

REVIEW

A review of population and landscape level dynamics associated with pneumonia outbreaks in bighorn sheep with implications for land management

Kelsey E. Paolini¹  | Michael K. Schwartz² | Megan M. Friggens³ | Samuel A. Cushman⁴ | Julie K. Weckworth^{2,5} | Joseph D. Holbrook¹

¹Haub School of Environment and Natural Resources, University of Wyoming, Laramie, Wyoming, USA

²U.S. Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA

³U.S. Forest Service, Rocky Mountain Research Station, Albuquerque, New Mexico, USA

⁴U.S. Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona, USA

⁵Center for Population Health Research, School of Public and Community Health Sciences, University of Montana, Missoula, Montana, USA

Correspondence

Kelsey E. Paolini, Haub School of Environment and Natural Resources, University of Wyoming, 1000 E University Avenue, Laramie, WY 82070, USA.
Email: kpaolini@uwyo.edu

Funding information

U.S. Forest Service

Abstract

Wildlife conservation necessitates understanding spatiotemporal drivers that facilitate disease outbreaks. Wildlife diseases are influenced by population and landscape level factors which affects host species' persistence through time. Recurrent pneumonia outbreaks in bighorn sheep have impeded population recovery throughout the western US. Recovery efforts have included translocating animals, limiting contact with known reservoirs, removing infected individuals, and depopulating herds, but pneumonia outbreaks continue to negatively impact recovery. Here, our objective was to systematically review the current literature focused on population and landscape level drivers that can contribute to pneumonia outbreaks in bighorn sheep. We reviewed 115 studies and discovered consistent themes important to address for future conservation. One of the primary themes to advance management includes understanding how population demographics, such as age and sex cohorts, can help elucidate drivers and maintenance of pathogens associated with respiratory disease. Second, broadening knowledge of landscape level processes including population connectivity and metapopulation dynamics can inform management and recovery efforts. We identified a need for comprehensive assessments that incorporate population dynamics, landscape genomics, and population connectivity across multiple spatiotemporal scales to advance landscape management. Finally, we provide directions for future research to help managers mitigate pneumonia outbreaks and aid bighorn sheep recovery.

KEYWORDS

bighorn sheep, land management, landscape dynamics, pneumonia, population dynamics

1 | INTRODUCTION

Historically, an estimated 1.5–2 million bighorn sheep (*Ovis canadensis*) traversed western North America, spanning from the Canadian Rockies, across the badlands south to the Trans-Pecos and west to the Cascades and Sierra Nevada (Buechner, 1960; Cowan, 1940). Within these landscapes, bighorn sheep formed metapopulations, or small groups of populations naturally distributed in a fragmented pattern with limited interaction (Bleich et al., 1990; Schwartz et al., 1986; Singer, Bleich, et al., 2000). Bighorn sheep likely evolved patchy distributions in rugged landscapes to access available resources, avoid predators, and limit the spread of disease (bolded terms are defined in Table 1; Bleich et al., 1990). In the late 1800s, however, bighorn sheep experienced rapid and severe population declines (i.e., currently less than 10% of historical estimates), due to unregulated hunting, fragmented habitat, livestock conflict, and respiratory disease (Buechner, 1960).

Bighorn sheep are particularly susceptible to respiratory disease, and pneumonia outbreaks have been a primary limiting factor negatively impacting species recovery (Cassirer et al., 2013; Manlove et al., 2016).

One factor that contributes to the slow recovery in bighorn sheep populations is high site fidelity which leads to limited dispersal, connectivity and likely amplifies the effects of restricted gene flow in small populations (e.g., inbreeding; Festa-Bianchet, 1986a, 1986b). In addition, recurrent pneumonia die-offs periodically decimate local populations. For example, a review of 82 pneumonia outbreaks across three decades reported median population declines of about 50% (Cassirer et al., 2018). Efforts to translocate and reintroduce bighorn sheep during the mid-1900s aimed to restore historical populations and prevent pneumonia related mortality (Singer et al., 2001; Singer, Papouchis, et al., 2000). Transporting individuals into isolated populations added genetic diversity, a technique called genetic rescue (Miller et al., 2012).

TABLE 1 Common terms used within the review and the definition of each term for context.

Term	Definition
Antibody	A molecule produced through an immune response to neutralize a specific pathogen contributing to immune memory ability to mount an immediate immune response if exposure occurs again. If present, these (acquired) antibodies indicate an animal has been exposed to a given pathogen in the past or is presently infected.
Disease	“A condition in which the normal function of some part of the body (cells, tissues, or organs) is disturbed. A variety of microorganisms and environmental agents are capable of causing disease” (Stevenson, 2010).
Density-dependent transmission	Probability of infection increases with increasing host density (number of hosts relative to the area). For example, disease will have a greater effect in limiting the growth of a large population, because overcrowding (higher density) facilitates host contact and pathogen spread.
Epizootic	A disease outbreak in an animal population, usually a discrete event, where widespread and high disease prevalence is reached rapidly.
Fitness	“A measure of the relative breeding success of an individual in a given population at a given time” (Stevenson, 2010).
Frequency-dependent transmission	Probability of infection increases with the proportion of infected hosts (# infected/total population); infection rates do not change respective to population density, e.g., sexually transmitted diseases.
Immune	“Resistant to infection or disease” (Aiello & Moses, 2016).
Landscape genomics	Field of study that focuses on describing the distribution of genetic variation under selection and adaptation on heterogeneous landscapes.
Leukotoxigenic	Describes a pathogen that possesses a leukotoxin, which may result in lowered immune system functioning in an infected host.
Pathogen	Agent that produces disease or has the capability to cause disease.
Pneumonia	“Inflammation of the lung tissue, often accompanied by inflammation of the trachea and other large airways” (Aiello & Moses, 2016).
Reservoir	Species capable of maintaining persistent infections by pathogens thus serving as a source of infection.
Susceptibility	“The likelihood of being affected or infected when exposed to agent; vulnerability” (Aiello & Moses, 2016).
Synoptic modeling	Analytical method that integrates population, behavior, and habitat selection characteristics to map population connectivity.
Transmission	“Passing of a pathogen from one individual to another” (Aiello & Moses, 2016).

Higher individual fitness in some augmented bighorn sheep populations has been attributed to genetic rescue (e.g., Hogg et al., 2006), but many populations have still failed to recover (Singer et al., 2001; Singer, Papouchis, et al., 2000). Despite translocating animals to restore populations, additional factors including local adaptation and strain-specific immunity may hinder translocation success (Bleich et al., 2018; Werdel et al., 2020), and local pneumonia-associated extirpations remain a substantial threat to bighorn sheep.

Pneumonia in bighorn sheep is a polymicrobial disease. Multiple bacterial and viral pathogens have been associated with pneumonia outbreaks in bighorn sheep. The primary bacterial pathogens commonly found co-infecting diseased animals includes *Mannheimia haemolytica* (formerly *Pasteurella haemolytica* serotype 2), *Bibersteinia trehalosi*, and *Mycoplasma ovipneumoniae* (Butler et al., 2017; Dassanayake et al., 2009, 2013; Tomassini et al., 2009). Research also linked *Pasteurella multocida* to some pneumonia outbreaks, but with less consistency than other bacterial pathogens (Besser et al., 2008; Callan et al., 1991; Rudolph et al., 2007). In addition to bacterial agents, researchers frequently isolated two viral pathogens in diseased sheep: respiratory syncytial virus and parainfluenza-3 (Herndon et al., 2011; Rudolph et al., 2007; Wolfe et al., 2010). Studying both viral pathogens in bighorn sheep indicate the viruses compromise the immune system and predispose sheep to bacterially derived pneumonia, although outbreaks still occur without the presence of viral pathogens (Al-Darraj et al., 1982; Dassanayake et al., 2013; Rudolph et al., 2007; Spraker et al., 1986). Therefore, a focus of disease research has centered on understanding the differences in disease outcome given infection with the various pathogens and how that may lead to heterogeneity in pneumonia outbreaks.

Each of the bacterial pathogens are comprised of multiple strains that lead to differences in severity of pneumonia. For example, exposure to the leukotoxin positive strain of *M. haemolytica* led to pneumonia associated mortality, while bighorn sheep developed only mild lung lesions when exposed to leukotoxin negative strains, (Dassanayake et al., 2009). Similarly, bighorn sheep with leukotoxin positive strains of *B. trehalosi* developed pneumonic lung lesions and those with leukotoxin negative strains failed to develop signs of pneumonia (Dassanayake et al., 2013). More recent studies on *M. ovipneumoniae* further suggest strain-specific vulnerability and transmission among populations (Besser et al., 2008; Epps et al., 2018; Gille et al., 2019). Direct exposure to *M. ovipneumoniae* did not consistently result in mortality across populations, rather the pathogen is considered a primary factor in predisposing bighorn sheep to fatal pneumonia (Besser et al., 2008; Besser, Cassirer, et al., 2012; Besser, Highland,

et al., 2012; Cassirer et al., 2018; Dassanayake et al., 2010; Plowright et al., 2017). Specifically, infection with *M. ovipneumoniae* causes reduced ciliary action in the lungs preventing individuals from adequately clearing co-infecting pathogens, which then cause or contribute to disease (Howard & Thomas, 1974; Rudolph et al., 2007). Although research has identified the bacterial pathogens likely contributing to pneumonia, the circumstances in which various strains and interactions among pathogens that consistently results in mortality remains unclear.

Once a bighorn sheep herd is exposed to pneumonia-associated pathogens through direct contact with a maintenance host, disease outbreaks occur through at least two pathways. First, pathogen introduction into naïve populations can spark an epizootic, causing disease and mortality in all age classes (Cassaigne et al., 2010; Cassirer & Sinclair, 2007; Plowright et al., 2013). Median declines of roughly 50% are observed as a result of epizootics, though population extirpation can occur (Cassirer et al., 2013, 2017, 2018). Secondly, infected survivors of the epizootic carry pathogens and expose naïve lambs within a population in subsequent lambing seasons. Endemic pneumonia pathogens in a population can cause recurrent high mortality in lambs, resulting in low recruitment and limit population recovery (Manlove et al., 2014). However, the presence of endemic pathogens, including *M. ovipneumoniae*, does not always lead to declines (Cassirer et al., 2017, 2018). The apparent heterogeneity in disease outcome given pneumonia pathogen introduction or pathogen persistence in bighorn sheep is not well understood (Cassirer et al., 2013, 2018).

Multiple population and landscape level factors influence pathogen exposure, disease outcome, and ultimately population-level effects. Heterogeneity across these variables spans multiple spatial scales and create unique challenges for wildlife and land managers. Pathogen introduction into a population depends on transmission from contact with reservoirs, or organisms capable of carrying and transmitting disease pathogens. For example, domestic sheep (*Ovis aries*) and goats (*Capra hircus*) are close relatives of bighorn sheep and can asymptotically harbor and transmit pneumonia-associated pathogens to wild sheep (Kamath et al., 2019; Lawrence et al., 2010). Variation in exposure risk among populations depends on where the population is located on the landscape with respect to reservoirs and connectivity among populations, which can ultimately drive management techniques such as depopulation in an effort to prevent subsequent pathogen spread. Additional population level factors that contribute to variation in disease dynamics following exposure includes population size and density. For example, larger populations may be more likely to persist but also more likely to disperse,

acquire, and/or spread pathogens (Gross et al., 2000; Singer, Moses, et al., 2000). Similarly, variation in exposure and disease outcome may be driven by landscape level processes. Heterogeneity in habitat quality across the landscape may lead to differences in overall health across populations and vulnerability to disease (Gilad et al., 2013; Lula et al., 2020). Gene flow and metapopulation processes may facilitate rescue or recolonization of populations but differ between populations given the configuration and connectivity between patches (Epps et al., 2018). Management across broader extents is complicated by these interacting factors. Therefore, understanding both population and landscape level drivers that consistently result in pneumonia outbreaks could help effectively manage bighorn sheep.

Managing bighorn sheep across heterogeneous landscapes with complex ownerships requires meeting multiple objectives. One of the primary management techniques has focused on geographically separating bighorn sheep herds from domestic flocks to reduce the risk of pathogen exposure (Heinse et al., 2016; Singer, Papouchis, et al., 2000). Techniques to isolate species have also included rotating seasonal grazing allotment use to create fallow years or closing domestic grazing allotments altogether. However, it remains unclear how often direct contact among domestic and wild sheep ultimately results in a pneumonia outbreak (Besser et al., 2014; Cassirer et al., 2018; Manlove et al., 2014; O'Brien et al., 2014).

Given the vast research on bighorn sheep ecology, yet the remaining uncertainty associated with disease outbreaks and population outcomes, we conducted a systematic literature review. Our goal was to identify knowledge gaps surrounding the drivers of transmission within and among populations to help direct future research and species management. Russell et al. (2020) provided a helpful framework for consideration when developing species recovery plans for wildlife populations facing recurrent disease outbreaks. Their approach outlines three primary principles to help maintain populations and limit the risk of future outbreaks: population level principles (e.g., population size, biotic reservoirs), landscape level principles (e.g., population connectivity, geographic distribution), and species level principles (e.g., adaptive capacity). These are synthetic principles that can be applied to many contexts, and thus we adapted the framework to understand factors related to pneumonia outbreaks in bighorn sheep and highlight knowledge gaps. Our specific objectives were to: (1) review literature on bighorn sheep ecology to understand how population and landscape level dynamics contribute to the risk of pneumonia outbreaks, and (2) use the existing knowledge base to identify knowledge gaps and provide direction for future management to aid bighorn sheep recovery.

2 | METHODS

Our literature review focused on bighorn sheep population and landscape level dynamics likely to facilitate disease outbreaks. We searched for articles in March 2021 using Web of Science. Our search terms included “bighorn sheep” AND (“connectivity” OR “dispersal” OR “movement”). We also conducted the same search with the addition of AND “pneumonia” to comprehensively review articles that could relate to pneumonia outbreaks. To fully cover the topics of interest and reduce bias from using a single search engine, we also scanned for additional relevant articles in GoogleScholar. Our collective searches returned a total of 292 articles (Figure 1). We then removed duplicate articles, filtered unrelated topics (e.g., articles focused on other species, such as mouflon [*Ovis gmelini*]), and only included peer reviewed articles which resulted in 115 full text articles.

For our systematic review, we identified the emergent theme(s) of an article and identified which principle(s) from Russell et al. (2020) the article corresponded with. We adapted the general framework of Russell et al. (2020) to structure our synthesis of population and landscape level variables that can impact disease outbreaks and pathogen spread in bighorn sheep. Finally, we reviewed our primary findings and proposed actionable advancements based on identified knowledge gaps in the existing literature.

2.1 | Population level variables

2.1.1 | Population variable 1—population size and demographic rates

Population size

Population size and density may influence disease dynamics and differences in population-level outcomes in bighorn sheep populations exposed to pneumonia-associated pathogens. Within 3 years of peak herd estimates, roughly 90% of bighorn sheep populations experiencing pneumonia outbreaks exhibited population declines, presumably associated with density-dependent mechanisms (Monello et al., 2001). Density-dependent transmission means pathogen spread increases with increasing population density. Another study followed nine bighorn sheep herds adjacent to a population that experienced an all-age die off in the Mojave Desert and found density dependent mechanisms influenced survival either from higher rates of contact or lower nutrition from increased resource competition (Dekelaita et al., 2020). Larger herds also face additional competitive pressures to obtain nutritional resources, which

FIGURE 1 An overview of our literature review processes to identify, filter, and incorporate relevant, accessible articles on bighorn sheep (*Ovis canadensis*).



can influence exposure to pathogens. Larger populations dispersed farther distances to mitigate intraspecific resource competition (Manlove et al., 2014; Monello et al., 2001). However, increased dispersal carries a higher risk of acquiring and spreading pathogens among populations.

Another possible mechanism for pathogen spread is through frequency-dependent transmission. Social grouping behaviors of bighorn sheep may facilitate frequency dependent pathogen spread. In a multi-year study, lamb survival varied across female nursery groups (i.e., groups of adult females and their offspring) regardless of group size during pneumonia outbreaks, implying pathogens circulated through frequency- rather than density-dependent mechanisms within subpopulations (Manlove et al., 2014). The implications of these observations is that where pathogen spread localizes within herds without expanding to the greater population (i.e., density-dependence), monitoring and targeting infected individuals for removal could help maintain viable populations by reducing the risk of pneumonia outbreaks.

Population demographics

Social grouping behaviors spread pneumonia pathogens differentially among bighorn sheep populations. Outside of the breeding season, males aggregate in bachelor groups and females form nursery groups with other females and their young (Mooring et al., 2003; Ruckstuhl, 1998; Woolf et al., 1970). Mother to lamb, and lamb to lamb transmission within nursery groups are believed to be key mechanisms for pathogen maintenance and spread proliferation (Manlove et al., 2014; Plowright et al., 2017; Raghavan et al., 2016). Adult females that survive an initial pneumonia outbreak, develop protective antibodies, and carry pneumonia pathogen(s) while consistently testing positive for the pathogen(s) are termed chronic carrier ewes. Chronic carrier ewes do not appear to transfer protective antibodies to offspring, and exposed lambs typically die of pneumonia during spring lambing seasons (Hanthorn, 2014; Miller, 2001; Raghavan et al., 2016). Infected lambs also transmit pneumonia pathogens to other lambs within herds, constraining long-term population growth (Cassirer et al., 2013, 2018; Manlove et al., 2016; Plowright et al., 2017). Variation in recruitment, or adding new individuals to a herd, is a primary driver of

population growth in large herbivores (Bowyer et al., 2020; Gaillard et al., 1998, 2000), and pneumonia outbreaks causing high lamb mortality negatively impacts long term herd growth and persistence. Therefore, assessing how different age or sex groupings within bighorn sheep can contribute to the severity of pneumonia outbreaks can enable more effective population management to target specific demographics and reduce pathogen transmission within herds.

Age class

Adult bighorn sheep and lambs appear to experience distinct clinical signs after exposure to pathogens. In both *M. haemolytica* and *B. trehalosi* infections, adults succumbed to decreased lung function and survivors asymptotically carried pathogens (Hanthorn, 2014; Miller, 2001). Lambs exposed to these carriers developed systemic infections which led to organ failure and mortality (Brogden et al., 1988; Hanthorn, 2014; Miller, 2001), suggesting an immature immune system in lambs throughout early development. Lambs at 2–3 weeks of age developed signs of infection with either *M. haemolytica* or *B. trehalosi*, while at around 8 weeks of age they exhibited clinical signs typical of *M. ovipneumoniae*; those lambs between 2 and 8 weeks of age had mixed pathologies (Wood et al., 2017). Targeted research that elucidates the drivers of observed variation in transmission and disease progression across age cohorts can help focus management actions to reduce lamb mortality and increase population recruitment.

2.1.2 | Population variable 2—Interactions with reservoirs

Animal reservoir are one critical component for understanding pathogen introduction and repeated reintroduction of disease-causing pathogens (Russell et al., 2020). Reservoirs carry pathogens and experience differing levels of response to disease (e.g., remain asymptomatic or develop mild to moderate symptoms) while exposing and transmitting pathogens to susceptible populations. Bighorn sheep themselves can transmit pathogens among other members of their herd or neighboring herds once exposed to pneumonia pathogens (Borg et al., 2017;

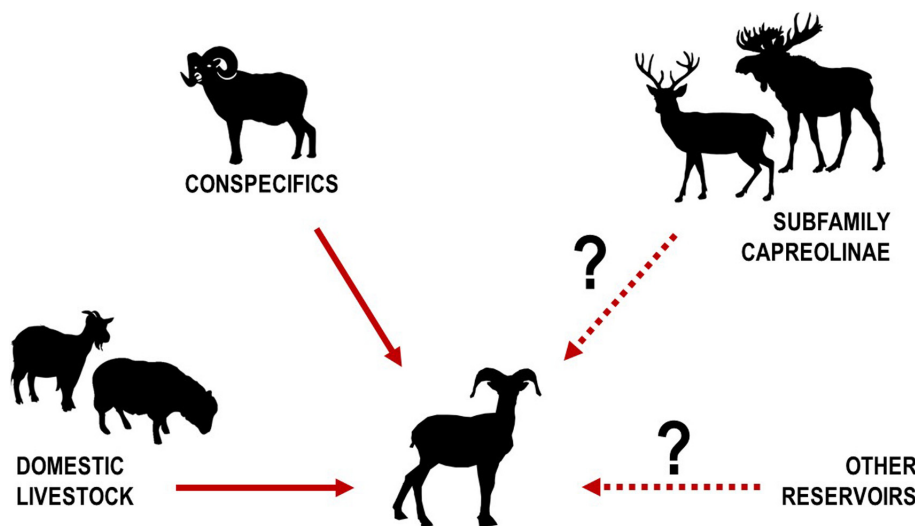


FIGURE 2 Multiple reservoir species are capable of carrying pneumonia pathogens that can lead to pneumonia in bighorn sheep. Pneumonia pathogens were only recently identified within the subfamily Capreolinae and it is unknown whether pathogen transmission to bighorn sheep has occurred.

Manlove et al., 2014). For example, introducing a single infected bighorn sheep in pen experiments demonstrated the high transmissibility of pneumonia pathogens to conspecifics in close contact (Besser et al., 2014). Multiple other species also harbor the primary pathogens associated with pneumonia outbreaks in bighorn sheep, including domestic sheep and goats and New World deer (e.g., moose, *Alces alces*) (Figure 2; Garwood et al., 2020; Highland et al., 2018; Lawrence et al., 2010).

A widely regarded reservoir for pneumonia pathogens infecting wild bighorn sheep are domestic sheep and goat herds (Callan et al., 1991; Carpenter et al., 2014; Foreyt et al., 1994; Foreyt & Jessup, 1982; Lawrence et al., 2010). Kamath et al. (2019) sampled *M. ovipneumoniae* bacterial strains across domestic and wild sheep and goats in the western US. Domestic sheep carried many strains of *M. ovipneumoniae*, whereas bighorn sheep populations circulated a few select strains that were related to strains found in domestics, suggesting multiple transmission events of *M. ovipneumoniae* between domestic and bighorn sheep (Kamath et al., 2019). Although studies have documented interactions between domestic and bighorn sheep leading to fatal pneumonia, inconsistent outcomes in disease severity further complicates our understanding of the potential population level impacts (Dassanayake et al., 2009; George et al., 2008; Lawrence et al., 2010). For example, some pathogen strains linked to mild symptoms in domestics, yet severe symptoms in bighorn sheep, indicate strain-specific immune responses may occur across species (Cassirer et al., 2017, 2018). While expanding upon strain specific immunity exceeds the scope of our review, these patterns highlight the need to further our understanding of domestic animals as a potential reservoir for pneumonia pathogens in bighorn sheep.

Recent research found possible pneumonia causing pathogens for bighorn sheep in other wild ungulates.

Multiple studies identified *M. ovipneumoniae* among individuals within the subfamily Carpreolinae (i.e., mule deer (*Odocoileus hemionus*), barren ground caribou (*Rangifer tarandus granti*)) plagued with respiratory disease (Highland et al., 2018; Rovani et al., 2019). Convoluting the issue, *M. ovipneumoniae* was identified in seemingly healthy individuals of these species (Highland et al., 2018). It is still unclear whether these species have introduced pneumonia pathogens leading to outbreaks into bighorn sheep populations. Additional research on potential reservoir species is needed to fully characterize the scope of management actions required to limit pathogen transmission to bighorn sheep.

2.2 | Landscape level variables

2.2.1 | Landscape variable 1—maintain multiple connected populations

Demographic or genetic rescue

Landscape connectivity, or the degree to which the landscape facilitates or impedes movement (Taylor et al., 1993), promotes gene flow among populations. Genetic diversity allows individuals, and ultimately populations, to respond to dynamic environments, internal parasites, and disease outbreaks (Vander Wal et al., 2013). Fragmented habitat and some innate behaviors of bighorn sheep, such as forming socially distinct subpopulations, limits population connectivity. Small, isolated populations lose genetic diversity over time which can lead to inbreeding depression and reduce population fitness. For example, bighorn sheep with lower genetic diversity carried heavier loads of lungworms, a damaging respiratory parasite (Luikart et al., 2008). In turn, reduced genetic diversity that leads to high parasite loads can increase

susceptibility to pneumonia pathogens and impact herd viability (Festa-Bianchet, 1991; Luikart et al., 2008; Spraker et al., 1986).

Managers frequently translocate bighorn sheep into new areas which can benefit adjacent populations or into unrelated populations, both of which can increase genetic diversity within the population, or to supplement population numbers. In many augmented populations, bighorn sheep exhibit greater reproductive success, larger-bodied offspring, and either maintained or increased genetic diversity (Gille et al., 2019; Jahner et al., 2019; Love Stowell et al., 2020; Miller et al., 2012; Poirier et al., 2019; Werdel et al., 2020). However, translocating animals as a management tool to preserve genetic diversity across landscapes also requires additional considerations (Gille et al., 2019; Olson et al., 2013; Roffler et al., 2016; Thompson et al., 2001). Translocating animals does not guarantee an increase in genetic diversity. Introduced animals often need time to integrate into established populations. In Alberta, Canada, for example, translocated bighorn sheep assimilated a year after reintroduction, experienced higher rates of aggressive encounters, and translocated females only successfully bred with natives 3 years after introduction (Poirier & Festa-Bianchet, 2018). Moreover, translocation may not appreciably increase genetic diversity across landscapes because gene flow between native and translocated populations can occur naturally (Flesch et al., 2020; Robinson et al., 2019).

Another challenge to maintaining connected, genetically diverse populations through translocation regards the potential loss of advantageous local adaptations. Selective pressures across heterogeneous landscapes shape genetic diversity and populations adapt to local environments over time. One study found that translocated bighorn sheep moved to geographically similar areas sustained improved survival relative to those moved to relatively distinct habitats (Bleich et al., 2018). Translocated animals without local adaptations face added challenges when placed in novel environments. Other studies found translocated bighorn sheep had an increased risk of acquiring detrimental pathogens as compared to native populations, which had developed some level of immunity (Plowright et al., 2013; Werdel et al., 2020). Similarly, translocated animals can present a risk to native populations by introducing pneumonia pathogens from developed strain-specific immunities or lack of knowledge surrounding their infection status (i.e., not all individuals are typically tested). In addition to the risks of spreading pneumonia pathogens among connected populations, successful breeding between native and translocated individuals may result in the loss of protective adaptations in offspring. A long-term study found that although population size in herds with translocated animals initially

increased, populations declined more so over a 5 year period relative to native populations, presumably due to fitness related consequences related to loss of local adaptations (Donovan et al., 2020). Additional research using landscape genomics, which identifies genes affected by selective pressures, could provide valuable information to improve successful animal translocations and identify factors that aid populations in surviving pneumonia outbreaks across landscapes.

Metapopulation connectivity

A bighorn sheep metapopulation is comprised of distinct but connected herds that experience increased gene flow when animals move through habitat corridors. For example, although some bighorn sheep populations naturally colonized new areas (Epps et al., 2010; Erwin et al., 2018), infrequent mixing—even among historically connected populations—remains problematic for maintaining genetic diversity (Flesch et al., 2020; Robinson et al., 2019). Changes to both structural and functional landscape connectivity imposed by physical (i.e., rivers) and anthropogenic barriers (e.g., fences, roadways), restricts movement (Buchalski et al., 2015; Deakin et al., 2020; Epps et al., 2005, 2018; Flesch et al., 2010), thus potentially limiting metapopulation dynamics and gene flow that could help herds survive and recover from pneumonia epidemics. Methods to reduce the impacts of barriers exist, such as co-locating translocated and isolated populations, but are challenged by a lack of suitable areas that allow sufficient room for bighorn sheep to maintain long-term genetic diversity and population connectivity (Epps et al., 2007). Reduced population connectivity can result in negative consequences (e.g., inbreeding depression), it can also serve to protect populations by limiting their exposure to pneumonia pathogens and reduced disease outbreaks. For example, population connectivity also presents increased risk of pathogen spread if one herd becomes exposed to pneumonia pathogens or has survived a previous outbreak and acquired immunity. Several recent studies suggest multifaceted management approaches are most likely to preserve connectivity by integrating both genetic and demographic networks across spatiotemporal extents (Couch et al., 2020; Creech et al., 2014; Epps et al., 2006; Fleishman et al., 2017), yet there are many additional considerations prior to action.

Spatiotemporal movements

Life history strategies shape animal movements and vary across spatiotemporal extents. Bighorn sheep are habitat specialists driven by strong site fidelity and seek areas with available escape terrain and clear visibility to avoid predators (DeCesare & Pletscher, 2004, 2006; Gilad et al., 2013; Merkle et al., 2016). The specific landscape

attributes encompassed by an area used to obtain all necessary resources to sustain fitness is called the home range of an animal (Burt, 1943). Many bighorn sheep populations migrate to seasonal ranges, whereas others exhibit year-round residency (Courtemanch et al., 2017; Geist & Petocz, 1977; Lula et al., 2020). However, bighorn sheep also display behavioral plasticity by switching between resident and seasonal migratory behaviors throughout their lifetime, which is also driven by local environmental conditions and life stages (Courtemanch et al., 2017; Spitz et al., 2018). Desert bighorn sheep (*Ovis canadensis nelsoni*) seasonally changed their behavior to access water resources and males used less rugged terrain than females (Lowrey & Longshore, 2017). In northern populations, Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) populations migrate to lower elevations in winter and higher elevations in summer in response to seasonal climate effects on resource availability (e.g., deep snow constraining winter resource availability, dense vegetation reducing summer visibility; Geist & Petocz, 1977). Both summer and winter ranges frequently consist of steep, southwesterly terrain; however, during the winter, bighorn sheep also select areas with more available forage often at lower elevations (Lula et al., 2020). Although elevational migration occurs in both altered (i.e., some or all animals were translocated) and native bighorn sheep populations, native herds exhibited less site fidelity, traveled further geographic distances, and dispersed more broadly across landscapes (Lowrey et al., 2019, 2020). This may mean that native populations experience a higher risk of acquiring and transmitting pneumonia pathogens among populations.

In addition to seasonal home ranging behavior, bighorn sheep make occasional long distance excursions, called forays, where individuals travel well outside their established home range. Forays connect socially distinct populations and increase the probability of contacting reservoirs and thus, transmitting pathogens. Both males and females exhibit foraging behavior to varying extents. For example, whereas females traveled up to 10 km from their established core home range, males forayed up to three times that distance and those movements often overlapped with domestic grazing allotments (DeCesare & Pletscher, 2006). This pattern of behavior increases the risk of pathogen spread among bighorn sheep herds during the breeding season. Interestingly, increasing foraging behavior by males during the winter rut has been correlated with all-age and widespread pneumonia outbreaks during winter seasons (Festa-Bianchet, 1986a; O'Brien et al., 2014). Therefore, males may be a mechanistic link connecting seemingly disjointed populations of sheep or other reservoirs, ultimately leading to

subsequent pneumonia outbreaks (Borg et al., 2017; George et al., 2008; Singer, Moses, et al., 2000).

2.2.2 | Landscape variable 2—broad geographic distributions

Environmental heterogeneity

Landscapes are heterogeneous in quality, disturbance, and climate. Heterogeneity in exposure to environmental stressors among populations may explain varying outcomes given exposure to pneumonia pathogens. Apparent differences in disease outcome across heterogeneous landscapes may be mediated by stress physiology (Enk et al., 2001; Monello et al., 2001). Acute or chronic stressors suppress the immune system and increase the risk of disease from pathogen exposure. For example, in Dall's sheep (*Ovis dalli*), transported animals experienced multiple stressors including herd fragmentation, increased temperatures, and human contact that were directly associated with subsequent stress-related pneumonia mortalities (Black et al., 1988).

Several studies assessed the role of human-mediated disturbance and the effects of nutrition on variation in population response to disease. Anthropogenic disturbance, that likely caused an increase in physiological stress, has been suggested as a contributor to pneumonia-associated mortalities in populations neighboring construction sites (Bailey, 1986; Spraker et al., 1984). Poole et al. (2016) found reclaimed mines were particularly important wintering habitat and limiting disturbance to winter ranges helped sustain bighorn sheep populations near human activities. Nutritional deficiencies have also been implicated in stress-related pneumonia, where low quality forage predisposed bighorn sheep to an immunocompromised state and successive pathogen invasion (Enk et al., 2001; Monello et al., 2001; Rudolph et al., 2007). Research on Mojave Desert populations found high quality summer and fall forage were likely cofactors across populations with differing exposure to *M. ovipneumoniae* (Dekelaita et al., 2020). Changes in nutritional quality are particularly important for translocated populations. For example, translocated populations moved into geographic areas resembling their original environment showed increased survival and recruitment (Bleich et al., 2018). This suggests that, although translocated animals experience handling-related stress, substantial changes to the environment and nutritional quality more strongly influence survival (Bleich et al., 2018; Creech et al., 2020; Singer, Papouchis, et al., 2000). Collectively, these studies highlight the importance of local variation in forage quality, quantity, and the distribution of suitable habitats across broad geographic scales that matches the

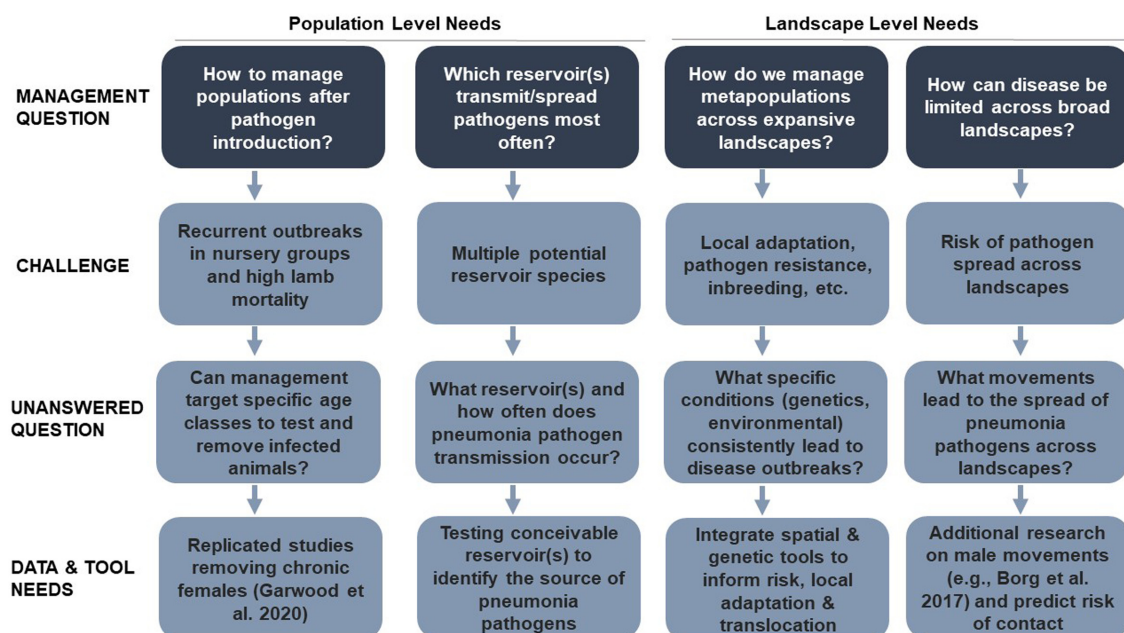


FIGURE 3 We delineate population and landscape level knowledge gaps identified in our review, highlight the challenges and unanswered questions, and describe data needs to help direct future research to advance bighorn sheep management.

requirements needed to maintain interconnected populations of bighorn sheep to optimize gene flow while minimizing disease exposure and transmission.

3 | SUMMARY

Pneumonia outbreaks and pathogen persistence in bighorn sheep continue to threaten the conservation of herds and populations despite several decades of research and management. Reviewing the current literature highlights key population level and landscape level research needs. Future population level management can benefit from a clearer understanding of how population structure (e.g., population size, age classes) and contact with reservoir species can lead to pneumonia outbreaks and poor population recovery (Cassirer et al., 2018; Dassanayake et al., 2009; Lawrence et al., 2010; Manlove et al., 2014; Rovani et al., 2019). Landscape level research on genetic variation, metapopulation connectivity, and environmental heterogeneity can assist in developing broad scale management to reduce pneumonia outbreaks (Borg et al., 2017; Dekelaita et al., 2020; Gille et al., 2019; Poirier et al., 2019; Werdel et al., 2020). From this review, we identify key management questions that remain at both the population and landscape levels (Figure 3). We summarize the primary challenges, describe the research questions and data requirements to help advance bighorn sheep management to mitigate future pneumonia outbreaks.

4 | FUTURE DIRECTIONS

4.1 | How can land managers manage populations following pathogen introduction?

Recurrent pneumonia outbreaks commonly happen in female nursery groups. Research suggests adult females that survived a pneumonia outbreak expose young lambs with immature immune systems to pneumonia pathogens, which can lead to high lamb mortality and negatively impact population recruitment (Cassirer et al., 2018; Manlove et al., 2014; Plowright et al., 2013, 2017; Raghavan et al., 2016). A 2020 study removed chronic carrier ewes infected with *M. ovipneumoniae* and found that lambs had lowered mortality rates and the population no longer exhibited signs of pneumonia (Garwood et al., 2020). The positive effects of removing chronic carrier ewes highlights two pathways forward. First, population testing and removal of infected carrier ewes may help long term population viability. Second, longitudinal monitoring of disease prevalence across age classes within nursery groups can help clarify the population drivers of recurrent outbreaks. Such studies may require intensive efforts to monitor outbreaks, however, this information can inform disease models that predict risk of outbreaks and factors associated with new or persistent pneumonia infections. Work expanding on the suggestions of Garwood et al. (2020) is needed.

4.2 | Which reservoir(s) are the most important with respect to pathogen maintenance and spread to focal bighorn sheep populations?

Preventing reservoirs from transmitting novel pathogens into naïve bighorn sheep populations can help reduce pneumonia outbreaks. Still, the frequency in which bighorn sheep acquire pathogens from reservoirs and subsequently develop pneumonia remains unclear. Since pneumonia pathogens were only recently identified within the subfamily Capreolinae (e.g., Highland et al., 2018; Rovani et al., 2019), gaining reliable knowledge on whether these species carry and transmit damaging pneumonia pathogens to bighorn sheep is needed.

Domestic sheep and goats can spread pneumonia-associated pathogens to bighorn sheep; fortunately, domestics are the most accessible species to monitor for public land management. Periodic pathogen testing on domestic herds with the potential to interact with bighorn sheep would provide a clearer understanding on whether additional management actions, such as livestock rotational grazing, could be taken.

Landscape level management to reduce pathogen transmission from domestic livestock to bighorn sheep necessitates educating both public and private landowners. In Washington, for example, more than one third of private landowners were unfamiliar with the risk of pathogen spread between species (Heinse et al., 2016). Land managers can help educate the public about domestic animals as a potential reservoir species and the importance of monitoring herds to promote both healthy domestic herds and bighorn sheep conservation. In addition to public education, land managers can study public perception and willingness to adopt management strategies to learn landowner values. Management plans can integrate landowner values and address potential concerns regarding actions impacting domestic livestock. For example, key management actions such as maintaining fencing for domestic animals and rotating or closing grazing allotments can be contentious, but with effective partnerships we help mutually beneficial solutions to prevent pathogen transmission to bighorn sheep and domestic animals. Additional management actions include tracking domestic and/or wild herds, accompanied by range riders with GPS technology, to identify whether domestic and wild sheep overlap. Partnering with landowners directly to work collaboratively to reduce potential pneumonia exposure to bighorn sheep can help lower the risk of spreading pneumonia pathogens across broad extents.

4.3 | How can land managers use genetics and spatial tools to help maintain connected populations across landscapes?

The vast differences in outcomes experienced among bighorn sheep populations exposed to pneumonia pathogens necessitates broad scale studies to explore the potential role of evolution of pathogen resistance and tolerance, and local adaptation to environmental conditions. Landscape genomics can identify genes affected by selective pressures in spatially explicit landscapes to help describe and map potential local environmental adaptations among populations (Storfer et al., 2018). Furthermore, genomic approaches such as genome wide association studies can identify candidate loci associated with disease or susceptibility. Moreover, diagnostic testing can help identify genetic markers related to changes in physiologic response, and could help characterize the interplay of various stressors contributing to pneumonia outbreaks in bighorn sheep (Bowen et al., 2020). Since many integrated factors appear to influence disease outcome in bighorn sheep, combining genomics with spatial data can improve our understanding of disease risk and pathogen dynamics to simulate pathogen spread (Kozakiewicz et al., 2018). Using individual-based, spatially explicit landscape genomic simulation models (e.g., Landguth et al., 2020) could enable modeling the interactive effects of different distributions, abundances, genetic characteristics, pathogen loads, and strains within complex landscapes (e.g., Creech et al., 2017).

4.4 | How can land managers limit disease risk across broad landscapes?

A crucial aspect for managing pneumonia epidemics in bighorn sheep is mapping the risk of pathogen spread across landscapes. Although current management techniques include depopulating infected herds, identifying how initial transmission occurs can help prevent pathogen acquisition and spread. Male bighorn sheep movements cover large distances, overlap domestic allotments, and connect distinct subpopulations, yet remain understudied relative to pneumonia outbreaks in bighorn sheep (Borg et al., 2017; DeCesare & Pletscher, 2006). Studying temporally dynamic movements integrated with habitat selection is central to advancing our understanding of pneumonia pathogen transmission. For example, male bighorn sheep traversing landscapes may only spend a limited amount of time near domestic grazing allotments. If viewed from a habitat selection perspective, the brief period a male spends in a location could result

in a seemingly low relative probability of use. In terms of pathogen transmission, however, the apparent low use of an area could still represent a critical source for pneumonia pathogens (i.e., males spend a short amount of time in an area, but could acquire and/or transmit pneumonia pathogens from/to domestics). Recognizing the potential for pathogen exposure and focusing on the intrinsic and extrinsic factors mediating male bighorn sheep movement would further our understanding on transmission dynamics.

Integrating population and behavioral characteristics, such as population density and dispersal ability, with fine-scale spatiotemporal selection patterns to predict connectivity provides a strong means to map physical interaction, an approach called synoptic modeling. Synoptic connectivity modeling has been implemented within a disease framework to provide researchers with spatiotemporal patterns of contact risk between buffalo and domestic cattle leading to foot and mouth disease (Kaszta et al., 2018). Utilizing this method to simulate alternative scenarios of land management to evaluate the potential impacts of anticipated change would be valuable to help assess pathogen transmission risk at the bighorn sheep and domestic livestock interface. Modeling approaches to predict landscape-level connectivity in other disease frameworks emphasized the primary finding from our review—comprehensively integrating demographic, genetic, and environmental factors across spatiotemporal extents can help preserve landscape connectivity while aiming to reduce pneumonia outbreaks (Allen et al., 2016; Gross et al., 2000; Keeley et al., 2016; O'Brien et al., 2014; Rubin et al., 2009; Spitz et al., 2017; Tucker et al., 2018).

5 | CONCLUSIONS

Future research in population- and landscape-driven dynamics can help advance our understanding of pneumonia outbreaks in bighorn sheep. Targeted research focused on age- and sex-specific cohorts can help uncover processes and behaviors leading to pneumonia-associated pathogen transmission and recurrent pneumonia outbreaks (Borg et al., 2017; Lula et al., 2020; Russell et al., 2020). Our review identified population level research needs that include studying the effectiveness of identifying, targeting, and removing chronic carrier ewes (e.g., Garwood et al., 2020) in populations with recurrent pneumonia outbreaks and identifying the reservoir species that may transmit pneumonia pathogens to bighorn sheep. At the landscape level, research directed at integrating genetic and spatial data to simulate disease risk and spread, as

well as understand local environmental adaptation and pathogen resistance, can help advance management and inform translocations. Finally, predicting male movements particularly during the breeding season with risk of contact to reservoirs can help in bighorn sheep recovery. Determining specific drivers that consistently lead to pneumonia outbreaks across multiple spatial and temporal scales can help provide meaningful direction to develop effective management strategies.

ACKNOWLEDGMENTS

We sincerely thank Katey Huggler, Dr. Patricia Klein Richard Truex, and anonymous reviewers for providing valuable comments that greatly improved this manuscript. This work was funded by the U.S. Forest Service.

CONFLICT OF INTEREST STATEMENT

The authors declare there are no conflicts of interest.

ORCID

Kelsey E. Paolini  <https://orcid.org/0000-0002-4947-2020>

REFERENCES

- Aiello, S. E., & Moses, M. A. (2016). *The Merck veterinary manual* (11th ed.). Wiley.
- Al-Darraj, A. M., Cutlip, R. C., Lehmkuhl, H. D., Graham, D. L., Kluge, J. P., & Frank, G. H. (1982). Experimental infection of lambs with bovine respiratory syncytial virus and *Pasteurella haemolytica*: Clinical and microbiologic studies. *American Journal of Veterinary Research*, 43, 236–240.
- Allen, C. H., Parrott, L., & Kyle, C. (2016). An individual-based modelling approach to estimate landscape connectivity for bighorn sheep (*Ovis canadensis*). *PeerJ*, 4, e2001.
- Bailey, J. A. (1986). The increase and die-off of Waterton Canyon bighorn sheep: Biology, management, and mismanagement. *Biennial Symposium of the Northern Wild Sheep and Goat Council*, 5, 325–340.
- Besser, T. E., Cassirer, E. F., Potter, K. A., Lahmers, K., Oaks, J. L., Shanthalingam, S., Srikumaran, S., & Foreyt, W. J. (2014). Epizootic pneumonia of bighorn sheep following experimental exposure to *Mycoplasma ovipneumoniae*. *PLoS One*, 9, e110039.
- Besser, T. E., Cassirer, E. F., Potter, K. A., VanderSchalie, J., Fischer, A., Knowles, D. P., Herndon, D. R., Rurangirwa, F. R., Weiser, G. C., & Srikumaran, S. (2008). Association of *Mycoplasma ovipneumoniae* infection with population-limiting respiratory disease in free-ranging Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*). *Journal of Clinical Microbiology*, 46, 423–430.
- Besser, T. E., Cassirer, E. F., Yamada, C., Potter, K. A., Herndon, C., Foreyt, W. J., Knowles, D. P., & Srikumaran, S. (2012). Survival of bighorn sheep (*Ovis canadensis*) commingled with domestic sheep (*Ovis aries*) in the absence of *Mycoplasma ovipneumoniae*. *Journal of Wildlife Diseases*, 48, 168–172.
- Besser, T. E., Highland, M., Baker, K., Cassirer, E. F., Anderson, N. J., Ramsey, J. M., Mansfield, K., Bruning, D. L.,

- Wolff, P., Smith, J. B., & Jenks, J. A. (2012). Causes of pneumonia epizootics among bighorn sheep, western United States, 2008–2010. *Emerging Infectious Diseases*, 18, 406–414.
- Black, S. R., Barker, I. K., Mehren, K. G., Crawshaw, G. J., Rosendal, S., Ruhnke, L., Thorsen, J., & Carman, P. S. (1988). An epizootic of *Mycoplasma ovipneumoniae* infection in captive Dall's sheep (*Ovis dalli dalli*). *Journal of Wildlife Diseases*, 24, 627–635.
- Bleich, V. C., Sargeant, G. A., & Wiedmann, B. P. (2018). Ecotypic variation in population dynamics of reintroduced bighorn sheep. *Journal of Wildlife Management*, 82, 8–18.
- Bleich, V. C., Wehausen, J. D., & Holl, S. A. (1990). Desert-dwelling mountain sheep: Conservation implications of a naturally fragmented distribution. *Conservation Biology*, 4, 383–390.
- Borg, N. J., Mitchell, M. S., Lukacs, P. M., Mack, C. M., Waits, L. P., & Krausman, P. R. (2017). Behavioral connectivity among bighorn sheep suggests potential for disease spread. *Journal of Wildlife Management*, 81, 38–45.
- Bowen, L., Longshore, K., Wolff, P., Klinger, R., Cox, M., Bullock, S., Waters, S., & Miles, A. K. (2020). Gene transcript profiling in desert bighorn sheep. *Wildlife Society Bulletin*, 44, 323–332.
- Bowyer, R. T., Stewart, K. M., Bleich, V. C., Witing, J. C., Monteith, K. L., Blum, M. E., & LaSharr, T. N. (2020). Metrics of harvest for ungulate populations: Misconceptions, lurking variables, and prudent management. *Alces*, 56, 15–38.
- Brogden, K. A., Rose, R., Cutlip, R. C., Lehmkuhl, H. D., & Tully, J. G. (1988). Isolation and identification of mycoplasmas from the nasal cavity of sheep. *American Journal of Veterinary Research*, 49, 1669–1672.
- Buchalski, M. R., Navarro, A. Y., Boyce, W. M., Winston Vickers, T., Tobler, M. W., Nordstrom, L. A., García, J. A., Gille, D. A., Penedo, M. C. T., Ryder, O. A., & Ernest, H. B. (2015). Genetic population structure of Peninsular bighorn sheep (*Ovis canadensis nelsoni*) indicates substantial gene flow across US-Mexico border. *Biological Conservation*, 184, 218–228. <https://doi.org/10.1016/j.biocon.2015.01.006>
- Buechner, H. K. (1960). The bighorn sheep in the United States, its past, present, and future. *Wildlife Monographs*, 53, 519–523.
- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24, 346–352.
- Butler, C. J., Edwards, W. H., Jennings-Gaines, J. E., Killion, H. J., Wood, M. E., McWhirter, D. E., Paterson, J. T., Proffitt, K. M., Almberg, E. S., White, P. J., Rotella, J. J., & Garrott, R. A. (2017). Assessing respiratory pathogen communities in bighorn sheep populations: Sampling realities, challenges, and improvements. *PLoS One*, 12, e0180689. <https://doi.org/10.1371/journal.pone.0180689>
- Callan, R. J., Bunch, T. D., Workman, G. W., & Mock, R. E. (1991). Development of pneumonia in desert bighorn sheep after exposure to a flock of exotic wild and domestic sheep. *Journal of the American Veterinary Medical Association*, 6, 1052–1056.
- Carpenter, T. E., Coggins, V. L., McCarthy, C., O'Brien, C. S., O'Brien, J. M., & Schommer, T. J. (2014). A spatial risk assessment of bighorn sheep extirpation by grazing domestic sheep on public lands. *Preventive Veterinary Medicine*, 114, 3–10.
- Cassaigne, I., Medellín, R. A., & Guasco, J. A. (2010). Mortality during epizootics in bighorn sheep: Effects of initial population size and cause. *Journal of Wildlife Diseases*, 46, 763–771.
- Cassirer, E. F., Manlove, K. R., Almberg, E. S., Kamath, P. L., Cox, M., Wolff, P., Roug, A., Shannon, J., Robinson, R., Harris, R. B., Gonzales, B. J., Plowright, R. K., Hudson, P. J., Cross, P. C., Dobson, A., & Besser, T. E. (2018). Pneumonia in bighorn sheep: Risk and resilience. *Journal of Wildlife Management*, 82, 32–45.
- Cassirer, E. F., Manlove, K. R., Plowright, R. K., & Besser, T. E. (2017). Evidence for strain-specific immunity to pneumonia in bighorn sheep. *Journal of Wildlife Management*, 81, 133–143.
- Cassirer, E. F., Plowright, R. K., Manlove, K. R., Cross, P. C., Dobson, A. P., Potter, K. A., & Hudson, P. J. (2013). Spatio-temporal dynamics of pneumonia in bighorn sheep. *Journal of Animal Ecology*, 82, 518–528.
- Cassirer, E. F., & Sinclair, A. R. E. (2007). Dynamics of pneumonia in a bighorn sheep metapopulation. *Journal of Wildlife Management*, 71, 1080–1088.
- Couch, C. E., Arnold, H. K., Crowhurst, R. S., Jolles, A. E., Sharpton, T. J., Witczak, M. F., Epps, C. W., & Beechler, B. R. (2020). Bighorn sheep gut microbiomes associate with genetic and spatial structure across a metapopulation. *Scientific Reports*, 10, 6582. <https://doi.org/10.1038/s41598-020-63401-0>
- Courtemanch, A. B., Kauffman, M. J., Kilpatrick, S., & Dewey, S. R. (2017). Alternative foraging strategies enable a mountain ungulate to persist after migration loss. *Ecosphere*, 8, 1–16.
- Cowan, I. M. (1940). Distribution and variation in the native sheep of North America. *American Midland Naturalist*, 24, 505.
- Creech, T. G., Epps, C. W., Landguth, E. L., Wehausen, J. D., Crowhurst, R. S., Holton, B., & Monello, R. J. (2017). Simulating the spread of selection-driven genotypes using landscape resistance models for desert bighorn sheep. *PLoS One*, 12, e0176960. <https://doi.org/10.1371/journal.pone.0176960>
- Creech, T. G., Epps, C. W., Monello, R. J., & Wehausen, J. D. (2014). Using network theory to prioritize management in a desert bighorn sheep metapopulation. *Landscape Ecology*, 29, 605–619.
- Creech, T. G., Epps, C. W., Wehausen, J. D., Crowhurst, R. S., Jaeger, J. R., Longshore, K., Holton, B., Sloan, W. B., & Monello, R. J. (2020). Genetic and environmental indicators of climate change vulnerability for desert bighorn sheep. *Frontiers in Ecology and Evolution*, 8, 1–21.
- Dassanayake, R. P., Shanthalingam, S., Herndon, C. N., Lawrence, P. K., Cassirer, E. F., Potter, K. A., Foreyt, W. J., Clinkenbeard, K. D., & Srikumaran, S. (2009). *Mannheimia haemolytica* serotype A1 exhibits differential pathogenicity in two related species, *Ovis canadensis* and *Ovis aries*. *Veterinary Microbiology*, 133, 366–371.
- Dassanayake, R. P., Shanthalingam, S., Herndon, C. N., Subramaniam, R., Lawrence, P. K., Bavananthasivam, J., Cassirer, E. F., Haldorson, G. J., Foreyt, W. J., Rurangirwa, F. R., Knowles, D. P., Besser, T. E., & Srikumaran, S. (2010). *Mycoplasma ovipneumoniae* can predispose bighorn sheep to fatal *Mannheimia haemolytica* pneumonia. *Veterinary Microbiology*, 145, 354–359. <https://doi.org/10.1016/j.vetmic.2010.04.011>
- Dassanayake, R. P., Shanthalingam, S., Subramaniam, R., Herndon, C. N., Bavananthasivam, J., Haldorson, G. J., Foreyt, W. J., Evermann, J. F., Herrmann-Hoesing, L. M., Knowles, D. P., & Srikumaran, S. (2013). Role of *Bibersteinia trehalosi*, respiratory syncytial virus, and parainfluenza-3 virus

- in bighorn sheep pneumonia. *Veterinary Microbiology*, 162, 166–172. <https://doi.org/10.1016/j.vetmic.2012.08.029>
- Deakin, S., Gorrell, J. C., Kneteman, J., Hik, D. S., Jobin, R. M., & Coltman, D. W. (2020). Spatial genetic structure of rocky mountain bighorn sheep (*Ovis canadensis canadensis*) at the northern limit of their native range. *Canadian Journal of Zoology*, 98, 317–330.
- DeCesare, N. J., & Pletscher, D. H. (2004). Bighorn sheep, horizontal visibility, and GIS. *Biennial Symposium of the Northern Wild Sheep and Goat Council*, 14, 181–190.
- DeCesare, N. J., & Pletscher, D. H. (2006). Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. *Journal of Mammalogy*, 87, 531–538.
- Dekelaita, D. J., Epps, C. W., Stewart, K. M., Sedinger, J. S., Powers, J. G., Gonzales, B. J., Abella-Vu, R. K., Darby, N. W., & Hughson, D. L. (2020). Survival of adult female bighorn sheep following a pneumonia epizootic. *Journal of Wildlife Management*, 84, 1268–1282.
- Donovan, V. M., Roberts, C. P., Wonkka, C. L., Beck, J. L., Popp, J. N., Allen, C. R., & Twidwell, D. (2020). Range-wide monitoring of population trends for Rocky Mountain bighorn sheep. *Biological Conservation*, 248, 108639.
- Enk, T. A., Picton, H. D., & Williams, J. S. (2001). Factors limiting a bighorn sheep population in Montana following a dieoff. *North-west Science*, 75, 280–291.
- Epps, C. W., Crowhurst, R. S., & Nickerson, B. S. (2018). Assessing changes in functional connectivity in a desert bighorn sheep metapopulation after two generations. *Molecular Ecology*, 27, 2334–2346.
- Epps, C. W., Palsbøll, P. J., Wehausen, J. D., Roderick, G. K., & McCullough, D. R. (2006). Elevation and connectivity define genetic refugia for mountain sheep as climate warms. *Molecular Ecology*, 15, 4295–4302.
- Epps, C. W., Palsbøll, P. J., Wehausen, J. D., Roderick, G. K., Ramey, R. R., & McCullough, D. R. (2005). Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters*, 8, 1029–1038.
- Epps, C. W., Wehausen, J. D., Bleich, V. C., Torres, S. G., & Brashares, J. S. (2007). Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology*, 44, 714–724.
- Epps, C. W., Wehausen, J. D., Palsbøll, P. J., & McCullough, D. R. (2010). Using genetic tools to track desert bighorn sheep colonizations. *Journal of Wildlife Management*, 74, 522–531.
- Erwin, J. A., Vargas, K., Blais, B. R., Bennett, K., Muldoon, J., Findysz, S., Christie, C., Heffelfinger, J. R., & Culver, M. (2018). Genetic assessment of a bighorn sheep population expansion in the Silver Bell Mountains, Arizona. *PeerJ*, 6, e5978.
- Festa-Bianchet, M. (1986a). Site fidelity and seasonal range use by bighorn rams. *Canadian Journal of Zoology*, 64, 2126–2132.
- Festa-Bianchet, M. (1986b). Seasonal dispersion of overlapping mountain sheep ewe groups. *Journal of Wildlife Management*, 50, 325–330.
- Festa-Bianchet, M. (1991). Numbers of lungworm larvae in feces of bighorn sheep: Yearly changes, influence of host sex, and effects on host survival. *Canadian Journal of Zoology*, 69, 547–559.
- Fleishman, E., Anderson, J., & Dickson, B. G. (2017). Single-species and multiple-species connectivity models for large mammals on the Navajo Nation. *Western North American Naturalist*, 77, 237–251.
- Flesch, A. D., Epps, C. W., Cain, J. W., Clark, M., Krausman, P. R., & Morgart, J. R. (2010). Potential effects of the United States-Mexico border fence on wildlife. *Conservation Biology*, 24, 171–181.
- Flesch, E. P., Graves, T. A., Thomson, J. M., Proffitt, K. M., White, P. J., Stephenson, T. R., & Garrott, R. A. (2020). Evaluating wildlife translocations using genomics: A bighorn sheep case study. *Ecology and Evolution*, 10, 13687–13704.
- Foreyt, W. J., & Jessup, D. A. (1982). Fatal pneumonia of bighorn sheep following association with domestic sheep. *Journal of Wildlife Diseases*, 18, 163–168.
- Foreyt, W. J., Snipes, K. P., & Kasten, R. W. (1994). Fatal pneumonia following inoculation of healthy bighorn sheep with *Pasteurella haemolytica* from healthy domestic sheep. *Journal of Wildlife Diseases*, 30, 137–145.
- Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, 13, 58–63.
- Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, 31, 367–393.
- Garwood, T. J., Lehman, C. P., Walsh, D. P., Cassirer, E. F., Besser, T. E., & Jenks, J. A. (2020). Removal of chronic mycoplasma ovipneumoniae carrier ewes eliminates pneumonia in a bighorn sheep population. *Ecology Evolution*, 10, 3491–3502.
- Geist, V., & Petocz, R. G. (1977). Bighorn sheep in winter: Do rams maximize reproductive fitness by spatial and habitat segregation from ewes? *Canadian Journal of Zoology*, 55, 1802–1810.
- George, J. L., Martin, D. J., Lukacs, P. M., & Miller, M. W. (2008). Epidemic pasteurellosis in a bighorn sheep population coinciding with the appearance of a domestic sheep. *Journal of Wildlife Diseases*, 44, 388–403.
- Gilad, O., Ben, W. X., & Armstrong, F. (2013). Assessing the feasibility for reintroducing desert bighorn sheep to Guadalupe Mountains National Park: Habitat, migration corridors and challenges. *Applied Geography*, 41, 96–104. <https://doi.org/10.1016/j.apgeog.2013.03.012>
- Gille, D. A., Buchalski, M. R., Conrad, D., Rubin, E. S., Munig, A., Wakeling, B. F., Epps, C. W., Creech, T. G., Crowhurst, R., Holton, B., Monello, R., Boyce, W. M., Penedo, M. C. T., & Ernest, H. B. (2019). Genetic outcomes of translocation of bighorn sheep in Arizona. *Journal of Wildlife Management*, 83, 838–854.
- Gross, J. E., Singer, F. J., & Moses, M. E. (2000). Effects of disease, dispersal, and area on bighorn sheep restoration. *Restoration Ecology*, 8, 25–37.
- Hanthorn, C. J. (2014). *Pathogenicity of Bibersteinia trehalosi in bovine calves*. Iowa State University. <https://lib.dr.iastate.edu/etd/13974>
- Heinse, L. M., Hardesty, L. H., & Harris, R. B. (2016). Risk of pathogen spillover to bighorn sheep from domestic sheep and goat flocks on private land. *Wildlife Society Bulletin*, 40, 625–633.
- Herndon, C. N., Shanthalingam, S., Knowles, D. P., Call, D. R., & Srikumaran, S. (2011). Comparison of passively transferred

- antibodies in bighorn and domestic lambs reveals one factor in differential susceptibility of these species to *Mannheimia haemolytica*-induced pneumonia. *Clinical and Vaccine Immunology*, 18, 1133–1138.
- Highland, M. A., Herndon, D. R., Bender, S. C., Hansen, L., Gerlach, R. F., & Beckmen, K. B. (2018). *Mycoplasma ovipneumoniae* in wildlife species beyond subfamily Caprinae. *Emerging Infectious Diseases*, 24, 2384–2386.
- Hogg, J. T., Forbes, S. H., Steele, B. M., & Luikart, G. (2006). Genetic rescue of an insular population of large mammals. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1491–1499.
- Howard, C. J., & Thomas, L. H. (1974). Inhibition by *Mycoplasma dispar* of ciliary activity in tracheal organ cultures. *Infection and Immunity*, 10, 405–408.
- Jahner, J. P., Matocq, M. D., Malaney, J. L., Cox, M., Wolff, P., Gritts, M. A., & Parchman, T. L. (2019). The genetic legacy of 50 years of desert bighorn sheep translocations. *Evolutionary Applications*, 12, 198–213.
- Kamath, P. L., Manlove, K., Cassirer, E. F., Cross, P. C., & Besser, T. E. (2019). Genetic structure of *Mycoplasma ovipneumoniae* informs pathogen spillover dynamics between domestic and wild Caprinae in the western United States. *Scientific Reports*, 9, 1–14.
- Kasza, Z., Cushman, S. A., Sillero-Zubiri, C., Wolff, E., & Marino, J. (2018). Where buffalo and cattle meet: Modelling interspecific contact risk using cumulative resistant kernels. *Ecography*, 41, 1–11.
- Keeley, A. T. H., Beier, P., & Gagnon, J. W. (2016). Estimating landscape resistance from habitat suitability: Effects of data source and nonlinearities. *Landscape Ecology*, 31, 2151–2162.
- Kozakiewicz, C. P., Burridge, C. P., Funk, W. C., VandeWoude, S., Craft, M. E., Crooks, K. R., Ernest, H. B., Fountain-Jones, N. M., & Carver, S. (2018). Pathogens in space: Advancing understanding of pathogen dynamics and disease ecology through landscape genetics. *Evolutionary Applications*, 11, 1763–1778.
- Landguth, E. L., Forester, B. R., Eckert, A. J., Shirk, A. J., Menon, M., Whipple, A., Day, C. C., & Cushman, S. A. (2020). Modelling multilocus selection in an individual-based, spatially-explicit landscape genetics framework. *Molecular Ecology Resources*, 20, 605–615.
- Lawrence, P. K., Shanthalingam, S., Dassanayake, R. P., Subramaniam, R., Herndon, C. N., Knowles, D. P., Rurangirwa, F. R., Foreyt, W. J., Wayman, G., Marciel, A. M., Highlander, S. K., & Srikumaran, S. (2010). Transmission of *Mannheimia haemolytica* from domestic sheep (*Ovis aries*) to bighorn sheep (*Ovis canadensis*): Unequivocal demonstration with green fluorescent protein-tagged organisms. *Journal of Wildlife Diseases*, 46, 706–717.
- Love Stowell, S. M., Gagne, R. B., McWhirter, D., Edwards, W., & Ernest, H. B. (2020). Bighorn sheep genetic structure in Wyoming reflects geography and management. *Journal of Wildlife Management*, 84, 1072–1090.
- Lowrey, C., & Longshore, K. M. (2017). Tolerance to disturbance regulated by attractiveness of resources: A case study of desert bighorn sheep within the River Mountains, Nevada. *Western North American Naturalist*, 77, 82–98.
- Lowrey, B., McWhirter, D. E., Proffitt, K. M., Monteith, K. L., Courtemanch, A. B., White, P. J., Paterson, J. T., Dewey, S. R., & Garrett, R. A. (2020). Individual variation creates diverse migratory portfolios in native populations of a mountain ungulate. *Ecological Applications*, 30, e2106.
- Lowrey, B., Proffitt, K. M., McWhirter, D. E., White, P. J., Courtemanch, A. B., Dewey, S. R., Miyasaki, H. M., Monteith, K. L., Mao, J. S., Grigg, J. L., Butler, C. J., Lula, E. S., & Garrett, R. A. (2019). Characterizing population and individual migration patterns among native and restored bighorn sheep (*Ovis canadensis*). *Ecology and Evolution*, 9, 8829–8839.
- Luikart, G., Pilgrim, K., Vistry, J., Ezenwa, V. O., & Schwartz, M. K. (2008). Candidate gene microsatellite variation is associated with parasitism in wild bighorn sheep. *Biology Letters*, 4, 228–231.
- Lula, E. S., Lowrey, B., Proffitt, K. M., Litt, A. R., Cunningham, J. A., Butler, C. J., & Garrett, R. A. (2020). Is habitat constraining bighorn sheep restoration? A case study. *Journal of Wildlife Management*, 84, 588–600. <https://doi.org/10.1002/jwmg.21823>
- Manlove, K. R., Frances Cassirer, E., Cross, P. C., Plowright, R. K., & Hudson, P. J. (2014). Costs and benefits of group living with disease: A case study of pneumonia in bighorn lambs (*Ovis canadensis*). *Proceedings of the Royal Society B: Biological Sciences*, 281, 1–8.
- Manlove, K., Frances Cassirer, E., Cross, P. C., Plowright, R. K., & Hudson, P. J. (2016). Disease introduction is associated with a phase transition in bighorn sheep demographics. *Ecology*, 97, 2593–2602.
- Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., Oates, B. A., Sawyer, H., Scurlock, B. M., & Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20160456.
- Miller, M. W. (2001). Pasteurellosis. In E. S. Williams & I. K. Barker (Eds.), *Infectious diseases of wild mammals* (pp. 330–339). Iowa State University Press.
- Miller, D. S., Weiser, G. C., Ward, A. C., Drew, M. L., & Chapman, P. L. (2012). *Pasteurellaceae* isolated from bighorn sheep (*Ovis canadensis*) from Idaho, Oregon, and Wyoming. *American Journal of Veterinary Research*, 73, 1024–1028.
- Monello, R. J., Murray, D. L., & Cassirer, E. F. (2001). Ecological correlates of pneumonia epizootics in bighorn sheep herds. *Canadian Journal of Zoology*, 79, 1423–1432.
- Mooring, M. S., Fitzpatrick, T. A., Benjamin, J. E., Fraser, I. C., Nishihira, T. T., Reisig, D. D., & Rominger, E. M. (2003). Sexual segregation in desert bighorn sheep (*Ovis canadensis mexicana*). *Behaviour*, 140, 183–207.
- O'Brien, J. M., O'Brien, C. S., McCarthy, C., & Carpenter, T. E. (2014). Incorporating foray behavior into models estimating contact risk between bighorn sheep and areas occupied by domestic sheep. *Wildlife Society Bulletin*, 38, 321–331.
- Olson, Z. H., Whittaker, D. G., & Rhodes, O. E. (2013). Translocation history and genetic diversity in reintroduced bighorn sheep. *Journal of Wildlife Management*, 77, 1553–1563.
- Plowright, R. K., Manlove, K. R., Besser, T. E., Páez, D. J., Andrews, K. R., Matthews, P. E., Waits, L. P., Hudson, P. J., & Cassirer, E. F. (2017). Age-specific infectious period shapes

- dynamics of pneumonia in bighorn sheep. *Ecology Letters*, 20, 1325–1336.
- Plowright, R. K., Manlove, K., Cassirer, E. F., Cross, P. C., Besser, T. E., & Hudson, P. J. (2013). Use of exposure history to identify patterns of immunity to pneumonia in bighorn sheep (*Ovis canadensis*). *PLoS One*, 8, e61919.
- Poirier, M. A., Coltman, D. W., Pelletier, F., Jorgenson, J., & Festa-Bianchet, M. (2019). Genetic decline, restoration and rescue of an isolated ungulate population. *Evolutionary Applications*, 12, 1318–1328.
- Poirier, M.-A., & Festa-Bianchet, M. (2018). Social integration and acclimation of translocated bighorn sheep (*Ovis canadensis*). *Biological Conservation*, 218, 1–9. <https://doi.org/10.1016/j.biocon.2017.11.031>
- Poole, K., Serrouya, R., Teske, I., & Podrasky, K. (2016). Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) winter habitat selection and seasonal movements in an areas of active coal mining. *Canadian Journal of Zoology*, 94, 733–745.
- Raghavan, B., Erickson, K., Kugadas, A., Batra, S. A., Call, D. R., Davis, M. A., Foreyt, W. J., & Srikumaran, S. (2016). Role of carriers in the transmission of pneumonia in bighorn sheep (*Ovis canadensis*). *Biology Open*, 5, 745–755.
- Robinson, R. W., Whiting, J. C., Shannon, J. M., Olson, D. D., Flinders, J. T., Smith, T. S., & Bowyer, R. T. (2019). Habitat use and social mixing between groups of resident and augmented bighorn sheep. *Scientific Reports*, 9, 14984. <https://doi.org/10.1038/s41598-019-51370-y>
- Roffler, G. H., Amish, S. J., Smith, S., Cosart, T., Kardos, M., Schwartz, M. K., & Luikart, G. (2016). SNP discovery in candidate adaptive genes using exon capture in a free-ranging alpine ungulate. *Molecular Ecology Resources*, 16, 1147–1164.
- Rovani, E. R., Beckmen, K. B., & Highland, M. A. (2019). Mycoplasma ovipneumoniae associated with polymicrobial pneumonia in a free-ranging yearling barren ground caribou (*Rangifer tarandus granti*) from Alaska, USA. *Journal of Wildlife Diseases*, 55, 733–736.
- Rubin, E. S., Stermer, C. J., Boyce, W. M., & Torres, S. G. (2009). Assessment of predictive habitat models for bighorn sheep in California's Peninsular ranges. *Journal of Wildlife Management*, 73, 859–869.
- Ruckstuhl, K. E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour*, 56, 99–106.
- Rudolph, K. M., Hunter, D. L., Rimler, R. B., Cassirer, E. F., Foreyt, W. J., DeLong, W. J., Weiser, G. C., & Ward, A. C. S. (2007). Microorganisms associated with a pneumonic epizootic in Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*). *Journal of Zoo and Wildlife Medicine*, 38, 548–558.
- Russell, R. E., DiRenzo, G. V., Szymanski, J. A., Alger, K. E., & Grant, E. H. C. (2020). Principles and mechanisms of wildlife population persistence in the face of disease. *Frontiers in Ecology and Evolution*, 8, 569016.
- Schwartz, O. A., Bleich, V. C., & Holl, S. A. (1986). Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation*, 37, 179–190.
- Singer, F. J., Bleich, V. C., & Gudorf, M. A. (2000). Restoration of bighorn sheep metapopulations in and near western national parks. *Restoration Ecology*, 8, 14–24.
- Singer, F. J., Moses, M. E., Bellew, S., & Sloan, W. (2000). Correlates to colonizations of new patches by translocated populations of bighorn sheep. *Restoration Ecology*, 8, 66–74.
- Singer, F. J., Papouchis, C. M., & Symonds, K. K. (2000). Translocations as a tool for restoring populations of bighorn sheep. *Restoration Ecology*, 8, 6–13.
- Singer, F. J., Zeigenfuss, L. C., & Spicer, L. (2001). Role of patch size, disease, and movement in rapid extinction of bighorn sheep. *Conservation Biology*, 15, 1347–1354.
- Spitz, D. B., Hebblewhite, M., & Stephenson, T. R. (2017). 'MigrateR': Extending model-driven methods for classifying and quantifying animal movement behavior. *Ecography*, 40, 788–799.
- Spitz, D., Hebblewhite, M., Stephenson, T., & German, D. (2018). How plastic is migratory behavior? Quantifying elevational movement in a partially-migratory alpine ungulate. *Canadian Journal of Zoology*, 96, 1385–1394.
- Spraker, T. R., Collins, J. K., Adrian, W. J., & Olterman, J. H. (1986). Isolation and serologic evidence of a respiratory syncytial virus in bighorn sheep from Colorado. *Journal of Wildlife Diseases*, 22, 416–418.
- Spraker, T. R., Hibler, C. P., Schoonveld, G. G., & Adney, W. S. (1984). Pathologic changes and microorganisms found in bighorn sheep during a stress-related die-off. *Journal of Wildlife Diseases*, 20, 319–327.
- Stevenson, A. (Ed.). (2010). *Oxford dictionary of English*. Oxford University Press.
- Storfer, A., Patton, A., & Fraik, A. K. (2018). Navigating the interface between landscape genetics and landscape genomics. *Frontiers in Genetics*, 9, 68.
- Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 68, 571–573. <http://www.jstor.org/stable/3544927>
- Thompson, J. R., Bleich, V. C., Torres, S. G., & Mulcahy, G. P. (2001). Translocation techniques for mountain sheep: Does the method matter? *The Southwestern Naturalist*, 46, 87–93.
- Tomassini, L., Gonzales, B., Weiser, G. C., & Sisco, W. (2009). An ecologic study comparing distribution of *Pasteurella trehalosi* and *Mannheimia haemolytica* between Sierra Nevada bighorn sheep, White Mountain bighorn sheep, and domestic sheep. *Journal of Wildlife Diseases*, 45, 930–940.
- Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., ... Mueller, T. (2018). Moving in the anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359, 466–469.
- Vander Wal, E., Garant, D., Festa-Bianchet, M., & Pelletier, F. (2013). Evolutionary rescue in vertebrates: Evidence, applications and uncertainty. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20120090.
- Werdel, T. J., Jenks, J. A., Besser, T. E., Kanta, J. T., Lehman, C. P., & Frink, T. J. (2020). Restoration of a bighorn sheep population impeded by *mycoplasma ovipneumoniae* exposure. *Restoration Ecology*, 28, 387–395.
- Wolfe, L. L., Diamond, B., Spraker, T. R., Sirochman, M. A., Walsh, D. P., Machin, C. M., Bade, D. J., & Miller, M. W. (2010). A bighorn sheep die-off in southern Colorado

involving a Pasteurellaceae strain that may have originated from syntopic cattle. *Journal of Wildlife Diseases*, 46, 1262–1268.

- Wood, M. E., Fox, K. A., Jennings-Gaines, J., Killion, H. J., Amundson, S., Miller, M. W., & Edwards, W. H. (2017). How respiratory pathogens contribute to lamb mortality in a poorly performing bighorn sheep (*Ovis canadensis*) herd. *Journal of Wildlife Diseases*, 53, 126–130.
- Woolf, A., O'Shea, T., & Gilbert, D. L. (1970). Movements and behavior of bighorn sheep on summer ranges in Yellowstone National Park. *Journal of Wildlife Management*, 34, 446–450.

How to cite this article: Paolini, K. E., Schwartz, M. K., Friggens, M. M., Cushman, S. A., Weckworth, J. K., & Holbrook, J. D. (2023). A review of population and landscape level dynamics associated with pneumonia outbreaks in bighorn sheep with implications for land management. *Conservation Science and Practice*, 5(7), e12956. <https://doi.org/10.1111/csp2.12956>