AN ABSTRACT OF THE DISSERTATION OF

Robert S. Spaan for the degree of Doctor of Philosophy in Wildlife Science presented on September 22, 2022.

Title: Characterizing the Spread and Consequences of *Mycoplasma ovipneumoniae* on Bighorn Sheep (*Ovis canadensis*) in the Northern Basin and Range Ecosystem

Abstract approved: _____

Clinton Wakefield Epps

North American bighorn sheep (*Ovis canadensis*) have experienced significant declines and population extirpations due to novel pathogens such as *Mycoplasma ovipneumoniae*. This disease continues to limit the population restoration of bighorn sheep. Therefore, understanding the demographic consequences of pathogen presence and the risk of contact between bighorn populations and potential sources of pathogens is vital to managing bighorn sheep populations effectively, especially for pathogens that cause respiratory pneumonia. My dissertation focuses on characterizing the spread and consequences of respiratory disease caused by *M. ovipneumoniae* in southeastern Oregon and northern Nevada.
I carried out four interdisciplinary studies involving extensive fieldwork, epidemiological, genetic, geospatial, and statistical methodologies to determine factors influencing bighorn sheep demography and spatial ecology. My research relied in part on data provided by two state wildlife management agencies, Oregon Department of Fish and Wildlife (ODFW) and Nevada Department of Wildlife (NDOW), that captured adult female and male bighorn sheep, fitted them with GPS collars that generated and remotely transmitted remotely location data, and sampled them to generate diagnostics and genetic testing. I collected additional observational and non-invasive data within the system.

In Chapter 2, I investigated the effect of *M. ovipneumoniae* on juvenile survival within our study system. I used observational data of juveniles and PCR-testing of juveniles that were found dead to analyze juvenile survival relative to *M. ovipneumoniae* presence, population genetic diversity, and forage characteristics. That study showed that the presence of *M. ovipneumoniae* can cause extremely low juvenile survival but found little influence of population genetic diversity or nutritional effects on juvenile survival. In addition, the study showed that even very low prevalence of *M. ovipneumoniae* in adults can have harmful effects on juveniles and that targeted removals of infected adults should be considered.

In Chapter 3, I investigated the effect of exposure and infection of *M. ovipneumoniae* and other factors on GPS-collared adults using known-fate models. *M. ovipneumoniae*-exposed adults had lower survival than unexposed individuals, and I found evidence, albeit weaker, that adult survival was lower for males and in populations where genetic diversity was lower. The low prevalence of *M. ovipneumoniae*-exposed individuals suggests that chronic shedders and birth pulses maintain the pathogen. While targeted removals have been used as an effective tool to manage juvenile survival in bighorn sheep, these results indicate adults may benefit from this action too. I also recommended that management increase genetic diversity of populations that have suffered from sequential founder effects, although such action would have to be weighed carefully against the risk of increased disease exposure.

For Chapter 4, I used GPS collar data to investigate space and habitat use patterns – key features of host behavior that impact pathogen exposure and transmission, as well as gene flow and metapopulation function. I assessed utilization distributions, site fidelity, social affinity, and resource selection functions separately for male and female bighorn. Although resource selection by both sexes was quite similar within the same seasons, female bighorn sheep exhibited extremely high site fidelity and social affinity, much higher than observed in other systems. Site fidelity and social affinity of male bighorn sheep were significantly lower, with numerous interpopulation movements. Our findings suggest that male bighorn sheep are responsible for disease transmission between the populations and maintain gene flow within the system. Still, females' high site fidelity and social affinity have resulted in the low potential for colonization of unused habitat, and I identified several areas of potential habitat that are unused by females but could increase distribution or enhance connectivity if occupied.

In Chapter 5, I used the methodology of O'Brien et al. (2014) to estimate the risk of contact for each study population with potential sources of *M. ovipneumoniae*, including domestic sheep grazing allotments, other bighorn sheep populations, or potential sources of domestic sheep and goats. I found that all study populations had some probability of contact with other possible sources of infection risk, although those sources did not include known domestic sheep grazing allotments. This study therefore provides a tool to prioritize outreach to private landowners or management of disease within affected bighorn populations that may pose risk to other populations.

This study highlights the adverse effects of *M. ovipneumoniae* persistence on bighorn sheep population recovery and the complications of managing metapopulation connectivity in a disease-impacted system. Management options to control pathogen spread must balance connectivity's negative and positive consequences. The management agencies responsible for these bighorn populations have initiated test and remove programs to deal with asymptomatic carriers within the system. However, our findings suggest further actions may be needed to improve genetic diversity and promote habitat colonization while considering disease risks associated with these actions. Hopefully, the data presented

here inform efforts that help mitigate further exposure to novel strains of *M. ovipneumoniae* while maintaining necessary metapopulation functions.

Characterizing the Spread and Consequences of *Mycoplasma ovipneumoniae* on Bighorn Sheep (*Ovis canadensis*) in the Northern Basin and Range Ecosystem

by
Robert S. Spaan

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APPROVED:

Major Professor, representing Wildlife Sciences

Head of the Department of Fisheries, Wildlife, and Conservation Sciences

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Robert S. Spaan, Author

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I am also grateful to Mike Cox of NDOW. He helped me acquire additional funds for captures and provisioned collars to expand the project into Nevada. I would also like to thank Phillip Milburn, Scott Torland and Autumn Larkins of ODFW for helping to initiate this project and Ed Partee of the NDOW for support when working with the neighboring Nevada populations. I would also like to thank ODFW and NDOW staff for capturing, collaring, and sampling bighorn sheep, particularly veterinarians Julia Burco (ODFW), Peregrine Wolff (NDOW), and their support staff. Finally, I would like to thank the field technicians Geoffrey Gerdes, Logan Gmuender, Lindsey Howard, and Colton Padilla for all their help and support. A special thanks to Geoffrey and Lindsey for putting up with having to share a living space with me.

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call at a moment's notice to work through problems, discuss papers, and with Brandon, discuss our shared love of African wildlife, research on African wildlife and photography.

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CONTRIBUTION OF AUTHORS

Robert Spaan contributed to the study design, assisted the Oregon Department of Fish and Wildlife (ODFW) and Nevada Department of Wildlife (NDOW) with captures, conducted and coordinated the collection of data, acquired additional funding, analyzed data, and drafted manuscripts in collaboration with coauthors. Clinton Epps contributed to the study design and research direction, obtained funding for the project, assisted ODFW and NDOW with captures, made field visits, interpreted results, and wrote manuscripts. Don Whittaker of ODFW, with other ODFW staff, initiated interest and visualized the project, obtained funding for the project, and organized and conducted the captures, interpretation of results, and writing of manuscripts. Mike Cox of NDOW, with other NDOW staff, assisted with acquiring additional funding and organized and conducted the captures, interpretation of results, and writing of manuscripts. Brianna Beechler and Rachel Crowhurst assisted ODFW and NDOW with captures, made field visits, and provided technical assistance with data analysis and manuscript writing. Adam Duarte and Matthew Weldy made field visits and provided technical assistance with data analysis and manuscript writing. Christina Aiello provided technical assistance with data analysis and manuscript writing.

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CHAPTER 1

GENERAL INTRODUCTION

Species select specific habitats to maximize their fitness through various mechanisms, such as nutrition acquisition, reproduction, or predator avoidance (Morris 2003). Habitat specialists, in particular, thrive within a narrow range of foraging or environmental conditions but tend to be sensitive to habitat disturbance or rapid change (Devictor et al. 2010). Moreover, given the heterogeneous nature of most landscapes (Wiens 1989), habitats favored by specialists are likely to be patchily distributed. As a result, they are often at risk of additional fragmentation by anthropogenic activities (Hanski 1998). Thus, managing habitat specialists usually requires ensuring connectivity among patches of suitable habitat to minimize inbreeding and maintain or restore metapopulation functionality by allowing demographic rescue and recolonization (Brown and Kodric-Brown 1977). While connectivity is necessary for healthy ecological function, it also risks exposure to novel pathogens in today's human-dominated landscapes (Borremans et al. 2019).

Bighorn sheep (*Ovis canadensis*), a habitat specialist, were extirpated from much of their range by the early 20th century, with pneumonia considered to have played a significant role (Cassirer et al. 2018). *Mycoplasma ovipneumoniae* is a bacterial pathogen considered to be the primary cause of pneumonia in bighorn sheep (Besser et al. 2008, 2014). It is typically initially transmitted to bighorn sheep by domestic sheep (*O. aries*) and goats (*Capra hircus*), with subsequent transmission among bighorn sheep, and initially results in high mortality of all age classes (often referred to as an “all age die-off”) due to a lack of immunity. While some individuals survive and clear the pathogen, subsequently gaining some degree of immunity to that strain of pathogen, others remain chronic carriers continuing to transmit the pathogen to previously unexposed juveniles (Plowright et al. 2017). This pattern of infection has been observed in several regions, including Oregon, Idaho, Washington, Nevada, and South Dakota (Smith et al. 2014, Cassirer et al. 2018, Garwood et al. 2020). Because immunity to *M. ovipneumoniae* is strain-specific, novel strains of pathogen result in new waves of infection (Cassirer et al. 2017).

Population-level responses to *M. ovipneumoniae* outbreaks, however, may vary widely. Considerable variation has been observed in levels of all-age mortality at first contact, subsequent adult survival, and juvenile survival in following years among populations and across evolutionary lineages and habitats (Cassirer et al. 2018, Dekelaita et al. 2020). Hypothesized causes of variation include strain virulence (Kamath et al. 2019), forage and population density (Cassirer et al. 2018), genetic diversity of host populations (Cassirer et al. 2018), and connectivity within a system (Manlove et al. 2017). Evolutionary history and the degree of adaptation to local condition may also influence fitness in disease outbreaks. Across the range of the species, bighorn sheep exhibit phenotypic variation and local

adaptation (Wehausen and Ramey II 2000, Wiedmann and Sargeant 2014, Malaney et al. 2015). Currently, three subspecies of bighorn sheep are recognized, the desert bighorn sheep (*O. c. nelsoni*), Rocky Mountain bighorn sheep (*O. c. canadensis*), and Sierra Nevada bighorn sheep (*O. c. sierrae*) (Wehausen and Ramey II 2000, Wehausen et al. 2005). However, debate exists whether the established lineages capture the independent evolutionary trajectories and local adaptation (Buchalski et al. 2016, Bleich et al. 2018, Barbosa et al. 2021).

Previous studies of population dynamics in the presence of *M. ovipneumoniae* suggest that disease dynamics should be evaluated across lineages and ecosystems. For instance, Rocky Mountain bighorn sheep in the Hells Canyon system of Idaho, Oregon, and Washington occupy relatively continuous habitat with cold winters (Cassirer and Sinclair 2007). In that system, *M. ovipneumoniae* tends to persist for long periods, resulting in constant disease in juveniles (Cassirer et al. 2018). The same pattern of infection was also observed in Rocky Mountain bighorn sheep in the Black Hills of western South Dakota and eastern Wyoming (Smith et al. 2014, Garwood et al. 2020). In the Mojave Desert of the southwestern United States of America, desert bighorn sheep occupy pockets of isolated mountain ranges surrounded by low-lying desert but linked by inter-mountain movements, resulting in natural metapopulations that have persisted with few translocations, unlike bighorn sheep across many other parts of their range (Bleich et al. 1996). *M. ovipneumoniae* in that system appears to have been present periodically for decades (Shirkey et al. 2021), and impacts on adult survival and juvenile recruitment appear to be highly variable (Dekelaita 2020).

Bighorn sheep in the northern Basin and Range ecosystem (including parts of southeastern Oregon, southwestern Idaho, and northern Nevada) occupy transitional habitats between the Mojave and Rocky Mountain systems and have a unique history. Native bighorn sheep from this region were considered the "California" subspecies (*O. c. californiana*; Cowan 1940), spanned from the Sierra Nevada of California north to British Columbia. In Oregon, all native bighorn sheep were extirpated by 1945 (Oregon Department of Fish and Wildlife 2003). Subsequently, morphometric and DNA analysis of the extinct native Oregon populations resulted in those populations being reassigned to the Great Basin Desert form of the desert bighorn sheep (*O. c. nelson*; Wehausen and Ramey II 2000). Bighorn sheep now existing in Oregon all stem from translocations and are managed as two lineages: Rocky Mountain bighorn sheep were introduced to northeastern Oregon, and "California" bighorn sheep were introduced to potential or former bighorn sheep habitat in other areas of the state using individuals from British Columbia. Both lineages are formally considered Rocky Mountain bighorn sheep subspecies at this time (*O. c. canadensis*; Wehausen and Ramey II 2000). Most of the restored populations in Oregon were sourced from a single translocation of 22 bighorn sheep from British Columbia in 1953 (Olson et al. 2013). However, in 2000 and 2001, as part of an experimental effort to increase population genetic

diversity and improve demographic performance, two populations in southeastern Oregon received augmentations of translocated bighorn sheep ultimately derived from different source populations in British Columbia (Olson et al. 2012). "California" bighorn sheep were also introduced to northern Nevada in 1972 from multiple source populations (Nevada Division of Wildlife 2001, Olson et al. 2013), and dispersal from these populations into southeastern Oregon has been observed (ODFW unpublished data). "California" bighorn populations in southwestern Idaho and northern Nevada share similar histories, although translocations to northern Nevada relied on a larger number of source populations than Oregon. Bighorn sheep habitat in the northern Basin and Range ecosystem exhibits a metapopulation-like structure, where bighorn uses discrete patches of steep escape terrain separated by vast areas of grassland or sagebrush. Due to their demographic history and spatial distribution, bighorn sheep in southeastern Oregon and northern Nevada have low genetic diversity (Olson et al. 2013, Malaney et al. 2015) compared to levels measured in studies of Rocky Mountain bighorn sheep in the Rocky Mountains of Colorado (Driscoll et al. 2015) and desert bighorn sheep in the Mojave Desert of California (Epps et al. 2018). Bighorn sheep in the northern Basin and Range ecosystem also experience different phenology of forage plants than observed in the desert or Rocky Mountain systems. Thus, disease dynamics may be expected to differ, as well.

In 2012 Oregon Department of Fish and Wildlife (ODFW) conducted disease testing in two bighorn sheep populations in southeastern Oregon to determine potential causes of apparently suppressed recruitment. The testing revealed the suspected presence of *M. ovipneumoniae* in these bighorn sheep populations. The origins of the pathogen are alleged to be bighorn sheep in the Santa Rosa Mountains of northern Nevada, transmitted to Oregon herds via long-distance movements by adult males (M. Cox, NDOW, personal communication). The effects of the pathogen were unclear, although *M. ovipneumoniae* is suspected to cause juvenile mortality. Moreover, the extent of *M. ovipneumoniae* infection in bighorn sheep populations of southeastern Oregon also was unknown, as well as parts of nearby Nevada. Therefore, the Oregon Department of Fish and Wildlife (ODFW) initiated a study of the consequences of respiratory disease by capturing bighorn sheep across nine populations, fitting them with GPS collars to provide remotely transmitted location data, and sampling them for infection or exposure to *M. ovipneumoniae* and other diseases. Subsequently, the Nevada Department of Wildlife (NDOW) likewise used captures to collect similar data in four nearby bighorn populations in northern Nevada. Both agencies provided these data for my dissertation research.

My dissertation focuses on characterizing the spread and consequences of respiratory disease caused by *M. ovipneumoniae* in southeastern Oregon. I carried out four interdisciplinary studies involving extensive fieldwork, epidemiological, genetic, geospatial, and statistical methodologies to determine factors influencing bighorn sheep demography and spatial ecology. The findings from this study will

provide information to ODFW and Nevada Department of Wildlife (NDOW) to make informed decisions regarding bighorn sheep management, with a specific emphasis on the management of disease and genetic health.

In Chapter 2, my objective was to determine the impact of *M. ovipneumoniae* on juvenile while also assessing population genetic diversity, forage and time effects. I used observational data in a known-fate analysis to generate semi-monthly and established 4-month capture histories to estimate juvenile survival using a known-fate model. The findings of this study will help determine the extent of *M. ovipneumoniae*-exposure and infection and the population genetic diversity within the system. In addition, the analysis will help determine the effects of *M. ovipneumoniae* or the other factors investigated on juvenile survival.

In Chapter 3, my objective was to determine if intrinsic or, most notably, the extrinsic effect of *M. ovipneumoniae*-exposure and infection on adult survival of bighorn sheep. To do this, I used the GPS collar data to generate monthly survival capture histories using known-fate models. The findings of this study further expand on the extent of *M. ovipneumoniae* exposure and infection within the system due to the inclusion of adult male disease data. In addition, the results of the sequential analysis will help determine the effects of *M. ovipneumoniae*-exposure and infection and other factors on adult survival.

In Chapter 4, my objective was to evaluate space and habitat use of male and female bighorn sheep to (1) estimate individual seasonal and inter-annual utilization distributions, (2) use the utilization distributions to assess site fidelity and population affinity, (3) develop resource selection models to estimate the effects of environmental conditions within the home-range habitat selection, and (4) develop predicted habitat distributions to help inform management decision-making and assess the degree to which unoccupied habitat is present within the system. The findings of this study will provide insight into the space and habitat use of bighorn sheep within the system. In addition, they may provide insight as to whether there is potential gene flow within the system and how *M. ovipneumoniae* may be moving within the system. Lastly, the predicted habitat distributions developed in this study are a critical input for the risk of contact modeling.

In Chapter 5, the objective was to determine the risk of contact between bighorn sheep populations and potential sources of *M. ovipneumoniae*. We employed the methodology of O'Brien et al. (2014) to (1) generate core herd home ranges, (2) determine sources of risk of *M. ovipneumoniae* exposure, and (3) generated separate seasonal foray frequencies and distance probabilities for male and female bighorn sheep in two metapopulations, and (4) used these components along with sex- and season-specific habitat suitability models to estimate the risk of contact for each study population with potential sources of *M. ovipneumoniae.* The findings of this study will provide insight into the risk of contact between the focal study populations and potential sources of *M. ovipneumoniae*. Overall, the results of my

dissertation research will hopefully contribute to informed decision-making for bighorn sheep management within this system.

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CHAPTER 2

Impact of *Mycoplasma ovipneumoniae* on juvenile bighorn sheep (*Ovis canadensis*) survival in the northern Basin and Range ecosystem

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Robert S. Spaan[1], Clinton W. Epps[1], Rachel S. Crowhurst[1], Donald G. Whittaker[2], Mike Cox[3] and Adam Duarte[1, 4]

[1] Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA
[2] Oregon Department of Fish and Wildlife, Salem, Oregon, USA
[3] Nevada Department of Wildlife, Reno, Nevada, USA
[4] USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington, USA

Abstract

Determining the demographic impacts of wildlife disease is complex because extrinsic and intrinsic drivers of survival, reproduction, body condition, and other factors that may interact with disease vary widely. *Mycoplasma ovipneumoniae* infection has been linked to persistent mortality in juvenile bighorn sheep (*Ovis canadensis*), although mortality appears to vary widely across subspecies, populations, and outbreaks. Hypotheses for that variation range from interactions with nutrition, population density, genetic variation in the pathogen, genetic variation in the host, and other factors. We investigated factors related to survival of juvenile bighorn sheep in reestablished populations in the northern Basin and Range ecosystem, managed as the formerly-recognized California subspecies (hereafter, "California lineage"). We investigated whether survival probability of 4-month juveniles would vary by (1) presence of *M. ovipneumoniae*-infected or exposed individuals in populations, (2) population genetic diversity, and (3) an index of forage suitability. We monitored 121 juveniles across a 3-year period in 13 populations in southeastern Oregon and northern Nevada. We observed each juvenile and GPS-collared mother semi-month and established 4-month capture histories for the juvenile to estimate survival. All collared adult females were PCR-tested at least once for *M. ovipneumoniae* infection. The presence of *M. ovipneumoniae*-infected juveniles was determined by observing juvenile behavior and PCR-testing dead juveniles. We used a known-fate model with different time effects to determine if the probability of survival to 4 months varied temporally or was influenced by disease or other factors. We detected dead juveniles infected with *M. ovipneumoniae* in only two populations.

Derived juvenile survival probability at four months in populations where infected juveniles were not detected was more than 20 times higher. Detection of infected adults or adults with antibody levels suggesting prior exposure was less predictive of juvenile survival. Survival varied temporally but was not strongly influenced by population genetic diversity or nutrition, although genetic diversity within most study area populations was very low. We conclude that the presence of *M. ovipneumoniae* can cause extremely low juvenile survival probability in translocated bighorn populations of the California lineage, but found little influence that genetic diversity or nutrition affect juvenile survival. Yet, after the PCR+ adult female in one population died, subsequent observations found 11 of 14 (~79%) collared adult females had surviving juveniles at 4-months, suggesting that targeted removals of infected adults should be evaluated as a management strategy.

Introduction

The study of population dynamics is essential for managing species (Williams, Nichols & Conroy, 2002). Recruitment is a crucial process for population dynamics, whereby populations gain individuals through births and immigration (Pradel, 1996). Recruitment varies strongly across species depending on whether they are k-selected, i.e., having fewer young with greater parental investment, or r-selected, i.e., having more young with reduced parental investment (MacArthur and Wilson 1967). For k-selected species such as large terrestrial herbivores, annual adult survival tends to be relatively high with little variation. In contrast, juvenile survival tends to be more variable, and therefore population growth tends to be more sensitive to juvenile survival parameters (Gaillard et al., 2000). Consequently, it is essential to consider variables affecting the survival of juveniles when managing such species.

Bighorn sheep (*Ovis canadensis*) have a relatively low reproductive output (Festa-Bianchet et al., 2019). Females rarely have more than one offspring per year and may not achieve full reproductive potential until their 4th year (Rubin, Boyce & Bleich, 2000). Thus, juvenile survival can have a significant impact on population trajectories (Manlove et al., 2019). Juvenile survival is influenced by disease (Cassirer & Sinclair, 2007; Smith et al., 2014), maternal body condition (Festa-Bianchet, 1998), forage quality (Feder et al., 2008), weather (Douglas, 2001), genetic diversity (Hogg et al., 2006) and predation (Rominger, 2018). Disease, particularly pneumonia, can have a dramatic effect on juvenile survival (Manlove et al., 2016; Garwood et al., 2020). More broadly, respiratory disease likely caused the decline of bighorn sheep across western North America and continues to inhibit the recovery of the species (Cassirer et al., 2018). Therefore, evaluating the interaction of disease and other factors acting simultaneously on juvenile survival is critical for the conservation and management of bighorn sheep.

Mycoplasma ovipneumoniae, a bacterial pathogen, is considered the primary causative agent of respiratory pneumonia in bighorn sheep (Besser et al., 2008; Cassirer et al., 2018). Transmission of *M.*

ovipneumoniae from domestic sheep (*O. aries*) and goats (*Capra hircus*) to bighorn sheep is typically followed by high mortality of individuals in all age classes in non-immune populations. Some survivors will clear the disease, while others remain chronic carriers that continue to shed the pathogen despite often appearing relatively healthy (Besser et al., 2013). Chronic carriers thus can transmit *M. ovipneumoniae* and sustain its presence within a population, especially by transmission to previously unexposed juveniles (Plowright et al., 2013). This infection pattern in bighorn sheep has been observed in multiple regions, including northeastern Oregon, Idaho, Washington, Nevada, and South Dakota (Cassirer et al., 2018; Garwood et al., 2020). Immunity to *M. ovipneumoniae* is thought to be strain-specific, with novel strains resulting in new waves of infection (Cassirer et al., 2017).

Population-level responses to *M. ovipneumoniae* outbreaks, however, may vary widely. Considerable variation has been observed in levels of all-age mortality at first contact, subsequent adult survival, and juvenile survival in following years among populations and across evolutionary lineages and habitats (Cassirer et al., 2018; Dekelaita et al., 2020). That variation has been hypothesized to stem from numerous causes, including strain virulence (Kamath et al., 2019), nutritional factors such as forage quality and population density (Dekelaita et al., 2020), stochastic factors such as the presence of chronic carriers (Cassirer et al., 2018; Garwood et al., 2020), genetic diversity of host populations (Cassirer et al., 2018), and phenological differences resulting in different patterns of aggregation, contact, and dispersal (Cassirer et al., 2018). Indeed, bighorn sheep inhabit ecosystems ranging from the arid deserts of northern Mexico and the southwestern United States of America to the frigid northern Rocky Mountains of Alberta and exhibit significant phenotypic variation and evidence of local adaptation (Wehausen & Ramey II, 2000; Wiedmann & Sargeant, 2014; Malaney et al., 2015). Currently, three subspecies of bighorn sheep are recognized, the desert bighorn sheep (*O. c. nelsoni*), the Rocky Mountain bighorn sheep (*O. c. canadensis*), and the Sierra Nevada bighorn sheep (*O. c. sierrae*) (Wehausen & Ramey II, 2000; Wehausen, Bleich & Ramey II, 2005). Previously, other subspecies were recognized (e.g., Peninsular bighorn sheep, *O. c. cremnobates*, and California bighorn sheep, *O. c. californiana*) (Cowan, 1940). Debate remains about whether those putative lineages reflect important independent evolutionary trajectories and important local adaptation (Buchalski et al., 2016; Bleich, Sargeant & Wiedmann, 2018; Barbosa et al. in review).

Previous studies of population dynamics in the presence of *M. ovipneumoniae* suggest that disease dynamics should be evaluated across lineages and ecosystems. For instance, Rocky Mountain bighorn sheep in the Hells Canyon system of Idaho, Oregon, and Washington occupy relatively continuous habitat with cold winters (Cassirer & Sinclair, 2007). In this system, *M. ovipneumoniae* tends to persist for long periods, resulting in constant disease in juveniles (Cassirer et al., 2018). The same pattern of infection was also observed in Rocky Mountain bighorn sheep in the Black Hills of western

South Dakota and eastern Wyoming (Smith et al., 2014; Garwood et al., 2020). In the Mojave Desert of the southwestern United States of America, desert bighorn sheep occupy pockets of isolated mountain ranges surrounded by low-lying desert but linked by inter-mountain movements, resulting in natural metapopulations (Bleich et al., 1996). *M. ovipneumoniae* in this system appears to have been present periodically (Shirkey et al. in press), and impacts on adult survival and juvenile recruitment appear to be highly variable (Dekelaita et al., 2020).

Bighorn sheep in the northern Basin and Range ecosystem (including parts of southeastern Oregon, southwestern Idaho, and northern Nevada) occupy transitional habitats between the Mojave and Rocky Mountain systems and have a unique history. Native bighorn sheep from this region was considered the "California" subspecies (*O. c. californiana*; Cowan, 1940), spanned from the Sierra Nevada of California north to British Columbia. In Oregon, all native bighorn sheep were extirpated by 1945 (Oregon Department of Fish and Wildlife, 2003). Subsequently, morphometric and DNA analysis of the extinct native Oregon populations resulted in those populations being reassigned to the Great Basin desert form of the desert bighorn sheep (*O. c. nelson*; Wehausen & Ramey II, 2000). Bighorn sheep now existing in Oregon all stem from translocations and are managed as two lineages: Rocky Mountain bighorn sheep were introduced to northeastern Oregon, and "California" bighorn sheep were introduced to potential or former bighorn sheep habitat in other areas of the state using individuals from British Columbia. Both lineages are formally considered Rocky Mountain bighorn sheep subspecies at this time (*O. c. canadensis*; Wehausen & Ramey II, 2000). Most of the restored populations in Oregon were sourced from a single translocation of 22 bighorn sheep from British Columbia in 1953 (Olson, Whittaker & Rhodes, 2013). However, in 2000 and 2001, as part of an experimental effort to increase population genetic diversity and improve demographic performance, two populations in southeastern Oregon received augmentations of translocated bighorn sheep ultimately derived from different source populations in British Columbia (Olson, Whittaker & Rhodes, 2012). "California" bighorn sheep were also introduced to northern Nevada in 1972 from multiple source populations (NDOW, 2001; Olson, Whittaker & Rhodes, 2013), and dispersal from these populations into southeastern Oregon has been observed (ODFW, unpublished data). "California" bighorn populations in southwestern Idaho and northern Nevada share similar histories, although translocations to northern Nevada relied on a larger number of source populations than Oregon.

Bighorn sheep habitat in the northern Basin and Range ecosystem exhibits a metapopulation-like structure, where bighorn uses discrete patches of steep escape terrain separated by vast areas of grassland or sagebrush. Due to their demographic history and spatial distribution, bighorn sheep in southeastern Oregon and northern Nevada have low genetic diversity (Olson, Whittaker & Rhodes, 2013; Malaney et al., 2015) compared to levels measured in studies of Rocky Mountain bighorn sheep in the Rocky

Mountains of Colorado (Driscoll et al., 2015) and desert bighorn sheep in the Mojave Desert of California (Epps, Crowhurst & Nickerson, 2018). Bighorn sheep in the northern Basin and Range ecosystem also experience different phenology of forage plants than observed in the desert or Rocky Mountain systems. Thus, disease dynamics may be expected to differ, as well.

Although cause-specific mortality in bighorn sheep juveniles has been widely studied in other systems (Smith et al., 2014; Cassirer et al., 2018; Cain et al., 2019; Garwood et al., 2020), it has not been evaluated in "California"-managed bighorn sheep. In this study, we evaluate the distribution and influence of *M. ovipneumoniae* on 13 "California"-managed bighorn sheep populations in southeastern Oregon and northern Nevada, and investigate juvenile mortality in relation to forage qualify and genetic diversity. Although presence of *M. ovipneumoniae* had previously been verified in at least one population, the effect of respiratory disease on the system was unknown. Genetic diversity of populations in this system likewise was unknown, although anticipated to be low, and forage quality was expected to vary widely given the broad range of elevations used by bighorn sheep and the strong influence of precipitation in this semi-arid system. We used telemetry and field-based observations to monitor the juveniles of GPS-collared adult females to estimate semi-monthly survival probability over a 3-year period. We hypothesized that survival of juveniles would be influenced by disease, nutrition, and genetic diversity. We predicted that the probability of 4-month juvenile survival would be lower in populations that (1) were exposed to *M. ovipneumoniae*, (2) had lower expected heterozygosity, and (3) that experienced lower forage quality, as indicated by pre- and post-parturition normalized differential vegetation index (NDVI). Additionally, after observing the mortality of an adult female suspected to be a chronic carrier in one of the study populations at the end of the 3-year period, we conducted a limited follow-up investigation of juvenile survival in that population in the following year.

Methods

Study area

The populations of bighorn sheep we studied were located in southeastern Oregon and northern Nevada, between 41.3 and 42.8 ºN, and 117.0 and 118.2 ºW (Fig. 2.1). The entire study area fell within the North Basin and Range (Level III classification of ecoregions in Omernik & Griffith, 2014). Five populations in our study fell within or largely within the Dissected High Lava Plateau (Blue Mountain [BSP], Bowden Hills [BHP], Rattlesnake [RSP], Three Forks [TFK], Upper Owyhee [UOP], Fig. 2.1), although BSP and RSP partly occurred within the High Lava Plains ecoregion (Omernik & Griffith, 2014). The Ten Mile (TMP) population fell within the High Lava Plains, while High Lava Plains and Semiarid Uplands (Omernik & Griffith, 2014) dominate bighorn sheep habitat within the Trout Creek

(Trout Creek – east [TCE], - south [TCS] and – west [TCW], Fig. 1) and Santa Rosa metapopulation (Calicos [CAL], Eight Mile [EML], Martin Creek [MCK], and Sawtooth [SAW], Fig. 2.1).

The Dissected High Lava Plateau and High Lava Plains ecoregions are both characterized by elevated plateaus, but the Dissected High Lava Plateau contains sheer-walled canyons as well as intermittent lakes, while the High Lava Plains contains isolated volcanic cones and buttes as well as intermittent lakes and ephemeral streams (Omernik & Griffith, 2014). Mountains of low to mid elevation, typically with steep slopes, and some ephemeral and perennial streams characterize the Semiarid Uplands (Omernik & Griffith, 2014). The most common geology types across all three ecotypes are basalt and rhyolite, interspersed with other rock types. The soils derived from these rock types are fairly shallow and poor (Omernik & Griffith, 2014). Mean precipitation across the study area is typically 22.5-35.0 cm per year, although some areas of the Trout Creeks and Santa Rosa Mountains, receive significantly more precipitation (Omernik & Griffith, 2014).

All three ecotypes contain sagebrush steppe. Big sagebrush (*Artemisia tridentata*) and low sagebrush (*A. arbuscular*) are the most common woody herbaceous species, while common indigenous herbaceous species being primarily made up of palatable perennial bunchgrasses such as Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Psudoroegneria spicata*), bottlebrush squirreltail (*Elymus elymoides*), Thurber needlegrass (*Achnatherum thurberianum*) and the less palatable Sandberg bluegrass (*Poa secunda*). Western juniper (*Juniperus occidentalis*) is the most common woody plant across 3 ecotypes, typically found in rocky areas, while the Semiarid Uplands are distinguished by willows (*Salix* spp.) in riparian areas, and quaking aspen (*Populus tremuloides*) and mountain mahogany (*Cercocarpus* spp.) in snow pockets (Omernik & Griffith, 2014). Ungulate species occurring in the study area include elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) (Omernik & Griffith, 2014). Potential bighorn sheep predavtors in the study area include cougar (*Puma concolor*), coyotes (*Canis latrans*), bobcat (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*; Omernik & Griffith, 2014).

The most common land-use practices are cattle ranching and cultivation of grains and hay (Omernik & Griffith, 2014). Heavy grazing of these lands and suppression of natural fires has led to the spread of large, uncontrollable fires and encroachment by invasive annual plants, such as the cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherium caput-medusae*; Omernik & Griffith, 2014). These grasses outcompete indigenous vegetation post-fire leading to the domination of these grasses. Wildlife and cattle here rely on springs, wetlands, and artificial water sources (Omernik & Griffith, 2014).

History of bighorn sheep populations within the study area

Reestablishment of bighorn sheep in the study area started in 1978 with the translocation of bighorn sheep into the Eight Mile area of the Santa Rosas (Fig. 2.1). The three Trout Creek populations, TCE, TCS, and TCW, and RSP were established with single translocations each from Hart Mountain (Table S2.1) in 1987 and 1992. Hart Mountain's bighorn sheep population was established in 1954 with a translocation of bighorn sheep from Williams Lake, British Columbia. Although bighorn sheep in TMP and UOP were translocated from various other populations in Oregon, all those populations were ultimately derived from the population established at Hart Mountain in 1954. Bighorn sheep in CAL, although translocated from the Pine Forest Range in Nevada, are also derived from Hart Mountain. The remaining bighorn sheep populations in the study were established from either a different original sources, e.g., MCK and SAW, which had stock from Kamloops, British Columbia, and Penticton, British Columbia, respectively, or more than one source, e.g., EML. Two populations were established by dispersal into unoccupied habitat: BSP was established with suspected dispersal events from the Trout Creek populations in the mid to late 1990s (pers. comm. S. Torland, ODFW), and BHP is thought to have been established by dispersing bighorn sheep from RSP. Other movements observed include the dispersal of collared adult males between the Santa Rosa Mountain Range and neighboring mountain ranges in southeastern Oregon, observed in 2009 and 2010 (NDOW, unpublished data).

Capture and sampling

All capture, handling, and disease testing were conducted by Oregon Department of Fisheries and Wildlife (ODFW) and Nevada Department of Wildlife (NDOW). Capture methodology followed the recommendations of Foster (2004) and the American Society of Mammalogists (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists, 2016). ODFW and NDOW captured, collared, and sampled adult female bighorn sheep across 13 populations in southeastern Oregon and northern Nevada between January 2016 and February 2018 (Fig. 2.1). Captures were conducted using a net gun fired from a helicopter, with individual bighorn sheep blindfolded and hobbled once captured (Krausman, Hervert & Ordway, 1985). Bighorn were brought to a centralized area at the base of their range to be fitted with a telemetry collar and to collect biological samples, except where capture location was too far from basecamp to transport them quickly, in which case they were field processed, at the capture location.

Each adult female was fitted with a Vertex Survey Globalstar collar (Vectronic Aerospace, Berlin, Germany). These collars provide a GPS location every 13 hours as well as VHF signal and were set to report a mortality if stationary for 12 hours. Each collar had its own unique VHF frequency, with the occasional duplicate placed on individuals in different populations between which dispersal was

deemed unlikely. The collars were also fitted with colored tags with unique numbers, allowing for identification of individuals observed in the field.

The age of each adult female was estimated from horn growth rings (Geist, 1966; Hoefs & Konig, 1984). Blood was obtained via jugular venipuncture to determine pregnancy status of adult females, obtain DNA, and to screen for disease. We determined pregnancy status of adult females using a serum pregnancy-specific protein B (PSPB) assay (Drew et al., 2001). Pregnancy testing of adult females was only conducted in the year in which they were captured; samples were sent to Sage Laboratories (Emmett, ID) conducted testing.

Diagnostics

Presence of *M. ovipneumoniae* was detected with polymerase chain reaction (PCR) tests using nasal, bronchial, and tympanic bullae swabs from each captured female bighorn sheep (Manlove et al., 2019). Previous exposure to *M. ovipneumoniae* was determined using a competitive enzyme-linked immunosorbent assay (cELISA) to detect antibodies in serum (Ziegler et al., 2014). All tests for *M. ovipneumoniae* were performed at Washington Animal Disease Diagnostic Laboratory (WADDL).

Monitoring of juvenile bighorn sheep

From 2016 to 2018, we conducted semi-monthly observations of all collared adult females between April 1 and August 31. Juvenile identification was determined via observation of physical contact between adult females and juveniles, such as nursing or bedding down together. Juveniles are weaned at approximately 4-months of age (Festa-Bianchet, 1988); thus, our observation period was intended to cover birth through weaning. We located adult females for observation using an R-1000 telemetry receiver fitted with an RA-23K VHF directional antenna (Telonics, Inc., Mesa, AZ). We conducted observations with Kowa TSN-601 spotting scopes fitted with a 20–60x magnification mounted on tripods. Once an adult female was confirmed to not or no longer have a juvenile, i.e., two consecutive observations where the adult female was observed without a lamb, we stopped tracking that individual adult female (e.g., Cassirer & Sinclair, 2007).

We opportunistically located dead juveniles and collected samples, including either the entire corpse, the pluck (heart, liver, and lungs), the head, nasal and ear swabs, and/or tissue samples depending on the state of decomposition. Swabs were inserted into vials dry or containing tryptic soy broth, and other samples put in a cooler until returning to our field base. We then stored both the samples and swabs at -20 ºC until laboratory submission. WADDL conducted gross- and histo-pathology on lung tissue samples and PCR tests on swabs. Additionally, *M. ovipneumoniae* strain-typing using multi-locus sequence typing (MLST) tests with four locus sequences, 16-23S intergenic spacer regions, the small

ribosomal subunit, the genes encoding RNA polymerase B, and gyrase B, was conducted on lung tissue and swab samples from two of the juvenile mortalities recovered (Cassirer et al., 2017). We then compared these strain-types to strain-typed samples from the Santa Rosa metapopulation (n = 6) and from the Rattlesnakes (n = 2). WADDL conducted the *M. ovipneumoniae* strain-typing.

Genetic sampling

We used a combination of both blood samples (n = 125) and feces (n = 66) as sources for DNA samples. Whole blood (3 mL) provided by ODFW and NDOW from captured bighorn sheep was collected in EDTA tubes and spun at 4,000 x *g* for 10 minutes to separate the buffy coat. We extracted DNA from this material using a Qiagen DNeasy Blood and Tissue Kit (Qiagen Inc., Valencia, CA, USA). Fecal samples were collected opportunistically while conducting observations of bighorn sheep across the different populations, and were generally a week or less in age, as estimated from pellet color, odor, and surface condition. Fecal samples that were still moist after deposition were dried and then stored at room temperature. Fecal pellets were scraped to target dried epithelial cells on the surface of the pellet (Wehausen, Ramey & Epps, 2004), and we extracted DNA from the scraped material using a modified version of the Aquagenomic Stool and Soil protocol (Multitarget Pharmaceuticals LLC, Colorado Springs, CO; see details in Appendix S4).

Genotyping, markers, individual identification, and marker

We used a suite of 16 microsatellite markers in three panels (Table S2.2) that had previously been used to investigate population connectivity and genetic variability in bighorn sheep (Creech et al., 2017, 2020; Epps, Crowhurst & Nickerson, 2018). Genotyping followed protocols outlined in Epps, Crowhurst & Nickerson (2018). Briefly, all samples were run in at least two (for blood) or three (for feces) independent PCR reactions to generate a consensus genotype for each individual at each locus. For blood samples, any discrepancy between the two replicates resulted in the sample being rerun at that panel, although consistency across replicates was very high. Because allelic dropout can be higher in fecal samples, for those samples a homozygous genotype was considered verified if the single allele was seen in all three replicates. A heterozygous genotype was considered to be verified if each allele was seen in at least two of the three replicates; any other discrepancies resulted in reruns. Other studies on bighorn (e.g., Epps, Crowhurst & Nickerson, 2018) reported screening for recaptures using as few as 6 loci to achieve a desired probability of identity [PID; Waits, Luikart & Taberlet (2001)] of <0.001 and a probability of identity for full siblings of < 0.05. However, our initial genotyping demonstrated that we needed to genotype at all 16 loci to achieve those thresholds. We identified recaptured individuals using CERVUS (Kalinowski, Taper & Marshall, 2007) by screening for individuals that matched at all 16 loci and

removing them from the data set. We repeated this analysis using successively reduced numbers of matching loci and the presence of one to two mismatches (to account for missing data and genotyping error, respectively), until the matches that the program returned seemed unlikely due to geographic location and/or the mismatches were not explainable by simple allelic dropout. Finally, we used GIMLET (Valière, 2002) to calculate two types of error rates in our genotypes: allelic dropout, and the presence of false alleles.

Linkage disequilibrium, Hardy-Weinberg tests, and genetic diversity

We used GENEPOP Version 4.2 on the Web (Rousset, 2008) to conduct the probability test for Hardy-Weinberg equilibrium (HWE) for each population by locus and then for each locus by population, as well as across populations for each locus and across loci for each population (Fisher's method, Fisher 1948). We then used GENEPOP 4.0 Desktop to test for linkage disequilibrium across each pair of loci within each population, and each pair of loci across all populations, applying a sequential Bonferroni correction in both cases across all loci. We used the R package *diveRsity* (Keenan et al., 2013) to calculate population genetic diversity metrics including expected heterozygosity (H_E), observed heterozygosity (H_O), and allelic richness (A_R). We accounted for imbalanced sample sizes amongst populations using rarefaction.

NDVI data

We used 14-day composite, 250 m resolution NDVI data from the Moderate Resolution Imaging Spectroradiometer (eMODIS). We utilized pre-processed data from 2016-2018 obtained from Earth Explorer (https://earthexplorer.usgs.gov/), which is managed by the United States Geological Survey's Earth Resources Observation Center (Jenkerson, Maiersperger & Schmidt, 2010).

We used GPS data from all collared adult females in each population to generate a single utilization distribution per population for each year from 2016–2018, using the R package *adehabitatHR* (Calenge, 2006). We estimated 95% utilization distributions using the kernel method with the default smoothing parameter (h_{ref}). We did not use least square cross validation (h_{lscv}) due to repeated use of locations, which may cause convergence issues (Kie et al., 2010).

We then extracted NDVI data from each population polygon for each 14-day composite image and generated a 90th percentile statistic using program R (R Core Team, 2019). Bighorn sheep are selective feeders; as such, we assume that the 90th percentile NDVI statistic represents a high-quality choice of forage, while accounting for the fact that maximum forage is not always attainable (Creech et al., 2016). Additionally, selecting the 90th percentile excludes the selection of false maximum values caused by measurement error. Finally, we averaged NDVI values across each 14-day composite for the 3-

months before and after the first juvenile observed in each population and used this variable as a measure for forage quality for each population pre- and post-parturition.

Drivers of juvenile survival

We analyzed our known-fate data in Program MARK (White & Burnham, 1999), to estimate juvenile survival (*S*) using a Kaplan-Meier estimator (Kaplan & Meier, 1958) with staggered entry (Pollock et al., 1989). First, we considered three population-level measures of exposure to *M. ovipneumoniae* in our models of juvenile survival (Table 2.1). Primarily, we considered the presence of *M. ovipneumoniae*-infected juveniles in each population, as the limited numbers of adults captured and tested in each population and the lack of annual testing precluded clear estimates of infection rates among adults. However, we also considered whether presence of infected adults (PCR) or exposed adults (cELISA) in each population influenced juvenile survival. Second, we considered two population-level measures of genetic diversity, expected heterozygosity (H_E) and allelic richness (A_R) (Table 2.1). We used univariate models of the three *M. ovipneumoniae* measures and the two genetic diversity measures as initial screening methods, using Akaike's information criterion, corrected for small sample sizes (AIC_c) to determine which *M. ovipneumoniae* and genetic diversity metric most strongly linked to juvenile survival before proceeding with subsequent analyses.

Subsequently, we conducted two analyses of juvenile survival. The first included all study populations (n = 13) and the selected measures of *M. ovipneumoniae* presence in each population, population-level metrics of forage quality (3-month pre- and post-parturition NDVI values) and genetic diversity (expected heterozygosity, H_E) (Table 2.1), and both additive and multiplicative effects of time. For each model that included the multiplicative effect of time and *M. ovipneumoniae*, we fixed survival interval 1 for the *M. ovipneumoniae* group, as no mortalities occurred during this period. The second analysis included all of the same variables except *M. ovipneumoniae* presence and was restricted to populations where *M. ovipneumoniae*-infected juveniles were not detected (n = 11, see Results). That second analysis was undertaken to determine whether effects of *M. ovipneumoniae* obscured the effect of the other covariates of interest. For both analyses, we used AIC_c and AIC_c weights (w_i) to select the best-supported model. We included a null model in both model selection sets to evaluate model performance (Burnham & Anderson, 2002). We selected the model with the lowest AIC_c and highest w_i as our best-supported model. We used evidence ratios between the top model and competitive models (those within 2 AIC_c units, to evaluate each model relative to the top model (Burnham & Anderson, 2002).

Post-study observations

After our final planned field season in 2018, the single PCR+ adult female in the RSP (of 21 tested) died of suspected bluetongue (*Orbivirus* spp.). Because prevalence of PCR+ adult females in this population was low (4.76% of tested - see Results), and no adult males tested PCR+ throughout the study, we considered it possible that no additional PCR+ individuals remained at RSP, potentially removing the source of infection for new juveniles. Therefore, we decided to conduct a single observation of juveniles in the RSP and BHP, populations in early August of 2019; we included BHP given its proximity to RSP. Juveniles in both these populations were typically 4-months old at that time; thus, that observation aligned closely with the 4-month juvenile survival we estimated during the study.

Results

Diagnostics

Between 2016 and 2018, 78 adult females were tested via cELISA to determine *M. ovipneumoniae* exposure, and 95 adult females were tested via PCR to determine active *M. ovipneumoniae* infections. The proportion of adult females PCR tested in each population varied from 0.10 to 0.43 ($\bar{x}$ = 0.27, Table S2.4). For the 10 adult females in the Santa Rosa metapopulation that were recaptured during our study and retested for infection via PCR, PCR status remained the same for the single positive individual in EML, and the rest were negative. None of the adult females in populations west of U.S. Route 95 (BSP, TCE, TCS, or TCW) showed evidence of *M. ovipneumoniae* exposure (Fig. 2.1, Table S2.3). However, all of the populations east of U.S. Route 95 (the four populations in the Santa Rosa Mountain's metapopulation, as well as BHP, RSP, TMP, and UOP (Fig. 2.1), except TFK, included adult females with evidence of exposure to *M. ovipneumoniae* (Table S2.3). We were unable to get a sample from the single individual adult female captured in TFK. The proportion of *M. ovipneumoniae* exposed adult females in those eight populations varied between 0.60 in CAL and EML to 1.00 in TMP ($\bar{x}$ = 0.75; Table S2.4). Only two adult females tested PCR+ to *M. ovipneumoniae* infection across all 13 populations (Table S2.3): one in EML on two occasions (2017 and 2018), and one in RSP in 2016. Additionally, one adult female in BHP yielded an indeterminate PCR test result, meaning *M. ovipneumoniae* detection could not be determined (Besser et al., 2019).

Linkage disequilibrium, Hardy-Weinberg tests, and genetic diversity

After removing the fecal samples from recaptured individuals (n = 28), the genetic data set contained 191 individuals at 16 microsatellite loci, representing 10 to 26 ($\bar{x}$ = 15.9) individuals per population (Table S2.5). The mean rate of false allele occurrence per locus was 0.001 and the mean allelic

dropout rate across all loci was 0.008 (range = 0.000-0.017). No locus was determined to be out of Hardy-Weinberg equilibrium by either test employed (Tables S2.6 & S2.7). Evaluating each locus pair by population showed no evidence of linkage disequilibrium ($p_{critical} = 0.000035$ for $\alpha = 0.05$); evaluating linkage for each pair of loci across populations using Fisher's test indicated that BL4 and HH62 were in disequilibrium ($p = 0.00039$; $p_{critical} = 0.00042$ for $\alpha = 0.05$). However, those loci have not appeared to be in disequilibrium in other bighorn sheep studies (e.g., Epps, Crowhurst & Nickerson, 2018), suggesting that this relationship may have been an artifact. Thus, and because linkage disequilibrium is more likely to bias estimates of genetic structure rather than estimates of genetic diversity as employed in this study, we retained all 16 loci in our analyses. H_E across the 13 study populations varied from 0.26 in BSP to 0.48 in EML ($\bar{x} = 0.37$; Table S2.5) and A_R varied from 1.82 in BSP to 2.88 in SAW ($\bar{x} = 2.37$; Table S2.5).

NDVI data

Pre- and post-parturition NDVI varied spatially and temporally (Table S2.8). BSP had consistently low pre-parturition NDVI, whilst EML and TMP had consistently high pre-parturition NDVI (Table S2.8). Post-parturition NDVI was lowest in BHP in 2018, was consistently low in RSP but was consistently high in TCE and EML (Table S2.8). Pre- and post-parturition NDVI values were not correlated (Table S2.9).

Pregnancy rates and observation of juvenile bighorn sheep

Seventy-six of the 82 (93%), pregnancy tests conducted across all 13 populations between 2016 and 2018 were positive (Table S2.10). Six of the 82 tests conducted were on recaptured adult females from EML ($n = 3$) and SAW ($n = 3$), all of which were positive. All populations had 100% pregnancy rates, except for TCE (67%; $n = 8/12$), TCS (50%; $n = 1/2$), and TFK (0%; $n = 0/1$) in 2016. The single collared adult female in TFK did not yield a positive pregnancy test result in January, but was later observed in early June with a juvenile, suggesting that the test was administered too early to detect a positive pregnancy result. Sixty-five of those 82 (79%) pregnant adult females survived to parturition; of those 59 (91%) were observed with juveniles. Population pregnancy rates were not correlated with genetic diversity (Pearson pairwise correlation; H_E, $r = 0.24$, $p = 0.272$; A_R, $r = 0.14$, $p = 0.529$).

We observed 121 juveniles with radio-collared adult females between 2016 and 2018; 78% of radio-collared adult females were observed with juveniles. Populations with the lowest proportion of radio-collared adult females with juveniles were BSP (2016 – 0.00; 2017 – 0.67; 2018 – 0.33), and TCE (2016 – 0.64; 2017 – 0.64; 2018 – 0.17), although sample sizes were small in BSP (n = 3). A set of twins was observed with a radio-collared adult female in both the BHP and MCK populations in 2018.

The observation rate of collared adult females with juveniles varied from 50 to 100%, with a mean observation rate of 94% across all semi-monthly sampling periods and study populations (Table S2.11). Throughout the study, we collected samples suitable for *M. ovipneumoniae* testing from 17 juvenile mortalities (Table S2.12). All juvenile mortalities (n = 15) recovered from the BHP (n = 1) and RSP (n = 14) populations tested positive for *M. ovipneumoniae*. None of the other juvenile mortalities from BSP (n = 1) or TCS (n = 1) tested positive for *M. ovipneumoniae*. The *M. ovipneumoniae* strain-type of the samples collected from the BHP and RSP juveniles matched the strain-type (NV_BHS_SantaRosas_2651_2014_4; Kamath et al., 2019) of all the other previously strain-typed bighorn sheep at the available sequences from the Santa Rosa meta-population and Rattlesnake population (Table S2.13).

Drivers of juvenile survival

Preliminary analyses with univariate models of the relationship between juvenile survival and different population-level measures of *M. ovipneumoniae* revealed that the presence of *M. ovipneumoniae*-infected juveniles in the population was a much stronger predictor of juvenile survival than the presence of infected (PCR+) or exposed (ELISA+) adults (Table S2.14). Preliminary analyses with univariate models of juvenile survival as a function of genetic diversity demonstrated that H_E was a stronger predictor of juvenile survival than A_R (Table S2.14). Therefore, in our subsequent multivariate models of juvenile survival, we used the presence of *M. ovipneumoniae*-infected juveniles in each population as our measure of *M. ovipneumoniae* presence, and H_E as our measure of genetic diversity. In those multivariate analyses, we identified two competing models predicting survival probability of juveniles across all populations (Table 2.2). Both models contained only two predictors: 1) whether *M. ovipneumoniae*-infected juveniles were detected, and 2) time. The model containing time as a multiplicative effect with *M. ovipneumoniae* had 2.36 times more support than the competing model that treated time as an additive effect (Table 2.2), meaning that the temporal pattern of juvenile mortality differed in populations where *M. ovipneumoniae*-infected juveniles were present. Neither forage quality (pre- and post-parturition NDVI), nor genetic diversity (H_E) predicted survival probability of juveniles (Table 2.2).

The odds of a juveniles surviving to 4-months of age in our study populations where *M. ovipneumoniae*-infected juveniles were detected were 8.00 (95% CI: -4.00–255.78) times less likely than juveniles in populations where we did not detect *M. ovipneumoniae*-infected juveniles (Table 2.3). The derived probability of survival for the entire 4-month annual study period for juveniles in populations where *M. ovipneumoniae*-infected juveniles were detected was 0.02 (95% CI: 0.00–0.13) compared to 0.44 (95% CI: 0.29–0.59) for juveniles in other populations (Fig. 2.2B).

We observed no significant difference in semi-monthly juvenile survival probability between populations where *M. ovipneumoniae*-infected juveniles were not detected in observations at 0.5, 1, and 1.5-months post-parturition (Fig. 2.2A). However, semi-monthly survival probability in populations where *M. ovipneumoniae*-infected juveniles were present were significantly lower 2-months (*S* exposed = 0.42, 95% CI: 0.24–0.62; *S* unexposed = 0.88, 95% CI: 0.75–0.95) and 2.5-months (*S* exposed = 0.40, 95% CI: 0.16–0.70; *S* unexposed = 0.94, 95% CI: 0.82–0.98) post-parturition (Fig. 2.2A). At 3, 3.5, and 4-months post-parturition, estimates in semi-monthly survival probability again did not differ between populations where *M. ovipneumoniae*-infected juveniles were or were not detected (Fig. 2.2A). The increase in uncertainty in our estimates is tied to decreasing sample size as individuals died.

Although no direct effect of either population genetic diversity or post-parturition NDVI was supported based on our model selection approach, both variables were highly correlated with the presence of *M. ovipneumoniae* (H_E = 0.58; post-NDVI = -0.66, Table S2.9). In fact, the two populations where *M. ovipneumoniae*-infected juveniles were present, BHP and RSP, had relatively high genetic diversity (H_E: BHP = 0.43; RSP = 0.45) compared to other study populations (Table S2.5). Similarly, RSP had low post-parturition NDVI values relative to the other populations in 2017 and 2018, while the same was the case for BHP in 2018 (Table S2.8).

In the second analysis, which excluded the two populations where *M. ovipneumoniae*-infected juveniles were present, competing models included both indices of forage quality and population genetic diversity as predictors of juvenile survival (Table 2.2), as well as a time-varying effect. However, the 95% confidence intervals for the parameter estimates of the nutritional and population genetic diversity model both overlapped zero, and the null model with no predictors was 2nd ranked. The top competing model, a time-varying model, had 1.69 times more support than the next best model, the null model (Table 2.2).

Post-study observations

In early August of 2019, following the death of the single adult female in RSP that tested PCR+ for *M. ovipneumoniae*, we located the two remaining collared individuals in the BHP (linked to RSP by adult male and female movements, data not shown). Neither the collared adult females nor any of the eight other adult females we observed in this population had juveniles (0% juvenile survival). We then located 14 of the RSP collared adult females, of which 11 had juveniles (~79% juvenile survival). We located approximately 35 adult females total in the RSP population and observed approximately 27 juveniles, which equates to an approximate 4-month survival rate of ~77%.

Discussion

We found that *M. ovipneumoniae* had a strong negative effect on juvenile survival in populations

where infected juveniles were detected. Juveniles in those populations had a 4-month survival probability more than 20 times lower than juveniles in populations where we did not detect infected juveniles. Indeed, in one affected population (RSP), only two juveniles out of 40 over three years survived. Presence of adult bighorn sheep with evidence of past exposure to *M. ovipneumoniae*, and in one population the presence of an adult infected at time of capture, were not strong predictors of juvenile survival. Moreover, juvenile survival was not detectably influenced by forage quality or population genetic diversity, even when excluding populations where *M. ovipneumoniae*-related juvenile mortality was observed. Strikingly, the death of a single infected adult female in a heavily impacted population appeared to drive an immediate recovery of juvenile survival in that population in the subsequent year, underscoring the potentially pivotal role of chronically infected adult females in outbreaks of this disease.

In our study, four-month juvenile survival probability in populations where infected juveniles were present (0.02; 95% CI: 0.00–0.13) were comparable to some of the lowest observed juvenile survival probabilities reported in other studies where pneumonia epizootics were present. In Rocky Mountain bighorn sheep in the Hells Canyon system of Idaho, Oregon, and Washington, survival to weaning at 4–5 months of age had a median value of 0.10, but ranged from <0.01–0.69, with peak mortality occurring between 1.5 and 2.5 months of age (Cassirer et al., 2013). In the Black Hills of South Dakota, Smith et al. (2014) reported 52-week survival to be only 0.02 (95% CI: 0.01–0.07), with the majority of juveniles (~75%) dying within the first 2 months after parturition. We observed similar temporal patterns to those studies, with most mortality related to disease in our study occurring between 1.5 and 3-months after parturition. In the Mojave Desert of California, in a 3-year study of desert bighorn sheep following an outbreak of *M. ovipneumoniae*, the proportion of juveniles surviving varied from 0.00 to 0.92 in populations where at least five juveniles were monitored, and survival in most populations improved in later years (Dekelaita 2020). Unlike Cassirer et al. (2013) and Smith et al. (2014), we did not address the effect of predators on juvenile survival. However, it should be noted that even if cause-specific mortality were to be assigned to a predator, the ultimate cause of mortality might still be *M. ovipneumoniae*. Although *M. ovipneumoniae* is considered the primary agent of pneumonia, other diseases, and the potential for co-infection effects may be important, but we did not assess them. Periods of low juvenile survival due to pneumonia can result in demographic consequences such as declining population growth rates (Manlove et al., 2016) and even skewed population structures (Festa-Bianchet, Gaillard & Côté, 2003).

Our study adds to the evidence that dynamics of respiratory pneumonia in bighorn sheep may be strongly influenced by the presence of only a small number of infected adults. We detected only one infected female adult bighorn sheep across two populations where *M. ovipneumoniae*-infected juvenile bighorn sheep were observed. However, the presence of infected adults at capture was not the strongest

predictor of juvenile survival. For instance, in EML, an infected female adult was present in 2017; she was still infected when retested in 2018. Despite that, one out of four juveniles born in 2017 and five of six juveniles born in 2018 survived. It is unclear why the presence of this apparently chronically-infected female did not lead to juvenile mortality in this case, although Plowright et al., (2017) noted that juvenile survival was not directly related to the mother's infection status in the study. The lack of juvenile die-off could be explained by other factors, e.g., the stochastic nature of exposure and the possibility of co-infection. We attempted to capture other factors that may play a role, e.g., measures of forage quality and population genetic diversity, but we did not detect any direct effect of those factors. Additionally, we were unable to assess the interaction of these variables with *M. ovipneumoniae* infection because our measures of those factors were at the population level. Conversely, juvenile survival in RSP was extremely poor from 2016–2018, where a single infected adult female was detected in 2016. Although we did not retest her and therefore do not know whether she was chronically infected, after her death in late 2018, juvenile survival rebounded sharply in 2019. In a satellite population discovered in the course of this study, BHP, one female out of three captured in 2018 yielded an indeterminate PCR result. We surmise that additional captures likely would have detected infected adults given that infected juveniles were detected in 2018 and no surviving juveniles were detected in either 2018 or 2019. Experimental removals of chronically-infected adult females in other bighorn sheep studies (e.g., Garwood et al., 2020) demonstrate that chronically-infected adult females can strongly influence juvenile survival when prevalence is low.

We did not detect influences of population genetic diversity on juvenile survival, although we observed low to very low population genetic diversity throughout our study area, with H_E ranging from 0.26–0.48 (Table S2.5). In contrast, H_E values derived for 11 native desert bighorn sheep populations in the Mojave Desert of California, using 15 of the 16 microsatellite loci we employed, ranged from 0.50–0.69 (Epps, Crowhurst & Nickerson, 2018). However, our study design did not account for possible interactions between these variables and presence of *M. ovipneumoniae*-infected juveniles, because *M. ovipneumoniae*-related juvenile mortalities were confirmed in only two of 13 populations. Our estimates of genetic diversity were also only derived from 16 microsatellite loci, most putatively neutral; estimates based on more markers across the genome or additional genes associated with immune function could have been more informative. Interestingly, the populations where *M. ovipneumoniae*-related juvenile mortality was confirmed had relatively high genetic diversity (Table S2.5). In fact, the higher genetic diversity observed at RSP likely resulted from gene flow from males dispersing from the Santa Rosa metapopulation (NDOW, unpublished data). Such movements also appeared to have spread this strain of *M. ovipneumoniae* from the Santa Rosa metapopulation to BHP and RSP; indeed, only one strain is known to occur throughout the populations where we detected infected individuals (Table S2.13). Genetic

diversity in populations to the west of U.S. Route 95, in particular, was strikingly low (H_E was 0.26–0.33) due to founder effects from translocation history (see above). Genetic diversity observed by Olson, Whittaker & Rhodes (2013) for the source population, Hart Mountain, was noticeably higher (H_E = 0.42). We note that the pregnancy rate in one of those populations (TCE) likewise was strikingly low (67%, n = 8/12) in 2016. Although the adult females that we had the opportunity to test in 2017 and 2018 (n = 3 total) were pregnant, the numbers of adult females observed with juveniles in 2017 and 2018 were equal to or lower than 2016. Yet, those populations were apparently free of *M. ovipneumoniae* during our study. Such low pregnancy rates suggest that inbreeding or low genetic diversity could influence performance of those populations (Olson, Whittaker & Rhodes, 2012), although we cannot rule out other factors. These contrasts highlight the challenges of maintaining genetic diversity while limiting spread of disease, particularly in reintroduced systems of populations where compounding founder effects have resulted in some of the lowest reported values for genetic diversity in wild bighorn sheep populations.

Forage quality as assessed by NDVI values pre- and post-parturition likewise did not appear to influence juvenile survival consistently across the study. Again, our ability to evaluate how variation in forage quality influenced survival when *M. ovipneumoniae* was present was limited. We note, however, that of the three populations where *M. ovipneumoniae*-infected adult females or juveniles were detected, juvenile survival was lowest where forage quality was lowest (BHP and RSP, Table S2.8, average juvenile survival = 0 and 0.07, respectively). In contrast, EML had the highest or second-highest pre- and post- parturition NDVI values (Table S2.8) and higher juvenile survival ($\bar{x}$ = 0.54; range = 0.25–0.83). Taken together, these anecdotal patterns suggest that the link between forage quality and *M. ovipneumoniae* dynamics within infected populations bears further investigation.

Our study demonstrated that reintroduced populations of "California"-managed bighorn sheep in southeastern Oregon and northern Nevada have been strongly influenced by respiratory disease, but not all populations are currently affected. Where infected juveniles were present, rates of juvenile mortality that we observed would lead to a dramatic decline in populations if those patterns persisted, as observed by (Manlove et al. 2016). However, the rapid improvement in juvenile survival in one badly-affected population following the death of the single adult female known to be infected with *M. ovipneumoniae* at the start of the study suggests that identification and removal of chronically-infected adult females could be a successful management strategy in this system, as tested for a Rocky Mountain bighorn sheep population by Garwood et al. (2020). The very low estimates of genetic diversity we observed in some populations suggest that actions to manage for improved genetic diversity may be warranted, although natural movements between several study populations simultaneously resulted in increased genetic diversity and spread of *M. ovipneumoniae*. Thus, any genetic management strategy employed would have to mitigate the potential impact on spread of disease.

Conclusions

We found that populations with *M. ovipneumoniae*-infected juveniles had significantly lower juvenile survival, while no direct effect of either genetic diversity or pre- and post-parturition forage quality on juvenile survival was detected. Presence of *M. ovipneumoniae*-infected or exposed adults was less predictive of juvenile survival. Our findings add to the body of evidence that *M. ovipneumoniae* can have deleterious effects on juvenile survival across the various bighorn sheep lineages and the different ecosystems they inhabit. After the mortality of the only PCR+ adult female that we detected in one of the populations most affected by respiratory disease during the first three years of our study, we found increased juvenile survival and detected no infected juveniles in the following year. This natural experiment suggests that in populations where prevalence of PCR+ adults is low, removal of infected adults or adults identified as chronic carriers of *M. ovipneumoniae*. However, our ability to detect those influences may have been limited by small number of populations where respiratory disease was observed and high correlations between genetic diversity and presence of disease resulting from translocation history and patterns of connectivity in this system. Future studies should evaluate the interaction of genetic diversity and disease in systems with larger numbers of populations affected by respiratory disease.

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Tables and Figures

Table 2.1 Description of variables considered in known-fate models predicting survival of juvenile bighorn sheep (*Ovis canadensis*) in populations across southeastern Oregon and northern Nevada. All statistical measures were considered at the population level.

Measure	Category	Measure type	Statistical measure (range)
. (null)		Intercept only model	
time	Temporal	Time-varying	
T	Temporal	Linear time trend	
M. ovipneumoniae status	Bacteria	*M. ovipneumoniae* status (+/-), as determined by presence of infected juveniles.	Binary
M. ovipneumoniae status	Bacteria	*M. ovipneumoniae* status (+/-) as determined by presence of infected (PCR+) adults	Binary
M. ovipneumoniae status	Bacteria	*M. ovipneumoniae* status (+/-) as determined by presence of infected (cELISA+) adults	Binary
A_R (Allelic richness)	Genetic	Measure of genetic diversity	Continuous (values btw. 1.82–2.88)
H_E (Expected heterozygosity)	Genetic	Measure of genetic diversity	Continuous (values btw. 0–1)
pre-NDVI (Pre-parturition NDVI)	Nutrition	90^{th} percentile 3-month pre-parturition mean NDVI	Continuous (values btw. -0.2–1)
post-NDVI (Post-parturition NDVI)	Nutrition	90^{th} percentile 3-month post parturition mean NDVI	Continuous (values btw. -0.2–1)

Table 2.2 Model selection results for known fate models predicting cumulative 4-month survival of juvenile bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada for the period 2016–2018. For analysis 1, we included a binary group variable for populations where *Mycoplasma ovipneumoniae* was (n = 2) and was not detected (n = 11). We modeled time as a constant (.), time-varying (time), linear (T), and random effect. Covariates modeled include expected heterozygosity (H_E), and pre- and post-parturition NDVI. For analysis 2, we only modeled populations (n = 11) with no observed *M. ovipneumoniae* mortalities. We modeled time as a constant (.), time-varying (time), and linear (T) effect. We included the same covariates in data set 2 that we used in data set 1.

Analysis	Model	K	AIC_c	ΔAIC_c	w_i	ML
1	*M. ovipneumoniae* × time	15*	366.51	0.00	0.30	1.00
	M. ovipneumoniae + time	9	368.23	1.71	0.13	0.42
	M. ovipneumoniae × time + H_E	16*	368.58	2.06	0.11	0.36
	M. ovipneumoniae × time + post-NDVI	16*	368.63	2.12	0.10	0.35
	M. ovipneumoniae × time + pre-NDVI	16*	368.64	2.12	0.10	0.35
	M. ovipneumoniae + time + H_E	10	370.02	3.51	0.05	0.17
	M. ovipneumoniae + time + pre-NDVI	10	370.23	3.72	0.05	0.16
	M. ovipneumoniae + time + post-NDVI	10	370.31	3.79	0.04	0.15
	M. ovipneumoniae × time + H_E + post-NDVI	17*	370.66	4.15	0.04	0.13
	M. ovipneumoniae × time + H_E + pre-NDVI	17*	370.69	4.18	0.04	0.12
	M. ovipneumoniae × time + pre-NDVI + post-NDVI	17*	370.77	4.25	0.04	0.12
	M. ovipneumoniae × time + H_E + pre-NDVI + post-NDVI	18*	372.80	6.29	0.01	0.04
	time + post-NDVI	9	383.02	16.51	0.00	0.00
	time + H_E	9	387.94	21.42	0.00	0.00
	Time	8	392.21	25.70	0.00	0.00
	time + pre-NDVI	9	394.22	27.71	0.00	0.00
	M. ovipneumoniae	2	400.46	33.94	0.00	0.00

	post-NDVI	2	412.59	46.08	0.00	0.00
	H_E	2	417.59	51.07	0.00	0.00
	T	2	418.76	52.24	0.00	0.00
	. (null)	1	422.68	56.17	0.00	0.00
	pre-NDVI	2	424.41	57.90	0.00	0.00
2	Time	8	210.79	0.00	0.23	1.00
	. (null)	1	211.84	1.05	0.14	0.59
	time + pre-NDVI	9	212.52	1.73	0.10	0.42
	time + H_E	9	212.70	1.91	0.09	0.38
	time + post-NDVI	9	212.78	1.99	0.09	0.37
	T	2	213.27	2.48	0.07	0.29
	post-NDVI	2	213.60	2.82	0.06	0.24
	pre-NDVI	2	213.67	2.88	0.05	0.24
	H_E	2	213.69	2.90	0.05	0.23
	time + H_E + pre-NDVI	10	214.19	3.41	0.04	0.18
	time + pre-NDVI + post-NDVI	10	214.41	3.62	0.04	0.16
	time + H_E + post-NDVI	10	214.78	4.00	0.03	0.14
	time + H_E + pre-NDVI + post-NDVI	11	216.25	5.46	0.02	0.07

*****Models where survival interval 1 for the *M. ovipneumoniae* group were fixed as no mortalities occurred during that interval

Table 2.3 The outputs from the top models in analysis 1 (*M. ovipneumoniae* × time) and analysis 2 (null) predicting survival of juvenile bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada. Analysis 1 includes all study populations, while analysis 2 only includes populations (n = 11) where *Mycoplasma ovipneumoniae* was not detected.

Analysis	Covariate	Effect on survival	Odds-ratio	Estimate	SE	95% CI	
						Lower	Upper
1	Intercept			2.08	1.06	0.00	4.16
	M. ovipneumoniae	↓	8.00	-2.08	1.77	-5.54	1.39
	time 1	↑	9.50	2.25	1.46	-0.61	5.12
	time 2	↑	1.00	0.00	1.13	-2.22	2.22
	time 3	↓	1.89	-0.64	1.12	-2.84	1.56
	time 4	↓	1.05	-0.05	1.16	-2.33	2.23
	time 5	↑	1.83	0.61	1.22	-1.78	2.99
	time 6	↑	2.44	0.89	1.28	-1.63	3.41
	time 7	↓	1.09	-0.09	1.23	-2.49	2.32
	M. ovipneumoniae × time 1*****	↑	1.00	0.00	0.00	0.00	0.00
	M. ovipneumoniae × time 2	↑	4.37	1.48	1.85	-2.16	5.11
	M. ovipneumoniae × time 3	↑	4.36	1.47	1.85	-2.15	5.09
	M. ovipneumoniae × time 4	↓	1.33	-0.29	1.88	-3.96	3.39
	M. ovipneumoniae × time 5	↓	2.75	-1.01	1.97	-4.88	2.86
	M. ovipneumoniae × time 6	↓	1.63	-0.49	2.12	-4.64	3.66
	M. ovipneumoniae × time 7	↑	2.18	0.78	2.24	-3.60	5.16
2	Intercept			2.08	1.06	0.00	4.16
	time 1	↑	9.50	2.25	1.46	-0.61	5.12
	time 2	↓	1.00	0.00	1.13	-2.22	2.22

time 3	↓	1.89	-0.64	1.12	-2.84	1.56
time 4	↓	1.05	-0.05	1.16	-2.33	2.23
time 5	↑	1.83	0.61	1.22	-1.78	2.99
time 6	↑	2.44	0.89	1.28	-1.63	3.41
time 7	↓	1.09	-0.09	1.23	-2.49	2.32

**M. ovipneumoniae* x time 1 is fixed as no mortalities were observed during this interval.

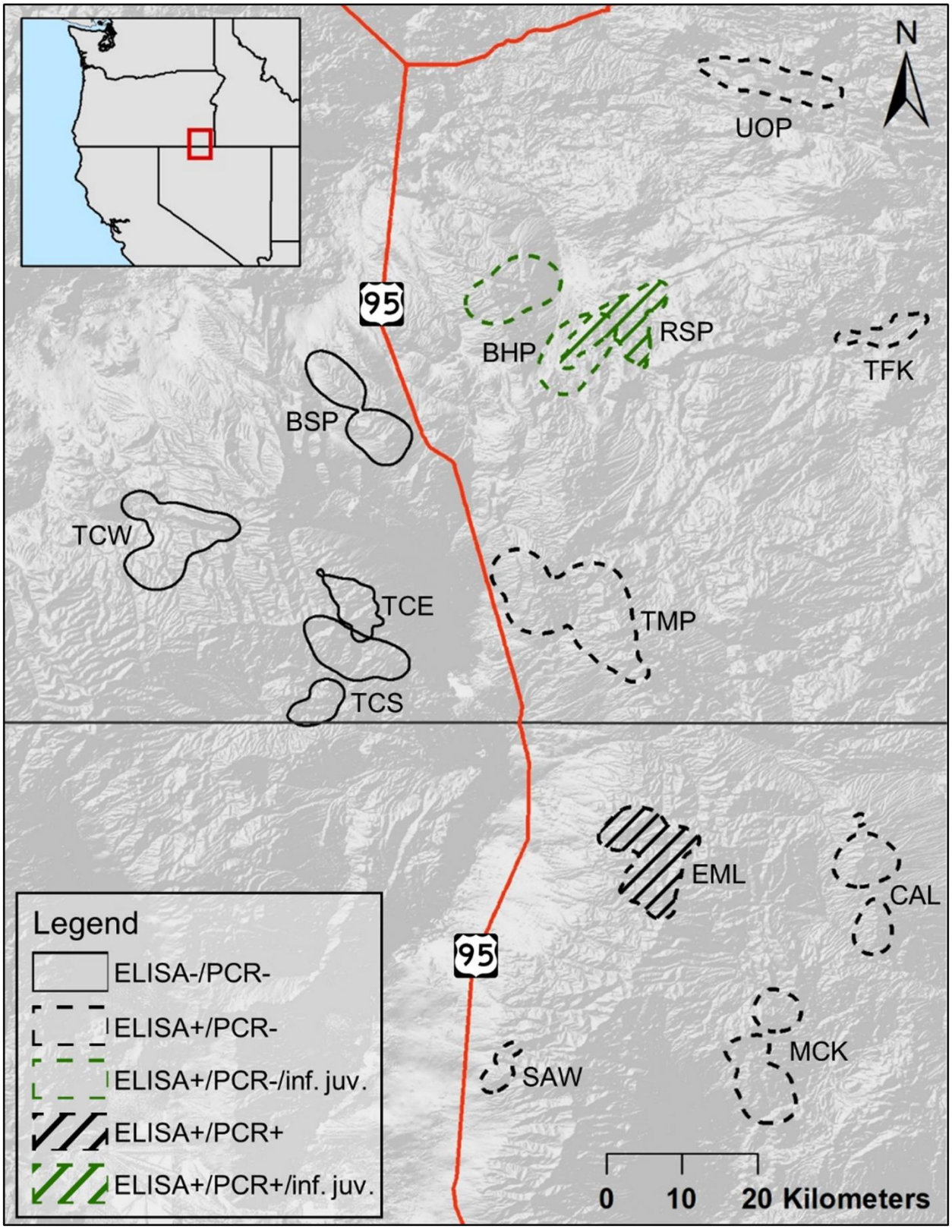
N
UOP
95
BHP
RSP
TFK
BSP
TCW
TCE
TMP
TCS
EML
CAL
95
SAW
MCK
Legend
ELISA-/PCR-
ELISA+/PCR-
ELISA+/PCR-/inf. juv.
ELISA+/PCR+
ELISA+/PCR+/inf. juv.
0 10 20 Kilometers

Figure 2.1 Cumulative summer utilization distributions of adult female bighorn sheep populations considered in this study. Overlapping polygons indicate shared habitat. Solid lined polygons, all to the west of U.S. Route 95, indicate populations unexposed to *Mycoplasma ovipneumoniae*, with dashed lines indicating exposed populations to the east of U.S. Route 95. Line fill indicates populations, EML and RSP, where a single adult female *M. ovipneumoniae* infection was detected. Green colored polygons indicate populations, BHP and RSP, where dead juveniles infected with *M. ovipneumoniae* were detected. Populations include – Bowden Hills (BHP), Blue Mountain (BSP), Calicos (CAL), Eight Mile (EML), Martin Creek (MCK), Rattlesnake (RSP), Sawtooth (SAW), Trout Creeks–east (TCE), Trout Creeks–south (TCS), Trout Creeks–west (TCW), Three Forks (TFK), Ten Mile (TMP) and Upper Owyhee (UOP).

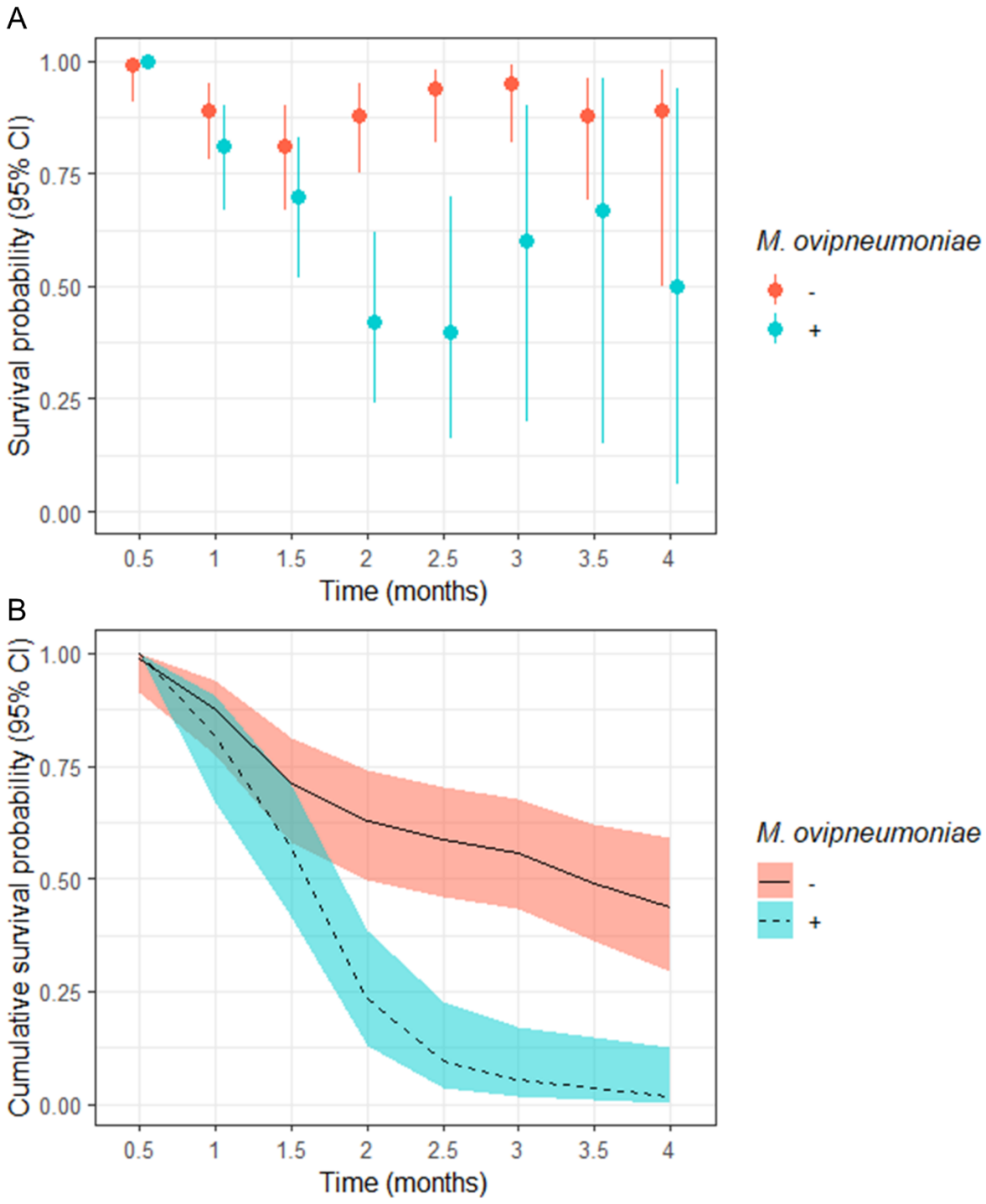

Figure 2.2 (A) Semi-monthly survival probabilities and (B) 4-month cumulative survival probabilities of juvenile bighorn sheep (*Ovis canadensis*) estimated using a Kaplan-Meier estimator with staggered entry and known-fate data collected in 13 populations in southeastern Oregon and northern Nevada. Survival probabilities and 95% confidence intervals are for populations where *Mycoplasma ovipneumoniae* was and was not detected.

Supplementary Material

Table S2.1 Translocation histories of bighorn sheep populations included in this study. Details include the population code (Pop) where the bighorn sheep were established or translocated to, translocation type (Trans_type), when the translocation took place (Year), the number of individuals (# ind.) translocated, the source population (Source pop.), the source state or province (S-State) population, the destination population (Destination pop.), and the destination state (D-State).

Population	Trans_type	Year	# individuals	Source population	S-State	Destination pop.	D-State
Bowden Hills	Colonization	unknown	?	Rattlesnake	OR	Bowden Hills	OR
Blue Mountain	Colonization	~1990s	?	Trout Ck.	OR	Blue Mountain	OR
Calicos	Import	1985	20	Williams Lake	BC	Pine Forest	NV
	Import	1988	18	Williams Lake	BC	Pine Forest	NV
	In jurisdiction	2011	25	Pine Forest	NV	Calico Mtn.	NV
Eight Mile	Import	1978	12	Penticton	BC	Eight Mile	NV
	In jurisdiction	2014	3	Pine Forest	NV	Three Mile Ck.	NV
Martin Creek*	Import	1984	13	Hart Mtn.	OR	Jackson Mtn.	NV
	Import	1985	20	Williams Lake	BC	Pine Forest	NV
	Import	1986	2	E fork of Owyhee Riv.	ID	Jackson Mtn.	NV
	Import	1987	15	Lower Owyhee	OR	Jackson Mtn.	NV
	Import	1988	18	Williams Lake	BC	Pine Forest	NV
	Import	1989	18	Kamloops	BC	High Rock/Calicos	NV
	In jurisdiction	1998	12	Jackson Mtn.	NV	Hinkey	NV
	In jurisdiction	1999	12	High Rock/Calicos	NV	Pine Forest	NV
	In jurisdiction	2006	21	Montana Mts.	NV	Martin Ck.	NV
	In jurisdiction	2011	27	Pine Forest	NV	Martin Ck.	NV
Rattlesnake	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1992	19	Hart Mtn.	OR	Rattlesnake Ck.	OR

Sawtooth	Import	1989	20	Penticton	BC	Sawtooth	NV
Trout Creeks – east	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1987	27	Hart Mtn.	OR	Trout Creek Mtn.	OR
Trout Creeks – south	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1990	14	Hart Mtn.	OR	Trout Creek Mtn.	OR
Trout Creeks – west	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1990	19	Hart Mtn.	OR	Trout Creek Mtn.	OR
Ten Mile	Import	1954	20	Williams Lake	BC	Hart Mtn.	OR
	In jurisdiction	1960	4	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1961	7	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1989	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1992	15	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	18	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	15	Steens Mtn.	OR	Ten Mile Rim	OR
Upper Owyhee*	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1960	4	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1961	7	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1965	17	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1983	21	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1983	14	Hart Mtn.	OR	Upper Owyhee	OR
	In jurisdiction	1987	15	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1987	16	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1989	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1992	15	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	17	Hart Mtn.	OR	Steens Mtn.	OR

In jurisdiction	1993	18	Hart Mtn.	OR	Steens Mtn.	OR
In jurisdiction	1993	36	Steens Mtn.	OR	Upper Owyhee	OR
In jurisdiction	1994	21	Lower Owyhee	OR	Upper Owyhee	OR
In jurisdiction	1995	17	Hart Mtn.	OR	Upper Owyhee	OR
In jurisdiction	2007	21	Philippi Canyon	OR	Upper Owyhee	OR

*****Indicates incomplete history

Table S2.2 Microsatellite loci used for analysis of bighorn sheep (*Ovis canadensis*) population genetic diversity in southeastern Oregon and Nevada, with allele sizes ranges observed in this study, fluorescent dye labels used, primer concentrations, and pre-PCR multiplex combination employed.

Locus	Reference	Allele size (bp)	Dye Label	Primer Concentration (µM)	Panel
AE129	Penty et al., 1993	166–177	Vic	0.25	1
AE16	Penty et al., 1993	84–100	Fam	0.20	3
BL4	Smith et al., 1997	158–162	Ned	0.30	2
FCB11	Buchanan & Crawford, 1993	125–131	Vic	0.20	3
FCB193	Buchanan & Crawford, 1993	105–119	Pet	0.25	1
FCB266	Buchanan & Crawford, 1993	89–101	Vic	0.20	3
FCB304	Buchanan & Crawford, 1993	142–150	Pet	0.20	3
HH62	Ede et al., 1994	102–130	Fam	0.15	1
JMP29	Crawford et al., 1995	121–133	Ned	0.20	3
MAF33	Buchanan & Crawford, 1992b	122–126	Vic	0.25	1
MAF36	Swarbrick et al., 1991	87–99	Vic	0.15	2
MAF48	Buchanan, Swarbrick & Crawford, 1991	122–126	Ned	0.20	1
MAF65	Buchanan, Swarbrick & Crawford, 1992	118–138	Fam	0.20	2
MAF209	Buchanan & Crawford, 1992a	110–122	Pet	0.20	2
TCRBV62	Crawford et al., 1995	171–175	Fam	0.25	3
TGLA387	Georges & Massey 1992	143–151	Pet	0.35	1

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Table S2.3 Breakdown of *Mycoplasma ovipneumoniae* test results for all female bighorn sheep captured and collared between 2016 and 2018 in populations (n = 13) across southeastern Oregon and northern Nevada. Tests included a PCR used to detect active infections of bighorn sheep to *M. ovipneumoniae* and an cELISA test, used to detect previous exposure to *M. ovipneumoniae* + indicates positive cases; - indicates negative cases; "indeterminate" indicates indeterminate; "unknown" indicates individuals for which there were no samples, and "recaptures" indicates recaptured individuals.

				***M. ovipneumoniae* status**							
				PCR				**cELISA**			
Population	**Year**	***n***	**recaptures**	**+**	**-**	**indeterminate**	**unknown**	**+**	**-**	**indeterminate**	**unknown**
Bowden Hills	2018	3	-	0	2	1	0	3	0	0	0
Blue Mountain	2016	3	-	0	3	0	0	0	3	0	0
Blue Mountain	2017	2	-	0	2	0	0	0	2	0	0
Calicos	2017	3	-	0	3	0	0	0	0	0	3
Calicos	2018	5	1	0	5	0	0	3	1	1	0
Eight Mile	2017	4	-	1	3	0	0	0	0	0	4
Eight Mile	2018	5	3	1	4	0	0	3	2	0	0
Martin Creek	2017	4	-	0	4	0	0	0	0	0	4
Martin Creek	2018	5	3	0	5	0	0	4	1	0	0
Rattlesnake	2016	10	-	1	9	0	0	6	1	3	0
Rattlesnake	2017	11	-	0	11	0	0	7	1	3	0
Sawtooth	2017	3	-	0	3	0	0	0	0	0	3
Sawtooth	2018	3	3	0	3	0	0	2	1	0	0
Trout Creeks – east	2016	12	-	0	12	0	0	0	11	0	1
Trout Creeks – east	2017	2	-	0	2	0	0	0	2	0	0
Trout Creeks – east	2018	1	-	0	1	0	0	0	1	0	0

Trout Creeks – south	2016	2	-	0	2	0	0	0	2	0	0
Trout Creeks – south	2017	1	-	0	1	0	0	0	1	0	0
Trout Creeks – south	2018	1	-	0	1	0	0	0	1	0	0
Trout Creeks – west	2016	2	-	0	2	0	0	0	2	0	0
Trout Creeks – west	2017	3	-	0	3	0	0	0	3	0	0
Trout Creeks – west	2018	1	-	0	1	0	0	0	1	0	0
Three Forks	2016	1	-	0	1	0	0	0	0	0	1
Ten Mile	2016	3	-	0	3	0	0	3	0	0	0
Ten Mile	2017	1	-	0	1	0	0	1	0	0	0
Upper Owyhee	2016	4	-	0	4	0	0	2	1	0	1
N		95		3	91	1	0	34	37	7	17

Table S2.4 Proportion of *Mycoplasma ovipneumoniae* exposed (exposed, indeterminate, and unexposed) and actively infected (positive (+), indeterminate, negative (-)) adult female bighorn sheep (*Ovis canadensis*), as determined by cELISA and PCR for populations (n = 13) in southeastern Oregon and northern Nevada. Pop. n = approximate number of adult females in each population, and n = number of individuals tested between 2016 and 2018.

	Pop.	***M. ovipneumoniae* cELISA**				***M. ovipneumoniae* PCR prevalence**			
Population	**n**	**n**	**Exposed**	**Indeterminate**	**Unexposed**	**n**	**+**	**Indeterminate**	**-**
Bowden Hills	14	3	1.00	0.00	0.00	3	0.00	0.33	0.67
Blue Mountain	12	5	0.00	0.00	1.00	5	0.00	0.00	1.00
Calicos	25	5	0.60	0.20	0.20	5	0.00	0.00	1.00
Eight Mile	32	5	0.60	0.00	0.40	6	0.17	0.00	0.83
Martin Creek	14	5	0.80	0.00	0.20	6	0.00	0.00	1.00
Rattlesnake	53	21	0.62	0.29	0.10	21	0.05	0.00	0.95
Sawtooth	11	3	0.67	0.00	0.33	3	0.00	0.00	1.00
Trout Creeks – east	35	14	0.00	0.00	1.00	15	0.00	0.00	1.00
Trout Creeks – south	20	4	0.00	0.00	1.00	4	0.00	0.00	1.00
Trout Creeks – west	43	6	0.00	0.00	1.00	6	0.00	0.00	1.00
Three Forks	10	0	-	-	-	1	0.00	0.00	1.00
Ten Mile	17	4	1.00	0.00	0.00	4	0.00	0.00	1.00
Upper Owyhee	17	3	0.67	0.00	0.33	5	0.00	0.00	1.00

Table S2.5 Genetic diversity (observed heterozygosity, H_O averaged across 16 loci; expected heterozygosity, H_E, averaged across 16 loci; allelic richness, A_R, averaged across 16 loci), for populations of bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada.

Population	n	H_O	H_E	A_R
Bowden Hills	18	0.481	0.428	2.575
Blue Mountain	15	0.307	0.257	1.815
Calicos	17	0.360	0.350	2.410
Eight Mile	14	0.557	0.476	2.656
Martin Creek	12	0.372	0.363	2.501
Rattlesnake	26	0.496	0.447	2.678
Sawtooth	12	0.445	0.422	2.880
Trout Creek – east	20	0.345	0.316	1.994
Trout Creek – south	17	0.316	0.281	1.890
Trout Creek – west	18	0.350	0.329	2.017
Ten Mile	12	0.482	0.457	2.699
Upper Owyhee	10	0.356	0.334	2.375

Table S2.6 Hardy-Weinberg multi-population test results by locus. Results were generated using Markov chain parameters for all tests (dememorization = 1,000; batches = 100; iterations per batch = 1,000).

Locus	p-values	SE
AE129	0.406	0.00
AE16	0.507	0.00
BL4	0.756	0.00
FCB11	0.899	0.00
FCB266	0.944	0.00
FCB304	0.924	0.00
HH62	0.912	0.00
JMP29	0.852	0.00
MAF209	0.796	0.00
MAF33	0.999	0.00
MAF36	0.807	0.00
MAF48	0.220	0.00
MAF65	0.124	0.00
OarFCB193	0.589	0.01

TCRBV62	0.527	0.01
TGLA387	0.933	0.00

Table S2.7 Hardy-Weinberg multi-population test results by population and subpopulation. Results were generated using Markov chain parameters for all tests (dememorization = 1,000; batches = 100; iterations per batch = 1,000).

Population	p-values
Bowden Hills	0.945
Blue Mountain	0.986
Calicos	0.481
Eight Mile	0.950
Martin Creek	0.430
Rattlesnake	0.991
Sawtooth	0.606
Three Forks*	0.600
Trout Creek east	0.793
Trout Creek south	0.943
Trout Creek west	0.520
Ten Mile	0.675
Upper Owyhee	0.600

Table S2.8 Mean pre- and post-parturition NDVI values across 13 populations of bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada for the period 2016-2018. Mean NDVI values were generated using pre-processed data obtain from Earth Explorer, managed by USGS's Earth Resource Observation Center. Superscripted numbers indicate rank, from lowest to highest, of NDVI, a proxy for forage quality. n/a indicates years where populations were not sampled.

	2016		**2017**		**2018**	
	$\bar{x}$ **NDVI**		$\bar{x}$ **NDVI**		$\bar{x}$ **NDVI**	
Population	**pre-parturition**	**post-parturition**	**pre-parturition**	**post-parturition**	**pre-parturition**	**post-parturition**
Bowden Hills	n/a	n/a	n/a	n/a	0.27^{6}	0.28^{1}
Blue Mountain	n/a	n/a	0.16^{1}	0.39^{2}	0.22^{3}	0.40^{4}
Calicos	n/a	n/a	n/a	n/a	0.19^{1}	0.42^{8}
Eight Mile	n/a	n/a	0.31^{10}	0.57^{11}	0.32^{11}	0.56^{11}
Martin Creek	n/a	n/a	0.22^{3}	0.40^{3}	0.26^{5}	0.41^{7}
Rattlesnake	0.39^{5}	0.44^{4}	0.20^{2}	0.37^{1}	0.28^{9}	0.32^{2}
Sawtooth	n/a	n/a	0.30^{9}	0.42^{5}	0.27^{6}	0.38^{3}
Trout Creeks –east	0.31^{1}	0.49^{6}	0.23^{4}	0.50^{10}	0.21^{2}	0.43^{10}
Trout Creeks – south	0.32^{2}	0.42^{4}	0.29^{8}	0.46^{9}	0.25^{4}	0.42^{8}
Trout Creeks – west	0.33^{3}	0.36^{1}	0.24^{7}	0.41^{4}	0.27^{6}	0.40^{4}
Three Forks*	0.47^{6}	0.41^{2}	0.23^{4}	0.42^{5}	n/a	n/a
Ten Mile	0.38^{4}	0.44^{5}	0.32^{11}	0.43^{8}	0.28^{9}	0.40^{4}
Upper Owyhee	0.47^{6}	0.41^{2}	0.23^{4}	0.42^{5}	n/a	n/a

*The data for Upper Owyhee (UOP) was used as a proxy for Three Forks (TFK) due to insufficient seasonal GPS locations for the single collared adult female bighorn sheep in the TFK population. Both TFK and UOP occur within the upper part of the Owyhee Canyon.

Table S2.9 Correlation of fixed effects predicting survival of bighorn sheep (*Ovis canadensis*) lamb survival. Fixed effects include *Mycoplasma ovipneumoniae* status, H_E (expected heterozygosity), pre-NDVI (pre-parturition NDVI), and post-NDVI (post-parturition NDVI).

Fixed effects	***M. ovipneumoniae***	H_E	**pre-NDVI**	**post-NDVI**
M. ovipneumoniae	-	0.58	-0.17	-0.66
H_E	0.58	-	0.07	-0.18
pre-NDVI	-0.17	0.07	-	0.28
post-NDVI	-0.66	-0.18	0.28	-

Table S2.10 Breakdown of collared adult female bighorn sheep (*Ovis canadensis*) productivity by population (n = 13) and years (n = 3) in southeastern Oregon and northern Nevada. Data includes the number of adult females at the start of each year, the number of adult females pregnancy tested, and the proportion ($\hat{p}$) pregnant, the number of adult females dead prior to the parturition period, and the proportion of adult females observed with juveniles by year.

Population	year	# adult females at start of year	# adult females pregnancy tested	$\hat{p}$ pregnant	# adult females dead pre-parturition	$\hat{p}$ adult females observed with juveniles
Bowden Hills	2018	3	3	1.00	0	1.00
Blue Mountain	2016	3	3	1.00	2	0.00
Blue Mountain	2017	3	2	1.00	0	0.67
Blue Mountain	2018	3	0	n/a	0	0.33
Calicos	2017	3	3	1.00	2	0.00
Calicos	2018	4	0	n/a	0	0.75
Eight Mile	2017	4	4	1.00	0	1.00
Eight Mile	2018	6	3	1.00	0	1.00
Martin Creek	2017	4	4	1.00	1	1.00
Martin Creek	2018	4	0	n/a	1	1.00
Rattlesnake	2016	10	10	1.00	1	0.78
Rattlesnake	2017	20	11	1.00	0	0.90
Rattlesnake	2018	18	0	n/a	0	0.83
Sawtooth	2017	3	3	1.00	0	1.00
Sawtooth	2018	3	3	1.00	0	1.00
Trout Creeks–east	2016	12	12	0.67	1	0.64
Trout Creeks–east	2017	11	2	1.00	0	0.64
Trout Creeks–east	2018	12	1	1.00	0	0.17

Trout Creeks–south	2016	2	2	0.50	0	0.50
Trout Creeks–south	2017	3	1	1.00	0	1.00
Trout Creeks–south	2018	4	1	1.00	0	0.75
Trout Creeks–west	2016	2	2	1.00	0	1.00
Trout Creeks–west	2017	5	3	1.00	3	1.00
Trout Creeks–west	2018	3	1	1.00	0	1.00
Three Forks	2016	1	1	0.00*****	0	1.00
Three Forks	2017	1	0	n/a	0	1.00
Ten Mile	2016	3	3	1.00	0	1.00
Ten Mile	2017	4	1	1.00	1	0.67
Ten Mile	2018	3	0	n/a	0	1.00
Upper Owyhee	2016	5	4	1.00	0	1.00
Upper Owyhee	2017	4	0	n/a	0	1.00

*****Three Forks adult female although not pregnant on the pregnancy test was observed with a lamb

Table S2.11 Number of collared adult female bighorn sheep (*Ovis canadensis*) in each population (*n*) at parturition of juvenile bighorn sheep, with observation rate (%) of juveniles accompanying collared adult females across all observation intervals for the period 2016 to 2018 in bighorn sheep populations (*n* = 13) in southeastern Oregon and northern Nevada.

	2016			**2017**			**2018**		
Population	***n***	**%**	**Range (%)**	***n***	**%**	**Range (%)**	***n***	**%**	**Range (%)**
Bowden Hills	n/a	n/a	n/a	n/a	n/a	n/a	4	96	83–100
Blue Mountain	n/a	n/a	n/a	2	100	100	1	100	100
Calicos	n/a	n/a	n/a	n/a	n/a	100	3	100	100
Eight Mile	n/a	n/a	n/a	4	100	100	6	92	67–100
Martin Creek	n/a	n/a	n/a	3	100	100	5	100	1.00
Rattlesnake	7	95	75–100	18	100	100	15	98	71–100
Sawtooth	n/a	n/a	n/a	3	78	60–100	3	100	1.00
Trout Creeks–east	7	72	50–88	7	93	83–100	2	100	1.00
Trout Creeks–south	1	100	100	3	100	100	3	100	1.00
Trout Creeks–west	2	85	83–88	2	100	100	3	95	86–100
Three Forks	1	100	100	1	80	80	n/a	n/a	n/a
Ten Mile	3	100	100	2	100	100	3	72	67–83
Upper Owyhee	4	88	67–100	3	90	83–100	n/a	n/a	n/a
	25	91	50–100	48	95	60–100	48	96	67–100

Table S2.12 Breakdown of juvenile bighorn sheep (*Ovis canadensis*) mortalities tested for *Mycoplasma ovipneumoniae* via polymerase chain reaction (PCR). Samples from juvenile mortalities were collected in the field between 2016 and 2018.

Mortality ID	Date collected	Population	Sex	*M. ovipneumoniae* status
RSP-01_16	26-May-2016	Rattlesnake	male	positive
RSP-02_16	26-May-2016	Rattlesnake	male	positive
RSP-03_16	31-May-2016	Rattlesnake	male	positive
RSP-01_17	28-May-2017	Rattlesnake	unknown	positive
RSP-02_17	28-May-2017	Rattlesnake	female	positive
RSP-03_17	31-May-2017	Rattlesnake	unknown	positive
RSP-04_17	5-Jun-2017	Rattlesnake	male	positive
RSP-05_17	7-Jun-2017	Rattlesnake	female	positive
RSP-06_17	7-Jun-2017	Rattlesnake	male	positive
RSP-09_17	25-Jun-2017	Rattlesnake	male	positive
RSP-10_17	25-Jun-2017	Rattlesnake	female	positive
TCP-01_17	8-May-2017	Trout Creeks – south	female	negative
BHP-01_18	16-Jul-2018	Bowden Hills	female	positive
BSP-01_18	5-Jul-2018	Blue Mountain	unknown	negative
RSP-01_18	16-Jun-2018	Rattlesnake	female	positive
RSP-04_18	18-Jun-2018	Rattlesnake	male	positive
RSP-06_18	18-Jun-2018	Rattlesnake	unknown	positive

Table S2.13 Strain-typed samples from bighorn sheep captured in southeastern Oregon and northern Nevada populations. All samples were multi-locus sequence typed (MLST) at the available sequences, 16S-23S intergenic spacer region (IGS), the small ribosomal subunit (16S), genes encoding RNA polymerase B (rpoB), and gyrase B (gyrB) were identical within loci. Details include year sample was collected, location of sample collection, WADDL processing number, animal details, and loci that were genotyped.

Date	Location	WADDL_#	Animal detail	IGS	16S	rpoB	gyrB
2004	Sawtooth, Santa Rosa Range	01370	adult male	x			
2004	Sawtooth, Santa Rosa Range	01370	adult male	x	x	x	
2012	Snowstorm Mountains*	12853	adult female	x	x	x	x
2014	Santa Rosa Range	00726	unknown	x			
2014	Santa Rosa Range	00726	unknown	x	x	x	x
2015	Santa Rosa Range	04278	unknown	x	x	x	x
2016	Rattlesnake	00793	adult female	x	x	x	x
2018	Bowden Hills	12749	juvenile female	x	x	x	x
2018	Rattlesnake	12749	juvenile male	x	x	x	x
2019	Rattlesnake	16781	unknown	x	x	x	x

***** Individual dispersed from Santa Rosa Range and was re-captured in the Snowstorm Mountains

Table S2.14 Univariate models examining the effects of various *Mycoplasma ovipneumoniae* and genetic diversity covariates on juvenile bighorn sheep (*Ovis canadensis*) survival in southeastern Oregon and northern Nevada.

Model	K	AIC_c	ΔAIC_c
M. ovipneumoniae (presence of infected juveniles)	2	400.46	-
M. ovipneumoniae (PCR)	2	409.59	9.13
M. ovipneumoniae (ELISA)	2	422.65	22.19
Expected heterozygosity (H_E)	1	417.59	-
Allelic richness (A_R)	1	420.85	3.26

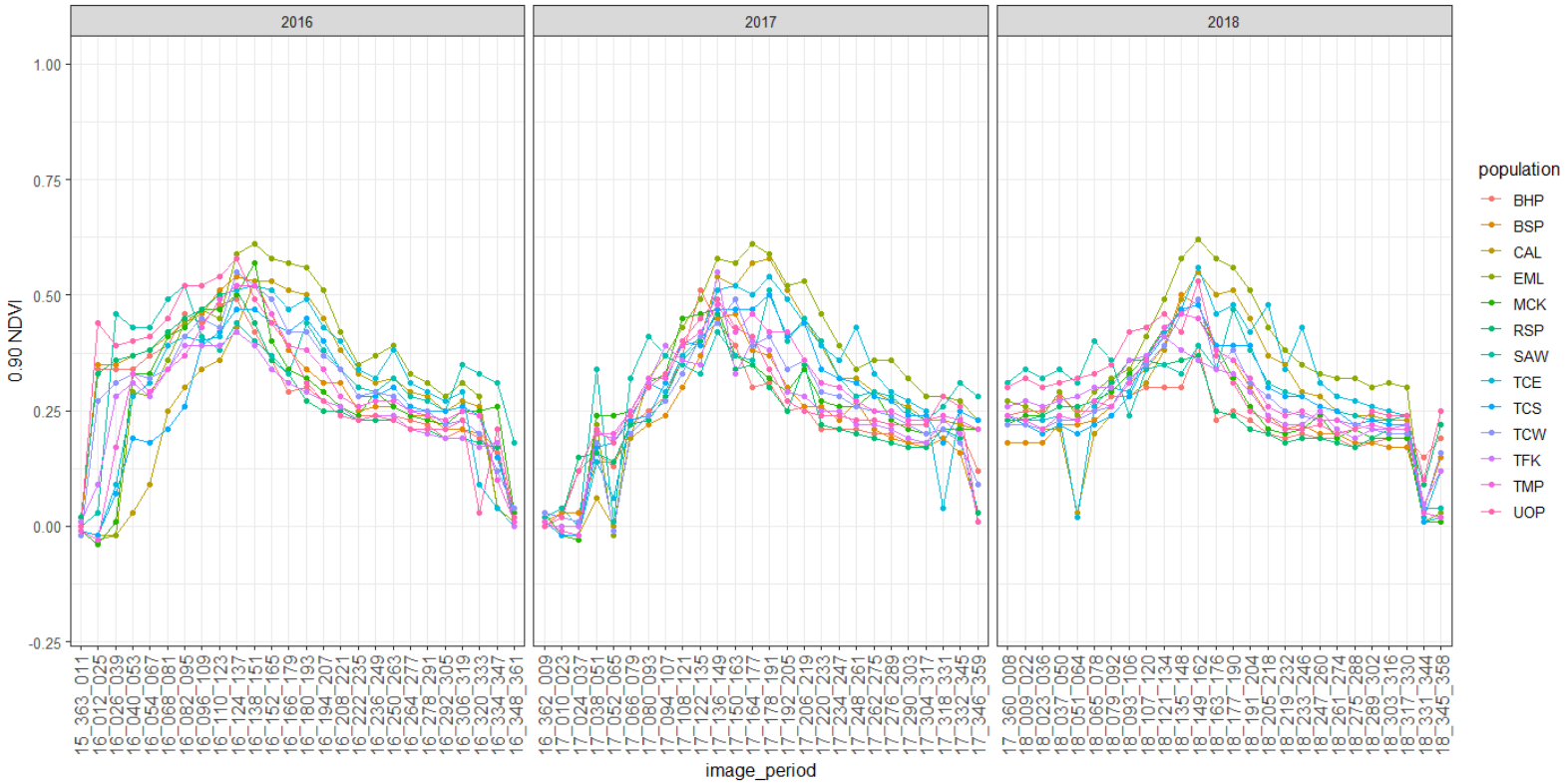

Figure S2.1 Ninetieth percentile normalized differential vegetation index (NDVI) values (scaled between -0.2 and 1.0) for all 13 bighorn sheep (*Ovis canadensis*) populations in southeastern Oregon and northern Nevada. Each value is derived from 14-day composite, 250 m resolution NDVI data from the Moderate Imaging Spectroradiometer (eMODIS) using annual composite 95% utilization distributions of collared adult females in each population to extract data. Population codes represent, BHP – Bowden Hills, BSP – Blue Mountain, CAL – Calicos, EMP – Eight Mile, MCK – Martin Creek, RSP – Rattlesnake, SAW – Sawtooth, TCE – Trout Creeks - east, TCS – Trout Creeks - south, TCW – Trout Creeks - west, TFK – Three Forks, TMP – Ten Mile and UOP - Upper Owyhee.

CHAPTER 3

Influences of sex, genetic diversity, and infectious disease on survival of adult California bighorn sheep (*Ovis canadensis*)

Robert S. Spaan[1], Clinton W. Epps[1], Adam Duarte[2], Rachel Crowhurst[1], Brianna R. Beechler[3], Donald G. Whittaker[4], Julia D. Burco[4], Mike Cox[5], and M. Weldy[6].

[1] Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA
[2] USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington, USA
[3] Department of Biomedical Sciences, Oregon State University, Corvallis, Oregon, USA
[4] Oregon Department of Fish and Wildlife, Salem, Oregon, USA
[5] Nevada Department of Wildlife, Reno, Nevada, USA
[6] Department of Forestry Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA

Corresponding Author:
Robert Spaan[1]
Nash Hall, 2820 SW Campus Way, Corvallis, OR, USA 97331
rob.spaan@oregonstate.edu

Abstract

Understanding drivers of survival in small populations of ungulates are essential, given that high adult survival is expected in stable or increasing populations. We investigated drivers of adult survival in California bighorn sheep populations in the northern Basin and Range ecosystem across two metapopulations with different histories of population translocation and exposure to respiratory pneumonia. We investigated whether the survival probability of adults varied by (1) age, (2) sex, (3) individual exposure to or infection with *Mycoplasma ovipneumoniae,* a key pathogen associated with respiratory pneumonia, (4) individual and population genetic diversity and (5) metapopulation identity. We tracked the monthly survival of 125 bighorn sheep fit using GPS collars with a mortality function from 2016–2020 in 13 southeastern Oregon and northern Nevada populations. We used a known-fate model and a sequential modeling strategy to 1) determine the temporal drivers of survival, 2) consider age-structured drivers of survival, and 3) consider the effects of sex, *M. ovipneumoniae* exposure or infection, genetic diversity, and metapopulation on the probability of survival. Positive *M. ovipneumonia*e exposures were limited to individuals in populations east of U.S. Route 95. We could not test for an *M. ovipneumoniae* infection effect due to the low number of PCR+ individuals. Throughout the study, 30 of

125 adults died. The top model predicting adult survival included sex, population genetic diversity, and *M. ovipneumoniae* exposure. However, the credible intervals for the estimated mean effects of sex and population genetic diversity overlapped zero. The odds of survival for *M. ovipneumoniae*-exposed individuals were 2.30 times lower than for unexposed individuals. The lack of temporal effects was likely due to insignificant variation in this long-lived species' monthly survival. We also failed to detect an age or metapopulation effect on survival. Throughout the study, the derived mean annual survival for female bighorn sheep unexposed to *M. ovipneumoniae* was 0.926 (95% CI [0.875–0.963]), compared to 0.840 (95% CI [0.753–0.910]) for exposed females, while male survival for unexposed individuals was 0.868 (95% CI [0.783–0.932]) compared to 0.723 (95% CI [0.538–0.865]) for exposed males. One bighorn sheep tested positive for exposure to bluetongue (*Orbivirus* spp.) at death; an additional five individuals were suspected of having died from this disease. The low prevalence of *M. ovipneumoniae*-infected individuals suggests that chronic shedders and birth pulses maintain the pathogen. Experimental removal of chronic carriers has been recommended and shown to be an effective management tool to increase juvenile survival. Our study suggests this action could also benefit unexposed individuals of all ages. Although we could not definitively document the role of bluetongue in this study, we also recommend monitoring the impact of that disease, especially during arid summer months.

Keywords

Bighorn sheep, adult survival, *Mycoplasma ovipneumoniae*, genetic diversity, metapopulation, disease fadeout, targeted removals, bluetongue, augmentation

Introduction

Understanding population dynamics is crucial to species management (Williams et al. 2002). For large, terrestrial herbivores, adult survival, most notably of females, tends to exhibit minimal variation, while juvenile survival tends to be more variable (Gaillard et al. 1998, 2000). Furthermore, in some large terrestrial herbivores exhibiting sexual dimorphism, survival in adult males tends to be lower for males than females (Toıgo and Gaillard 2003). Thus, adult survival of large terrestrial herbivores, particularly of adult females, provides stability to populations, while population growth tends to be more sensitive to juvenile survival parameters due to adult survival being so invariant (Gaillard et al. 1998, 2000). However, adult survival can be essential for small populations' persistence (Rubin et al. 2002, Festa-Bianchet et al. 2006). Therefore, it is vital to consider the variables driving mortality.

The causes of mortality in adult bighorn sheep (*Ovis canadensis*), a large, terrestrial herbivore exhibiting sexual dimorphism, are diverse. However, observed causes of adult mortality in bighorn sheep include intrinsic effects such as sex (Jorgenson et al. 1997, Cassirer and Sinclair 2007, Paterson et al.

2021), age (Jorgenson et al. 1997, Conner et al. 2018), low genetic diversity (Hogg et al. 2006), and extrinsic effects such as forage (Conner et al. 2018, Proffitt et al. 2021), density dependence (Jorgenson et al. 1997), precipitation and temperature (Jorgenson et al. 1997, Dekelaita et al. 2020), predation (Festa-Bianchet et al. 2006, Conner et al. 2018, Proffitt et al. 2021), environmental disasters, such as avalanches (Conner et al. 2018), and disease (Jorgenson et al. 1997, Cassirer and Sinclair 2007, Dekelaita et al. 2020). Indeed, disease is considered a major contributor to the decline and extirpation of bighorn sheep across North America and it continues to hamper the recovery and management of the species across its range (Cassirer et al. 2018).

Mycoplasma ovipneumoniae, a bacterial pathogen, is the primary causative agent of pneumonia in bighorn sheep (Besser et al. 2008, 2014). The pathogen is usually transmitted to bighorn sheep by domestic sheep and goats (Besser et al. 2014, Cassirer et al. 2018) but can be transmitted among bighorn sheep populations. Initial infection of bighorn sheep by *M. ovipneumoniae* is typically followed by an all-age die-off (Cassirer et al. 2013, Manlove et al. 2016), with variable mortality rates (Cassirer et al. 2018). The disease can be maintained in the system by chronic carrier females, transmitting the pathogen to naïve lambs, which may inhibit population recovery, resulting in declining populations (Manlove et al. 2016). Persistence of the pathogen in the system can lead to low recruitment and declining population growth with age skewed towards older individuals (Manlove et al. 2016). Chronic carrier males are responsible for most pathogen spillover events into other populations, given their propensity for frequent and longer-distance forays (DeCesare and Pletscher 2006, O'Brien et al. 2014). Bighorn sheep appear to lack cross-strain immunity to *M. ovipneumoniae*, meaning that exposure to novel strains will likely result in similar mortality patterns (Cassirer et al. 2017).

Annual survival of adult bighorn sheep across their range and subspecies tends to be consistently high (0.80–1.00) in the absence of disease or high-density mountain lion populations (Jorgenson et al. 1997, Cassirer and Sinclair 2007, Conner et al. 2018, Dekelaita et al. 2020, Proffitt et al. 2021, Werdel et al. 2021). However, during early phases of pneumonia outbreaks or when mountain lions occur at high densities, annual survival is generally lower (<0.80) (Rominger et al. 2004, Festa-Bianchet et al. 2006). Other patterns of survival commonly observed across the range of bighorn sheep where pneumonia is absent include prime-aged (2–7 years of age) individuals having higher survival than older (> 7 years of age) individuals (Jorgenson et al. 1997, Festa-Bianchet et al. 2006, Conner et al. 2018, Proffitt et al. 2021), and females generally having higher survival than males (Jorgenson et al. 1997, Festa-Bianchet et al. 2006, Cassirer and Sinclair 2007). However, exceptions exist where estimated male survival is higher (Conner et al. 2018).

In the past, the loss of bighorn sheep from large portions of their range to disease and other factors resulted in widespread restoration through translocations, sometimes from very distant source

populations (Singer et al. 2000). For bighorn sheep populations reestablished with either small numbers or single source translocations, and where gene flow with other populations is limited, genetic diversity may decline sharply due to founder effects (Hedrick et al. 2001). Low genetic diversity is widespread in some restored systems, as in Oregon (Olson et al. 2013), and has been hypothesized to contribute to poor survival and reproduction (Hedrick et al. 2001, Hogg et al. 2006, Johnson et al. 2011, Olson et al. 2012). Mediating the loss of genetic diversity through augmentation with individuals from other source populations has been demonstrated to have positive fitness effects on reproduction (Hogg et al. 2006, Johnson et al. 2011) and survival (Hogg et al. 2006). Further, Cassirer et al. (2018) suggests that genetically diverse metapopulations may provide for better outcomes related to pathogen invasion due to more robust immunity. However, the influence of individual- or population-level genetic diversity on survival in disease-affected systems has rarely been assessed.

This study aimed to determine drivers of adult survival in the reestablished (n = 13) bighorn sheep populations in the northern Basin and Range ecosystem from 2016–2020. We used a known fate model structure with a sequential modeling strategy to build an inferential model. In the first step, we considered temporal drivers of survival. In the second step, we considered age-structured drivers of survival. In the third step, we considered covariates characterizing the effects of sex, disease and genetic diversity in the system, and metapopulation. We hypothesized that adult survival would be influenced by sex, *M. ovipneumoniae* infection or exposure, and genetic diversity. We predicted that the probability of monthly adult survival would be lower in individuals that are (1) male, (2) have been exposed to or have *M. ovipneumoniae*, and (3) or have lower genetic diversity.

Materials & Methods

Study area

Our study encompassed thirteen bighorn sheep populations, all located in southeastern Oregon and northern Nevada, between 41.2 and 42.3°N and 116.9 and 118.4°W (Fig. 3.1). Elevation across the study area ranged from approximately 1,050 m in the Owyhee Canyon to 2,957 m in the Santa Rosa Mountains. Mean precipitation for the study area was approximately 22.5–35.0 cm per annum (Omernik and Griffith 2014). The study area terrain types included elevated plateaus, sheer-walled canyons with intermittent lakes and ephemeral streams, and mountains of low-to-mid elevation with primarily steep slopes and ephemeral or perennial streams (Omernik and Griffith 2014). For more detailed information on geology, vegetation, wildlife, and land use practices, please refer to Spaan et al. (2021).

U.S. Route 95 runs north-south through the study area dividing the study area's populations into two metapopulations. The western metapopulation included the Blue Mountain (BSP), Trout Creek east

(TCE), Trout Creek south (TCS), and Trout Creek west (TCW) populations, all of which are mostly in Oregon (Fig. 3.1). The eastern metapopulation includes the populations in Nevada's Santa Rosa Mountains, i.e., the Calicos (CAL), Eight Mile (EML), Martin Creek (MCK), and Sawtooth (SAW), and the Bowden Hills (BHP), Rattlesnakes (RSP), Ten Mile (TMP), Three Forks (TFK), and the Upper Owyhee (UOP) populations in Oregon (Fig. 3.1). Although established with single translocations in the late 1980s and early 1990s, the three Trout Creek populations trace their lineage to Williams Lake, British Columbia (Table S3.1, Supporting Information). In addition, dispersing bighorn sheep from the Trout Creeks colonized Blue Mountain in the mid to late 1990s (pers. comm. S. Torland, ODFW). Comparatively, the eastern metapopulation's bighorn sheep populations have several different translocation sources, e.g., Kamloops, Penticton, and Williams Lake, BC, and were established in some cases by multiple translocation sources (Table S3.1, Supporting Information).

Capture and sampling

ODFW and NDOW captured, collared, and sampled adult male and female bighorn sheep across 13 populations in southeastern Oregon and northern Nevada between January 2016 and February 2018 (Fig. 3.1). Captures were conducted using a net gun fired from a helicopter, with individual bighorn sheep blindfolded and hobbled once captured (Krausman et al. 1985). The bighorn sheep were then brought to a nearby processing location to collect biological samples and fit with a GPS collar. In some instances, flight distances were prohibitive and captured sheep were processed at the capture site. Bighorn sheep age was determined at capture using tooth eruption patterns for individuals less than or equal to four years of age and horn annuli used for those individuals older than four years of age (Geist 1966). All female bighorn sheep included in this study (n = 79) were fit with Vertex Survey Globalstar collars (Vectronic Aerospace, Berlin, Germany). The majority of the male bighorn sheep (n = 41) were fit with Vertex Survey Globalstar collars with the rest (n = 5) fit with Telonics Globalstar collars (Telonics, Mesa, AZ, USA). All capture, handling, and disease testing were conducted by Oregon Department of Fisheries and Wildlife (ODFW) and Nevada Department of Wildlife (NDOW) according to the recommendations of (Foster 2004) and the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

Diagnostics

M. ovipneumoniae presence was determined using polymerase chain reaction (PCR) tests of nasal, bronchial, and tympanic bullae swabs from each captured bighorn sheep (Manlove et al. 2019). The PCR test has a diagnostic sensitivity of 100% and diagnostic specificity of 98.7% (Manlove et al. 2019). *M. ovipneumoniae* exposure was determined using a competitive enzyme-linked immunosorbent assay

(cELISA) to detect antibodies in serum (Ziegler et al. 2014). The cELISA tests has a diagnostic sensitivity of 88% and a diagnostic specificity of 99.3% (Johnson et al. 2022). All testing for *M. ovipneumoniae* was performed at the Washington Animal Disease Diagnostic Laboratory (WADDL).

Genetic sampling

We used a combination of blood samples (n = 125) and feces (n = 66) as sources for DNA samples. Whole blood (3 mL) provided by ODFW and NDOW from captured bighorn sheep was collected in EDTA tubes and spun at 4,000 × g for 10 min to separate the buffy coat. We extracted DNA from this material using a Qiagen DNeasy Blood and Tissue Kit (Qiagen Inc., Valencia, CA, USA). Fecal samples were collected opportunistically while conducting observations of bighorn sheep across the different populations, and were generally a week or less in age, as estimated from pellet color, odor, and surface condition. Fecal samples that were still moist after deposition were dried and then stored at room temperature. Fecal pellets were scraped to target dried epithelial cells on the surface of the pellet (Wehausen et al. 2004), and we extracted DNA from the scraped material using a modified version of the Aquagenomic Stool and Soil protocol (Multitarget Pharmaceuticals LLC, Colorado Springs, CO).

Genotyping, markers, individual identification, and marker

We used a suite of 16 microsatellite markers in three panels (Table S3.2) that had previously been used to investigate population connectivity and genetic variability in bighorn sheep (Epps et al. 2018, Creech et al. 2020, Spaan et al. 2021). Genotyping followed protocols outlined in Epps et al. (2018). Briefly, all samples were run in at least two (for blood) or three (for feces) independent PCR reactions to generate a consensus genotype for each individual at each locus. For blood samples, any discrepancy between the two replicates resulted in the sample being rerun at that panel, although consistency across replicates was very high. Because allelic dropout can be higher in fecal samples, for those samples a homozygous genotype was considered verified if the single allele was seen in all three replicates. A heterozygous genotype was considered to be verified if each allele was seen in at least two of the three replicates; any other discrepancies resulted in reruns. Other studies on bighorn (e.g., Epps et al. 2018) reported screening for recaptures using as few as 6 loci to achieve a desired probability of identity (PID; Waits et al. 2001) of <0.001 and a probability of identity for full siblings of <0.05. However, our initial genotyping demonstrated that we needed to genotype at all 16 loci to achieve those thresholds. We identified recaptured individuals using CERVUS (Kalinowski et al. 2007) by screening for individuals that matched at all 16 loci and removing them from the data set. We repeated this analysis using successively reduced numbers of matching loci and the presence of one to two mismatches (to account for missing data and genotyping error, respectively), until the matches that the program returned seemed unlikely due to

geographic location and/or the mismatches were not explainable by simple allelic dropout. Finally, we used GIMLET (Valière 2002) to calculate two types of error rates in our genotypes: allelic dropout, and the presence of false alleles.

Linkage disequilibrium, Hardy-Weinberg tests, and genetic diversity

We used GENEPOP Version 4.2 on the Web (Rousset 2008) to conduct the probability test for Hardy-Weinberg equilibrium (HWE) for each population by locus and then for each locus by population, as well as across populations for each locus and across loci for each population (Fisher 1948). We then used GENEPOP 4.0 Desktop to test for linkage disequilibrium across each pair of loci within each population, and each pair of loci across all populations, applying a sequential Bonferroni correction in both cases across all loci. We used the R package *diveRsity* (Keenan et al. 2013) to calculate population genetic diversity metrics including expected heterozygosity (H_E), observed heterozygosity (H_O), and allelic richness (A_R). We accounted for imbalanced sample sizes amongst populations using rarefaction.

To calculate individual genetic diversity, heterozygous alleles were allocated a value of one and homozygous alleles allocated a value of zero. In the case of missing loci, we assigned said loci the mean value for that specific loci from individuals within the same population. Finally, we averaged the scores across all 16 loci to generate individual genetic diversity scores.

Drivers of adult survival

We used a known-fate model to estimate adult survival (S) of female and male bighorn sheep using a Kaplan-Meier estimator (Kaplan and Meier 1958) with staggered entry (Pollock et al. 1989). We use a sequential model-building strategy consisting of three phases. First, we modeled temporal effects, including time as a constant, linear trend, monthly, seasonal, and annual, as factors with independent effects and a zero-centered random effect that varied by year, as well as the interaction of all temporal effects, except the cumulative effect with sex (Table 3.1). Second, we modeled age effects, including a linear trend age effect and a categorical age effect adapted from (Jorgenson et al. 1997). For the categorical age effect, individuals aged one to seven years were considered to be in their prime, and individuals older than seven were regarded as non-prime aged, plus variants of these models, including interaction with sex (Table 3.1). Lastly, we modeled the effects of sex, *M. ovipneumoniae* exposure, expected population genetic heterozygosity (H_E), individual genetic heterozygosity, and metapopulation (Table 3.1). We did not model the effect of *M. ovipneumoniae* infection due to inadequate sample size (n = 3 out of 125).

We used the Watanabe-Akaike information criterion (WAIC; (Watanabe 2010)) to select the most supported model structure. We considered the model with the smallest WAIC value and highest model

support weight (w), the most supported model. We used the relative change in WAIC (ΔWAIC) to evaluate the support for individual models relative to the top-ranked model.

Our model selection procedure did not support temporal variation in survival with monthly intervals. However, we were concerned that minor variations in monthly survival could propagate into significant differences in derived annual survival. So, we derived additional annual estimates from a variant of the top-ranking model that included a zero-centered random effect which allowed monthly survival to vary around mean monthly survival.

We conducted all analyses using R version 4.1.2 (R Core Team 2021). We used JAGS software version 4.3.0 (Plummer 2003) using R2jags package version 0.7-1 (Su and Yajima 2021) to fit models. For all models, we used an uninformative normally distributed prior for the intercept and slope parameters, where $\mu = 0$, and $\tau = 0.368$. For random effect models, we used a zero-centered random affect with a uniformed hyper prior ranging from 0 to 5 for precision. For model selection, each model was estimated with three independent chains of 10,000 iterations following a burn-in period of 5,000 iterations. We assessed model convergence by visual examination of trace plots and monitored the Brooks–Gelman–Rubin convergence diagnostic to make sure $\hat{R} < 1.01$ (Brooks and Gelman 1998). We described the posterior distributions for each parameter estimated by their mean and 95% credible interval. We assessed the magnitude of the effect based on the degree to which the 95% credible intervals of the estimate overlapped zero. We assessed model convergence by visual examination of trace plots and monitored the Brooks–Gelman–Rubin convergence diagnostic to make sure $\hat{R} < 1.01$ (Brooks and Gelman 1998).

Results

Diagnostics

The bighorn sheep included in the known fate model (79 females and 46 males) were captured between December 2015 and February 2018. Ten of the females and a single male were recaptured and retested during the study and neither *M. ovipneumoniae* infection nor exposure status changed between recaptures (Table S3.3). None of the female (n = 26) nor male (n = 23) bighorn sheep in populations west of U.S. Route 95, i.e., BSP, TCE, TCS, or TCW, had evidence of infection or exposure to *M. ovipneumoniae* (Fig. 3.1, Table S3.3). However, all of the bighorn sheep in populations east of U. S. Route 95, which include the four Santa Rosa metapopulation populations, as well as BHP, RSP, TMP, and UOP (Fig. 3.1), except TFK, had evidence of exposure to *M. ovipneumoniae* (Table S3.4). We were unable to determine *M. ovipneumoniae* exposure for the single TFK female bighorn sheep as we were unable to attain a blood sample (Table S3.4). The proportion of *M. ovipneumoniae* exposed adult females

in those eight populations included in the survival analysis varied from 0.60 in RSP to 1.00 in TMP ($\bar{x}$ = 0.78; Table S3.4). In the six populations where males were tested, the proportion of *M. ovipneumoniae*-exposed males varied from 0.00 in SAW and UOP, where only a single individual was sampled to 0.80 in RSP ($\bar{x}$ = 0.64 when excluding populations where a single individual was sampled; Table S3.4). Only three individuals tested PCR+ to *M. ovipneumoniae* infection across all 13 populations (Table S3.4): one female in EMP on two occasions in 2017 and 2018, one female in RSP in 2016, and an MCK male in 2018 (Table S3.4). Two individuals, a BHP female and an RSP male, yielded indeterminate PCR test results (Table S3.4), indicating that *M. ovipneumoniae* detection was indeterminate (Besser et al. 2019).

Population and individual genetic diversity

Population genetic diversity (H_E) across the 13 study populations ranged from 0.26 in BSP to 0.48 in EML ($\bar{x}$ = 0.37; Table S3.5). However, H_E was lower in all populations west of U. S. Route 95 ($\bar{x}$ = 0.30; range = 0.26–0.33) compared to the populations east of U. S. Route 95 ($\bar{x}$ = 0.41; range = 0.35–0.48) (Table S3.5). Individual heterozygosity for the bighorn sheep west of U. S. Route 95 ranged from 0.19 in the TCE and TCS to 0.63 in TCE and TCW ($\bar{x}$ = 0.33, $\tilde{x}$ = 0.31; Table S3.6). For bighorn sheep east of U.S. Route 95, individual heterozygosity ranged from 0.19 in RSP and TFK to 0.81 in RSP ($\bar{x}$ = 0.47, $\tilde{x}$ = 0.44; Table S3.6).

Drivers of adult survival

We monitored 125 GPS-collared bighorn sheep (79 females and 46 males) for a period of five years, 2016–2020. Mean age at capture was 4.8 ± 1.8 (SD) years of age with a range of 1 to 10 for females and 4.3 ± 2.2 (SD) years of age with a range of 2 to 11 for males. Over the course of the study we experienced a high collar failure rate, most notably with the collars fit to males. Excluding the male mortalities, 45% (n = 15) of the GPS collars fit to males failed in the first year of deployment, and an additional 21% (n = 7) failed in the second year. Excluding the female mortalities, 13% (n = 8) of the GPS collars fit to females failed in the first year of deployment, and an additional 18% (n = 11) failed in the second year.

During the study 30 GPS-collared individuals (17 females and 13 males) died. Mean mortality age was 6.9 years of age (range: 4–12) for females and 6.5 years of age (range: 3–10) for males. For the 40% of the mortalities to which we could assign cause-specific mortality, mountain lions accounted for 42% (n = 5), injury for 17% (n = 2), blue tongue for 8% (n = 1), and hunters for 33% (n = 4). During the course of the study ODFW issued six tags per year for the Whitehorse unit, which encompasses the Oregon study populations, and NDOW issued two to five tags per year for the Santa Rosa populations

over the same period. All four individuals taken by hunters were adult males with a mean age of 8.5 years of age (range: 5–10).

Our first step of the sequential modeling revealed no evidence of a temporal effect (Table 3.2). The second step of the sequential modeling revealed weak evidence of an age effect, but support was less than the null model (Table 3.2). In the last step of the sequential modeling we found a small ΔWAIC of 0.13 between individual heterozygosity and population genetic diversity (H_E), so we proceeded with H_E, given that genetic diversity is managed at the population level for wild populations (e.g., Olson et al. 2012). The last step of the sequential modeling revealed several competing models within 2 WAIC of the top model (Table 3.2). However, we used the top model in order to evaluate our hypotheses. The top model included sex, H_E, and *M. ovipneumoniae* exposure (Table 3.2). We did not detect a metapopulation effect on survival. All models converged in all cases.

Model selection suggested that individuals in more heterozygous populations had higher survival, with an ~83% probability of an increase in survival across the potential measure of heterozygosity based on the posterior distribution of the coefficient estimate (Table 3.3, Fig. 3.2). Likewise, adult females were 1.86 (95% CI [0.90–3.80]) times more likely to survive than male bighorn sheep (Table 3.3). However, the credible intervals for both H_E and sex overlapped zero (Table 3.3). The credible interval for *M. ovipneumoniae* exposure did not overlap zero, and adult bighorn sheep that were unexposed to *M. ovipneumoniae* were 2.30 (95% CI [1.07–4.89]) times more likely to survive during the 5-year study period than those that were exposed (Table 3.3).

For female bighorn sheep, derived annual survival of individuals unexposed to *M. ovipneumoniae* was slightly higher (0.926; 95% CI [0.875-0.963]) than exposed individuals (0.840; 95% CI [0.753-0.910]; Fig.3.3). Likewise, for male bighorn sheep, derived mean annual survival of unexposed individuals was slightly higher (0.868; 95% CI [0.783–0.932]) compared to exposed individuals (0.723; 95% CI [0.538–0.865]; Fig. 3.3).

The lack of a temporal effect was likely due to minimal variation in monthly survival of this long-lived species. Therefore, we fitted a random temporal effect to the top model to propagate annual survival estimates (Table S3.7). The temporal random effect model indicated that the lowest year of annual survival for female and male bighorn sheep was observed in 2019 and the highest in 2016 (Fig. 3.3, Table S3.8).

Discussion

We found that the survival of adult bighorn sheep was negatively affected by individual-level exposure to *M. ovipneumoniae.* We could not test the effect of active *M. ovipneumoniae* infection on survival due to the low prevalence (n = 3/125) of actively infected individuals, but two of the three such

individuals, both females, died. Moreover, we did not detect a direct temporal effect of month, season, or year on survival, and neither age (categorical or continuous) nor metapopulation identity influenced survival. Although the effects were not unequivocal, our analyses also suggested that low genetic diversity was associated with lower survival, and that survival was higher for adult females than for adult males.

Our derived annual survival estimates were similar to those observed in other systems. For example, our derived annual survival of 0.926 (95% CI [0.875-0.963]) for adult female bighorn sheep unexposed to *M. ovipneumoniae* was similar to values reported for unexposed prime-aged female Rocky Mountain bighorn sheep across their range (Jorgenson et al. 1997, Proffitt et al. 2021), PCR- female desert bighorn sheep in the Mojave (Dekelaita et al. 2020), and females in most populations of Sierra Nevada bighorn sheep (Conner et al. 2018). Interestingly, our derived survival estimates for *M. ovipneumoniae*-exposed adult female bighorn sheep (0.840; 95% CI [0.753-0.910]) too were similar to those of older or non-prime aged adult female Rocky Mountain bighorn sheep in temperate regions (Jorgenson et al. 1997, Proffitt et al. 2021). Likewise, our derived annual survival for male bighorn sheep unexposed to *M. ovipneumoniae* (0.868; 95% CI [0.783–0.932]) was similar to values reported for prime-aged Rocky Mountain bighorn sheep in Alberta, Canada (Jorgenson et al. 1997) and slightly lower to values reported for male Sierra Nevada bighorn sheep (Conner et al. 2018). Again, our derived annual survival estimates of bighorn sheep exposed to *M. ovipneumoniae* (0.723; 95% CI [0.538–0.865]) were somewhat similar to those of older or non-primed aged male Rocky Mountain bighorn sheep annual survival in Alberta, Canada (Jorgenson et al. 1997).

To our knowledge, this study is the first to report a negative association between adult survival and individual-level exposure to *M. ovipneumoniae*. We consider several possible explanations for this effect. First, although Dekelaita et al. (2020) found no direct effect of *M. ovipneumoniae* exposure on survival, animals found to be infected with *M. ovipneumoniae* at capture had lower survival over the next 3.5 years. Dekelaita et al. (2020) suggested that chronic infection could explain those mortalities, although of the ten mortalities that were PCR tested postmortem, only 2 (20%) were infected at the time of death. However, negative tests may have been unreliable due to carcass degradation. One postmortem in that study found no active infection but observed acute active pneumonia, suggesting that clearing *M. ovipneumoniae* could still have resulted in lung damage. We hypothesize that long-term lung damage from *M. ovipneumoniae* infection, even if the infection clears, could negatively influence survival. We also note that the *M. ovipneumoniae* outbreak described by Dekelaita et al. (2020) appeared to be a new outbreak of a novel strain, leading to much higher rates of infection observed at capture than observed in our study (Shirkey et al. 2021). Secondly, we note that the adverse effect of *M. ovipneumoniae*-exposure on survival might be explained by the cost of individuals mounting an antibody immune response to the

pathogen. Tavalire et al. (2018) observed this immunological pattern in African buffalo (*Syncerus caffer*), where individuals with an "infection resistance" immune phenotype mounted an innate immune response to bovine tuberculosis (*Mycobacterium bovis*), resulting in fitness costs. The low prevalence of *M. ovipneumoniae*-infected individuals in exposed populations (<5%) within this system may indicate that the pathogen is in the process of fading out. However, infected individuals may maintain the pathogen within the system as chronic carriers by shedding the pathogen (Cassirer et al. 2017, Plowright et al. 2017). Therefore, test-and-removal of *M. ovipneumoniae*-infected individuals, where pathogen prevalence is low, may help facilitate pathogen fadeout (Cassirer et al. 2018). Additionally, Almberg et al. (2022) modeled several management actions suggesting that test-and-remove, depopulation-and-reintroduction, and range expansion could help bighorn sheep population recovery post-*M. ovipneumoniae* epidemic. Our study suggests that the benefits of clearing populations of this pathogen could extend to increased adult survival as well as much higher lamb recruitment.

Another pathogen detected in an RSP bighorn sheep mortality was bluetongue (*Orbivirus* spp.), transmitted by midges (*Culicoides spp.*) (Saminathan et al. 2020). Bluetongue has been identified as a mortality source in desert bighorn sheep in California (Blaisdell 1975) and Texas (Robinson et al. 1967, Daily et al. 2022). Jessup (1985) suggested that bighorn sheep exposure to bluetongue may occur in areas with abundant artificial and natural water at lower elevations. Interestingly, five bighorn sheep from which we could not attain samples for bluetongue testing, along with the confirmed bluetongue mortality, died within a ~four-week window (September/October 2018) in BHP and RSP. These populations are two of the lower elevation populations in the study. All six bighorn sheep mortalities were located within a ~7 km radius and in a creek or canyon bottom. Saminathan et al. (2020) state that clinical signs of the bluetongue include fever, respiratory distress, lameness, and muscular necrosis resulting in death. We surmise that bluetongue may have contributed to the mortality of these bighorn sheep and contributed to the lack of a detected age effect on survival as all individuals were prime-aged (Jorgenson et al. 1997) at death ($\bar{x}$ = 5.3 years of age; range = 3–7).

We observed a marginal positive relationship between population genetic diversity and adult bighorn sheep survival. Generally, population genetic diversity within the system was low, with H_E for study populations ranging from 0.26–0.48 (Table S3.5). However, the genetic diversity of populations west of U.S. Route 95 was notably lower, with H_E = 0.26–0.33 (Table S3.5). The genetic diversity values are extremely low compared to those observed in Sierra Nevada bighorn sheep (Johnson et al. 2011) and desert bighorn sheep in the Mojave (Epps et al. 2018), both of which used neutral microsatellite loci to assess genetic diversity. These low genetic diversity estimates likely point to a founder effect from these translocations, as Olson et al. (2013) reported noticeably higher genetic diversity for the source of these populations (H_E = 0.42). Comparatively, the populations east of U.S. Route 95 had higher genetic

diversity with H_E = 0.35–0.48 (Table S3.5). The translocation history for the populations east of U.S. Route 95 is variable, with some having single and others multiple translocation sources (Table S3.1). However, the single source populations appear to have benefitted from gene flow from males moving between the Santa Rosa populations in Nevada and Oregon (Chapter 2). Although we could not test interactions between *M. ovipneumoniae* and genetic diversity, we noted that two of the PCR+ individuals had very low individual genetic diversity (≤ 0.25). We further note that the populations with lowest genetic diversity were unexposed to *M. ovipneumoniae* during the course of this study, meaning that they did not suffer from one of the leading negative influences on adult survival that we observed, which may likewise have made it more difficult to detect this effect.

Our study demonstrated that *M. ovipneumoniae*-exposed bighorn sheep had lower survival compared to unexposed individuals. More generally, California bighorn sheep in the northern Basin and Range continue to be negatively impacted by the sustained presence of *M. ovipneumoniae* due to chronic shedders and birth pulses (Spaan et al. 2021). When prevalence of *M. ovipneumoniae* infected bighorn sheep is low, targeted removals of infected individuals can be an effective management tool to improve juvenile survival (Garwood et al. 2020). Such management actions would not only benefit future juvenile survival but also reduce the potential for infection of older individuals unexposed to *M. ovipneumoniae* and facilitate disease fade-out (Almberg et al. 2022), in addition to potentially increasing adult survival. Management should also consider addressing the low genetic diversity, most notably for the populations of bighorn sheep west of U.S. Route 95. Although we did not find concrete evidence of a bluetongue effect, this could have been an important mortality event and should warrant monitoring. While population augmentation could improve genetic diversity (Hogg et al. 2006, Poirier et al. 2019), disease management must also be considered, given that translocations may increase the risk of disease transmission.

Conclusions

We found that adult bighorn sheep exposed to *M. ovipneumoniae* had a lower probability of survival. No temporal, age, or metapopulation effects on survival were detected. Due to the inadequate number of actively infected individuals, we could not assess the relationship between *M. ovipneumoniae* infection and survival. However, two of the three *M. ovipneumoniae* infected individuals, both female, died during the study. The negative relationship between *M. ovipneumoniae* exposure and survival may be due to long-term damage from infection, or possibly may be associated with immunological phenotype, whereby individuals mounting an antibody response to infection do so at a cost to survival. Targeted removal of chronic carriers of *M. ovipneumoniae* has previously been suggested for the populations east of U.S. Route 95 as a potential management action for bighorn sheep populations to

improve juvenile survival. Our study suggests these actions would also benefit unexposed individuals of all ages, improving adult survival. Lastly, although the link we observed between lower survival and lower genetic diversity was not conclusive, populations west of U.S. Route 95 might benefit from population augmentation to enhance genetic diversity. However, the risk of the potential introduction of novel *M. ovipneumoniae* strains and increased transmission due to increased population density and movements of translocated bighorn sheep post-release should be considered (Werdel et al. 2021).

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Tables

Table 3.1 Description of variables considered in known-fate models predicting survival (*S*) of adult bighorn sheep (*Ovis canadensis*) in thirteen southeastern Oregon and northern Nevada populations from 2016–2020. The reference level is provided for binary factors.

Measure	**Category**	**Measure type**	**Statistical measure (range)**
Constant		Intercept only model	
Time (cumulative month)	Temporal	Time-varying (1–5×12)	Factor with independent effect
Month	Temporal	Monthly time	Factor with independent effect
Season	Temporal	Seasonal – summer (April–September) & winter (October–March)	Factor with independent effect
Year	Temporal	2016–2020	Factor with independent effect
tRE	Temporal	Temporal effect – 2016–2020 treated as a zero-centered normally distributed random effect	Random intercept
Sex	Intrinsic	Male or female	Binary factors – female
$Age_{CONTINUOUS}$	Intrinsic	Age (years) – treated as a continuous variable	Continuous (values: 1–12)
$Age_{CATEGORICAL}$*	Intrinsic	Age (years) – prime: 1–7, and non-prime >7	Binary factors – prime
H_E (Expected heterozygosity)	Genetic	Measure of population genetic diversity	Continuous (values: 0–1)
Individual heterozygosity	Genetic	Measure of individual genetic diversity	Continuous (values: 0–1)
M. ovipneumoniae exposure	Bacteria	*M. ovipneumoniae* exposure status (+/-), as determined by cELISA	Binary factors – unexposed
M. ovipneumoniae infection	Bacteria	*M. ovipneumoniae* infection status (+/-), as determined by PCR	Binary factors – uninfected
Metapopulation	Spatial	Metapopulations separated by U.S. Route 95	Binary factors – eastern

*Using age structure described by (Jorgenson et al. 1997)

Table 3.2 Model selection results for known fate models predicting monthly survival of adult bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada for the period 2016–2020. Initially, we assessed temporal patterns in the data using month, cumulative month, season, year, and with the interaction of sex. Secondarily, we moved forward with the top temporal model, the null model, and incorporated age effects. Finally, we moved forward with the top model, the null model, and included sex, expected heterozygosity (H_E), individual heterozygosity, *Mycoplasma ovipneumoniae* exposure (*M. ovi* exposure), and metapopulation.

Phase	Model	*K*	WAIC	ΔWAIC	*w*
1	constant	1	334.80	0.00	0.717
	season	2	337.60	2.80	0.177
	sex × season	4	340.03	5.23	0.053
	tRE	2	341.74	6.94	0.022
	month	12	342.42	7.61	0.016
	year	5	342.97	8.17	0.012
	sex × tRE	11	345.90	11.10	0.003
	sex × year	10	350.56	15.76	0.000
	sex × month	24	357.52	22.72	0.000
	cumulative month	60	417.16	82.36	0.000
2	constant	1	334.87	0.00	0.336
	$age_{CONTINUOUS}$	2	335.46	0.59	0.250
	$age_{CATEGORICAL}$	2	336.33	1.46	0.162
	sex × $age_{CATEGORICAL}$	3	336.62	1.75	0.140
	sex × $age_{CONTINUOUS}$	3	337.07	2.20	0.112
3	sex + H_E + *M. ovi* exposure	4	333.11	0.00	0.212
	sex + *M. ovi* exposure	3	333.17	0.06	0.205
	H_E + *M. ovi* exposure	3	334.01	0.90	0.135
	M. ovi exposure	2	334.42	1.31	0.110
	constant	1	334.87	1.76	0.088
	sex	2	335.31	2.20	0.070
	individual heterozygosity	2	335.68	2.57	0.059
	H_E	2	335.81	2.70	0.055
	sex + H_E	3	336.51	3.41	0.039
	metapopulation	2	337.12	4.01	0.029

Table 3.3 The output from the top known fate model, which included sex, population heterozygosity (H_E), and *M. ovipneumoniae* exposure, predicting adult survival of bighorn sheep (*Ovis canadensis*) in populations (n = 13) across southeastern Oregon and northern Nevada for the period 2016–2020. Included are the direction of effect on survival, the odds-ratios, intercept and coefficient estimates and associated 95% credible intervals.

Covariate	**Effect on survival**	**Odds-ratio**	**Estimate**	**95% CI**	
				Lower	**Upper**
Intercept			4.41	3.30	5.52
Sex	↓	1.86	-0.62	-1.33	0.11
H_E	↑	6.14	1.81	-0.94	4.58
M. ovipneumoniae exposure	↓	2.30	-0.83	-1.59	-0.07

Figures

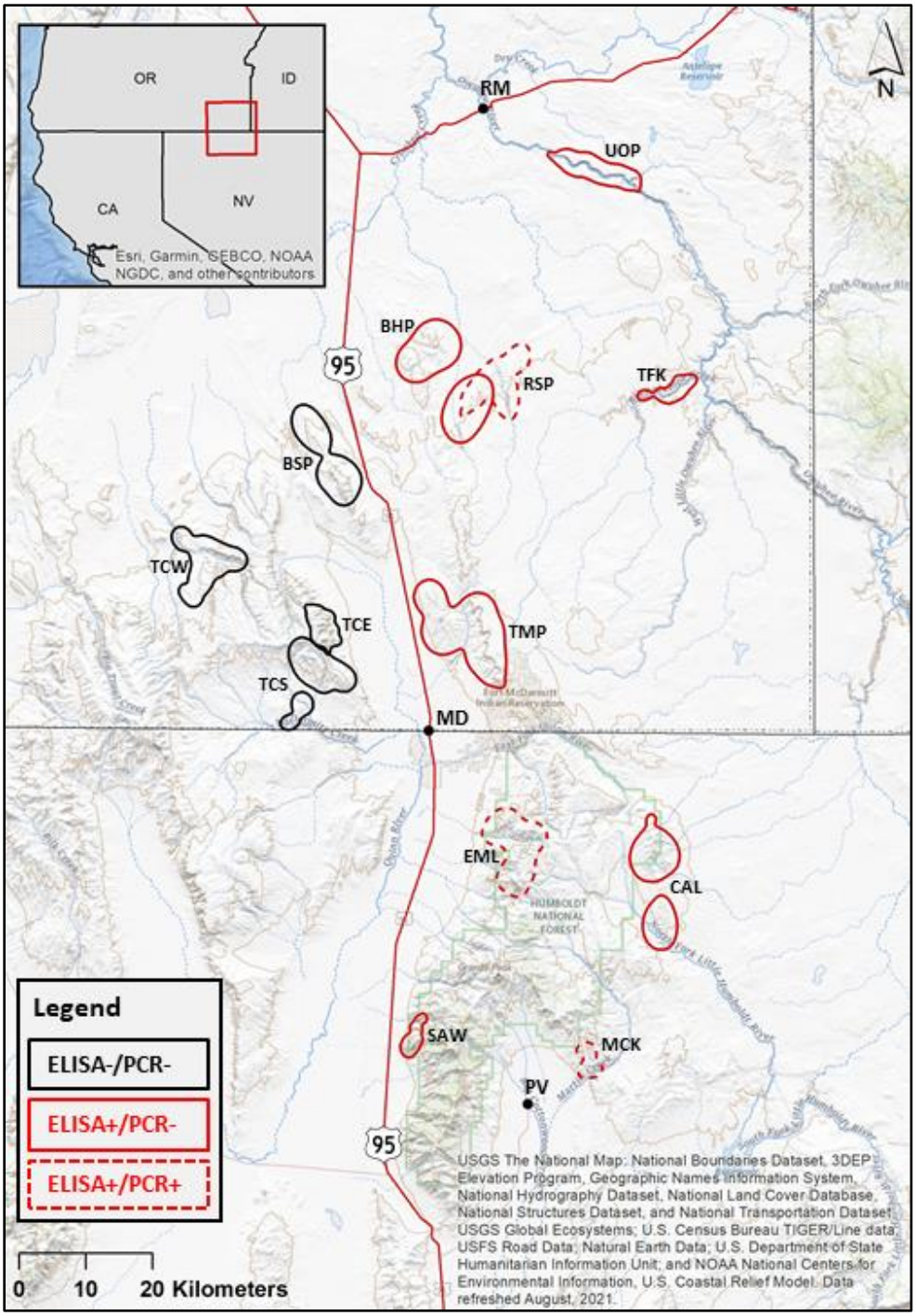

Figure 3.1 Utilization distributions (95%) of thirteen adult female bighorn sheep (*Ovis canadensis*) populations in southeastern Oregon and northern Nevada, derived from spatial data collected between 2016 and 2020 adapted from Spaan et al. (2021). As indicated by black polygons, populations west of U. S. Route 95 had no bighorn sheep test ELISA or PCR+ for *M. ovipneumoniae*. All populations east of U. S. Route 95, characterized by red polygons, showed either bighorn sheep populations with exposures (solid, red line) or had exposures and active *M. ovipneumoniae* infections (red dash line).

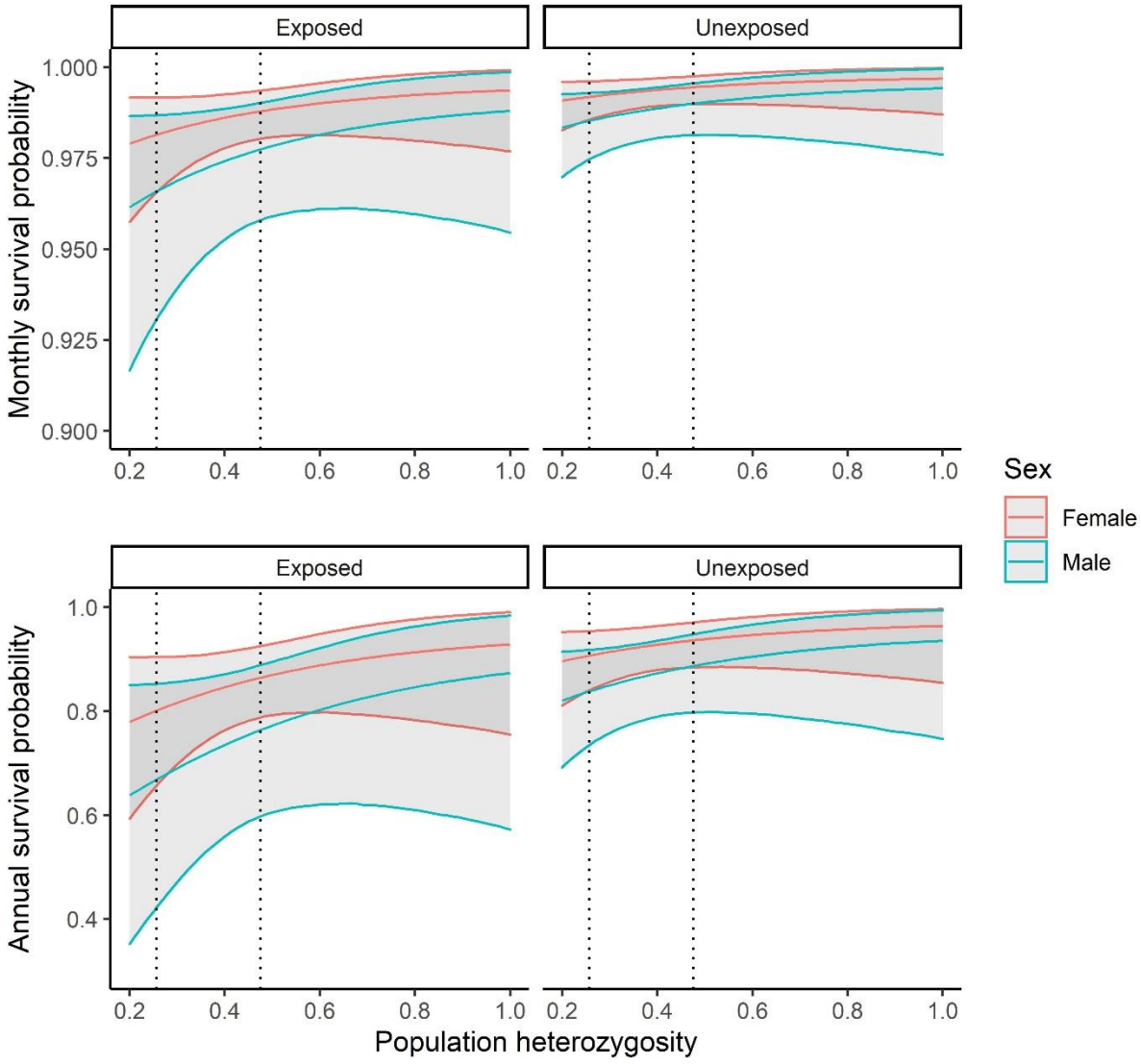

Figure 3.2 Monthly estimated and derived annual survival probabilities for adult male and female bighorn sheep (*Ovis canadensis*) as a function of population heterozygosity (H_E) while accounting for *Mycoplasma ovipneumoniae* exposure status. Predictions are from a known-fate model. The vertical dotted lines at 0.26 and 0.48 represent the minimum and maximum population genetic diversity of the bighorn sheep study populations. Shaded areas indicate 95% credible bands.

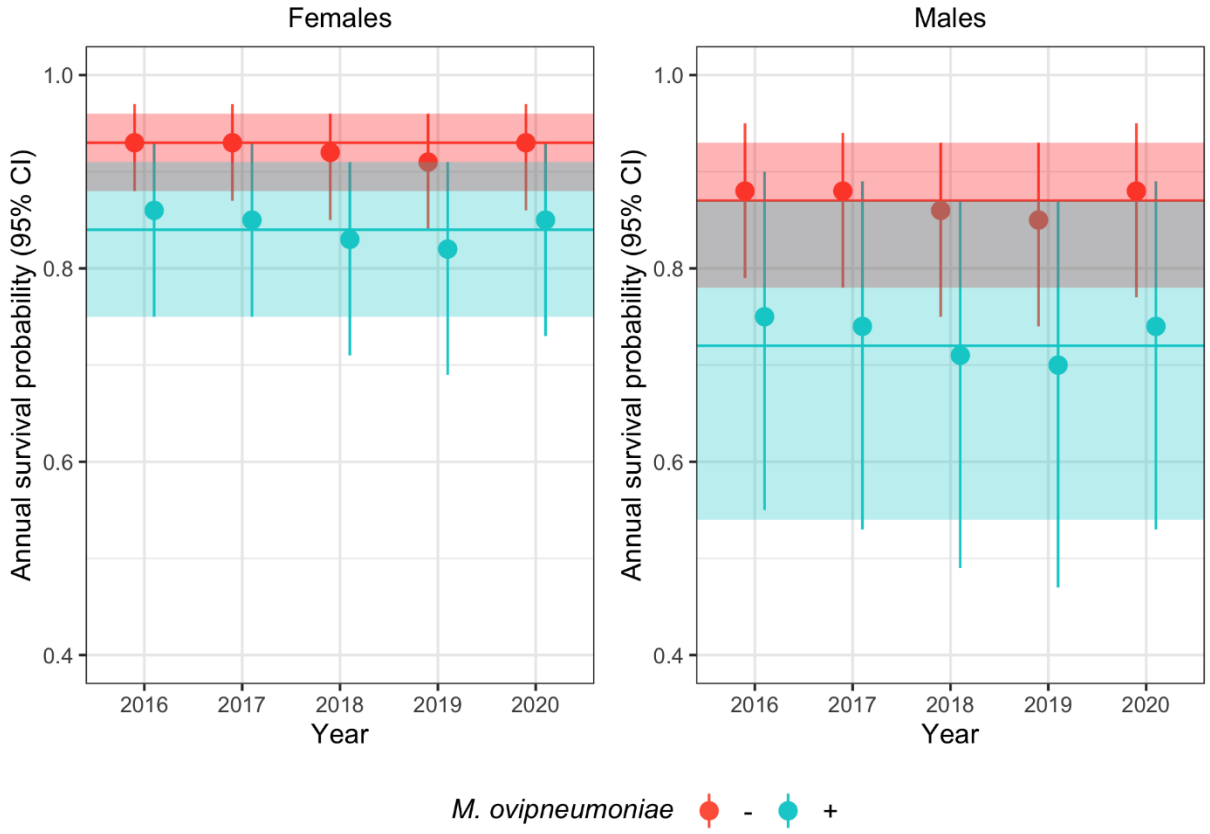

Figure 3.3 Derived annual (2016–2020) survival probabilities for *Mycoplasma ovipneumoniae*-exposed (+) and unexposed (-), female and male bighorn sheep (*Ovis canadensis*) generated using the most supported known-fate model structure, which included effects for sex, population genetic diversity, and *M. ovipneumoniae*-exposure, and a random intercept for year. The solid horizontal lines and shaded areas indicate the derived annual survival probability estimate and 95% credible intervals of *M. ovipneumoniae*-exposed and unexposed female and male bighorn sheep for the entire study period.

Supplementary Tables

Table S3.1 Translocation histories of bighorn sheep (*Ovis canadensis*) populations included in this study. Details include the population code (Pop.) where the bighorn sheep were established or translocated to, translocation type (Trans_type), when the translocation took place (Year), the number of individuals (# ind.) translocated, the source population (Source pop.), the source state or province (S-State) population, the destination population (Destination pop.), and the destination state (D-State).

Pop.	Trans.-type	Year	# individuals	Source pop.	S-State	Destination pop.	D-State
Bowden Hills	Colonization	unknown	?	Rattlesnake	OR	Bowden Hills	OR
Blue Mountain	Colonization	~1990s	?	Trout Ck.	OR	Blue Mountain	OR
Calicos	Import	1985	20	Williams Lake	BC	Pine Forest	NV
	Import	1988	18	Williams Lake	BC	Pine Forest	NV
	In jurisdiction	2011	25	Pine Forest	NV	Calico Mtn.	NV
Eight Mile	Import	1978	12	Penticton	BC	Eight Mile	NV
	In jurisdiction	2014	3	Pine Forest	NV	Three Mile Ck.	NV
Martin Creek*	Import	1984	13	Hart Mtn.	OR	Jackson Mtn.	NV
	Import	1985	20	Williams Lake	BC	Pine Forest	NV
	Import	1986	2	E fork of Owyhee Riv.	ID	Jackson Mtn.	NV
	Import	1987	15	Lower Owyhee	OR	Jackson Mtn.	NV
	Import	1988	18	Williams Lake	BC	Pine Forest	NV
	Import	1989	18	Kamloops	BC	High Rock/Calicos	NV
	In jurisdiction	1998	12	Jackson Mtn.	NV	Hinkey	NV
	In jurisdiction	1999	12	High Rock/Calicos	NV	Pine Forest	NV
	In jurisdiction	2006	21	Montana Mts.	NV	Martin Ck.	NV
	In jurisdiction	2011	27	Pine Forest	NV	Martin Ck.	NV

Rattlesnake	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1992	19	Hart Mtn.	OR	Rattlesnake Ck.	OR
Sawtooth	Import	1989	20	Penticton	BC	Sawtooth	NV
Trout Creeks – east	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1987	27	Hart Mtn.	OR	Trout Creek Mtn.	OR
Trout Creeks – south	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1990	14	Hart Mtn.	OR	Trout Creek Mtn.	OR
Trout Creeks – west	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1990	19	Hart Mtn.	OR	Trout Creek Mtn.	OR
Ten Mile	Import	1954	20	Williams Lake	BC	Hart Mtn.	OR
	In jurisdiction	1960	4	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1961	7	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1989	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1992	15	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	18	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	15	Steens Mtn.	OR	Ten Mile Rim	OR
Upper Owyhee*****	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1960	4	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1961	7	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1965	17	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1983	21	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1983	14	Hart Mtn.	OR	Upper Owyhee	OR
	In jurisdiction	1987	15	Hart Mtn.	OR	Lower Owyhee	OR

In jurisdiction	1987	16	Hart Mtn.	OR	Lower Owyhee	OR
In jurisdiction	1989	17	Hart Mtn.	OR	Steens Mtn.	OR
In jurisdiction	1992	15	Hart Mtn.	OR	Steens Mtn.	OR
In jurisdiction	1993	17	Hart Mtn.	OR	Steens Mtn.	OR
In jurisdiction	1993	18	Hart Mtn.	OR	Steens Mtn.	OR
In jurisdiction	1993	36	Steens Mtn.	OR	Upper Owyhee	OR
In jurisdiction	1994	21	Lower Owyhee	OR	Upper Owyhee	OR
In jurisdiction	1995	17	Hart Mtn.	OR	Upper Owyhee	OR
In jurisdiction	2007	21	Philippi Canyon	OR	Upper Owyhee	OR

*****Indicates incomplete history

Table S3.2 Microsatellite loci used for analysis of bighorn sheep (*Ovis canadensis*) population genetic diversity in southeastern Oregon and Nevada, with allele sizes ranges observed in this study, fluorescent dye labels used, primer concentrations, and pre-PCR multiplex combination employed.

Locus	Reference	Allele size (bp)	Dye Label	Primer Concentration (µM)	Panel
AE129	Penty et al., 1993	166–177	Vic	0.25	1
AE16	Penty et al., 1993	84–100	Fam	0.20	3
BL4	Smith et al., 1997	158–162	Ned	0.30	2
FCB11	Buchanan & Crawford, 1993	125–131	Vic	0.20	3
FCB193	Buchanan & Crawford, 1993	105–119	Pet	0.25	1
FCB266	Buchanan & Crawford, 1993	89–101	Vic	0.20	3
FCB304	Buchanan & Crawford, 1993	142–150	Pet	0.20	3
HH62	Ede et al., 1994	102–130	Fam	0.15	1
JMP29	Crawford et al., 1995	121–133	Ned	0.20	3
MAF33	Buchanan & Crawford, 1992b	122–126	Vic	0.25	1
MAF36	Swarbrick et al., 1991	87–99	Vic	0.15	2
MAF48	Buchanan, Swarbrick & Crawford, 1991	122–126	Ned	0.20	1
MAF65	Buchanan, Swarbrick & Crawford, 1992	118–138	Fam	0.20	2
MAF209	Buchanan & Crawford, 1992a	110–122	Pet	0.20	2
TCRBV62	Crawford et al., 1995	171–175	Fam	0.25	3
TGLA387	Georges & Massey 1992	143–151	Pet	0.35	1

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Table S3.3 Breakdown of *Mycoplasma ovipneumoniae* test results for all female (♀) and male (♂) bighorn sheep (*Ovis canadensis*) west and east of U. S. Route 95 included in the known-fate analyses. All individuals were captured between 2016 and 2018 in thirteen populations across southeastern Oregon and northern Nevada. Bighorn sheep were tested via PCR for active *M. ovipneumoniae* infections and via cELISA for previous exposure. + indicates positive cases; - indicates negative cases; "ind." indicates indeterminate; "unk." indicates individuals for which there were no samples, and "recaptures" indicates recaptured individuals.

						***M. ovipneumoniae* status**							
						PCR				**cELISA**			
MP	**Population**	**Year**	**n**	**sex**	**recap**	**+**	**-**	**ind.**	**unk.**	**+**	**-**	**ind.**	**unk.**
West	Blue Mountain	2016	2	♀	-	0	2	0	0	0	2	0	0
	Blue Mountain	2017	2	♀	-	0	2	0	0	0	2	0	0
	Blue Mountain	2016	1	♂	-	0	1	0	0	0	1	0	0
	Blue Mountain	2017	1	♂	-	0	1	0	0	0	1	0	0
	Blue Mountain	2018	2	♂	-	0	2	0	0	0	2	0	0
	Trout Creek east	2016	11	♀	-	0	11	0	0	0	10	0	1
	Trout Creek east	2017	2	♀	-	0	2	0	0	0	2	0	0
	Trout Creek east	2018	1	♀	-	0	1	0	0	0	1	0	0
	Trout Creek east	2016	5	♂	-	0	5	0	0	0	5	0	0
	Trout Creek east	2017	1	♂	-	0	0	0	1	0	1	0	0
	Trout Creek east	2018	3	♂	-	0	3	0	0	0	3	0	0
	Trout Creek south	2016	2	♀	-	0	2	0	0	0	2	0	0
	Trout Creek south	2017	1	♀	-	0	1	0	0	0	1	0	0
	Trout Creek south	2018	1	♀	-	0	1	0	0	0	1	0	0
	Trout Creek south	2016	2	♂	-	0	2	0	0	0	2	0	0
	Trout Creek south	2017	1	♂	-	0	1	0	0	0	1	0	0
	Trout Creek south	2018	2	♂	-	0	2	0	0	0	2	0	0
	Trout Creek west	2016	2	♀	-	0	2	0	0	0	2	0	0
	Trout Creek west	2017	1	♀	-	0	1	0	0	0	1	0	0
	Trout Creek west	2018	1	♀	-	0	1	0	0	0	1	0	0
	Trout Creek west	2016	2	♂	-	0	2	0	0	0	2	0	0

	Trout Creek west	2017	1	♂	-	0	0	0	1	0	1	0	0
	Trout Creek west	2018	2	♂	-	0	2	0	0	0	2	0	0
N			49			0	47	0	2	0	48	0	1
East	Bowden Hills	2018	3	♀	-	0	2	1	0	3	0	0	0
	Calicos	2017	1	♀	-	0	1	0	0	0	0	0	1
	Calicos	2018	4	♀	1	0	4	0	0	3	1	0	0
	Calicos	2017	1	♂	-	0	1	0	0	0	0	0	1
	Eight Mile	2015	2	♀	-	0	2	0	0	2	0	0	0
	Eight Mile	2017	4	♀	-	1	3	0	0	0	0	0	4
	Eight Mile	2018	5	♀	3	1	4	0	0	3	2	0	0
	Eight Mile	2015	1	♂	-	0	1	0	0	0	0	1	0
	Eight Mile	2018	1	♂	-	0	1	0	0	0	1	0	0
	Martin Creek	2017	4	♀	-	0	4	0	0	0	0	0	4
	Martin Creek	2018	5	♀	3	0	5	0	0	4	1	0	0
	Martin Creek	2018	2	♂	-	1	1	0	0	2	0	0	0
	Rattlesnake	2016	9	♀	-	1	8	0	0	5	1	3	0
	Rattlesnake	2017	11	♀	-	0	11	0	0	7	1	3	0
	Rattlesnake	2016	5	♂	-	0	5	0	0	5	0	0	0
	Rattlesnake	2017	2	♂	-	0	2	0	0	1	1	0	0
	Rattlesnake	2018	3	♂	-	0	2	1	0	2	1	0	0
	Sawtooth	2017	3	♀	-	0	3	0	0	0	0	0	3
	Sawtooth	2018	3	♀	3	0	3	0	0	2	1	0	0
	Sawtooth	2017	1	♂	-	0	1	0	0	0	0	0	1
	Three Forks	2016	1	♀	-	0	1	0	0	0	0	0	1
	Ten Mile	2016	3	♀	-	0	3	0	0	3	0	0	0
	Ten Mile	2017	1	♀	-	0	1	0	0	1	0	0	0
	Ten Mile	2016	2	♂	-	0	2	0	0	2	0	0	0
	Ten Mile	2017	2	♂	-	0	2	0	0	1	1	0	0
	Ten Mile	2018	2	♂	1	0	1	0	1	1	1	0	0
	Upper Owyhee	2016	4	♀	-	0	4	0	0	2	1	0	1
	Upper Owyhee	2016	2	♂	-	0	1	0	1	0	1	0	1
N			87		11	4	79	2	2	49	14	7	17

Table S3.4 Proportion of *Mycoplasma ovipneumoniae* infected (positive (+), negative (-), indeterminate, and unknown), and exposed (exposed, indeterminate, unexposed, and unknown), female (♀) and male (♂) bighorn sheep (*Ovis canadensis*), as determined by cELISA and PCR for populations (*n* = 13) in southeastern Oregon and northern Nevada. MP = metapopulation, population, and *n* = number of individuals tested by population and sex between 2016 and 2018.

			Pop.	***M. ovipneumoniae* prevalence**				***M. ovipneumoniae* exposure**			
MP	**Population**	**sex**	***n***	***n***	**+**	**Indeterminate**	**-**	***n***	**Exposed**	**Indeterminate**	**Unexposed**
West	Blue Mountain	♀	16	4	0.00	0.00	1.00	4	0.00	0.00	1.00
	Blue Mountain	♂	9	4	0.00	0.00	1.00	4	0.00	0.00	1.00
	Trout Creeks east	♀	30	14	0.00	0.00	1.00	14	0.00	0.07	0.93
	Trout Creeks east	♂	15	9	0.00	0.11	0.89	9	0.00	0.00	1.00
	Trout Creeks south	♀	20	4	0.00	0.00	1.00	4	0.00	0.00	1.00
	Trout Creeks south	♂	10	5	0.00	0.00	1.00	5	0.00	0.00	1.00
	Trout Creeks west	♀	40	4	0.00	0.00	1.00	4	0.00	0.00	1.00
	Trout Creeks west	♂	20	5	0.00	0.20	0.80	5	0.00	0.00	1.00
East	Bowden Hills	♀	14	3	0.00	0.33	0.67	3	1.00	0.00	0.00
	Calicos	♀	35	4	0.00	0.00	1.00	4	0.75	0.00	0.25
	Calicos	♂	10	1	0.00	0.00	1.00	0	-	-	-
	Eight Mile	♀	30	7	0.14	0.00	0.86	7	0.71	0.00	0.29
	Eight Mile	♂	5	2	0.00	0.00	1.00	2	0.50	0.50	0.00
	Martin Creek	♀	11	6	0.00	0.00	1.00	5	0.80	0.20	0.00
	Martin Creek	♂	5	2	0.50	0.00	0.50	2	0.50	0.50	0.00
	Rattlesnake	♀	45	20	0.05	0.95	0.00	20	0.60	0.30	0.10
	Rattlesnake	♂	20	10	0.00	0.00	1.00	10	0.80	0.00	0.20
	Sawtooth	♀	12	3	0.00	0.00	1.00	3	0.67	0.00	0.33

Sawtooth	♂	3	1	0.00	0.00	1.00	1	0.00	0.00	1.00
Three Forks	♀	10	1	0.00	0.00	1.00	0	-	-	-
Ten Mile	♀	20	4	0.00	0.00	1.00	4	1.00	0.00	0.00
Ten Mile	♂	10	4	0.00	0.00	1.00	4	0.75	0.00	0.25
Upper Owyhee	♀	40	4	0.00	0.00	1.00	3	0.67	0.00	0.33
Upper Owyhee	♂	20	2	0.00	0.50	0.50	1	0.00	0.00	1.00

Table S3.5 Genetic diversity (observed heterozygosity, H_O averaged across 16 loci; expected heterozygosity, H_E, averaged across 16 loci; allelic richness, A_R, averaged across 16 loci), for bighorn sheep (*Ovis canadensis*) populations in southeastern Oregon and northern Nevada.

MP	Population	*n*	H_O	H_E
West	Blue Mountain	15	0.307	0.257
	Trout Creek east	20	0.345	0.316
	Trout Creek south	17	0.316	0.281
	Trout Creek west	18	0.350	0.329
East	Bowden Hills	18	0.481	0.428
	Calicos	17	0.360	0.350
	Eight Mile	14	0.557	0.476
	Martin Creek	12	0.372	0.363
	Rattlesnake	26	0.496	0.447
	Sawtooth	12	0.445	0.422
	Three Forks	-	-	-
	Ten Mile	12	0.482	0.457
	Upper Owyhee	10	0.356	0.334

*The single Three Forks individual's genetic data was incorporated with the Upper Owyhee data

Table S3.6 Summary of individual genetic diversity data across 16 loci with *n* indicating the number of individuals from each population, and na indicating unsampled individuals included in the survival analysis, and the mean, minimum, and maximum values for each population of bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada.

MP	Population	*n*	na	mean	min	max
West	Blue Mountain	8	2	0.292	0.250	0.375
	Trout Creek east	23	6	0.350	0.188	0.625
	Trout Creek south	9	0	0.285	0.188	0.375
	Trout Creek west	9	0	0.361	0.250	0.625
East	Bowden Hills	3	0	0.417	0.375	0.438
	Calicos	5	0	0.444	0.328	0.625
	Eight Mile	10	3	0.518	0.313	0.625
	Martin Creek	8	1	0.411	0.250	0.563
	Rattlesnake	30	5	0.498	0.188	0.813

Sawtooth	4	0	0.422	0.313	0.625
Three Forks	1	0	0.188	-	-
Ten Mile	9	0	0.524	0.313	0.750
Upper Owyhee	6	2	0.375	0.313	0.438

Table S3.7 The output from the top known fate model, which included sex, population heterozygosity, and *M. ovipneumoniae* exposure (*M. ovi* exposure), plus a random effect for year ($\sigma^2 = 0.65$), predicting adult survival of bighorn sheep (*Ovis canadensis*) in populations ($n = 13$) across southeastern Oregon and northern Nevada for the period 2016–2020. Included are the direction of effect on survival, the odds-ratio, estimates and associated 95% credible intervals.

Covariate	**Effect on survival**	**Odds-ratio**	**Estimate**	**95% CI**	
				Lower	**Upper**
Intercept			4.66	3.52	5.94
Sex	↓	1.82	-0.60	-1.33	0.11
M. ovi exposure	↓	2.29	-0.83	-1.60	-0.06
H_E	↑	6.27	1.84	-0.99	4.60

Table S3.8 Derived mean annual survival estimates with 95% credible intervals from the top known fate model, which included sex, population heterozygosity, and *M. ovipneumoniae* exposure (*M. ovi* exposure), plus a year random effect for year (σ = 0.72) used to predict adult survival of bighorn sheep (*Ovis canadensis*) in populations (n = 13) across southeastern Oregon and northern Nevada for the period 2016–2020.

Group	**Sex**	**Year**	**Estimate**	**95% CI**	
				LB	**UB**
Unexposed ♀	females	2016	0.933	0.876	0.972
Unexposed ♀	females	2017	0.930	0.874	0.969
Unexposed ♀	females	2018	0.918	0.851	0.963
Unexposed ♀	females	2019	0.915	0.841	0.963
Unexposed ♀	females	2020	0.930	0.863	0.971
M.ovi exposed ♀	females	2016	0.855	0.751	0.931
M.ovi exposed ♀	females	2017	0.849	0.746	0.925
M.ovi exposed ♀	females	2018	0.826	0.710	0.910
M.ovi exposed ♀	females	2019	0.820	0.687	0.910
M.ovi exposed ♀	females	2020	0.850	0.731	0.931
Unexposed ♂	males	2016	0.882	0.788	0.948
Unexposed ♂	males	2017	0.876	0.779	0.945
Unexposed ♂	males	2018	0.858	0.753	0.933
Unexposed ♂	males	2019	0.852	0.735	0.932
Unexposed ♂	males	2020	0.877	0.771	0.948
M.ovi exposed ♂	males	2016	0.751	0.553	0.896
M.ovi exposed ♂	males	2017	0.741	0.534	0.891
M.ovi exposed ♂	males	2018	0.708	0.494	0.868
M.ovi exposed ♂	males	2019	0.698	0.470	0.866
M.ovi exposed ♂	males	2020	0.743	0.527	0.895

CHAPTER 4

Spatial, temporal, and sexual variation in site fidelity, social affinity, and resource selection of bighorn sheep (*Ovis canadensis*): implications for metapopulation-level restoration

Robert S. Spaan[1], Clinton W. Epps[1], Matthew J. Weldy[2], Christina M. Aiello[1], Donald G. Whittaker[3], Mike Cox[4], and Adam Duarte[5].

[1] Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA
[2] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA
[3] Oregon Department of Fish and Wildlife, Salem, Oregon, USA
[4] Nevada Department of Wildlife, Reno, Nevada, USA
[5] USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington, USA

Corresponding Author:
Robert Spaan[1]
Nash Hall, 2820 SW Campus Way, Corvallis, OR, USA 97331
rob.spaan@oregonstate.edu

Abstract

Habitat specialists tend to have patchy distributions. An understanding of space and habitat use allows for evaluation of patch quality and potential connectivity among patches, which are essential to minimize inbreeding and maintain or restore metapopulation function. With these objectives in mind, we evaluated space and habitat use from 2016 to 2020 of a restored metapopulation of bighorn sheep (*Ovis canadensis*), a habitat-specialist in the northern Basin and Range ecosystem. First, we estimated seasonal and inter-annual individual utilization distributions using GPS data from 104 adults (68 female, 36 male) across thirteen populations. Second, we used the utilization distributions to assess an individual's tendency to remain in its home range (site fidelity) and to stay in a population (social affinity). Third, we used resource selection models to estimate the effects of environmental conditions on within-home range (third-order) habitat selection. Fourth, we developed predicted habitat distribution maps to help inform management decision-making and assess the degree to which unused habitat is present in the system. Summer utilization distributions for female bighorn sheep were significantly smaller than winter utilization distributions, with no seasonal effect detected for males. The mean utilization distributions of female bighorn sheep were 2.00 times smaller than males. After accounting for season, the odds of individual site fidelity were 1.99 times higher for females than males, while after accounting for sex, the

odds of individual site fidelity were 1.47 times higher in the summer compared to the winter. For social affinity, the odds for females were 5.81 times higher than males. Although resource selection by both sexes was quite similar within the same seasons, female bighorn sheep exhibited extremely high site fidelity and social affinity, much higher than observed in other systems. Indeed, no interpopulation movements of female bighorn sheep were observed. Site fidelity and social affinity of male bighorn sheep were significantly lower, with numerous interpopulation movements. Our findings suggest that male bighorn sheep primarily drive the spread of disease and maintain gene flow within the system, but the high site fidelity and social affinity of females we observed has resulted in low potential for colonization of unused habitat. We identified areas of suitable habitat that could, if populated by colonization or translocation, increase the number of occupied patches and enhance population connectivity.

Keywords

Translocations, Brownian Bridge utilization distributions, Site fidelity, Social affinity, Habitat selection

Introduction

Characterizing habitat selection is essential from an evolutionary (Shafer et al. 2012; Fattebert et al. 2015), management (Chetkiewicz and Boyce 2009), and conservation (La Morgia et al. 2011) standpoint. Species select specific habitats to maximize their fitness through various mechanisms, such as nutrition acquisition, reproduction, or predator avoidance. This is particularly important for habitat specialists that thrive within a narrow range of foraging or environmental conditions but tend to be sensitive to habitat disturbance or rapid change (Devictor et al. 2010). Moreover, given the heterogeneous nature of most landscapes (Wiens 1989), habitats favored by specialists are likely to have patchy distributions, which are often at risk of additional fragmentation by anthropogenic activities (Hanski 1998). Thus, managing habitat specialists often requires ensuring connectivity among patches of suitable habitat to minimize inbreeding and maintain or restore metapopulation function by allowing for demographic rescue and recolonization (Brown and Kodric-Brown 1977).

In more extreme cases, habitat specialists might require restoration on large landscapes where extirpation has occurred. In such cases, spatially explicit predictive maps of space and habitat use have proven to be useful tools (Peters et al. 2015; Hunter-Ayad et al. 2020). For instance, habitat predictions have identified translocation sites for the meadow butterfly (*Maniola jurtina*) (Heikkinen et al. 2015) and determined unoccupied habitats that, with improved functional connectivity, could improve gene flow for the bezoar goat (*Capra aegagrus*) (Kuemmerle et al. 2020). Likewise, patterns of an organism's fidelity to its area of use (hereafter, site fidelity) can influence the success of reestablished populations or managed metapopulations**.** Site fidelity is exhibited across taxa from diel to seasonal scales (Merkle et al.

2022) and is strongly related to metapopulation function (Matthiopoulos et al. 2005). For instance, strong site fidelity in either sex may lead to lower probabilities of recolonization of unoccupied habitat patches. In contrast, species with high site fidelity are less likely to adapt to climate change and extreme disturbance events (Kreling et al. 2021).

Bighorn sheep (*Ovis canadensis*) are habitat specialists with patchy populations often functioning as a metapopulation (Bleich et al. 1996). Although described as poor colonizers (Geist 1971), colonization and interpopulation movements by bighorn sheep have become recognized as essential life history traits (Bleich et al. 1990; Epps et al. 2005, 2010; DeCesare and Pletscher 2006). Across their range from the arid deserts of southwest USA and Mexico to the more temperate environments of the northern USA and Canada, bighorn sheep consistently select steep, rugged habitats within proximity to escape terrain (DeCesare and Pletscher 2006; Villepique et al. 2015; Poole et al. 2016; Lula et al. 2020; Gedir et al. 2020). However, selection of specific resources, e.g., access to water (Gedir et al. 2020), forage quality (Lula et al. 2020; Gedir et al. 2020), roads and development avoidance (Poole et al. 2016), and canopy cover (Lula et al. 2020), can be both system and seasonally dependent. For translocation purposes, Singer et al. (2000a) recommend areas with suitable amounts of escape terrain (slopes $\geq 27^{o}$), the presence of perennial water, good visibility, and the absence of natural and artificial barriers and developments.

An understanding of site fidelity is crucial to assess metapopulation dynamics of bighorn sheep. Although site fidelity in bighorn sheep has yet to be reviewed per se, it can describe how individuals move within or among populations, which is informative for demographic, disease, and genetic management (Creech et al. 2017) and metapopulation structure (Creech et al. 2014). Explorative movements such as dispersal, intermountain movements, and seasonal migrations influence site fidelity. In the Mojave Desert, where the habitat tends to be isolated patches separated by minimal escape terrain, desert bighorn sheep rarely migrate seasonally. However, desert bighorn sheep make periodic dispersal events (Epps et al. 2010, 2018) and intermountain movements (Dekelaita 2020). In the more temperate latitudes occupied by Rocky Mountain bighorn sheep in Colorado, Idaho, Montana and Wyoming, habitat tends to be more connected resulting in seasonal and inter-population movements being more common, particularly for males (Borg et al. 2017; Lowrey et al. 2019). Yet, Morrison et al. (2021) found Rocky Mountain bighorn sheep in temperate latitudes showed no seasonal pattern in site fidelity. Instead, Morrison et al. (2021) found site fidelity varied across study sites and increased where inter-population habitat was more homogenous. Interestingly, translocated bighorn sheep are more limited in their movements than native bighorn sheep, suggesting a loss in learned behavior (Jesmer et al. 2018; Lowrey et al. 2019). Thus, the relationship between habitat and site fidelity is context-dependent.

The wide diversity of site fidelity behaviors complicates translocation efforts, which have been a primary tool in bighorn sheep conservation (Singer et al. 2000b). Indeed, since 1922 over 21,500 bighorn sheep have been translocated to restore bighorn sheep populations to much of their range (Wild Sheep Working Group 2015). In some cases, this has occurred in habitat patches unoccupied by bighorn sheep in otherwise occupied systems, e.g., desert bighorn sheep (*O. c. nelsoni*) in California's Mojave Desert (Bleich et al. 1990). Still, in others, wholesale restoration of metapopulations has been required to reestablish bighorn sheep. For instance, bighorn sheep in Washington, Oregon, and northern Nevada were wholly extirpated by the mid-1940s (Johnson 1983; Nevada Division of Wildlife 2001; Oregon Department of Fish and Wildlife 2003). Although the taxonomic classification of the original populations in those regions has been debated, restoration across that portion of the range used bighorn sheep from western British Columbia as the ultimate source (Wild Sheep Working Group 2015). Considered to be a distinct subspecies at one point, the California bighorn (*O. c. californiana*) was synonymized with the Rocky Mountain subspecies (*O. c. canadensis*) based on morphology (Wehausen and Ramey II 2000) but has been maintained as distinct lineages by most states. California bighorn sheep in Washington, southeastern Oregon, southwestern Idaho, and British Columbia are genetically distinct from Rocky Mountain bighorn populations currently in that region (Barbosa et al. 2021). Although the full degree of genetic differentiation of the two lineages has not yet been established, due to translocation history, habitat differences, and the possibility of adaptive differences, California-lineage bighorn sheep (hereafter, California bighorn) may exhibit different patterns of habitat use and site fidelity than other subspecies and lineages. Characterizing those patterns would facilitate management across a large portion of the total range of bighorn sheep that is now occupied by California bighorn originating from 20th century translocations.

In this study, we collected GPS collar data from reintroduced California bighorn sheep populations to gain insight into their habitat selection and connectivity, and the broader implications of those processes for disease and genetic management. We pursued four objectives. First, we estimated seasonal and inter-annual individual utilization distributions for thirteen southeastern Oregon and northern Nevada populations. Second, we used the utilization distributions to assess site fidelity and social affinity, defined as an individual's tendency to remain in a population. Third, we used resource selection models to estimate the effects of ten variables on the within-home range (third order) habitat selection. Fourth, we used these models to derive predicted habitat distribution maps across our study area.

Materials & Methods

Study area

Our study encompassed thirteen bighorn sheep populations, all located in southeastern Oregon and northern Nevada, between 41.2 and 42.3°N and 116.9 and 118.4°W (Fig. 4.1). Elevation across the study area ranged from approximately 1,050 m in the Owyhee Canyon to 2,957 m in the Santa Rosa Mountains. Mean precipitation for the study area was about 22.5–35.0 cm per annum (Omernik and Griffith 2014). The study area terrain types included elevated plateaus, sheer-walled canyons with intermittent lakes and ephemeral streams, and mountains of low to mid-elevation with primarily steep slopes and ephemeral or perennial streams (Omernik and Griffith 2014). For more detailed information on the northern Basin and Range's geology, vegetation, wildlife, and land use practices, please refer to (Spaan et al. 2021).

U.S. Route 95 runs north-south through the study area, dividing the study area's populations into two metapopulations. The western metapopulation included the Blue Mountain (BSP), Trout Creek east (TCE), Trout Creek south (TCS), and Trout Creek west (TCW) populations, all of which are mostly in Oregon (Fig. 4.1). The eastern metapopulation includes the populations in Nevada's Santa Rosa Mountains, i.e., the Calicos (CAL), Eight Mile (EML), Martin Creek (MCK), and Sawtooth (SAW), and the Bowden Hills (BHP), Rattlesnakes (RSP), Ten Mile (TMP), Three Forks (TFK), and the Upper Owyhee (UOP) populations in Oregon (Fig. 4.1). Although established with single translocations in the late 1980s and early 1990s, the three Trout Creek populations trace their lineage to Williams Lake, British Columbia (Table S4.1, Supporting Information). In addition, dispersing bighorn sheep from the Trout Creeks colonized Blue Mountain in the mid to late 1990s (pers. comm. S. Torland, ODFW). Comparatively, the eastern metapopulation's bighorn sheep populations have several different translocation sources, e.g., Kamloops, Penticton, and Williams Lake, BC, and were established in some cases by multiple translocation sources. For more detailed information on the translocation history, please refer to (Spaan et al. 2021).

Capture and collaring

All capture, handling, and disease testing were conducted by Oregon Department of Fisheries and Wildlife (ODFW) and Nevada Department of Wildlife (NDOW). Capture methodology followed the recommendations of Foster (2004) and the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016). ODFW and NDOW captured, collared, and sampled adult female and male bighorn sheep across 13 and 11 populations respectively in southeastern Oregon and northern Nevada between January 2016 and February 2018 (Fig. 4.1). Captures

were conducted using a net gun fired from a helicopter, with individual bighorn sheep blindfolded and hobbled once captured (Krausman et al. 1985). ODFW and NDOW brought bighorn sheep to a centralized area at the base of their range to be fitted with a telemetry collar and to collect biological samples. When capture locations were too far from basecamp to transport animals quickly, they were processed at the capture location.

All adult female (n = 68) and most of the adult male bighorn sheep (n = 31) were fitted with Vertex Survey Globalstar collars (Vectronic Aerospace, Berlin, Germany). The remaining adult male bighorn sheep (n = 5) were fitted with Telonics Globalstar collars (Telonics, Mesa, AZ, USA). Most collars provided GPS locations every 13 hours and operated on the same cycle, except for two collars that reported locations every 11 hours.

Utilization distributions and fidelity

We used GPS data from all collared bighorn sheep to generate individual seasonal utilization distributions for the period 2016–2020, using the R package *adehabitatHR* (Calenge 2006). We defined summer as April 1–September 30 and winter as October 1–March 31. Lambing in parts of this system starts at the end of March - early April (Spaan et al. 2021b), with the rutting period starting as early as late September - early October. We estimated 99% Brownian bridge utilization distributions (BBUDs) which incorporates σ^1, a parameter associated with the speed of each individual animal, and σ^2, the associated telemetry error of the collar types (Kranstauber et al. 2012). For σ^2, we used GPS data from mortalities to assess error rates for both the Vectronic Aerospace (n = 41) and Telonics (n = 1) collars. First, we generated median collar location centers as the GPS errors tended to have a skewed distribution to calculate σ^1. We then calculated the distance between each location and the median collar location centers to calculate the mean error. Utilization distribution estimators, such as BBUD estimator, are considered more rigorous than more traditional methods because they account for these parameters (Walter et al. 2015). We used Welch's two-sample *t*-test to compare the seasonal and sexual differences in BBUD variation.

We evaluated site fidelity and social affinity by assessing BBUD overlap with Bhattacharyya's affinity (BA) index (Bhattacharyya 1943) within the package *adehabitatHR.* The BA index estimates the joint distributions of the two utilization distributions under the hypothesis of independence (Clapp and Beck 2015). The index compares the intensity of use between two distributions, i.e., 0 (no overlap) to 1 (equal space use). We compared utilization distributions between subsequent years of an individual bighorn sheep within the same season to estimate individual site fidelity. To estimate social affinity, we compared the utilization distributions of an individual relative to other members of the same population. Population fidelity comparisons were only done between bighorn sheep of the same sex.

To determine the effect of sex, season, and the interaction between sex and season on site fidelity and social affinity, we fit linear mixed effect models within the package *lme4* (Bates et al. 2015). In addition, we accounted for imbalanced sample numbers from the different populations with a zero-centered population random intercept for each population. Finally, we logit transformed the proportional response variables for both models to fulfill linear model assumptions and added 0.0001 to all social affinity values to transform 0 values (Warton and Hui 2011). For both analyses, we used Akaike's information criterion (AIC) to select the best-supported model. We selected the model with the lowest AIC and highest w_i as our best supported model. We used evidence ratios between the top model and competitive models to evaluate each model relative to the top model (Burnham and Anderson 2002).

Resource selection modeling

To evaluate how individual bighorn sheep select for habitat characteristics, we estimated resource selection at 3rd order selection, defined by Johnson (1980) as use of habitat components within the home range. We applied a used-available design (Manly et al. 2002) using a 1:10 (used: available) ratio. The used locations were the GPS locations of individual bighorn sheep within seasons, and available locations were drawn randomly from within the season specific BBUDs. We generated individual models for four subsets of data: female summer, female winter, male summer, and male winter. We fit mixed-effects logistic regression models with a random intercept for each individual and population (Gillies et al. 2006) using the *lme4* package in software R (version 4.1.2, nAGQ optimization algorithm, R Core Team, 2021).

We included several topographic, forage, and environmental variables in the models (Table 4.1). For topographic variables, we downloaded digital elevation models (DEM) at 10 m^2 resolution from Earth Explorer (http://earthexplorer.usgs.gov/) as one" tiles. Using a mosaicked DEM, we then estimated slope, topographic position index (TPI), vector ruggedness measure (VRM), a layer identifying ridges, distance to escape terrain, and aspect at 10 m^2 resolution in R version 4.1.2 (R Core Team 2021). We calculated TPI, which was scaled from -39.1 to 43.8, as the mean difference of the central point to a focal square of the surrounding 5 × 5 grid cells. Thus, low and high values represent lower and higher slopes respectively (Weiss 1999). We then estimated VRM, which integrates the variation in slope and aspect, using the methods described in Sappington et al. (2007). VRM provides a better measure of variability of terrain compared to slope and elevation (Sappington et al. 2007). From the TPI data, we created a binary ridge layer, defined as any cells with a TPI score greater than six, after visually inspecting the layer. We also calculated distance to escape terrain, shown by DeCesare and Pletscher (2006) to be a good predictor of bighorn sheep resource selection. We assessed distance to escape terrain, measured in meters, at different slopes, namely ≥ 27º, ≥ 37º, and ≥ 45º (Lula et al. 2020). We then estimated aspect, which ranged from -1 (south) to 1 (north).

To assess forage, we used 14-day composite, 250 m^2 resolution normalized differential vegetation index (NDVI) data (Pettorelli et al. 2005) from the Moderate Resolution Imaging Spectroradiometer (eMODIS). We used pre-processed data from 2016–2020 obtained from Earth Explorer (https://earthexplorer.usgs.gov/), which is managed by the U. S. Geological Survey's Earth Resources Observation Center (Jenkerson et al. 2010). For each NDVI raster, cells labelled as cloudy, negative, or fill, in the eMODIS quality data were assigned NA values (i.e., no data), and cells labeled as snow were assigned the 0.025 quantile of the entire NDVI times series for the cell (Bischof et al. 2012; Merkle et al. 2016). All resulting NDVI values were then smoothed using the modified Whittaker smoother, which is designed to address the negative-biased noise often present in NDVI and other remotely sensed data (Atzberger and Eilers 2011). From the smoothed NDVI data, we estimated mean greenness ($NDVI_{MEAN}$), and greenness amplitude (i.e., the difference between the lowest and highest values for each cell, $NDVI_{AMP}$) for each season.

We also quantified tree canopy and snow cover (Table 4.1). We used the 2016 national land cover database (NLCD) for canopy cover, which has a 30 m^2 resolution image with canopy cover represented by percentage cover at the pixel level (Coulston et al. 2012). We derived annual winter snow data from the eMODIS 250 m^2 resolution quality data. Snow cover was calculated as the proportion of 14-day time points each pixel was covered by snow during the winter season.

We aimed to use a global model for male and female bighorn sheep in each season to derive predictive surfaces of resource use to the extent of the study area. However, selection of topographical and forage covariates can occur at different spatial scales and functional forms (Lowrey et al. 2018). Thus, we fit univariate models for three topographical covariates, slope, TPI, and VRM, assessed at their original 10 m^2 resolution, and then each at a buffering distance of 50, 100, and 500 m (Table 4.1), given that bighorn sheep may select attributes more broadly than at the minimum resolution of the data (Laforge et al. 2015). We also used univariate models to assess distance to escape terrain, determined at three different slope cutoffs (i.e., $\geq 27^{\circ}$, $\geq 37^{\circ}$ and $\geq 47^{\circ}$). To determine our best forage measure, $NDVI_{AMP}$ and $NDVI_{MEAN}$, we also used univariate models of forage measures at their original resolution of 250 m and with a 500 m buffer (Table 1). We used area under the receiver-operating curve (AUC) to compare and select the spatial scale and form of univariate models (Boyce et al. 2002). We used k-folds (n = 10) cross validation to generate the AUC scores and the associated 95% CIs, which represent the uncertainty of the AUC score. The AUC statistical range is 0–1, where higher values indicate increased model predictive ability, and values > 0.5 indicate models are better predictive classifiers than random classification (Phillips and Dudík 2008; Jiménez-Valverde 2012). The global models predicting resource selection for both adult female and male bighorn sheep for the summer periods included topographical variables, elevation, slope, TPI, VRM, distance to escape terrain, ridge, and aspect, the forage variable NDVI, and

the environmental variable canopy cover, whilst the winter models also included the environmental variable snow cover. We included two random intercepts, namely animal and population ID to account for repeated measures and suspected variation by population. Correlations between covariates included in the global models were assessed using Pearson correlation matrices between all variables for all data sets using a cutoff of $|r| \geq 0.7$ (Hosmer and Lemeshow 2000).

We standardized all the continuous covariates (*z*-score) used in the models to improve model performance and to allow for comparison of effect sizes across variables (Schielzeth 2010). We then exponentiated the logistic regression coefficients to determine the odds ratio for each effect. We considered the effect significant if the 95% CI of the odds ratio did not overlap one.

Results

Between 2016 and 2020, we collected GPS data from 68 adult female in 13 populations and 36 adult male bighorn sheep in 11 populations across southeastern Oregon and northern Nevada. In total, we assessed 362 individual seasons: 261 individual females and 101 individual males. The mean number of female adult bighorn sheep assessed per summer and winter season was 31 (range: 14–41) and 26.5 (range: 16–36) respectively (Table S4.1), while the mean number of male adult bighorn sheep assessed per summer and winter season was 13 (range: 6–20) and nine (range: 5–16) respectively (Table S4.1). The mean fix probability for all collars was 0.90 with a standard deviation of 0.08 (Fig. S4.1). The four datasets included 1,207,884 locations, of which 512,215 locations were included in the adult female summer, 350,661 locations in the adult female winter, 218,299 locations in the adult male summer, and 126,709 locations in the adult male winter datasets.

Utilization distributions and fidelity

The number of locations used to generate the GPS error rates varied from three to 948 ($\bar{x}$ = 53.8) for the 41 Vectronic Aerospace collars and 248 locations for the single Telonics collar. Mean GPS error rate for the Vectronic Aerospace collars and the Telonics collar were 6.36 m and 4.91 m respectively (Fig. S4.1).

The summer BBUDs for female bighorn sheep ($\bar{x}$ = 41.1 km^2; range: 8.6–127.1 km^2) were 1.2 times smaller (t = -3.04, df = 223.55, p = 0.003) than the winter BBUDs ($\bar{x}$ = 49.4 km^2; range: 8.8–109.8 km^2). For male bighorn sheep there was no significant difference (t = -1.25, df = 89.45, p = 0.213) between summer ($\bar{x}$ = 82.4 km^2; range: 17.4–445.9 km^2) and winter BBUDs ($\bar{x}$ = 99.3 km^2; range: 38.2–371.4 km^2). BBUDs for female bighorn sheep were 2.00 times smaller than male bighorn sheep in the summer (t = -4.29, df = 68.32, $p < 0.001$) and 2.01 times in the winter (t = -5.05, df = 38.44, $p < 0.001$). At the population level, the mean utilization distributions of female bighorn sheep tended to be smaller in

MCK, SAW, and TCE, and larger in TMP and TCW, across all seasons (Fig. S4.3). For male bighorn sheep there was less pattern with utilization distributions, due to periodic forays by individuals across both seasons (Figs. 4.1, S4.3).

The top model predicting individual site fidelity via BA included the effect of sex and season (Table 4.2). After accounting for season, the odds of individual site fidelity were 1.99 times higher for females than males, while after accounting for sex, the odds of individual site fidelity were 1.47 times higher in the summer compared to the winter (Table 4.3). Predicted individual site fidelity 0.76 (95% CI [0.70–0.82]) for males and 0.87 (95% CI [0.83–0.89]) for females, while predicted individual site fidelity was 0.83 (95% CI [0.78-0.87)] in summer and 0.76 (95% CI [0.70-0.82]) in winter (Fig. 4.2). The top model predicting social affinity only included a single effect, sex (Table 4.2). The odds of social affinity were 5.81 times higher for females than males (Table 4.3). Predicted social affinity was 0.76 (95% CI [0.62–0.86]) for males and 0.95 (95% CI [0.91–0.97]) for females (Fig. 4.2).

Resource selection modeling

Based on univariate models, the best-performing buffer distance or slope cutoff within each topographic variable was the same for both female and male bighorn sheep across seasons, except for TPI in the summer (Table S4.4). Slope was best represented with a buffer of 50 m, VRM with a buffer of 100 m, distance to escape terrain at a slope cutoff of ≥ 27º, and TPI with a 100 m buffer across all data sets, except TPI for adult females in the summer, which was best represented with a buffer of 50 m (Table S4.4). For forage variables, the best performing univariate models for both female and male bighorn sheep were $NDVI_{MEAN}$ in the summer and $NDVI_{AMP}$ in the winter (Table S4.5).

We chose to draw inference from the global model as it allowed us to address covariate hypotheses across each sex in each season. For all four data subsets, the AUC score for the global model was indistinguishable from the most parsimonious model, and both had high model predictive accuracy (Table 4.4). The global model for adult female bighorn sheep was the highest ranked model in the summer and fourth ranked model in the winter with AUC scores of 0.83 (95% CI: [0.82–0.83]) and 0.81 (95% CI: [0.81–0.82]) respectively (Table 4.4). The global model for adult male bighorn sheep was the second ranked model in both the summer and winter datasets with AUC scores of 0.79 (95% CI: [0.78-0.79]) and 0.82 (95% CI: [0.81; 0.83]) respectively (Table 4.4). The magnitude, coefficient estimates and associated odds ratios across the top models in each of the datasets varied little, likely due to the large sample sizes leading to robust inferences.

All the variables from the global model for both summer and winter resource selection by female bighorn sheep had strong support as predictors of resource selection, as evidenced by the odds ratios and associated 95% CIs (Table 4.5, Fig. 4.3). Consistent across both seasons, female bighorn sheep selected

for steeper slopes, higher TPI, areas closer to steeper terrain of ≥ 27º, ridges, and southerly facing slopes, but avoided areas with more canopy cover (Table 4.5, Fig. 4.4). Female bighorn sheep selection differed for elevation and rugged terrain between seasons: they selected higher elevations with rugged terrain in the summer, but selected lower elevations with less rugged terrain and avoided snow cover in the winter (Table 4.5, Fig. 4.4). Female bighorn sheep selected for areas of lower forage value, in terms of mean and amplitude NDVI, in both the summer and winter seasons (Table 4.5, Fig. 4.4).

For male bighorn sheep, the 95% CIs for the odds ratio overlapped zero, indicating VRM did not influence habitat selection during summer, while there was only marginal support for ridges (Table 4.5, Fig. 4.3). In the winter season, all the variables included in the global model except elevation influenced habitat selection (Table 4.5, Fig. 4.3). Consistent across both seasons, male bighorn sheep selected for higher slopes, higher TPI, and remained close to escape terrain ≥ 27º, but avoided areas of canopy cover (Table 4.5, Fig. 4.4). Additionally, in the winter they selected rugged terrain, ridges, and avoided snow cover (Table 4.5, Fig. 4.4). Like female bighorn sheep, male bighorn sheep selected areas with lower forage values, in terms of mean and amplitude NDVI, in the summer and winter seasons (Table 4.5, Fig. 4.4).

Discussion

We evaluated habitat selection and site fidelity for California bighorn sheep and determined that site fidelity varied strongly by sex and season while social affinity varied by sex. Although resource selection by both sexes was quite similar within season (Table 4.3, Fig. 4.3), female bighorn sheep in this study system exhibited extremely high site fidelity and social affinity (Fig. 4.2). Indeed, no interpopulation movements of female bighorn sheep were observed over the course of the study. As a consequence, metapopulation function may be inhibited as low colonization rates will lead to areas of suitable habitat not being used. Both site fidelity and social affinity of male bighorn sheep was significantly lower, meaning they are responsible for both gene flow and the spread of disease within the metapopulation.

Bighorn sheep in our system exhibited similar patterns of home range use to desert bighorn sheep. In desert bighorn sheep in the arid southwest, male bighorn sheep used larger areas than female bighorn sheep (Krausman et al. 1989; Hoglander et al. 2015), while areas of use were also larger in the winter compared to the summer (Hoglander et al. 2015). Hoglander et al. (2015) found that the smaller summer ranges were associated with greater intensity of use around escape terrain, particularly for females, suggesting predator avoidance, as we observed in our system. Comparatively, for Rocky Mountain bighorn sheep in British Columbia, sex did not influence the size of home ranges (Poole et al. 2016). Observed sex differences are likely the result of forays by males to access females during the rut in the

winter, as observed with desert bighorn sheep (Dekelaita 2020), and to access higher quality forage in the summer.

While we expected males to exhibit lower site fidelity and use larger areas than females, the high site fidelity and lack of interpopulation movements observed for females were striking and may have implications for managing these restored metapopulations. Although male forays may facilitate gene flow among parts of this system (Spaan et al. 2021), the lack of female forays likely inhibits demographic connectivity, i.e., limiting the potential colonization of unoccupied habitat patches (Creech et al. 2014). There is evidence that females have made extra-population movements in the past, given that BHP and BSP were established via colonization (Spaan et al. 2021). In other study systems, female bighorn sheep make frequent intermountain and interpopulation movements. For example, in the Mojave Desert, 17 out of 108 female desert bighorn sheep monitored for a minimum of six months made intermountain movements (Dekelaita 2020). Likewise, monthly probabilities of movement by female Rocky Mountain Bighorn Sheep between different groups in central Idaho ranged between 0.05 to 0.24 (Borg et al. 2017). The reasons for such high female site fidelity and social affinity in this system are unclear. However, the propensity to disperse has been shown to be a heritable trait (Hansson et al. 2003, Doligez et al. 2009). Extremely low genetic diversity was documented for many of these populations, primarily due to founder effects: founding populations, particularly those in the western metapopulation, were 14–27 individuals, and those individuals were in turn drawn from other populations previously subjected to strong founder effects (Spaan et al. 2021). Thus, we speculate that inbreeding might contribute to a reduction in or loss of this trait, particularly in the western metapopulation which has not experienced gene flow from more genetically diverse populations nearby (Spaan et al. 2021).

Based upon the sex-based differences in site fidelity, size of use area, and the lack of evidence of interpopulation movements by female bighorn sheep during the study, male bighorn sheep appear to drive both the spread of disease and gene flow within this system. However, even male movements may be restricted by the presence of a fenced, two-lane highway, US Route 95. The bighorn captured for this study were all tested to determine exposure of *Mycoplasma ovipneumoniae*, a transmissible bacterial pathogen that causes pneumonia and can result in all-age die-offs and subsequent lower recruitment (Cassirer et al. 2018). All populations east of U.S. Route 95 (Fig. 4.1) showed evidence of exposure to *M. ovipneumoniae*, while populations west of the highway showed no such evidence (Spaan et al. 2021). In support of this conclusion, testing of the bighorn captured for this study showed that exposure to *Mycoplasma ovipneumoniae*, a transmissible bacterial pathogen resulting in pneumonia, that often causes all-age die-offs and subsequent lower recruitment (Cassirer et al. 2018), differed across the highway. All the populations east of U.S. Route 95 (Fig. 4.1) contained individuals showing evidence of exposure to *M. ovipneumoniae*, but no individuals in populations west of U. S. Route 95 showed such evidence (Spaan et

al. 2021). Also, while the populations west of U.S. Route 95 and two populations east of U. S. Route 95 (RSP and TMP) share similar translocation histories, RSP and TMP have much higher population genetic diversity due to gene flow with the more diverse neighboring Nevada populations (Spaan et al. 2021).

Resource selection was similar overall among males and females, but some minor and significant seasonal differences occurred (Fig. 4.5). Male and female bighorn sheep used higher elevation areas during the summer, likely to take advantage of forage green-up (Merkle et al. 2016). While in the winter, female bighorn sheep, most notably those in the higher elevation populations, e.g., EML, SAW, and TMP, moved to lower elevations than males. This was likely to avoid snow. Snow avoidance is common in bighorn sheep although Rocky Mountain and Sierra Nevada bighorn sheep are also known to avoid snow by using higher elevation windswept areas (Poole et al. 2016; Courtemanch et al. 2017; Spitz et al. 2020). The stronger effect of snow avoidance in the winter was likely due to thermoregulatory needs, i.e., trying to keep warmer in the winter by avoiding higher lying areas with greater snow accumulation (Mahoney et al. 2018). Predator avoidance is an alternative hypothesis for avoiding tree cover (Holl et al. 2004). However, minimal tree cover exists at lower elevations within this system.

Male and female bighorn sheep displayed slightly different resource selection behaviors related to topographical variables. Female bighorn sheep selected more rugged terrain in the summer, likely to reduce predation risk during the pre- and post-parturition periods, while in the winter, they selected less rugged terrain likely to access forage. In comparison, male bighorn sheep only selected for rugged terrain in the winter. Female and male bighorn sheep selected for ridges across all seasons, although the 95% confidence interval for the coefficient estimates overlapped zero for males in the summer. Bleich et al. (1997) observed similar patterns in desert bighorn sheep where adult males, segregated from adult females, used less rugged habitats to access higher quality forage, suggesting they were less predator averse than female desert bighorn sheep.

Metapopulation persistence typically increases when more occupied patches are present (Hanski et al. 1995), and managers have sought to maintain restored bighorn sheep populations and increase harvest opportunity. If additional populations are desired to achieve those goals, our analyses of habitat suggest there is potential to establish more populations in this system. We identified several large patches of suitable habitat that remain unused by bighorn sheep (Fig. 4.5). For example, east of U. S. Route 95, the habitat connecting TMP in Oregon with neighboring EML and CAL populations in northern Nevada is used by males throughout the year (Fig. 4.1) but is unused by females. We also identified suitable habitat for both sexes south of EML that is only used by males in the summer. West of U. S. Route 95, some suitable habitat also remains unoccupied. The most notable example is the canyonland to the northeast of TCW which was explored by a single dispersing male from BSP. Given the lack of interpopulation movements by females that we observed compared to other systems (Borg et al. 2017;

Dekelaita 2020), translocation could accelerate establishment of populations in these areas. In addition, translocations could improve genetic diversity if new source populations were used, particularly for the populations west of U.S. Route 95 that exhibit very low population genetic diversity (Spaan et al. 2021). However, the benefits of translocation must always be weighed against the risk of disease. New translocations can increase densities and foray behavior due to competition for forage and mating opportunities, resulting in more connect habitat patches, potentially facilitating disease transmission (Werdel et al. 2020). Our models of site fidelity and habitat use, as well as the predictive maps of habitat use, will help inform those management decisions.

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Tables

Table 4.1 Covariates used to assess habitat use of male and female bighorn sheep (*Ovis canadensis*) evaluated via resource selection function. TPI – topographic position index, VRM – vector ruggedness measure, NDVI – normalized differential vegetation index.

Covariates	Type	Image resolution (m)	Buffer (m)	Predicted relationship summer/winter (+/-) ♀	Predicted relationship summer/winter (+/-) ♂	Observed value range
Elevation (m)	continuous	10	na	+/-	+/-	1,053.3–2,661.4
Slope (º)	continuous	10	50, 100, 500	+/+	+/+	0–80.3
Topographic position index (TPI)	continuous	10	50, 100, 500	+/+	+/+	-39.1–43.8
Vector ruggedness measure (VRM)	continuous	10	50, 100, 500	+/+	+/+	0–0.38
Distance (m) to escape terrain (≥ 27º, 37º, and 45º)	continuous	10	na	-/-	-/-	0–8,882.9
Ridge	binary	10	na	+/+	+/+	0 or 1
Aspect (northness)	continuous	10	na	+/-	+/-	-1–1
$NDVI_{AMP}$	continuous	250	500	+/+	+/+	0.02–0.72
$NDVI_{MEAN}$	continuous	250	500	+/+	+/+	0.01–0.62
Canopy cover (%)	continuous	30	na	-/-	-/-	0–50
Snow cover (mean proportion)	continuous	250	na	na/-	na/-	0–0.35

Table 4.2 Model selection results for linear mixed effects model predicting individual site and social affinity of bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada for the period 2016–2020. Covariates for both models included sex, season, and the interaction between sex and season. We controlled for uneven sample sizes across the study area in both analyses by including populations as a random effect. (σ^2 for the site fidelity model < 0.01, while σ^2 for the social affinity model = 0.01). Models in bold text indicate most parsimonious models within 2 AIC of the top model.

Analysis	Model	*K*	AIC	Δ AIC	w_i	ML
Site fidelity	**sex + season**	**5**	**401.14**	**0.00**	**0.69**	**1.00**
	sex + season + sex × season	6	402.83	1.69	0.30	0.43
	sex	4	409.49	8.35	0.01	0.02
	season	4	420.37	19.23	0.00	0.00
Social affinity	sex + season + sex × season	6	1,988.20	0.00	0.52	1.00
	sex	**4**	**1,989.00**	**0.80**	**0.35**	**0.67**
	sex + season	5	1,990.90	2.70	0.13	0.26
	season	4	2,064.60	76.40	0.00	0.00

Table 4.3 The outputs from the most parsimonious models within 2 AIC of the top model predicting site and social affinity of bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada for the period 2016–2020. The reference-level for sex in both models is male, while the reference level for season in the site fidelity model is winter.

Analysis	Covariate	Effect on fidelity	Odds-ratio	Estimate	95% CI		p-value
					Lower	Upper	
Site fidelity	intercept			1.18	0.84	1.51	< 0.001
	sex-female	+	1.99	0.69	0.40	0.97	< 0.001
	season-summer	+	1.47	0.38	0.15	0.62	0.002
Social affinity	intercept			1.16	0.49	1.83	0.004
	sex-female	+	5.81	1.76	1.37	2.14	< 0.001

Table 4.4 Model selection results for within home range, third-order resource selection by adult male and female bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada for the period 2016–2020. The highlighted models indicate the global model. Models were evaluated using area under the receiver-operating curve (AUC), where higher AUC values indicate models with better predictive power; lower (LB) and upper (UB) bounds of the 95% CI are also presented.

			95% AUC	
Data set	**Model**	**AUC**	**LB**	**UB**
Adult ♀	**Elevation + $Slope_{50}$ + TPI_{50} + VRM_{100} + d2esc27 + Ridge + Aspect + $NDVI_{MEAN}$ + Canopy cover**	**0.825**	**0.821**	**0.828**
summer	Elevation + $Slope_{50}$ + TPI_{50} + VRM_{100} + d2esc27 + Ridge + Aspect + $NDVI_{MEAN}$	0.825	0.821	0.828
	Elevation + $Slope_{50}$ + TPI_{50} + VRM_{100} + d2esc27 + Aspect + $NDVI_{MEAN}$ + Canopy cover	0.825	0.821	0.828
	Elevation + $Slope_{50}$ + TPI_{50} + VRM_{100} + d2esc27 + Aspect + $NDVI_{MEAN}$	0.825	0.821	0.828
	Null model	0.499	0.496	0.500
Adult ♀	Elevation + $Slope_{50}$ + TPI_{100} + d2esc27 + Ridge + Aspect + $NDVI_{AMP}$ + Canopy cover + Snow cover	0.814	0.808	0.819
winter	Elevation + $Slope_{50}$ + TPI_{100} + d2esc27 + Aspect + $NDVI_{AMP}$ + Canopy cover + Snow cover	0.814	0.808	0.819
	$Slope_{50}$ + TPI_{100} + d2esc27 + Ridge + Aspect + $NDVI_{AMP}$ + Canopy cover + Snow cover	0.814	0.808	0.819
	Elevation + $Slope_{50}$ + TPI_{100} + VRM_{100} + d2esc27 + Ridge + Aspect + $NDVI_{AMP}$ + Canopy cover + Snow cover	**0.814**	**0.808**	**0.819**
	Null model	0.500	0.498	0.500
Adult ♂	Elevation + $Slope_{50}$ + TPI_{100} + d2esc27 + Ridge + Aspect + $NDVI_{MEAN}$ + Canopy cover	0.785	0.779	0.790
summer	**Elevation + $Slope_{50}$ + TPI_{100} + VRM_{100} + d2esc27 + Ridge + Aspect + $NDVI_{MEAN}$ + Canopy cover**	**0.785**	**0.779**	**0.790**
	Elevation + $Slope_{50}$ + TPI_{100} + VRM_{100} + d2esc27 + Aspect + $NDVIM_{EAN}$ + Canopy cover	0.785	0.779	0.790
	Elevation + $Slope_{50}$ + TPI_{100} + d2esc27 + Ridge + Aspect + $NDVI_{MEAN}$	0.785	0.779	0.790
	Null model	0.500	0.499	0.500
Adult ♂	Elevation + $Slope_{50}$ + TPI_{100} + VRM_{100} + d2esc27 + Aspect + $NDVI_{AMP}$ + Canopy cover + Snow cover	0.824	0.815	0.831
winter	**Elevation + $Slope_{50}$ + TPI_{100} + VRM_{100} + d2esc27 + Ridge + Aspect + $NDVI_{AMP}$ + Canopy cover + Snow cover**	**0.824**	**0.815**	**0.832**
	$Slope_{50}$ + TPI_{100} + VRM_{100} + d2esc27 + Aspect + $NDVI_{AMP}$ + Canopy cover + Snow cover	0.823	0.815	0.831
	$Slope_{50}$ + TPI_{100} + VRM_{100} + d2esc27 + Ridge + Aspect + $NDVI_{AMP}$ + Canopy cover + Snow cover	0.823	0.815	0.831
	Null model	0.499	0.497	0.500

TPI = topographical position index, VRM = vector ruggedness measure, d2esc = distance to escape terrain, $NDVI_{MEAN}$ = normalized differential vegetation index, $NDVI_{AMP}$ = normalized differential vegetation index amplitude. Values after parameters indicate buffers, and values after "d2esc" indicate a cut-off of ≥ 27°.

Table 4.5 Summary results of scaled, continuous data for each fixed effect from the global generalized linear mixed effects models predicting winter and summer resource selection by adult male and female bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada. Explanatory variables include elevation, slope, topographical position index, vector ruggedness measure, distance to escape terrain, ridges, aspect, mean and amplitude normalized differential vegetation index, canopy- and snow cover for the winter datasets. Positive values for aspect indicate more northerly-facing aspect, while negative aspects indicate more southerly-facing aspect.

				95% CI	
Data set	**Variables**	**Direction of effect**	**Odds-ratio**	**LB**	**UB**
Adult ♀	Elevation	+	1.64	1.60	1.68
summer	$Slope_{50}$	+	2.57	2.52	2.62
	TPI_{50}	+	1.41	1.40	1.42
	VRM_{100}	+	1.04	1.03	1.06
	Distance to escape terrain (≥27º)	-	2.50	2.40	2.61
	Ridge	+	2.16	1.96	2.38
	Aspect	-	1.11	1.10	1.12
	$NDVI_{MEAN}$	-	1.24	1.22	1.26
	Canopy cover	-	1.05	1.03	1.06
Adult ♀	Elevation	-	1.11	1.08	1.14
winter	$Slope_{50}$	+	2.38	2.32	2.43
	TPI_{100}	+	1.50	1.48	1.51
	VRM_{100}	-	1.04	1.02	1.05
	Distance to escape terrain (≥27º)	-	2.90	2.75	3.05
	Ridge	+	1.61	1.40	1.87
	Aspect	-	1.17	1.15	1.18
	$NDVI_{AMP}$	-	1.10	1.08	1.13
	Canopy cover	-	1.22	1.18	1.26
	Snow cover	-	1.37	1.34	1.40
Adult ♂	Elevation	+	1.55	1.51	1.59
summer	$Slope_{50}$	+	1.94	1.89	1.99
	TPI_{100}	+	1.39	1.37	1.41
	VRM_{100}	0	1.00	-1.02	1.02
	Distance to escape terrain (≥27º)	-	2.50	2.40	2.61
	Ridge	**(+)**	1.34	0.99	1.83

	Aspect	**(+)**	1.02	1.00	1.03
	$NDVI_{MEAN}$	-	1.36	1.33	1.39
	Canopy cover	-	1.03	1.01	1.05
Adult ♂	Elevation	0	1.03	0.99	1.07
winter	$Slope_{50}$	+	1.81	1.75	1.88
	TPI_{100}	+	1.67	1.63	1.70
	VRM_{100}	+	1.10	1.07	1.12
	Distance to escape terrain (≥27º)	-	5.10	4.57	5.70
	Ridge	+	1.48	1.09	2.01
	Aspect	-	1.23	1.21	1.26
	$NDVI_{AMP}$	-	1.33	1.28	1.38
	Canopy cover	-	1.13	1.08	1.18
	Snow cover	-	1.44	1.38	1.49

TPI = topographical position index, VRM = vector ruggedness measure, d2esc = distance to escape terrain, $NDVI_{MEAN}$ = normalized differential vegetation index, $NDVI_{AMP}$ = normalized differential vegetation index amplitude. Values after parameters indicate buffers, and values after "d2esc" indicate a cut-off of ≥ 27°.

Figures

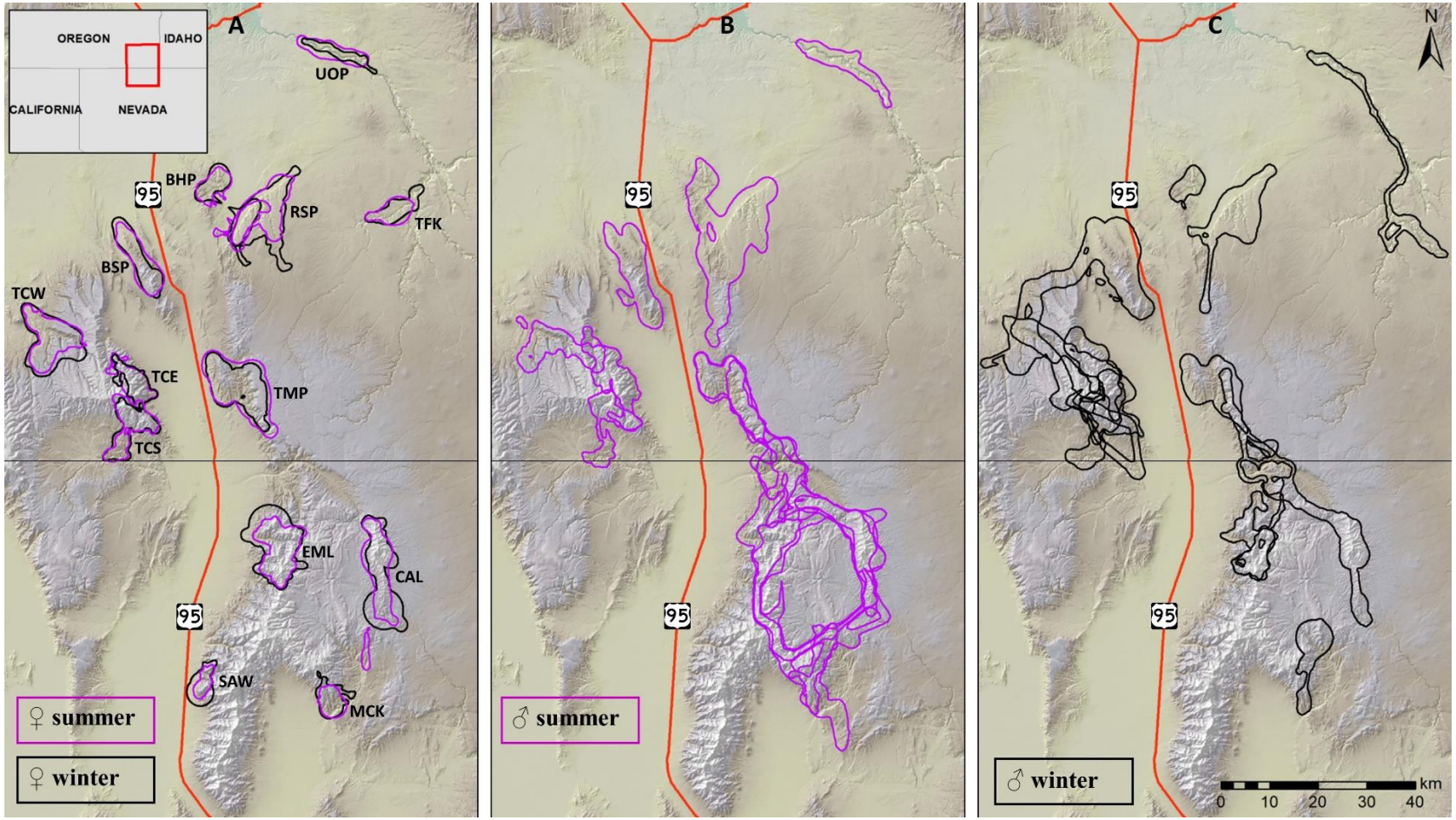


Figure 4.1 Cumulative 99% Brownian bridge utilization distributions for adult female bighorn sheep (*Ovis canadensis*) in the summer and winter seasons (A), and adult male bighorn sheep in the summer (B) and winter seasons (C). Populations west of U.S. Route 95 include Blue Mountain (BSP), Trout Creeks – east (TCE), Trout Creeks south (TCS), Trout Creeks – west (TCW). Populations east of U.S. Route 95 include Bowden Hills (BHP), Calicos (CAL), Eight Mile (EML), Martin Creek (MCK), Rattlesnake (RSP), Sawtooth (SAW), Three Forks (TFK), Ten Mile (TMP), and Upper Owyhee (UOP). Overlapping polygons indicate overlapping utilization distributions. Utilization distributions were not generated for adult male bighorn sheep in SAW and TFK, due to the absence of collared males.

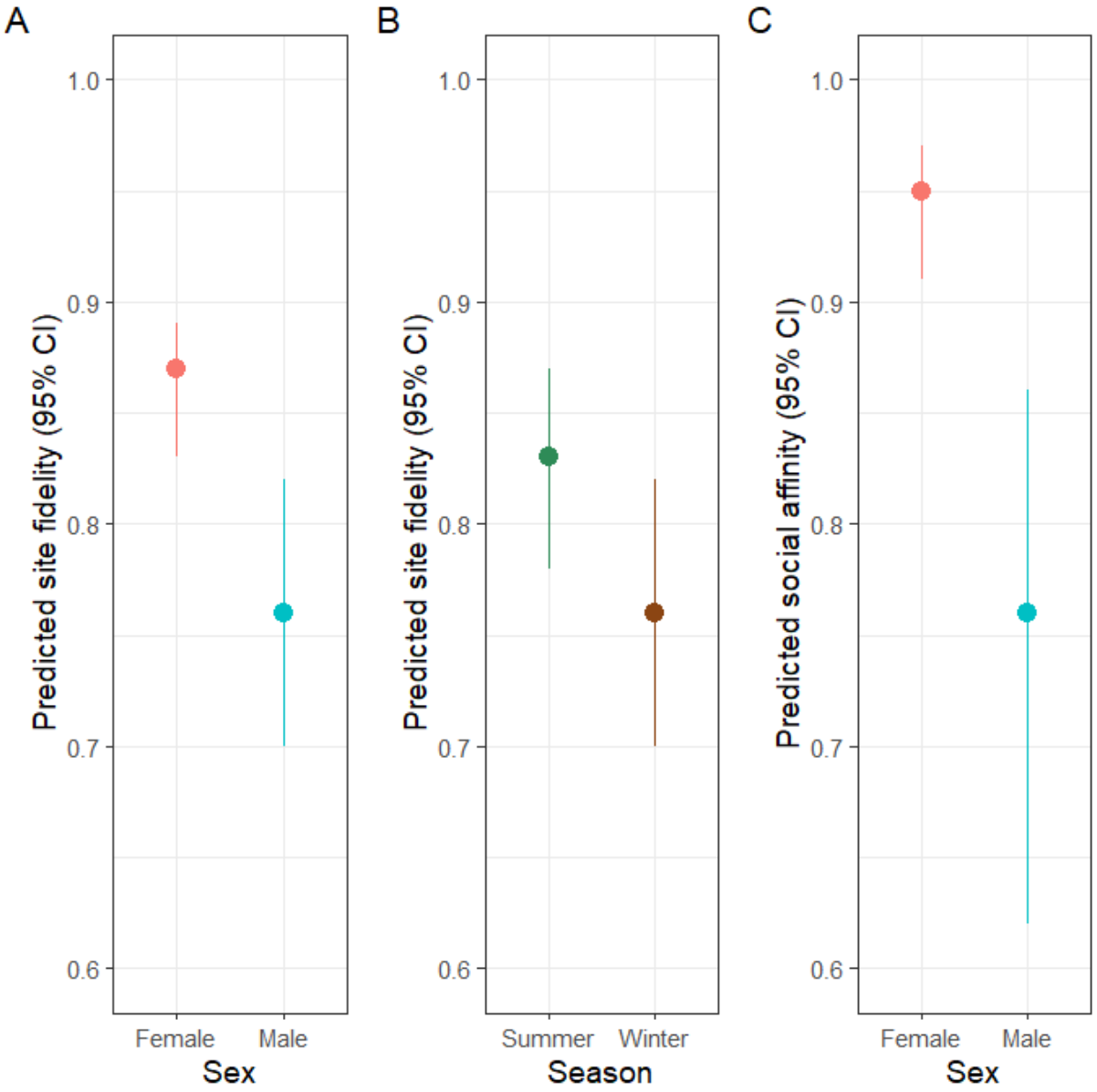


Figure 4.2 Predicted values of site fidelity by sex (A) and season (B), and variation in social affinity by sex (C) for bighorn sheep (*Ovis canadensis*), in southeastern Oregon and northern Nevada, as determined by 95th percentile kernel overlap of utilization distributions using Bhattacharyya's affinity index. The reference category for (A) is male, (B) is winter, and (C) is male.

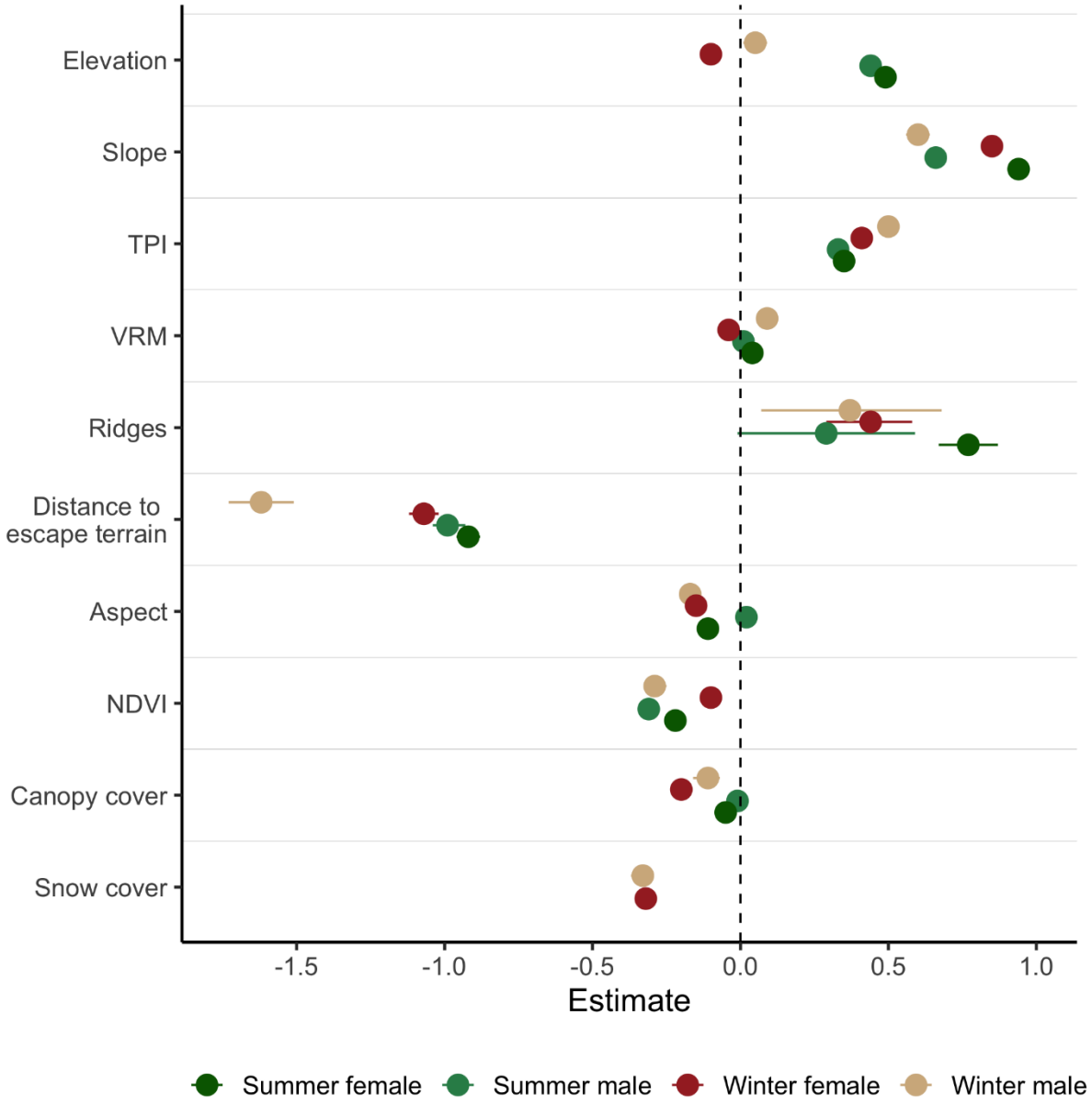


Figure 4.3 Coefficient estimates and 95% confidence intervals of the scaled variables included in the global models predicting female and male bighorn sheep (*Ovis canadensis*) summer and winter habitat use in southeastern Oregon and northern Nevada from 2016 to 2020. Variables include elevation, slope, topographical position index (TPI), vector ruggedness measure (VRM), ridges, distance to escape terrain, aspect, normalized differential vegetation index (NDVI), and canopy and snow cover.

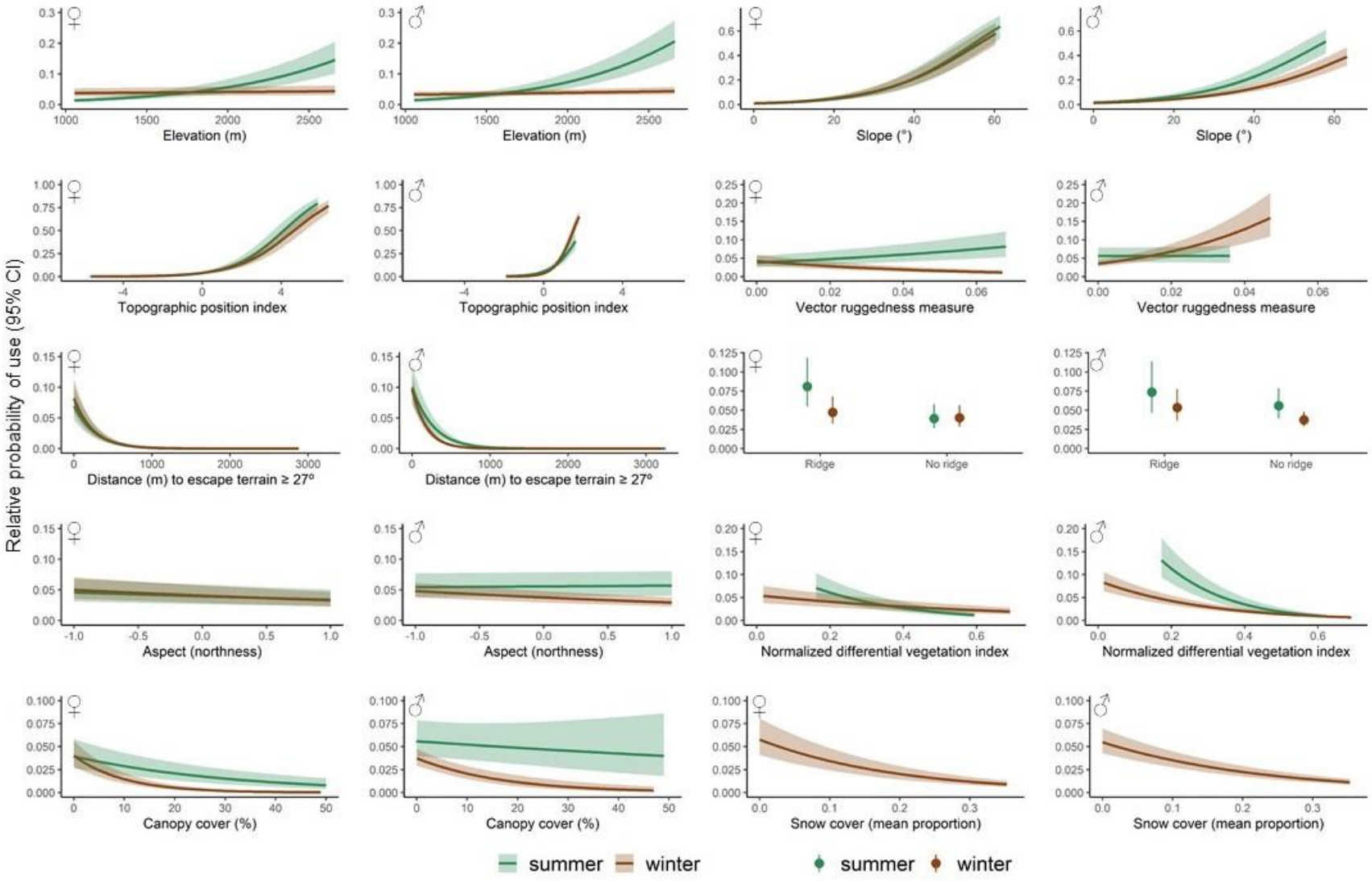
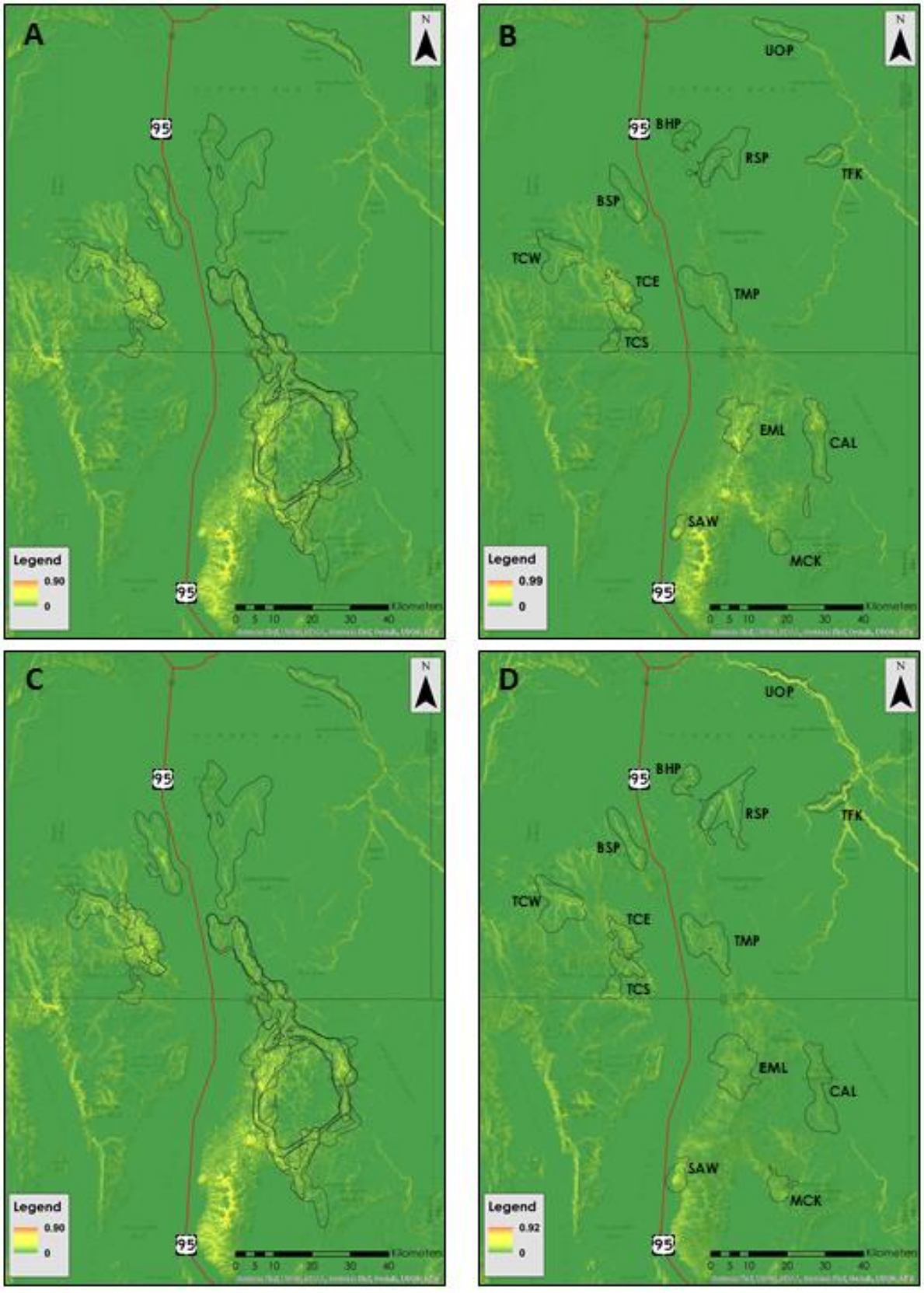

Relative probability of use (95% CI)
♀
♂
Elevation (m)
Slope (°)
Topographic position index
Vector ruggedness measure
Distance (m) to escape terrain ≥ 27°
Ridge
No ridge
Aspect (northness)
Normalized differential vegetation index
Canopy cover (%)
Snow cover (mean proportion)
summer
winter

Figure 4.4 Prediction plots showing seasonal relative probabilities of use of resources (± 95% CI) by female and male bighorn sheep (*Ovis canadensis*) in southeastern Oregon and northern Nevada. The symbols indicate sex (♂ - male, ♀ - female), with seasons represented by green (summer) and brown (winter).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TMP
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MCK
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Legend
0.90
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D
Legend
0.92
0

Figure 4.5 Predicted bighorn sheep (*Ovis canadensis*) probability of use for A. male summer, B. female summer, C. male winter, and D. female winter seasons. Three letter codes indicate the summer core herd home ranges representing: BHP – Bowden Hills, BSP – Blue Mountain, CAL – Calico, EML – Eight Mile, MCK – Martin Creek, RSP – Rattlesnakes, SAW – Sawtooth, TCE – Trout Creek east, TCS – Trout Creek south, TCW – Trout Creek west, TFK – Three Forks, TMP – Ten Mile, and UOP – Upper Owyhee populations.

Supplementary Tables

Table S4.1 Sample size (*n*) of male and female bighorn sheep (*Ovis canadensis*) assessed via resource selection function by season (S = summer, W = winter).

Sex	2016S	2016-17W	17S	2017-18W	2018S	2018-19W	2019S	2019-20W	2020S	Total
♀	32	27	41	36	41	27	27	16	14	261
♂	17	6	6	5	20	16	16	9	6	101
Total	49	33	47	41	61	43	43	25	20	**362**

Table S4.2 Breakdown of male and female bighorn sheep (*Ovis canadensis*) assessed via resource selection function by population and season (S = summer, W = winter).

Population	2016S		2016/17W		2017S		2017/18W		2018S		2018/19W		2019S		2019/20W		2020S		Total	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
BHP	-	-	-	-	-	-	-	-	3	-	2	-	2	-	2	-	2	-	11	-
BSP	1	1	1	1	3	1	3	1	2	3	2	3	2	3	-	-	-	-	14	13
CAL	-	-	-	-	1	1	1	1	3	1	3	1	3	1	3	-	2	-	16	5
EML	1	1	1	-	5	-	5	-	6	1	6	1	5	1	5	1	5	1	39	6
MCK	-	-	-	-	3	-	3	-	4	2	1	1	2	1	2	1	1	1	16	6
RSP	9	4	9	1	13	1	12	1	10	3	7	-	7	-	-	-	-	-	67	10
SAW	-	-	-	-	2	-	3	-	3	-	2	-	2	-	2	-	2	-	16	-
TCE	10	5	6	1	5	-	3	1	4	3	2	3	2	3	1	3	1	2	34	21
TCS	2	1	2	-	2	-	2	-	2	2	1	2	1	2	-	1	-	1	12	9
TCW	1	1	2	1	2	1	1	1	2	3	1	3	1	3	1	2	1	1	12	16
TFK	1	-	1	-	1	-	1	-	1	-	-	-	-	-	-	-	-	-	5	-
TMP	3	2	3	1	3	2	2	-	1	2	-	2	-	2	-	1	-	-	12	12
UOP	4	2	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	7	3
Total	32	17	27	6	41	6	36	5	41	20	27	16	27	16	16	9	14	6	261	101

Table S4.3 Mean summer (S) and winter (W) home range size (km^2) of adult female and male bighorn sheep (*Ovis canadensis*) populations in southeastern Oregon and northern Nevada estimated using Brownian Bridge utilization distributions.

Pop	2016S		2016/17W		2017S		2017/18W		2018S		2018/19W		2019S		2019/20W		2020S	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
BHP	-	-	-	-	-	-	-	-	58.7	-	65.6	-	51.9	-	51	-	27.8	-
BSP	11.3	73.5	49	69.6	40.2	97.5	43.8	111.7	50.8	71.1	47.9	202.4	37.7	73	-	-	-	-
CAL	-	-	-	-	32.5	224.9	56.7	159.6	32.6	167.4	71	202.7	65	201.5	52.6	-	41.5	-
EML	46.6	174.6	60.1	-	48.2	-	59.1	-	-	445.9	89	82.4	37.8	43.3	51.5	65.7	50.4	67.4
MCK	-	-	-	-	15	-	19.5	-	18.7	41.6	25.7	50.2	22.9	32.7	29.7	52.2	19.6	30.6
RSP	42.5	83.6	50.9	130.9	60.5	158.3	54	108.8	43.7	173.6	59.2	-	54.4	-	-	-	-	-
SAW	-	-	-	-	10.3	-	9.7	-	12	-	27.2	-	8.6	-	12.7	-	14.8	-
TCE	17.6	32.7	24.7	53.6	23.5	-	30.2	64.2	23.7	51.1	28	73	23.5	48.2	27.7	102	29.8	33.7
TCS	41	48.2	39.4	-	42.4	-	35.4	-	34.3	17.6	48.2	68.4	36.1	50.7	-	101	-	29.7
TCW	46.1	31.7	64.4	48.8	46.6	65.6	80	-	55.9	40.3	68.6	73.6	51	45.7	54.1	100.5	50.0	48.2
TFK	22.3	-	34.1	-	21.9	-	33	-	35	-	-	-	-	-	-	-	-	-
TMP	94.8	127.1	81.4	126.6	104	101.9	87.2	-	127.1	332.6	-	83.9	-	95.9	-	96.8	-	-
UOP	24.9	56.3	22.7	102.9	33.2	-	-	-	-	-	-	-	-	-	-	-	-	-

Table S4.4 Univariate models assessing resource selection of topographic variables, slope, topographic position index (TPI), vector ruggedness measure (VRM) at the original resolution (10 m) and with various buffers (50, 100, and 500 m), and distance to escape terrain (d2esc) with three different slope cutoffs (≥ 27°, ≥ 37°, ≥ 45°) for bighorn sheep (*Ovis canadensis*) using area under the curve (AUC).

Data set	Parameter	AUC	95% AUC CI LB	95% AUC CI UB
Adult ♀ summer	**$Slope_{50}$**	**0.794**	**0.791**	**0.798**
	$Slope_{100}$	0.792	0.788	0.794
	Slope	0.769	0.766	0.774
	$Slope_{500}$	0.740	0.737	0.742
	TPI_{50}	**0.656**	**0.644**	**0.668**
	TPI_{100}	0.652	0.642	0.660
	TPI	0.601	0.593	0.613
	TPI_{500}	0.552	0.547	0.558
	VRM_{100}	**0.732**	**0.726**	**0.736**
	VRM_{50}	0.720	0.715	0.725
	VRM_{500}	0.708	0.703	0.715
	VRM	0.682	0.676	0.685
	d2esc27	**0.778**	**0.775**	**0.781**
	d2esc37	0.776	0.772	0.780
	d2esc45	0.760	0.754	0.767
Adult ♀ winter	**$Slope_{50}$**	**0.771**	**0.766**	**0.778**
	$Slope_{100}$	0.766	0.761	0.773
	Slope	0.754	0.749	0.761
	$Slope_{500}$	0.711	0.704	0.717
	TPI_{100}	**0.634**	**0.623**	0.644
	TPI_{50}	0.608	0.599	0.617
	TPI	0.566	0.558	0.575
	TPI_{500}	0.547	0.544	0.551
	VRM_{100}	**0.704**	**0.697**	**0.708**
	VRM_{50}	0.688	0.679	0.692
	VRM_{500}	0.683	0.678	0.687
	VRM	0.649	0.644	0.653
Adult ♂ summer	**$Slope_{50}$**	**0.740**	**0.729**	**0.747**
	$Slope_{100}$	0.734	0.721	0.742
	Slope	0.726	0.718	0.733
	$Slope_{500}$	0.698	0.683	0.707
	TPI_{100}	**0.621**	**0.613**	**0.634**
	TPI_{50}	0.585	0.574	0.599
	TPI_{500}	0.580	0.573	0.584
	TPI	0.539	0.529	0.546
	VRM_{100}	**0.652**	**0.639**	**0.660**
	VRM_{500}	0.651	0.636	0.658
	VRM_{50}	0.643	0.632	0.651
	VRM	0.635	0.624	0.646
	d2esc27	**0.734**	**0.723**	**0.738**
	d2esc37	0.644	0.632	0.651
	d2esc45	0.408	0.382	0.562
Adult ♂ winter	**$Slope_{50}$**	**0.751**	**0.735**	**0.759**
	$Slope_{100}$	0.748	0.732	0.756
	Slope	0.730	0.716	0.740
	$Slope_{500}$	0.681	0.667	0.692
	TPI_{100}	**0.680**	**0.668**	**0.689**
	TPI_{50}	0.663	0.653	0.673
	TPI	0.609	0.597	0.623
	TPI_{500}	0.556	0.552	0.580
	VRM_{100}	**0.705**	**0.694**	**0.715**
	VRM_{50}	0.696	0.684	0.705
	VRM_{500}	0.676	0.666	0.683
	VRM	0.662	0.657	0.667

	d2esc27	**0.768**	**0.763**	**0.774**	**d2esc27**	**0.765**	**0.752**	**0.773**
	d2esc37	0.741	0.735	0.746	d2esc37	0.755	0.747	0.767
	d2esc45	0.714	0.709	0.718	d2esc45	0.722	0.711	0.733

Table S4.5 Univariate models assessing resource selection of forage variables, NDVIMEAN and NDVIAMP at the original resolution (250 m) and with various buffers (250 and 500 m) for bighorn sheep (*Ovis canadensis*) using area under the curve (AUC).

Data set	**Parameter**	**AUC**	**95% AUC CI**		**Data set**	**Parameter**	**AUC**	**95% AUC CI**	
			LB	**UB**				**LB**	**UB**
Adult ♀ summer	**$NDVI_{MEAN}$**	**0.522**	**0.518**	**0.528**	Adult ♂ summer	**$NDVI_{MEAN}$**	**0.529**	**0.524**	**0.535**
	$NDVI_{MEAN250}$	0.518	0.514	0.523		$NDVI_{MEAN250}$	0.527	0.522	0.532
	$NDVI_{AMP500}$	0.513	0.511	0.516		$NDVI_{MEAN500}$	0.518	0.512	0.524
	$NDVI_{MEAN500}$	0.511	0.507	0.515		$NDVI_{AMP250}$	0.508	0.499	0.513
	$NDVI_{AMP250}$	0.510	0.508	0.512		$NDVI_{AMP}$	0.507	0.500	0.513
	$NDVI_{AMP}$	0.508	0.506	0.511		$NDVI_{AMP500}$	0.507	0.495	0.513
Adult ♀ winter	**$NDVI_{AMP}$**	**0.545**	**0.541**	**0.554**	Adult ♂ winter	**$NDVI_{AMP}$**	**0.555**	**0.542**	**0.574**
	$NDVI_{AMP250}$	0.544	0.539	0.553		$NDVI_{AMP250}$	0.555	0.539	0.573
	$NDVI_{AMP500}$	0.535	0.531	0.540		$NDVI_{AMP500}$	0.549	0.533	0.564
	$NDVI_{MEAN500}$	0.520	0.517	0.522		$NDVI_{MEAN500}$	0.524	0.512	0.539
	$NDVI_{MEAN250}$	0.515	0.513	0.517		$NDVI_{MEAN250}$	0.521	0.508	0.535
	$NDVI_{MEAN}$	0.512	0.510	0.515		$NDVI_{MEAN}$	0.519	0.506	0.534

$NDVI_{MEAN}$ = normalized difference vegetation index means and $NDVI_{AMP}$ = normalized difference vegetation index amplitude.

Table S4.6 Pearson correlation coefficient matrix used to asses variables used in resource selection models of bighorn sheep (*Ovis canadensis*). Variables include elevation, slope, topographic position index (TPI), vector ruggedness measure (VRM), distance to escape terrain (d2esc), ridge, and aspect, $NDVI_{AMP}$ or $NDVI_{MEAN}$, canopy and snow cover.

Data set	Covariate	Elevation	$Slope_{50}$	TPI_{50}	VRM_{100}	d2esc	Ridge	Aspect	$NDVI_{MEAN}$	Canopy cover	Snow cover
Adult ♀	Elevation	x	0.40	0.09	0.06	0.00	-0.13	-0.38	**0.51**	0.08	na
summer	$Slope_{50}$	0.40	x	0.05	**0.64**	0.14	-0.15	**-0.69**	0.32	0.06	na
	TPI_{50}	0.09	0.05	x	0.04	0.15	-0.02	-0.04	-0.01	-0.06	na
	VRM_{100}	0.06	**0.64**	0.04	x	0.22	-0.06	-0.39	0.10	0.05	na
	d2esc	0.00	0.14	0.15	0.22	x	-0.02	-0.04	0.00	0.00	na
	Ridge	-0.13	-0.15	-0.02	-0.06	-0.02	x	0.18	-0.01	0.08	na
	Aspect	-0.38	**-0.69**	-0.04	-0.39	-0.04	0.18	x	-0.32	-0.05	na
	$NDVI_{MEAN}$	**0.51**	0.32	-0.01	0.10	0.00	-0.01	-0.32	x	0.15	na
	Canopy cover	0.08	0.06	-0.06	0.05	0.00	0.08	-0.05	0.15	x	na
Data set	Covariate	Elevation	$Slope_{50}$	TPI_{100}	VRM_{100}	d2esc	Ridge	Aspect	$NDVI_{AMP}$	Canopy cover	Snow cover
Adult ♀	Elevation	x	0.40	0.09	0.07	0.00	-0.14	-0.36	0.40	**0.68**	0.13
winter	$Slope_{50}$	0.40	x	0.02	**0.64**	0.12	-0.15	**-0.67**	0.13	0.15	0.08
	TPI_{100}	0.09	0.02	x	-0.02	0.12	-0.01	-0.03	0.00	0.01	-0.07
	VRM_{100}	0.07	**0.64**	-0.02	x	0.20	-0.06	-0.39	0.03	-0.02	0.05
	d2esc	0.00	0.12	0.12	0.20	x	-0.01	-0.03	0.01	-0.01	0.00
	Ridge	-0.14	-0.15	-0.01	-0.06	-0.01	x	0.18	0.03	-0.07	0.10
	Aspect	-0.36	**-0.67**	-0.03	-0.39	-0.03	0.18	x	-0.12	-0.16	-0.07
	$NDVI_{AMP}$	0.40	0.13	0.00	0.03	0.01	0.03	-0.12	x	0.48	0.15
	Canopy cover	**0.68**	0.15	0.01	-0.02	-0.01	-0.07	-0.16	0.48	x	0.13
	Snow cover	0.13	0.08	-0.07	0.05	0.00	0.10	-0.07	0.15	0.13	x

Data set	Covariate	Elevation	$Slope_{50}$	TPI_{100}	VRM_{100}	d2esc	Ridge	Aspect	$NDVI_{AMP}$	Canopy cover	Snow cover
Adult ♂	Elevation	x	0.29	0.16	-0.02	-0.01	-0.06	-0.34	0.41	0.04	na
summer	$Slope_{50}$	0.29	x	-0.04	**0.57**	0.07	-0.07	**-0.64**	0.23	0.04	na
	TPI_{100}	0.16	-0.04	x	-0.11	0.03	-0.01	-0.02	-0.04	-0.07	na
	VRM_{100}	-0.02	**0.57**	-0.11	x	0.14	-0.01	-0.38	0.10	0.06	na
	d2esc	-0.01	0.07	0.03	0.14	x	0.00	-0.02	0.00	0.00	na
	Ridge	-0.06	-0.07	-0.01	-0.01	0.00	x	0.09	0.08	0.07	na
	Aspect	-0.34	**-0.64**	-0.02	-0.38	-0.02	0.09	x	-0.29	-0.04	na
	$NDVI_{MEAN}$	0.41	0.23	-0.04	0.10	0.00	0.08	-0.29	x	0.12	na
	Canopy cover	0.04	0.04	-0.07	0.06	0.00	0.07	-0.04	0.12	x	na
Data set	Covariate	Elevation	$Slope_{50}$	TPI_{100}	VRM_{100}	d2esc	Ridge	Aspect	$NDVI_{AMP}$	Canopy cover	Snow cover
Adult ♂	Elevation	x	0.27	0.16	-0.04	-0.02	-0.06	-0.36	0.42	**0.63**	0.09
winter	$Slope_{50}$	0.27	x	-0.02	**0.60**	0.10	-0.09	**-0.63**	0.23	0.13	0.06
	TPI_{100}	0.16	-0.02	x	-0.07	0.04	-0.01	-0.03	-0.01	0.01	-0.09
	VRM_{100}	-0.04	**0.60**	-0.07	x	0.17	-0.03	-0.37	0.11	-0.01	0.07
	d2esc	-0.02	0.10	0.04	0.17	x	-0.01	-0.03	0.00	-0.02	0.00
	Ridge	-0.06	-0.09	-0.01	-0.03	-0.01	x	0.13	0.02	-0.06	0.10
	Aspect	-0.36	**-0.63**	-0.03	-0.37	-0.03	0.13	x	-0.27	-0.16	-0.06
	$NDVI_{AMP}$	0.42	0.23	-0.01	0.11	0.00	0.02	-0.27	x	0.41	0.13
	Canopy cover	**0.63**	0.13	0.01	-0.01	-0.02	-0.06	-0.16	0.41	x	0.09
	Snow cover	0.09	0.06	-0.09	0.07	0.00	0.10	-0.06	0.13	0.09	x

Supplementary figures

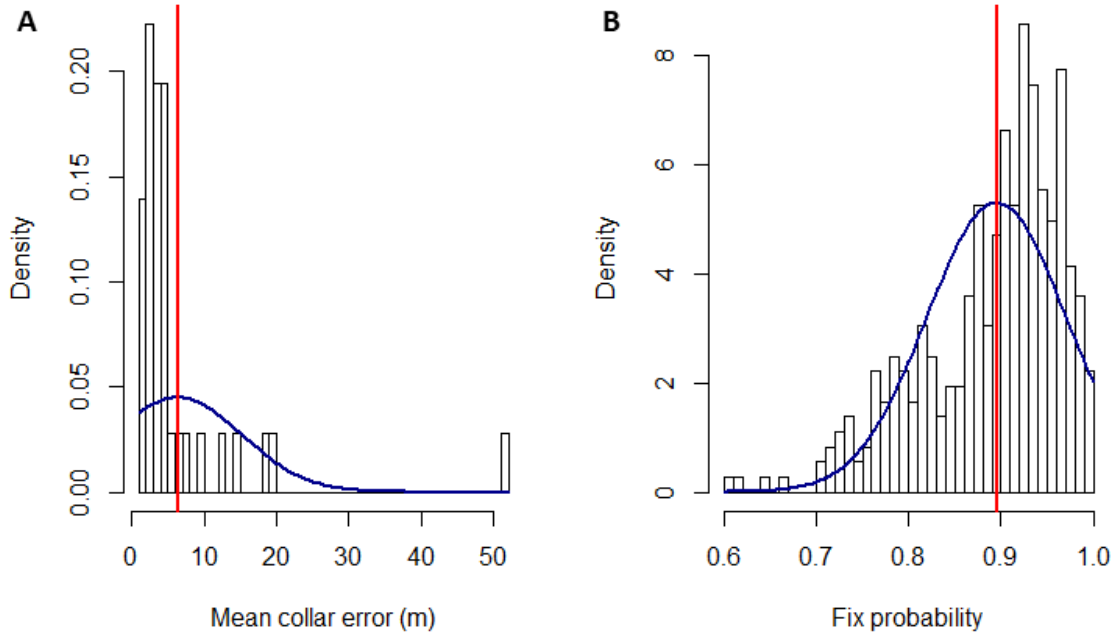

Figure S4.1 (A) Histogram showing error rates of Vectronics Aerospace collars. Individual collar error binned to one-meter intervals representing the proportion of collars within each bin. The red line indicates the mean collar error (m), and the blue line indicates a smoothed density curve of collar error. (B) Histogram showing the fix probability of Vectronics Aerospace collars. The individual bins represent the number of collars within each bin; the red line indicates the mean fix probability, and the blue line the distribution of the fixes.

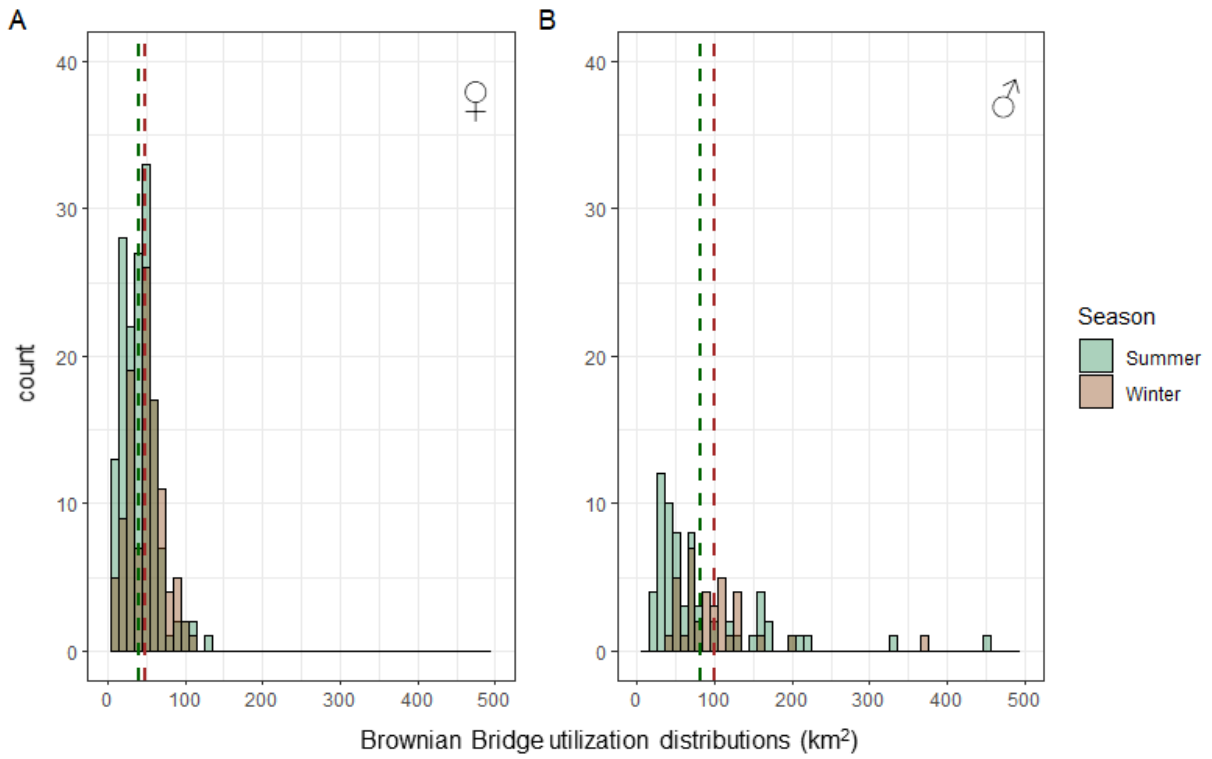

Figure S4.2 Distribution of summer and winter Brownian Bridge utilization distribution (BBUDs) sizes for (A) female (♀) and (B) male (♂) bighorn sheep (*Ovis canadensis*). The x-axis indicates the size (km^2) of the BBUDs, while the y-axis shows the number of BBUDs in each 10 km^2 bin. The dashed lines indicate the mean BBUD size for each season.

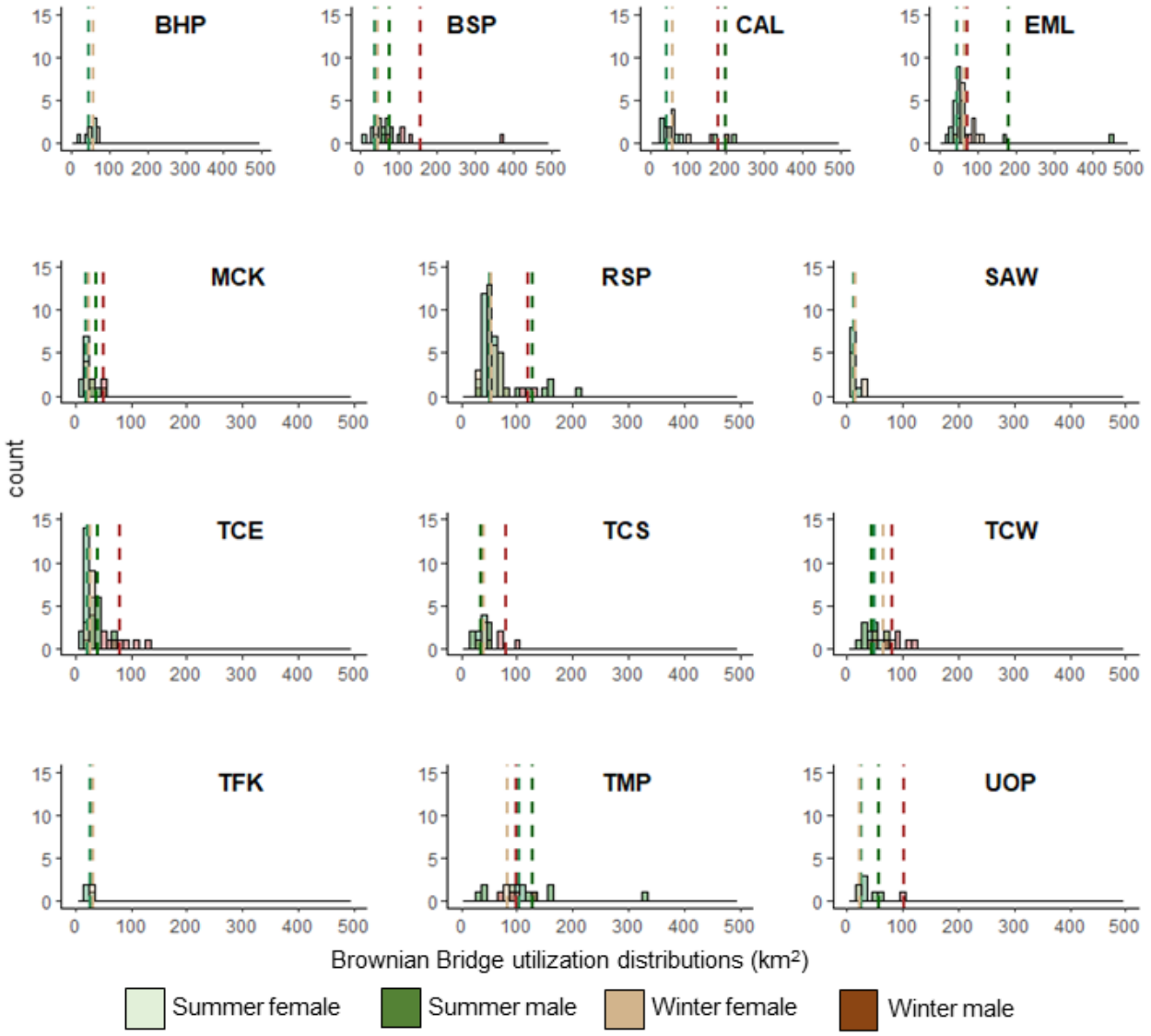

Figure S4.3 Distribution of population-specific summer and winter Brownian Bridge utilization distribution (BBUDs) sizes for adult female and male bighorn sheep (*Ovis canadensis*). The x-axis indicates the size (km^2) of the BBUDs, while the y-axis shows the number of BBUDs in each 10 km^2 bin. The dashed lines indicate the mean BBUD size for each season.

CHAPTER 5

Assessing risk of contact between California-managed bighorn sheep (*Ovis canadensis*) and potential sources of respiratory disease in the northern Basin and Range ecosystem

Robert S. Spaan[1], Clinton W. Epps[1], Donald G. Whittaker[2], and Mike Cox[3].

[1] Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA

[2] Oregon Department of Fish and Wildlife, Salem, Oregon, USA

[3] Nevada Department of Wildlife, Reno, Nevada, USA

Corresponding Author:

Robert Spaan[1]

Nash Hall, 2820 SW Campus Way, Corvallis, OR, USA 97331

rob.spaan@oregonstate.edu

Information

Abstract

North American bighorn sheep (*Ovis canadensis*) have experienced significant declines and population extirpations due to novel pathogens such as *Mycoplasma ovipneumoniae*, and disease continues to limit population restoration. Understanding the risk of contact between bighorn populations and potential sources of pathogens is vital to managing bighorn sheep populations effectively, especially for pathogens that cause respiratory pneumonia. This study evaluated the risk of contact with potential sources of *M. ovipneumoniae* for restored bighorn sheep populations in southeastern Oregon and northern Nevada. Although evaluations in other systems have focused on potential contact with domestic sheep grazing allotments, in this case, we also considered other bighorn sheep populations both within and outside the study area as potential sources of risk, allowing managers to consider consequences of management actions in the event of disease outbreak. We also considered private or other lands where domestic sheep or goats could be present. We used GPS collar data from 43 male and 68 female bighorn sheep collected from 2016–2020 and employed the methodology of O'Brien et al. (2014) to pursue four objectives regarding the risk of contact among the sampled populations. First, we generated seasonal core herd home ranges for each population. Second, we determined potential sources of risk for *M. ovipneumoniae* exposure. Third, we generated separate seasonal foray frequencies and probabilities for male and female bighorn sheep west and east of the highway, U.S. Route 95, given different population histories and other evidence that suggested the system is divided into two metapopulations. Fourth, we used those

components along with sex- and season-specific habitat suitability models to estimate the risk of contact for each study population with potential sources of *M. ovipneumoniae*. Male bighorn sheep had higher foray frequencies and probabilities, and forays were longer than females. Foray distances for male and female bighorn sheep west of U. S. Route 95 were lower in the summer than males and females east of U. S. Route 95. Across the system, the expected number of contacts with potential risk sources was almost entirely male-driven. However, multiple populations on each side of U. S. Route 95 had overlapping core herd home ranges, indicating a high degree of contact and thus disease spread probability within each metapopulation. The risk of contact with populations outside the study area was negligible, except that the Upper Owyhee population had non-zero risk of contact with neighboring populations in Idaho. The risk of contact between bighorn within the study area and domestic sheep grazing allotments on the periphery likewise appeared negligible. Still, all study populations had some probability of contact with other potential sources of risk. Although the model suggested contact could occur between metapopulations separated by U. S. Route 95, movement, genetic, and disease evidence to date suggests such contacts have not occurred recently.

Introduction

Novel pathogens, often carried by non-native livestock and wild species, present a significant risk to wildlife (Cunningham et al. 2017). Wild species often struggle to defend themselves from novel pathogens due to being immunologically naïve (Tompkins et al. 2015, Escobar et al. 2021), as observed for African buffalo (*Syncerus caffer*) infected with bovine tuberculosis (*Mycobacterium bovis*) (Jolles et al. 2005), European boars (*Sus scrofa*) infected with African swine fever (*Asfivirus* spp.) (Bergmann et al. 2021), and in various African ungulates infected with brucellosis (*Brucella abortus*) or rinderpest (*Morbillivirus* spp.) (Dobson 1995, Gorsich et al. 2015). Responses to novel diseases can include increased mortality of adults or juveniles, or reduced reproductive capacity, resulting in population declines (Jolles et al. 2005, Gorsich et al. 2015). Thus, infectious diseases can significantly affect wildlife species, including population decline and even population extirpation (De Castro and Bolker 2004, Preece et al. 2017).

Several strategies exist for managing directly transmitted novel diseases. These include reducing disease in the population of organisms in which the pathogen survives (reservoir species), reducing disease in populations to which the pathogen is transmitted (target species), and the reduction or prevention of transmission between reservoir and target species (Wobeser 2002). Reservoir species are populations of organisms in which infectious pathogens reside and reproduce (Haydon et al. 2002). In some cases, wildlife acquires novel pathogens from livestock, which continue to serve as a reservoir if present in the system. However, exposed populations of wildlife can also subsequently act as reservoirs,

as was historically the case for African buffalo (*Syncerus caffer*) infected with bovine tuberculosis (*Mycobacterium bovis*) (Caron et al. 2003). In that case, management may require limiting further contact between wildlife and livestock and between exposed and unexposed populations of wildlife (Cross et al. 2007).

Bighorn sheep (*Ovis canadensis*) in North America exemplify the challenge of managing disease from novel pathogens in systems where livestock and native wildlife populations might act as reservoirs. Bighorn experienced widespread declines and population extirpations across their distribution by the early 20th century (Risenhoover et al. 1988). Exposure to various pathogens is hypothesized to have played a significant role in their decline, and continues to hinder bighorn sheep recovery (Wehausen et al. 2011, Cassirer et al. 2018). However, *Mycoplasma ovipneumoniae*, an novel bacterial pathogen transmitted via direct contact from domestic sheep (*O. aries*) and goats (*Capra hircus*) to bighorn sheep, was recently determined to be a primary causative agent of bighorn sheep decline (Besser et al. 2008, Cassirer et al. 2018, Garwood et al. 2020). Exposure of bighorn sheep to a novel strain of *M. ovipneumoniae* typically results in mortalities across all age classes, with surviving animals maintaining some immunity to that strain. However, the disease often persists due to chronic adult carriers (often referred to as chronic shedders) that infect the annual influx of newborn offspring (lambs) (Cassirer and Sinclair 2007, Cassirer et al. 2013). Those lambs lack immunity and mortality is often high for years after that strain becomes established (Cassirer and Sinclair 2007, Cassirer et al. 2013, Spaan et al. 2021). Immunity to *M. ovipneumoniae* appears to be symptomatic, with exposure to new strains of *M. ovipneumoniae* resulting in similar outcomes as previously unexposed populations (Cassirer et al. 2017). Moreover, bighorn to bighorn transmission subsequently also plays a vital role in exposure and persistence of *M. ovipneumoniae* in wild populations of bighorn, which often exhibit significant spatial structuring with occasional inter-population movements (Dekelaita et al. 2020, Shirkey et al. 2021).

Diverse management responses to *M. ovipneumoniae* have been employed following exposure of bighorn populations to novel strains. Those responses include the test and removal of chronic shedders (Bernatowicz et al. 2016, Garwood et al. 2020), depopulation followed by reintroduction (Bernatowicz et al. 2016), range expansion which would result in reduced densities (Lula et al. 2020), herd augmentation, and density reduction. Almberg et al. (2022) simulated management strategies and found that only test and remove, depopulation and reintroduction, or range expansion would result in population recovery following an epidemic. In contrast, herd augmentation and density reduction increased *M. ovipneumoniae* persistence and population size (Almberg et al. 2022). However, there is general agreement that avoiding contact between bighorn sheep populations and potential sources of novel strains of *M. ovipneumoniae* is one of the most critical aspects of managing this novel pathogen.

To date, several studies have attempted to characterize risk of contact between populations of bighorn sheep and sources of potential respiratory disease (Clifford et al. 2009, Carpenter et al. 2014, O'Brien et al. 2014). Clifford et al. (2009) used GPS collar data to determine potential contact rates for Sierra Nevada bighorn sheep (*O. c. sierrae*) in California by determining the proportion of 100% bighorn sheep utilization distributions overlapping domestic sheep grazing allotments or non-federal land. O'Brien et al. (2014) also used radio telemetry data to determine contact risk. However, O'Brien et al. (2014) differentiated their model from previous iterations by incorporating foray behavior. Forays are periodic, long-distance exploratory movements made outside the home range by male and female bighorn sheep (Singer et al. 2001, DeCesare and Pletscher 2006). O'Brien et al. (2014) used core herd home ranges, foray behavior, habitat suitability models, and demographic data to assess bighorn sheep's risks of contact with sources of disease. The risk of contact model estimates the probability that a foray movement will reach any given point on the landscape (O'Brien et al. 2014).

This study aimed to determine the risk of contact for bighorn sheep populations within California bighorn sheep in the northern Basin and Range ecosystem of southeastern Oregon and northern Nevada. Our approach to modeling risk was novel in that we not only modeled risk of contact between bighorn sheep from the thirteen focal study populations with grazing allotments but considered all potential sources of *M. ovipneumoniae*, i.e., domestic sheep and goats as well as bighorn sheep within the study area extent on both federal and private lands. To do this, we employed GPS collar data and followed the methodology of O'Brien et al. (2014) in pursuing four objectives. First, we generated seasonal core herd home ranges for each population of male and female bighorn sheep. Second, we determined potential risk sources. Third, we generated seasonal foray frequencies and probabilities for male and female bighorn sheep west and east of the highway, U. S. Route 95. Fourth, we used the generated data, along with seasonal habitat suitability models generated for male and female bighorn sheep in this system from a previous study (Chapter 4), and herd demographics provided by the Oregon Department of Fish and Wildlife and Nevada Department of Wildlife to compute bighorn sheep risk of contact.

Materials & Methods

Study area

The populations of bighorn sheep we studied were located in southeastern Oregon and northern Nevada, between 41.2 and 42.3°N and 116.9 and 118.4°W (Fig. 5.1). Elevation across the study area ranged from approximately 1,050 m in the Owyhee Canyon to 2,957 m in the Santa Rosa Mountains. Mean precipitation for the study area is approximately 22.5–35.0 cm per annum. However, parts of the Santa Rosa and Trout Creek Mountains receive significantly more rainfall (Omernik and Griffith 2014).

The area is characterized by terrain types including elevated plateaus, sheer-walled canyons with intermittent lakes and ephemeral streams, and mountains of low to mid-elevation with primarily steep slopes and ephemeral or perennial streams (Omernik and Griffith 2014). Basalt and rhyolite are the dominant geological types, with other rocks interspersed, which give rise to primarily shallow, poor soils (Omernik and Griffith 2014).

Sagebrush steppe is the dominant vegetation type. The most common woody species include quaking aspen (*Populus tremuloides*) and mountain mahoganies (*Cercocarpus* spp.), found in snow pockets, Western juniper (*Juniperus occidentalis*), located in rocky areas, and willows (*Salix* spp.), found in riparian areas (Omernik and Griffith 2014). Common shrubs include big sagebrush (*Artemisia tridentate*) and low sagebrush (*A. arbuscular*) (Omernik and Griffith 2014). The most common palatable herbaceous species for ungulates include perennial bunchgrass, e.g., bluebunch wheatgrass (*Psudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), Thurber needlegrass (*Achnatherum thurberianum*), bottlebrush squirreltail (*Elymus elymoides*), and the less palatable Sandberg bluegrass (*Poa secunda*). Ungulates in the study area include "California" managed bighorn sheep, pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and elk (*Cervus canadensis*) (Omernik and Griffith 2014), while potential bighorn predators include golden eagles (*Aquila chrysaetos*), mountain lion (*Puma concolor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) (Omernik and Griffith 2014).

Standard land-use practices include cattle ranching and grain and hay cultivation (Omernik and Griffith 2014). Overgrazing and fire suppression have led to the spread of fires and encroachment of invasive annuals such as medusahead (*Taeniatherium caput-medusae*) and cheatgrass (*Bromus tectorum*), which tend to outcompete indigenous species (Omernik and Griffith 2014). In addition, local wildlife and cattle rely on artificial water sources, wetlands, springs, and streams for water (Omernik and Griffith 2014).

The study includes thirteen bighorn sheep populations, which we considered two separate metapopulations due to genetic, disease exposure, and space use differences that became apparent over the course of the study (see Results below, and Spaan et al. 2021). A highway separates these metapopulations, U. S. Route 95 (Fig. 5.1). The western metapopulation includes the Blue Mountain (BSP) and Trout Creek east (TCE), south (TCS), and west (TCW) populations (Fig. 5.1). The eastern metapopulation includes the Calico (CAL), Eight Mile (EML), Martin Creek (MCK), and Sawtooth (SAW) populations in the Santa Rosas of northern Nevada, and the Bowden Hills (BHP), Rattlesnakes (RSP), Ten Mile (TMP), Three Forks (TFK), and the Upper Owyhee (UOP) populations in Oregon (Fig. 1). Although established with single translocations in the late 1980s and early 1990s, the three Trout Creek populations trace their lineage to Williams Lake, British Columbia (Table S5.1). In addition, dispersing bighorn sheep from the Trout Creeks colonized Blue Mountain in the mid to late 1990s (pers.

comm. S. Torland, ODFW). The eastern metapopulation's bighorn sheep populations are derived from at least three different translocation sources, i.e., Kamloops, Penticton, and Williams Lake, BC (Table S5.1). Consequently, population genetic diversity in this system for bighorn sheep, derived from 16 microsatellite loci, is variable. The western metapopulation of bighorn sheep has a mean population expected heterozygosity (H_E) of 0.30 (range = 0.26–0.33) compared to 0.41 (range = 0.33–0.48) for the eastern metapopulation (Spaan et al. 2021).

Another justification for considering the study populations as two separate metapopulations is the historical and spatial distribution of *M. ovipneumoniae* within the system (Spaan et al. 2021). All populations within the eastern metapopulation have been exposed to *M. ovipneumoniae*, with the first recorded detections occurring in SAW in 2003. Until recently, only a single strain of *M. ovipneumoniae* was detected within this system, although the strain type for TFK and UOP has yet to be determined (Spaan et al. 2021).

Capturing and collaring

All capture, handling, and disease testing were conducted by the Oregon Department of Fisheries and Wildlife (ODFW) and the Nevada Department of Wildlife (NDOW). The bighorn sheep capture methodology followed the recommendations of Foster (2004) and the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016). Between January 2016 and February 2018, NDOW and ODFW captured, collared, and sampled adult male and female bighorn sheep across 13 populations in southeastern Oregon and northern Nevada (Fig. 5.1). Bighorn sheep were captured by firing a netgun from a helicopter, blindfolded and hobbled (Krausman et al. 1985). They then fit each bighorn sheep with a GPS collar and took biological samples.

In this paper, we used data from adult females (n = 68) and adult males (n = 38), fit with Vertex Globalstar collars (Vectronic Aerospace, Berlin, Germany). In addition, five adult male bighorn sheep (n = 5) were fit with Telonics Globalstar collars (Telonics, Mesa, AZ, USA). Most collars provided GPS locations every 13 hours and operated on the same time cycle, except for three collars that reported locations every 11 hours.

Core herd home ranges

We generated core herd home ranges, defined as the core use areas of an entire population (Carpenter et al. 2014, O'Brien et al. 2014). Core herd home ranges for the summer period included April 1 – September 30, and the winter period was October 1 – March 31. Lambing in some populations within this system begins at the end of March, or early April (Spaan et al. 2021), with rutting, thus beginning in

late September or early October. We used the bighorn sheep risk of contact tool (RoC Tool; O'Brien et al. 2020) to generate seasonal core herd home ranges for each population, where core herd home ranges are derived using 95% utilization distributions using the kernel method with the default reference (h_{ref}) smoothing parameter (Fieberg 2007). All core herd home ranges were generated with data from males and females, except for the BHP, SAW, and TFK populations, which only had spatial data from females (Fig. 5.2).

Sources of risk

Potential sources of infection risk include both other bighorn sheep populations and potential sources of domestic sheep and goats. Excluding the thirteen bighorn sheep focal study populations, defined as populations containing collared bighorn sheep, the study area extent fully or partially included an additional ten bighorn sheep populations (hereafter, non-focal populations), which could present additional risk. Non-focal populations within the study area extent included the Owyhee Front (OWF) and Owyhee River (OWR) populations in Idaho, Andorno (AND), Double H's (DHP), Jackson Mountain (JMP), and Snowstorms (SSP) populations in Nevada, and the Black Point (BPP), Juniper Ridge (JRP), Sheepheads (SHP) and Steen Mountain (STP) populations in Oregon (Fig. 5.1). Additionally, we included the population polygon for the Montana Mountains (MTP) in Nevada, which was depopulated in 2015 due to a virulent outbreak of *M. ovipneumoniae* (pers. comm. E. Partee, NDOW), to determine the risk of contact between the Trout Creek populations and MTP (Fig. 5.1).

To assess potential sources of domestic sheep and goats, we accessed the Bureau of Land Management's (BLM) "Land Surface Management" shapefiles for Idaho, Nevada, and Oregon (https://navigator.blm.gov) for landownership. We did not try to determine if sheep or goats were present on private or Bureau of Indian Affairs (BIA) land. We simply treated them as places where sheep and goats could be present now or in the future. Landownership types within the study area extent included BLM cattle grazing allotments, BLM sheep grazing allotments, private land, BIA land, state of Oregon land, U.S. Forest Service (USFS) land, and other minor designations such as Department of Energy (DOE) land (Fig. S5.1). We then reclassified the layer to potential risk sources, which included BLM sheep grazing allotments, private, and BIA lands (Fig. S5.2). In a 2011 survey of 453 domestic sheep operations across 22 USA states, the USDA's National Animal Health Monitoring System found that 88.5% of operations had *M. ovipneumoniae* infected domestic sheep (USDA-APHIS 2015). Heinse et al. (2016) surveyed 40 domestic sheep and goat flocks in Washington and detected *M. ovipneumoniae* in 37.5% of the flocks, and 78% had escapee incidents.

Foray behavior

To determine foray frequencies and foray distance probabilities of male and female bighorn sheep across summer and winter, we used the 'multiple ring buffer' and 'intersect tools' in ArcMap 10.8 (Environmental Systems Research Institute, Inc., Redlands, CA). First, we delineated concentric rings of 1 km distance around each core herd home range until the rings reached all locations (Fig. 5.3). The 'intersect function' was then applied to determine the maximum distance of each individual from each core herd home range. We then calculated the foray frequency, which equated to the number of individuals located outside the core herd home range within a given season. Next, the foray distance probability, calculated as the Euclidean distance or straight-line distance between the edge of the core herd home range and the furthest point, was calculated as the proportion of foraying individuals reaching each 1-km-interval out to the maximum foray distance. Finally, we applied a Gaussian kernel to the distance probabilities to smooth the foray probabilities (Fig. S5.1) (O'Brien et al. 2014).

Habitat preferences

Four predictive habitat surfaces were generated as part of a previous resource selection study assessing space use and habitat selection of the same populations of bighorn sheep in the northern Basin and Range ecosystem (chapter 3). The predictive habitat surfaces, representing summer and winter habitat selection by male and female bighorn sheep were used to model bighorn sheep's risk of contact with the core herd home ranges of bighorn sheep populations and potential sources of domestic sheep and goats (Fig. 5.1). The focal study population UOP was the closest to the border of the study area extent, ~18 km away (Fig. 5.1). The nearest of the three domestic sheep grazing allotments in the study area, the Wilder-Quinn Allotment, was ~25 km from the closest focal study population, TCS (Fig. 5.1).

Estimation of risk of contact

We used the Risk of Contact Tool (RoCT) an R-based implementation of the Risk of Contact model described in O'Brien et al. (2014) to model the risk of contact between bighorn sheep populations and potential sources of domestic sheep and goats. Model inputs include the foray frequencies and foray distances, along with the individual habitat suitability models and herd demographic data, provided by the Oregon Department of Fish and Wildlife and Nevada Department of Wildlife. From the model inputs we generated individual male and female, total male and female, and cumulative risk of contacts for each population of bighorn sheep with all focal and non-focal study populations as well as potential sources of domestic sheep and goats.

The formulas and description of the risk of contact calculations can be found in O'Brien et al. (2014). Briefly, the model first calculates a risk of contact of a single bighorn sheep in a particular season

is a joint probability with three components, the probability of a foray, the conditional probability of said individual reaching a specific foray distance given the foray happened, and the conditional probability of risk at a foray distance given that distance was reached. Next, the model determines the probability of intersecting a risk source as being proportional to the risk area within a band of homogenous habitat. If the habitat within the risk source is more favorable, the probability of a bighorn sheep intersecting the risk source is greater. The probability of an animal reaching the risk source is equal to the maximum probability of a single band within the bounds of the risk source being reached. Finally, population-level contact rates are generated by summing the individual male and female bighorn sheep within each population.

Results

Core herd home ranges

Core herd home ranges varied greatly in size among populations and seasons. For example, the three core herd home ranges where we only had adult female GPS collar data had a mean size of 51.0 km^2 (14.1–120.1 km) in the summer and 59.6 km^2 (14.2–126.3 km^2) in the winter (Table S5.2). In comparison, where we had data from adult males and females core herd home ranges (n = 10) had a mean home range size of 227.1 km^2 (71.4–674.2 km^2) in the summer and 171.3 km^2 (42.3–355.5 km^2) in the winter (Table S5.2). Core herd home ranges for the western metapopulation had a mean size of 107.4 km^2 (76.1–159.2 km^2) in the summer and 128.6 km^2 (95.1–145.8 km^2) in the winter, while core herd home ranges for the eastern metapopulation had a mean size of 295.0 km^2 (71.4–674.2 km^2) in the summer and 192.8 km^2 (42.3–355.5 km^2) in the winter (Table S5.2).

Foray frequency and probabilities

Male bighorn sheep had higher foray frequencies (Table S5.3), foray distance probabilities (Table S5.4), and forayed further (Tables 5.1 and S5.4) across all seasons compared to female bighorn sheep. For males, foray frequencies did not vary much between seasons in either metapopulation and each population had at least one individual make a foray (Tables 5.1 and S5.4). The males west of U. S. Route 95 had a foray frequency of 0.568 in the summer and 0.669 in winter, while males east of U. S. Route 95 had a foray frequency of 0.669 in the summer and 0.597 in the winter (Table S5.3). Foray distances were more variable relative to the foray probabilities. The maximum Euclidean foray distance for males west of U. S. Route 95 was 5.2 km in the summer and 35.9 km in the winter (Table 5.1). In comparison, the maximum Euclidean foray distance for males east of U. S. Route 95 was 35.8 km in the summer and 28.9 km in the winter (Table 5.1).

For females, foray frequencies were lower across both seasons for the western metapopulation with females not foraying far from their core herd home ranges (Tables 5.1 and S5.4). The females west of U. S. Route 95 had a foray frequency of 0.168 in the summer and 0.033 in winter (Table S5.3). Conversely, females east of U. S. Route 95 had a foray frequency of 0.218 in the summer and 0.418 in the winter (Table S5.3). Females west of U. S. Route 95 had a maximum Euclidean foray distance of 1.3 km in the summer and 2.4 km in the winter (Table 5.1). In comparison, females east of U. S. Route 95 had a maximum Euclidean foray distance of 9.1 km in the summer and 5.8 km in the winter (Table 5.1).

Intraspecies risk of contact

Across the entire system in both seasons, the expected number of contacts by the bighorn sheep population with core herd home ranges was almost entirely male-driven. For bighorn sheep populations west of U. S. Route 95, the risk of contact model predicted no contact risk between focal-study populations and focal or non-focal study populations (Tables 5.2 and 5.3). In the Trout Creeks, the core herd home ranges of TCE overlapped, indicating a high number of potential contacts with TCS and TCW in the summer and winter (Tables 5.2 and 5.3, Fig. 5.2). In contrast, the core herd home ranges of TCS and TCW did not overlap with each other in either season (Tables 5.2 and 5.3, Fig. 5.2). The BSP core herd home range did not overlap with any population across all seasons (Tables 5.2 and 5.3, Fig. 5.2). Overlapping core herd home ranges indicate a high number of potential contacts between respective bighorn sheep from the respective populations.

For bighorn sheep populations east of U. S. Route 95, the TMP core herd home range overlapped with CAL and EML across all seasons (Tables 5.2 and 5.3, Fig. 5.1). Likewise, the core herd home ranges of BHP and RSP overlapped (Tables 5.2 and 5.3, Fig. 5.1). The risk of contact model predicted 0.25 and 0.32 expected contacts by CAL bighorn sheep with the core herd home ranges of EML and MCK in the summer and 0.21 and 0.20 contacts in the winter, respectively (Tables 5.2 and 5.3). EML bighorn sheep had 0.01 and 0.03 expected contacts with CAL, and 0.13 and 0.04 expected contacts with MCK in the summer and winter, and MCK had < 0.01 expected contacts with the TMP core herd home range in the summer (Tables 5.2 and 5.3). On the other hand, SAW only had a predicted 0.11 expected contacts with the AND core herd home range in the summer (Table 5.2). TMP did not have any expected contacts with any populations in the winter, but in the summer had <0.01 and 0.11 expected contacts with the MCK and RSP core herd home ranges, and RSP had 1.98 expected contacts with the TMP core herd home range in the summer (Table 5.2).

The risk of contact model predicted 0.73 and 0.08 expected contacts by RSP and TMP bighorn sheep respectively with the BSP core herd home range and 0.04 and 0.05 expected contacts by TMP bighorn sheep respectively with TCE and TCS core herd home ranges of the western metapopulation

(Table 5.2). Lastly, in the Upper Owyhee, TFK bighorn sheep had 0.01 and 0.05 expected contacts with the UOP core herd home range in the summer and winter. In contrast, UOP bighorn sheep had 0.63 and 0.83 expected contacts with the TFK core herd home range and 0.71 and 0.01 expected contacts with the OWR polygon, a non-focal study population in the summer and winter (Tables 5.2 and 5.3).

Bighorn sheep risk of contact to potential domestic sources

Across the study area, there were no expected contacts between bighorn sheep and domestic sheep grazing allotments (Tables S5.5–S5.17). For bighorn sheep populations west of U. S. Route 95, the mean number of expected contacts ≥ 0.05 with other potential sources of domestic stock sheep and goats was 1.5 (range = 0–3) during the summer and 2.8 (range = 0–4) in the winter (Tables 5.4 and S5.5–S5.8). All potential risk sources with an expected number of contacts ≥ 0.05 were private properties with a mean size of 51.2 km^2 (range = 0.2–257.1 km^2) in the summer and 29.2 km^2 (range = 0.2–257.1 km^2) in the winter (Tables 5.4 and S5.5–S5.8). Additionally, 67% of the potential domestic risk sources overlapped with the core herd home ranges of bighorn sheep in the summer and 64% in the winter (Tables 5.4 and S5.5–S5.8).

For bighorn sheep east of U. S. Route 95, the mean number of expected contacts with potential sources of domestic stock sheep and goats with an expected number of contacts ≥ 0.05 was 13.6 (range = 1–38) during the summer and 10.4 (range = 1–32) in the winter (Tables 5.4 and S5.9–S5.17). Potential risk sources with a probability ≥ 0.05 included private properties and Bureau of Indian Affairs land with a mean size of 13.6 km^2 (range = 0.03–461.3 km^2) in the summer and 15.2 km^2 (range = 0.03–461.3 km^2) in the winter (Tables 5.4 and S5.9–S5.17). Additionally, 70% of the potential domestic risk sources overlapped with the core herd home ranges of bighorn sheep in the summer and 71% in the winter (Tables 5.4 and S5.9–S5.17).

Discussion

All focal study populations of bighorn sheep in southeastern Oregon and northern Nevada were at risk of either intraspecies population contact or potential contact with domestic sheep and goats largely due to the presence of private or other lands where livestock could be present. The risk of contact within this system was driven by male bighorn sheep due to higher foray frequencies and foray distance probabilities (Tables S5.3 and S5.4). In addition, the risk of contact was greater in the eastern than the western metapopulations due to higher foray probabilities of individuals making longer distances forays. However, the risk of contact between the Trout Creek bighorn sheep populations in the west metapopulation was high due to overlapping core herd home ranges. Female bighorn sheep in this system contribute very little to the risk of any population because they are highly philopatric (Chapter 3). In

addition, females exhibited much lower foray frequencies and shorter foray distances across all seasons relative to male bighorn sheep (Table S5.3 and S5.4).

Foray frequencies were generally higher than those observed in other systems. For example, Singer et al. (2001) recorded 0.100 (range: 0–0.230) forays per bighorn sheep of either sex across ten translocated populations, while O'Brien et al. (2014) recorded summer foray rates of 0.141 and 0.015 forays per male and female respectively for Hells Canyon populations. Comparatively, summer foray frequencies for males and females for the two metapopulations ranged from 0.568–0.669 for males and 0.168–0.218 for females. While the foray frequencies we measured may seem high, most forays were close to the boundaries of the core herd home ranges, especially for the western metapopulation. Additionally, Singer et al. (2001) and O'Brien et al. (2014) generated foray frequencies with VHF telemetry data that were much sparser over time, making it harder to detect short forays. Indeed, O'Brien et al. (2014) noted that the foray frequencies and foray distances recorded in the Hells Canyon system were most certainly underestimated due to the collection of more temporally coarse data. The high resolution of our GPS collar data likely generated more realistic foray frequencies, particularly for short forays of limited duration.

Foray distances for male and female bighorn sheep, conversely, were lower than most forays observed in other systems. Foray distances by bighorn sheep were similar to those recorded in Montana by DeCesare and Pletscher (2006), where a maximum foray distance of 32.9 km for males and 9.8 for females was observed. However, longer foray distances of 48 km in southwestern Alberta (Festa-Bianchet 1986) and over 50 km by male bighorn sheep in the Hells Canyon (O'Brien et al. 2014) and Sierra Nevada systems (Anderson et al. 2022) have been observed. In the Hells Canyon, female bighorn sheep made forays of more than 30 km in the summer and 50 km in the winter (O'Brien et al. 2014). The lower foray distances observed in our system could be because these bighorn sheep use discrete patches of steep escape terrain, separated by flatter and more open sagebrush and grassland (Spaan et al. 2021). In contrast, Rocky Mountain and Sierra Nevada bighorn sheep habitat is more continuous, facilitating extra home range movements. Another potential reason for the shorter observed forays could that bighorn in this system lack long-term knowledge of the system because of relatively recent (1978–2011) reestablishment of populations via translocation. Native populations of Rocky Mountain bighorn sheep in Idaho, Montana, and Wyoming make far more migratory and elevational movements to access quality forage than re-established and augmented populations (Jesmer et al. 2018, Lowrey et al. 2019). Jesmer et al. (2018) suggest that this may be due to learned and cultural transmission between generations of bighorn sheep.

The RoC model performed reasonably well based on the spatial distribution of the Santa Rosa *M. ovipneumoniae* strain-type and bighorn sheep movements within this system. The overlap in core ranges

or high predicted contacts among bighorn populations in the eastern metapopulation conforms with the distribution of the Santa Rosa strain, which is present in all the Santa Rosa populations, as well as BHP, RSP, and TMP (Spaan et al. 2021). Recently, a new strain of *M. ovipneumoniae*, hereafter referred to as the Snowstorms strain because it was first detected in SSP bighorn sheep (pers. comm. E. Partee, NDOW), has been detected in bighorn sheep on the southern end of the Santa Rosas in the AND population (Fig. 5.1). The RoC models did not predict contact between the focal-study populations in the Santa Rosas and the non-focal study population SSP (Fig. 5.1). However, we did not model the risk of contact between the non-focal populations AND and SSP (Fig. 5.1). Another yet-to-be strain-typed strain of *M. ovipneumoniae* was recently detected in TMP (pers. comm. E. Partee, NDOW). This strain of *M. ovipneumoniae* is suspected to originate from the Upper Owyhee Canyon system east of U.S. Route 95. Again, the RoC models did not suggest a risk of contact between either TMP and TFK or UOP, nor vice versa. However, other bighorn sheep subpopulations occupy habitats within the Upper Owyhee Canyon system, which we could not model. In both cases, connective habitat exists in the form of canyons along the north fork of the Little Humboldt between SSP and the Santa Rosas and the West Little Owyhee River between the Upper Owyhee Canyon system and TMP.

Although BSP is thought to have been naturally colonized by dispersing Trout Creek bighorn sheep (pers. comm. S. Torland, ODFW), the model did not predict that risk of contact. The low foray distance frequencies in the western metapopulation (Table S5.4), where only a single male made a foray greater than 18 km (Table 5.1), may explain the risk of contact not being detected. Additionally, minimal, suitable habitat exists between BSP and the Trout Creeks (Fig 5.2 A-D). Despite the lack of risk predicted between BSP and the Trout Creeks, a foraying bighorn sheep from BSP generated a maximum straight-line foray distance of 35.9 km while intersecting the core herd ranges of TCS and TCW on his foray to and from BSP to the McDermitt River. No risk of contact value was derived as the foray probability for a distance of 12 km or greater was only 0.06 and 18 km or greater was only 0.03. In addition, minimal predicted habitat exists between BSP and the Trout Creek populations.

The RoC models predicted contact between the two metapopulations on either side of U.S. Route 95, with < 0.01 to 0.73 expected contacts per summer between bighorn sheep from BHP, RSP, and TMP with BSP, TCE, and TCS core herd home ranges. However, genetic, disease, and movement data suggest no evidence of contact between these two metapopulations. As such, the RoC model poorly handles rigid boundaries, such as U. S. Route 95. While highways act as a barrier to movement, highway crossings occasionally occur (Epps et al. 2010, 2018, Dekelaita 2020), notably when facilitated by crossing structures (Creech et al. 2020). In addition, the generally flat terrain bordering either side of U.S. Route 95 further inhibits bighorn sheep crossings. While we can consider U.S. Route 95 a barrier to movement, this barrier is not impermeable.

The risk of contact tool has some methodological limitations. For instance, it would be more appropriate to generate cost resistance surfaces using foray data to assess the risk of contact (Anderson et al. 2022), as foraying bighorn sheep are expected to select habitat differently when foraying. However, we lacked sufficient foray data to parameterize a cost resistance surface. In addition, most forays that we observed in this system fell within bighorn sheep habitat on the periphery of core herd home ranges: as such, while technically forays, they were not long-distance movements resulting in contact with populations or locations separated by significant areas of non-habitat. In fact, we only observed a single incidence of a long-distance foray where an individual crossed unsuitable habitat. Additionally, the model fails to address the attraction between bighorn sheep and domestic sheep and goats, or bighorn sheep from other populations (O'Brien et al. 2014), nor does the model address the possibility of domestic sheep and goats making forays into bighorn sheep occupied areas, which has been shown to be a somewhat common occurrence in other systems where domestic sheep are present (Heinse et al. 2016).

Management Implications

Understanding the risk of contact between potential sources of diseases within a system is essential for disease and population management. In our study, we assessed the risk of contact between bighorn sheep focal study populations and potential sources of the bacterial pathogen *M. ovipneumoniae*, the primary causative agent of pneumonia in bighorn sheep. To that end, we applied the risk of contact model (O'Brien et al. 2014) to determine the risk of contact between bighorn sheep and potential sources of domestic sheep and goats. While most potential sources of domestic sheep and goats of *M. ovipneumoniae* in our study area are not known to host domestic sheep and goats currently, they might do so in the future. Thus, our modeling exercise will help managers determine which areas or landowners might be worth targeting with outreach if the addition of domestic livestock seems possible or likely. Additionally, we assessed the potential risk of contact amongst bighorn sheep populations, which is not usually formally considered. Doing so is essential as the focal study populations contain *M. ovipneumoniae*-exposed and unexposed populations. The risk of contact modeling results can be used in several ways to better inform managers or potentially drive the decision-making process, e.g., by incorporating the data into a structured decision-making process (Sells et al. 2016). The risk of contact models should be updated with new spatial and demographic data whenever possible, as changes to model parameters will result in different risk estimates.

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Tables

Table 5.1 Foray details for male (*n* = 11) and female (*n* = 13) bighorn sheep (*Ovis canadensis*) across southeastern Oregon and northern Nevada. Data was collected from GPS collared bighorn sheep between 2016 and 2020.

			Summer forays			Winter forays		
				Distance (km)			Distance (km)	
Population	**Sex**	**Pop.**	**Frequency**	**Mean**	**Max**	**Frequency**	**Mean**	**Max**
Blue Mountain[1]	♂	9	1/9	1.3	1.3	6/9	8.8	35.9
Trout Creek - east[1]	♂	15	15/17	2.3	5.2	12/19	3.6	7.2
Trout Creek - south[1]	♂	10	4/6	1.1	1.3	4/7	3.3	4.3
Trout Creek - west[1]	♂	20	4/11	0.6	1.0	5/12	3.7	17.2
Calicos[2]	♂	10	3/3	11.6	18.1	2/3	13.7	17.0
Eight Mile[2]	♂	5	3/4	17.0	35.8	2/4	15.9	28.9
Martin Creek[2]	♂	5	3/4	0.9	2.0	4/4	3.0	3.4
Rattlesnake[2]	♂	20	9/10	3.8	10.4	6/13	7.9	14.2
Ten Mile[2]	♂	10	3/9	7.6	19.8	3/9	8.5	20.0
Upper Owyhee[2]	♂	20	1/4	8.5	8.5	1/4	14.0	14.0
Blue Mountain[1]	♀	16	0/9	-	-	0/9	-	-
Trout Creek - east[1]	♀	30	1/25	0.4	0.4	2/30	1.4	2.4
Trout Creek - south[1]	♀	20	4/8	0.3	0.5	0/9	-	-
Trout Creek - west[1]	♀	40	3/8	0.7	1.3	0/9	-	-
Bowden Hills[2]	♀	14	3/7	1.5	1.6	1/7	1.3	1.3
Calicos[2]	♀	35	1/10	9.1	9.1	0/10	-	-
Eight Mile[2]	♀	30	0/23	-	-	4/24	1.1	1.1
Martin Creek[2]	♀	11	7/11	0.1	0.4	5/13	0.9	3.2
Rattlesnake[2]	♀	45	4/41	0.6	0.6	31/46	1.1	5.8
Sawtooth[2]	♀	12	7/10	0.5	0.9	2/4	1.3	2.1
Ten Mile[2]	♀	20	0/8	-	-	0/9	-	-
Three Forks[2]	♀	10	3/3	0.5	0.6	2/4	1.3	2.1
Upper Owyhee[2]	♀	40	0/6	-	-	0/9	-	-

[1] indicates bighorn sheep populations west and [2] east of U.S. Route 95

Table 5.2 Expected number of male, female, and cumulative summer contacts between bighorn sheep (*Ovis canadensis*) focal-study populations on the y-axis with bighorn sheep populations on the x-axis. INF indicates bighorn sheep populations where core herd home ranges overlap. (-) means no predicted contacts between populations. Non-focal study populations, BPP, DHP, JRP, JMP, MTP, OWF, SHP, SSP, and STP, are not included in the table as they did not generate any risk.

Data	Pop.	AND	BHP	BSP	CAL	EML	MCK	OWR	RSP	SAW	TCE	TCS	TCW	TFK	TMP	UOP
♂	BSP	-	-	NA	-	-	-	-	-	-	-	-	-	-	-	-
	CAL	-	-	-	NA	0.24	0.31	-	-	-	-	-	-	-	INF	-
	EML	-	-	-	0.01	NA	-	-	-	-	-	-	-	-	INF	-
	MCK	-	-	-	0.13	-	NA	-	-	-	-	-	-	-	<0.01	-
	RSP	-	INF	0.71	-	-	-	-	NA	-	-	-	-	-	1.92	-
	SAW	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	TCE	-	-	-	-	-	-	-	-	-	NA	INF	INF	-	-	-
	TCS	-	-	-	-	-	-	-	-	-	INF	NA	-	-	-	-
	TCW	-	-	-	-	-	-	-	-	-	INF	-	NA	-	-	-
	TMP	-	-	0.08	INF	INF	<0.01	-	0.11	-	0.04	0.05	-	-	NA	-
	UOP	-	-	-	-	-	-	0.69	-	-	-	-	-	0.61	-	NA
♀	BHP[1]	-	NA	<0.01	-	-	-	-	INF	-	-	-	-	-	-	-
	BSP	-	-	NA	-	-	-	-	-	-	-	-	-	-	-	-
	CAL	-	-	-	NA	0.01	0.01	-	-	-	-	-	-	-	INF	-
	EML	-	-	-	<0.01	NA	-	-	-	-	-	-	-	-	INF	-
	MCK	-	-	-	<0.01	-	NA	-	-	-	-	-	-	-	<0.01	-
	RSP	-	INF	0.02	-	-	-	-	NA	-	-	-	-	-	0.06	-
	SAW	0.01	-	-	-	-	-	-	-	NA	-	-	-	-	-	-
	TCE	-	-	-	-	-	-	-	-	-	NA	INF	INF	-	-	-
	TCS	-	-	-	-	-	-	-	-	-	INF	NA	-	-	-	-
	TCW	-	-	-	-	-	-	-	-	-	INF	-	NA	-	-	-
	TFK[1]	-	-	-	-	-	-	-	-	-	-	-	-	NA	-	0.01
	TMP	-	-	<0.01	INF	INF	<0.01	-	<0.01	-	<0.01	<0.01	-	-	INF	-
	UOP	-	-	-	-	-	-	0.02	-	-	-	-	-	0.02	-	INF
∑	BHP[1]	-	NA	<0.01	-	-	-	-	INF	-	-	-	-	-	-	-
	BSP	-	-	NA	-	-	-	-	-	-	-	-	-	-	-	-
	CAL	-	-	-	NA	0.25	0.32	-	-	-	-	-	-	-	INF	
	EML	-	-	-	0.01	NA	-	-	-	-	-	-	-	-	INF	-
	MCK	-	-	-	0.13	-	NA	-	-	-	-	-	-	-	<0.01	-

RSP	-	INF	0.73	-	-	-	-	NA	-	-	-	-	-	1.98	-
SAW	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TCE	-	-	-	-	-	-	-	-	-	NA	INF	INF	-	-	-
TCS	-	-	-	-	-	-	-	-	-	INF	NA	-	-	-	-
TCW	-	-	-	-	-	-	-	-	-	INF	-	NA	-	-	-
TFK[1]	-	-	-	-	-	-	-	-	-	-	-	-	NA	-	0.01
TMP	-	-	0.08	INF	INF	<0.01	-	0.11	-	0.04	0.05	-	-	NA	-
UOP	-	-	-	-	-	-	0.71	-	-	-	-	-	0.63	-	NA

[1] Contact rates assessed using only female bighorn sheep data

Pop. codes: AND – Andorno; BHP – Bowden Hills; BPP – Black Pt.; BSP – Blue Mt.; CAL – Calicos; DHP – Double H's; EML – Eight Mile; JMP – Jackson Mt.; JRP – Juniper Ridge; MCK – Martin Ck.; MTP – Montanas; OWF – Owyhee Front; OWR – Owyhee Rvr.; RSP – Rattlesnakes; SAW – Sawtooth; SHP – Sheepheads; SSP – Snowstorms; STP – Steens Mt.;TCE – Trout Ck. east; TCS – Trout Ck. south; TCW – Trout Ck. west; TFP – Three Forks; TMP – Ten Mile; UOP – Upper Owyhee.

Table 5.3 Expected number of male, female, and cumulative winter contacts between bighorn sheep (*Ovis canadensis*) focal-study populations on the y-axis with bighorn sheep populations on the x-axis. INF indicates bighorn sheep populations where core herd home ranges overlap. (-) means no predicted contacts between populations. Non-focal study populations, AND, BPP, DHP, JRP, JMP, MTP, OWF, SHP, SSP, and STP, are not included in the table as they did not generate any risk.

Data	Pop.	BHP	BSP	CAL	EML	MCK	OWR	RSP	SAW	TCE	TCS	TCW	TFK	TMP	UOP
♂	BSP	-	NA	-	-	-	-	-	-	-	-	-	-	-	-
	CAL	-	-	NA	0.19	0.18	-	-	-	-	-	-	-	INF	-
	EML	-	-	0.03	NA	-	-	-	-	-	-	-	-	INF	-
	MCK	-	-	0.04	-	NA	-	-	-	-	-	-	-	-	-
	RSP	INF	-	-	-	-	-	NA	-	-	-	-	-	-	-
	SAW	-	-	-	-	-	-	-	NA	-	-	-	-	-	-
	TCE	-	-	-	-	-	-	-	-	NA	INF	INF	-	-	-
	TCS	-	-	-	-	-	-	-	-	INF	NA	-	-	-	-
	TCW	-	-	-	-	-	-	-	-	INF	-	NA	-	-	-
	TMP	-	-	INF	INF	-	-	-	-	-	-	-	-	NA	-
	UOP	-	-	-	-	-	0.01	-	-	-	-	-	0.78	-	NA
♀	BHP[1]	NA	-	-	-	-	-	INF	-	-	-	-	-	-	-
	BSP	-	NA	-	-	-	-	-	-	-	-	-	-	-	-
	CAL	-	-	NA	0.02	0.01	-	-	-	-	-	-	-	INF	-
	EML	-	-	<0.01	NA	-	-	-	-	-	-	-	-	INF	-
	MCK	-	-	<0.01	-	NA	-	-	-	-	-	-	-	-	-

	RSP	INF	-	-	-	-	-	NA	-	-	-	-	-	-	-
	SAW	-	-	-	-	-	-	-	NA	-	-	-	-	-	-
	TCE	-	-	-	-	-	-	-	-	NA	INF	INF	-	-	-
	TCS	-	-	-	-	-	-	-	-	INF	NA	-	-	-	-
	TCW	-	-	-	-	-	-	-	-	INF	-	NA	-	-	-
	TFK[1]	-	-	-	-	-	-	-	-	-	-	-	NA	-	0.05
	TMP	-	-	INF	INF	-	-	-	-	-	-	-	-	NA	-
	UOP	-	-	-	-	-	<0.01	-	-	-	-	-	0.08	-	NA
∑	BHP[1]	NA	-	-	-	-	-	INF	-	-	-	-	-	-	-
	BSP	-	NA	-	-	-	-	-	-	-	-	-	-	-	-
	CAL	-	-	NA	0.21	0.20	-	-	-	-	-	-	-	INF	-
	EML	-	-	0.03	NA	-	-	-	-	-	-	-	-	INF	-
	MCK	-	-	0.04	-	NA	-	-	-	-	-	-	-	-	-
	RSP	INF	-	-	-	-	-	NA	-	-	-	-	-	-	-
	SAW	-	-	-	-	-	-	-	NA	-	-	-	-	-	-
	TFK[1]	-	-	-	-	-	-	-	-	-	-	-	NA	-	0.05
	TCE	-	-	-	-	-	-	-	-	NA	INF	INF	-	-	-
	TCS	-	-	-	-	-	-	-	-	INF	NA	-	-	-	-
	TCW	-	-	-	-	-	-	-	-	INF	-	NA	-	-	-
	TMP	-	-	INF	INF	-	-	-	-	-	-	-	-	NA	-
	UOP	-	-	-	-	-	0.01	-	-	-	-	-	0.86	-	NA

[1] Contact rates assessed using only female bighorn sheep data

Pop. codes: Pop. codes: AND – Andorno; BHP – Bowden Hills; BPP – Black Pt.; BSP – Blue Mt.; CAL – Calicos; DHP – Double H's; EML – Eight Mile; JMP – Jackson Mt.; JRP – Juniper Ridge; MCK – Martin Ck.; MTP – Montanas; OWF – Owyhee Front; OWR – Owyhee Rvr.; RSP – Rattlesnakes; SAW – Sawtooth; SHP – Sheepheads; SSP – Snowstorms; STP – Steens Mt.;TCE – Trout Ck. east; TCS – Trout Ck. south; TCW – Trout Ck. west; TFP – Three Forks; TMP – Ten Mile; UOP – Upper Owyhee.

Table 5.4 Expected number of seasonal contacts between bighorn sheep (*Ovis canadensis*) population with potential sources of domestic sheep (*Ovis aries*) and goats (*Capra hircus*) with a probability ≥ 0.05 in both the summer and winter for summer and winter. Size indicates the mean and range of property sizes (km^2) with which each bighorn sheep population is predicted to make contact.

		summer			**winter**		
			size (km^2)			**size (km^2)**	
Metapop.	**Pop.**	**contacts**	**mean**	**range**	**contacts**	**mean**	**range**
western	BSP[1]	-	NA	NA	-	NA	NA
western	TCE[1]	2	12.8	3.8–21.8	3	8.7	0.7–21.8
western	TCS[1]	1	2.6	NA	4	2.9	0.2–7.0
western	TCW[1]	3	93.0	0.2–257.1	4	70.9	0.2–257.1
western	$\bar{x}$	**1.5**	**51.2**	0.2–257.1	**2.8**	**29.2**	0.2–257.1
eastern	BHP[2]	1	3.1	NA	1	3.1	NA
eastern	CAL[2]	34	6.4	0.03–78.3	32	6.9	0.2–78.3
eastern	EML[2]	18	13.1	0.1–78.3	15	10.2	0.1–78.2
eastern	MCK[2]	10	49.8	0.2–461.3	7	70.9	0.3–461.3
eastern	RSP[2]	9	0.8	0.2–3.1	7	1.0	0.2–3.1
eastern	SAW[2]	1	199.5	NA	1	199.5	NA
eastern	TFK[2]	1	0.8	NA	2	1.1	0.8–1.4
eastern	TMP[2]	38	7.1	0.03–78.3	24	13.6	0.1–78.3
eastern	UOP[2]	10	22.5	0.7–207.8	5	3.3	0.2–7.7
eastern	$\bar{x}$	**13.6**	**13.6**	**0.03–461.3**	**10.4**	**15.2**	**0.03–461.3**

[1]western- and [2]eastern metapopulation

Figures

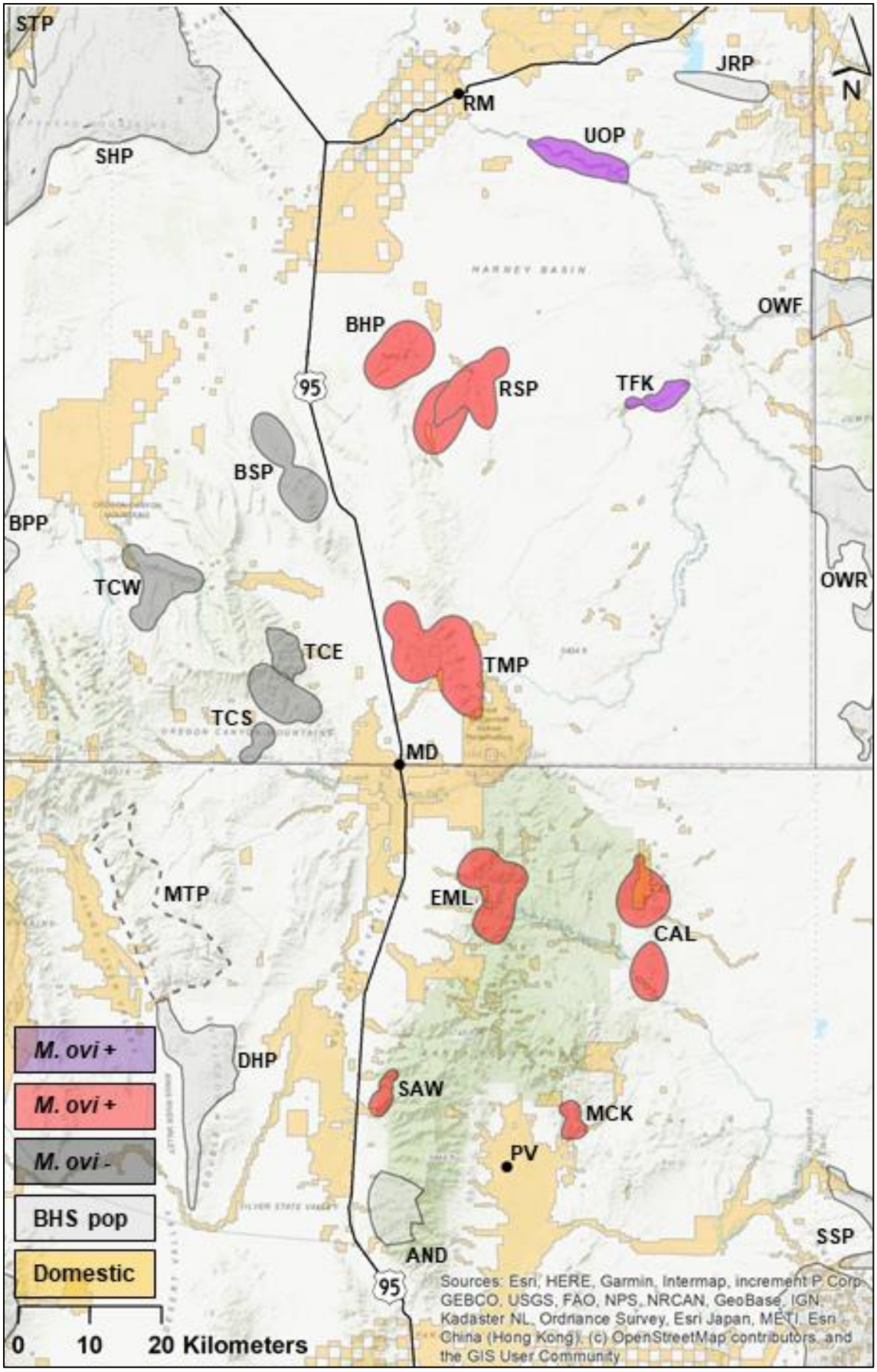
STP
JRP
N
RM
UOP
SHP
HARNEY BASIN
OWF
BHP
95
RSP
TFK
BSP
BPP
TCW
OWR
TCE
TMP
TCS
MD
MTP
EML
CAL
M. ovi +
M. ovi +
M. ovi -
BHS pop
Domestic
DHP
SAW
MCK
PV
SSP
AND
95
0 10 20 Kilometers
Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

Figure 5.1 The focal study populations, indicated by polygons with *Mycoplasma ovipneumoniae* status within the study area, represent the 95% KDE of female bighorn sheep (*Ovis canadensis*) for the summer. The colors of the polygons indicate *M. ovipneumoniae* exposure status with U. S. Route 95 separating exposed and unexposed focal study populations, and the colors show a single known (red) and unknown (purple) strain. The three-letter codes representing the focal study populations are BHP – Bowden Hills, BSP – Blue Mountain, CAL – Calico, EML – Eight Mile, MCK – Martin Creek, RSP – Rattlesnakes, SAW – Sawtooth, TCE – Trout Creek east, TCS – Trout Creek south, TCW – Trout Creek west, TFK – Three Forks, TMP – Ten Mile, and UOP – Upper Owyhee populations. The three-letter codes representing the non-focal study population polygons provided by the Oregon Department of Fish and Wildlife and Nevada Department of Wildlife are AND – Andorno, BPP – Black Point, DHP – Double H, JRP – Juniper Ridge, MTP – Montana, OWF – Owyhee Front, OWR – Owyhee River, SHP – Sheepheads, SSP – Snowstorms, and STP – Steens populations. The orange polygons represent potential domestic sheep and goat sources, and the dashed polygon outline indicates the recently (~2015) extirpated MTP. The two-letter codes represent the towns: MD – McDermitt, PV – Paradise Valley, and RM – Rome.

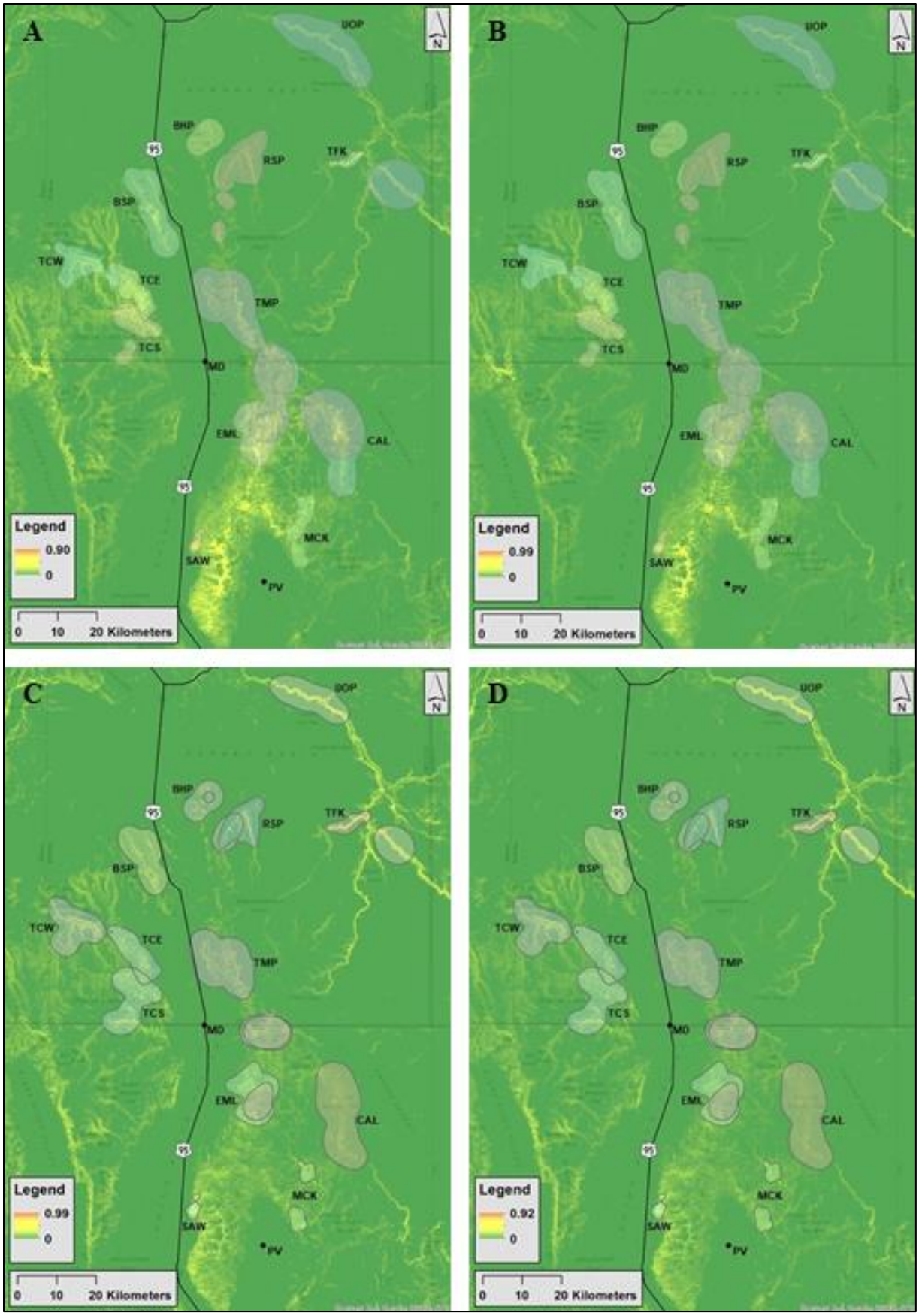
A
B
C
D
UOP
BHP
RSP
TFK
BSP
TCW
TCE
TMP
TCS
MD
EML
CAL
MCK
SAW
PV
95
N
Legend
0.90
0
0.99
0.92
0 10 20 Kilometers

Figure 5.2 Predicted habitat surfaces show A. summer male, B. summer female, C. winter male, and D. winter female bighorn sheep (*Ovis canadensis*) probability of use. Three letter codes indicate the summer core herd home ranges representing: BHP – Bowden Hills, BSP – Blue Mountain, CAL – Calico, EML – Eight Mile, MCK – Martin Creek, RSP – Rattlesnakes, SAW – Sawtooth, TCE – Trout Creek east, TCS – Trout Creek south, TCW – Trout Creek west, TFK – Three Forks, TMP – Ten Mile, and UOP – Upper Owyhee populations. The two-letter codes represent the towns: MD – McDermitt, and PV – Paradise Valley.

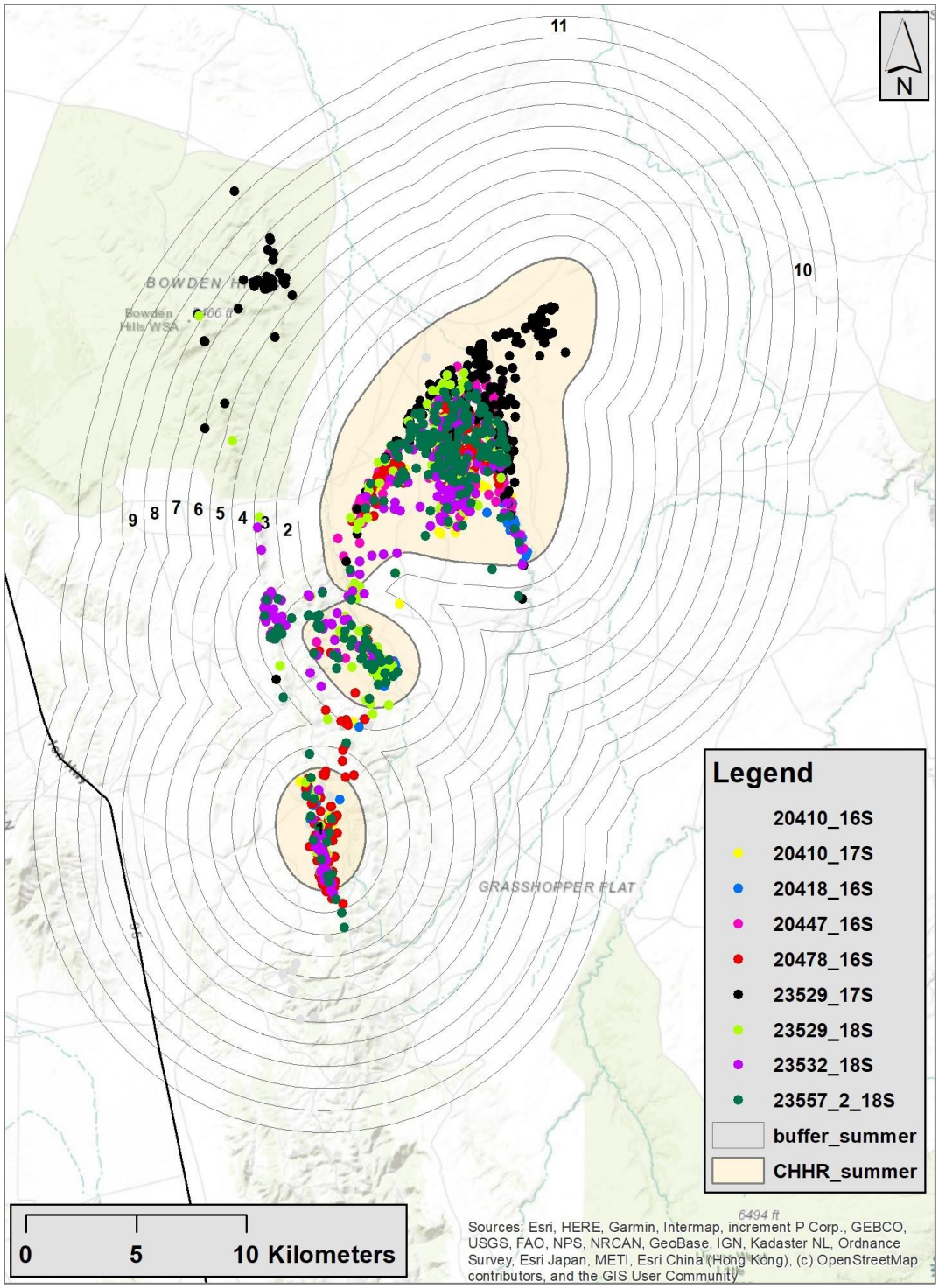

Figure 5.3 GPS point location data from individual male bighorn sheep (*Ovis canadensis*) collars in the Rattlesnake population for the entire study period (2016-2020). The core herd home range (CHHR) is derived from male and female bighorn sheep locations. The buffers extending to 11 km in this map are generated using ArcMap's "multiple line buffer" tool. We then use the intersect tool to determine if and how far individual bighorn sheep made linear forays from the CHHR.

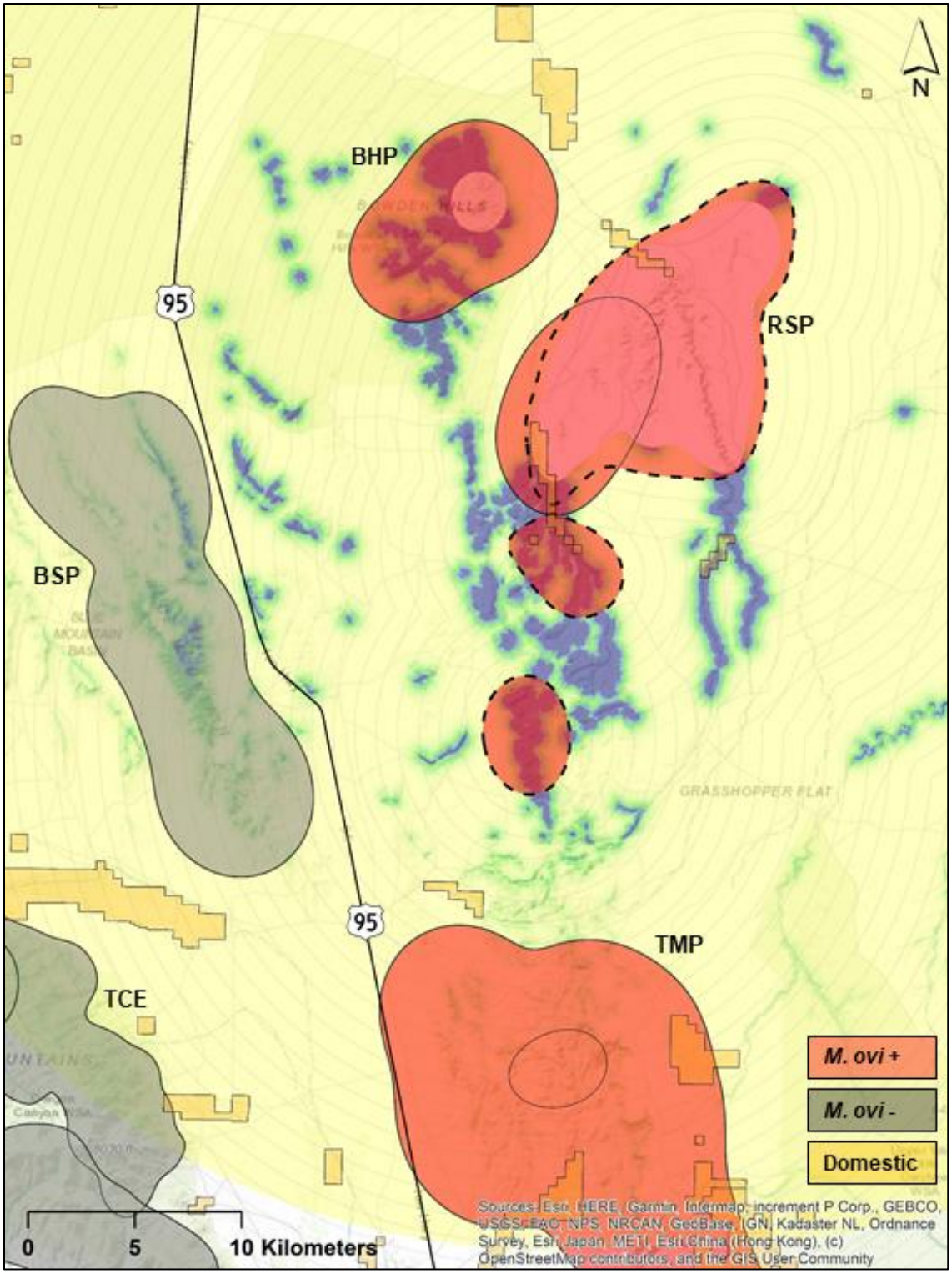

Figure 5.4 Map showing foray probability of RSP male bighorn sheep. The color denotes the relative probability of a bighorn sheep reaching different areas including core herd home ranges of neighboring bighorn sheep populations (red and grey polygons) and potential sources of domestic sheep and goats (orange polygons).

Supplementary Material

Supplementary Tables

Table S5.1 Translocation histories of bighorn sheep populations included in this study. Details include the population code (Pop) where the bighorn sheep were established or translocated to, translocation type (Trans_type), when the translocation took place (Year), the number of individuals (# ind.) translocated, the source population (Source pop.), the source state or province (S-State) population, the destination population (Destination pop.), and the destination state (D-State).

Pop	Trans_type	Year	# individuals	Source pop.	S-State	Destination pop.	D-State
Bowden Hills	Colonization	unknown	?	Rattlesnake	OR	Bowden Hills	OR
Blue Mountain	Colonization	~1990s	?	Trout Ck.	OR	Blue Mountain	OR
Calicos	Import	1985	20	Williams Lake	BC	Pine Forest	NV
	Import	1988	18	Williams Lake	BC	Pine Forest	NV
	In jurisdiction	2011	25	Pine Forest	NV	Calico Mtn.	NV
Eight Mile	Import	1978	12	Penticton	BC	Eight Mile	NV
	In jurisdiction	2014	3	Pine Forest	NV	Three Mile Ck.	NV
Martin Creek*	Import	1984	13	Hart Mtn.	OR	Jackson Mtn.	NV
	Import	1985	20	Williams Lake	BC	Pine Forest	NV
	Import	1986	2	E fork of Owyhee Riv.	ID	Jackson Mtn.	NV
	Import	1987	15	Lower Owyhee	OR	Jackson Mtn.	NV
	Import	1988	18	Williams Lake	BC	Pine Forest	NV
	Import	1989	18	Kamloops	BC	High Rock/Calicos	NV
	In jurisdiction	1998	12	Jackson Mtn.	NV	Hinkey	NV
	In jurisdiction	1999	12	High Rock/Calicos	NV	Pine Forest	NV
	In jurisdiction	2006	21	Montana Mts.	NV	Martin Ck.	NV
	In jurisdiction	2011	27	Pine Forest	NV	Martin Ck.	NV
Rattlesnake	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1992	19	Hart Mtn.	OR	Rattlesnake Ck.	OR
Sawtooth	Import	1989	20	Penticton	BC	Sawtooth	NV
Trout Creeks – east	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1987	27	Hart Mtn.	OR	Trout Creek Mtn.	OR
Trout Creeks – south	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1990	14	Hart Mtn.	OR	Trout Creek Mtn.	OR

Trout Creeks – west	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1990	19	Hart Mtn.	OR	Trout Creek Mtn.	OR
Ten Mile	Import	1954	20	Williams Lake	BC	Hart Mtn.	OR
	In jurisdiction	1960	4	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1961	7	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1989	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1992	15	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	18	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	15	Steens Mtn.	OR	Ten Mile Rim	OR
Upper Owyhee*	Import	1954	20		BC	Hart Mtn.	OR
	In jurisdiction	1960	4	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1961	7	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1965	17	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1983	21	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1983	14	Hart Mtn.	OR	Upper Owyhee	OR
	In jurisdiction	1987	15	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1987	16	Hart Mtn.	OR	Lower Owyhee	OR
	In jurisdiction	1989	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1992	15	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	17	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	18	Hart Mtn.	OR	Steens Mtn.	OR
	In jurisdiction	1993	36	Steens Mtn.	OR	Upper Owyhee	OR
	In jurisdiction	1994	21	Lower Owyhee	OR	Upper Owyhee	OR
	In jurisdiction	1995	17	Hart Mtn.	OR	Upper Owyhee	OR
	In jurisdiction	2007	21	Philippi Canyon	OR	Upper Owyhee	OR

*****Indicates incomplete history

Table S5.2 Seasonal core herd home ranges (km^2) assessed using a 95% kernel density estimate for bighorn sheep (*Ovis canadensis*) populations in southeastern Oregon and northern Nevada.

Population	summer (km^2)	winter (km^2)
Bowden Hills*	120.1	126.3
Blue Mountain	159.2	135.3
Calicos	397.6	337.7
Eight Mile	160.1	141.5
Martin Creek	71.4	42.3
Rattlesnakes	158.9	103.0
Sawtooth*	14.1	14.2
Trout Creeks - east	76.1	95.1
Trout Creeks - south	90.5	145.8
Trout Creeks - west	103.8	138.0
Three Forks*	18.7	37.2
Ten Mile	674.2	355.5
Upper Owyhee	379.1	218.8

* Assessed with only female bighorn sheep spatial data

Table S5.3 Summer and winter foray frequencies of bighorn sheep (*Ovis canadensis*) west and east of U. S. Route 95. Populations west of U. S. Route 95 include Blue Mountain, the Trout Creeks, east, south, and west, while those to the east of U. S. Route 95 include Bowden Hills, Calicos, Eight Mile, Martin Creek, Rattlesnakes, Sawtooth, Three Forks, Ten Mile, and Upper Owyhee.

		Foray frequencies	
Metapopulation	Season	♂	♀
west	summer	0.568	0.168
west	winter	0.669	0.033
east	summer	0.669	0.218
east	winter	0.597	0.418

Table S5.4 Summer and winter Gaussian-adjusted foray probabilities for male and female bighorn sheep (*Ovis canadensis*) west and east of U. S. Route 95. Foray distances are Euclidean (straight line distance from the core herd home range edge to the furthest foray point from the core herd home range).

	Male				Female			
	west		east		west		east	
Distance (km)	summer	winter	summer	winter	summer	winter	summer	winter
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2	0.439	0.613	0.565	0.579	0.021	0.008	0.035	0.229
3	0.109	0.572	0.408	0.536		0.008	0.009	0.058
4	0.083	0.542	0.314	0.450			0.009	0.049
5	0.005	0.314	0.314	0.307			0.009	0.019

6	0.005	0.246	0.314	0.294	0.009	0.010
7		0.215	0.282	0.294	0.009	
8		0.185	0.282	0.294	0.009	
9		0.123	0.282	0.294	0.009	
10		0.123	0.220	0.294	0.009	
11		0.123	0.220	0.294		
12		0.062	0.188	0.207		
13		0.062	0.157	0.207		
14		0.062	0.157	0.207		
15		0.062	0.157	0.164		
16		0.062	0.126	0.104		
17		0.062	0.126	0.104		
18		0.062	0.094	0.104		
19		0.031	0.094	0.061		
20		0.031	0.063	0.061		
21		0.031	0.031	0.061		
22		0.031	0.031	0.030		
23		0.031	0.031	0.030		
24		0.031	0.031	0.030		
25		0.031	0.031	0.030		
26		0.031	0.031	0.030		
27		0.031	0.031	0.030		
28		0.031	0.031	0.030		
29		0.031	0.031			
30		0.031	0.031			
31		0.031	0.031			
32		0.031	0.031			
33		0.031	0.031			
34		0.031	0.031			
35		0.031	0.031			
36		0.031	0.031			

Table S5.5 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Blue Mountain population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	-	-	-	-	-	-	-
Winter	-	-	-	-	-	-	-

Table S5.6 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Trout Creek – east population and potential sources of domestic sheep and goats with a probability (*p*) ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT455	3.77	Inf	Inf	Inf	Inf	Inf
	PVT474	21.77	Inf	Inf	Inf	Inf	Inf
Winter	PVT455	3.77	Inf	Inf	Inf	Inf	Inf
	PVT462	0.65	Inf	Inf	Inf	Inf	Inf
	PVT474	21.77	Inf	Inf	Inf	Inf	Inf

Table S5.7 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Trout Creek – south population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT399	2.61	<0.01	<0.01	0.05	0.01	0.06
Winter	PVT385	7.03	Inf	Inf	Inf	Inf	Inf
	PVT399	2.61	Inf	Inf	Inf	Inf	Inf
	PVT375	1.67	0.01	-	0.14	-	0.14
	PVT376	0.15	<0.01	<0.01	0.05	0.01	0.06

Table S5.8 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Trout Creek – west population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT469	0.16	Inf	Inf	Inf	Inf	Inf
	PVT522	257.05	Inf	Inf	Inf	Inf	Inf
	PVT474	21.77	0.01	<0.01	0.17	0.04	0.21
Winter	PVT469	0.16	Inf	Inf	Inf	Inf	Inf
	PVT522	257.05	Inf	Inf	Inf	Inf	Inf
	PVT474	21.77	0.01	<0.01	0.25	<0.01	0.25
	PVT451	4.51	0.01	<0.01	0.21	<0.01	0.21

Table S5.9 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Bowden Hills population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT503	3.14	Inf	Inf	Inf	Inf	Inf
Winter	PVT503	3.14	Inf	Inf	Inf	Inf	Inf

Table S5.10 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Calico population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT233	0.62	Inf	Inf	Inf	Inf	Inf
	PVT239	0.49	Inf	Inf	Inf	Inf	Inf
	PVT249	0.66	Inf	Inf	Inf	Inf	Inf
	PVT284	0.31	Inf	Inf	Inf	Inf	Inf
	PVT287	0.16	Inf	Inf	Inf	Inf	Inf
	PVT288	0.86	Inf	Inf	Inf	Inf	Inf
	PVT290	0.16	Inf	Inf	Inf	Inf	Inf
	PVT292	0.52	Inf	Inf	Inf	Inf	Inf
	PVT294	0.52	Inf	Inf	Inf	Inf	Inf
	PVT299	0.16	Inf	Inf	Inf	Inf	Inf
	PVT303	0.16	Inf	Inf	Inf	Inf	Inf
	PVT306	0.49	Inf	Inf	Inf	Inf	Inf
	PVT307	0.16	Inf	Inf	Inf	Inf	Inf
	PVT311	0.16	Inf	Inf	Inf	Inf	Inf
	PVT317	0.16	Inf	Inf	Inf	Inf	Inf
	PVT318	0.33	Inf	Inf	Inf	Inf	Inf
	PVT322	0.16	Inf	Inf	Inf	Inf	Inf
	PVT324	17.87	Inf	Inf	Inf	Inf	Inf
	PVT349	0.65	Inf	Inf	Inf	Inf	Inf
	PVT362	0.65	Inf	Inf	Inf	Inf	Inf
	PVT365	1.2	Inf	Inf	Inf	Inf	Inf
	PVT369	0.63	Inf	Inf	Inf	Inf	Inf
	PVT370	0.16	Inf	Inf	Inf	Inf	Inf
	PVT372	0.16	Inf	Inf	Inf	Inf	Inf
	PVT377	0.16	Inf	Inf	Inf	Inf	Inf
	PVT382	0.03	Inf	Inf	Inf	Inf	Inf
	PVT625	2.59	Inf	Inf	Inf	Inf	Inf
	BIA010	78.24	Inf	Inf	Inf	Inf	Inf
	BIA011	78.27	Inf	Inf	Inf	Inf	Inf
	PVT331	3.25	<0.01	<0.01	0.06	0.13	0.19
	PVT210	24.96	0.01	<0.01	0.13	0.01	0.14
	PVT344	0.98	<0.01	<0.01	0.04	0.07	0.11
	PVT325	0.82	0.01	<0.01	0.08	0.03	0.11
	PVT280	2.04	<0.01	<0.01	0.03	0.06	0.09
Winter	BIA010	78.24	Inf	Inf	Inf	Inf	Inf
	PVT226	3.21	Inf	Inf	Inf	Inf	Inf
	PVT233	0.62	Inf	Inf	Inf	Inf	Inf
	PVT239	0.49	Inf	Inf	Inf	Inf	Inf
	PVT249	0.66	Inf	Inf	Inf	Inf	Inf
	PVT257	0.34	Inf	Inf	Inf	Inf	Inf
	PVT288	0.86	Inf	Inf	Inf	Inf	Inf
	PVT290	0.16	Inf	Inf	Inf	Inf	Inf
	PVT292	0.52	Inf	Inf	Inf	Inf	Inf

PVT294	0.52	Inf	Inf	Inf	Inf	Inf
PVT306	0.49	Inf	Inf	Inf	Inf	Inf
PVT307	0.16	Inf	Inf	Inf	Inf	Inf
PVT311	0.16	Inf	Inf	Inf	Inf	Inf
PVT318	0.33	Inf	Inf	Inf	Inf	Inf
PVT322	0.16	Inf	Inf	Inf	Inf	Inf
PVT324	17.87	Inf	Inf	Inf	Inf	Inf
PVT365	1.2	Inf	Inf	Inf	Inf	Inf
PVT369	0.63	Inf	Inf	Inf	Inf	Inf
PVT370	0.16	Inf	Inf	Inf	Inf	Inf
PVT371	0.32	Inf	Inf	Inf	Inf	Inf
PVT372	0.16	Inf	Inf	Inf	Inf	Inf
PVT377	0.16	Inf	Inf	Inf	Inf	Inf
BIA011	78.27	Inf	Inf	Inf	Inf	Inf
PVT382	0.03	Inf	Inf	Inf	Inf	Inf
PVT625	2.59	Inf	Inf	Inf	Inf	Inf
PVT349	0.65	0.01	0.01	0.11	0.24	0.35
PVT317	0.16	<0.01	<0.01	0.03	0.07	0.10
PVT210	24.96	0.01	<0.01	0.06	0.01	0.08
PVT331	3.25	0.01	<0.01	0.06	0.02	0.08
PVT327	1.46	<0.01	<0.01	0.01	0.05	0.05
PVT325	0.82	<0.01	<0.01	0.04	0.01	0.05
PVT280	2.04	<0.01	<0.01	0.04	0.01	0.05

Table S5.11 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Eight Mile population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT267	0.32	Inf	Inf	Inf	Inf	Inf
	PVT269	0.16	Inf	Inf	Inf	Inf	Inf
	PVT296	3.22	Inf	Inf	Inf	Inf	Inf
	PVT297	0.83	Inf	Inf	Inf	Inf	Inf
	PVT298	0.08	Inf	Inf	Inf	Inf	Inf
	PVT305	1.76	Inf	Inf	Inf	Inf	Inf
	PVT310	1.97	Inf	Inf	Inf	Inf	Inf
	PVT327	1.46	Inf	Inf	Inf	Inf	Inf
	PVT331	3.25	Inf	Inf	Inf	Inf	Inf
	PVT334	1.62	Inf	Inf	Inf	Inf	Inf
	PVT278	58.37	0.03	0.02	0.15	0.55	0.70
	PVT325	0.82	0.01	0.02	0.04	0.54	0.59
	BIA011	78.27	0.02	<0.01	0.09	0.01	0.10
	BIA010	78.24	0.01	<0.01	0.06	0.04	0.10
	PVT289	1	<0.01	<0.01	0.02	0.06	0.08

	PVT308	0.64	<0.01	<0.01	0.02	0.06	0.08
	PVT229	1.61	0.01	<0.01	0.05	0.00	0.05
	PVT234	1.43	0.01	<0.01	0.05	0.00	0.05
Winter	BIA010	78.24	Inf	Inf	Inf	Inf	Inf
	PVT269	0.16	Inf	Inf	Inf	Inf	Inf
	PVT296	3.22	Inf	Inf	Inf	Inf	Inf
	PVT297	0.83	Inf	Inf	Inf	Inf	Inf
	PVT298	0.08	Inf	Inf	Inf	Inf	Inf
	PVT305	1.76	Inf	Inf	Inf	Inf	Inf
	PVT310	1.97	Inf	Inf	Inf	Inf	Inf
	PVT327	1.46	Inf	Inf	Inf	Inf	Inf
	PVT331	3.25	Inf	Inf	Inf	Inf	Inf
	PVT334	1.62	Inf	Inf	Inf	Inf	Inf
	PVT278	58.37	0.06	0.03	0.29	1.04	1.33
	PVT333	0.32	0.01	<0.01	0.03	0.13	0.16
	PVT267	0.32	0.01	<0.01	0.03	0.09	0.12
	PVT325	0.82	0.01	<0.01	0.06	0.03	0.09
	BIA006	0.48	<0.01	<0.01	0.01	0.07	0.08

Table S5.12 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Martin Creek population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT171	1.1	Inf	Inf	Inf	Inf	Inf
	PVT183	461.31	Inf	Inf	Inf	Inf	Inf
	PVT184	6.32	Inf	Inf	Inf	Inf	Inf
	PVT186	1.15	Inf	Inf	Inf	Inf	Inf
	PVT192	0.16	Inf	Inf	Inf	Inf	Inf
	PVT197	0.99	Inf	Inf	Inf	Inf	Inf
	PVT200	0.67	Inf	Inf	Inf	Inf	Inf
	PVT206	0.33	Inf	Inf	Inf	Inf	Inf
	PVT210	24.96	Inf	Inf	Inf	Inf	Inf
	PVT204	0.63	0.01	<0.01	0.06	<0.01	0.06
Winter	PVT171	1.1	Inf	Inf	Inf	Inf	Inf
	PVT183	461.31	Inf	Inf	Inf	Inf	Inf
	PVT184	6.32	Inf	Inf	Inf	Inf	Inf
	PVT200	0.67	Inf	Inf	Inf	Inf	Inf
	PVT206	0.33	Inf	Inf	Inf	Inf	Inf
	PVT210	24.96	Inf	Inf	Inf	Inf	Inf
	PVT179	1.45	0.01	<0.01	0.06	0.01	0.07

Table S5.13 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Rattlesnakes population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT490	0.17	Inf	Inf	Inf	Inf	Inf
	PVT493	0.17	Inf	Inf	Inf	Inf	Inf
	PVT494	0.17	Inf	Inf	Inf	Inf	Inf
	PVT503	3.14	Inf	Inf	Inf	Inf	Inf
	PVT512	0.16	Inf	Inf	Inf	Inf	Inf
	PVT513	1.75	Inf	Inf	Inf	Inf	Inf
	PVT495	1.29	0.01	<0.01	0.20	0.01	0.21
	PVT493	0.17	<0.01	<0.01	0.10	0.01	0.10
	PVT494	0.17	<0.01	<0.01	0.07	0.00	0.08
Winter	PVT503	3.14	Inf	Inf	Inf	Inf	Inf
	PVT512	0.16	Inf	Inf	Inf	Inf	Inf
	PVT513	1.75	Inf	Inf	Inf	Inf	Inf
	PVT495	1.29	0.01	<0.01	0.20	0.03	0.23
	PVT493	0.17	0.01	<0.01	0.14	0.02	0.16
	PVT494	0.17	<0.01	<0.01	0.09	0.02	0.11
	PVT490	0.17	<0.01	<0.01	0.06	0.01	0.07

Table S5.14 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Sawtooth population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT235	199.53	Inf	Inf	Inf	Inf	Inf
Winter	PVT235	199.53	Inf	Inf	Inf	Inf	Inf
	PVT187	2.27	0.00	0.00	0.01	0.03	0.05

Table S5.15 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Three Forks population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT506	0.8	Inf	Inf	Inf	Inf	Inf
Winter	PVT506	0.8	Inf	Inf	Inf	Inf	Inf
	PVT517	1.36	na	0.01	na	0.08	0.08

Table S5.16 Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Ten Mile population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	BIA010	78.24	Inf	Inf	Inf	Inf	Inf
	PVT287	0.16	Inf	Inf	Inf	Inf	Inf
	PVT288	0.86	Inf	Inf	Inf	Inf	Inf
	PVT290	0.16	Inf	Inf	Inf	Inf	Inf
	PVT292	0.52	Inf	Inf	Inf	Inf	Inf
	PVT294	0.52	Inf	Inf	Inf	Inf	Inf
	PVT297	0.83	Inf	Inf	Inf	Inf	Inf
	PVT299	0.16	Inf	Inf	Inf	Inf	Inf
	PVT303	0.16	Inf	Inf	Inf	Inf	Inf
	PVT305	1.76	Inf	Inf	Inf	Inf	Inf
	PVT306	0.49	Inf	Inf	Inf	Inf	Inf
	PVT307	0.16	Inf	Inf	Inf	Inf	Inf
	PVT308	0.64	Inf	Inf	Inf	Inf	Inf
	PVT311	0.16	Inf	Inf	Inf	Inf	Inf
	PVT317	0.16	Inf	Inf	Inf	Inf	Inf
	PVT318	0.33	Inf	Inf	Inf	Inf	Inf
	PVT322	0.16	Inf	Inf	Inf	Inf	Inf
	PVT323	0.49	Inf	Inf	Inf	Inf	Inf
	PVT324	17.87	Inf	Inf	Inf	Inf	Inf
	PVT325	0.82	Inf	Inf	Inf	Inf	Inf
	PVT326	0.34	Inf	Inf	Inf	Inf	Inf
	PVT327	1.46	Inf	Inf	Inf	Inf	Inf
	PVT331	3.25	Inf	Inf	Inf	Inf	Inf
	PVT339	0.48	Inf	Inf	Inf	Inf	Inf
	PVT349	0.65	Inf	Inf	Inf	Inf	Inf
	PVT365	1.2	Inf	Inf	Inf	Inf	Inf
	PVT369	0.63	Inf	Inf	Inf	Inf	Inf
	PVT370	0.16	Inf	Inf	Inf	Inf	Inf
	PVT372	0.16	Inf	Inf	Inf	Inf	Inf
	PVT377	0.16	Inf	Inf	Inf	Inf	Inf
	BIA011	78.27	Inf	Inf	Inf	Inf	Inf
	PVT382	0.03	Inf	Inf	Inf	Inf	Inf
	PVT438	2.61	Inf	Inf	Inf	Inf	Inf
	PVT441	8.58	Inf	Inf	Inf	Inf	Inf
	PVT446	0.16	Inf	Inf	Inf	Inf	Inf
	PVT464	6.01	Inf	Inf	Inf	Inf	Inf
	PVT625	2.59	Inf	Inf	Inf	Inf	Inf
	PVT278	58.37	0.04	<0.01	0.37	0.01	0.38
Winter	BIA010	78.24	Inf	Inf	Inf	Inf	Inf
	PVT296	78.27	Inf	Inf	Inf	Inf	Inf
	PVT297	0.83	Inf	Inf	Inf	Inf	Inf
	PVT298	0.08	Inf	Inf	Inf	Inf	Inf
	PVT305	1.76	Inf	Inf	Inf	Inf	Inf

PVT365	1.2	Inf	Inf	Inf	Inf	Inf
PVT369	0.63	Inf	Inf	Inf	Inf	Inf
PVT370	0.16	Inf	Inf	Inf	Inf	Inf
PVT371	0.32	Inf	Inf	Inf	Inf	Inf
PVT372	0.16	Inf	Inf	Inf	Inf	Inf
PVT377	0.16	Inf	Inf	Inf	Inf	Inf
BIA011	78.27	Inf	Inf	Inf	Inf	Inf
PVT382	0.03	Inf	Inf	Inf	Inf	Inf
PVT438	2.61	Inf	Inf	Inf	Inf	Inf
PVT441	8.58	Inf	Inf	Inf	Inf	Inf
PVT446	0.16	Inf	Inf	Inf	Inf	Inf
PVT464	6.01	Inf	Inf	Inf	Inf	Inf
PVT625	2.59	Inf	Inf	Inf	Inf	Inf
PVT278	58.37	0.03	<0.01	0.35	0.05	0.40
PVT331	3.25	0.01	<0.01	0.11	0.02	0.13
PVT349	0.65	<0.01	<0.01	0.04	0.06	0.10
PVT325	0.82	0.01	<0.01	0.06	0.01	0.07
PVT473	1.79	<0.01	<0.01	0.03	0.04	0.06
PVT327	1.46	<0.01	<0.01	0.04	0.01	0.05

Table S5.17. Expected number of annual contacts between bighorn sheep (*Ovis canadensis*) from the Upper Owyhee population and potential sources of domestic sheep and goats with a probability ≥ 0.05 in both the summer and winter.

Season	land	size (km^2)	ram_C_*p*	ewe_C_*p*	all_ram_C_*p*	all_ewe_C_*p*	herd_C_*p*
Summer	PVT499	1.52	Inf	Inf	Inf	Inf	Inf
	PVT500	0.32	Inf	Inf	Inf	Inf	Inf
	PVT505	0.8	Inf	Inf	Inf	Inf	Inf
	PVT507	7.72	Inf	Inf	Inf	Inf	Inf
	PVT575	1.13	Inf	Inf	Inf	Inf	Inf
	PVT583	1.95	Inf	Inf	Inf	Inf	Inf
	PVT003	0.65	0.01	<0.01	0.15	0.07	0.22
	PVT517	1.36	0.01	<0.01	0.19	<0.01	0.20
	PVT525	1.55	0.01	<0.01	0.12	<0.01	0.13
	PVT623	207.76	<0.01	<0.01	0.07	<0.01	0.07
Winter	PVT505	0.8	Inf	Inf	Inf	Inf	Inf
	PVT507	7.72	Inf	Inf	Inf	Inf	Inf
	PVT575	1.13	<0.01	<0.01	0.08	0.12	0.20
	PVT504	0.16	<0.01	<0.01	0.07	0.04	0.11
	PVT573	6.47	<0.01	<0.01	0.05	0.01	0.06

Supplementary Figures

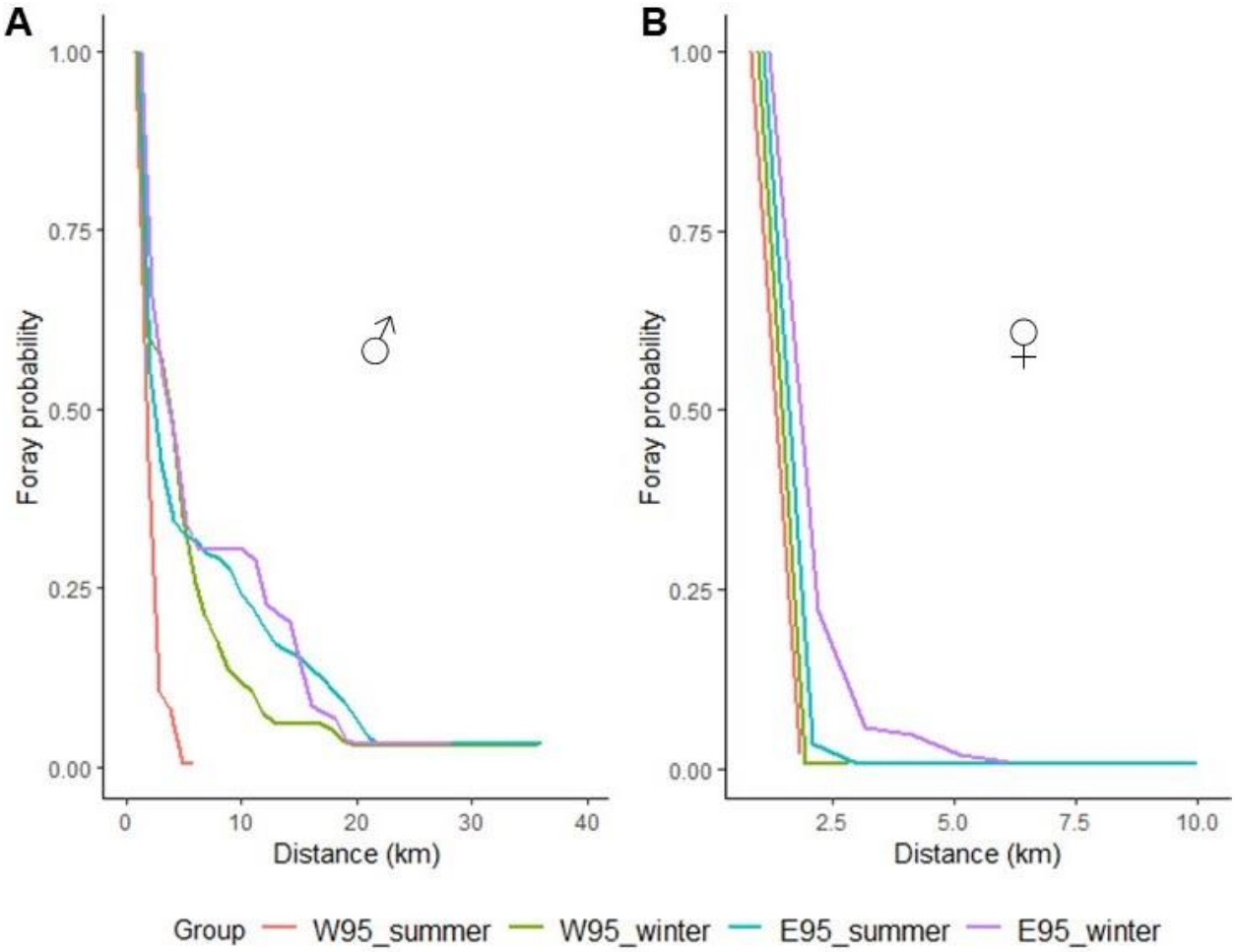

Figure S5.1 Gaussian-adjusted summer and winter foray probabilities for A. male and B. female bighorn sheep (*Ovis canadensis*) west and east of U. S. Route 95.

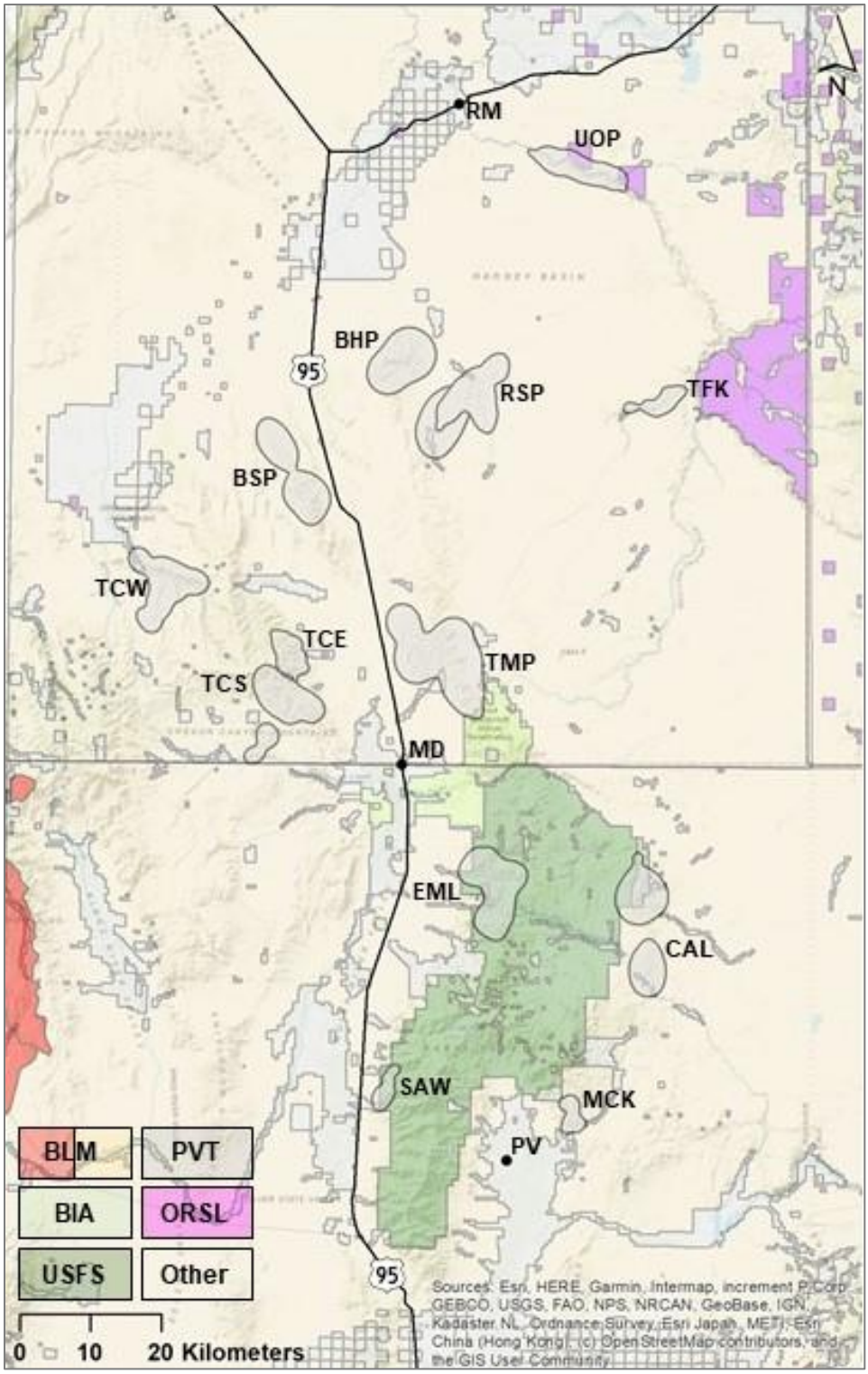

Figure S5.2 Landownership types found within the study area extent, including BLM (red) – Bureau of Land Management domestic sheep grazing allotments, BLM (beige) – Bureau of Land Management other, PVT – private, BIA – Bureau of Indian Affairs, ORSL – Oregon State lands, USFS – United States Forest Service, and Other – includes Department of Energy and Federal Aviation Authority land.

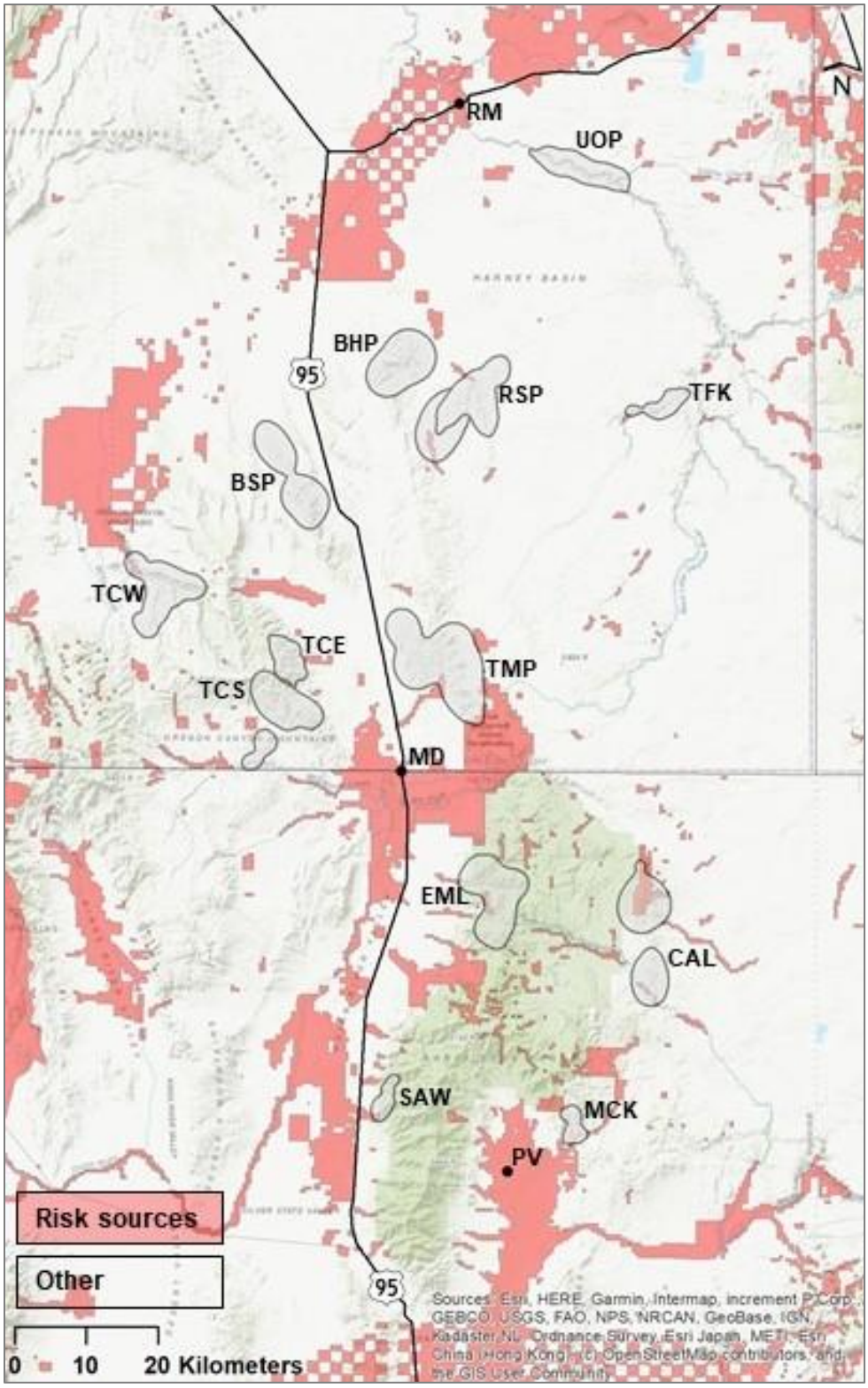

Figure S5.3 Potential sources of domestic sheep and goats presenting a disease risk to bighorn sheep (*Ovis canadensis*). Potential sources of domestic sheep and goats are made up of BLM domestic sheep grazing allotments, private, and Bureau of Indian Affairs land.

CHAPTER 6
CONCLUSION

My dissertation focuses on characterizing the spread and consequences of *Mycoplasma ovipneumoniae* to bighorn sheep (*Ovis canadensis*) in the northern Basin and Range ecosystem. To accomplish this task, I carried out four interdisciplinary studies involving extensive fieldwork, epidemiological, genetic, geospatial, and statistical methodologies to determine factors influencing bighorn sheep demography and spatial ecology. The findings from this study will facilitate the Oregon Department of Fish and Wildlife (ODFW) and Nevada Department of Wildlife (NDOW) in managing bighorn sheep genetic health and disease, specifically *M. ovipneumoniae,* within the study system.

The spatial analyses conducted in Chapters 4 and 5 revealed much about the distribution and pattern of *M. ovipneumoniae* transmission within the system. Interpopulation movements observed in the raw spatial data, overlapping utilization distributions in Chapter 4, and the risk of contact modeling in Chapter 5 reflects similar risk patterns and actual infection of the single strain of *M. ovipneumoniae* observed within the system up until 2020. Although the risk of contact model in Chapter 5 suggested potential contact between some populations west and east of U.S. Route 95, no evidence of such movements exists. All the populations west of U.S. Route 95 are unexposed to *M. ovipneumoniae*. The finding indicates that U.S. Route 95 likely acts as a barrier to movement but is not impermeable. However, should a pathogen enter any of the Trout Creek populations, the risk for transmission to the other Trout Creek populations would be very high due to overlapping utilization distributions and core herd home ranges observed in Chapters 4 and 5. From the risk of contact modeling in Chapter 5, the most significant external threat to the study populations appears to be neighboring Owyhee Canyon populations in Idaho. In contrast, all populations were at risk from potential domestic sheep and goat sources, i.e., private or Bureau of Indian Affairs lands where landowners could choose to bring domestic sheep or goats in at any time.

Transmission of *M. ovipneumoniae* and gene flow within this system appear male-driven. My Chapter 4 findings support this argument with no interpopulation movement observed by females across the entire system, the high site fidelity and social affinity of females within the system, and the low foray frequency and distance probabilities observed in Chapter 5. These findings suggest that the potential for colonization of unused habitat within this system is low.

In Chapters 2 and 3, disease testing of captured bighorn sheep in this system revealed high *M. ovipneumoniae*-exposure rates in all populations east of U.S. Route 95. However, the prevalence of *M. ovipneumoniae*-infected individuals was extremely low, with only two females and a single male in three different populations testing PCR+. In Chapter 2, I detected dead juveniles infected with *M.*

ovipneumoniae in only two populations. In both these populations, the impact of *M. ovipneumoniae* on juvenile survival was catastrophic, with a derived survival probability 20 times lower than in populations where no dead juveniles with *M. ovipneumoniae* were detected. Interestingly, when the single known *M. ovipneumoniae*-infected individual in one of these populations died, the subsequent post-study observations found a high percentage of the collared adult females had surviving juveniles at four months of age.

We could not test the direct effects of *M. ovipneumoniae*-infection on adult survival of bighorn sheep in Chapter 3 due to inadequate sample sizes. However, we found that *M. ovipneumoniae*-exposure predicted survival, with *M. ovipneumoniae*-exposed bighorn sheep having 2.3 times lower survival than *M. ovipneumoniae*-unexposed individuals. Possible explanations for this effect include potential lung damage or the cost of mounting an immune response.

There is potential for *M. ovipneumoniae* to fade from this system, given the low prevalence of infection in adults observed in Chapters 2 and 3. In addition, the effects of *M. ovipneumoniae* on juvenile recruitment were significant. Therefore, we suggested the potential targeted removal of infected adults by the respective management agencies. ODFW and NDOW have recently initiated test-and-remove programs, which could aid pathogen fadeout, improve juvenile survival, and benefit *M. ovipneumoniae*-unexposed individuals as well.

Our risk of contact modeling exercise will help managers determine which areas or landowners might be worth targeting with outreach if the addition of domestic livestock seems possible or likely. The risk of contact modeling results can also be used in several ways to better inform managers or potentially drive the decision-making process, e.g., by incorporating the data into a structured decision-making process (Sells et al. 2016), or potentially guiding outreach to landowners. In addition, these results can inform managers of the potential spread of other novel pathogens or strains of *M. ovipneumoniae.*

While we did not find direct evidence of population genetic diversity on juvenile survival, we did find suggestive evidence of a negative effect on adult survival. In addition, the lowest pregnancy rates were in bighorn sheep populations in the western metapopulation, where population genetic diversity was the lowest. This low population genetic diversity is due to founder effects from sequential translocations from the same small source population. Translocations of individuals from populations with different ancestry would benefit the populations west of U.S. Route 95, improving genetic diversity. However, the benefits of translocation must always be weighed against the risk of disease. New translocations can increase densities and foray behavior due to competition for forage and mating opportunities, resulting in more connected habitat patches, potentially facilitating disease transmission.