.1%	3.5%	

Yellowstone Area. Our analysis includes some of the same HDs as those studied by Flesch et al. (2016), although we focus only on a recent time period, 2000–2016. This

statistical approach has been shown to perform well with a minimum of 5 data points spanning a ten-year survey period (Humbert et al. 2009, Flesch et al. 2016). For our analyses we identified a set of 21





survey areas for which at least 5 surveys were conducted during unique years of a 16-year period. After estimating trends and statistical uncertainty for each area, we used linear-log regression to test for a curvilinear relationship between the standard errors of growth rate estimates and the respective average number of individuals counted in each area.

Expert opinion questionnaire

We developed an original, standardized questionnaire for completion by MFWP area biologists. We emailed this 25question survey to eighteen MFWP biologists in Regions 1–5 who have management responsibility for currently delineated mountain goat HDs. Responses were compiled and summarized separately for native and introduced mountain goat HDs. We treated HDs as population sample units for summarizing results, because population surveys are typically conducted on a HD basis. Populations not currently within an administrative HD were included as independent samples. For a subset of questions, we asked respondents to rank a set of possible answers by their relative importance within each HD. In these cases, respondents were free to select and rank as many or as few options as were applicable, with their top choice receiving at rank of 1. We summarized answers to these questions in 2 ways: 1) first we recorded the number of times (the count) a given answer was selected, and 2) we scored rankings in reverse order such that ranks of 1 received the most points. For example, in a question with 7 possible answers, a ranking of 1 received a score of 7, a ranking of 2 received a score of 6, and so on. Scores were then summed for each possible answer across all responses.

With our first question (Question 1), we asked biologists to provide population estimates for a total of 58 population units, including 26 HDs with native populations, 26 HDs with introduced populations, and 6 populations (4 native and 2 introduced) not currently within an HD. These were not statistical estimates, but expert opinion estimates derived from the best available information, including aerial and ground surveys, knowledge of sightability corrections from populations elsewhere (Cichowski et al. 1994, Gonzalez-Voyer et al. 2001), and professional judgment. We also asked biologists to provide a "range of confidence" surrounding each population estimate, which was not a statistical confidence interval but rather a "best guess" at the range of possible values of true abundance. When pooling estimates for summary purposes across multiple HDs, we used the sum of point estimates, low range of confidence boundaries, and high range of confidence boundaries to characterize total estimates and range of confidence boundaries for the pooled area.

The second suite of questions (Questions 2-8) concerned biologists' impressions of the historic (1960-2010) and current (2010–2015) status of each population (per HD) and the relative roles of various potential limiting factors during each time period. The third suite of questions (Questions 9-16) were focused on the goals and means with which biologists set harvest quotas. This section also included questions about biologists' perceptions of the interest and ability of hunters to correctly identify the sex of targeted mountain goats in the field. The fourth suite of questions (Questions 17–19) concerned the methodology (e.g., aircraft platform, time of year, and frequency) used to conduct population trend counts. Next



we asked questions about habitat concerns specific to mountain goat populations (Question 20–21), interest in translocation as a management tool (Question 22), and the most pressing management and research needs (Question 23–25). Details concerning this questionnaire and biologist responses beyond what is presented here are available in an unpublished report (Smith and DeCesare 2017; found online at: http://fwp.mt.gov/fwpDoc.html?id=81144).

RESULTS

Hunter harvest

The availability of hunting licenses during 1960-2015 peaked in 1963 at 1,371 licenses, primarily for hunting of native populations (Figure 2a). Unlimited licenses were available for several native populations at the beginning of the study period in 1960, although regulations for these HDs were gradually switched to limited, draw-based licensing during the subsequent decade. The last unlimited hunting occurred in 1971 in a portion of the Bob Marshall Wilderness, after which only limited licenses were offered in all HDs. In 2015, 16,643 hunters applied to the lottery for 241 mountain goat licenses, with a 1.4% chance of successfully drawing.

Mirroring trends in license availability, total harvest of mountain goats was highest during the early 1960s, peaking at 513 animals in 1963. By the late 1970s and throughout the 1980s, total harvest became somewhat stable, averaging 216 (range 170–242) mountain goats per year during 1977–1989. Similar harvests have been achieved since, including during the 1990s (mean=212, range=197–228), the 2000s (mean=221, range=184–250), and most recently 2010–2015 (mean=198, range=174–214). Less visible during this 40-

year period of stability in total harvest has been a dramatic shift in harvest from native to introduced populations. In the early 1960s, 87–88% of harvested animals were from native populations, averaging 377 native mountain goats harvested per year compared to 55 introduced mountain goats. Since that time, the proportionate harvest of native mountain goats has declined substantially as a result of both reduced licenses in native populations and increased licenses in introduced populations. In 2015, 25 mountain goats were harvested from native ranges compared to 155 from introduced ranges.

The success rates of hunters, measured as kills per license sold, were lowest during the beginning of this study period, averaging 34% for native populations and 41% for introduced populations during the 1960s (Figure 2b). During subsequent decades, as licenses were reduced in native ranges and increased in introduced ranges, success rates for both increased. Throughout this period, hunter success in introduced range has remained consistently higher than in native range. Thus far during the 21st century (2000-2015), success rates have averaged 65% for hunters of native populations and 74% for hunters of introduced populations.

There was no statistical difference in proportionate harvest of females among native and introduced populations (t_{110} =0.543, P=0.588; Figure 3). A decreasing trend in the annual proportion of females in the harvest was evident among both native (θ =-0.002, P=0.001) and introduced (θ =-0.002, P=0.001) subsets of the statewide harvest, showing an average decrease of 0.2% per year (Figure 3). For example, an average of 42.2% of the annual harvest was females during the 1960s





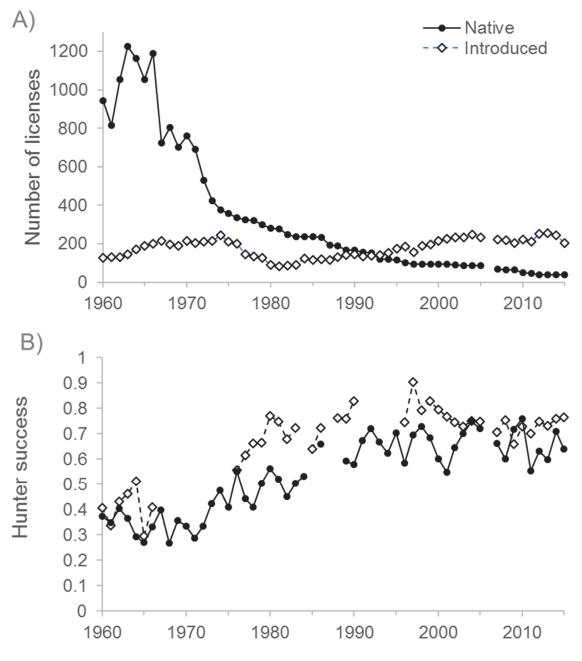


Figure 2. Trends in A) the availability of hunting licenses and B) hunter success rates (kills per license) for native and introduced populations of mountain goats in Montana, 1960–2015.



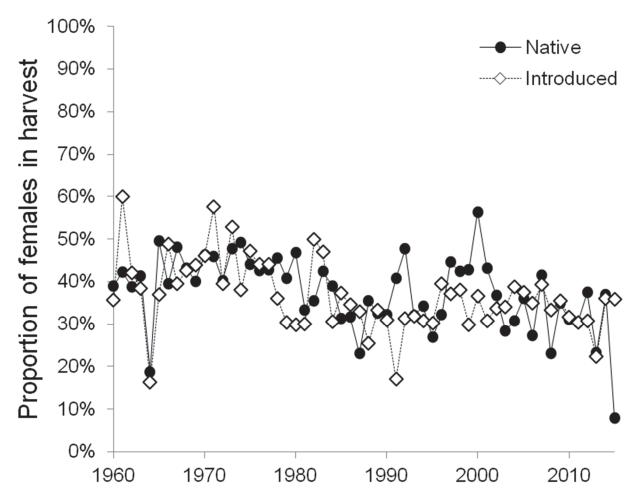


Figure 3. Proportion of females within the annual harvest of mountain goats, among native and introduced populations, in Montana, 1960–2015

(excluding an outlier value of 18% from 1964), while an average of 30.7% of the harvest was females during 2010–2015.

Among 13 extant native regional population units (groups of HDs), 7 were closed to hunting and 6 provided hunting opportunity in 2015. The average license rate (using population estimates derived from expert opinion questionnaires) among the hunted native population units was 5.5%, and the harvest rate averaged 2.0% (Table 1). Among the 14 introduced population units, 4 were closed to hunting and 10 provided hunting opportunity in 2015. The average license rate among the

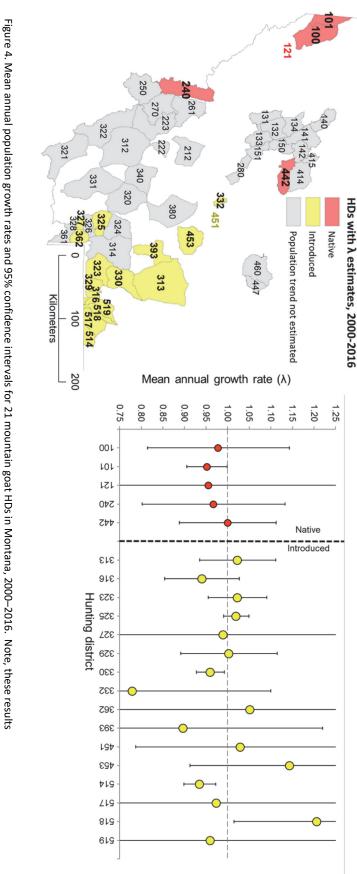
hunted introduced population units was 7.7%, and the harvest rate averaged 6.3% (Table 1).

Population trend surveys

We estimated survey-based population growth rates for 5 native HDs and 16 introduced HDs during 2000–2015 (Figure 4). For native HDs, point estimates of λ were <1 for 4 of 5 populations. However, 95% confidence intervals of λ overlapped 1.0 for all native HDs except HD 101, West Cabinet Mountains where λ was significantly <1.0. Among introduced HDs, point estimates of λ were <1.0 for half (8 of







include 2 former HDs (121, 451) that have since been closed and thus are not represented with polygon boundaries. Figure 4. Mean annual population growth rates and 95% confidence intervals for 21 mountain goat HDs in Montana, 2000–2016. Note, these results



16) of populations and >1.0 for the other half. Confidence intervals of λ overlapped 1.0 for 14 of 16 introduced HDs, while confidence intervals for the remaining 2 (HD 330, North Absaroka, and HD 514, Line Creek) indicated estimates of λ that were significantly <1.0. Given the wide confidence intervals surrounding most estimates of λ , little can be said with statistical certainty about trends in survey data for many of these mountain goat HDs using survey data alone. Linear-log regression of the standard errors of λ estimates relative to the log (number of individuals counted per survey area) suggested a negative relationship between the magnitude of counts and the subsequent estimate's standard error (θ =-0.034, *P*=0.021; Figure 5). Thus, statistically rigorous estimates of trends are more

difficult to attain under survey conditions of small populations and infrequent surveys.

Among all mountain goat survey areas (including HDs as well as populations outside of HD boundaries) with at least one survey during 2000–2015, the average count was 39 animals. For the subset of 21 survey areas with >5 surveys the average count was 56 animals. When comparing the standard error of estimates of lambda by the magnitude of these counts per area, it appears that there is potential for a high amount of uncertainty (i.e., SE estimates >0.05 would lead to confidence intervals >0.2 units wide surrounding λ) when the average number of mountain goats counted is <100 animals. This would apply to 48 of all 52 survey areas flown during 2000–2015, unless surveys were designed such that data could be pooled among multiple

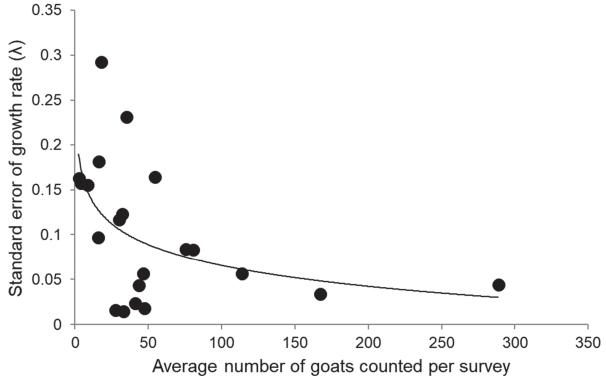


Figure 5. Standard error of mountain goat population growth rate estimates as a function of the average number of individuals counted during trend surveys in 21 survey areas across Montana, 2000–2015. The fitted line was derived from a linear-log regression showing a significant negative effect of log (mean number counted) on the resulting standard error.





survey areas prior to interpretation. However, a formal power analysis of simulated mountain goat survey data would provide an improved depiction of the precision of trend estimates under various scenarios of monitoring goats with aerial surveys.

Expert opinion questionnaire

Population estimates. —According to results from this questionnaire, the estimated total population (and range of confidence) of mountain goats in 2016 in native populations was 1,159 (885–1,537), and in introduced populations was 2,526 mountain goats (1,842-2,958). The combined statewide population (excluding the 2 national parks) was 3,685 (2,727-4,495). An additional 2,000 (1,700-2,300) mountain goats are estimated to live in native populations within Glacier National Park (Belt and Krausman 2012, J. Belt pers. comm.), and 225 (200-250) mountain goats from introduced populations inhabiting northern Yellowstone National Park, either year-round or seasonally (Flesch et al. 2016). Including animals within national parks yields statewide estimates of 3,159 native mountain goats and 2,751 introduced mountain goats totaling 5,910 in all.

Trends and limiting factors. —Area biologists estimated that 77% (23 of 30) of native mountain goat HDs have declined between 1960 and 2010, including 1 extirpated population. An additional 13% (4 of 30) were judged to be stable and 10% (3 of 30) had uncertain trends over this period. For introduced HDs, biologists estimated that 43% (12 of 28) declined during this 50-year period, 11% (3 of 28) remained stable, 43% (12 of 28) increased, and trend for the

remaining HD was uncertain. The most commonly cited factors limiting mountain goat numbers over this historic period of 1960–2010 were total hunter harvest followed by unknown reasons, harvest of female mountain goats, habitat changes, and predation (Table 2). That ranking was very similar for both native and introduced populations of mountain goats, with ORV/snowmobile use a concern in several HDs of native mountain goats, and predation a greater concern for introduced populations. Several respondents noted a high degree of uncertainty surrounding declines in native mountain goat populations, sometimes as a consequence of insufficient population data needed to assess changes.

With regards to the more recent period of 2010–2015, biologists responded that 75% of native HDs declined during this time or their status was uncertain; whereas 75% of introduced HDs were judged to be stable or increasing, with the remainder judged as declining or of uncertain trend. The most commonly cited factors currently limiting mountain goat numbers were habitat changes, followed by harvest of female mountain goats, total mountain goat harvest, predation, small population risks, and ORV/snowmobile disturbance (Table 3). There were marked differences between perceived factors limiting contemporary mountain goats in native versus introduced HDs. For introduced HDs, predation, harvest of females, total harvest, and habitat changes ranked similarly as most important. For native mountain goats, habitat changes were most important, followed by small population risks, ORV/snowmobile disturbance, and climate change concerns. Regarding native mountain goat populations, several biologists noted that the cumulative effects





Table 2. Relative importance of factors limiting mountain goat populations historically (1960–2010) in 29 native and 27 introduced HDs (as well as local populations outside of HD boundaries) in Montana. Count data indicate the number of populations to which a limiting factor applies. Weighted scores reflect both the number of populations to which a factor applies and the relative rankings of that factor among others selected.

		Disease	Predation	Hunter harvest (total # animals)	Hunter harvest (proportion of females)	Habitat changes (non-anthropogenic)	ORV/Snowmobile disturbance	Energy exploration	Logging and/or road construction	Non-motorized recreation	Climate change	Small population risks (inbreeding,)	Other (describe in Q4)	Unknown
Native	Count	7	10	21	10	17	14			3	10	9		21
	Weighted score	23	49	126	70	78	79			15	13	52		123
Introduced	Count	4	12	11	10	10				1		4	5	8
	Weighted score	14	63	56	54	43				3		23	30	54
Total	Count	11	22	32	20	27	14			4	10	13	5	29
	Weighted score	37	112	182	124	121	79			18	33	75	30	177

of specific factors may be perpetuating suppression of mountain goat numbers that may have begun prior to 2010. Regarding introduced populations, biologists raised concerns about suspected predation on mountain goats as well as the need for careful monitoring of harvest rates and potential overuse of available range by mountain goats.

Harvest management. —In response to a question about the goals of harvest management, biologists managing native populations took an almost unanimously conservative approach to harvest, with the goal of minimizing impact on populations in 94% of HDs. To the contrary, biologists managing introduced populations had more varied objectives, including the goal of minimizing impact in 42% of HDs but also

goals of limiting or decreasing population growth in 58% of HDs. Survey minimum counts and survey recruitment ratios were the two types of data on which biologists place the greatest reliance in setting harvest regulations. The next two factors most relied on to set regulations were FWP harvest data (number of animals harvested relative to number of licenses issued) and hunter effort data (number of days/animal harvested). With mandatory reporting of mountain goat kills and consistent annual hunter harvest surveys, these may be the most consistently available data at biologists' disposal.

We also asked biologists 2 questions regarding how considerations of the sex of animals entered hunters' decisions when targeting a mountain goat. Responses indicated that an average of 55% (range 0–





Table 3. Relative importance of factors limiting mountain goat populations in recent times (2010–2015) in 29 native and 27 introduced HDs (as well as local populations outside of HD boundaries) in Montana. Count data indicate the number of populations to which a limiting factor applies. Weighted scores reflect both the number of populations to which a factor applies and the relative rankings of that factor among others selected.

		Disease	Predation	Hunter harvest (total # animals)	Hunter harvest (proportion of females)	Habitat changes (non-anthropogenic)	ORV/Snowmobile disturbance	Energy exploration	Logging and/or road construction	Non-motorized recreation	Climate change	Small population risks (inbreeding,)	Other (please describe in Q4)	Ltd Available Habitat
Native	Count	10	14	14	13	18	21			4	20	16	4	
	Weighted score	50	66	74	81	101	95			20	91	99	15	
Introduced	Count	6	13	11	11	12	3			3		3		2
	Weighted score	41	69	62	67	60	17			11		17		14
Total	Count	16	27	25	24	30	24			7	20	19	4	2
	Weighted score	91	135	136	148	161	112			31	91	116	15	14

90%) of hunters intend to harvest a male rather than a female; and biologists estimated that an average of 52% (range 0–90%) of hunters can correctly identify a mountain goat's sex under field hunting conditions. These results suggested that approximately half of license-holders may be as likely to kill a female as a male, particularly with female-biased sex ratios being typical in the adult cohort of mountain goat populations (Chadwick 1973, Rideout 1974, Gonzalez-Voyer et al. 2003).

Biologists identified a wide array of research needs that would benefit their understanding and management of mountain goat populations. Of 12 topics mentioned, 3 research themes or areas of study captured 62% of all topics respondents offered: assessments of habitat condition, use, and carrying capacity

(9 responses); population demographics: productivity, recruitment, kid survival, and adult survival (7); and causes of mortality (5). The other 9 topics were each mentioned 3 times or less. Biologists also identified 8 management or monitoring needs that would assist mountain goat management. The 2 topics most often mentioned, and constituting 68% of all responses, were: better/more frequent monitoring of populations (10 responses); and sightability correction models and improved, standardized, survey methodology (5). Ten additional topics of relevance to mountain goat management and conservation in Montana were mentioned 1 or 2 times each by questionnaire respondents.





DISCUSSION

Population estimates and trends

To put current numbers in historical perspective, Casebeer et al. (1950) reviewed estimates of the statewide mountain goat population during 1919-1942, as recorded by the US Forest Service, and during 1943-1948 from estimates made by the Montana Fish and Game Department (Rognrud and Lancaster 1947). From these records it appears that about 4,100 mountain goats occupied native ranges across Montana during 1943-1946 (excluding national parks), a figure 3.5 times larger than the 1,159 native mountain goats estimated by Montana's biologists in 2016 in our study (Figure 6). Establishment of new herds in previously unoccupied mountain ranges began in 1941 (Picton and Lonner 2008). While the program to expand mountain goat distributions to unoccupied ranges was still in its infancy, Casebeer et al. (1950) recorded an annual maximum of 97 mountain goats among all introduced populations during 1943-1946. Additional translocations and growth of introduced populations resulted in our estimate of 2,526 in 2016 (Figure 6).

For native mountain goat populations, numbers of licenses and harvested mountain goats have plummeted from an average of 967 licenses and 329 harvested annually during the decade of the 1960s to an average of 50 licenses and 33 mountain goats harvested during 2007–2015 (39 licenses and 25 mountain goats harvested in 2015). In contrast, licenses and mountain goats harvested from introduced populations have increased from an average 169 licenses and 71 mountain goats harvested annually during the 1960s to an average of 225 licenses and 165 mountain goats harvested during

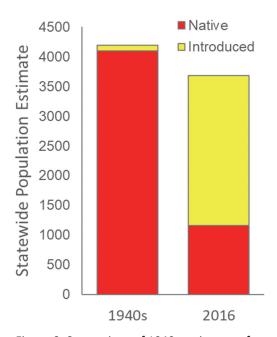


Figure 6. Comparison of 1940s estimates of mountain goat abundance in native and introduced populations of Montana, excluding national parks, by Casebeer et al. (1950) with those of this study for 2016.

2007–2015 (202 licenses and 155 mountain goats harvested from introduced populations in 2015).

Harvest management of mountain goats has been a topic of much interest and debate. Corroborating our questionnaire results concerning the important role that hunter harvest played in reducing historic mountain goat populations (Table 2), overharvest has been implicated as a source of population declines in native mountain goats in other parts of their range. Rice and Gay (2010) used population modeling to evaluate historical trends of mountain goats in Washington and found that population declines were primarily attributable to harvest. Mountain goat populations, numbering less than 100 animals, are generally no longer hunted in Washington (Rice and Gay 2010). Hamel et al. (2006) modeled population dynamics of mountain goats in Alberta and showed high sensitivity of population dynamics to adult female



survival and a subsequently detrimental role of female harvest in affecting population trends. As a result of these findings, the authors recommended closure of hunting in populations numbering <50 total individuals, and conservative harvest rates of 1-4% for larger populations depending on the population size and proportionate female harvest (Hamel et al. 2006, Rice and Gay 2010). In our study, the average license rates were 5.5% across hunted native population units and 7.7% across hunted introduced populations, while harvest rates averaged 2.0% for native and 6.3% for introduced populations. It is important to note that these estimates rely on population estimates from expert opinion rather than from repeatable, statistical population estimation procedures, and thus have unknown accuracy and precision. Twelve of the state's 52 currently delineated HDs have been closed to hunting, ostensibly due to populations too small to support harvest (note: following the completion of this study an additional 7 native populations were closed to hunting for the 2018 season).

Harvest rates of introduced population units have typically been higher, including cases of harvesting as many as 7.5–20% of the population in some areas (reviewed by Williams 1999 and Côté et al. 2001). Williams (1999) noted that introduced mountain goat populations likely occur in different stages of Caughley's (1970) 4 states of an ungulate irruption, as regulated by density-dependent quality of habitat. Because introductions began as early as the 1940s, it is evident that some of Montana's introduced herds have already experienced multiple cycles of increase and decline. Thus, a single optimal harvest rate prescription may not apply to all

populations after accounting for other limiting factors such as density dependence or predation rates. However, all authors have recommended caution with harvest of mountain goats in particular due to the difficulties of limiting harvest to males as well as their generally modest reproductive capacity.

Population monitoring

Our results suggested that current monitoring practices using aerial surveys alone have not, for the most part, been adequate to reasonably distinguish increasing vs. decreasing population trends with statistical rigor over the most recent 15-year time period. Biologists offered that better and more frequent monitoring of populations was their top management need and suggested research leading to a better understanding of population demographics of mountain goats was a high priority. Minimum counts documented during population surveys are a valid means of monitoring trend, even with annual variation in sightability of animals, provided the average sightability over long periods of time does not change (reviewed by DeCesare et al. 2016). In other words, an equal proportion of the population is assumed to be within the survey area and mean sightability of those within the area is assumed to be constant. While these counts provide a means of estimating trend, they cannot be used to estimate abundance without specific estimates of sightability. Measured sightability rates of marked mountain goats have varied from ~40% to 80% in studies in British Columbia, Idaho, and Washington (Poole et al. 2000, Pauley and Crenshaw 2006, Rice et al. 2009). Sightability likely varies among mountain goat populations and habitats in Montana, making it unlikely that a single sightability



model would apply across the state (Harris et al. 2015). Accounting for sightability bias across would Montana would likely require multiple studies and multiple models to fit varying conditions.

Managers of species that tend to occur in small populations commonly face an additional challenge of lacking statistical power when interpreting trend surveys. The precision of population estimates is known to decrease as the size of the population being monitored decreases (Taylor and Gerrodette 1993, Barnes 2002, DeCesare et al. 2016). For example, Barnes (2002) found that the confidence intervals for estimates for a West African elephant monitoring program were likely to be >100% of the point estimates when the population was below 600 animals. While this threshold doesn't necessarily apply directly to mountain goat monitoring in Montana, our results do suggest a positive relationship between the magnitude of counts and their precision (Figure 5). Thus, lumping subpopulations together into larger groups whether during surveys or during data analysis may increase our power to detect trends if done so consistently over time and if population dynamics can be assumed to be the same across the larger group. A formal power analysis of simulated and empirical mountain goat survey data would offer an improved depiction of how various survey sampling designs might affect the strength of results. Additionally, review of other survey techniques or monitoring practices (such as monitoring of trend via survival and reproductive rates of marked individuals or non-invasive DNA-based population estimation) may aid in evaluating current practices compared to those employed for mountain goats in other jurisdictions (Poole et al. 2011).

In addition to minimum counts, biologists indicated frequent use of recruitment ratios when monitoring mountain goat populations. These ratios are typically formulated as young/adult ratios, though the definition of the adult denominator appeared to vary across surveys depending on efforts to distinguish yearling or 2-year-old mountain goats from older animals. Of significance to interpretation of these data is the important life history detail that the age of first reproduction for female mountain goats is 3 years of age (Rideout 1975) and primiparity can average >4 years-old for native populations (Festa-Bianchet and Côté 2008). It is likely that many of the adults counted in recruitment ratios are not in fact breeding-aged adults. Thus, variation in age structure of adults across years or populations should be expected to confound interpretation of recruitment ratio data.

Area biologists also indicated that other data, in addition to survey data, are used when managing mountain goats. These included hunter harvest data, hunter effort data, and data concerning the age and sex of harvested individuals. Statistical modeling of these forms of data is not typically employed, and it is currently unclear if catch-effort or age-at-harvest data would be sufficient to glean meaningful patterns statistically, whether as a stand-alone analysis or incorporated into an integrated population model (Skalski et al. 2007, Udevitz and Gogan 2012). Hunter success, in particular, may be of limited value in assessing the population status of mountain goats, particularly native mountain goats in Montana. Over the past 60 years as harvest success has increased (Figure 2), we found that Montana's native mountain goats have clearly been in decline



as have the number of licenses issued annually. In HDs where only one or two licenses are issued annually, hunter success of 100% or 50% in a HD is difficult to interpret, and potentially misleading. Fidelity of mountain goats to preferred areas of their ranges contributes to the ability of hunters to find and harvest mountain goats, even when populations are small (Chadwick 1973, Smith 1976, Taylor et al. 2006, Festa-Bianchet and Côté 2008). This natural history trait may predispose hunted mountain goat populations to apparent "hyperstability" when monitored with hunter statistics alone (Hatter 2001). In such cases, hunter harvest statistics may convey a deceptively stable trend even for declining populations, because hunters continue to find and harvest mountain goats in the same areas and with the same efficiency regardless of decreased numbers overall (Hatter 2001). Survey responses suggested that Montana's mountain goat managers recognize the limited value of harvest success compared to biological data obtained from population surveys on which they place greater importance when establishing annual regulations. Consequently, population monitoring ranked highest among management priorities.

Limiting factors

Concerns about small population effects raised by several biologists are justified, given the small and potentially isolated nature of many of Montana's mountain goat populations. Biologists estimated that >50% of the state's HDs (and 69% of extant native HDs) may support fewer than 50 mountain goats. Such populations risk heightened consequences of stochastic events and inbreeding depression, compared to large populations

or metapopulations (Hebblewhite et al. 2010, Johnson et al. 2011). Effective conservation of mountain goats may require additional understanding of the extent to which populations face such risks. Research on movement and yearlong distributional patterns are needed for some of Montana's larger landscapes to determine where populations may now be reproductively isolated.

Unique among large mammal species, the mountain goat's distribution in Montana is almost completely on federally or state-managed lands, including national forest multiple-use lands, national forest wilderness areas, two national parks, state lands, and tribal land. Because of their high, rugged nature, mountain goat ranges tend to be less subject to human development and alteration than habitats of the state's other big game species. Yet, the biologists we surveyed offered a range of direct or indirect effects, both natural and anthropogenic, that are either suspected or known to be affecting mountain goats. Road construction into mountain goat habitat to facilitate mining, energy and timber extraction, and motorized recreation can alter habitat with implications for mountain goat distributions and demography (Fox et al. 1989, White and Gregovich 2017), and increased vulnerability of mountain goats to harvest (Mountain Goat Management Team 2010). Numerous studies in Canada and the U.S. have demonstrated that mountain goats are particularly sensitive to helicopter disturbance (Foster and Rahs 1983, Côté, 1996, Gordon and Wilson, 2004).

In Montana, some of the most pertinent research conducted on habitat-mediated impacts on mountain goats includes documentation of how helicopter over-flights associated with seismic testing





affects population dynamics (Joslin 1986), and how road intrusion and timber harvest alter mountain goat behavior and distribution (Chadwick 1973). However, little is known about the effects of commercial and recreational activities on most mountain goat populations in the state, or about the condition and carrying capacity of most mountain goat ranges and how that may relate to population performance. Likewise, the effects of wildfire, or contrarily fire suppression, on mountain goats through changes in habitat structure, plant succession, and forage are little known. These are noteworthy areas for research regarding the differing status and trends we identified of native versus introduced populations generally. Mountain goats may also be among those species most sensitive to climate change because of their cold-adapted nature and because the climate is warming (and cascading environmental changes occurring) twice as rapidly at high elevations compared to the global mean rate of warming (Beever and Belant 2011).

Future directions

Montana is unique among the 8 U.S. and Canadian jurisdictions within the native range of the mountain goat by now supporting greater numbers of mountain goats in introduced populations than those in the state's native populations. Clearly one size fits all prescriptions for management would not serve the state's mountain goat populations well. Management and conservation efforts require consideration of the wide range of habitats Montana's mountain goats occupy with special attention to differences between native and introduced mountain goats. However, statewide coordination of management planning and research

prioritization may serve to leverage resources to address needs and answer questions for broad landscapes and multiple populations of mountain goats.

From our findings, important topics deserving of future attention in comprehensive planning for Montana's mountain goats include:

- 1) Recommendations for harvest of mountain goats: These may well differ for native and introduced populations. Not only population harvest rates, but sex-specific harvest prescriptions dependent on maintaining viable population size could be addressed. Wildlife managers can influence mountain goat conservation largely through regulation of public harvest in comparison to other factors beyond their control.
- 2) Evaluation of monitoring practices: MFWP biologists rely heavily on population survey data to establish harvest levels of populations. Improved survey techniques, sightability modeling, and informed/optimal monitoring frequencies are all important management needs. Although biologists overwhelmingly felt that monitoring needed to be herd or hunting district specific because of local conditions, some consensus on data collected may be important for comparing populations and analyzing multi-year trends. The most difficult task in this study was analysis of population survey data due to inconsistencies in monitoring frequency and protocols. A formal power analysis of simulated and





empirical mountain goat survey data would offer an improved depiction of how various survey sampling designs might affect the strength of results.

- support area biologists' efforts to formally design, prescribe, and document monitoring protocols for mountain goats in their respective areas with the goal of detecting changes in population status that require management actions. These would greatly benefit future area biologists in their jurisdictions and efforts such as this study by collecting comparable data streams over time.
- 4) Species management plan: MFWP does not currently have a statewide management plan for mountain goats. Examples of such plans exist for other species in Montana, and for mountain goats in neighboring jurisdictions (e.g., Alberta, British Columbia, Idaho, Oregon, Utah, and Washington). Those state and provincial plans have brought together much of the pertinent literature and identified key planning elements, some unique to mountain goat conservation. Development of such a plan has been previously identified as a priority by MFWP, yet has not occurred in the face of limited time and resources. Relative to other ungulate species in Montana, a management plan for mountain goats may be particularly useful for a variety of reasons. First, various life history traits make them more
- sensitive to harvest management than other ungulates, which justifies a unique approach to harvest management of this species. Second, some of the variation in monitoring practices and/or harvest rates identified in this report might benefit from regional or statewide coordination or guidelines. Third, the reproductive isolation of many populations may render mountain goats more vulnerable to natural and anthropogenic changes in their environment across broad areas of their distribution. Lastly, individual biologists have less funding and time to devote to this species relative to other more abundant and/or controversial species, which might increase the value of a statewide resource for information and guidance.
- 5) Ecological research: In addition to the monitoring-based research questions we identified above, our questionnaire indicated a variety of potential avenues for important research into mountain goat ecology. These included, but were not limited to, assessments of mountain goat foraging ecology and habitat condition, demographic vital rates and population dynamics, and causes of mortality.

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Habitat Selection, Movement, Disease, and Population Structure of a Re-Introduced Bighorn Sheep Population in a Canyon Environment

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ABSTRACT: We comprehensively assessed multiple management concerns for a re-introduced sheep herd in Dinosaur National Monument, Colorado, USA. We captured 20 bighorn sheep in late 2006, collected genetic and disease samples and deployed GPS collars that recorded locations every 2.5 hours for 18 months. We evaluated habitat selection and movement at 2 spatial scales. Bighorns selected home ranges near the river, where canopy cover was low, and for grasslands, shrublands, and woodlands versus non-vegetated areas. Within the home range, in summer, assessed with an integrated step selection function, bighorns selected for areas near escape terrain, low solar radiation, more westerly slopes, moderate variation in local topography, and the canyon bottom or the rim, thus selecting against moderate elevations. Selection patterns in winter were similar, with additional selection for areas near permanent water and away from intermittent water. In terms of movement, bighorns strongly avoided crossing rivers, and selected areas with lower forest cover that were further from escape terrain. We detected movement across the rivers in one region, near the juncture of the Green and Yampa Rivers and found no genetic signal of population structure. Combined, these analyses suggest that the rivers and rugged canyons do not impede either demographic or genetic connectivity of bighorn sheep in the Monument and that they should be treated as a single herd. Results from the ELISA test suggest widespread exposure to M. ovi. These methods will help analysts working in other canyon systems and these findings will help local management of this re-introduced population.

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KEYWORDS Bighorn sheep; *Ovis canadensis*; management; home range; movement; habitat selection; disease; Dinosaur National Monument; Colorado.



Is Habitat Constraining Bighorn Sheep (*Ovis canadensis*) Distribution and Restoration? A Case Study in the Greater Yellowstone Ecosystem

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ABSTRACT: Rocky Mountain Bighorn Sheep (Ovis canadensis) are believed to have historically existed within geographically distinct areas (e.g., mountain ranges) as naturally structured metapopulations, and efforts focused on restoring metapopulations may provide currently unrealized restoration opportunities. By rebuilding metapopulations, managers may not only increase bighorn sheep abundance and distribution, but may also promote natural recolonization, improve genetic heterozygosity and improve population resiliency to stochastic disease events. The Madison Mountain Range, located on the western edge of the Greater Yellowstone Ecosystem (GYE), is a good example of a mountain complex with apparent unrealized potential for restoration. We hypothesized that the range is capable of supporting a metapopulation of bighorn sheep, and that current distributions are not primarily limited by habitat availability. We instrumented 27 adult female bighorn sheep in the Taylor-Hilgard population, located on the southern end of the Madison Range, with GPS radio collars programmed to record spatial data for approximately 18 months. Based on these data, we generated resource selection function (RSF) models to describe the seasonal movement of this population and evaluated their ability to predict current distributions of bighorn sheep within the Madison Range. Next, we extrapolated predictive models to identify areas of unoccupied habitat that could be considered for future translocation efforts aimed at establishing a continuous bighorn sheep metapopulation. Here, we discuss our models' performance, and utility for informing future bighorn sheep management within the Madison Range.

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KEYWORDS Bighorn sheep; *Ovis canadensis*; resource selection function; predictive habitat models; translocation potential; Madison Range; Montana.





Evaluating Success for an Intramountain Range Transplant of Bighorn Sheep in Southwestern Montana

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ABSTRACT: Montana Fish, Wildlife and Parks (MFWP) performed three bighorn sheep transplants within the Madison Mountains of southwest Montana to repopulate a historic, but unoccupied, winter range. The existing (source) herd had endured and recovered from several all-age die-offs and numbered approximately 200 animals prior to the start of transplants. An unoccupied winter range approximately 14 miles north was chosen as the release site due to a combination of biological and social factors. MFWP and Montana State University captured bighorn sheep using a drop net, and moved 52, 22, and 23 bighorn sheep in wintertime 2015, 2016, and 2018 (total = 97 bighorn sheep). The drop net enabled selection of social and family groups for transplant. We transplanted 16 lambs, 57 ewes, 23 rams, and 1 unclassified sheep. Older rams (>3.5) were avoided in transplant to prevent them from injuring lambs or smaller sheep in the trailer during transport. A sample of released bighorn ewes were fitted with LOTEK Lifecycle GPS collars at each transplant (10 in 2015, 6 in 2016, and 11 in 2018), which provided location data daily for up to 3 years. Mortalities included 4 predations, 2 injuries, and 1 unknown cause of death. Mortalities can be compared to non-transplanted, collared study animals from the source herd (8 mortalities across 32 VHF and GPS collars on ewes 2012-2018). Transplant success, defined by the percentage of bighorn sheep which remained in the transplant area after 1 year (i.e., did not return to the capture site) varied from approximately 20% in 2015 to approximately 80% in 2016, with 2018 still underway. Released bighorn sheep did not necessarily stay together in groups and individual movements varied across an area of approximately 625 km². Results suggest managers can use intramountain range captures and transplants to achieve success in expanding occupiable winter ranges and establishing a





desirable metapopulation structure. Intramountain transplants have advantages of using local animals familiar to the ecological landscape and local predator suite, and with common movement behaviors (i.e., migratory or non-migratory strategies) and pathogen communities. Managers may have to capture and release for several years to see success.

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KEYWORDS Bighorn sheep; *Ovis canadensis*; intramountain transplant; translocation evaluation; Madison Range; Montana.

Seasonal Use Patterns and Movement of Mountain Goats in the Mount Evans Wilderness, Colorado

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ABSTRACT: Mountain goats (*Oreamnos americanus*) were introduced into the Mount Evans area in 1961. From 1961 until the mid-1970s the mountain goat population stayed mainly below tree line and were occasionally observed in the alpine. By the mid-1980s, use shifted to the alpine near Lincoln Lake year-round. Based on summer ground surveys, established in 1978, the population used more of the available alpine habitat than was observed in the mid-1980s and mountain goat numbers have fluctuated over time from a low of 44 (1978) to a high of 167 (2001) (minimum count). In 2013, there was an unknown disease outbreak affecting kids and yearlings resulting in loss of almost an entire age class in this herd. Satellite collars were placed on mountain goats (n=20) between 2015 and 2016 to determine if habitat use had changed since the 1980s, evaluate the overall and seasonal habitat use, and monitor condition of kids associated with collared females for potential reoccurrence of the 2013 disease outbreak. Results suggest habitat use by mountain goats has changed dramatically since the 1980s. Mountain goats used more available alpine habitat compared to the 1980s, but no collared animals were observed in the Lincoln Lake area. Collared animals used 18.4% (16.13 km²) of the overall available habitat (87.3 km²). Seasonal habitat use is markedly different between summer and winter use. Based on MaxEnt (for maximum entropy) modeling, elevation had the highest relative importance to the summer model (>0.60); whereas for winter it was the terrain ruggedness index (>0.80).

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KEY WORDS Mountain goat, *Oreamnos americanus*, seasonal habitat use; disease; Mount Evans; Colorado.





Niche Similarities Among Introduced and Native Mountain Ungulates

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ABSTRACT: When two ecologically similar species are sympatric, theory predicts they will occupy distinct ecological niches to reduce competition. We evaluated the niche partitioning hypothesis with sympatric mountain ungulates – native bighorn sheep (BHS; Ovis canadensis) and introduced mountain goats (MTG; Oreamnos americanus) in the northeast Greater Yellowstone Area. We characterized seasonal niches using two-stage resource selection functions with a used-available design and descriptive summaries of the niche attributes associated with used GPS locations. We evaluated seasonal similarity in niche space according to confidence interval overlap of model coefficients and similarity in geographic space by comparing model predicted values with Schoener's D metric. Our sample contained 37,962 summer locations from 53 individuals (BHS = 31, MTG = 22), and 79,984 winter locations from 57 individuals (BHS = 35, MTG = 22). Slope was the most influential niche component for both species and seasons, and showed the strongest evidence of niche partitioning. Bighorn sheep occurred on steeper slopes than mountain goats in summer and mountain goats occurred on steeper slopes in winter. The pattern of differential selection among species was less prevalent for the remaining covariates, indicating strong similarity in niche space. Model predictions in geographic space showed broad seasonal similarity (summer D = 0.88, winter D = 0.87), as did niche characterizations from used GPS locations. Our results suggest that reducing densities of mountain goats in hunted areas where they are sympatric with bighorn sheep and impeding their expansion may reduce the possibility of competition and disease transfer.

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KEY WORDS Mountain goat, *Oreamnos americanus*, bighorn sheep; *Ovis canadensis*; niche overlap; niche partitioning; resource selection function; Greater Yellowstone Area.





Pneumonia in Bighorn Sheep: A Recent Review

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ABSTRACT: In this presentation, we review the literature and recent unpublished data to present a brief overview of the biology and management of pneumonia in bighorn sheep. Association of domestic sheep has long been linked to pneumonia outbreaks in free-ranging bighorn sheep and has been confirmed in 13 captive commingling experiments. Epizootic pneumonia in bighorn sheep is polymicrobial but *Mycoplasma ovipneumoniae*, a bacterium





specific to Caprinae and commonly carried by healthy domestic sheep and goats, appears to be a necessary primary agent. All-age epizootics following introduction of M. ovipneumoniae along with other pathogens into bighorn sheep populations are usually severe (median mortality 48%) but fatality rates vary widely, from 5 – 100%. Disease outcomes may be influenced by the strain of M. ovipneumoniae, by co-infection with other bacterial and viral pathogens, and by factors associated with transmission and host immunity. Once introduced, M. ovipneumoniae can persist in bighorn sheep populations for decades. Carrier dams transmit the pathogen to their susceptible lambs, triggering fatal pneumonia outbreaks in nursery groups, which limit recruitment and slow or prevent population recovery. The result is that demographic costs of pathogen persistence often outweigh the impacts of the initial introduction. Strain typing suggests that spillover of M. ovipneumoniae into bighorn sheep populations from domestic small ruminants is ongoing, and that consequences of spillover are amplified by movements of infected bighorn sheep across populations. Current disease management strategies focus on reducing risk of spillover from reservoir populations of domestic sheep and goats and on limiting transmission among bighorn sheep. A broad array of approaches has been tried and more are needed to prevent pathogen introduction, induce disease fadeout in persistently infected populations, and promote population resilience across the diverse landscapes bighorn sheep inhabit.

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KEY WORDS Bighorn sheep; *Ovis canadensis*; pneumonia; *Mycoplasma ovipneumoniae*; epizootic; strains; co-infection; transmission; immunity; management.





Fatal Pneumonia in Bighorn Sheep Lambs: The Critical Role of *Mycoplasma* ovipneumoniae Carrier Ewes

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ABSTRACT: Mycoplasma ovipneumoniae is a candidate primary etiologic agent of pneumonia in bighorn sheep (Ovis canadensis). Introduction of M. ovipneumoniae into bighorn populations may result in severe all-age epizootics (5-100% mortality), followed by years of pneumoniainduced mortality in lambs (20-100% mortality). Recurrent lamb pneumonia in post-epizootic bighorn populations significantly reduces recruitment, impairing population growth and threatening population viability. It is hypothesized that ewes that are chronic nasal carriers of M. ovipneumoniae serve as the source of transmission of this pathogen to lambs. During the peri- and post- natal periods, initial dam-lamb infections are amplified by lamb-lamb transmission within lamb social contact networks, exposing all lambs in the group to the pathogen, even if only a small proportion of the dams are carriers. Captive bighorn sheep were used to test the hypothesis that the presence of M. ovipneumoniae carrier ewes within a nursery group precipitates lamb pneumonia outbreaks. Post-epizootic bighorn ewes (n=6) were commingled and longitudinally sampled for M. ovipneumoniae carriage over a 2-year period. One carrier and five non-carriers were identified. In 2017, these ewes were placed into two pens, with pen C1 (carrier 1) containing the carrier and one non-carrier ewe, and pen N (noncarrier) containing four non-carrier ewes. Both lambs born in pen C1 developed pneumonia, while the four lambs born in pen N remained non-pneumonic and survived. In 2018 we will repeat this experiment after moving the non-carrier ewe in pen C1 to pen N, and replacing her with two non-carrier ewes previously held in pen N. We have also added two additional pens (C2 and C3) containing one or more chronic carrier ewes. We predict all lambs born in the carrier pens will develop pneumonia, while all lambs born in pen N will again remain nonpneumonic. If this prediction holds true, both here and in parallel experiments at South Dakota State University, our hypothesis for the role of carrier ewes in precipitating pneumonia outbreaks in lambs will be strongly supported.

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KEY WORDS Bighorn sheep; *Ovis canadensis*; pneumonia; *Mycoplasma ovipneumoniae*; epizootic; carrier ewes; lamb mortality; captive animal study.



The Implications of Imperfect Detection for Establishing the Presence/Absence of Pathogens: A Web-Based Resource for Managers

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ABSTRACT: A key factor for the informed management of populations of wild animals is the ability to accurately determine the presence or absence of pathogens. The infection status of groups has important implications for the translocations of individuals, herd-level accreditation of freedom from infection, as well as understanding the risks of pathogen transmission between wild and domestic animals. However, accurately assessing the presence of pathogens is complicated by imperfect detection, which results in uncertainty regarding pathogen presence even in the face of no positive test results. The accurate assessment of pathogen presence also requires evaluating the consequences of assuming binomial or hypergeometric sampling. Here, we develop a flexible, Bayesian-based framework for estimating the probability of pathogen presence and its uncertainty. We demonstrate our approach by evaluating the consequences of imperfect detection for a variety of respiratory pathogens in bighorn sheep (Ovis canadensis). We then generalize this framework by developing a webbased application to make this estimation methodology more widely available. Using test results, this application allows users to estimate the probability of pathogen presence, or prevalence in the event of positive tests, by controlling parameters related to sampling design and detection probabilities. Furthermore, it informs sampling design by allowing users to determine the sample size and number of replicate tests per individual that are required to achieve a specified confidence in the probability of pathogen presence. Overall, this work has produced a practical, readily-accessible, and easily-used tool that will allow managers to assess the probability of pathogen presence/absence in wild populations.

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KEY WORDS Bighorn sheep; *Ovis canadensis*; pathogen presence; pathogen detection; prevalence; web-based application; sampling design.





Detection Error and Demographic Variability Amid Pervasive Pneumonia Pathogens in Bighorn Sheep

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ABSTRACT: Respiratory disease (pneumonia) has been a persistent challenge for bighorn sheep (Ovis canadensis) conservation and its cause has been attributed to numerous bacteria including Mycoplasma ovipneumoniae and several Pasteurellaceae family species. This study sought to investigate efficacy of diagnostic protocols in detecting Pasteurellaceae and Mycoplasma ovipneumoniae, generate sampling recommendations for different protocols, assess the distribution of these disease agents among 21 bighorn sheep populations in Montana and Wyoming, and evaluate what associations existed between detection of these agents and demographic performance of bighorn sheep populations. Analysis of replicate samples from individual bighorn sheep revealed that detection probability for regularly used





diagnostic protocols was generally low (<50%) for Pasteurellaceae and was high (>70%) for Mycoplasma ovipneumoniae, suggesting that routine pathogen sampling likely mischaracterizes respiratory pathogen communities. Power analyses found that most pathogen species could be detected with 80% confidence at the population-level by conducting regularly used protocols multiple times per animal. Each pathogen species was detected in over half of the study populations, but after accounting for detection probability there was low confidence in negative test results for populations where Pasteurellaceae species were not detected. Eighty percent of study populations hosted both Mycoplasma ovipneumoniae and leukotoxigenic Pasteurellaceae pathogens, yet a number of these populations were estimated to have recruitment rates greater than 30% and positive population growth. The results of this work suggest that disease severity is influenced by ecological factors and/or differences in pathogen communities that cannot be assessed using methods currently available to most wildlife managers. These results also suggest that continued respiratory disease epizootics may be caused by pathogens already resident in bighorn sheep populations as well as by the introduction of novel pathogens. We present a framework to evaluate these hypotheses and develop management strategies aiming to minimize the effects of respiratory disease in bighorn sheep amid pervasive respiratory pathogens.

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KEY WORDS Bighorn sheep; *Ovis canadensis*; pneumonia; *Mycoplasma ovipneumoniae*; *Pasteurellaceae*; detection probability; recruitment.

Use of Rapid Field-Based PCR Testing to Detect *Mycoplasma ovipneumoniae* Infection in Bighorn Sheep

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ABSTRACT: Mycoplasma ovipneumoniae (Movi) induced epizootic pneumonia has resulted in significant declines in bighorn sheep (Ovis canadensis, BHS) populations in the USA. Testing of BHS nasal swabs with real-time PCR (RT-PCR) for Movi infection has proven valuable in epidemiologic and ecologic studies of the disease but does not produce results in time to support individual animal management actions without special arrangements for animal holding. The objective of this study was to evaluate rapid, animal-side testing using RT-PCR (Biomeme, Inc.) to detect Movi in sheep nasal swabs. Duplicate nasal swabs were collected from 53 BHS in Hells Canyon. Animals were considered positive if Movi was detected in either or both swabs. DNA was extracted from one swab using Biomeme reagents and analyzed in the field using the Biomeme RT-PCR instrument/two3 PCR machine (B-DNA/B-PCR) and the second swab was extracted and tested by Conventional laboratory analysis (C-DNA/C-PCR). Movi was not detected using B-DNA/B-PCR in any of the tested BHS, while C-DNA/C-PCR detected Movi in 2 animals. C-PCR detected Movi using B-DNA from one of these two animals. Biomeme and conventional laboratory PCRs were also used to test duplicate nasal swabs from 33 domestic sheep (DS). B-DNA/B-PCR detected Movi in 58% (19/33), compared to 64% (21/33) for C-DNA/C-PCR. Movi was detected by B-DNA/B-PCR in two DS that were negative by C-DNA/C-PCR, while C-DNA/C-PCR detected Movi in four DS that were negative by B-DNA/B-PCR. C-PCR also detected Movi using B-DNA from these latter four animals. In all, 86 BHS and DS were tested by B-DNA/B-PCR and C-DNA/C-PCR; Movi was detected in 25 animals by one or both methods. Considering these 25 animals as 'true positives', the diagnostic sensitivity for Movi detection was 76% for B-DNA/B-PCR and 92% for C-DNA/C-PCR. Results indicated that swab-to-swab variation in sampling and the presence of inhibitory substances in DNA extracts contributed to the imperfect sensitivity of both tests. This study demonstrates the field applicability of Biomeme test and identified areas where improvement is needed.

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KEY WORDS Bighorn sheep; *Ovis canadensis*; pneumonia; *Mycoplasma ovipneumoniae*; domestic sheep; real-time PCR; animal-side test development.





Use of Intra-nasal Antibiotics as an Aid to Clearing *Mycoplasma ovipneumoniae* Carriage by Domestic Sheep

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ABSTRACT: Mycoplasma ovipneumoniae is the primary cause of epizootic pneumonia of bighorn sheep (Ovis canadensis). Contacts with reservoir hosts of M. ovipneumoniae, domestic sheep and goats, may result in transmission of this bacterium initiating outbreaks of this disease. Efforts to control the disease have emphasized physical separation of bighorn sheep from these reservoir hosts; however, separation is challenged by the natural movements of bighorn sheep, by straying reservoir hosts, and by the apparent mutual attraction of these sheep species. The effectiveness of separation would be complemented by elimination of M. ovipneumoniae from reservoir host operations near bighorn sheep ranges. Elimination of M. ovipneumoniae may be achieved by removal of adult chronic carriers and by segregated weaning of replacement stock, but these practices are limited by lack of facilities for effective on-farm segregation, by infection of replacements prior to weaning age, or by carrier prevalences exceeding the operator's tolerance for culling. Clearing M. ovipneumoniae with antimicrobial drug therapy would circumvent these limitations. Here we report that combined systemic and local therapy can eliminate this pathogen from domestic sheep. Pilot studies of systemic (subcutaneous) treatment of chronic carrier ewes with enrofloxacin, gamithromycin, tildipirosin, and tulathromycin failed to eliminate M. ovipneumoniae nasal carriage. However, combined systemic and intranasal enrofloxacin treatment successfully cleared M. ovipneumoniae from two carrier domestic ewes for >3 months. Two subsequent enrofloxacin trials examined yearling lamb (n=28) and adult ewe (n=15) carriers randomly assigned to one of 4 treatment groups in 2x2 factorial designs. Factors were 1) systemic treatment (yes or no) and 2) intranasal wash dosage (low or high). In both trials, animals treated with systemic enrofloxacin combined with either high or low dose intranasal treatment became PCR negative for M. ovipneumoniae. Carrier animals that failed to clear M. ovipneumoniae following intranasal-only therapy did clear the infection when subsequently treated with combined therapy. These results indicate that combined antimicrobial therapy can eliminate M. ovipneumoniae carriage by domestic sheep. Further studies are needed to 1) document the durability of M. ovipneumoniae clearance, 2) determine the efficacy of combined therapy in domestic goats, and 3) optimize antimicrobial drug choices and dosing levels.

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KEY WORDS Pneumonia; *Mycoplasma ovipneumoniae*; domestic sheep; antibiotics; subcutaneous treatment; intra-nasal treatment; combined therapy.





A Pilot Program to Create a Source of Domestic Sheep Free of *M. ovipneumoniae* for Cooperating Private Owners

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EXPANDED ABSTRACT: Small ruminant owners indicate interest in lowering risk of pathogen transmission to bighorns while continuing to maintain their flocks. One promising approach is for owners to hold only animals free of *M. ovipneumoniae*, but managers lack sources for animals certified free of this pathogen to which they could refer partnering flock-owners. Because development of a *M. ovipneumoniae*-free flock was an experimental and untested process likely to entail up-front costs, the Washington Department of Fish and Wildlife (WDFW) decided to pave the way rather than expecting a private firm to shoulder these risks. We further reasoned that if we were successful, our experience would be useful to private breeders interested in expanding the program.

An avenue for cooperation had previously been established by Washington's Sustainability in Prisons Project, which has raised endangered turtles and butterflies in state correctional facilities, providing valuable life-lessons for participating inmates. In early 2016, WDFW collaborated with the Washington Department of Corrections (DOC) to begin raising and breeding for sale domestic sheep that could be certified free of *M. ovipneumoniae* at the Washington State Penitentiary in Walla Walla. WDFW contracted with 2 sheep experts to lead day-to-day operations, paid for testing and purchase of founder individuals, and, together with DOC, funded necessary infrastructure improvements. Fifteen Suffolk ewes, originating from 2 nearby herds, arrived onsite in late September 2017, and a (< 1 yr-old) ram was added in mid-October. In addition to testing PCR-negative (on nasal swabs) twice for *M. ovipneumoniae*, as well as once for ovine progressive pneumonia virus, paratuberculosis and Caseous lymphadenitis (CL), all founder individuals were genotyped either RR or QR (for scrapie), vaccinated against Campylobacter and CL, and inspected by a veterinarian.

Despite our precautions, the ram tested PCR-positive for *M. ovipneumoniae* in late November 2017, approximately 5 weeks after arrival, and a week later, a ewe was also positive. Rapid isolation of infected individuals, coupled with 5-day antibiotic treatment with via nasal wash and subcutaneous injection was evidently successful in both preventing further spread and clearing the infected animals of this particular infection. All 16 animals were PCR-negative





on 5 successive tests conducted over an abbreviated 2 week period. Lambing occurred from 13 March to 2 April 2018, a total of 30 lambs were produced, of which 28 (9 females, 19 males) survived.

However, follow-up swabbing and PCR testing for *M. ovipneumoniae* on April 30, 2018 unexpectedly revealed positive or indeterminate results for 7 ewes, only 2 of which were part of the previous infection. Strain-typing indicated that the 2 infections were separate, one originating from each of the 2 source herds. This suggested either that the bacteria had entered the flock a 2nd time (presumably through fomites, as the herd had been kept entirely closed), or that the founding individuals carried 2 strains, only one of which was detected in our initial (November 2017) outbreak. Correlations of strain types with source herds strongly supported the 2nd of these hypotheses. This, in turn, suggested that even our extensive testing had earlier yielded some false negatives. Further investigation identified the presence of strong PCR inhibitors in some sheep nasal mucus, and the PCR method was modified to reduce the effect of those inhibitors.

Additional testing in mid-July 2018 suggested that 5 of the newly infected animals may have cleared this 2nd strain (pending additional testing), 1 or 2 ewes seemed to be persistent carriers, but that the bacteria had spread to most of the lambs.

To attain our goal of *M. ovipneumoniae*-free status, we are currently planning a combination of separation, removal, and treatment. Although we have not yet met that goal, we have learned that more extensive testing than we'd anticipated – particularly prior to selecting animals to originate the herd — is needed to ensure that no undetected infections enter the herd. Once introduced, additional infections are likely. We remain optimistic that creating pathogen-free herds is possible and is a useful strategy for assisting cooperative owners, but caution that it will require substantial resources and patience.

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KEY WORDS Pneumonia; *Mycoplasma ovipneumoniae*; domestic sheep; *M. ovipneumoniae*-free flock; repeated testing; antibiotic treatment.



Variation in the Annual Cost of Living of an Endangered Population of Bighorn Sheep

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ABSTRACT: Energy is fundamental to survival, growth, and reproduction with effects that scale up to influence larger-scale processes including movements, habitat selection, and population productivity. Estimates of the amount of energy wild animals need to make a living rarely have been quantified or related to larger-scale processes. Our objective was to develop a tool to calculate energy budgets of bighorn sheep based on body mass, reproductive status, and movement data. We used empirical data from 37 Sierra Nevada bighorn sheep (Ovis canadensis sierrae) that were captured during 2009–2014 and fitted with GPS collars, weighed, and assessed for reproductive status. Resting metabolic rates (reported in the literature) were the foundation of energy budgets; we added costs for eating, walking, and sinking in snow. Empirical data for reproduction and replenishment of body fat for bighorn sheep were not available in the literature, so we estimated these costs based on data for related species while correcting for allometric scaling relationships. Annual energy requirements varied with sex, reproductive status, and migratory tactic. Our model provides the basis for quantifying energetic implications of migration tactic for sheep and estimates of energy intake needed for optimal reproductive output. Coupling our model with estimates of food supplies may provide insights into energetic motivations of habitat selection and aid in establishing estimates of nutritional carrying capacity. Our energy model can be adapted to any population of freeranging sheep if annual body mass (and fat) dynamics, reproductive status, and movement rates are known.

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KEYWORDS Sierra Nevada bighorn sheep; *Ovis canadensis sierrae*; energy budget; metabolic rates; energy model.