

Chapter 5

Genetic Attributes and Research Interests

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THE GENOMICS REVOLUTION AND YELLOWSTONE

Genetic research and engineering have infiltrated our daily lives in countless ways. New advances due to genomics are in the news almost every day. Genomics involves identifying the structure and function of genomes, which consist of the genetic information in individuals. Prior to the 1980s, scientists had a limited ability to study genetic material called DNA, which is short for deoxyribonucleic acid. Unlike today, they could not identify criminals using forensics, diagnose certain medical conditions and inherited diseases, or genetically modify plant crops for resistance to diseases and drought. In 1985, scientists invented an approach to make many copies of a small amount of genetic material. Scientists called this replication a polymerase chain reaction (PCR). A microorganism, *Thermus aquaticus*, discovered in a Yellowstone hot spring, provided the critical ingredient, Taq polymerase, to make this reaction possible. Taq polymerase assists in the steps necessary to replicate DNA and can withstand the heat necessary for the procedure. Today, laboratories produce many versions of this enzyme for a wide range of studies and applications. The technology that emerged from studying a Yellowstone hot spring now helps us understand, manage, and conserve the web of life in the Yellowstone area and throughout the world.

WHAT IS DNA AND HOW DO WILDLIFE BIOLOGISTS USE IT?

Just as in people, DNA provides the instruction book for life within bighorn sheep and mountain goats. Multiple influences on the DNA of a wildlife population, including gene flow through the movement of breeding individuals from one area to another, mutation, selection, and chance, operate on different timescales. Not only does DNA code for an individual's appearance and biological processes, but it is also the source of adaptation to specific diseases, environmental conditions, and food resources. Genetic diversity, variation in the DNA of an individual or population, provides the potential for adaptation to changing conditions, such as exposure to new diseases. Scientists study the genetics of bighorn sheep and mountain goats in the Greater Yellowstone Area to identify how past events have shaped today's populations, which can aid in future conservation and management decisions. (Carlson et al. 2014, Smith et al. 2014, Frankham et al. 2017)

To evaluate wildlife genetic information, scientists must first obtain samples that contain DNA. You can read about the types of samples that biologists collect, such as blood samples, in the "How We Learn" box. If you looked at a blood sample under a microscope, you would observe many different cells. White blood cells, which help the immune system respond to disease, contain a nucleus. The nucleus holds genetic material, called nuclear DNA, with instructions not only for the white blood cell but also for the entire organism. Each cell contains only a single copy of nuclear DNA, arranged in chromosomes that look like bundles of thread. Just as in humans, these chromosomes occur in pairs in mountain ungulates, with one chromosome from the father and one from the mother, and nuclear DNA codes for most traits of an individual, such as eye and hair color. If you looked at one strand of DNA, it would look like a ladder, with pairs of nucleotides that make up the rungs. Geneticists use different letters to represent these nucleotides (also called bases), including A for adenine, G for guanine, T for thymine, and C for cytosine. These letters are the alphabet that code for the processes that make up an organism.

Bighorn sheep and mountain goat genomes consist of about 2.9 and 2.5 billion base pairs, respectively. (“*Oreamnos americanus* (ID 17040) - Genome - NCBI” n.d., “*Ovis canadensis* (ID 10514) - Genome - NCBI” n.d.)

The nucleus is not the only place containing DNA in a cell. The mitochondria, a subcellular organelle that regulates cell energy, has its own DNA in a circular shape that is different from nuclear DNA. Mitochondrial DNA consists of about 16,000 base pairs and codes for proteins that are involved in energy metabolism. In most species mitochondrial DNA is inherited only from the mother, which means that the variation found within this type of DNA comes from mutation rather than a combination of DNA inherited from both parents. Thus, biologists can use mitochondrial DNA to track inheritance of DNA from mothers over many generations. In addition, the lower variability of mitochondrial DNA makes it useful in distinguishing genetic differences among wildlife populations and species. Because each cell has many copies of mitochondrial DNA, it is also easier to isolate than nuclear DNA in non-invasive samples that are lower in quality or not fresh. Thus, scientists can use mitochondrial DNA to track genetic information over long periods of time, such as when and where groups of humans moved out of Africa thousands of years ago. (Quintana-Murci et al. 1999, Barr et al. 2005, Olivieri et al. 2006, Frankham et al. 2010, 2017; Garrett and Grisham 2013, Davenport et al. 2018)

Although everyone has their own unique genome (except for identical twins or clones), there are many genetic similarities across people and species. Domestic sheep and humans share 76% of their genomes. When comparing the DNA of two different people, 99.9% of their genomes are the same, but the remaining 0.1% difference accounts for variability in appearance, susceptibility to diseases, and many other traits. Thus, researchers identify the limited areas (called loci) of DNA in wildlife that show differences among individuals to address research questions about their populations. In the Greater Yellowstone Area, scientists have evaluated genomes of bighorn sheep and mountain goats to understand how their populations

have changed over time, determine the level of genetic differences among today's populations and individuals, and identify the origin of animals that dispersed into new areas. These research questions can help improve our understanding of the history of wildlife populations and provide information for future decisions to enhance their long-term well-being. (Poissant et al. 2010, Auton et al. 2015, "*Ovis aries* Annotation Report" 2015)

ANCIENT AND CONTEMPORARY BIGHORN SHEEP POPULATIONS

LEARNING ABOUT BIGHORN SHEEP FROM THOUSANDS OF YEARS AGO

Bighorn sheep have inhabited the Greater Yellowstone Area for thousands of years as a significant large herbivore (plant eater) in the ecosystem and an important food source to native people. Following European colonization across the west, market hunting and domestic sheep grazing resulted in drastic reductions in bighorn sheep populations. The Greater Yellowstone Area was no exception (see chapter 2). The 1877 Yellowstone Superintendent's report indicated several thousand bighorn sheep were removed from the area, mostly for pelts, between 1870 and 1877. This drastic reduction in the population size likely contributed to a loss of genetic diversity in the area. Superintendent Norris indicated thousands of bighorn sheep still ranged in the mountains along the eastern side of the park, but these remaining bighorn sheep were potentially impacted by exotic respiratory diseases introduced by contact with domestic sheep grazing near the park. The introduction of exotic respiratory diseases into the Greater Yellowstone Area undoubtedly resulted in catastrophic die-offs of bighorn sheep and strong selection for individuals that could mount successful immune defenses. Recent sampling of bighorn sheep populations in the region indicated these exotic pathogens are present in nearly all population segments (see chapter 6). These findings suggest current bighorn sheep populations have likely been under continuous selection pressure for resistance



Ancient bighorn sheep skull thousands of years old. Scientists have extracted DNA from ancient bighorn sheep bones and skulls to compare the bighorn sheep of the past with today's populations. Photo by Craig Lee, University of Colorado-Boulder.

against the exotic pathogens since domestic sheep were introduced into the area approximately 150 years ago. Genetic research can help evaluate how these past events influenced the bighorn sheep that roam the region today. (Norris 1878, Buechner 1960, Avise et al. 1988, Lee and Puseman 2017, Butler et al. 2018)

Anthropologists studying artifacts from receding ice patches in alpine areas of the Greater Yellowstone Area recovered ancient skull caps, horn cores, and bones from bighorn sheep in the northern area of the Beartooth-Absaroka Mountains. They suspect native people left bighorn sheep remains at the same site over many hundreds of human generations. Multiple bighorn sheep specimens were radio-carbon dated to 685 to 5,530 years before present. Scientists can compare DNA from these ancient samples to the genomes of today's bighorn sheep by determining the order of their base pairs (A, G, T, and C), which is called sequencing.

Because ancient DNA degraded into smaller pieces over time, determining the order of the base pairs that made up the original genome is like putting together a complex jigsaw puzzle. Thus, studying mitochondrial DNA is useful in this case because it degrades less over time and there are more copies per cell than nuclear DNA. In addition, the smaller size of mitochondrial DNA makes it easier for geneticists to reconstruct, as there are fewer puzzle pieces that need to be put together to rebuild the full mitochondrial genome. Scientists expect the genome of the pre-settlement bighorn sheep to represent the historic condition of native bighorn sheep when their populations were numerous and free of diseases introduced by domestic sheep. This approach can help us determine how the population inhabiting the Beartooth-Absaroka Mountains has changed over thousands of years.

Researchers plan to compare 26 mitochondrial DNA genomes from contemporary bighorn sheep in the Beartooth-Absaroka Mountains with six ancient samples by constructing a phylogenetic tree. Like a family tree, which shows how individuals are related by birth, a phylogenetic tree shows how ancient and contemporary animals are similar based on their DNA sequences. Using this information, scientists plan to evaluate both how market hunting and domestic sheep diseases influenced the bighorn sheep population. In addition, recall that mitochondrial DNA is only inherited from the mother, and bighorn sheep groups of mothers and daughters maintain a similar home range (geographic area where they live) over multiple generations. Thus, scientists also can evaluate how stability of ewe home ranges might affect how bighorn sheep are related across geography over thousands of years. This effort represents an exciting and unique opportunity to help us understand the relatively rare, but important, process of female dispersal across time. (Hunter and Milner 1963, Geist 1971, Avise 2000, Nei and Kumar 2000, Fisher and Matthews 2001, Frankham et al. 2010)

EVALUATING GENETIC DIFFERENCES BETWEEN TODAY'S BIGHORN SHEEP HERDS

Following the loss of many bighorn sheep populations across the West, wildlife managers relocated more than 21,500 bighorn sheep in over 1,460 translocations across many states to start new herds and supplement existing herds. As a result, today's populations originated in one of three ways: reintroduced herds started by animals from distant sources; native herds supplemented with animals from other areas; and native herds that did not receive additional animals from other populations. It is not always clear which animals survived and reproduced after many of the attempted translocations. If we knew which translocations were successful, and how this depended on the environment where the source herd came from, we could improve the success of future translocations. Genetics can help us understand how bighorn sheep populations are related and inform future translocation planning. (Wild Sheep Working Group 2015)

To account for male genetic contributions and obtain more detailed information than what mitochondrial DNA can provide, researchers studied nuclear DNA from populations of bighorn sheep. The nuclear genome is much larger than the mitochondrial genome and sequencing many animals requires considerable resources and laboratory effort. To optimize the efficiency of nuclear DNA research, scientists employed a different approach that targets only the variable areas of DNA, capitalizing on the fact that most of the genome is similar between two individuals. One specific location, where the nucleotides forming the "rungs" of the DNA ladder commonly vary, is a single nucleotide polymorphism or SNP (pronounced "snip"). For example, at the same place in a DNA strand, one bighorn sheep may have a C (cytosine), whereas another may have a T (thymine). This difference may be functional, contributing to one individual having darker fur than another, or may be neutral, meaning that the difference has no effect that scientists have detected yet. In the human genome, one SNP occurs on average every

1,000 nucleotides, meaning that each person has about 4 to 5 million SNP sites. Scientists can target specific locations in the bighorn sheep genome where the nucleotide tends to vary by using a SNP chip. A SNP chip is a slide that holds short DNA sequences that attach to portions of the DNA that contain a SNP, enabling a laboratory machine to identify which nucleotide is found at the SNP site. Researchers developed an Ovine High Density SNP chip to evaluate domestic sheep that contains over 600,000 different SNPs found at known locations throughout the genome. Bighorn sheep and domestic sheep diverged as separate species from a common ancestor about three million years ago. These two species can interbreed and produce viable offspring, and still have the same number of chromosomes. Thus, the SNP chip developed for domestic sheep is also useful for bighorn sheep and contains about 24,000 SNPs that are informative for wild sheep. (Young and Manville 1960, Avise 2004, Bunch et al. 2006, Kim and Misra 2007, Poissant et al. 2010, Miller et al. 2015, Reference 2019)

Prior to evaluating genetic differences among herds using the SNP chip, scientists developed hypotheses describing what they expected to find. Both movement of males among herds due to geographic proximity and movement of animals to new areas via translocations by wildlife managers could increase genetic similarities among populations. Researchers predicted that bighorn sheep herds near one another or with shared translocation histories would have similar genomics. However, the degree of genetic similarity could vary depending on landscape features for natural movement of animals and if animals survived and bred after managers released them for translocations. To address this hypothesis, scientists summarized variation of SNPs into a graph using a technique called principle component analysis (PCA). Scientists discovered they could detect genetic differences among bighorn sheep populations using the Ovine High Density SNP chip. Researchers compared bighorn sheep from the Taylor Hilgard population on the west side of the Greater Yellowstone Area that had a history of multiple translocations with bighorn sheep

from the Beartooth-Absaroka population on the east side of the Greater Yellowstone Area that had no history of translocations from distant herds. These two populations differed genetically from one another, suggesting there has not been recent movement of breeding animals between these two areas. However, the Taylor Hilgard and Beartooth-Absaroka populations were genetically more similar to one another than the bighorn sheep population found in Glacier National Park on the United States-Canadian border, suggesting the Glacier population has been genetically separated from the other two populations for a longer period. These findings are like the large genetic differences detected by researchers in grizzly bear populations found in the Greater Yellowstone Area compared to those in Glacier National Park. Identifying how neighboring populations are genetically distinct can also be useful in identifying individuals that are descendants of translocations. For example, geneticists can



Bighorn sheep in Glacier National Park were found to be genetically different than those in the Greater Yellowstone Area. Photo by Elizabeth Flesch, Montana State University

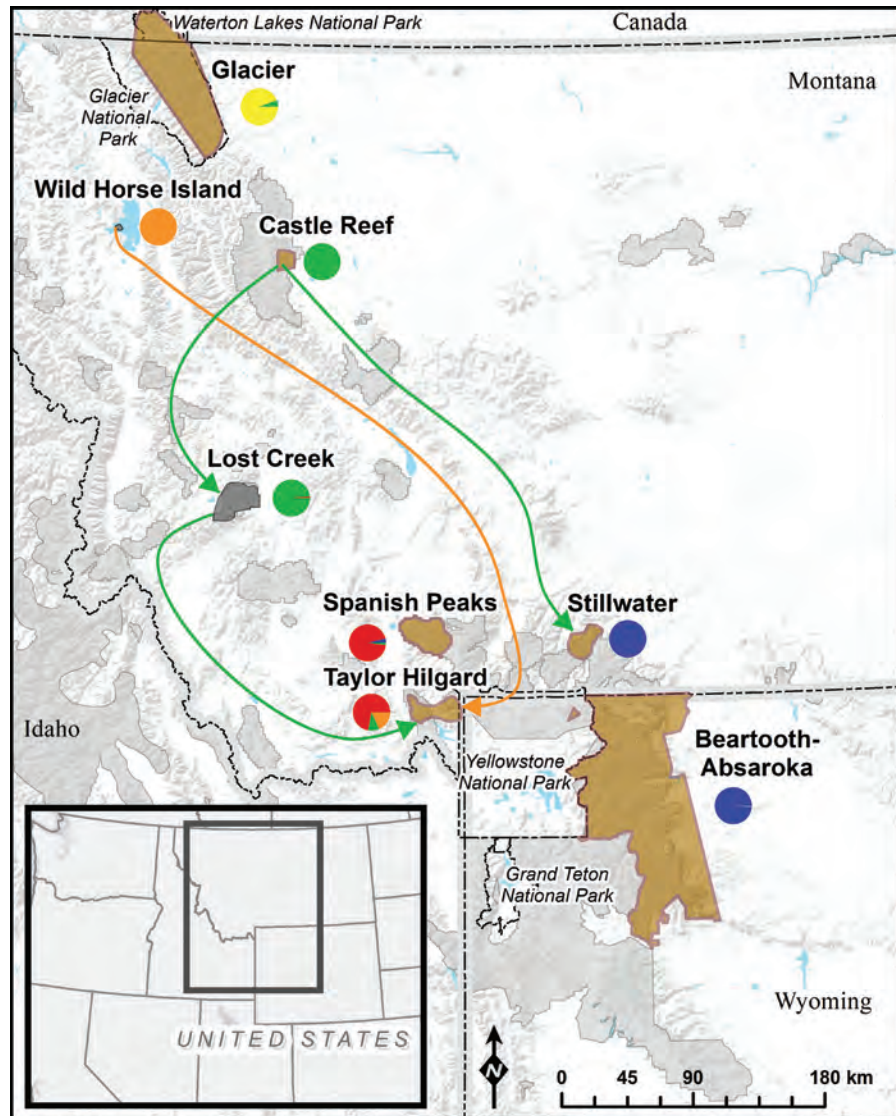


Figure 1. Genetic analyses revealed relationships among bighorn sheep individuals and populations in the Greater Yellowstone Area due to natural and human influences. Approximate range of evaluated bighorn sheep herds are shown in brown (native herds) and dark gray (reintroduced herds). Each pie chart represents the estimated ancestry for that population based on a STRUCTURE analysis. Herd pie charts containing the same color show genetic connections due to natural movement of animals or translocations by managers (symbolized by arrows). Estimated range of bighorn sheep herds not included in this analysis are shown in gray polygons. Map by Elizabeth Flesch, Montana State University.

determine whether translocations of male or female bighorn sheep made a larger genetic contribution to the recipient herd. This information can help inform and improve future translocation efforts that may seek to augment herd genetic diversity. (Reich et al. 2008, Haroldson et al. 2010, Francois et al. 2010, Flesch et al. 2018)

To evaluate the success of past translocation efforts in the Greater Yellowstone Area, scientists identified genetically distinct populations. A pie chart composed of two or more colors indicates the population had mixed ancestry from different sources (Figure 1). The analysis, performed using a classification approach called STRUCTURE, indicated there is some genetic connectivity between native herds in the Stillwater and Beartooth-Absaroka areas on the east side of the Greater Yellowstone Area. On the west side, the native Spanish Peaks and Taylor Hilgard herds, which are in geographic proximity, showed genetic connectivity. No genetic connections occurred between herds in geographically distant Glacier National Park and the Greater Yellowstone Area. Both Taylor Hilgard and Stillwater received translocations of bighorn sheep, implemented to enhance bighorn sheep conservation, from other areas in the state of Montana. Some of the animals transported from Lost Creek and Wild Horse Island to Taylor Hilgard made a genetic contribution (bred successfully in the new area), as their genetic influences on today's Taylor Hilgard population were detected by the analysis and represented by the source's population color. In contrast, a translocation from Castle Reef to Stillwater did not appear to make a genetic contribution, as the genetic signature of the Castle Reef population, symbolized by a different color, was not detected in the Stillwater population. The two translocations received by Taylor Hilgard were composed of 18 to 26 animals, including males and females, whereas the translocation received by the Stillwater herd included only two rams. Thus, based on the information from these translocations, scientists suspect that releasing a larger number of animals composed of males and females was more effective in genetically contributing to the recipient herd than releasing a small number of rams. (Pritchard et al. 2000, Montana Fish, Wildlife and Parks 2010, Raj et al. 2014, Flesch et al. 2020)

DETERMINING HOW INDIVIDUALS ARE RELATED WITHIN BIGHORN SHEEP HERDS

Scientists can also use the SNP chip to evaluate genetic diversity and determine how individuals within a bighorn sheep herd are related. Large, connected populations usually have high genetic diversity and potential to adapt to new environmental conditions. Conversely, a population is at risk for inbreeding depression if it is small and does not have gene flow, with potential parents moving in from other areas, over multiple generations. Inbreeding depression describes a phenomenon where close relatives breeding with one another results in reduced reproduction or survival at the individual and population level, through mechanisms such as reduced pregnancy rates and increased disease susceptibility. This negative impact on survival and reproduction can increase the risk of the population dying out. Genetic research can help identify populations where inbreeding may be a concern, and managers may choose to intervene by connecting areas of fragmented habitat or bringing unrelated individuals into the population through translocation. (Saccheri et al. 1998, Frankham et al. 2010, 2017)

To help determine if there is inbreeding in populations that are small and isolated, scientists calculate mean kinship. Kinship measures the level of genetic similarity between two individuals. It is used, for example, to determine optimal breeding pairs for captive wildlife in zoos to minimize inbreeding. Kinship also represents the probability that the two nucleotides drawn at random from two individuals will be the same, due to a recent shared ancestor. Thus, the value of kinship represents the level of inbreeding of any offspring born from breeding the two compared individuals. For example, a mother and daughter bighorn sheep would have kinship at the level of about 0.25, as the daughter inherited 50% of the mother's DNA. Biologists can use the average of the kinship values for animals sampled from a herd to determine how related everyone is to one another, called mean kinship. A large, randomly breeding population would have a mean kinship value near zero. (Frankham et al. 2017)



Bighorn sheep on Specimen Ridge in Yellowstone National Park. Photo by Elizabeth Flesch, Montana State University. .

Researchers sought to predict the level of mean kinship observed for different herds based on their origin and history, as many influences in the past can affect how related individuals currently are. First, scientists expected native and reintroduced herds to have different mean kinship because initial genetic composition and diversity of founders of a newly established herd can have a strong impact on the population's genetics. When a herd is founded by a small number of individuals, it could have low genetic diversity. In contrast, native herds are more likely to contain more genetic diversity. Second, population size could affect herd genetics. Small population size can increase inbreeding due to low availability of unrelated, potential mates. Third, past bottlenecks of severe reductions in population size

could also result in a loss of genetic variation. Finally, connectivity with other bighorn sheep herds is important to consider, as isolation and consequent lack of gene flow can cause a decline in genetic diversity. Thus, researchers summarized all these herd attributes to predict what the genetic information would show. The Beartooth-Absaroka is a native, large herd with high genetic connectivity across the mountain range and little potential for past bottlenecks. The Taylor Hilgard is a native, small herd with a past bottleneck due to a disease die-off and little to no connectivity with other herds. Thus, biologists predicted the Beartooth-Absaroka population would have lower mean kinship than Taylor Hilgard herd. (Nei et al. 1975, Fitzsimmons et al. 1997, Hedrick et al. 2001, Reed and Frankham 2003, Epps et al. 2005, Frankham 2007, Olson et al. 2013, Love Stowell et al. 2020)

Using genetic information for each of the herds generated using the Ovine SNP chip, geneticists determined the mean kinship values were consistent with their expectations. Bighorn sheep in the Beartooth-Absaroka herd were not very related, with a mean kinship value near zero. In contrast, the Taylor Hilgard had a higher mean kinship of 0.064, which was consistent with the herd's history, but still low and not concerning for population management. However, there can be multiple causes and interpretations of mean kinship values and evaluating these values alone cannot definitively determine if a herd is experiencing problematic levels of inbreeding. In general, mean kinship serves as a helpful piece of information to consider along with other factors to evaluate herd health. Scientists quantified mean kinship of bighorn sheep to explore the differences in genetic diversity among herds due to differing herd histories, and future research could evaluate the relationship between mean kinship within herds and population growth. (Waples 2015, Flesch et al. 2018)

MOUNTAIN GOAT GENETIC RESEARCH

Mountain goats in and near Yellowstone National Park are not native to the area. A total of 170 mountain goats were released in the Greater Yellowstone Area at seven locations north of Yellowstone National Park in Montana in the late 1940s and early 1950s, and at two locations southwest of Grand Teton National Park in Idaho in the late 1960s and 1970s. At each location, managers introduced 5 to 33 mountain goats. When populations originate from only a few individuals, limited genetic variation exists in the new population, and variation is lower than the source population. Usually, only some animals successfully reproduce, which can further reduce genetic variation. Geneticists refer to this loss of genetic variation in small populations due to chance as genetic drift. The relatively fast differentiation helps researchers evaluate whether substantial gene flow, and thus movement, recently occurred among herds. In addition, because some genetics are still shared with the original source herd, genetics can also be used to track the origin of animals. (Frankham et al. 2010, Flesch et al. 2016)



Teton mountain range. Photo by Elizabeth Flesch., Montana State University

Biologists can use a part of the DNA called microsatellites to assess movements and isolation among groups of mountain ungulates. Microsatellites consist of short sequences of 1 to 5 nucleotides that repeat, such as AT AT AT. They are on chromosomes between the parts of the genome that code for traits such as hair color. Geneticists call the number of repeats at that location (locus) an allele. When DNA replication occurs, sometimes a copy of the repeating sequence (AT) is accidentally inserted or deleted on the new DNA strand, which leads to fewer or more repeats. Because they are non-coding (neutral) loci, mutations can occur in these loci without affecting the survival of the animal. At each locus, many different alleles (numbers of repeats) are possible. Thus, biologists can use microsatellites from a group of animals to detect genetic drift within a population and movements between populations. When no movements occur between groups, scientists predict that each group will have a distinct pattern of alleles. When an individual has alleles atypical for the group of animals where it was found, the individual or close relative of the individual may have moved from a different group of animals. As microsatellites are found throughout nuclear genomes of plants and animals and on mitochondrial DNA in animals, they can be used to understand the movement of both males and females, only females, or only males, depending on which microsatellite locus is studied. (Hamada et al. 1984, Weber and Wong 1993, Lunt et al. 1998, Avise 2004, Frankham et al. 2010)

Some microsatellite laboratory processes only provide information regarding the number of repeats found at the microsatellite site. Newer laboratory approaches sequence the nucleotides in the DNA using more automated processes, which provides improved certainty, objectivity, and speed. However, approaches that sequence tens to hundreds of thousands of loci, such as the SNP chip discussed above, provide more power to detect variation among individuals. The high rate of mutation in microsatellites also means that some alleles of the same length may have evolved independently in different groups of animals, which can sometimes cause confusion in studies evaluating which groups are isolated from each other. Nonetheless, because geneticists can identify microsatellites from

samples with degraded or little DNA, such as hair and fecal pellets, they can be useful for non-invasive sampling. (Balloux and Lugon-Moulin 2002)

USING GENETICS TO ASSESS ISOLATION AND SOURCE OF NON-NATIVE MOUNTAIN GOATS IN GRAND TETON NATIONAL PARK

Managers in Grand Teton National Park have been concerned about the effect of non-native mountain goats on the small, isolated bighorn sheep population in the Tetons. The first observations of solitary, likely transient, mountain goats in the Teton Range occurred in the late 1970s. Sporadic sightings of goats occurred through the 1980s and 1990s, including some of nannies with kids, but a population was not established. People observed a nanny and kid near the Grand Targhee ski resort in 2005, after which observations of mountain goats in the Tetons became more frequent. In December 2018, managers observed 88 mountain goats during a winter helicopter survey. As managers considered whether a removal program of the non-native mountain goats would be successful, they asked questions about the isolation and source of the mountain goats in the Teton Range.

The nearest mountain goat population is in the Snake River Range, southwest of the Tetons. The population originated from the introduction of 12 goats during 1969 to 1971 near Palisades, Idaho, that subsequently expanded 19 to 25 miles (30 to 40 kilometers) east into Wyoming. Most mountain goats in the Snake River Range are over 25 miles (40 kilometers) from the core range of mountain goats in the Teton Range, but in recent years, people have observed one billy and a few other scattered goats in the Snake River Range only 12 to 25 miles (20 to 40 kilometers) away from Teton Range goats. Concurrently, the closest mountain goat populations to the north, about 62 miles (100 kilometers) away, have expanded across the Beartooth and Absaroka Mountains. The nearest native goats to the Tetons are about 106 miles (170 kilometers) northwest in the Lemhi Range and Lima Peaks in Idaho and Montana. (Hayden 1984, Flesch et al. 2016)

To evaluate the likely source herd and assess recent gene flow with neighboring populations, biologists genotyped samples from 30 mountain goats captured in the Snake River Range, 28 in the Beartooth-Absaroka Mountains, and 13 in the Teton Range. They supplemented this with 34 fecal samples from the Teton Range in 2017. This resulted in 11 loci microsatellite-genotypes of 27 goats (13 males, 14 females) from the Snake River, 27 goats (9 males, 18 females) from the Beartooth-Absaroka Mountains, and 29 goats (12 males, 17 females) from the Teton Range. Three classification approaches, including PCA and STRUCTURE analyses, analogous to those applied to evaluate bighorn sheep populations, supported that the three areas are composed of three genetically distinct populations. Mountain goats in the Teton Range are genetically more similar to those in the Snake River Range than those in the Beartooth-Absaroka (Figure 2). In addition, genetic variation patterns and the presence of many private alleles found only in one area suggest the Beartooth-Absaroka population of mountain goats has multiple distinct subgroups.

Together, these analyses support the hypothesis that the most likely source of mountain goats in the Teton Range is the Snake River population and that migration between the three populations has not been common in recent generations. However, researchers may not have detected very recent movements because they did not have genotypes from all individuals in the Teton Range. Because the analysis also indicated potential substructure or variation within the Beartooth-Absaroka, scientists have limited confidence they have sufficiently characterized the genetic structure of that population. Researchers also do not have samples from a non-native herd about 73 miles (117 kilometers) away in the southern portion of the Madison Valley, Montana. Biologists need to conduct additional sampling to characterize the patterns of gene flow and genetic drift among those herds and more fully search for very recent movements.

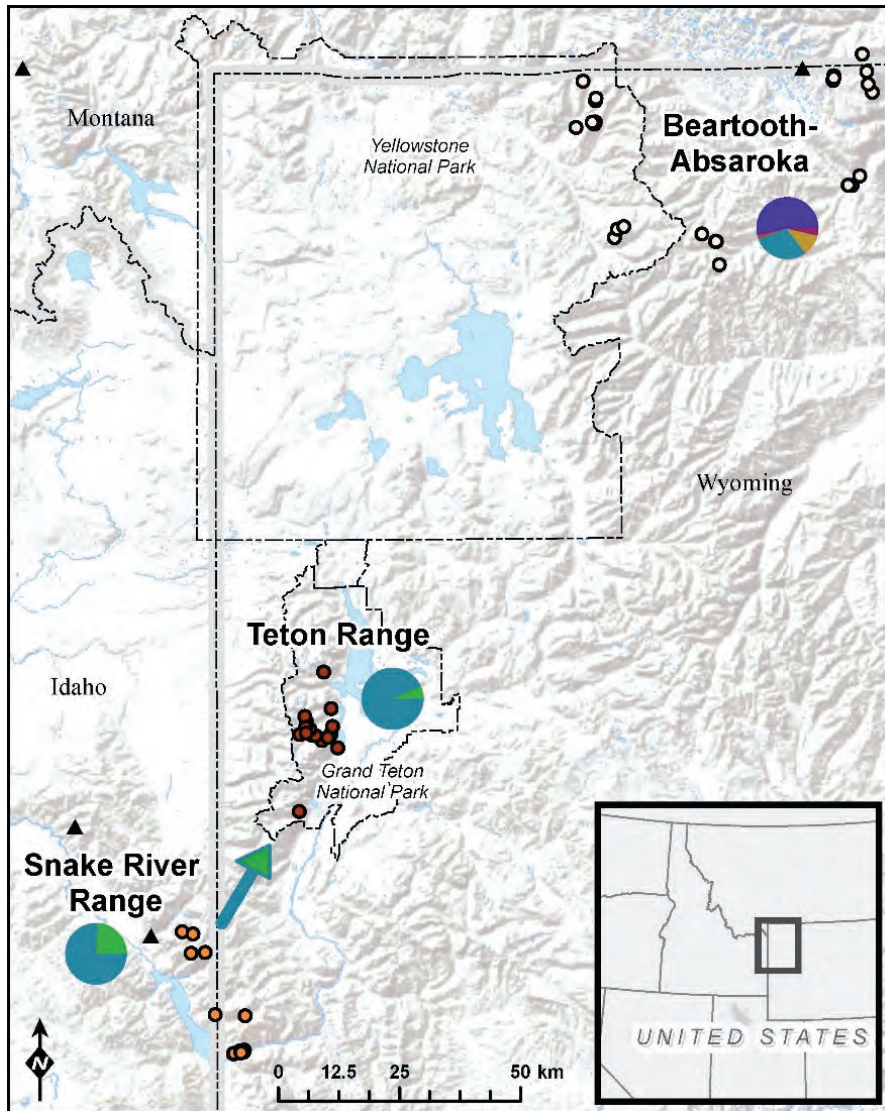


Figure 2. This map illustrates a microsatellite locus where allele frequencies are more similar for mountain goats in the Teton and Snake River Range than those in the Beartooth-Absaroka. Each color in a pie chart represents the frequency of alleles found at that locus for each population. The blue and green arrow indicates the likely dispersal direction of mountain goats given their genetic similarity and history. Points indicate locations where mountain goat genetic samples were obtained; black triangles indicate historic locations where mountain goats were released. Map by Elizabeth Flesch, Montana State University.

CONCLUSIONS

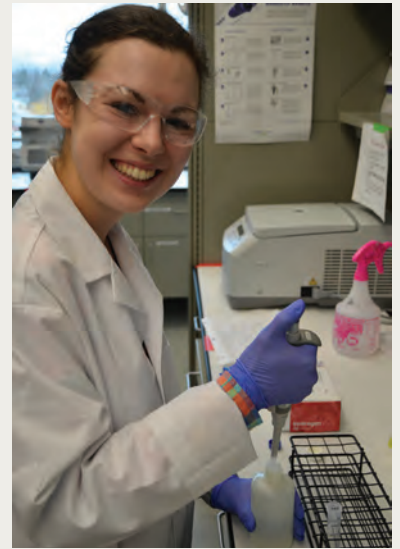
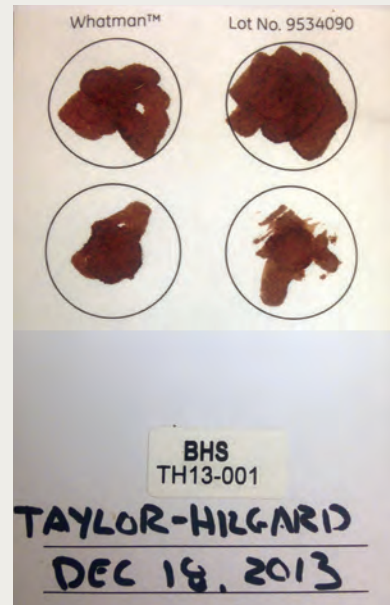
Efforts to study the DNA of bighorn sheep and mountain goats in the Greater Yellowstone Area have helped illuminate how past events shaped today's populations, which can aid future conservation and management decisions. Comparing the mitochondrial genomes of ancient and contemporary bighorn sheep can provide information regarding how the population changed over time due to natural and human influences. Genetic similarities between domestic sheep and bighorn sheep allowed for an in-depth study of today's bighorn sheep genomes, including identifying how populations in different regions are related and determining which translocated animals were successful in breeding at their new location. History of disease die-offs or small population size can affect how related individuals in the same herd are to one another, and researchers can assess the potential for a harmful level of inbreeding by calculating mean kinship using genomic data. Future work can explore if existing levels of inbreeding in bighorn sheep populations have influenced population growth and recruitment of young animals into the herd. Disease can also serve as an important influence on bighorn sheep population dynamics. Because the natural selection process has been ongoing since the introduction of exotic diseases, bighorn sheep herds may have evolved to be more resilient to the pathogens through a stronger immune response or some other mechanism that may be at least partially determined by genetics. Exploration of genetic differences that could affect individual immune system response may be able to improve understanding and management of this issue. Genetic research regarding mountain goats revealed similarities and differences among geographically disparate, introduced populations and identified the most likely source of dispersing animals that founded the population in Grand Teton National Park. These efforts can serve to inform decisions regarding the conservation of mountain ungulate populations in the Greater Yellowstone Area. Genomic research will likely become an increasingly valuable tool to enhance our understanding of the natural world and ourselves.



A group of bighorn sheep feeding in winter. Photo by Mark Gocke.

HOW WE LEARN: OBTAINING DNA SAMPLES FOR WILDLIFE GENOMICS STUDIES

To study the genetics of bighorn sheep and mountain goats, biologists collect blood, ear punches, tissue, and fecal pellets. Biologists label each sample with the animal's identification, location, date of sample, sex, and age (if known). When biologists capture an animal for sampling, they can safely collect a blood sample from a vein using a needle and syringe, in the same way that people have blood drawn for testing. Alternatively, biologists can place a few drops of whole blood onto a gene card, a paper treated with chemicals that stabilize DNA, for storage at room temperature for long periods. Biologists also collect ear punches with high quality DNA by punching a small hole in the ear with a sterile biopsy tool prior to ear tagging. In addition, scientists can extract DNA from muscle and lung tissue from animals harvested by hunters or killed by vehicles. Biologists can also obtain DNA by collecting fecal pellets or hair that animals have left behind, using a non-invasive collection approach. For example, researchers have placed barbed wire on rub trees and corrals of wire around scent lures to collect samples of hair from grizzly bears. Usually, less DNA is present in such non-invasively collected samples because DNA breaks down in sunlight. After researchers have collected samples, they extract the DNA from the sample in a laboratory.



Biologists collecting genetic samples from blood (upper left), which is put on a gene card (upper right), ear punches (lower left), and fecal pellets (lower middle). Biologist checking the quality of a bighorn sheep DNA sample in a laboratory at Montana State University (lower right). Photos by Elizabeth Flesch (upper left and right, lower left), Adrian Sanchez Gonzalez (lower middle), and Phil Merta (lower right) from Montana State University.



Bighorn sheep ram skull in a patch of heartleaf arnica. Photo by Jacob Frank, National Park Service.

Chapter 6

Health and Diseases

Mary E. Wood, Carson J. Butler, and Robert A. Garrott

INTRODUCTION

Bighorn sheep have been a focus of wildlife health investigations for over a century and reports of disease in bighorn sheep in the Greater Yellowstone Area date back to at least the 1880s. Many diseases have been identified and described in bighorn sheep and, to a lesser extent, mountain goats. It appears that mountain ungulates are susceptible to many of the diseases carried by domestic livestock and, in some cases, results of infection can be catastrophic. What is still poorly understood is the interaction of diseases that may have been native in mountain ungulate populations, those that were introduced through contact with domestic livestock but have attenuated over time, and those introduced by domestic livestock that still constitute a significant threat to the health and viability of mountain ungulate populations.

Despite some uncertainty regarding specific pathogens, which are agents that cause disease, most wildlife managers agree respiratory disease represents one of the most significant obstacles to bighorn sheep restoration. Outbreaks, called epizootics, occur in bighorn sheep populations with varying frequency and severity. Respiratory disease agents already present in a population can affect young lambs and the introduction of new diseases can lead to significant die-offs of animals across all ages followed by variable periods of poor lamb recruitment. Population-level responses to respiratory disease can vary dramatically from mild and sporadic, to long-term lamb losses with modest adult survival, to catastrophic all age die-offs and near population elimination.

While all-age die-offs can be highly visible and concerning, the prolonged poor lamb recruitment during or following an outbreak can be the most challenging factor to address. In some cases, poor lamb recruitment has continued in populations for decades after the initial disease event. This can lead to continually declining numbers of animals that are incapable of recruiting enough healthy lambs to support long-term population viability.

ORIGIN AND TRANSMISSION OF RESPIRATORY DISEASE

Most respiratory disease pathogens likely originated from domestic livestock and were introduced to North America during European settlement and subsequent imports of livestock. Early reports of large bighorn sheep die-offs consistently coincided with the introduction of domestic livestock to an area. Bighorn sheep are gregarious animals with a tendency to form larger social groups. It is this social nature that sometimes draws them to domestic livestock, particularly domestic sheep, resulting in the potential for disease transmission. While these pathogens can cause significant health concerns in domestic livestock, they have likely harbored them for centuries resulting in some amount of immune tolerance over time. In contrast, mountain ungulate populations did not evolve with these livestock pathogens and appear to be very sensitive to them, particularly when new pathogen species or strains are introduced.

While pathogens were likely initially introduced into populations through contact with domestic livestock, current evidence suggests new exposures can occur from contact with both domestic livestock and other mountain ungulate populations. Therefore, wildlife managers must consider internal conservation and translocation (relocation) efforts, natural movements of wild sheep and goats, as well as proximity to domestic livestock when evaluating the causes of respiratory disease events.

A COMPLEX HISTORY OF DISEASE

For over a century, wildlife managers have been documenting and researching disease-related die-offs in bighorn sheep populations. Many pathogens have been identified that cause respiratory disease, and new pathogens are still being identified. Thus, respiratory disease in bighorn sheep holds a complex history of continual search for the primary agents causing outbreaks, with each newly discovered pathogen bringing hope for a clearer management solution.

Early reports of die-offs in the late 1800s attributed disease and mortality to psoroptic mange, which is caused by mites (*Psoroptes ovis*) and typically associated with infestations in domestic sheep. Psoroptic mange in bighorn sheep causes crusty lesions or scabs with occasional yellowish or white discharge, mostly around the head and ears. Early reports of psoroptic mange in bighorn sheep date back to the late 1800s shortly after the arrival of domestic sheep, and this parasite is likely present to some extent in many populations in the Greater Yellowstone Area. The true population impact of psoroptic mange is unclear because disease diagnostics were limited until the late 20th century and concurrent conditions such as respiratory disease may have been under-recognized. (Honest and Frost 1942, Buechner 1960)

Starting in 1927, a new potential cause for bighorn sheep population die-offs was described when lungworm larvae were found in bighorn sheep dying of respiratory disease. Lungworm is a parasite caused by nematodes, primarily *Protostrongylus*, and is a native parasite of bighorn sheep. Initially, researchers speculated lungworm infestations caused damage and irritation to the lungs, allowing for secondary bacterial infections resulting in pneumonia. Reports of pneumonia in bighorn sheep became more and more common through the mid-1900s. Decades of work ensued, focusing on investigation, treatment, and management of lungworm infections in bighorn sheep with limited success in the overall management of populations. Experimental infection of lambs with lungworms did not cause fatal pneumonia and lungworms also were found in

apparently healthy bighorn sheep. This suggested lungworm may not be the sole agent causing respiratory disease, though it may still be a component in areas where it is prevalent. (Rush 1927, Forrester 1971, Samson et al. 1987, Muschenheim et al. 1990, Miller et al. 2000)

During the same period when research focused heavily on lungworm, some researchers began to investigate the potential role of viruses and bacteria. Work in the 1960s identified bighorn sheep exposure to common livestock respiratory viruses including bovine respiratory syncytial virus and parainfluenza 3, leading to questions about whether viruses could be the underlying cause of respiratory disease. Research into viruses in association with respiratory disease have continued over the years but, to date, investigations have failed to find a common thread in respiratory disease die-offs. (Howe et al. 1966, Parks and England 1974, Spraker et al. 1986, Miller et al. 2011, Dassanyake et al. 2013)

Research in 1962 began to suggest respiratory disease in bighorn sheep shared many similarities with shipping fever in cattle and that *Pasteurella* bacteria may be a primary causative agent. By the 1980s, work began to focus more on bacteria from the Pasteurellaceae family as a primary disease agent, referred to as pasteurellosis in bighorn sheep. For decades, research had identified *Pasteurella* bacteria in lungs of bighorn sheep dying of respiratory disease. However, investigators often considered these bacteria a secondary invader and continued searching for a primary disease agent. More research began to accumulate demonstrating consistent identification of *Pasteurella* bacteria in the lungs of sick sheep. In addition, the rapid disease course leading to mortality was inconsistent with lungworm infection, and experimental transmission of *Pasteurella* bacteria to bighorn sheep resulted in fatal pneumonia. The history of Pasteurellaceae evaluation in the face of respiratory disease is complicated by changes in the nomenclature of *Pasteurella* bacteria over time. While the same bacteria have been consistently identified in bighorn lungs (*Mannheimia* sp., *Pasteurella* sp., *Bibersteinia* sp.), the nomenclature of these bacteria

has changed significantly, leading to some difficulty in tracing commonalities in bacterial agents over time. Additionally, different strains of Pasteurella bacteria have been identified, which appear to lead to a variable effect in animals. In some cases, Pasteurella bacteria were isolated from apparently healthy sheep as well as those with respiratory disease. This complicated efforts to identify a single cause since disease expression in populations seemed highly variable with no clear understanding of underlying factors that may contribute to that variability. Research began to return to earlier reports and suspicions that underlying factors including stress, parasites, nutrition, and habitat may play a role in the variation of disease outcomes associated with Pasteurella bacteria, like shipping fever in cattle. (Post 1962, Monello et al. 2001, Miller et al. 2012)

Beginning in 2008, scientists began focusing on another bacterium, *Mycoplasma ovipneumoniae*, in the respiratory disease complex. Like work on Pasteurella, this new research was a follow up of earlier work identifying Mycoplasma bacteria in bighorn sheep in 1970. Infection with Mycoplasma bacteria can cause clinical signs of respiratory disease in bighorn sheep; however, it does not consistently lead to mortality. One of the main concerns for this bacteria is its' capacity to impair an animal's ability to clear other pathogens from the respiratory tract. Researchers began to consider the potential for Mycoplasma to act as a primary infectious agent that would then make bighorn sheep more susceptible to infection with Pasteurella bacteria. A flurry of research followed with heavy focus on Mycoplasma as a primary cause of respiratory disease in bighorn sheep. Studies began to focus on the potential to identify and remove Mycoplasma-infected animals with the hope that this may prove a viable management strategy. As research on *Mycoplasma ovipneumoniae* accrued, many of the same issues that plagued Pasteurella as a primary causative agent were identified. For example, different strains of Mycoplasma bacteria appear to lead to different disease outcomes and Mycoplasma bacteria have been isolated from apparently healthy bighorn sheep and in populations without indication of clinical respiratory disease.



*Sampling a mountain goat for respiratory pathogens. This biologist is collecting a tonsil swab sample.
Photo by Mark Gocke, Wyoming Game and Fish Department.*

Again, these findings complicate efforts to identify a single cause of respiratory disease in bighorn sheep. As research on *Mycoplasma ovipneumoniae* continues, more focus has been placed on understanding variations in bacterial strains that may cause some strains of Mycoplasma to be more capable of causing disease than others. (Woolf et al. 1970, Besser et al. 2008, Butler et al. 2018, Kamath et al. 2019)

Amidst the flurry of research on *Mycoplasma ovipneumoniae*, researchers in Colorado began noticing unusual changes to the sinuses of bighorn sheep culled from populations with respiratory disease. These sheep had chronic sinus infections as well as overgrowth of the sinus lining and bone. These growths, currently referred to as sinus tumors, can fill the sinuses of bighorn sheep and occasionally even erode through the skull. The tumors appear to be infectious and a viral cause is suspected; however, the definitive causative agent has yet to be identified. Sinus tumors can obstruct the sinus cavities of a bighorn sheep and may impair clearance of respiratory pathogens from the sinuses. In this way, sinus tumors appear to provide an ideal environment for bacterial proliferation as well as a mechanism for bacterial shedding and transmission. (Fox et al. 2011, 2015, 2016)

Each new discovery of a potential causative agent led to a new wave of research and debates among researchers. Significant effort was put forth to identify the single pathogen responsible for respiratory disease in mountain ungulates. What has become apparent is that each newly identified disease agent was likely additive to the disease complex rather than a replacement of agents previously identified. Ultimately, it appears respiratory disease is a complex syndrome that likely results from the convergence of numerous disease agents interacting with other ecological factors at the population level. Both respiratory disease and the pursuit to better understand its causes are ongoing.

RESPIRATORY DISEASE – CURRENT UNDERSTANDING

Many pathogens have been implicated in bighorn sheep respiratory disease and the relative importance of each has been vigorously debated among researchers. Most researchers agree respiratory disease is characterized by multiple pathogens combined with multiple outside factors leading to variable disease expression in a population. Current research suggests the primary pathogens involved in the disease syndrome include the bacterium *Mycoplasma ovipneumoniae* and multiple species of bacteria belonging to the Pasteurellaceae family, some of which carry a toxin (leukotoxin) that attacks white blood cells. Further research indicates infectious tumors found in bighorn sheep sinuses may be a significant contributor to the respiratory disease complex by preventing normal clearance of bacterial pathogens from the sinus lining. In addition to these pathogens, other bacteria such as *Fusobacteria necrophorum*, as well as respiratory viruses including parainfluenza, bovine respiratory syncytial virus, and bovine herpesvirus-1 (infectious bovine rhinotracheitis), and parasites such as lungworm or psoroptes mites have been implicated as potential co-factors.

Data suggests some pathogens are sufficiently virulent to cause severe disease outbreaks in the absence of other ecological factors. Captive studies involving the comingling of bighorn sheep with domestic sheep consistently result in the mortality of bighorn sheep. However, the broad variability in disease outcomes among free-ranging bighorn sheep populations in the West also suggests that, in some scenarios, other factors may significantly contribute to disease outcomes at the population level. These could include ecological factors such as habitat availability and use, forage quality, trace minerals, population density and crowding, predation, translocation efforts, loss of population knowledge of optimal landscape use, as well as animal factors such as nutritional status and immune competence and responses to disease agents. These factors may be particularly important in populations in the Greater Yellowstone Area that tend to be large and robust with diverse habitat

utilization, potentially resulting in more disease tolerance than smaller, transplanted populations in other areas across the West. (Besser et al. 2012b, Dassanyake et al. 2013, Fox et al. 2015, Shanthalingam et al. 2016, Butler et al. 2018)

RESPIRATORY DISEASE IN MOUNTAIN GOATS

Most research and understanding of respiratory disease in mountain ungulates focuses on bighorn sheep; however, more recent research has begun to investigate disease in mountain goats. Most respiratory pathogens of bighorn sheep have also been documented in mountain goats including lungworm, *Mycoplasma ovipneumoniae*, multiple *Pasteurella* species, respiratory viruses, and sinus tumors. Population responses to these respiratory pathogens in mountain goats are less well documented than in bighorn sheep. However, clinical signs of disease and negative population impacts from these pathogens have been described in recent literature. Documentation of respiratory pathogens in mountain goat populations brings a concern for negative population impacts, as well as concern over the potential for disease transmission between bighorn sheep and mountain goats on shared ranges. (Dunbar et al. 1986, Blanchong et al. 2018, Lowrey et al. 2018a, Wolff et al. 2019)

EPIDEMIOLOGY AND SIMILARITIES TO DOMESTIC DISEASES

Throughout the years, multiple researchers have suggested respiratory disease in bighorn sheep shares many similarities with shipping fever (also known as bovine respiratory disease) in cattle. This is a complex disease syndrome where multiple factors come together to result in respiratory disease in cattle, particularly in calves. Typically, this disease is caused by the interaction of primary stressors such as weaning, shipping, handling, and nutrition that may weaken the immune response of the animal and allow for bacteria to infect the lungs and cause pneumonia. Effective management of this syndrome in livestock includes managing stressors, reducing overcrowding, vaccination, and implementing treatment of sick animals.

It is only through this combined approach that effective management of shipping fever is achieved.

Shipping fever provides an excellent example of why we must recognize the role of multiple factors on disease expression in a population. Epidemiology is the basic study of the patterns, causes, and distribution of disease in a population. This field of study is highly valuable when trying to understand what factors affect an outbreak of disease in a population. One of the simplest epidemiology concepts is the Epidemiologic Triad, where disease expression in a population can be considered a function of the relationship between a disease agent, a host (such as an animal that can get the disease), and the environment. There are many complex interactions that can occur between an agent, host, and the environment to result in various disease outcomes within a population. To understand disease outcomes and identify potential preventative measures or management options, one must assess all three components and their interactions.

HISTORY OF RESPIRATORY DISEASE AND OUTCOMES IN THE GREATER YELLOWSTONE AREA

The Greater Yellowstone Area holds one of the greatest remaining concentrations of bighorn sheep in the United States. As such, it may surprise many to learn the ecosystem has a long history of disease die-offs, dating back to the 1880s. By the early 20th century hundreds of thousands of domestic sheep grazed even the most remote areas. Die-offs caused by pneumonia were recorded as early as the 1920s in Yellowstone National Park and records of psoroptic mange die-offs date back to the 1880s in the Wind River Range, the Absaroka Range, and the Beartooth Range. It is plausible pneumonia also contributed to these early die-offs attributed to psoroptic mange. In the Meeteetse, Wyoming area, a disease die-off in 1880 reduced the number of bighorn sheep that could be counted in the foothills above the Greybull River from 'thousands' to several dozen in 1881. In the Gros Ventre

mountain range, a pneumonia die-off reduced the number of animals counted in the area from 1,207 in 1934 to 234 in 1938. Though early records are sparse, examples such as these suggest bighorn sheep throughout the Greater Yellowstone Area suffered immense disease-related losses following the introduction of domestic sheep to the region. Despite the devastating impacts of disease, bighorn sheep populations managed to persist in many parts of the ecosystem and most contemporary populations are 'native' populations whose ancestors occupied the region for millennia and survived the introduction of non-native diseases. (Honest and Frost 1942, Buechner 1960)

Disease continues to affect bighorn sheep throughout the Greater Yellowstone Area, with a wide range of severity and outcomes. The most well-known example is the pneumonia die-off that struck the renowned Whiskey Basin population in 1991. Nearly 30 years after the all-age die-off, lamb recruitment remains well below pre die-off levels and the population is less than half of its former size. In contrast, the neighboring Jackson population, which occupies the Gros Ventre and northern Wyoming ranges, went through two pneumonia die-offs since 2000 but quickly rebounded to pre die-off levels in both cases. Like the Jackson population, the Upper Yellowstone population, which is spread throughout the upper Yellowstone River drainage in Montana and Yellowstone National Park, experiences chronic, relatively mild, pneumonia symptoms, but managed to maintain and rebound after recent disease events. In the Madison Range, the Hilgard population was nearly extirpated after a second pneumonia die-off during the severe winter of 1996-1997 left only a few dozen animals alive. However, the population rapidly recovered and grew to nearly 300 individuals by 2013. A population introduced to the lower Boulder River drainage of Montana went extinct following a pneumonia outbreak that occurred in 2000. Other populations in the Absaroka, Beartooth, Teton, and northern Madison ranges have no confirmed history of pneumonia die-offs, though it seems likely that historical die-offs occurred. Additional pneumonia die-offs have likely occurred in modern

times; however, many populations occupy such remote locations that confirming pneumonia as a cause of sudden population declines is nearly impossible. For example, between 2011 and 2013 bighorn sheep counts and lamb recruitment in the southern Absaroka Range declined sharply and hikers recovered over 150 skulls of recently deceased rams in the area over multiple years. The pattern strongly suggests a pneumonia die-off occurred, but no conclusive evidence exists. Cases of pneumonia in individual animals are relatively common throughout the ecosystem. (Ryder et al. 1992, Montana Fish, Wildlife and Parks 2010, Sells et al. 2015, Butler et al. 2018)

As newcomers to the Greater Yellowstone Area, mountain goats do not have the same history of disease as bighorn sheep. The steady expansion of mountain goats across the area suggests disease is not currently having a significant impact on their populations. However, isolated cases of pneumonia mortality have been reported.

RESPIRATORY PATHOGENS IN BIGHORN SHEEP AND MOUNTAIN GOAT POPULATIONS

The bacteria linked to pneumonia in bighorn sheep are essentially ubiquitous among bighorn sheep populations in the Greater Yellowstone Area. *Pasteurella* bacteria are present in all tested populations, as is *Mycoplasma ovipneumoniae* except in the Teton Range. This likely reflects a long-history of respiratory disease in the ecosystem, as well as intact historical lineages and connectivity among most remaining populations. The pathogens found in present populations may have been circulating since the arrival of domestic sheep to the ecosystem nearly 150 years ago, though it is impossible to know their origins with certainty. The same bacteria also have been found in most mountain goat populations that have been tested in the ecosystem, once again, except for the Teton Range. (Butler et al. 2018, Lowrey et al. 2018a)

The effects of respiratory pathogens can be catastrophic to bighorn sheep populations, as they were for the, now extinct, population in the Boulder River. However, the common presence of these pathogens in one of the continent's

strongholds for bighorn sheep indicate populations in the Greater Yellowstone Area may possess some resiliency in the face of respiratory disease. The reasons for this resiliency are currently unknown but may be a combination of factors such as habitat availability and utilization, population size, and possibly some attenuation (or lessening of severity) of pathogens over time. Since many of the populations are large, native populations that have developed population-knowledge of the landscape over millennia, it may be that their ability to occupy a diverse range of habitats and utilize varied survival strategies is what provides them with some buffer in the face of respiratory disease.

OTHER DISEASES AND PARASITES

While respiratory disease currently represents the most significant disease concern facing mountain ungulate populations, multiple other diseases and parasites have been identified with varying levels of impact and concern to populations. Contagious ecthyma, otherwise known as orf, sore mouth, or scab mouth, is a viral disease documented in both bighorn sheep and mountain goats. The disease results in scabby lesions primarily on the lips and muzzle, but also occasionally on the legs, feet, udder, and labia. Lesions typically heal in 1 to 2 months and animals develop some amount of immunity after infection. While contagious ecthyma does not typically result in high mortality, severe cases with significant lesions around the mouth can reduce foraging and lead to poor body condition and sporadic mortality. While some amount of contagious ecthyma is seen in mountain ungulate populations in the Greater Yellowstone Area, periodic larger outbreaks may be seen when many naïve animals are exposed to the disease. Contagious ecthyma is a zoonotic disease and humans can develop painful sores after handling affected animals. (Samuel et al. 1975)

Infectious keratoconjunctivitis or 'pink-eye' is a contagious disease affecting the eyes. The disease is associated with low mortality but can affect large numbers of animals within a population given the right conditions. Clinical signs in bighorn sheep



Bighorn sheep ram with contagious ecthyma (sore mouth). Although deaths can be associated with this disease, animals can, and do recover. Photo by Jacob Frank, National Park Service.



Keratoconjunctivitis, or pinkeye, has caused the cloudy left eye of this bighorn sheep ewe. Although not fatal itself, this disease leaves animals vulnerable to predation and accidents. Photo by Doug McWhirter, Wyoming Game and Fish Department.

have been reported as mild to severe discharge from the eyes, swelling of the eyelids, cloudy or milky eyes, and blindness in severe cases. The disease can affect either one or both eyes. An outbreak of keratoconjunctivitis associated with a *Chlamydia sp.* bacteria was reported in bighorn sheep in Yellowstone National Park in the early 1980s. The outbreak was reported to cause a die-off of approximately 60% of a population estimated at 500 bighorn sheep. While there are occasional reports of outbreaks in mountain ungulate populations, additional die-offs associated with keratoconjunctivitis have not been reported in the Greater Yellowstone Area. Sporadic cases of keratoconjunctivitis undoubtedly still occur, however, it is not currently considered a disease of significant concern at the population level. (Meagher et al. 1992)

Additional diseases have been documented in mountain ungulates; however, cases appear to be sporadic in the Greater Yellowstone Area and do not currently appear to cause significant persistent population-level impacts. These diseases include, but may not be limited to, bluetongue virus, anaplasmosis, Johne's disease, malignant catarrhal fever, bovine viral diarrhea, necrobacillosis, and a variety of internal and external parasites.

ASSESSING NUTRITION AND PHYSIOLOGICAL STATUS

Mountain ungulates live in a seasonal environment that typically provides nutritious and abundant forage during the 5 to 6 month growing season with energy and protein in excess of what the animals need for daily body maintenance. The excess nutritional resources are converted to muscle mass and fat that are used by the animals during the remaining 6 to 7 months of the year when nearly all plants are dry and dormant and lack the nutrition to meet daily metabolic demands. The typical deep winter snows experienced in the Greater Yellowstone Area add to nutritional stress because animals must expend additional energy to move through the snow pack and uncover plants when foraging.

In a typical year, air temperatures and precipitation during the spring and summer result in a growing season that produces an adequate quantity and quality of forage for mountain ungulates to store enough body reserves to survive the prolonged period of winter shortages as well as nourish the unborn young conceived in the fall until birth in spring. Weather conditions, however, are quite variable from year-to-year and from place-to-place across the expansive landscape. Droughts, extended growing seasons due to good late summer and fall precipitation, annual differences in the duration and depth of snow, and grazing by other wildlife and livestock all impact the forage resources available to mountain ungulates. Changes to plant communities due to fire suppression, wild fires, invasive plants, and human activities and development can also influence the seasonal ranges traditionally used by mountain ungulates and the availability of resources they need to maintain health, survive, and reproduce. Hence, wildlife managers are keenly interested in developing and employing practical techniques that can allow them to assess animal nutrition and physiological status.

One such technique to evaluate the nutritional status of a population is to utilize ultrasonography in combination with physical palpation and measurement of an animal to generate an overall body condition score and measure subcutaneous fat thickness. This information can be taken from multiple animals within a population to give an estimate of the overall nutritional condition of the population. While only providing a snapshot in time, the nutritional status of animals in a population may reflect on ecological factors influencing population dynamics such as habitat quality and forage availability on the landscape. This information may be useful when evaluating outside factors that may influence a population and its response to respiratory disease. (Cook et al. 2001, 2007)

While body condition scoring and ultrasound measurements are providing biologists insight into the nutritional status of wild ungulates in the Greater Yellowstone Area, newer techniques may provide opportunity for expanded information. Metabolomics is a relatively new field of science that holds promise to expand the



Sampling a big horn sheep for pregnancy using ultrasonography. Another method used to assess pregnancy is based on the presence of hormones in collected blood samples. Photo by Mark Gocke, Wyoming Game and Fish Department.



Nuclear magnetic resonance spectroscopy machine used to detect biological molecules (metabolites) in blood samples that may hold promise as a technique to assess the nutritional and health status of animals. Photo by Bob Garrott, Montana State University.

ability of veterinarians, managers, and researchers to characterize the health and physiological status of wild animals. Metabolomics identifies and measures the quantities of metabolites, which are biological molecules, that represent intermediate and end products of the myriad complex biochemical processes that occur inside cells that support life. This rapidly expanding research field may better explain the functional nutritional and health states of plants and animals and is currently routinely used in the fields of human health, crop characterization, domestic livestock production, food and nutritional analyses, and environmental monitoring. Over the past five years, many hundreds of bighorn sheep and mountain goats have been captured in the Greater Yellowstone Area for ecological research. Serum extracted from blood samples obtained from these animals is being used to explore the potential of metabolomics to improve our understanding of the health and physiological status of the many populations managed by state and federal agencies in the area.

HOW WE LEARN: HEALTH AND DISEASES

Wildlife managers, veterinarians, and researchers collect samples and take measurements from mountain ungulates to test for disease agents and evaluate their general health and nutritional status. Samples collected may vary depending upon funding, research interests, and availability of diagnostic testing. Commonly collected samples and measurements may include feces to evaluate for parasites; nasal and tonsil or oropharyngeal swabs to test for bacterial pathogens; blood to test for exposure to viruses, evaluate trace minerals, look at white blood cells, and obtain DNA for genetics; ear swabs to check for mites; and ultrasound to check pregnancy status and evaluate nutritional condition.



Biologists collect samples and take measurements from mountain ungulates to test for disease agents and evaluate their general health and nutritional status. Photos by Mark Gocke, Wyoming Game and Fish Department (upper left and right), Montana Fish, Wildlife and Parks (lower left), and Jim Berardinelli, Montana State University (lower right).



A pair of bighorn sheep lambs in early winter. Photo by Mark Gocke.

Chapter 7

Population Dynamics

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Kelly M. Proffitt, Jay J. Rotella, and Kevin Monteith*

INTRODUCTION

When you see wildlife in a natural environment such as an alpine meadow, you notice and appreciate the individual animals, their physical characteristics and behavior, whether they are alone or in a group, how they interact with others, and so on. In short, you are conscious of, and value, animals as individuals. Except for extremely rare species, which may number only in the tens or hundreds of individuals, conservation and management focuses on populations, which are aggregations of freely interacting individuals of the same species occupying a defined area at the same point in time. When there are isolated aggregations of animals occupying a distinct portion of the landscape it is relatively easy to define the distribution of the animals that make up that population. Such is the case for the Spanish Peaks bighorn population found in the northern portion of the Madison Range in the western portion of the Greater Yellowstone Area, as well as the bighorn population found in the Teton Range of Grand Teton National Park. However, when animals occur over a large landscape because of the routine seasonal movements to access disparate ranges, defining populations becomes more difficult. For example, mountain goats found throughout the northern portion of the Greater Yellowstone Area, as well as bighorn sheep distributed from the Beartooth Range in Montana all the way south along the Absaroka Range in Wyoming adjacent to the eastern boundary of

Yellowstone National Park (Figure 1). Despite the difficulty of defining populations, it is important because effectiveness of conservation and management is evaluated at the population level where agencies with administrative responsibilities routinely conduct surveys to collect data on abundance and other demographic attributes of the population. These surveys are generally conducted over a fixed area that is practical to survey and is the biologist's best estimate of the landscape occupied by an aggregation of freely interacting individuals. Surveys are performed to answer the fundamental question of 'how well are they doing', this is, are the number of animals within the survey area stable, increasing, or decreasing. If the trend in abundance is not meeting conservation or management objectives then the important question is why? For populations that are relatively isolated from one another biologists can focus on assessing reproduction and survival in an attempt to ferret out the underlying mechanisms driving the trend. When animals are more broadly distributed and split into multiple population units, the sleuthing for underlying mechanisms becomes more challenging as movements of animals among adjacent areas also may come into play.

Studies of seasonal movements of bighorn sheep and mountain goats in these areas (see chapter 4) indicate animals within localized regions interact more freely than animals in more distant locales, resulting in population substructure called a metapopulation, or what might be considered an interacting set of subpopulations. These subpopulations experience largely independent trends in reproduction and survival, but their fates are somewhat connected because movements of some animals among subpopulations loosely link them together. From the perspective of conservation, metapopulations are more desirable than isolated populations because when local conditions result in poor reproduction and survival in one subpopulation, movements of animals from other subpopulations experiencing more favorable conditions can bolster the struggling subpopulation. Thus, metapopulations are more resilient to the vagaries of climate and nature than isolated populations and,

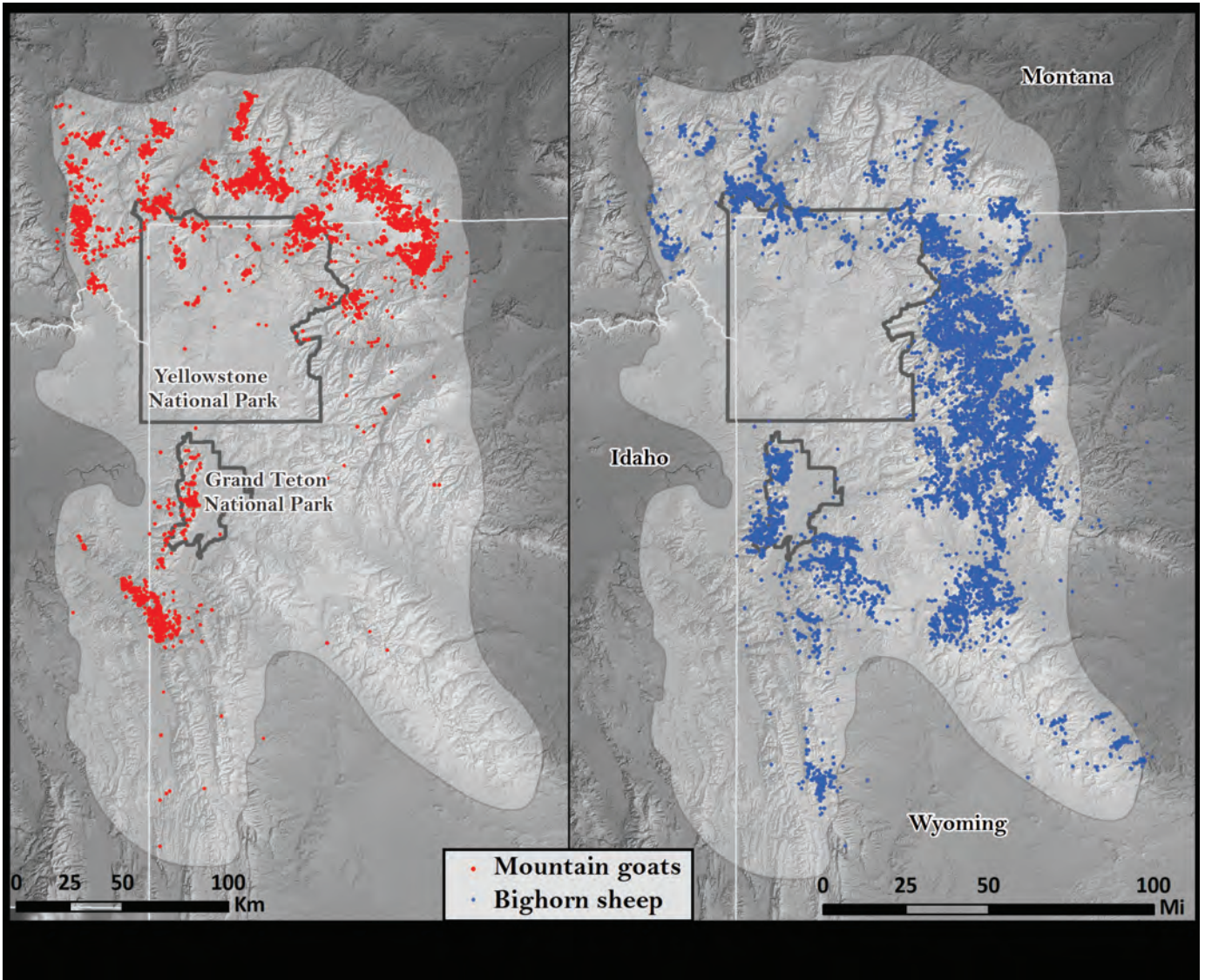


Figure 1. The distribution of bighorn sheep (blue) and mountain goats (red) in the Greater Yellowstone Area. Figure by Elizabeth Fleisch, Montana State University, and colleagues (2016).

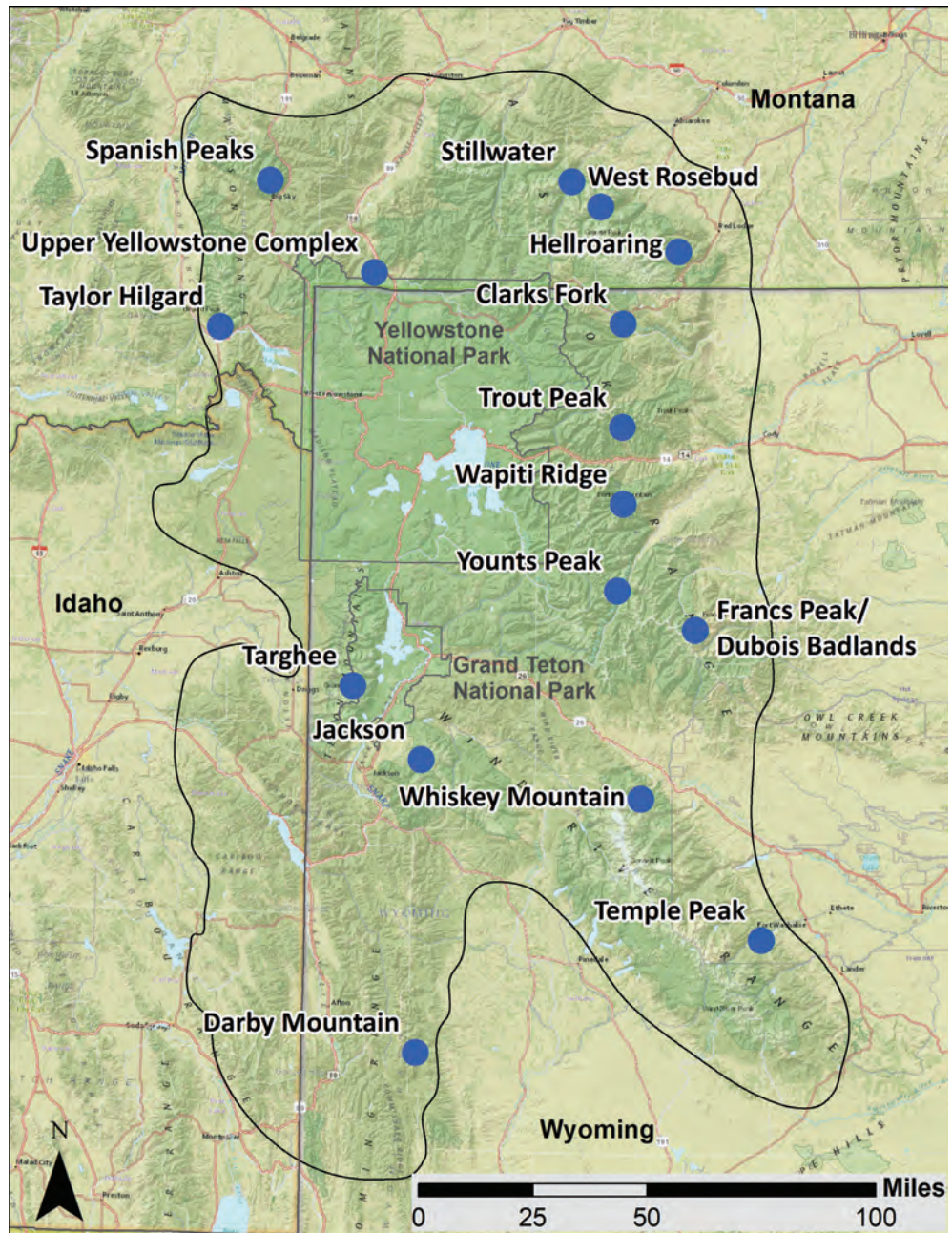


Figure 2. Bighorn sheep population locations and names. Map by Blake Lowrey, Montana State University.

as a result, they are less likely to undergo large changes in abundance over time. (Hanski 1999)

There are 16 recognized bighorn sheep populations distributed throughout the mountain ranges of the Greater Yellowstone Area (Figure 2). Relatively distinct and isolated populations include the Spanish Peaks and Taylor-Hilgard herds in the Madison Range, the Stillwater, Hellroaring, and West Rosebud herds in the northern Absaroka Range, Whiskey Mountain and Temple Peak herds in the Wind River Range, Jackson in the Gros Ventre Range, Targhee in the Teton Range, and Darby Mountain in the Wyoming Range. There is a large metapopulation of bighorn sheep in the eastern Absaroka Range composed of five population units, including the Clarks Fork, Trout Peak, Wapiti Ridge, Younts Peak, and Francs Peak. In addition, the Upper Yellowstone metapopulation complex is composed of about a dozen small groups of 20-80 animals that winter along the Yellowstone River and migrate into surrounding high-elevation mountainous areas during summer.

Identifying distinct mountain goat populations is difficult because they have been slowly expanding their distribution in the Greater Yellowstone Area since their introduction and there has been limited ecological research on them. Mountain goats occur throughout the Madison, Gallatin, north Absaroka, and Beartooth Ranges in Montana, as well as the northern portion of Wyoming's Absaroka Range and the Snake River Range spanning the Idaho-Wyoming border. Mountain goats have recently established a reproducing population in the Teton Range and distributions are expanding southward in Wyoming's Absaroka Range along the eastern border of Yellowstone National Park. The limited data on seasonal movements in the Greater Yellowstone Area suggest that individual mountain goats generally occupy relatively restricted home ranges; thus in those mountain ranges where mountain goats are broadly distributed we expect a metapopulation structure.

Biologists with the state and federal agencies responsible for conserving and managing these bighorn sheep and mountain goat populations conduct surveys on

an annual or semiannual time frame to obtain estimates of abundance and the number of young animals added to the population. Agencies also track the location, age and sex of all harvested bighorn sheep and mountain goats. In recent years, many populations have also been incorporated into regional research projects using radio-collared adults to provide estimates of pregnancy and survival rates, as well as insights into common sources of mortality.

REPRODUCTION

The annual cycle of reproduction is similar for bighorn sheep and mountain goats. Mature females ovulate and become receptive to mating with males in autumn. Female bighorn are typically sexually mature by the time they reach 2.5 years of age, whereas mountain goat females are slower to mature, normally breeding for the first time at 3.5 to 4.5 years of age. In general, the breeding season in the Greater Yellowstone Area for bighorn sheep and mountain goats is mid-November to mid-December, but there is some variation in the timing of the breeding season from population to population. The timing of breeding and births in populations generally is synchronized to local environmental conditions such that young are born when resources required for their successful rearing to independence are maximized. Large herbivores (plant eaters) like bighorn sheep and mountain goats time breeding such that young are born in spring when plant communities are initiating seasonal growth, which provides the most nutritious forage to support nursing and maximize the time young have access to high-quality forage after weaning and prior to the onset of winter. There is considerable variability in the timing of the growing season for plants across the Greater Yellowstone Area depending on the elevation of bighorn sheep and mountain goat spring and summer ranges. A good example of synchronization of the breeding season to local environmental conditions is the Stillwater bighorn sheep herd that summers on the high-elevation Beartooth Plateau in the northeastern portion of the Greater Yellowstone Area. These animals breed approximately

one month later than what is typical for most bighorn populations in the area such that lambing occurs in late June to early July. In contrast, bighorn living 200 miles north of the Stillwater herd in the low-elevation prairies associated with the Missouri River in eastern Montana breed two months earlier, lambing in late-April to early May. (Geist 1971, Stewart 1982, Festa-Bianchet and Côté 2008)

When bighorn sheep and mountain goats breed in late-fall, they are in their peak body condition. They have recovered from the nutritional stress incurred during the winter by foraging on nutritious green vegetation throughout the spring and summer growing season and have increased substantially in weight by converting the energy and protein of the plants they have consumed into both muscle mass and fat. Growing season conditions on summer ranges in the Greater Yellowstone Area are normally sufficient for females to accrue adequate body fat during the summer to sustain a pregnancy the next fall, winter and spring. Extensive testing of mature bighorn sheep females captured for research indicates that typical annual pregnancy rates for most herds in this area are high, ranging from 87 to 95%. However, annual variation in weather can result in considerable year-to-year variation in the growing season and available forage resources. After severe winters, deep snow can persist up to a month longer in the spring than average, resulting in a delay in the initiation of the growing season. Likewise, the duration of the growing season can vary annually, with hot dry summers resulting in relatively short growing seasons and cooler wetter summers extending the growing season into the fall. The plants that bighorn sheep and mountain goats consume yield the most energy and protein when they are green and growing, so annual variation in length of the growing season due to the capriciousness of weather conditions can affect the amount of nutrition available and the muscle and fat that animals can accrue over summer. In years when the growing season is abbreviated, some females may not attain adequate body condition by fall to ovulate and breed. Indeed, bighorn herds throughout the Greater Yellowstone Area show evidence of poor years in forage conditions with pregnancy rates declining



A nanny-kid group of mountain goats on the Beartooth Plateau. The body condition of females determines pregnancy, and combined with weather, disease, and predation determine the productivity of a population. Photo by Mark Gocke.

to as low as 42 to 80%. Although data on pregnancy rates of mountain goats for populations in the Greater Yellowstone Area are not available, intensive studies of a Canadian mountain goat population suggest a similar range in annual pregnancy rates as that documented for bighorn sheep (Festa-Bianchet and Côte 2008)

As breeding season begins, mature males of both species, which have been generally on their own throughout the summer, join the nursery groups of females, young of year, and immature males. Both bighorn sheep and mountain goats are polygamous, with males intensely competing with each other for opportunities to mate receptive females. In most polygamous large mammals, males tend to be larger than females, a trait that likely evolved because of intense competition among males during the breeding season. Mature male bighorn sheep are approximately 40% larger than adult females, with adult males weighing 175 to 250 pounds (79 to 113 kilograms) compared with the typical weight of females of 130 to 190 pounds (59 to 86 kilograms). The difference in body size between the sexes is similar for mountain goats with males weighing 190 to 245 pounds (86 to 111 kilograms) while females range from 120 to 160 pounds (56 to 73 kilograms). During the breeding season, males display their bodies and horn sizes to one another during ritualized posturing behaviors with larger, older males tending to be dominant over younger, smaller males. Physical competition between males of similar size and dominance is common and on spectacular display when two large bighorn sheep rams square off a short distance from one another. They rear up on their hind legs, charge forward, and use the full weight and strength of their bodies to clash their horns together with a resounding crack that people can hear from as far as a mile away. The shock of the impact can frequently drive one of the combatants backward and sometimes damage their horns. Physical competition among mature mountain goat males is not as dramatic, likely because their thin, short, dagger-like horns could easily inflict mortal wounds. In contrast to the head-to-head confrontation of bighorn rams, competing male mountain goats stand broadside to one another, oriented head to



Bighorn rams preparing to clash heads during the rutting season. These clashes cause horn tips to become splintered or broken, sometimes significantly (inset). Rams also use body postures and horn displays as a non-combative way to establish dominance. Photo of rams clashing by Kenneth R. Whitten; photo of ram with broken horn by Jacob Frank, National Park Service.

rump, and use their horns to attempt to strike their opponent on the flank or rump. Serious wounds are rare, but minor punctures and slashes are common. Older males have a thick dermal shield on the rump approximately 0.6 to 0.9 inches (1.5 to 2.3 centimeters) that likely minimizes the damage caused by horning during escalated fights. (Geist 1967, 1971, Festa-Bianchet and Côte 2008)

Gestation length for both mountain goats and bighorn sheep is approximately 6 months (170 to 180 days). As date of birth nears, the female usually separates herself from her normal social group and seeks out an isolated location in rugged terrain where she will remain secluded for several days to a week after the birth. Bighorn sheep normally give birth to a single lamb, and twinning is rare. Twins are more common in mountain goats and there are occasional reports of triplets. The frequency of twinning is an index of the relative quality and quantity of forage available on the summer range. The level of nutrition a female obtains before entering winter as well as conditions experienced during the winter will influence the growth rate of the fetus, with young of both species typically weighing between 7 and 9 pounds (3.2 to 4.1 kilograms) at birth. Animals on poor quality summer or winter ranges or those that experience exceptionally severe winter conditions may give birth to underweight young that have a low probability of surviving the first few days of life. After the birthing season both bighorn sheep and mountain goats aggregate into nursery groups that can exceed 50 animals. Although young nurse through the summer, they begin eating vegetation within a week to 10 days after birth and are routinely grazing by the time they are 3 weeks old. Weaning may occur anytime between late July and September, but occasional suckling occurs through the fall and winter. There is a strong social bond between the mother and her young during the summer, but in bighorn sheep the bond weakens over the winter with lambs essentially independent by spring. In contrast, the social bond between mountain goat mothers and their young commonly extends into the second year. (Lentfer 1955, Geist 1971, Festa-Bianchet and Côte 2008)



A mountain goat nanny and kid. Tight bonds are formed between mother and offspring, as the nanny is responsible not only for sustenance and defense, but also for showing her kid how to navigate the landscape and find foraging areas at various seasons. Photo by Mark Gocke.

SURVIVAL RATES AND CAUSES OF MORTALITY

Survival rate is defined as the probability that an animal alive at the start of some defined time period (normally a year) will still be alive at the end of the time period. Studies of survival rates of long-lived large mammals have documented that survival probabilities for individuals vary depending on an animal's age. Survival probability is relatively low from birth through the first year of life, increases rapidly to a maximum as animals mature and reach adult body size, and declines in the oldest age classes. One of the major mechanisms believed responsible for declining survival rates for older animals is tooth wear. Plant material is hard to digest, and large herbivores like bighorn sheep and mountain goats use their teeth to both crop plants and to chew the plant material extensively to break it into small fragments that microbes in their complex stomachs can efficiently digest. If you watch these animals going about their daily lives you will notice that much of their time is spent eating, whether they are slowly walking along an alpine meadow or grassy bench on a cliff biting off plants, or bedded and chewing a bolus of plant material they have regurgitated. Plants are abrasive because of their structure and chemical composition as well as the fine soil that clings to their surface. As a result, the constant biting and chewing wears down the sharp ridges on their teeth making them less efficient at the critical task of processing and digesting their food, thus, contributing to their physiological decline as they age. Survival rates also differ for males and females due to the differences in their behavior, body size, and demands placed on each sex for reproduction (females—gestation and lactation; males—competition for mating opportunities), with males generally having lower survival rates and shorter longevity than females. (Laws 1981)

Survival is an important attribute of wildlife populations that has a strong influence on whether or not the number of animals in a population is increasing, decreasing, or remaining stable. Adult survival can vary from one population to the next because the Greater Yellowstone Area is a large and diverse landscape with each bighorn sheep and mountain goat population occupying a somewhat different environment.



A ram chews its cud. Chewing coarse vegetation can take its toll, and an herbivore's life span is dictated by how long its teeth last. Photo by Kenneth R. Whitten.

For example, the physical characteristics of the landscape including the geology and topography affects the mosaic of plant communities and their productivity, which of course is of fundamental importance to large herbivores. The abundance of other species of animals present in the local community can also influence competition for important resources such as forage and the risk of being killed by predators. In addition, local and regional climate conditions impact how long plants are growing and nutritious each summer and how extensive and persistent snowpack is each winter, which influences the energy required for mountain goats and bighorn sheep to access the forages they need and can also make the animals more vulnerable to predation. (Dailey and Hobbs 1989)

Trends in the abundance of bighorn sheep and mountain goat populations are particularly sensitive to the survival rates of adult females. Because of the difficulty and expense, most management agencies do not routinely measure or monitor survival rates. However, over the past decade biologists have radio-collared hundreds of female bighorn sheep (see chapter 3 and 4), which has allowed the survival rates of adult females to be estimated for nearly all the bighorn sheep populations in the Greater Yellowstone Area. This work has revealed that, on average, annual survival rates of adult females vary among populations from a low of 80% to a high of 93%. Mountain goats are one of the most challenging large mammals to capture and, as a result, researchers pooled data on the modest numbers of radio-collared males and females to obtain adequate sample sizes for estimating survival rates. This research, concentrated in the Snake River Range in the southwestern Greater Yellowstone Area and the Beartooth-Absaroka region of the northeastern portion of the area, found slightly lower average annual adult mountain goat survival rates of 80% to 86%, likely due to the inclusion of males which tend to have lower survival rates than females. (Proffitt et al. 2021)

As with nearly all wildlife species, many factors can result in the death of an animal; bighorn sheep and mountain goats are no exception. The Greater Yellowstone Area

has the full complement of predators that were present at the time Euro-Americans first explored the region. Mountain lions, wolves, grizzly bears, black bears, and coyotes are the most abundant predators capable of killing bighorn sheep and mountain goats and records from regional studies of these predators have documented kills of both mountain ungulates. It is also likely that golden eagles are effective predators of lambs and kids. Observations of nursery groups of bighorn sheep and mountain goats fleeing to seek shelter under ledges and in caves when golden eagles fly into view provide anecdotal evidence golden eagles are routinely attempting to prey on young mountain ungulates in some areas. Investigations of radio-collared animals that have died also indicate that accidents, particularly falls from cliffs and avalanches, are an important cause of mortalities. For those herds that occupy ranges bisected by roads, vehicle collisions also occasionally kill animals. As described in chapter 6, disease, particularly respiratory pneumonia likely caused by pathogens originally introduced into the wild populations by domestic animals, is common throughout the herds with some populations of bighorn sheep occasionally experiencing severe outbreaks that result in the deaths of significant numbers of animals. Long, severe winters in much of the Greater Yellowstone Area and the associated extensive snowpack reduces nutritional intake to sub-maintenance levels for many months each year. Prolonged snowpack leading to starvation, therefore, is another common source of mortality in bighorn sheep and mountain goats. Finally, outside the national parks, both mountain ungulate species are hunted, with state wildlife management agencies strictly controlling the number of hunters and generally limiting the annual harvest to approximately 2 to 4% of the estimated total population size.

RECRUITMENT

Throughout the Greater Yellowstone Area, large numbers of newborn animals are added to mountain goat and bighorn sheep populations when females give birth



A group of three bighorn lambs with a ewe in winter. The number of young born and their survival through their first year determines how many animals are “recruited” into the adult population. Photo by Mark Gocke.

each spring. This annual 'birth pulse' has the potential to cause dramatic increases in size of populations. However, young animals are extremely vulnerable and in most years a large proportion of the young die before they reach their first birthday. When the young do survive until their first birthday, biologists consider them 'recruited' into the adult population. Thus, recruitment is an important attribute of bighorn sheep and mountain goat populations. Unlike adult survival rates, which are usually only estimated infrequently during research studies, biologists annually collect information on recruitment for most populations in the Greater Yellowstone Area. This is done by conducting aerial surveys to locate as many animals in a population as possible during mid- to late-winter and recording the number and sex of adults and the number of lambs or kids (young-of-the-year) observed. Because these surveys normally occur a month or more before young would reach their first birth day the data collected is biased high as additional mortalities are likely between the time of the survey and when animals become 1 year old. Biologists convert this information into a recruitment rate, reported as a ratio of young-of-the-year to adult females such as 28 lambs per 100 adult females or a proportion such as 0.28 lambs per adult female. It is difficult to distinguish the sex of adult mountain goats at the distances biologists normally are classifying the age and sex of animals during surveys. Thus, biologists often express mountain goat recruitment rates as kid to adult ratios. This important metric of population productivity incorporates aspects of both pregnancy rates, that determined the number of young born, and the survival rates of those vulnerable young animals into an index of the number of new animals that survive to be successfully recruited into the adult population. (Gaillard et al. 2000, Skalski et al. 2005)

In contrast with adult survival rates, which tend to be high and relatively consistent from year-to-year, recruitment rates tend to be much lower with considerable variation within a population annually as well as among populations. An examination of annual recruitment rates during 2013 to 2017 for two different bighorn herds at opposite ends of the Greater Yellowstone Area illustrates this variability. The recruitment rates

recorded for the upper Yellowstone bighorn complex in the northern region were 40, 38, 26, 30, and 28 lambs per 100 adult females, while the rates recorded for the Jackson bighorn herd during the same time period trended the opposite direction and were 21, 31, 36, 41, and 34 per 100 adult females. Similar annual variation is also common in mountain goat populations in the region. For example, biologists survey the Snake River Range population biennially and recruitment rates recorded for years 2004, 2006, 2008, 2010, and 2012 were 30, 19, 28, 35, and 26 kids per 100 adults. Given the high pregnancy rates of most bighorn sheep herds in the area, the lamb to adult female ratio at birth is typically about 80, indicating that at least half of the young born each year succumb to various mortality sources before reaching their first birthday, which is relatively common for mountain ungulates. Recruitment rates needed to maintain a population will depend on other demographic attributes but are most dependent on adult female survival. Under a typical range of annual adult female survival rates of 85% or better, recruitment rates less than 20 lambs per 100 adult females would likely indicate the population is declining. (Western Association of Fish and Wildlife Agencies 2015)

DISPERSAL

While most animals born into a population remain within the natal population range, once they reach the age where they become independent of their mother, some individuals may leave and settle in a new area, a behavior known as dispersal. The factors motivating animals to disperse are not well known. It is possible that some animals just have a propensity to wander, but the most likely driver of dispersal behavior is the search for some important resource the animal needs but cannot find in adequate abundance within its local environment. As populations grow, the density of animals in a given area increases and competition for food or access to mates and potential social tension and aggression among animals increasingly crowded into a limited space can cause animals to strike out to find new areas to live. The most

obvious example of dispersal by mountain ungulates in the Greater Yellowstone Area is the gradual range expansion of mountain goats following their relocation to the region. Since being introduced into just a hand full of sites in the northern mountains of the Greater Yellowstone Area in Montana in the 1940s and 1950s, populations have grown and animals have spread widely from introduction sites into surrounding areas. Mountain goats have fully occupied the northern mountains of the Greater Yellowstone Area and are now dispersing south into the northern portion of Yellowstone National Park and the Absaroka mountain chain in Wyoming. Similarly, the few mountain goats introduced into Idaho's Snake River Range in the late 1960s and early 1970s have spread throughout the Range and have dispersed northward into Wyoming's Teton Range and Grand Teton National Park (chapter 2). (Lemke 2004, Flesch et al. 2016)

In contrast, bighorn sheep do not demonstrate the same tendency to disperse. Throughout the historic range of bighorn sheep where native populations have been reduced to remnant herds or reestablished via translocations, populations tend to maintain a localized distribution even as densities increase. The history of bighorn sheep in Montana's Madison Range in the western Greater Yellowstone Area is perhaps the best example of bighorn sheep's reluctance to disperse. Historic records indicate bighorn sheep were widely distributed throughout the range, but currently only two remnant populations occupy relatively small portions of the available landscape with the Spanish Peaks herd at the northern end of the range and the Taylor-Hilgard herd at the southern end of the range. Despite increases in population size over the past several decades, the populations have demonstrated little expansion into adjacent high-quality habitat. As a consequence, as the populations grow they concentrate in higher densities on relatively small winter ranges where the entire population is more vulnerable to potential localized severe snowpack conditions, predators concentrating on bighorn sheep, and contagious diseases. Indeed, the Taylor-Hilgard herd has experienced two catastrophic pneumonia-related die-offs that reduced the population by an estimated 60-80%, once in the

mid-1980s and again in the mid-1990's. This apparent reluctance of bighorn sheep to disperse has prompted the state management agency to begin trapping animals and translocating them into unoccupied habitat between the two populations to repopulate the entire mountain range and establish a broadly distributed metapopulation (see chapter 9). Creating a spatially-structured broadly distributed population would reduce the potential for the entire population to be impacted by deleterious factors, thus creating a more resilient population by reducing the potential for dramatic changes in abundance. (Bleich et al. 1996, Festa-Bianchet et al. 2006, Jesmer et al. 2018, Lowrey et al. 2019, Lula et al. 2020)

ABUNDANCE AND POPULATION TRENDS

Anyone with an interest in the conservation and management of a wildlife population, whether a professional biologist, agency administrator, member of a non-government advocacy group, or simply a person that cares about the animals, wants to know how many animals are in the population and how population size has been changing through time. These two seemingly simple questions are often some of the most difficult for wildlife biologists to address. Counting wild animals in the mountainous landscapes inhabited by bighorn sheep and mountain goats is a challenging task. The animals are scattered over large complex landscapes with distributions changing dramatically over time as animals respond to seasonal changes in the quantity and quality of the plants they eat, the accumulation and melting of snowpack, interactions with predators and other animals, and a host of other factors. They tend to be in small groups that are easily hidden from an observer by rock outcrops, trees and shrubs, and the complexity of the topography. Even when standing in the open, animals can be difficult to spot from an airplane or when scanning a mountain slope with a spotting scope. One simply cannot find and count all the animals in a population. The proportion of the animals in a population that biologists detect and count varies from survey to survey and is

Table 1. Fall/winter estimates of size and trends of bighorn sheep and mountain goat populations in the Greater Yellowstone Area. Acronyms are MFWP = Montana Fish, Wildlife and Parks; NPS = National Park Service; USFS = U.S. Forest Service; WGF = Wyoming Game and Fish Department, WRR = Wind River Reservation. and YNP = Yellowstone National Park.

Herd	Management Agencies	Population Size	Population Trend
Bighorn Sheep			
Spanish Peaks	MFWP, USFS	150-200	Stable
Taylor Hilgard	MFWP, USFS	220-240	Stable
Upper Yellowstone Complex	MFWP, USFS, NPS	350-450	Stable
Stillwater	MFWP, USFS	100-120	Increasing
Hellroaring	MFWP, USFS	30-40	Stable
West Rosebud	MFWP, USFS	60-80	Stable
Clarks Fork	WGF, USFS, NPS	550	Declining
Trout Peak	WGF, USFS, NPS	675	Declining
Wapiti Ridge	WGF, USFS, NPS	800	Stable
Younts Peak	WGF, USFS	750	Declining
Francs Peak/Dubois Badlands	WGF, USFS, NPS, WRR	825	Declining
Whiskey Mountain	WGF, USFS, WRR	500	Declining
Temple Peak	WGF, USFS, WRR	75	Stable
Jackson	WGF, USFS	400	Stable
Targhee	WGF, USFS, NPS	125	Stable
Darby Mountain	WGF, USFS	75	Stable
	Total	5,685-5,905	
Mountain Goat			
Madison Range	MFWP, USFS	447-760	Increasing
Gallatin Range	MFWP, USFS, NPS	140-275	Increasing
MT Absaroka	MFWP, USFS, NPS	250-350	Declining
MT Beartooth	MFWP, USFS, NPS	240-372	Stable
WY Absaroka (including YNP)	WGF, USFS, NPS	175	Increasing
WY-MT Beartooth	WGF, USFS	75	Stable
Teton Range	WGF, USFS, NPS	50	Declining
Snake River Range	WGF, IDFG, USFS	300	Stable
	Total	1,677-2,357	

generally unknown. Intensive research studies focused on this topic, however, suggest that routine population surveys conducted under good observation conditions likely detect 60 to 80% of the animals. (Bodie et al. 1995, Gonzalez-Voyer et al. 2001, Williams et al. 2002, Rice et al. 2009)

Despite the challenges of counting mountain ungulates, agency biologists climb into planes and helicopters every year to do the best job they can to inventory populations throughout the Greater Yellowstone Area. These surveys indicate the region contains approximately 5,700 to 5,900 bighorn sheep and 1,700 to 2,400 mountain goats (Table 1). With the exception of the restored Darby Mountain and Temple Peak herds, all the bighorn sheep populations in the Greater Yellowstone Area are native. Sheep in these populations survived the period of market hunting, competition with domestic sheep that were grazed in nearly every mountain range (Figure 2, chapter 2), and disease outbreaks caused by exotic pathogens introduced by domestic sheep in the late 1800s and early 1900s.

The survival of the native bighorn sheep herds in the Greater Yellowstone Area and their subsequent recovery is a remarkable conservation success because most bighorn sheep populations in western North America were extirpated during the period of over-exploitation, which reduced the continental population from an estimated one half to one and a half million animals to less than 25,000. Over the past century concerted efforts by natural resource agencies to restore populations throughout historic range have yielded modest success as over 1,400 translocations involving 21,500 animals have increased the continental population to approximately 50,000 in 2016. Most restored populations, however, occupy restricted ranges isolated from other bighorn herds, display weak demographic performance, and consequently are relatively small. The native herds in the Greater Yellowstone Area, especially those along the eastern boundary of Yellowstone National Park in Wyoming, represent the largest continuous distribution of bighorn sheep in North America. (Seton 1929, Buechner 1960, Singer et al. 2000, Brewer et al. 2014, Wild Sheep Working Group 2015)

Most populations of bighorn sheep in the Greater Yellowstone Area, however, have experienced substantial fluctuations in numbers. Numerous pathogens associated with pneumonia are present in all the populations, and many of the bighorn sheep populations have experienced disease related die-offs of varying magnitude (see chapter 6). Most populations have recovered from disease events, although populations generally experience a period of poor lamb recruitment prior to returning to more typical recruitment. An exception to this pattern is the Whiskey Mountain metapopulation that occupies the northern Wind River Range. The major portion of the population that winters on the east side of the range represented the largest wintering concentration of bighorn sheep in the United States, but experienced a pneumonia-related die-off during the winter of 1990-1991. Lamb recruitment in this herd has been consistently poor since then, resulting in a steady decline in the population over the subsequent three decades. Unusually severe winters have also been associated with significant mortality events and temporary declines in abundance, most commonly in populations that winter at high elevations. The Stillwater bighorn herd provides another example of population fluctuations over time. This small migratory population winters along the Stillwater River, a drainage on the northern slopes of Montana's Absaroka Mountains. The population experienced a gradual decline through most of the 1980s and into the mid-1990s associated with the development of a mine within the core of the winter range. In the late 1990s, however, the trajectory of the population reversed and numbers have been increasing slowly and steadily for the past two decades.

Mountain goats have become broadly distributed and well established following introductions into mountain ranges in the northern and southwestern Greater Yellowstone Area. Mountain goat populations in the Snake River Range, along the Wyoming-Idaho border in the southwestern Greater Yellowstone Area, and the mountains spanning the northern border of Yellowstone National Park, where Montana initially introduced mountain goats, experienced decades of gradual

increases in abundance as the populations became established. These populations now appear to have stabilized with some declines noted in more localized areas. In other regions of the Greater Yellowstone Area, however, mountain goat populations are increasing. Mountain goats occur throughout the Madison and Gallatin Ranges along the western border of Yellowstone National Park and populations are continuing to increase in abundance. Along the eastern border of Yellowstone National Park, mountain goats are continuing their decades-long slow range expansion southward along Wyoming's Absaroka Range with a consequent increase in abundance. Mountain goats have also recently colonized the Teton Range and Grand Teton National Park, and this small population is increasing in size.

CONCLUSIONS

Population dynamics of mountain goats and bighorn sheep are the result of the interactions of animals' births, deaths, and movements that dictate trends in abundance and distribution of these iconic mammals across the diverse and expansive landscape of the Greater Yellowstone Area. The interactions of many factors influence these population processes, including weather, availability and quality of forage plants, predators, competition for food and space with other wildlife species, and disease. Human activities influence population processes through our direct and indirect impacts on the attributes of the landscapes that bighorn sheep and mountain goats depend on, management of other wildlife species and domestic animals that interact with these mountain ungulates, and purposeful conservation and management actions. Monitoring the many populations of bighorn sheep and mountain goats in the region by numerous state, federal, and tribal government agencies is challenging due to the remote and rugged environments that these animals occupy. Although data on pregnancy and survival rates are not always available, biologists routinely assess the abundance and recruitment of populations via surveys to count and classify (sex/age) as many animals that can be detected in the areas occupied by each population.

Bighorn sheep populations in the region have recovered from the era of overexploitation following settlement of the region by Euro-Americans, and mountain goats have become broadly distributed and well established following introductions into mountain ranges in the northern and southwestern Greater Yellowstone Area. Individual populations fluctuate over time, but biologists consider most populations healthy and stable. As would be expected with so many populations distributed across a vast landscape, some individual populations present specific conservation challenges that management agencies are addressing with strong participation from the public.

HOW WE LEARN: POPULATION DEMOGRAPHICS AND TRENDS

Wildlife managers throughout the Greater Yellowstone Area conduct and rely on counts and classifications, such as the number of bighorn sheep ewes, rams, and lambs, to monitor the demographic vigor of populations. These surveys are often conducted once or twice per season when animals are most concentrated on winter ranges. Small populations of generally less than 200 animals that spend winter in localized areas accessible from roads can be surveyed by biologists from the ground using binoculars and spotting scopes. However, many of the bighorn sheep and mountain goat populations in the region are distributed across vast areas of remote and rugged wilderness where aircraft are the only practical means of surveying the populations. Both small fixed-wing planes and helicopters are used depending on the elevations of winter ranges, distances that must be traveled, and need to fly into steep canyons. Flights can vary from 3 to more than 6 hours with aircraft routinely buffeted by strong winds, making the surveys challenging for both pilots and biologists. Poor weather conditions, limited availability of aircraft and skilled pilots, and periodic shortages of funds result in years where surveys cannot be completed; however, management agencies are committed to monitoring surveys.

In addition to the routine management surveys, intensive short-duration (3-10 years) research projects often focus on obtaining more detailed demographic insights by studying survival and reproduction, which are the major drivers of changes in the abundance of populations. Survival studies depend on the same types of radio collars used to study how animals use various habitats and migrate between seasonal ranges (see chapters 3 and 4). Built into nearly all radio collars is a motion sensing device that can detect when an animal has not moved for an extended period (6-8 hours), indicating the animal has likely died. This information is conveyed to the biologists via a

distinctive change in the pattern of the transmitted radio signal, or in the case of collars that communicate with satellites, the biologist may receive an email or a cell phone text message. Determining the cause of an animal's death, however, requires finding the dead animal and carefully examining the carcass and surrounding area. In most cases, visiting the site of a mortality does not occur immediately but may be delayed by weeks or months due to a combination of rugged terrain, remoteness, seasonally swollen rivers and streams, deep snowpack, avalanche conditions, and several other factors. Typically, all a biologist finds is a radio collar among a scattering of hair and bones, making it difficult to definitively determine the cause of the animal's death.

Insights into reproduction are obtained by determining the pregnancy status of captured females either from levels of hormones in blood samples or detecting a fetus with a portable ultrasound machine. Both survival and reproduction can vary depending on the age of the animal which can be determined based on the eruption pattern of incisor teeth as one pair of deciduous teeth are replaced with permanent incisors annually for the first 3½ years of an animal's life. Older ages can be determined for dead animals by extracting an incisor from the jaw and sending it to a laboratory that can prepare and stain the tooth and count the annual rings of cementum in the root like counting the annual rings of a tree. In addition to these field activities, an equally important aspect of monitoring and conserving mountain ungulate populations in the region is integrating all the various types of data collected in the field. This requires many hours working in the office on computers and often personnel with specialized expertise in sophisticated statistical, mapping, and modeling tools to understand the complex dynamics of populations and inform management decisions.



Monitoring efforts can include aerial surveys, ground observations, documentation of mortality through radio collars, and health sampling. Photos by Mark Gocke, Wyoming Game and Fish Department (upper left, lower left), Chris Queen, Wyoming Game and Fish Department (upper right), and Bob Garrott, Montana State University (lower right).



Mountain goats on Sepulcher Mountain in Yellowstone National Park. Photo by Diane Renkin, National Park Service.