AN ABSTRACT OF THE DISSERTATION OF

Daniella J. Dekelaita for the degree of Doctor of Philosophy in Wildlife Science presented on April 20, 2020.

Title: <u>Assessing Apparent Effects on Survival and Movement of Desert Bighorn Sheep</u> (*Ovis canadensis nelsoni*) Following a Pneumonia Outbreak

Abstract approved:

Clinton W. Epps

In the western United States, bighorn sheep (*Ovis canadensis*) have suffered major die-offs in every state since the mid-1800s, and disease from domestic sheep (*Ovis aries*) has been a primary factor in these events. Beginning in the early 1900s, poly-factorial, poly-microbial pneumonia was identified as a major disease affecting bighorn populations, and within the last 12 years *Mycoplasma ovipneumoniae* (*M. ovi*) has been identified as a primary causal agent associated with pneumonia outbreaks; other pneumonic pathogens that have been widely implicated include leukotoxigenic *Mannheimia* (formerly *Pasteurella*) *haemolytica* (*M. haemolytica*), *Bibersteinia* (formerly *Pasteurella*) *trehalosi* (*B. trehalosi*), and *Pasteurella multocida*. Pneumonia outbreaks typically follow from direct contact between domestic animals and wild sheep, but as yet, respiratory disease dynamics in bighorn populations are not completely understood. My research identifies factors that are correlated with variation in the expression and occurrence of the disease both spatially and temporally within bighorn populations of California.

In Chapter 1, I investigated post-outbreak survival of adult female bighorn across 9 populations and evaluated the relationship between *M. ovi* infection and survival, while testing effects of range factors that could potentially drive differences in adult female survival (i.e., forage quality, winter precipitation, and population abundance). I used survival data from radio-collars on 115 females that were captured and screened for *M. ovi* infection between 2013 and 2015, and I evaluated potential effects on survival from November 2013 to March 2017 using the known-fate model in Program MARK. Annual survival was negatively correlated with positive infection status at capture but varied across populations with respect to differences in range conditions. Summer and autumn forage quality, as measured using the normalized difference vegetation index (NDVI), was positively correlated with overwinter survival, while winter precipitation (a proxy for winter severity) was negatively correlated with overwinter survival. I also found that population abundance was negatively correlated with annual survival, suggesting a potential density-dependent effect. My findings suggest that summer and autumn forage quality, indexed by NDVI, may partially offset the negative effect associated with *M. ovi* infection on host survival. Additionally, the negative effect associated with population abundance suggests that density-dependence further added to effects associated with infection.

Reduced neonate survival has been identified as a major factor limiting population recovery for bighorn sheep following pneumonia epizootics. In Chapter 2, I investigated lamb survival in 7 populations of desert bighorn (*O. c. nelsoni*) exposed to *M. ovi*. I applied beta regression to late-season (15 August to 30 September) lambewer ratios from 2014-2016 to model lamb survival and evaluate effects of precipitation and population abundance, in order to better understand neonate survival trends in these populations. I detected a quadratic effect of precipitation in October-April, coincident with the period of mid-gestation to lambing for parturient females, whereby precipitation up to an optimum level was positively associated with lamb survival. In contrast, precipitation in May-August, coincident with the period, was associated with a negative effect on lamb survival, but this effect was not robust to additional testing with yearly effects and may have been spurious. My findings suggest that higher precipitation in October-April likely increases forage availability and thereby nutrition for parturient females, although excessive precipitation might have a deleterious effect in terms of neonate survival.

In Chapter 3, I used GPS-collar data from 135 radio-collared bighorn (27 males and 108 females) from 14 populations to evaluate movement trends. Animals were captured in November 2013-2015 and March 2017 and location data were

collected from November 2013 to December 2018. My objective was to model intermountain movement as a binary response and evaluate effects of sex, age, and M. ovi infection status at capture (determined from PCR testing of nasal swabs collected from animals at capture), in order to assess the potential transmission risk individuals posed between populations by inferring potential for contact from movement behavior. I also examined seasonal trends by calculating proportions of intermountain movements by season for males and females. In a secondary analysis, I tested effects on mean seasonal daily movement rates using linear regression. I found that males were more likely to undertake intermountain movements than females, older animals (> 5 years old) were more likely than younger animals (< 5 years old), and individuals that were PCR-positive for *M. ovi* at capture were less likely than those that were PCR-negative. Additionally, intermountain movements were more frequent during the breeding season (July-November) for males and during the period of midgestation to lambing (October-April) for females. The breeding season was also associated with higher mean daily movement rates for males, while effects of age and PCR status at capture were not supported. For females, positive PCR status and the period of mid-gestation to lambing were both negatively associated with mean daily movement rates and the effect of age was not supported. My findings suggest that the potential transmission risk posed within and across populations by an individual varies depending on time of year and sex in this system, while M. ovi infection may also inhibit animal movement and consequently potential transmission risk.

Results from this study corroborate findings from other studies regarding factors influencing survival and movement of bighorn sheep. We found evidence that *M. ovi* infection may have lingering effects on survival and movement as well, which has clear implications for disease transmission. Additional investigation may be needed to gain a better understanding of how the pathogen specifically interacts with host and environment to prolong its existence within and across populations. Findings from my research can help direct future studies and management efforts aimed at mitigating effects of respiratory disease in bighorn populations.

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Assessing Apparent Effects on Survival and Movement of Desert Bighorn Sheep (Ovis canadensis nelsoni) Following a Pneumonia Outbreak

by Daniella J. Dekelaita

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APPROVED:

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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.

Daniella J. Dekelaita, Author

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CONTRIBUTION OF AUTHORS

Daniella Dekelaita collected data, contributed to study design, assisted with captures, analyzed data, and wrote manuscripts in joint collaboration with coauthors. Clinton Epps obtained funding for the project and contributed to study design and ideas, interpretation of results and writing of manuscripts. Jenny Powers, Ben Gonzales, and Regina Abella-Vu helped visualize the project, established protocols for disease testing, and facilitated lab work, live animal captures and collar deployments. Neal Darby and Debra Hughson provided ongoing field support and essential assistance to meet project objectives in Mojave National Preserve and neighboring areas. Kelley Stewart, James Sedinger, and David German provided technical assistance with data analysis, idea implementation, and manuscript writing. Taal Levi provided technical guidance with data analysis and visualization, and contributed to analysis development.

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GENERAL INTRODUCTION

At present, there are many challenges facing wildlife management and conservation including habitat loss, fragmentation, climate change, and disease. Habitat loss and fragmentation from human activity reduce viability of wildlife populations by reducing habitable space and by limiting connectivity between populations, which is critical for maintaining genetic diversity and ultimately fitness and viability of individuals within populations (Rudnick et al. 2012). Coupled with climate change, loss of suitable habitat for wildlife species is predicted to increase and cause local population extinctions and eventual extinction of species on a massive scale (Holmes 2006, Barnosky et al. 2011). Additionally, wildlife disease, which can reach epidemic proportions, further complicates efforts to recover and conserve populations and may hasten the demise of species (Cunningham et al. 2017). For species that are struggling to maintain a foothold in our modern world, attempts to solve conservation challenges and recover populations may come too late, but hope endures for those species that are not yet on the brink (Holmes 2006). Bighorn sheep (Ovis canadensis) are an example of a species whose conservation is complicated by the aforementioned challenges (Epps et al. 2005, 2006, Besser et al. 2013), but for which hope still endures. Bighorn sheep metapopulations are especially sensitive to loss of habitat and connectivity given the structural network required to sustain metapopulation dynamics (Bleich et al. 1990, Epps et al. 2005), and with the looming specter of climate change, bighorn are becoming increasingly more vulnerable to the threat of extinction, especially in desert environments (Epps et al. 2006). While climate change remains an overarching threat, however, epizootic pneumonia may be the biggest challenge facing current management of this iconic species at present.

Beginning in the early 1900s, pneumonia has contributed to major die-offs of bighorn sheep in the western United States (Buechner 1960). Pneumonia outbreaks typically follow from direct contact between domestic animals and wild sheep, but as yet, respiratory disease dynamics in bighorn populations are not completely understood. An all-age die-off is often the first signal of a pneumonia invasion into a naïve population, and is typically followed by high lamb mortality in subsequent years, likely due to chronically infected adult females passing pathogens to their offspring through physical contact (Cassirer et al. 2013, 2018, Manlove et al. 2014, Wood et al. 2017). Not all surviving adults become chronically infected, but those that do can maintain infection within populations for decades, suppressing lamb survival and ultimately limiting population recovery (Plowright et al. 2017, Cassirer et al. 2018). Within the last 12 years *Mycoplasma ovipneumoniae* (*M. ovi*) has been identified as a primary causal agent associated with pneumonia outbreaks (Besser et al. 2008, 2012*b*, 2014, Plowright et al. 2017, Cassirer et al. 2018); other pneumonic pathogens that have been widely implicated include leukotoxigenic *Mannheimia* (formerly *Pasteurella*) *haemolytica* (*M. haemolytica*), *Bibersteinia* (formerly *Pasteurella*) *trehalosi* (*B. trehalosi*), and *Pasteurella multocida* (*P. multocida*; Tomassini et al. 2009, Monello et al. 2001, Besser et al. 2008, 2012*b*, Wood et al. 2017, Cassirer et al. 2018).

In the Mojave Desert of California, reduced connectivity between populations of desert bighorn sheep (O. c. nelsoni) has been identified as an impediment to metapopulation dynamics and consequently gene flow and long-term viability of populations (Epps et al. 2007). The Mojave Desert ecosystem features an assemblage of mountain ranges separated by low-lying areas that are fragmented by roads, freeways and other anthropogenic structures, and populations of desert bighorn sheep inhabit many of these ranges. In May and June of 2013, a pneumonia outbreak linked to M. ovi led to an all-age die-off of desert bighorn sheep at Old Dad Peak (Kelso Mountains) in the Mojave Desert, California, USA (Epps et al. 2016). Previously, bighorn sheep in this region of the Mojave were believed to be insulated from the threat of pneumonia because of reduced connectivity with neighboring bighorn populations and domestic sheep herds. The incident that occurred at Old Dad Peak is the only confirmed pneumonia induced die-off observed in the Mojave Desert ecosystem in California, although retrospective screening of banked serum collected in 1983-2006 revealed that some neighboring populations were in fact seropositive for *M. ovi* antibodies as early as 1986, while bighorn at Old Dad Peak were seropositive in 1989 (California Department of Fish and Wildlife, unpublished data). Subsequent to the die-off, asymptomatic individuals were screened for M. ovi infection in several nearby populations and many tested positive. Given what

appeared to be differences in response to *M. ovi* across populations, I wanted to focus my research on identifying factors that could be influencing variation in the expression and occurrence of the disease both spatially and temporally.

In Chapter 1, my objective was to examine post-outbreak survival of adult female bighorn across 9 populations in the Mojave Desert and evaluate the relationship between *M. ovi* infection and survival, while testing effects of exogenous factors relating to range condition that could potentially drive differences in adult female survival (i.e., forage quality, winter precipitation/severity, and female population abundance). I used survival data from 115 females that were fitted with radio-collars and screened for *M. ovi* infection between 2013 to 2015, and I evaluated potential effects on survival from November 2013 to March 2017 using the knownfate model in Program MARK (version 8.2; White and Burnham 1999, Cooch and White 2017). I found that *M. ovi* infection was associated with a reduction in adult female survival and that range factors appeared to influence survival as well. These findings validate observed differences in survival trends of adult females across populations exposed to pneumonia associated with *M. ovi*.

In Chapter 2, I investigated differences in neonate survival from 2014 to 2016 in 7 bighorn populations exposed to the *M. ovi* pathogen, although I could not study direct effects associated with infection in neonates for lack of screening. The peak of lambing in the Mojave Desert occurs in February-April and I therefore used lateseason (15 August to 30 September) lamb-ewe ratios from each population across years to index lamb survival up to at least 4-5 months of age when weaning begins (Festa-Bianchet et al. 1994); lamb-ewe ratios are commonly used to gauge lamb survival at the population level (Picton 1984, Douglas and Leslie 1986, Wehausen et al. 1987). I applied beta regression to model survival based on ratios and evaluated effects associated with seasonal precipitation and female population abundance, which have been identified as important factors affecting bighorn lamb survival (Douglas and Leslie 1986, Portier et al.1998, Wehausen 2005). My results indicated support for October-April and May-August precipitation, whereby lamb survival appeared to increase with October-April precipitation up to an optimum level, while survival appeared to decrease with May-August precipitation. The apparent effect of May-August precipitation lost support with the inclusion of yearly effects in a subsequent analysis, however, suggesting that it may have been spurious. I considered several potential explanations for these patterns including the possibility that excessive precipitation in October-April may lead to loss of carbon and nitrogen in soil (Austin et al. 2004) that could negatively affect neonate health. The correlation between higher precipitation during hotter months and lower neonate survival, if not spurious, may be further explained by aerosol transmission of *M. ovi*, which may increase with increasing humidity as seen with *M. pneumoniae* in humans (Onozuka et al. 2009).

In Chapter 3, I addressed potential transmission risk between populations by analyzing intermountain movement trends among individuals. I used GPS data from 135 radio-collared bighorn (27 males and 108 females) from 14 populations to model intermountain movement as a binary response and evaluate effects of sex, age, and *M. ovi* infection, in order to assess the potential transmission risk individuals posed between populations by inferring potential for contact from movement behavior. I also examined seasonal trends by calculating proportions of intermountain movements by season for males and females. Additionally, I conducted a supporting analysis in which I tested the same effects on mean seasonal daily movement rates using linear regression. My findings suggest that potential transmission risk posed within and across populations by an individual varies depending on time of year and sex, while *M. ovi* infection may also inhibit animal movement and consequently potential transmission risk.

Conservation of bighorn sheep will likely remain a management challenge into the future given current threats to populations. This research specifically addresses factors associated with survival, movement, and disease. My hope is that findings from this study will help direct future research aimed at mitigating effects of pneumonia in bighorn populations and influence planning efforts to conserve existing populations and restore those affected by respiratory disease.

LITERATURE CITED

- Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221-235.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction arrived? Nature 471:51-57.
- Besser, T. E., E. F. Cassirer, K. A. Potter, J. VanderSchalie, A. Fischer, D. P. Knowles, D. R. Herndon, F. R. Rurangirwa, G. C. Weiser, and S. Srikumaran. 2008. Association of *Mycoplasma ovipneumoniae* infection with population limiting respiratory disease in free-ranging Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*). Journal of Clinical Microbiology 46:423-430.
- Besser, T. E., M. A. Highland, K. Baker, E. F. Cassirer, N. J. Anderson, J. M. Ramsey, K. Mansfield, D. L. Bruning, P. Wolff, J. B. Smith, and J. A. Jenks. 2012b. Causes of pneumonia epizootics among bighorn sheep, western United States, 2008-2010. Emerging Infectious Diseases 18:406-414.
- Besser, T. E., E. F. Cassirer, M. A. Highland, P. Wolff, A. Justice-Allen, K. Mansfield, M. A. Davis, and W. Foreyt. 2013. Bighorn sheep pneumonia: sorting out the cause of polymicrobial disease. Preventive Veterinary Medicine 108:85-93.
- Besser, T. E., E. F. Cassirer, K. A. Potter, K. Lahmers, J. L. Oaks, S. Shanthalingam, S. Srikumaran, and W. J. Foreyt. 2014. Epizootic pneumonia of bighorn sheep following experimental exposure to *Mycoplasma ovipneumoniae*. PLOS ONE 9:1-9.
- Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Conservation Biology 4:383-390.
- Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildlife Monographs 4:3-174.
- Cassirer, E. F., R. K. Plowright, K. R. Manlove, P. C. Cross, A. P. Dobson, K. A. Potter, and P. J. Hudson. 2013. Spatio-temporal dynamics of pneumonia in bighorn sheep. Journal of Animal Ecology 82:518-528.
- Cassirer, E. F., K. R. Manlove, E. S. Almberg, P. Kamath, M. Cox, P. Wolff, A. Roug, J. Shannon, R. Robinson, R. B. Harris, B. J. Gonzales, R. K. Plowright, P. J. Hudson, P. C. Cross, A. Dobson, and T. E. Besser. 2018. Pneumonia in bighorn sheep: risk and resilience. Journal of Wildlife Management 82:32-45.
- Cooch, E. G., and G. C. White, editors. 2017. Program MARK: a gentle introduction. Seventeenth edition. Colorado State University, Fort Collins, Colorado, USA.
- Cunningham, A. A., P. Daszak, and J. L. N. Wood. 2017. One Health, emerging infectious diseases and wildlife: two decades of progress? Philosophical Transactions B 372: 20160167.

- Douglas, C. L. and D. M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. Journal of Wildlife Management 50:153-156.
- Epps, C. W., D. Dekelaita, and B. Dugovich. 2016. Updates on respiratory disease affecting bighorn sheep in and near Mojave National Preserve. Mojave National Preserve, Sweeney Granite Mountains Desert Research Center Science Newsletter. https://www.nps.gov/moja/learn/science-newsletter.https://www.nps.gov/moja/learn/science-newsletter.htm>. Accessed 20 November 2018.
- Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714-724.
- Epps, C. W., P. J. Palsboll, J. D. Wehausen, G. K. Roderick, and D. R. McCullough. 2006. Elevation and connectivity define genetic refugia for mountain sheep as climate warms. Molecular Ecology 15:4295-4302.
- Epps, C. W., P. J. Palsboll, J. D. Wehausen, G. K. Roderick, R. R. Ramey II, and D. R. McCullough. 2005. Highways block gene flow and cause rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8:1029-1038.
- Festa-Bianchet, M., J. T. Jorgenson, and W. D. Wishart. 1994. Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not females. Behavioral Ecology 5:21-27.
- Holmes, B. 2006. Earth without humans. New Scientist 192:37-41.
- Manlove, K., E. F. Cassirer, P. C. Cross, R. K. Plowright, and P. J. Hudson. 2014. Costs and benefits of group living with disease: a case study of pneumonia in bighorn lambs (*Ovis canadensis*). Proceedings of the Royal Society 281:20142331. doi 10.1098/rspb. 2014. 2331.
- Monello, R. J., D. L. Murray, and E. F. Cassirer. 2001. Ecological correlates of pneumonia epizootics in bighorn sheep herds. Canadian Journal of Zoology 79:1423-1432.
- Onozuka, D., M. Hashizume, and A. Hagihara. 2009. Impact of weather factors on *Mycoplasma pneumoniae* pneumonia. Thorax 64:507-511.
- Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology 21:869-879.
- Plowright, R. K., K. R. Manlove, T. E. Besser, D. J. Paez, K. R. Andrews, P. E. Matthews, L. P. Waits, P. J. Hudson, and E. F. Cassirer. 2017. Age-specific infectious period shapes dynamics of pneumonia in bighorn sheep. Ecology Letters 20:1325-1336.
- Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology 245:271-278.
- Rudnick, D. A., S. J. Ryan, P. Beier, S. A. Cushman, F. Dieffenbach, C. W. Epps, L.
 R. Gerber, J. Hartter, J. S. Jenness, J. Kintsch, A. M. Merenlender, R. M.
 Perkl, D. V. Preziosi, and S. C. Trombulak. 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology, Ecological Society of America. Report 16.
- Tomassini, L., B. Gonzales, G. C. Weiser, and W. Sischo. 2009. An ecological study comparing *Pasteurella trehalosi* and *Mannheimia haemolytica* between

Sierra Nevada bighorn sheep, White Mountain bighorn sheep, and domestic sheep. Journal of Wildlife Diseases 45:930-940.

- Wehausen, J. D. 2005. Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. Pages 37-50 in J. Goerrissen and J. M. Andre, editors. Sweeney Granite Mountains Desert Research Center 1978-2003: A Quarter Century of Research and Teaching. University of California Natural Reserve Program, Riverside, USA.
- Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California sheep population. Journal of Wildlife Management 51:86-98.
- White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-139.
- Wood, M. E., K. A. Fox, J. Jennings-Gaines, H. J. Killion, S. Amundson, M. W. Miller, and W. H. Edwards. 2017. How respiratory pathogens contribute to lamb mortality in a poorly performing bighorn sheep (*Ovis canadensis*) herd. Journal of Wildlife Diseases 53:126-130.

CHAPTER 1: SURVIVAL OF ADULT FEMALE BIGHORN SHEEP FOLLOWING A PNEUMONIA EPIZOOTIC

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ABSTRACT

Beginning in the early 1900s, poly-factorial, poly-microbial pneumonia was identified as a disease affecting bighorn sheep (Ovis canadensis) and it continues to threaten bighorn populations, posing an ongoing management challenge. In May and June of 2013, a pneumonia outbreak linked to the pathogen Mycoplasma ovipneumoniae (M. ovi) led to an all-age die-off of desert bighorn sheep (Ovis canadensis nelsoni) at Old Dad Peak (Kelso Mountains) in the Mojave Desert, California, USA. Subsequently, clinical signs of respiratory disease were observed in multiple neighboring ranges. Our objective was to investigate post-outbreak survival of adult female bighorn across 9 populations from 2014 to 2017 in the Mojave Desert and evaluate the relationship between *M. ovi* infection and survival, while testing effects of range factors that could potentially drive differences in adult female survival (i.e., forage quality, winter precipitation, and population abundance). We fitted adult females with radio-collars following the outbreak and collected serum and nasal swab samples for competitive enzyme-linked immunosorbent assay (cELISA) and polymerase chain reaction (PCR) testing to determine exposure and infection status at time of capture. We tracked survival of 115 adult females with radio-collars and used the known-fate model in Program MARK to evaluate effects and estimate survival from November 2013 to March 2017. Annual survival was negatively

correlated with positive infection status at capture but varied across populations with respect to differences in range conditions. Summer and autumn forage quality, as represented by mean normalized difference vegetation index (NDVI) values, was positively correlated with overwinter survival, while winter precipitation (a proxy for winter severity) was negatively correlated with overwinter survival. We also found that population abundance was negatively correlated with annual survival, suggesting a potential density-dependent effect. Model-averaged annual survival estimates ranged from 0.700 (\pm 0.07 SE) to 0.945 (\pm 0.026 SE) for infected individuals and 0.896 (+ 0.03 SE) to 0.983 (+ 0.011 SE) for uninfected individuals. We conclude that summer and autumn forage quality, indexed by NDVI, may partially offset the negative effect associated with *M. ovi* infection on host survival. Our survival modeling results suggest that chronic infection may have afflicted adult females that were PCR-positive (i.e., infected with *M. ovi*) at time of capture. One strategy we propose as a next step is programmatic re-testing of infected individuals to assess pathogen persistence at the individual level and evaluate whether selective culling might potentially help to reduce prevalence and transmission within populations.

INTRODUCTION

In the western United States, bighorn sheep (*Ovis canadensis*) have suffered major die-offs in every state since the mid-1800s, and disease from domestic sheep (*Ovis aries*) has been a primary factor in these events (Valdez and Krausman 1999, Wehausen et al. 2011). Since the 1950s, poly-factorial, poly-microbial pneumonia was identified as the major disease affecting bighorn populations, and within the last 12 years *Mycoplasma ovipneumoniae* (*M. ovi*) has been identified as a primary causal agent associated with pneumonia outbreaks (Besser et al. 2008, 2012*b*, 2014, Plowright et al. 2017, Cassirer et al. 2018); other pneumonic pathogens that have been widely implicated include leukotoxigenic *Mannheimia* (formerly *Pasteurella*) *haemolytica* (*M. haemolytica*), *Bibersteinia* (formerly *Pasteurella*) *trehalosi* (*B. trehalosi*), and *Pasteurella multocida* (*P. multocida*; Tomassini et al. 2009, Monello et al. 2001, Besser et al. 2008, 2012*b*, Wood et al. 2017, Cassirer et al. 2018). Pneumonia outbreaks may follow from direct contact between domestic animals and wild sheep, but direct livestock exposure cannot be confirmed in all cases (Besser et al. 2018).

al. 2012*b*), which was true in 6 out of 9 events documented in the western United States in 2009 and 2010 (WAFWA 2010).

In May and June of 2013, a pneumonia outbreak linked to M. ovi led to an allage die-off of desert bighorn sheep (O. c. nelsoni) at Old Dad Peak (Kelso Mountains) in the Mojave Desert, California (Epps et al. 2016). Previously, bighorn sheep in this region of the Mojave were believed to be insulated from the threat of pneumonia because of reduced connectivity with neighboring wild sheep systems and domestic herds. How the pathogen entered the population is unknown, but subsequent to the outbreak, clinical signs of disease were observed in multiple neighboring bighorn sheep populations. In November 2013, 2014, and 2015, adult bighorn from Old Dad Peak and 8 neighboring ranges (i.e., South Soda, Cady, North Bristol, South Bristol, Marble, Clipper, Hackberry, and Woods Mountains) were captured and tested for *M. ovi* infection via polymerase chain reaction (PCR) of nasal swab samples. The same strain of *M. ovi* was detected in adult bighorn from all ranges except the South Soda Mountains, where animals were *M. ovi*-negative but seropositive for *M. ovi* antibodies. Attempts to screen for additional respiratory pathogens, including leukotoxigenic M. haemolytica and B. trehalosi, were also undertaken but were unsuccessful due to complications with the storage and transport of samples (California Department of Fish and Wildlife [CDFW], unpublished data).

To date, the incident that occurred at Old Dad Peak is the only confirmed pneumonia induced die-off observed in the Mojave Desert ecosystem in California, although retrospective screening of banked serum collected in 1983-2006 revealed that some bighorn in neighboring ranges were in fact seropositive for *M. ovi* antibodies as early as 1986, while bighorn at Old Dad Peak were seropositive in 1989 (CDFW, unpublished data). The strain of *M. ovi* that animals were exposed to during this earlier time remains unknown. Additionally, *M. haemolytica*, *B. trehalosi*, and *P. multocida* were detected via culture testing of oropharyngeal swab samples (Caine Veterinary Teaching Center, Caldwell, ID; Miller et al. 2011) collected from bighorn at Old Dad Peak in 2005 and 2006, and the South Bristol Mountains in 2002 (CDFW, unpublished data).

As yet, disease dynamics of epizootic pneumonia in bighorn sheep are not completely understood, and likely vary by region, host ecology, and causal pathogens, but pneumonia outbreaks seem to have a common pattern. An all-age dieoff is often the first signal of a pneumonia invasion into a naïve population, and is typically followed by high lamb mortality in subsequent years, likely due to chronically infected adult females passing pathogens to their offspring through physical contact (Cassirer et al. 2013, 2018, Manlove et al. 2014, Wood et al. 2017). Not all surviving adults become chronically infected, however those that do can maintain infection within populations for decades (Plowright et al. 2017, Cassirer et al. 2018), and adult survival can be relatively stable in years following an initial outbreak (Cassirer et al. 2013, Manlove et al. 2016). There also appears to be a seasonal component associated with acute pneumonia-induced mortality, whereby age-specific die-offs in adults typically occur during the breeding season when contact rates increase (Cassirer et al. 2013). Aside from seasonality, how other factors contribute to disease patterns remains unclear, but population density along with stochastic variables, such as weather and range condition, may also influence expression of the disease (Dunbar 1992, Ryder et al. 1992, Monello et al. 2001, Singer et al. 2001, Wolfe et al. 2010). For example, precipitation is strongly linked to productivity in desert bighorn sheep populations through quality and quantity of forage (Wehausen et al. 1987, Wehausen 2005), but harsh winter weather has also been identified as a possible factor influencing pneumonia in both wild and domestic sheep (McIlroy et al. 1989, Ryder et al. 1992, Wolfe et al. 2010).

Our objective was to investigate post-outbreak survival of adult female bighorn (> 2 years old) across 9 populations for 3.5 years (Nov 2013 to Mar 2017) in the Mojave Desert, California. We evaluated the relationship between *M. ovi* and seasonal survival, and tested effects of range factors that could potentially drive differences in adult female survival. We had 2 hypotheses: *H1*) *M. ovi infection lowers post-outbreak survival of adult females*. We assumed that females who were carrying the *M. ovi* pathogen at capture could suffer fatality from acute infection, experience reduced health from disease post-recovery, or incur debilitating effects from prolonged infection. Mycoplasmal species are known to induce chronic and

latent disease states in animals and humans (Waites and Talkington 2004), and bighorn sheep exposed to *M. ovi* can become chronic, non-clinical carriers of the pathogen (Plowright et al. 2017). H2) Range factors, specifically seasonal forage quality, population size, and inclement weather, further influence survival of adult *females*. We assumed that females in ranges with higher forage quality would have better nutrition and overall health (Bender and Weisenberger 2005) and we predicted that higher forage quality would therefore partially offset the effect of infection (Wehausen et al. 1987, Dunbar 1992, Miller et al. 2012). In larger populations, we predicted increased resource competition might cause a negative density-dependent effect (McCullough 1979, Clutton-Brock et al. 1997, Bowyer et al. 2014), and we assumed effects of infection and density would be additive to forage quality. We also considered that larger populations could have lower survival owing to higher contact rates and levels of disease prevalence if disease transmission was density-dependent (Begon et al. 2002, Lloyd-Smith et al. 2005, Cassirer et al. 2013). Finally, we predicted that inclement weather (i.e., heavy precipitation during colder months of the year) would add to the effect of infection (McIlroy et al. 1989, Ryder et al. 1992, Wolfe et al. 2010) and that higher winter precipitation would have a negative effect on winter survival.

STUDY AREA

The Mojave Desert ecosystem, which supports a metapopulation of bighorn sheep, consists of a patchwork of mountain ranges separated by low-lying areas of desert scrub and wash communities that are fragmented by roads, freeways, and other anthropogenic developments (Bleich et al. 1997, Epps et al. 2007). The Mojave is considered high desert, characterized by dry, hot summers and cold, wet winters, but also experiences late summer monsoons that account for at least 25% of the total annual rainfall (Hereford et al. 2004, National Geographic Society 2008). Temperatures and precipitation vary with elevation; temperatures typically range from average lows of -1°C in the winter to average highs of 34°C in the summer, and can exceed 40°C in the lower lying areas (NPS 2016). Mean annual precipitation is approximately 21 cm, with lower elevations receiving as little as 9 cm and higher elevations receiving as much as 25 cm annually (NPS 2016).

Our study occurred from November 2013 to March 2017. The study area comprised 9 focal bighorn sheep populations that were defined by mountain ranges in the Eastern Mojave Desert: Old Dad Peak/Kelso, South Soda, Cady, North Bristol, South Bristol, Marble, Clipper, Hackberry, and Woods Mountains (Epps et al. 2005); bighorn populations occupying these ranges were connected by occasional intermountain movements (Epps et al. 2018). The ranges were located east of Barstow, California, with Interstate 15 bounding the northern edge of the study area and Interstate 40 dividing the southern portion (Fig. 1.1). The entire study area spanned approximately 6,000 km² and occurred on lands managed by the Bureau of Land Management (BLM) and National Park Service, Mojave National Preserve (MNP). Dominant land use consisted of mining, hunting, recreation, and a cattle ranch allotment immediately adjacent to Woods Mountains that extended into the surrounding valleys. The study area also featured scattered private inholdings, the Union Pacific Railroad, and the Mojave Gas Pipeline. The first 3 years of the study occurred during a 5-year drought in California (Preisler et al. 2017), which resulted in less water availability and drier vegetation across the landscape from November 2013 to November 2016, with higher rainfall averages occurring in December 2016 to March 2017 (Climate Engine 2017).

The South Soda, North Bristol, South Bristol, and Marble Mountains were lower in elevation with peak elevations ranging from approximately 740 m to 1,200 m. Old Dad Peak/Kelso, Cady, Clipper, Hackberry, and Woods Mountains were higher in elevation with peak elevations ranging from approximately 1,300 m to 1,600 m. Mountain ranges were composed largely of volcanic flow and granitic rocks, but also featured unique differences in overall composition with respect to other rock types and geologic deposits, including sandstone, limestone, and metamorphic complexes (USGS 2018). Dominant vegetation in these ranges included catclaw acacia (*Senegalia greggii*), creosote bush (*Larrea tridentata*), rabbitbrush (*Ericameria sp.*), brittlebush (*Encelia farinosa*), white bur-sage (*Ambrosia dumosa*), blackbrush (*Coleogyne ramosissima*), Mormon tea (*Ephedra sp.*), silver and buckhorn cholla (*Cylindropuntia echinocarpa* and *Cylindropuntia acanthocarpa*), Mojave yucca (*Yucca schidigera*), California barrel cactus (*Ferocactus cylindraceus*), and annual grasses and forbs that appeared seasonally in response to rainfall (Digonnet 2013, Creech et al. 2016). Sparse pinyon pine (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) also occurred at higher elevation in the Hackberry and Woods Mountains. Common resident mammal species included antelope ground squirrel (*Ammospermophilus leucurus*), black-tailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), kit fox (*Vulpes macrotis*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and desert bighorn sheep. Two other ungulate species also occurred in the Hackberry and Woods Mountains: mule deer (*Odocoileus hemionus*) and free-ranging burro (*Equus asinus*); feral burros are not native to the Mojave Desert.

Additionally, natural and man-made water features (i.e., guzzlers) were present in all 9 ranges. Guzzlers are artificial catchments connected to storage tanks that can hold water to be dispensed gradually through a drinker box or trough (Swift el al. 2000). Natural water features included point-source springs and the Mojave River (the Mojave River only occurred in the Cady Mountains). Each mountain range had at least 1 water source, and some ranges contained multiple water features of varying types.

METHODS

Collaring, Disease Testing, and Mortality Recovery

Adult female bighorn sheep were captured and radio-collared in November 2013, 2014, and 2015. Animals were located aerially and captured using a net-gun fired from helicopter (Krausman et al. 1985), and were processed in the field following guidelines approved by CDFW and the National Park Service Institutional Animal Care and Use Committee (ACUP PWR_MOJA_Epps.Powers_DesertBighorn 2013.A3, 2013-2015), and as established by the American Society of Mammalogists for use of wild animals in research (Sikes et al. 2016). Adult females were fitted with both Global Positioning Systems (GPS) and very high frequency (VHF) radio-collars, and received ear tags with unique color and number combinations.

Blood and nasal swabs were collected from individuals at time of capture. Prior to testing, blood serum was stored in cryogenic vials at -20° C, and swabs were stored dry at -20° C. Serology was performed for *M. ovi* specific antibodies in serum samples using competitive enzyme-linked immunosorbent assays (cELISA) by Washington Animal Disease Diagnostic Laboratory (WADDL; Pullman, WA). Nasal swabs were used to detect *M. ovi* specific DNA sequences via PCR testing by WADDL; strain typing consisted of multi-locus sequence typing based on partial DNA sequences of the 16S-23S intergenic spacer region, the 16S ribosomal subunit, and RNA polymerase B and gyrase B genes, as described in Cassirer et al. (2017). Additionally, we estimated minimum age of females based on horn growth (i.e., number of horn annuli) and tooth eruption patterns (Deming 1952, Geist 1966, Heffelfinger 1997, Rubin et al. 2000).

Adult females were monitored and tracked via satellite- and radio-telemetry. The GPS data were received through the Iridium and Globalstar satellite systems (Iridium Communications, McLean, Virginia; Globalstar, Inc., Covington, Louisiana); collar locations were recorded between 2 times a day and once every 3 days, and collars signaled a mortality if they were motionless for more than 8 hours. If GPS collars stopped reporting locations because of technical failure, CDFW staff monitored survival status via radio-telemetry surveys conducted from fixed-wing aircraft at approximately 1-2-month intervals (GPS collars had an average lifespan of 2 years and VHF collars had an average lifespan of 9 years). Mortalities were typically recovered from within 24 hours to 2 days after detection during the spring and summer, and from within 24 hours to 2 weeks during the autumn and winter, depending on availability of field personnel.

During post-mortem recovery, inner ear, nasal, and lung swab samples were collected for *M. ovi* PCR. Lung tissue samples were also collected from dead animals < 12 hours post-mortem for histological examination. Swab and tissue samples were kept on ice in the field; swabs were stored dry or in a tryptic soy broth media at -20°C and lung samples were stored in 10% neutral buffered formalin at 4°C prior to laboratory submission. The California Health and Food Safety Laboratory (CAHFS; San Bernardino, CA) and Colorado State University Veterinary Diagnostic Lab (CSU VDL; Fort Collins, CO) performed gross- and histo-pathology on lungs and WADDL performed PCR on swabs collected post-mortem. Additionally, field personnel also conducted mortality site investigations, which included examination of the condition of the carcass for signs potentially indicative of cause of death (i.e., lacerations, bite marks, broken bones, body position, bullet wounds, color of bone marrow), and inspection of surrounding areas for other evidence (i.e., predator tracks, scat, drag marks, cache sites, blood trailing, steep terrain), to determine whether predation, falling, gunshot, or poor nutrition may have contributed to mortality. We note that while mortality investigations allowed us to rule out potential causes of death, we could not reliably determine cause of death based on evidence from these investigations and used the information largely to determine if a mortality was human-caused and should therefore be censored from the study.

Death dates from GPS collars were assumed to be the actual time of death for individuals with active GPS collars (i.e., the day movement stopped); if a mortality was detected via VHF signal, we deduced an approximate time of death based on the mortality detection date, last known live detection date, and the condition of the carcass at the time of recovery. Assessments of carcass condition were informed by mortalities we recovered that had known death dates, and corresponded with designations defined by Galloway et al. (1989). Generally, if a carcass was intact or bloated, with organs still present, we inferred that the carcass was fresh and death had occurred within the last 1-3 days. If a carcass had been scavenged but was partially articulated with some muscle tissue intact, we inferred the carcass was in the early decomposition stage and between 4 and 7 days old. If the carcass appeared heavily scavenged (i.e., largely or wholly disarticulated) with bones bearing mummified muscle tissue, we assumed the carcass to be in a state of advanced decomposition and at least 2 or 3 weeks old. Finally, if remains consisted of dry bone and bone fragments, we concluded that the carcass had reached the skeletonization stage and was \geq 4 weeks old (we did not collect samples from carcasses in advanced stages of decomposition).

Environmental Variables

We calculated seasonal home ranges at the population level for animals in each mountain range to extract data reflecting environmental conditions within ranges for each population. Seasonal home ranges were estimated in each mountain range by grouping collar location data for all individuals by season. Seasons were defined based on a climograph for Mojave National Preserve (McKee et al. 2015), whereby October and November represented autumn, December through March represented winter, April through June represented spring, and July through September represented summer. We used the kernel density tool in ArcGIS 10.5 (ESRI 2016) to produce home range estimates with fixed kernels and reference bandwidth (h_{ref;} Silverman 1986). A 95% contour was used to capture the majority of use per season (Seaman and Powell 1996, Börger et al. 2006, Formica et al. 2010) and generate seasonal home ranges that captured 96-98% of realized locations for each population.

We used the Normalized Difference Vegetation Index (NDVI) as an index of forage quality (Pettorelli et al. 2011, Ryan et al. 2012, Hurley et al. 2014, Creech et al. 2016, Heffelfinger et al. 2017), and extracted both NDVI and precipitation data from Climate Engine (2017; Huntington et al. 2017). For NDVI, we used a composite of Landsat 4, 5, 7, 8, which had a temporal scale of 16 days and spatial resolution of 30 m, and calculated mean seasonal NDVI within each seasonal home range for every year of the study. To obtain winter precipitation data, we calculated rainfall totals within winter seasonal home ranges using 5-day estimates from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS; Funk et al. 2015, Climate Engine 2017).

Abundance Estimates for Evaluating a Density-Dependent Effect

Bighorn sheep frequently use both man-made and natural water features for hydration in the Mojave, especially during the hot summer months (Bleich et al. 1997). As such, we set up remote cameras at 1-3 point-source water features in each mountain range to collect visual survey data, targeting all sites regularly visited by bighorn (established water sources were well-documented in these ranges). Survey data from cameras were then used to generate counts of marked and unmarked individuals for abundance estimation. We used Bushnell Trophy cameras (standard and hybrid 8MP) set to a 1-second delay to collect photos and video from June through September 2016, when bighorn reliably use water, and serviced cameras every 2 weeks.

We applied the generalized form of Bowden's estimator (\tilde{N} ; Bowden and Kufeld 1995) to the total number of marked and unmarked adult females observed on camera for selected days in each mountain range to estimate population abundance of

adult female bighorn. To obtain numbers of marked and unmarked individuals, photos and videos were first sorted into activity periods by day and were then scored (videos provided better coverage with larger groups). We defined an activity period as beginning from the time when the first bighorn sheep in a group appeared at water and ending at the time when the last bighorn sheep in a group left, with activity typically ceasing for ≥ 20 minutes between periods. Days were generally censored if there were any activity periods that elapsed for > 1.5 hours with > 5 adult females present, as longer time periods with more individuals could render uncertainty in count totals. We counted all marked and unmarked adult females (i.e., > 2 years old) in each activity period and calculated totals for each day in which we could obtain reliable counts, treating a single day as a sampling unit. We define occasion in this context as a single sampling day. Unmarked individuals were identified by unique horn and pelage characteristics, and marked individuals were identified by ear tag combinations. We compared identities of individuals across all activity periods within a given occasion to prevent double-counting. If any unmarked or marked individuals were indistinguishable (usually because of image quality), we censored the entire occasion.

We attempted to use at least 16 occasions for each population in order to achieve an average of marked animal sightings per marked individual > 1 (i.e., at least > 1 sighting of each marked animal on average), with a higher proportion of the marked sample detected (> 0.7 in most cases), so as to reduce variance and increase precision (Bowden and Kufeld 1995, Diefenbach 2009), and adjusted the number of occasions given the usable data available. Frequency of visitation varied across mountain ranges and sites, and not all sites received daily visitation; additionally, there were occasional gaps in consecutive sampling days owing to downed cameras and other temporary technical failings remedied when cameras were serviced. We drew occasions consecutively beginning from July through August (when activity was highest), and subsequently from September and June to add occasions as needed. In ranges where camera data were collected from > 1 point-source water feature, we drew occasions evenly across sites.
We acknowledge that double-counting of unmarked individuals across activity periods may have occurred despite efforts to control for replacement within occasions. We therefore estimated a potential inflation factor for each range based on the rate of revisitation, which we calculated from the total number of times a marked individual was observed in 2 different activity periods within an occasion divided by the sum of marked individuals present across all occasions. We assumed the rate of revisitation to be the same for marked and unmarked individuals and used this rate to adjust our counts of unmarked adult females in order to calculate the percentage by which we may have overestimated abundance within each mountain range as a result of double-counting.

We also recognize that our estimates may have an unknown negative bias because we did not directly account for individual heterogeneity (White and Cooch 2017), and Bowden's estimator relaxes the assumption of "equal catchability" for abundance estimation (Krebs 1999, McClintock et al. 2006, McClintock and White 2007, Cooch and White 2017). Our estimates are also based on count data collected in 2016, the last year of the study, and are only representative of the number of adult females that used point-source water features. As such, our estimates serve as a relative index for the true population size, or abundance of adult females, within each mountain range over the study period.

Survival Modeling

We used the known-fate model in Program MARK (version 8.2; White and Burnham 1999, Cooch and White 2017) with a logit link function to model seasonal adult female survival from November 2013 to March 2017. We created individual encounter histories for each animal, whereby every month was a sampling occasion for evaluating survival, and an animal was recorded as either dead or alive at the beginning and end of each sampling occasion. Infection status (i.e., whether an individual was PCR-positive [infected] or negative [not infected] for *M. ovi* at capture) was included as an individual covariate in our models, while population abundance, NDVI, and winter precipitation were included as group covariates (Cooch and White 2017). Winter precipitation and NDVI were time-varying covariates, while population abundance was a constant index.

We used a multi-step modeling approach to assess several potentially important parameters. We first fit models containing all combinations of mean seasonal NDVI and tested for effects on monthly survival within the same season and lag effects on monthly survival within the following season (Table 1.1). The best model had a single covariate, the lag effect of mean autumn NDVI (i.e., autumn forage quality) on winter survival, which was the only informative NDVI parameter in the initial model set (i.e., 90% confidence interval [CI] did not overlap 0). We then developed a candidate model set to test this variable along with varying combinations of our other *a priori* covariates, and included single covariate models, a null model with a single intercept, and a range effect model with 9 intercepts parameterizing each range for comparison. Given the late summer monsoon season in the Mojave, we also decided to evaluate a lag effect of summer forage quality (i.e., mean summer NDVI) on winter survival *post hoc*, which we added to our candidate model set. Additionally, we tested a quadratic effect of winter precipitation on winter survival *post hoc* as well. We modeled infection status as a dummy variable (Cooch and White 2017) whereby individuals received a covariate value of 1 if they were PCR-positive at time of capture (i.e., infected with M. ovi), a value of 0 if they were PCR-negative (i.e., not infected), and a mean of 0.5 if a test result was indeterminate based on results from WADDL, or status was otherwise unknown due to missing data (we assumed information was missing at random and imputed missing values assuming a probability of 0.5 for either outcome, which we believe to be conservative insofar as accounting for uncertainty in the status of these individuals). All of our continuous variable inputs (i.e., NDVI, winter precipitation, and population abundance) were zstandardized; we used the Pearson correlation coefficient to assess relatedness of these variables prior to model fitting.

Lastly, we conducted 2 separate *a posteriori* analyses to evaluate effects of age and exposure to *M. ovi* (i.e., cELISA status) on survival (Appendix A). We decided to test these covariates because we found a strong negative effect associated with PCR-positive status on survival that we wanted to explore further, and older age has been linked to higher rates of *M. ovi* infection among adult bighorn (Plowright et al. 2017). Age and exposure status were included as individual covariates and coded

as dummy variables (Cooch and White 2017). Females estimated to be 2-9 years old received a covariate value of 0, and females > 9 years old received a value of 1. Females that became older than 9 years during the study, based on minimum age estimates, were moved from the former cohort to the latter upon aging out. Individuals received covariate values of 1 if they were cELISA-positive at time of capture (i.e., *M. ovi* antibodies were detected), values of 0 if they were negative (i.e., antibodies were not detected), and a mean value of 0.5 if a test result was indeterminate or otherwise unknown.

Models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc; Akaike 1973, Hurvich and Tsai 1989). In the candidate model set, we considered the effects of all variables in models with Δ AICc scores < 2 and interpreted covariate effects based on model-averaged estimates with 90% confidence intervals (Burnham and Anderson 2010, Arnold 2010, Symonds and Moussalli 2011, Monteith et al. 2014), which we compared to results from our top 2 models. We identified predictor variables with relative variable importance, *w*+(*j*), closer to 1 as most important (Burnham and Anderson 2010, Symonds and Moussalli 2011).

Annual and winter survival estimates for infected and uninfected individuals were produced for every population by multiplying model-averaged monthly survival probabilities; we calculated model-averaged standard error (SE) estimates using the Delta method (Cooch and White 2017: Appendix B). Annual survival was estimated from January through December for a given year. Winter survival was estimated from December through March across successive years.

RESULTS

Sample Sizes

We radio-collared a total of 122 adult female bighorn sheep between 2013 and 2015. We censored 4 animals that may have died from post-capture stress (i.e., mortalities occurred within 4 weeks following capture; Kock et al. 1987, Beringer et al. 1996), and removed from the study another 2 individuals that were illegally killed and 1 individual whose death was attributed to a tight collar, which ultimately yielded a sample size of 115 individuals across the 9 populations. Of these animals, 31 females died and 84 females survived. Sample sizes within each range varied from 6

individuals (Hackberry and Woods Mountains [12 total]) to 24 individuals (Marble Mountains; Table 1.2). Seventeen females were > 9 years old during the study.

M. ovi Status

Of the 115 animals in our sample, 36 tested positive for *M. ovi* infection at time of capture and 15 had indeterminate PCR results or otherwise unknown infection status, while 70 were seropositive and 21 had indeterminate cELISA results (i.e., 40%-50% inhibition) or otherwise unknown exposure status. Of the 17 older females in our sample, 3 were PCR-positive for *M. ovi* at capture, 5 were PCR-negative, and 9 were of unknown infection status. The total proportion of PCR-positive individuals among our samples within each range varied from 0% (South Soda Mountains) to 75% (South Bristol Mountains), and the proportion of mortalities varied from 0% (Hackberry, Woods, and Clipper Mountains) to 54% (Marble Mountains; Table 1.2) over the study period. The lowest proportions of PCR-positive individuals (< 20%) occurred in the South Soda (0%) and North Bristol Mountains (14%; Table 1.2). Intermediate proportions (20-40%) occurred in the Hackberry, Woods, Old Dad Peak/Kelso, and Cady Mountains (Table 1.2). Highest proportions of infected individuals (> 40%) occurred in the Marble, Clipper, and South Bristol Mountains (Table 1.2). No study animals showed clinical signs of illness at time of capture. Both PCR and cELISA tests have high diagnostic sensitivity (> 99% and > 88% respectively; WADDL 2017) and specificity (> 98.7% and > 98.6%, respectively; WADDL 2020), but we acknowledge that *M. ovi* pathogen and antibody detection can fail, and while false positives are highly unlikely, false negatives may occur due to low pathogen load or antibody levels that become less over time (Plowright et al. 2017), or from mishandling of samples.

Abundance Estimates

Marked animals detected on camera were typically within 9 km of point-source water features during the sampling period (June-September); although Bowden's estimator allows for individual heterogeneity and temporary movement off the study area (White 1996, McClintock et al. 2006, McClintock and White 2007), we assumed that marked animals located > 9 km away from point-source water features throughout the sampling period were not available for sampling during any occasions, and therefore

we censored between 1 and 5 animals from population estimates in 3 ranges (Cady [1], Marble [4], and North Bristol Mountains [5]). We used count data from 14 to 19 occasions (i.e., sampling days) in each mountain range to estimate abundance of adult females. Occasions typically had > 5 activity periods separated by breaks of ≥ 20 minutes, with activity periods rarely exceeding 1.5 hours.

Estimated abundance was lowest in Hackberry, Woods, and South Soda Mountains (< 40 adult females), intermediate in Old Dad Peak/Kelso, South Bristol, Clipper and Cady Mountains (40-80 adult females), and highest in North Bristol and Marble Mountains (> 80 adult females; Table 1.3). We recorded 214 marked animal sightings (detecting 78% of our total sample) and 858 unmarked animal sightings across all mountain ranges (Table 1.4), and documented 12 occurrences of marked animals visiting the same site in 2 different activity periods during the same occasion. As such, we calculated a revisitation rate of 0.056, which yielded a potential inflation factor that may have increased our abundance estimates by 3.3 to 5.1% (Table 1.4). We also tested repeatability of our method for generating counts by using a second observer to re-score 21 occasions (3 separate occasions from 7 different mountain ranges); first and second observer counts were highly correlated (r = 0.98), indicating that counts provided a reasonably accurate assessment of the number of animals present on each sampling occasion.

Environmental Conditions

Seasonal NDVI averages for summer and autumn were highest in Hackberry, Woods, and Clipper Mountains, intermediate in Old Dad Peak/Kelso and Marble Mountains, and lowest in South Soda, South Bristol, Cady, and North Bristol Mountains (Table 1.3). Yearly winter precipitation varied widely across ranges, with totals ranging from 14mm to 118mm (Table 1.3). Hackberry and Woods Mountains received the highest rainfall in winter, followed by North Bristol, Old Dad Peak/Kelso, Cady, Clipper, and South Soda Mountains, which received up to 42% less (Table 1.3). South Bristol and Marble Mountains received the lowest levels of yearly winter precipitation, which were up to 65% less than Hackberry and Woods Mountains. Winter precipitation was highest in 2016-17 in all ranges, with totals doubling those from the previous year (Table 1.3).

Survival Modeling

We used Pearson correlation coefficients to examine pairwise correlations between winter precipitation and NDVI in summer (r = 0.30) and autumn (r = 0.047) and found no statistical support for relationships (i.e., P > 0.05). There was a small negative correlation between population abundance and summer NDVI that was significant (r = -0.40, P = 0.024), whereas a correlation between population abundance and autumn NDVI lacked statistical support (r = -0.33, P = 0.062). There was strong evidence for a positive correlation between summer and autumn NDVI (r = 0.92, P << 0.05), and we therefore tested these variables separately in the candidate model set (Table 1.5).

Our global models alternately containing summer and autumn NDVI were the most strongly supported (Table 1.5). As per the results from these 2 top models, summer and autumn NDVI were associated with a positive lag effect on winter survival, winter precipitation was negatively correlated with winter survival, and population abundance and PCR-positive status (as determined at capture) were associated with negative effects on survival across all seasons (Table 1.6). Modelaveraged parameter estimates substantiated these results (Table 1.6). Summer and autumn NDVI were competing predictor variables, although the relative variable importance (w+[j]; Burnham and Anderson 2010) for summer NDVI was slightly higher (summer NDVI: 0.59; autumn NDVI: 0.39; combined: 0.98). Among the other 3 supported predictor variables, PCR status had the highest relative variable importance (0.97), followed by population abundance (0.85), with winter precipitation being comparably less important (0.63). Winter precipitation also had weak statistical support in our second highest ranking model (i.e., 90% CI slightly overlapped zero). We tested a quadratic effect of winter precipitation on winter survival post hoc, which was not informative in any models and appeared to cancel out the main effect of winter precipitation.

Estimated Effects

Based on the model-averaged estimates of factor effects, monthly survival in winter was approximately 3 times higher with every 0.03 increase in mean summer or autumn NDVI (i.e., the mean ratio comparing differences in reflectance measurements of infrared and near-infrared light). Monthly odds of survival were 33.3% (90% CI = 11.4, 49.7) less with every 40-animal increase in population abundance, 70.8% (90% CI = 41.5, 85.4) less if an animal was PCR-positive for M. ovipneumoniae at capture, and 30.2% (90% CI = 4.3, 49.1) less with every 21 mm increase in winter precipitation. Model-averaged effects for summer and autumn NDVI are not jointly additive unless effects are weighted using the full-model averaging approach described by Symonds and Moussalli (2011), because these variables are correlated and therefore explain much of the same variance in the data (i.e., overwinter survival can be explained by one or the other in simplified terms).

The precision of our abundance estimates varied depending on population and sample sizes, with smaller sample sizes and larger populations having wider confidence intervals. Consequently, we tested the sensitivity of the apparent population abundance effect, given the uncertainty in the data, by reevaluating our models using the upper and lower bounds of the 90% confidence intervals for population abundance (confidence intervals were scaled back from 95% to provide minimum values > 0 in the Hackberry and Cady Mountains). Abundance remained an informative parameter at both lower and upper bounds (respective model-averaged estimates: $\beta = -0.39$, 90% CI = -0.66, -0.13 and $\beta = -0.40$, 90% CI = -0.70, -0.11), but the estimated effect shifted with respect to increases in abundance. Based on model-averaged estimates, monthly odds of survival would decrease by approximately 33% with every 20-animal increase at the lower bound and with every 55-animal increase at the upper bound.

Survival Estimates

Model-averaged annual survival probabilities for adult female bighorn varied across populations with respect to range conditions and population abundance, and were higher for uninfected animals in a given population and year (Table 1.7). Estimated annual survival was highest in the Hackberry, Woods, and Clipper Mountains, ranging from 0.958 (\pm 0.016 SE) to 0.983 (\pm 0.011 SE) for uninfected females and from 0.869 (\pm 0.034 SE) to 0.945 (\pm 0.026 SE) for infected females, intermediate in Old Dad Peak/Kelso, South Bristol, and South Soda Mountains (uninfected: 0.943 [\pm 0.026 SE] to 0.966 [\pm 0.017 SE]; infected: 0.828 [\pm 0.057 SE] to 0.893 [\pm 0.038 SE]),

and lowest in the Cady, Marble, and North Bristol Mountains (uninfected: 0.896 [\pm 0.030 SE] to 0.953 [\pm 0.017 SE]; infected: 0.700 [\pm 0.070 SE] to 0.856 [\pm 0.036 SE]; Table 1.7).

Sixty-five percent (n = 20) of all 31 mortalities among collared females occurred during winter. In winter 2016-17, which was the most severe winter in terms of precipitation, observed mortality among collared females was highest with a total of 10 deaths, and estimated overwinter survival was lowest in some populations (Table 1.8). As with annual survival, estimated overwinter survival reflected differences in average summer and autumn forage quality, population abundance, and total winter precipitation across ranges for uninfected and infected individuals (Fig. 1.2).

A Posteriori Covariate Testing

We evaluated estimated age and *M. ovi* exposure (i.e., cELISA status) *a posteriori*. The potential effect of older age (i.e., > 9 years) on survival was not supported (i.e., 90% CIs overlapped 0), although age was included in 3 of 7 top models (Δ AICc scores < 2; Appendix A). The parameter estimate for age in the highest ranked model containing age was $\beta = -0.60$, 90% CI [-1.32, 0.13] and the relative variable importance for age was 0.44. The potential effect of *M. ovi* exposure on survival, based on cELISA testing, was not supported in our evaluation. The cELISA covariate occurred in models with Δ AICc scores ≥ 8 (Appendix A) and all estimates for the effect had 90% CIs overlapping 0. The relative variable importance of cELISA was 0.024, providing further evidence that this variable was not informative.

Post-Mortem Diagnostics

We recovered all 31 mortalities included in the study and collected and analyzed post-mortem samples from 10 of these individuals; remains were too old (\geq 2 weeks) for sampling in 18 cases, and in 3 cases field sampling failed. Thirteen of the 31 mortalities were detected via VHF signal, and in 8 of these cases, the last live detection and mortality detection occurred within the same season. There was no clear evidence of predation in any mortality cases. Of the 10 individuals that were tested post-mortem, 2 animals were PCR-positive for *M. ovi* at death and at time of capture (1 and 2 years prior to death), 1 of which had chronic active pneumonia at

time of death as determined by lung histopathology (we were unable to collect a lung sample from the other individual, and therefore could not test for disease). Another animal had acute active pneumonia at death, but did not test positive for *M. ovi* at death or time of capture. In the 7 other mortality cases, *M. ovi* infection was not confirmed post-mortem, but 5 animals tested positive for *M. ovi* infection < 1 year (n = 1) and 1-4 years (n = 4) prior. The infection status of the 2 remaining cases was not confirmed at time of capture. Of the 31 mortalities, 84% occurred > 1 year after capture; mean estimated age at death was 7 years old and range of estimated ages at death was 3 to 16. We note that negative results from samples collected post-mortem are not reliable due to the likelihood of pathogen degeneration following host mortality.

Eight individuals were also screened for leukotoxigenic *Pasteurellaceae* postmortem via PCR testing of lung swabs (WADDL; Besser et al. 2012*b*) and sinus tissue (Colorado Parks and Wildlife, Fort Collins, CO; Fox et al. 2015). Of these animals, only1 tested positive. Post-mortem tests for *Pasteurellaceae* were not carried out systematically because detection rates associated with standard testing protocol for the pathogens are low (< 0.5; Butler et al. 2017) and samples were difficult to collect, store, and transport in a timely manner.

DISCUSSION

We found that *M. ovi* infection was associated with a reduction in survival of adult female bighorn for 3.5 years following a pneumonia outbreak that occurred in the Mojave Desert in 2013. The negative effect of *M. ovi* infection on adult female bighorn sheep survival is consistent with other studies that have linked *M. ovi* to pneumonia epizootics and acute mortality in bighorn sheep populations (Besser et al. 2012*a*, *b*, Cassirer et al. 2017, 2018), although our study suggests a lingering postoutbreak effect. Environmental variables also appeared to influence survival, and in particular, higher forage quality in summer and autumn (as approximated by NDVI) was associated with increased probability of survival for infected and uninfected individuals. We also found that winter survival was higher in mountain ranges with higher summer and autumn NDVI for both infected and uninfected individuals. The positive relationship between increased nutrition during summer and autumn with overwinter survival has been well documented in ungulates (Mautz 1978, Cook et al. 2004, sensu Tollefson et al. 2008, Monteith et al. 2014), and many studies have also shown that immune function and disease resistance are dependent on nutrition (Ullrey 1993, Lochmiller and Deerenberg 2000, Cotter et al. 2011, Brunner et al. 2014).

Estimated population abundance was negatively correlated with survival of adult female bighorn, although there was uncertainty in the strength of the effect because precision of abundance estimates varied. We also note that population sizes may have fluctuated over the 3-year period and abundance estimates therefore served as a relative index across populations. We conclude that larger populations may be experiencing a density-dependent effect on survival that can be attributed to either increased pressure on resources resulting in lower nutrition (McCullough 1979, Clutton-Brock et al. 1997, Bowyer et al. 2014), especially during summer and autumn, or increased contact rates that beget higher rates of disease transmission (Lloyd-Smith et al. 2005, Cassirer et al. 2013, 2018), or both. Although disease transmission can be frequency-dependent in bighorn sheep populations (Manlove et al. 2014, Cassirer et al. 2018), transmission is more likely to be density-dependent during summer months in the Mojave when groups converge at point-source water features, causing homogeneous mixing (Begon et al. 2002).

There was also an apparent negative effect of winter precipitation on overwinter survival, but the effect had weak statistical support in our second highest ranking model, which implies uncertainty. Previous studies have implicated stress from severe winter conditions as likely triggers of pneumonia-induced mortality in bighorn populations (Ryder et al. 1992, Wolfe et al. 2010), and McIlroy et al. (1989) found that rain and windchill were directly associated with the development of pneumonic lung lesions in domestic sheep. We therefore used winter precipitation as a proxy for winter severity. In our study, survival was lowest during winter months and in winter 2016-17, which was the most severe in terms of precipitation, mortality among collared ewes was highest. Perhaps there was uncertainty in this parameter because it did not account for other weather conditions like windchill and temperature that may have been more informative. We did not test other possible correlates of winter severity because we could not reliably obtain such data for all mountain ranges in the study, but we did test quadrature of winter precipitation to determine whether sub-optimal precipitation might be associated with lower survival in winter and found no effect.

Additionally, previous exposure to *M. ovi* (as per cELISA testing and demonstration of *M. ovi* specific antibodies), barring infection status at capture, did not appear to affect adult female survival. Given that estimated survival was lower for individuals that tested positive for infection at capture, while past exposure alone did not lower survival probability, we deduce that many infected individuals may have remained infected until death. Recent studies have reported that bighorn sheep can become chronically infected with M. ovi (Cassirer et al. 2017, Plowright et al. 2017, Wood et al. 2017), and infectious periods can last up to 3 years or longer (Plowright et al. 2017). Eighty-four percent of mortalities in the study occurred > 1 year after capture, and we confirmed *M. ovi* infection at time of death in 2 recovered mortalities that were PCR-positive at capture 1 and 2 years prior (we were unable to determine infection status at death in 21 other cases), 1 of which had chronic active pneumonia at time of death (we could not obtain a lung sample from the other mortality to test disease status). In view of our results and current literature, we propose that chronic infection may have led to lower survival among adult females that tested positive for the *M. ovi* pathogen at capture. We recognize, however, that false-negative PCR results could potentially invalidate this conclusion if there were infected individuals who tested negative and did not experience lower survival. Even so, selective culling of bighorn that are chronically infected with M. ovi has been identified as a way to control pathogen persistence in infected populations (Cassirer et al. 2018). As such, we propose programmatic re-testing of infected animals to evaluate the propensity for chronic infection among bighorn in the Mojave Desert and to assess whether selective culling could be an effective management tool for reducing prevalence and transmission of *M. ovi* within infected populations, granted female bighorn who were PCR-positive for *M. ovi* at time of capture had lower survival odds which implies natural culling from populations over time.

Finally, we tested an age effect on survival of adult females estimated to be 2-9 years of age and > 9 years. Plowright et al. (2017) found that *M. ovi* prevalence in adults (i.e., individuals > 2 years old) decreased between ages 2 and 9, and increased after 9 years of age, with highest prevalence occurring among individuals > 15 years old. This finding suggests that older animals are more likely to become chronic carriers of the pathogen. We did not find a compelling effect associated with older age, although the age covariate was included in 3 top performing models. We suspect that our sample of older age females may have been too small (n = 17) for the parameter estimate to be supported, but there was likely a weak signal that resulted in the covariate appearing in supported models. We also did not have information on infection status for 9 older females, and of the 8 remaining, only 3 were PCR-positive for *M. ovi* at capture. We therefore conclude that the negative effect associated with *M. ovi* infection in our study largely reflects the impact on survival of adult females estimated to be between 2 and 9 years of age.

In applying a maximum likelihood framework, we acknowledge the limitation in our ability to account for uncertainty in variable inputs. We note that corresponding parameter estimates are based on mean values and the variance of these estimates partially represents uncertainty associated with variable inputs. Although we cannot overcome the error such uncertainty may have introduced to our analysis, we have employed methods to evaluate the robustness of our results (i.e., model-averaging parameter estimates, testing the reliability of count data with a second observer, estimating potential inflation of abundance estimates, and testing the sensitivity of the apparent population abundance effect), which have demonstrated strong support for our findings. Moreover, we also model-averaged estimated annual and winter survival to account for model selection uncertainty (Cooch and White 2017).

While many studies have suggested that forage quality, winter severity, and population size may influence the survival of bighorn sheep exposed to pneumonia (Dunbar 1992, Ryder et al. 1992, Monello et al. 2001, Bender and Weisenberger 2005, Wolfe et al. 2010), Cassirer et al. (2018) noted a lack of evidence in the literature to support nutritional condition as a factor affecting susceptibility to respiratory disease, and Jorgenson et al. (1997) concluded that winter severity and population size had no apparent effect on adult female survival in 2 Rocky Mountain populations (one infected with pneumonia) in Alberta, Canada. We speculate that our study of adult female bighorn survival in populations recently exposed to M. ovi across mountain ranges with varying environmental conditions in a desert system, where carrying capacity is arguably lower than that in non-arid mountain environments (Bender and Weisenberger 2005, Bowyer et al. 2014), may have afforded the conditions to detect signals that could be less pronounced across populations with more homogeneous conditions and in less stochastic environments. Moreover, drought conditions preceding the outbreak may have also produced carry over effects (Harrison et al. 2011) that contributed to lower survival and may have added to the observed effect associated with infection. Additionally, we recognize that our analysis focused on the effect associated with M. ovi infection, and while M. ovi has been identified as a primary causal agent in pneumonia outbreaks and associated mortality among bighorn sheep over the past several years (Besser et al. 2008, 2012*a*, *b*, 2013, 2014, Plowright et al. 2017, Cassirer et al. 2018), other respiratory pathogens (i.e., M. haemolytica, B. trehalosi, and P. multocida) were detected in some of our study populations before the pneumonia outbreak in 2013 and may have also influenced adult female survival during the study. On a final note, there are other factors that can also influence disease resistance and overall health, including forage quality associated with micronutrients and soil composition (Ullrey 1993, Spears 1994, Hnilicka et al. 2002), genetics (Coltman et al. 1999, Luikart et al. 2008, Plowright et al. 2017), and chronic physiological stress (Belden et al. 1990, Dhabhar and McEwen 1997, Pruett 2003, Romero 2004, Martin 2009). Such factors may further explain observed differences in adult female response and warrant investigation in future studies.

MANAGEMENT IMPLICATIONS

We speculate that if bighorn sheep distributions were more diffuse during summer and autumn, use of forage would become more evenly distributed and nutrition less limited for adult females. A more diffuse distribution might also reduce contact rates between infected and uninfected individuals, and reduce transmission of M. ovipneumoniae within populations. One way to achieve a broader spatial distribution of populations during summer and autumn might be to reconfigure placement of artificial water features, and perhaps add new installations in a way that would give animals greater access to quality forage and allow for greater use of forage throughout the range, although this strategy could ultimately increase population size and produce higher densities over time.

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LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Proceedings of the 2nd International Symposium on Information Theory Akademiai Kiado, Budapest. (Reproduced in pages 610-624 *in* S. Kotzand and L. S. Johnson, editors. 1992. Breakthroughs in Statistics, Volume One, Foundations and Basic Theory. Springer-Verlag, New York, New York, USA).
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178.
- Begon, M., M. Bennett, R. G. Bowers, N. P. French, S. M. Hazel, and J. Turner. 2002. A clarification of transmission terms in host-microparasite models: numbers, densities, and areas. Epidemiology and Infection 129:147-153.
- Belden, E. L., E. S. Williams, E. T. Thorne, H. J. Harlow, K. White, and S. L. Anderson. 1990. Effect of chronic stress on immune system function of Rocky

Mountain Bighorn Sheep. Biennial Symposium of the Northern Wild Sheep and Goat Council 7:76-91.

- Bender, L. C., and M. E. Weisenberger. 2005. Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. Wildlife Society Bulletin 33:956-964.
- Beringer, J., L. P. Hansen, W. Wilding, J. Fischer, and S. L. Sheriff. 1996. Factors affecting capture myopathy in white-tailed deer. Journal of Wildlife Management 60: 373-380.
- Besser, T. E., E. F. Cassirer, K. A. Potter, J. VanderSchalie, A. Fischer, D. P. Knowles, D. R. Herndon, F. R. Rurangirwa, G. C. Weiser, and S. Srikumaran. 2008. Association of *Mycoplasma ovipneumoniae* infection with population limiting respiratory disease in free-ranging Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*). Journal of Clinical Microbiology 46:423-430.
- Besser, T. E., E. F. Cassirer, C. Yamada, K. A. Potter, C. Herndon, W. J. Foreyt, D. P. Knowles, and S. Srikumaran. 2012a. Survival of bighorn sheep (*Ovis canadensis*) commingled with domestic sheep (*Ovis aries*) in the absence of *Mycoplasma ovipneumoniae*. Journal of Wildlife Diseases 48:168-172.
- Besser, T. E., M. A. Highland, K. Baker, E. F. Cassirer, N. J. Anderson, J. M. Ramsey, K. Mansfield, D. L. Bruning, P. Wolff, J. B. Smith, and J. A. Jenks. 2012b. Causes of pneumonia epizootics among bighorn sheep, western United States, 2008-2010. Emerging Infectious Diseases 18:406-414.
- Besser, T. E., E. F. Cassirer, M. A. Highland, P. Wolff, A. Justice-Allen, K. Mansfield, M. A. Davis, and W. Foreyt. 2013. Bighorn sheep pneumonia: sorting out the cause of polymicrobial disease. Preventive Veterinary Medicine 108:85-93.
- Besser, T. E., E. F. Cassirer, K. A. Potter, K. Lahmers, J. L. Oaks, S. Shanthalingam, S. Srikumaran, and W. J. Foreyt. 2014. Epizootic pneumonia of bighorn sheep following experimental exposure to *Mycoplasma ovipneumoniae*. PLOS ONE 9:1-9.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:3-50.
- Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz, and T. Coulson. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. The American Naturalist 168:471-485.
- Bowden, D. C. and R. C. Kufeld. 1995. Generalized mark-resight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840-851.
- Bowyer, R. T., V. C. Bleich, K. M. Stewart, J. C. Whiting, and K. L. Monteith. 2014. Density dependence in ungulates: a review of causes and concepts with some clarification. California Fish and Game 100:550-572.
- Brunner, F. S., P. Schmid-Hempel, and S. M. Barribeau. 2014. Protein-poor diet reduces host-specific immune gene expression in *Bombus terrestris*.
 Proceedings of the Royal Society 281:20140128. doi 10.1098/rspb.2014.0128.

- Burnham, K. P., and D. R. Anderson. 2010. Model selection and multimodel inference: a practical-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Butler, C. J., W. H. Edwards, J. E. Jennings-Gaines, H. J. Killion, M. E. Wood, D. E. McWhirter, J. T. Paterson, K. M. Proffitt, E. S. Almberg, P. J. White, J. J. Rotella, and R. A. Garrott. 2017. Assessing respiratory pathogen communities in bighorn sheep populations: sampling realities, challenges, and improvements. PLOS ONE 12:e0180689.
- Cassirer, E. F., R. K. Plowright, K. R. Manlove, P. C. Cross, A. P. Dobson, K. A. Potter, and P. J. Hudson. 2013. Spatio-temporal dynamics of pneumonia in bighorn sheep. Journal of Animal Ecology 82:518-528.
- Cassirer, E. F., K. R. Manlove, R. K. Plowright, and T. E. Besser. 2017. Evidence for strain-specific immunity to pneumonia in bighorn sheep. Journal of Wildlife Management 81:133-143.
- Cassirer, E. F., K. R. Manlove, E. S. Almberg, P. Kamath, M. Cox, P. Wolff, A. Roug, J. Shannon, R. Robinson, R. B. Harris, B. J. Gonzales, R. K. Plowright, P. J. Hudson, P. C. Cross, A. Dobson, and T. E. Besser. 2018. Pneumonia in bighorn sheep: risk and resilience. Journal of Wildlife Management 82:32-45.
- Climate Engine. 2017. Desert Research Institute and University of Idaho. https://app.climateengine.org. Accessed 26 Aug 2017.
- Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. The American Naturalist 149:195-219.
- Coltman, D. W., J. G. Pilkington, J. A. Smith, and J. M. Pemberton. 1999. Parasitemediated selection against inbred Soay sheep in a free-living island population. Evolution 53:1259-1267.
- Cooch, E. G., and G. C. White, editors. 2017. Program MARK: a gentle introduction. Seventeenth edition. Colorado State University, Fort Collins, Colorado, USA.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1-61.
- Cotter, S. C., S. J. Simpson, D. Raubenheimer, and K. Wilson. 2011. Macronutrient balance mediates trade-offs between immune function and life history traits. Functional Ecology 25:186-198.
- Creech, T. G., C. W. Epps, R. J. Monello, and J. D. Wehausen. 2016. Predicting diet quality and genetic diversity of a desert adapted ungulate with NDVI. Journal of Arid Environments 127:160-170.
- Deming, O. V. 1952. Tooth development of the Nelson bighorn sheep. California Fish and Game 38:523-529.
- Dhabhar, F. S. and B. S. McEwen. 1997. Acute stress enhances while chronic stress suppresses cell-mediated immunity *in vivo*: a potential role for leukocyte trafficking. Brain, Behavior, and Immunity 11:286-306.
- Diefenbach, D. R. 2009. Estimating avian population size using Bowden's estimator. The Auk 126:211-217.
- Digonnet, M. 2013. Hiking the Mojave Desert: natural and cultural heritage of Mojave National Preserve. Wilderness Press, Palo Alto, California, USA.

- Dunbar, M. R. 1992. Theoretical concepts of disease versus nutrition as primary factors in population regulation of wild sheep. Biennial Symposium of the Northern Wild Sheep and Goat Council 8:174-192.
- Epps, C. W., D. Dekelaita, and B. Dugovich. 2016. Updates on respiratory disease affecting bighorn sheep in and near Mojave National Preserve. Mojave National Preserve, Sweeney Granite Mountains Desert Research Center Science Newsletter. https://www.nps.gov/moja/learn/science-newsletter.htm. Accessed 20 November 2018.
- Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714-724.
- Epps, C. W., P. J. Palsboll, J. D. Wehausen, G. K. Roderick, R. R. Ramey II, and D. R. McCullough. 2005. Highways block gene flow and cause rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8:1029-1038.
- Epps, C. W., R. S. Crowhurst, B. S. Nickerson. 2018. Assessing change in functional connectivity in desert bighorn sheep metapopulation after two generations. Molecular Ecology 27:2334-2346.
- ESRI. 2016. ArcGIS Desktop: Release 10.5. Environmental Systems Research Institute, Inc. Redlands, California.
- Formica, V. A., M. E. Augat, M. E. Barnard, R. E. Butterfield, C. W. Wood, and E. D. Brodie III. 2010. Using home range estimates to construct social networks for species with indirect behavioral interactions. Behavioral Ecology and Sociobiology 64:1199-1208.
- Fox, K. A., N. M. Rouse, K. P. Huyvaert, K. A. Griffin, H. J. Killion, J. Jennings-Gaines, W. H. Edwards, S. L. Quackenbush, and M. W. Miller. 2015. Bighorn sheep (*Ovis canadensis*) sinus tumors are associated with coinfections by potentially pathogenic bacteria in the upper respiratory tract. Journal of Wildlife Diseases 51:19-27.
- Funk, C., P. Peterson, M. Landsfeld, D. Pedreros, J. Verdin, S. Shukla, G. Husak, J. Rowland, L. Harrison, A. Hoell, and J. Michaelsen. 2015. The climate hazards infrared precipitation with stations – a new environmental record for monitoring extremes. Scientific Data 2:150066. doi 10.1038/sdata.2015.66.
- Galloway, A, W. H. Birkby, A. M. Jones, T. E. Henry, and B. O. Parks. 1989. Decay rates of human remains in an arid environment. Journal of Forensic Sciences 34:607-616.
- Geist. V. 1966. Validity of horn segment counts in aging bighorn sheep. Journal of Wildlife Management 30:634-635.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carryover effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4-18.
- Heffelfinger, J. 1997. Age criteria for Arizona game species. Arizona Game and Fish Department, Special Report No. 19. Arizona Game and Fish Department, Phoenix, Arizona, USA.
- Heffelfinger, L. J., K. M. Stewart, A. P. Bush, J. S. Sedinger, N. W. Darby, and V. C. Bleich. 2017. Timing of precipitation in an arid environment: effects on

population performance of a large herbivore. Ecology and Evolution 2017:1-13. doi 10.1002/ece3.3718.

- Hereford, R., R. H. Webb, and C. I. Longpre. 2004. Precipitation history of the Mojave Desert Region, 1893-2001. USGS Fact Sheet 117-03. https://doi.org/10.3133/fs11703. Accessed 20 November 2018.
- Hnilicka, P. A., J. Mionczynski, B. J. Mincher, J. States, M. Hinschberger, S. Oberlie, C. Thompson, B. Yates, and D. D. Siemer. 2002. Bighorn sheep lamb survival, trace minerals, rainfall, and pollution: are there any connections? Biennial Symposium of the Northern Wild Sheep and Goat Council 13:69-94.
- Huntington, J. L., K. C. Hegewisch, B. Daudert, C. G. Morton, J. T. Abatzoglou, D. J. McEvoy, and T. Erickson. 2017. Climate Engine: Cloud computing of climate and remote sensing data for advanced natural resource monitoring and process understanding. Bulletin of the American Meteorological Society 98:2397-2410.
- Hurley, M. A., M. Hebblewhite, J.-M. Gaillard, S. Dray, K. A. Taylor, W. K. Smith, P. Zager, and C. Bonenfant. 2014. Functional analysis of Normalized Difference Vegetation Index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. Philosophical Transactions of the Royal Society 369:20130196. doi 10.1098/rstb.2013.0196.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. Ecology 78:1019-1032.
- Kock, M. D., R. K. Clark, C. E. Franti, D. A. Jessup, and J. D. Wehausen. 1987.
 Effects of capture on biological parameters in free-ranging bighorn sheep (*Ovis canadensis*): evaluation of normal, stressed and mortality outcomes and documentation of postcapture survival. Journal of Wildlife Diseases 23:652-662.
- Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71-73.
- Krebs, C. J. 1999. Ecological Methodology. Second edition. Addison-Wesley Education Publishers, Inc., Menlo Park, California, USA.
- Lloyd-Smith, J. O., P. C. Cross, C. J. Briggs, M. Daugherty, W. M. Getz, J. Latto, M. S. Sanchez, A. B. Smith, and A. Swei. 2005. Should we expect population thresholds for wildlife disease. Trends in Ecology and Evolution 20:511-519.
- Lochmiller, R. L. and C. Deerenberg. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? Oikos 88:87-98.
- Luikart, G., K. Pilgrim, J. Visty, V. O. Ezenwa, and M. K. Schwartz. 2008. Candidate gene microsatellite variation is associated with parasitism in wild bighorn sheep. Biology Letters 4:228-231.
- Manlove, K., E. F. Cassirer, P. C. Cross, R. K. Plowright, and P. J. Hudson. 2014. Costs and benefits of group living with disease: a case study of pneumonia in bighorn lambs (*Ovis canadensis*). Proceedings of the Royal Society 281:20142331. doi 10.1098/rspb.2014.2331.

- Manlove, K., E. F. Cassirer, P. C. Cross, R. K. Plowright, and P. J. Hudson. 2016. Disease introduction is associated with a phase transition in bighorn sheep demographics. Ecology 97:2593-2602.
- Martin, L. B. 2009. Stress and immunity in wild vertebrates: timing is everything. General and Comparative Endocrinology 163:70-76.
- Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88-90.
- McClintock, B. T. and G. C. White. 2007. Bighorn sheep abundance following a suspected pneumonia epidemic in Rocky Mountain National Park. Journal of Wildlife Management 71:183-189.
- McClintock, B. T., G. C. White, and K. P. Burnham. 2006. A robust design markresight abundance estimator. Journal of Agricultural, Biological, and Environmental Statistics 11:231-248.
- McCullough, D. R. 1979. The George Reserve Deer Herd: Population Ecology of a K-Selected Species. University of Michigan Press, Ann Arbor, USA.
- McIlroy, S. G., E. A. Goodall, R. M. McCracken, and D. A. Stewart. 1989. Rain and windchill as factors in the occurrence of pneumonia in sheep. The Veterinary Record 125:79-82.
- McKee, C. J., K. M. Stewart, J. S. Sedinger, A. P. Bush, N. W. Darby, D. L. Hughson, and V. C. Bleich. 2015. Spatial distributions and resource selection by mule deer in an arid environment: responses to provision of water. Journal of Arid Environments 2015:76-84.
- Miller, D. S., E. Hoberg, G. Weiser, K. Aune, M. Atkinson, and C. Kimberling. 2012. A review of hypothesized determinants associated with bighorn sheep (*Ovis canadensis*) die-offs. Veterinary Medicine International 2012:1-19.
- Miller, D. S., G. C. Weiser, A. C. S. Ward, M. L. Drew, P. L. Chapman. 2011. Domestic sheep (*Ovis aries*) *Pasteurellaceae* isolates from diagnostic submissions to the Caine Veterinary Teaching Center (1990–2004). Veterinary Microbiology 150:284-288.
- Monello, R. J., D. L. Murray, and E. F. Cassirer. 2001. Ecological correlates of pneumonia epizootics in bighorn sheep herds. Canadian Journal of Zoology 79:1423-1432.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Connor, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1-56.
- National Geographic Society. 2008. Mojave National Preserve [map]. National Geographic Maps, Evergreen, Colorado, USA.
- National Park Service [NPS]. 2016. Mojave weather. https://www.nps.gov/moja/planyourvisit/weather.htm>. Accessed 9 Apr 2018.
- Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15-27.
- Plowright, R. K., K. R. Manlove, T. E. Besser, D. J. Paez, K. R. Andrews, P. E. Matthews, L. P. Waits, P. J. Hudson, and E. F. Cassirer. 2017. Age-specific

infectious period shapes dynamics of pneumonia in bighorn sheep. Ecology Letters 20:1325-1336.

- Preisler, H. K., N. E. Grulke, Z. Heath, and S. L. Smith. 2017. Analysis and out-year forecast of beetle, borer, and drought-induced tree mortality in California. Forest Ecology and Management 399:166-178.
- Pruett, S. B. 2003. Stress and the immune system. Pathophysiology 9:133-153.
- Romero, L. M. 2004. Physiological stress in ecology: lessons from biomedical research. Trends in Ecology and Evolution 19:249-255.
- Rubin, E. S., W. M. Boyce, and V. C. Bleich. 2000. Reproductive strategies of desert bighorn sheep. Journal of Mammalogy 81:769-786.
- Ryan, S. J., P. C. Cross, J. Winnie, C. Hay, J. Bowers, and W. M. Getz. 2012. The utility of normalized difference vegetation index for predicting African buffalo forage quality. Journal of Wildlife Management 76:1499-1508.
- Ryder, T. J., E. S. Williams, K. W. Mills, K. H. Bowles, and E. T. Thorne. 1992. Effect of pneumonia on population size and lamb recruitment in Whiskey Mountain bighorn sheep. Biennial Symposium of the Northern Wild Sheep and Goat Council 8:136-146.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.
- Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235-253.
- Silverman, B. W. 1986. Density estimation for statistics and data analysis. Monographs on Statistics and Applied Probability. Chapman and Hall, London, England.
- Singer, F. J., L. C. Zeigenfuss, and L. Spicer. 2001. Role of patch size, disease, and movement in rapid extinction of bighorn sheep. Conservation Biology 15:1347-1354.
- Spears, J. W. 1994. Minerals in forages. Pages 281-317 in G. C. Fahey, Jr., editor. Forage Quality, Evaluation, and Utilization. American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, Madison, Wisconsin, USA.
- Swift, P. K., J. D. Wehausen, H. B. Ernest, R. S. Singer, A. M. Pauli, H. Kinde, T. E. Rocke, and V. C. Bleich. 2000. Desert bighorn sheep mortality due to presumptive type c botulism in California. Journal of Wildlife Diseases 36:184-189.
- Symonds, M. R. E. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13-21.
- Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keisler, and N. Dasgupta. 2008. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. Journal of Wildlife Management 74:974-986.

- Tomassini, L., B. Gonzales, G. C. Weiser, and W. Sischo. 2009. An ecological study comparing *Pasteurella trehalosi* and *Mannheimia haemolytica* between Sierra Nevada bighorn sheep, White Mountain bighorn sheep, and domestic sheep. Journal of Wildlife Diseases 45:930-940.
- Ullrey, D. E. 1993. Nutrition and predisposition to infectious disease. Journal of Zoo and Wildlife Medicine 24:304-314.
- United States Geological Survey [USGS]. 2018. Mineral resources online spatial data. https://mrdata.usgs.gov/. Accessed 9 Apr 2018.
- Valdez, R. and P. R. Krausman. 1999. Description, distribution and abundance of mountain sheep. Pages 1-22 in R. Valdez and P. R. Krausman, editors. Mountain Sheep of North America. University of Arizona Press, Tucson, USA.
- Waites, K. B., and D. F. Talkington. 2004. *Mycoplasma pneumoniae* and its role as a human pathogen. Clinical Microbiology Reviews 17:697-728.
- Washington Animal Disease Diagnostic Laboratory [WADDL]. 2017. Washington State University. https://waddl.vetmed.wsu.edu/animal-disease-faq/mycoplasma-ovipneumoniae-diagnostics-in-domestic-and-wild-sheep-and-goats>. Accessed 17 Oct 2018.
- Washington Animal Disease Diagnostic Laboratory [WADDL]. 2020. Washington State University. https://waddl.vetmed.wsu.edu/search-tests/Panels/Test-Details?id=455>. Accessed 22 May 2020.
- Wehausen, J. D. 2005. Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. Pages 37-50 in J. Goerrissen and J. M. Andre, editors. Sweeney Granite Mountains Desert Research Center 1978-2003: A Quarter Century of Research and Teaching. University of California Natural Reserve Program, Riverside, USA.
- Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California sheep population. Journal of Wildlife Management 51:86-98.
- Wehausen. J. D., S. T. Kelley, and R. R. Ramey II. 2011. Domestic sheep, bighorn sheep, and respiratory disease: a review of the experimental evidence. California Fish and Game 97:7-24.
- Western Association of Fish and Wildlife Agencies (WAFWA). 2010. Summary on 9 bighorn sheep die-offs in 5 western states in Winter 2009-2010. www.wafwa.org>. Accessed 26 March 2016.
- White, G. C. 1996. Program NOREMARK Software Reference Manual. https://sites.warnercnr. colostate.edu/gwhite / wpcontent/uploads/sites/73/2017/05/noremark.pdf>. Accessed 21 November 2018.
- White, G. C. and E. G. Cooch. 2017. Population abundance estimation with heterogeneous encounter probabilities using numerical integration. Journal of Wildlife Management 81:322-336.
- White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-139.
- Wolfe, L. L., B. Diamond, T. R. Spraker, M. A. Sirochman, D. P. Walsh, C. M. Machin, D. J. Bade, and M. W. Miller. 2010. A bighorn sheep die-off in

southern Colorado involving a *Pasteurellaceae* strain that may have originated from synoptic cattle. Journal of Wildlife Diseases 46:1262-1268.

Wood, M. E., K. A. Fox, J. Jennings-Gaines, H. J. Killion, S. Amundson, M. W. Miller, and W. H. Edwards. 2017. How respiratory pathogens contribute to lamb mortality in a poorly performing bighorn sheep (*Ovis canadensis*) herd. Journal of Wildlife Diseases 53:126-130.

TABLES AND FIGURES

Table 1.1. Preliminary results from known-fate modeling in Program MARK of monthly adult female bighorn survival from 2013-2017 across populations occupying 9 different mountain ranges, following a pneumonia outbreak in the Mojave Desert, California, USA. We tested combinations of mean seasonal NDVI (Normalized Difference Vegetation Index) on monthly survival within the same season and lag effects on monthly survival within the following season to identify which NDVI parameters were informative. We evaluated models using Akaike's Information Criterion adjusted for small sample sizes (AICc).

No. 1 Autumn NDVI lag 2 0.00 0.33 2 Autumn NDVI lag + Summer NDVI lag 3 1.57 0.15 3 Autumn NDVI lag + Winter NDVI lag 3 1.77 0.14 4 Autumn NDVI lag + Spring NDVI lag 3 1.82 0.13 5 Autumn NDVI lag + Spring NDVI lag + Winter NDVI lag 4 3.36 0.06 6 Autumn NDVI lag + Spring NDVI lag + Summer NDVI lag 4 3.44 0.06 7 Autumn NDVI lag + Spring NDVI lag + Winter NDVI lag 4 3.58 0.06	339.59 339.16 339.36 339.41 338.94 339.02 339.16
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7 Autumn NDVI lag + Spring NDVI lag + Winter NDVI lag 4 3.58 0.06	339.16
	557.10
8 Autumn NDVI lag + Spring NDVI lag + Summer NDVI lag + Winter NDVI lag 5 5.23 0.02	338.80
9 Null 1 8.37 0.01	349.96
10 Summer NDVI 2 8.87 0.00	348.46
11 Autumn NDVI 2 9.47 0.00	349.06
12 Winter NDVI 2 9.74 0.00	349.33
13 Spring NDVI lag 2 9.85 0.00	349.44
14 Winter NDVI lag 2 10.03 0.00	349.63
15 Autumn NDVI + Summer NDVI 3 10.07 0.00	347.65
16 Summer NDVI + Winter NDVI 3 10.21 0.00	347.79
17 Summer NDVI lag 2 10.31 0.00	349.90
18 Spring NDVI 2 10.33 0.00	349.92
19 Autumn NDVI + Winter NDVI 3 10.86 0.00	348.45
20 Spring NDVI + Summer NDVI 3 10.87 0.00	348.45
21 Autumn NDVI + Spring NDVI 3 11.40 0.00	348.99
22Autumn NDVI + Summer NDVI + Winter NDVI411.430.00	347.01
23Spring NDVI lag + Winter NDVI lag311.500.00	349.09
24 Spring NDVI + Winter NDVI 3 11.71 0.00	349.30
25 Spring NDVI lag + Summer NDVI lag 3 11.82 0.00	349.40
26Summer NDVI lag + Winter NDVI lag311.990.00	349.57
27Autumn NDVI + Spring NDVI + Summer NDVI412.040.00	347.63
28Spring NDVI + Summer NDVI + Winter NDVI412.210.00	347.79
29Autumn NDVI + Spring NDVI + Winter NDVI412.810.00	348.40
30Autumn NDVI + Spring NDVI + Summer NDVI + Winter NDVI513.410.00	346.99
31Spring NDVI lag + Summer NDVI lag + Winter NDVI lag413.480.00	240.05

^aNumber of model parameters.

^bAkaike model weight.

Table 1.2. Sample sizes and results of PCR (polymerase chain reaction) testing for *Mycoplasma ovipneumoniae* (*M. ovi*) from adult female bighorn radio-collared between 2013 and 2015 for survival monitoring from 2013-2017 in the Mojave Desert, California, USA. Notation is as follows: D = M. *ovi* detected (PCR-positive at capture), ND = M. *ovi* not detected (PCR-negative at capture), Unk = infection status unknown at time of capture; totals are in parentheses. Table also indicates mortalities by population and proportions of samples that were PCR-positive (i.e., infected with M. ovi) and seropositive for M. ovi antibodies (i.e., previously exposed).

Range	Adult F Sample				Mortalities	Infected (%) ^a	Mortalities (%) ^b	Exposed (%) ^c
(Population)	2013-14	2014-15	2015-16/17	All years				
Marble	19	18	21	$7^{D}/9^{ND}/8^{Unk}$ (24)	$6^{D}/2^{ND}/5^{Unk}$ (13)	43.8	54.2	100
S. Bristol	16	15	15	$12^{D}/4^{ND}/5^{Unk}(21)$	$4^{D}/3^{Unk}$ (7)	75.0	33.3	100
ODP/Kelso	13	13	14	$5^{D}/11^{ND}/1^{Unk}$ (17)	$3^{D}/1^{ND}/1^{Unk}$ (5)	31.3	29.4	73.3
N. Bristol	5	5	14	$2^{D}/12^{ND}$ (14)	$1^{ND}(1)$	14.3	7.1	30.0
Hackberry	4	5	5	$2^{D}/2^{ND}/1^{Unk}$ (5)	0	40.0	0.0	66.7
Woods	0	0	7	$1^{D}/6^{ND}(7)$	0	16.7	0.0	14.3
Clipper	3	3	11	$5^{D}/6^{ND}$ (11)	0	45.5	0.0	100
Cady	0	9	7	$2^{D}/7^{ND}$ (9)	$1^{D}/3^{ND}(4)$	22.2	44.4	75.0
S. Soda	4	4	7	7 ND (7)	$1^{ND}(1)$	0.0	14.3	60.0
Total	64	72	101	36 ^D /64 ND /15 ^{Unk} (115)	$14^{D}/8^{ND}/9^{Unk}(31)$	36.0	27.0	75.2

^aPercentage of individuals that tested positive for *M. ovi* at time of capture. Individuals with unknown infection status removed from total.

^bPercentage of individuals that suffered mortality between 2013 and 2017.

^cPercentage of individuals that were previously exposed to *M. ovi* and were seropositive at time of capture, based on cELISA (competitive enzyme-linked immunosorbent assay) results. Individuals of unknown status removed from total.

Table 1.3. Estimated population abundance for adult female bighorn in 2016, mean summer and autumn NDVI for 2013-2016, and total precipitation in winter 2013-14 to winter 2016-17 in 9 mountain ranges in the Mojave Desert, California, USA. Abundance estimates were derived from remote camera data we collected at point-source water features in each mountain range in summer 2016. Mean summer and autumn NDVI (Normalized Difference Vegetation Index) were obtained from Landsat 4, 5, 7, 8, and winter precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS).

		2013	2013-14	2014	2014-15	2015	2015-16	2016	2016-17
Range (Population)	Adult F Abundance ^a (95% CI)	Mean NDVI Summer/ Autumn	Total Winter Precipitation (mm)						
Hackberry	14 (0-28)	0.16/0.18	27.56	0.17/0.18	63.46	0.13/0.15	49.72	0.16/0.15	118.22
Woods	18 (6-29)	0.16/0.18	27.56	0.17/0.18	63.46	0.13/0.15	49.72	0.16/0.15	118.22
Clipper	65 (28-102)	0.13/0.14	20.54	0.13/0.17	38.29	0.11/0.13	34.67	0.11/0.11	82.75
Old Dad Peak	41 (18-63)	0.10/0.11	23.18	0.10/0.14	40.81	0.10/0.13	36.23	0.10/0.11	77.73
Marble	135 (67-202)	0.11/0.12	14.27	0.10/0.13	26.33	0.09/0.11	24.86	0.09/0.10	58.10
S. Soda	28 (5-52)	0.09/0.10	21.66	0.09/0.10	39.09	0.09/0.10	32.56	0.09/0.10	68.76
S. Bristol	46 (25-68)	0.10/0.12	14.05	0.10/0.12	22.22	0.09/0.10	19.43	0.09/0.09	52.15
Cady	71 (0-144)	0.09/0.10	26.35	0.11/0.12	42.27	0.10/0.10	35.64	0.10/0.10	70.32
N. Bristol	101 (26-175)	0.09/0.10	28.23	0.09/0.11	44.21	0.09/0.10	39.36	0.09/0.09	87.73

^aOur estimates are based on the population of adult females using point-source water features and serve as an index for true population size; estimates were generated using Bowden's estimator and are rounded to nearest whole numbers.

Table 1.4. Sample sizes of marked adult female bighorn, estimated abundance, and adjusted abundance in 9 populations in the Mojave Desert, California, USA. We used data collected in summer 2016 from remote cameras at water sites to obtain numbers of marked and unmarked adult females, and applied Bowden's estimator to generate abundance estimates. Marked and unmarked sightings are numbers of marked and unmarked adult females observed for a set of sampling occasions. Adjusted unmarked sightings and corresponding abundance estimates were calculated by applying a revisitation rate of 0.056 (based on the number of marked individuals we detected 2 times within the same occasion) to the number of unmarked sightings we recorded. The inflation percentage indicates by how much we may have overestimated abundance of adult female bighorn as a result of double-counting unmarked individuals.

Range (Population)	Sample Size	Marked Sightings	Unmarked Sightings	Mean Sightings ^a	Abundance Estimate	Adjusted Unmarked Sightings	Adjusted Abundance Estimate	Inflation (%)
Hackberry	5	13	23	2.60	14	22	13	3.51
Woods	7	17	26	2.43	18	25	17	3.31
S. Soda	7	21	64	3.00	28	61	27	4.16
Old Dad Peak	14	63	120	4.50	41	114	39	3.60
S. Bristol	15	32	67	2.13	46	63	45	3.72
Clipper	11	16	78	1.45	65	74	62	4.60
Cady	6	18	195	3.00	71	185	68	5.10
N. Bristol	9	12	122	1.33	101	116	96	5.07
Marble	16	22	163	1.38	135	154	128	4.90

^aAverage number of marked sightings per marked individual.

Table 1.5. Results from known-fate modeling in Program MARK of monthly adult female bighorn survival from 2013-2017 across populations occupying 9 different mountain ranges, following a pneumonia outbreak in the Mojave Desert, California, USA. PCR status was based on results from PCR (polymerase chain reaction) testing for *Mycoplasma ovipneumoniae* infection using nasal swabs collected from females at time of capture. Adult female population abundance was derived from remote camera data we collected at point-source water features in 2016 in each mountain range. We tested effects of winter precipitation totals, and mean summer and autumn NDVI (Normalized Difference Vegetation Index) in each mountain range on survival in winter months only. Models were evaluated using Akaike's Information Criterion adjusted for small sample sizes (AICc).

Model	Model Structure	K^{a}	ΔAICc	W_i^{b}	Deviance
INO.					
1	Summer NDVI lag + Winter precipitation + PCR status + Abundance	5	0.00	0.34	322.88
2	Autumn NDVI lag + Winter precipitation + PCR status + Abundance	5	1.38	0.17	324.25
3	Autumn NDVI lag + PCR status + Abundance	4	1.46	0.16	326.35
4	Summer NDVI lag + PCR status + Abundance	4	1.84	0.14	326.72
5	Summer NDVI lag + Winter precipitation + PCR status	4	3.38	0.06	328.27
6	Summer NDVI lag + PCR status	3	4.87	0.03	331.75
7	Autumn NDVI lag + Winter precipitation + PCR status	4	5.18	0.03	330.06
8	Autumn NDVI lag + PCR status	3	5.33	0.02	332.21
9	Winter precipitation + PCR status + Abundance	4	6.07	0.02	330.95
10	Summer NDVI lag + Winter precipitation + Abundance	4	7.68	0.01	332.56
11	Summer NDVI lag + Abundance	3	7.77	0.01	334.66
12	Autumn NDVI lag + Abundance	3	8.13	0.01	335.02
13	Autumn NDVI lag + Winter precipitation + Abundance	4	9.05	0.00	333.93
14	Summer NDVI lag	2	9.76	0.00	338.65
15	Summer NDVI lag + Winter precipitation	3	9.90	0.00	336.78
16	Autumn NDVI lag	2	10.70	0.00	339.59
17	PCR status + Abundance	3	11.19	0.00	338.08
18	Autumn NDVI lag + Winter precipitation	3	11.61	0.00	338.49
19	Winter precipitation + Abundance	3	12.67	0.00	339.55
20	Winter precipitation + PCR status	3	12.69	0.00	339.58
21	Range	9	14.90	0.00	329.73
22	PCR status	2	15.24	0.00	344.13
23	Abundance	2	15.80	0.00	344.69
24	Winter precipitation	2	17.80	0.00	346.69
25	Null	1	19.07	0.00	349.96

^aNumber of model parameters.

^bAkaike model weight.

Table 1.6. Parameter estimates from our top 2 models and model-averaged parameter estimates derived from known-fate modeling (Program MARK) of monthly adult female bighorn survival from 2013-2017 across populations occupying 9 different mountain ranges, following a pneumonia outbreak in the Mojave Desert, California, USA. PCR status was based on results from PCR (polymerase chain reaction) testing for *Mycoplasma ovipneumoniae* infection using nasal swabs collected from females at time of capture, and was modeled as a dummy variable, whereby positive infection status received a value of 1. Adult female population abundance was derived from remote camera data we collected at point-source water features in 2016 in each mountain range. We tested effects of winter precipitation totals (mm), and mean summer and autumn NDVI (Normalized Difference Vegetation Index) in each mountain range on survival in winter months only. We evaluated models using Akaike's Information Criterion adjusted for small sample sizes (AICc).

	Model 1	Model 2	Model averages
Intercept			
β	6.07	5.85	5.87
SE	0.42	0.39	0.52
90% CI	5.38, 6.76	5.21, 6.49	5.02, 6.72
Summer NDVI lag ^a			
β	0.95		1.03
SE	0.36		0.37
90% CI	0.36, 1.55		0.42, 1.64
Autumn NDVI lag ^a			
β		1.06	1.24
SE		0.45	0.46
90% CI		0.31, 1.80	0.48, 2.01
PCR-positive			
β	-1.29	-1.29	-1.23
SE	0.42	0.42	0.42
90% CI	-1.98, -0.60	-1.98, -0.59	-1.93, -0.54
Population abundance			
β	-0.40	-0.42	-0.40
SE	0.17	0.17	0.17
90% CI	-0.69, -0.12	-0.70, -0.13	-0.69, -0.12
Winter precipitation			
β	-0.39	-0.32	-0.36
SE	0.18	0.20	0.19
90% CI	-0.69, -0.08	-0.65, 0.02	-0.68, -0.04

*Summer and autumn NDVI are correlated and model-averages are not jointly additive.

Table 1.7. Annual survival estimates with standard errors (SE) for adult female bighorn in 9 populations from 2014-2016, following a pneumonia outbreak in the Mojave Desert, California, USA; estimates were generated using the known-fate model in Program MARK. Table indicates different levels of mean NDVI (Normalized Difference Vegetation Index) and estimated adult female population abundance for mountain ranges and shows estimates for individuals that were PCR-positive for *Mycoplasma ovipneumoniae* infection at capture (i.e., infected) and PCR-negative at capture (i.e., not infected). PCR status was based on results from PCR (polymerase chain reaction) testing for *Mycoplasma ovipneumoniae* infection using nasal swabs collected from females at time of capture. Female population abundance was derived from remote camera data we collected at point-source water features in 2016 in each mountain range. Annual survival was estimated from January through December for a given year; estimates are model-averaged.

	PCR-positi	ve						tive					
	2014		2015		2016		2014	2014		2015		2016	
Range (Population)	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	
Hackberry***/+	0.945	0.026	0.941	0.028	0.932	0.033	0.983	0.011	0.981	0.012	0.978	0.013	
Woods***/+	0.944	0.026	0.940	0.028	0.930	0.033	0.982	0.011	0.981	0.012	0.978	0.013	
Clipper***/++	0.904	0.030	0.900	0.031	0.869	0.034	0.969	0.014	0.968	0.014	0.958	0.016	
Old Dad Peak**/++	0.886	0.038	0.893	0.038	0.878	0.039	0.963	0.018	0.966	0.017	0.960	0.018	
Marble**/+++	0.781	0.080	0.762	0.083	0.709	0.091	0.927	0.032	0.920	0.033	0.900	0.038	
S. Soda*/+	0.869	0.051	0.863	0.051	0.854	0.052	0.957	0.023	0.955	0.023	0.952	0.024	
S. Bristol*/++	0.882	0.039	0.871	0.039	0.828	0.057	0.962	0.019	0.958	0.019	0.943	0.026	
Cady*/++	0.827	0.048	0.856	0.036	0.809	0.048	0.943	0.023	0.953	0.017	0.937	0.022	
N. Bristol*/+++	0.754	0.070	0.762	0.060	0.700	0.070	0.917	0.031	0.920	0.026	0.896	0.030	

* Lowest summer and autumn NDVI averages (0.09-0.12), **Intermediate summer and autumn NDVI averages

(0.09-0.14), ***Highest summer and autumn NDVI averages (0.13-0.18).

+ Lowest population abundance (< 40 adult females), ++Intermediate population abundance (40-80 adult females),

+++ Highest population abundance (> 80 adult females).

Table 1.8. Overwinter survival estimates with standard errors (SE) for adult female bighorn in 9 populations from Winter 2013-14 to Winter 2016-17, following a pneumonia outbreak in the Mojave Desert, California, USA; estimates were generated using the known-fate model in Program MARK. Table indicates different levels of mean NDVI (Normalized Difference Vegetation Index) and estimated adult female population abundance for mountain ranges and shows survival estimates for individuals that were PCR-positive for *Mycoplasma ovipneumoniae* infection at capture (i.e., infected) and PCR-negative at capture (i.e., not infected). PCR status was based on results from PCR (polymerase chain reaction) testing for *Mycoplasma ovipneumoniae* infection using nasal swabs collected from females at time of capture. Female population abundance was derived from remote camera data we collected at point-source water features in 2016 in each mountain range. Winter survival was estimated from December through March across successive years; estimates are model-averaged.

	PCR-positive								PCR-negative							
	Winter 2013-14		Winter 2014-15		Winter 2015-16		Winter 2016-17		Winter 2013-14		Winter 2014-15		Winter 2015-16		Winter 2016-17	
Range (Population)	Estimate	e SE	Estimate	e SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	e SE	Estimate	e SE	Estimate	e SE
Hackberry***/+	0.996	0.005	0.994	0.009	0.983	0.012	0.979	0.035	0.999	0.002	0.998	0.003	0.995	0.004	0.994	0.011
Woods***/+	0.996	0.005	0.994	0.009	0.982	0.013	0.978	0.036	0.999	0.002	0.998	0.003	0.994	0.004	0.993	0.011
Clipper***/++	0.978	0.010	0.980	0.014	0.957	0.014	0.894	0.053	0.993	0.004	0.994	0.005	0.987	0.006	0.967	0.017
Old Dad Peak**/++	0.942	0.020	0.954	0.024	0.949	0.024	0.900	0.048	0.981	0.009	0.986	0.009	0.984	0.009	0.968	0.016
Marble**/+++	0.916	0.034	0.901	0.048	0.856	0.058	0.747	0.092	0.973	0.013	0.969	0.017	0.953	0.021	0.915	0.032
S. Soda*/+	0.923	0.034	0.915	0.032	0.915	0.036	0.879	0.052	0.975	0.014	0.973	0.013	0.972	0.015	0.961	0.019
S. Bristol*/++	0.944	0.025	0.943	0.023	0.899	0.043	0.849	0.054	0.982	0.010	0.982	0.010	0.967	0.018	0.951	0.021
Cady*/++	0.886	0.038	0.945	0.017	0.894	0.031	0.843	0.056	0.963	0.016	0.983	0.007	0.966	0.013	0.949	0.019
N. Bristol*/+++	0.837	0.057	0.862	0.046	0.822	0.054	0.674	0.136	0.946	0.022	0.955	0.017	0.941	0.020	0.885	0.050

* Lowest summer and autumn NDVI averages (0.09-0.12), **Intermediate summer and autumn NDVI averages

(0.09-0.14), ***Highest summer and autumn NDVI averages (0.13-0.18).

+ Lowest population abundance (< 40 adult females), ++Intermediate population abundance (40-80 adult females),

+++ Highest population abundance (> 80 adult females).



Figure 1.1. Delineations of 9 bighorn sheep populations in the Mojave Desert, California, USA that were monitored from 2013-2017 following a pneumonia outbreak.



Figure 1.2. Model-averaged estimates of overwinter survival for selected populations of adult female bighorn from 2013-2017, following a pneumonia outbreak in the Mojave Desert, California, USA, based on known-fate modeling in Program MARK. Circles symbolize estimates for individuals that were PCR-negative for *Mycoplasma ovipneumoniae* infection at capture (not infected), triangles symbolize estimates for individuals that were PCR-negative for *Mycoplasma ovipneumoniae* infection at capture (not infected), and error bars indicate standard errors. Colors represent levels of mean summer and autumn NDVI for a given mountain range; red represents highest values (0.13-0.18), green represents intermediate values (0.09-0.14), and blue represents lowest values (0.09-0.12). *N* denotes population estimates of adult female bighorn.

CHAPTER 2: VARIATION IN SURVIVAL OF DESERT BIGHORN LAMBS IN A METAPOPULATION FOLLOWING A PNEUMONIA EPIZOOTIC

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ABSTRACT

Reduced neonate survival has been identified as a major factor limiting population recovery for bighorn sheep (Ovis canadensis) following pneumonia epizootics. Our objective was to investigate lamb survival in 7 populations of desert bighorn (O. c. *nelsoni*) exposed to the respiratory pathogen *Mycoplasma ovipneumoniae* (*M. ovi*) in the Mojave Desert, California, USA, following a pneumonia outbreak in 2013. We applied beta regression to late-season (15 August to 30 September) lamb-ewe ratios from 2014-2016 to model lamb survival and evaluate effects of precipitation and population abundance in order to better understand neonate survival trends in these populations. We detected a quadratic effect of precipitation in October-April, coincident with the period of mid-gestation to lambing for parturient females, whereby precipitation up to an optimum level was positively associated with lamb survival. In contrast, precipitation in May-August, coincident with the post-lambing period, was associated with a negative effect on lamb survival, but this effect was not robust to additional testing with yearly effects. The effect of population abundance was not supported in top models. We consider that higher precipitation in October-April likely increases forage availability and thereby nutrition for parturient females, but higher levels of precipitation may have undetermined consequences in terms of neonate health. We further consider that the correlation between higher precipitation

during hotter months and lower neonate survival could be a function of aerosol transmission of *M. ovi*, which may increase with increasing humidity, but the apparent effect of May-August precipitation may have also been spurious. Our results suggest that precipitation was an important factor influencing lamb survival, and that environmental variation likely contributes to variation in lamb survival in bighorn populations infected with *M. ovi*.

INTRODUCTION

Pneumonia epizootics have been a major threat affecting bighorn sheep (Ovis canadensis) populations since the early 1900s, and in recent years Mycoplasma ovipneumoniae (M. ovi) has been identified as a primary causal agent associated with pneumonia outbreaks (Besser et al. 2008, 2012b, 2014, Plowright et al. 2017, Cassirer et al. 2018); other pneumonic pathogens that have been widely implicated include leukotoxigenic Mannheimia (formerly Pasteurella) haemolytica (M. haemolytica), Bibersteinia (formerly Pasteurella) trehalosi (B. trehalosi), and Pasteurella multocida (P. multocida; Tomassini et al. 2009, Monello et al. 2001, Besser et al. 2008, 2012b, Wood et al. 2017, Cassirer et al. 2018). Outbreaks often follow from direct contact between domestic sheep (O. aries) and wild sheep, and once a pneumonia pathogen is introduced into a wild system, it can be maintained within populations for decades and have lingering consequences (Plowright et al. 2017, Cassirer et al. 2018). An all-age die-off typically occurs after a pneumonia invasion into a naïve population, and while adult survival can be relatively stable in the years following, reduced neonate survival can limit population recovery (Cassirer et al. 2013, 2018, Manlove et al. 2016, Plowright et al. 2017). Lambs in infected populations typically contract pneumonia and die within the first 3 to 4 months of life (Cassirer et al. 2013, Manlove et al. 2016), likely because chronically infected females pass pneumonia pathogens to their offspring who then pass the pathogen to other offspring (Cassirer et al. 2018).

In May and June of 2013, a pneumonia outbreak linked to *M. ovi* led to an allage die-off of desert bighorn sheep (*O. c. nelsoni*) at Old Dad Peak (Kelso Mountains) in the Mojave Desert, California, USA (Epps et al. 2016, Dekelaita et al. *In review*; Fig. 2.1). Following the outbreak, sick animals were observed in several nearby ranges, although no other die-offs were detected. In November 2013, 2014, and 2015, adult bighorn from Old Dad Peak (Kelso Mountains) and neighboring ranges (i.e., South Soda, Cady, North Bristol, South Bristol, Marble, and Clipper Mountains) were captured, collared, and tested for *M. ovi* infection via polymerase chain reaction (PCR) of nasal swab samples, under the management authority of California Department of Fish and Wildlife (CDFW) and the National Park Service (NPS). The same strain of *M. ovi* was detected in adult bighorn from all ranges except the South Soda Mountains, where animals were *M. ovi*-negative but seropositive for *M. ovi* antibodies. Sick neonates displaying classic clinical signs of pneumonia infection (i.e., coughing, nasal discharge, and head shaking; Wood et al. 2017) were also documented in these ranges during summers 2014-2016 via remote cameras.

Apparent effects of *M. ovi* infection on adult female survival were previously studied in these ranges following the 2013 pneumonia outbreak, and females who were PCR-positive for *M. ovi* at time of capture were found to have lower survival, which may have resulted from chronic infection (Dekelaita et al. *In review*). Lamb survival also appeared to be lower in several ranges following the initial outbreak as indicated by lamb-ewe ratios from ground observations. Lamb survival is influenced by a host of different factors, including forage quality, nutritional condition of the mother, population density, weather, genetics, and predation in addition to disease (Douglas and Leslie 1986, Hass 1989, Douglas 2001, Wehausen 2005, Cassirer and Sinclair 2007). Our objective was to investigate lamb survival across 7 ranges in the Mojave Desert and evaluate potentially important factors influencing survival in order to better understand neonate survival trends following the outbreak. We could not test directly for an effect associated with *M. ovi* infection since we did not collect samples from individual neonates, and instead focused our analysis on range factors to indirectly assess how disease might affect recruitment.

We identified 2 variables, precipitation and population size, that were strongly correlated with lamb survival in previous studies (Picton 1984, Douglas and Leslie 1986, Portier et al.1998, Wehausen 2005). Accordingly, we developed the following hypotheses: *H1*) *Higher precipitation in October through April (October-April) increases lamb survival.* Precipitation in autumn through early spring is critical for

plant productivity through the spring season in the Mojave Desert (Beatley 1974), and more specifically, higher precipitation in October-April was linked to higher diet quality in February through June (February-June), when lambing (i.e., parturition) typically occurs in the Mojave Desert, and with higher lamb-ewe ratios in summer as reported by Wehausen (2005); lambing generally occurs from February to April in the Mojave, but can extend earlier or later in populations (Bunnell 1982, Thompson and Turner 1982, Hass 1997, Wehausen 2005). Other studies have similarly found precipitation in autumn and winter to be highly correlated with lamb survival in the desert as well (Douglas and Leslie 1986, Douglas 2001). We therefore predicted that higher precipitation in October-April would increase available nutrition for parturient females and lambs in winter and spring which would positively influence lamb survival. H2) Higher precipitation in May through August (May-August) further increases lamb survival. High temperatures in May-August increase evapotranspiration and cause soil-moisture deficits to occur in the desert, thereby reducing the effect of precipitation on plant growth and forage nutrition in summer (Douglas et al. 2001), which is typically when weaning occurs in the Mojave Desert. We predicted that lamb survival to weaning would therefore be influenced further by precipitation in May-August and that higher levels of precipitation during this period would be correlated with higher survival, although the magnitude of the effect might differ from the earlier period (i.e., October-April). We also note that our study occurred during a 5-year drought in California and we therefore assumed that higher precipitation during hotter months would have a pronounced positive effect on lamb survival. H3) Increased population size lowers lamb survival. Previous studies have detected negative effects of population density on lamb survival, suggesting that lamb survival may be density-dependent, but these effects are not detectable in all bighorn populations and likely depend on environmental conditions and carrying capacity as well (Douglas and Leslie 1986, Portier et al. 1998, Bowyer et al. 2014). We assumed that resource competition might cause a negative density-dependent effect on lamb survival in larger populations (McCullough 1979, Clutton-Brock et al. 1997, Bowyer et al. 2014) given the limited availability of resources in the desert, especially during
hotter months, and predicted that lamb survival would be negatively associated with population size as a result.

STUDY AREA

The Mojave Desert hosts a metapopulation of bighorn sheep that occupy a large assemblage of mountain ranges separated by low-lying desert scrub and wash communities that are fragmented by roads, freeways, and other anthropogenic developments (Bleich et al. 1997, Epps et al. 2007). Our study focused on bighorn sheep populations in the eastern Mojave Desert and spanned the following 7 ranges: Old Dad Peak/Kelso, South Soda, Cady, North Bristol, South Bristol, Marble, and Clipper Mountains (Fig. 2.1). The study area was located east of Barstow, CA, spanning approximately 5500 km² and occurring largely between Interstates 15 and 40 on lands managed by the Bureau of Land Management (BLM) and National Park Service, Mojave National Preserve (MNP). Elevation ranged from approximately 300 m to 2,000 m. Mountain ranges were composed largely of volcanic flow and granitic rocks (USGS 2018). Common desert scrub species included catclaw acacia (Senegalia greggii), creosote bush (Larrea tridentata), rabbitbrush (Ericameria sp.), brittlebush (Encelia farinosa), white bur-sage (Ambrosia dumosa), blackbrush (Coleogyne ramosissima), Mormon tea (Ephedra spp.), silver and buckhorn cholla (Cylindropuntia echinocarpa and Cylindropuntia acanthocarpa), Mojave yucca (Yucca schidigera), California barrel cactus (Ferocactus cylindraceus), and annual grasses and forbs that appeared seasonally in response to rainfall (Digonnet 2013, Creech et al. 2016). Common native mammal species included antelope ground squirrel (Ammospermophilus leucurus), black-tailed jackrabbit (Lepus californicus), desert cottontail (Sylvilagus audubonii), kit fox (Vulpes macrotis), coyote (Canis latrans), bobcat (Lynx rufus), and desert bighorn sheep. Mountain lion (Puma *concolor*) appeared rare to nonexistent in these ranges during the study.

Dry, hot summers and cold, wet winters typify the climate of the Mojave Desert, but there is a late summer monsoon season that accounts for at least 25% of the total annual precipitation as well (Hereford et al. 2004, National Geographic Society 2008). Temperatures and precipitation vary with elevation; temperatures typically range from average lows of -1°C in the winter to average highs of 34°C in the summer, and can exceed 40°C in the lower lying areas (NPS 2016). Mean annual precipitation is approximately 21 cm, with lower elevations receiving as little as 9 cm and higher elevations receiving as much as 25 cm annually (NPS 2016). Our study occurred during a 5-year drought in California (Preisler et al. 2017), which likely resulted in less water availability and drier vegetation across the landscape from autumn 2013 through summer 2016.

Additionally, natural and man-made water features were present in all 7 ranges. Natural water features included point-source springs and the Mojave River (the Mojave River only occurred in the Cady Mountains). Man-made water features, or guzzlers, are artificial catchment and supply systems that dispense water gradually through a drinker box or trough for the benefit of wildlife species (Swift el al. 2000). Each mountain range contained at least 1 water source, with some ranges featuring several of varying types.

METHODS

Lamb Survival Indices

Lamb-ewe ratios have been commonly used to gauge lamb survival at the population level (Picton 1984, Douglas and Leslie 1986, Wehausen et al. 1987, Douglas 2001). As such, we used mean late-season (15 August to 30 September) lamb-ewe ratios as an index for lamb survival through weaning. Lambs usually begin weaning at 4-5 months of age (Festa-Bianchet et al. 1994) and are typically in the weaning phase by late August or early September in the Mojave Desert. We assumed adult female survival was stable over the late-season period.

To obtain late-season ratios, we used observations from camera survey data collected at point source water features in August and September; bighorn sheep frequently use both man-made and natural water features for hydration in the Mojave, especially during the hot summer months (Bleich et al. 1997), and cameras installed at these sites allow for population surveillance during this time. Data were collected from May through September in 3 ranges in 2014 (i.e., Old Dad Peak/Kelso, Marble, and South Bristol Mountains), and 7 ranges in 2015 and 2016 (Old Dad Peak/Kelso, Marble, South Bristol Mountains, Cady, South Soda, North Bristol and Clipper Mountains). We set up remote cameras at 1-3 point-source water features in each

mountain range, targeting all known sites regularly visited by bighorn sheep. Data from cameras were then used to generate counts of adult females and young. We used Bushnell Trophy cameras (standard and hybrid 8MP) set to a 1-second delay to collect photos and video from August through September 2016, when bighorn sheep reliably use water, and serviced cameras every 2 weeks.

Photos and videos were first sorted into activity periods by day and were then scored (videos provided better coverage with larger groups). We defined an activity period as beginning from the time when the first bighorn sheep in a group appeared at water and ending at the time when the last bighorn sheep in a group left, with activity typically ceasing for >20 minutes between periods. Days were generally censored if there were any activity periods that elapsed for >1.5 hours with >5 adult females present, as longer time periods with more individuals could render uncertainty in count totals. We counted all adult females and lambs in each activity period and calculated totals for each day in which we could obtain reliable counts, treating a single day as a sampling occasion. We attempted to use at least 8 occasions from each camera site (4 occasions each from August and September) within a given range per year, and calculated ratios by dividing the sum of all daily lamb totals by the sum of all daily adult female totals for each range and year. Some adult females were previously collared and could be identified by ear tag combinations (Dekelaita et al. In review), while unmarked adult females and lambs were identified by unique horn and pelage characteristics. We compared identities of individuals across all activity periods within a given occasion to prevent double-counting. If any unmarked or marked individuals were indistinguishable (usually because of image quality), we censored the entire occasion.

Validation of Camera-Derived Ratios

To validate camera-derived late-season ratios as a proxy for survival to weaning, we tracked survival of lambs with collared adult females up to 5 months (i.e., approximately 18-20 weeks) using camera and field observations to develop a secondary metric for comparison. Field observations were gathered opportunistically (i.e., during site visits or helicopter surveys conducted by CDFW) and systematically (i.e., targeting specific individuals and conducting ground searches using telemetry).

Females were identified as having a lamb if they were seen with a lamb at heel and engaged in nurturing or otherwise associative behavior (i.e., nursing, nuzzling, traveling to and from a site together, or appearing repeatedly together), and if ewes were lactating. We aged lambs by horn length and rostrum size (Bleich 1982), and visually monitored lactation in ewes by examining udder condition and estimating size when possible (i.e., full, ½ full, ¼ full, <¼ full). If lambs survived to 5 months of age, we concluded they had survived to the start of weaning.

For adult females that were collared in the autumn preceding the lambing season, pregnancy status prior to lambing was determined by testing blood serum collected during capture for Pregnancy-Specific Protein B (Wood et al. 1986; lab work was performed by BioTracking, Inc., Moscow, Idaho); collared animals were captured and processed following guidelines approved by CDFW and the National Park Service Institutional Animal Care and Use Committee (ACUP#PWR MOJA Epps.Powers DesertBighorn_2013.A3, 2013-2015), and as established by the American Society of Mammalogists for use of wild animals in research (Sikes et al. 2016). For females collared in previous years, we inferred pregnancy status for that season by visually inspecting the udder for signs of swelling when females first appeared on camera, if they were nonparous. Females identified as nonpregnant from serum testing or barren (i.e., no lamb present and no indication that lactation occurred) based on visual assessment were classified as unknown status and were censored. Females with inconclusive serum test results were also censored.

We assumed that females had lost their lambs to mortality if they were pregnant prior to the lambing season but were never seen with lambs, or became solitary over the course of the field season and their udders dried prematurely. Generally, given confirmation of pregnancy (i.e., via serum testing or observation with a lamb), if 2 of the 3 following criteria were met, we assumed the lamb had died: 1) the dam's udder went dry prematurely, 2) the lamb was never observed or stopped appearing on camera, 3) the dam was observed alone in the field. We concluded that a female was without a lamb in the field if she was observed alone in areas where a lamb could be easily seen if present; these observations were typically confirmed with follow-up observations as well. If we were unable to determine whether a lamb had survived or died, we identified the ewe as an unknown case and removed her from the sample. We then calculated proportions of lambs surviving up to 5 months of age with collared females and used the Pearson correlation test to evaluate how well mean late-season lamb-ewe ratios corresponded with these proportions across all populations and years for which we had both types of data.

A Priori Covariates

We obtained precipitation totals from October-April, and May-August, from Climate Engine (2017; Huntington et al. 2017) for each range and year using annual home range estimates based on Global Positioning System (GPS) collar location data from females as described by Dekelaita et al. (Chapter 1). Home ranges were estimated with fixed kernels and reference bandwidth (Silverman 1986) using the kernel density tool in ArcGIS 10.5 (ESRI 2016). We used a 95% contour to capture the majority of annual use across years (96-98% of realized locations) for each population. We then calculated rainfall totals within annual home ranges using 5-day estimates from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS; Funk et al. 2015, Climate Engine 2017). Population abundance estimates were produced by Dekelaita et al. (*In review*) and are based on counts of marked and unmarked adult females rendered from camera survey data collected in 2016. The estimates were generated using Bowden's estimator (Bowden and Kufeld 1995) and serve as an index for adult female abundance, or a relative index of population size.

Modeling Approach

We developed a candidate model set to evaluate all combinations of our *a priori* covariates, and included single covariate models and a null model with a single intercept. We used the Pearson correlation coefficient to assess relatedness of covariates prior to model fitting. We then applied beta regression for proportions (Ferrari and Cribari-Neto 2004, Ferrari 2011) with a logit link function for the mean (μ) submodel and log link function for the precision (ϕ) submodel to estimate lamb survival using late-season lamb-ewe ratios as the response variable. We used the betareg package in Program R (Cribari-Neto and Zeileis 2010, Zeileis et al. 2019; R Development Core Team 2019) to fit our models and assumed constant dispersion for ϕ (i.e., we did not include regressors to model ϕ). Additionally, we fit models with

quadratic and pseudothreshold (i.e., natural log) functional forms of precipitation to further investigate relationships between precipitation and survival. Models were evaluated using Akaike's Information Criterion adjusted for small sample sizes (AICc; Akaike 1973, Hurvich and Tsai 1989) and the AICcmodavg package in Program R (Mazerolle 2019; R Development Core Team 2019). We considered the effects of all variables in our top models (Δ AICc scores <2) and interpreted covariate effects based on 90% confidence intervals (CIs) for a conservative evaluation of parameter importance (Arnold 2010, Burnham and Anderson 2010). Lastly, we refit our most strongly supported model with the same predictor variables for μ and different sets of those variables for ϕ , testing them individually as well, to account for possible variable dispersion and potentially improve model fit. We interpreted goodness-of-fit based on pseudo R^2 calculated for beta regression (Ferrari and Cribari-Neto 2004).

We then examined relationships between survival and predictor variables associated with precipitation by comparing pairwise scatterplots to bivariate regression curves. Plots were generated using the ggplot2 package in Program R (Wickham et al. 2020; R Development Core Team 2019). To test the assumption that observed precipitation was independent over time, we subsequently fit 4 alternate models containing yearly fixed effects and predictor variables from our top model, and added them to our candidate model set for comparison. We estimated yearly effects by modeling 2014 and 2015 as indicator variables and 2016 as the reference category.

RESULTS

Camera-Derived Lamb-Ewes Ratios and Validation

We used camera count data from 6 to 10 occasions (i.e., sampling days) at each site in each mountain range per year to produce lamb-ewe ratios; the number of occasions depended on site activity. Lamb survival varied across populations and years as indicated by late-season lamb-ewe ratios and proportions of lambs that survived to 5 months with collared ewes (Table 2.1). We observed a strong correlation between those metrics across populations and years (r = 0.92, $p = 4.4 \times 10^{-6}$; Appendix B). Estimates from the Clipper and North Bristol mountains for 2016 and 2015 were

censored from the correlation test, however, because samples sizes of marked females were small (≤ 6), and estimated survival based on proportions of surviving lambs with collared females appeared spurious. We used the proportions of lambs with collared ewes to substantiate camera-derived ratios, and we believe that late-season lamb-ewe ratios more accurately reflect lamb survival to weaning within populations because these estimates are based on observations from the population at large, whereas proportions are based on finite samples and therefore tend toward greater sampling error.

Covariate Measures

Precipitation in October-April fluctuated throughout the study but appeared to be consistently higher in some ranges (Table 2.2); Old Dad Peak/Kelso, Cady, North Bristol, South Soda, and Clipper Mountains experienced some of the highest totals (51-81 mm), while Marble and South Bristol Mountains experienced lowest levels (31-57 mm). Precipitation in May-August appeared more variable across ranges and vears; all ranges experienced lower (<15 mm) and higher levels (>20 mm), with the exception of Old Dad Peak/Kelso Mountains which had consistently higher levels. Estimated mean adult female abundance was lowest in the South Soda Mountains (28 adult females), intermediate in Old Dad Peak/Kelso, Cady, Clipper and South Bristol Mountains (40-80 adult females), and highest in North Bristol and Marble Mountains (>80 adult females; Table 2.2). We used Pearson correlation coefficients to examine pairwise correlations between the following covariates and concluded that covariates were not confounding: October-April precipitation and May-August precipitation (r =-0.43, p = 0.085), October-April precipitation and population abundance (r = -0.17, p = 0.52), May-August precipitation and population abundance (r = -0.15, p = 0.57; Appendix C).

Model Estimates

We tested linear, quadratic, and pseudothreshold forms of October-April and May-August precipitation and present the model set containing linear and alternate functional forms most strongly supported for each covariate (Table 2.3). Our top model indicated that the quadratic form of October-April precipitation and the pseudothreshold form of May-August precipitation were the most important variables influencing lamb survival (pseudo $R^2 = 0.32$). As we predicted, October-April precipitation was associated with a positive effect on lamb survival ($\beta = 0.41$, SE = 0.10), but the effect decreased with increasing precipitation ($\beta_{quadratic term} = -0.0034$, SE = 0.00091; Table 2.4). Contrary to our predictions, the pseudothreshold form of May-August precipitation was associated with a negative effect on lamb survival ($\beta = -$ 1.44, SE = 0.51), but this effect lost support with the inclusion of yearly effects in our subsequent analysis (Table 2.5). Population abundance, which we predicted would have a negative effect on lamb survival, was not supported in any of our top models (Δ AICc scores <2). Additionally, model fit of our top model did not improve with regressors for ϕ (pseudo $R^2 \leq 0.32$) which suggests that dispersion was constant as originally estimated by our top model (β_0 for $\phi = 2.01$, SE = 0.36).

Based on our top model without yearly effects, the optimum level of precipitation in October-April was 60 mm, with estimated lamb survival predicted to reach 97.3% (90% CI [86.2, 100]) at this limit and decreasing at higher levels (Fig. 2.2a). Lamb survival declined with increasing May-August precipitation, decreasing the most between 0-20 mm (Fig. 2.2b). For example, given 60 mm of rainfall in October-April, estimated lamb survival decreased to 32.8% (90% CI [9.2, 61.9]) with the first 20 mm of rainfall in May-August, and to 15.2% (90% CI [1.2, 39.9]) with the next 20 mm of rainfall. Pairwise scatterplots and bivariate regression curves visualizing these relationships suggested a lack of independence in yearly observations, however, especially for May-August precipitation (Fig. 2.3).

In our subsequent analysis, yearly effects were more strongly supported than the effect of May-August precipitation given AICc ranking (Table 2.5). The highest ranking model indicated support for the quadratic effect of October-April precipitation ($\beta_{\text{linear term}} = 0.27$, SE = 0.095; $\beta_{\text{quadratic term}} = -0.0026$, SE = 0.00083) and negative yearly effects that decreased from 2014 to 2016 ($\beta_{2014} = -3.43$, SE = 0.81; $\beta_{2015} = -1.81$, SE = 0.47; $\beta_0 = -6.70$, SE = 2.69; Table 2.6) with improved fit (pseudo $R^2 = 0.45$). Based on this model, estimated lamb survival was lowest in 2014 and highest in 2016 assuming a constant level of October-April precipitation. For example, given 60 mm of rainfall in October-April, predicted lamb survival was 4.4% (90% CI [0.01, 16.8]) in 2014, 18.9% (90% CI [3.9, 40.5]) in 2015, and 58.7% (90% CI [34.2, 81.3]) in 2016.

DISCUSSION

We found that October-April and May-August precipitation were both important factors associated with lamb survival in our initial analysis, but apparent effects were not all consistent with our hypotheses and predictions, and further testing with yearly effects revealed that the negative effect associated with May-August precipitation might be spurious. We detected a quadratic effect of October-April precipitation, whereby precipitation up to an optimum level was positively associated with lamb survival, corroborating the importance of precipitation during this period, although the net effect became negative above the optimum. Autumn-spring precipitation is critical in terms of plant productivity during gestation and lambing in the Mojave Desert and has been linked to winter-spring nutrition and consequently productivity in bighorn sheep (Douglas and Leslie 1986, Douglas 2001, Wehausen 2005). Nevertheless, some studies have also observed that higher levels of precipitation can be associated with lower survival of lambs, although an explanation for this phenomenon remains unclear (DeForge and Scott 1982, Wehausen et al. 1987, Douglas 2001, Wehausen 2005). DeForge and Scott (1982) and Wehausen et al. (1987) speculated that higher levels of precipitation might increase insect populations and contribute to higher transmission rates and fatality associated with vector-borne diseases, although that effect should act on the mother as well as the offspring. Douglas (2001) proposed that above average precipitation coupled with colder temperatures could cause thermal stress in lambs and contribute to lower survival. Since October-April rainfall was largely concurrent with the period of gestation, such an effect would have to be indirect through the mother. While both explanations seem plausible, we also consider that nutrient cycling of nitrogen and carbon is largely influenced by wet-dry cycles in the desert, and increased pulses of rainfall during the growing season may diminish nitrogen and carbon mineralization, thereby lowering forage nutrition (Austin et al. 2004). As such, perhaps excessive rainfall could in turn compromise nutritional condition in parturient females and ultimately reduce lamb survival, since maternal nutrition affects lamb health (Douglas 2001).

We also detected a negative effect associated with May-August precipitation on lamb survival contrary to our hypothesis, although this effect was displaced by yearly effects in a secondary analysis. Yearly effects were negative and decreased over time, indicating that lamb survival improved with each year following the outbreak when controlling for effects of October-April precipitation. This finding could be potentially explained by a natural decrease in infection rates that may have occurred across populations over time, which would presumably result in less infection among lambs, but we note that yearly effects appeared to be correlated with October-April precipitation and partially correlated with May-August precipitation. Average October-April precipitation across ranges increased in each year of the study, while average May-August precipitation was comparable in 2014-2015 and decreased by nearly half in 2016. As such, without additional years of data, we cannot ascertain whether the effect associated with May-August precipitation was an artifact or was displaced because of data limitations.

Many studies generally agree that precipitation during the autumn-spring period affects forage nutrition and therefore greatly influences lamb survival by affecting maternal nutrition, while fluctuations in summer precipitation may have little to no effect on nutritional availability and lamb survival (Douglas and Leslie 1986, Douglas 2001, Wehausen 2005). Douglas (2001) observed that during summer months in the Mojave, high ambient temperatures reduce nutrient and moisture content of plants, and cause soil moisture deficits that limit the potential for plant growth in response to rainfall. Similarly, Wehausen (2005) noted that summer rains in the Mojave contributed minimally to mean diet quality for bighorn, as indicated by fecal nitrogen content. A study by Hnilicka et al. (2002), however, reported lower lamb survival during wetter summers in Wyoming following a pneumonia outbreak and concluded that the negative effect associated with higher precipitation was the result of reduced selenium uptake by forage plants. Selenium, which is important to immune function and disease resistance (Hefnawy and Tortora-Perez 2010), might be a factor worth considering in the desert as well. Alternately, Onozuka et al. (2009) found that *M. pneumoniae* in humans became more infectious with increasing ambient humidity and temperature as a result of prolonged airborne survival of the

pathogen. If the effect associated with May-August precipitation was real, perhaps higher levels of precipitation during hotter months might have increased aerosol transmission rates leading to higher disease incidence and related mortality among lambs.

Finally, population density has been identified in several studies as an important factor affecting lamb survival (Douglas and Leslie 1986, Wehausen 1987, Portier et al. 1998). Larger populations are likely to experience increased resource competition and lower nutrition, considered to be density-dependent effects that ultimately lower neonate survival (Gaillard et al. 1998). We tested the relationship between population abundance and lamb survival and found no support for a density effect, although abundance was negatively correlated with survival of adult female bighorn in these ranges in a separate study by Dekelaita et al. (*In review*). We suspect that the population-limiting effect of density may have been overwhelmed by density-independent factors associated specifically with disease and was therefore not detectable in our study (see Portier et al. 1998). For example, different levels of precipitation during spring and summer likely influenced animal aggregations, specifically group sizes and distributions with respect to available forage, which may have further influenced disease transmission and obscured an effect associated with population abundance.

There was a high level of unexplained variance associated with our top models. We believe that some unexplained variance may have resulted from uncertainty in lamb-ewe ratios, because ratios were mean values based on observations over the late-season period (15 August to 30 September). We verified that lamb-ewe ratios reflected lamb survival in our study given the strong correlation with collared females that had surviving lambs, but using lamb-ewe ratios as a proxy for survival also assumes that pregnancy rates were stable if not high across all populations and years, which we cannot verify. Many studies have used lamb-ewe ratios as a measure of lamb survival (Picton 1984, Douglas and Leslie 1986, Wehausen et al. 1987, Douglas 2001) and we have no reason to believe they were not a good index in our study, but we acknowledge that they may have introduced some variance for which we could not account. Additionally, predation may have been a factor contributing to lamb mortality that we were unable to measure and test, and for this reason may have also contributed to unspecified variance. Coyotes and bobcats are potential predators of neonates (McCoy et al. 2013, Smith et al. 2014, Schuman et al 2017, Cain et al. 2019) and were common species across our study area, but assessing additive effects of predation was beyond the scope of our study. Lastly, pathogen prevalence within populations is another factor that may influence lamb survival, and could therefore introduce additional error. Manlove et al. (2014) determined that pathogen transmission in lambs during pneumonia epidemics is frequency-dependent (i.e., dependent on the proportion of the population infected) and lamb survival may be therefore largely controlled by the number of infected individuals in a population. We had limited information regarding infection rates in our study populations, but pathogen prevalence presumably varied across populations throughout this study and likely resulted in additional error we could not overcome.

Our findings indicate that precipitation was an important factor influencing lamb survival, with pneumonia being indirectly implicated as well. Additional investigation will be needed to examine direct effects associated with the disease and how it might be effectively managed. For example, if a connection between selenium deficiency and reduced lamb survival can be ascertained, perhaps selenium fortified mineral blocks can be used to help offset lamb mortality. Assessing pathogen prevalence in populations through programmatic retesting of individuals could further help determine to what degree prevalence influences lamb survival and whether selective culling, which has been identified as a way to control pathogen persistence in infected populations (Cassirer et al. 2018), might benefit lamb survival.

On a final note, we recognize connectivity in a metapopulation, while important to maintaining genetic diversity and ultimately long-term persistence and viability of populations (Simberloff and Cox 1987, Hanski 1998, Lande 1998), can also help enable the spread and maintenance of a disease within a system (Hess 1996, Keeling and Eames 2005). Bighorn populations that have higher connectivity may therefore also experience prolonged exposure to *M. ovi*, and consequently suppressed lamb survival and recruitment over the long-term. In a *post ho*c analysis, we evaluated the effect of a genetic covariate, allelic richness at locus BL4, which could potentially reflect connectivity among populations, since heterozygosity is typically indicative of gene flow across populations (analysis explained in Appendix D). Locus BL4 is near the interferon gamma locus associated with ovine resistance to strongyle infection (Coltman et al. 2000) and was linked to immunoglobulin A activity among Scottish Blackface lambs (Davies et al. 2006). We found a negative effect associated with BL4 richness but we did not consider the apparent effect to be directly associated with connectivity since our study occurred over a short-term period and alleles at this locus are likely under selective pressure as well. Moreover, intermountain movements made by collared animals during this time occurred between most neighboring ranges, as reported by Dekelaita et al. (Chapter 3), which also suggests that connectivity was not likely driving differences in lamb survival during this study. In light of our findings, we hope new research can further develop our understanding of factors influencing population dynamics in this system and help guide future management efforts to mitigate effects of respiratory disease in populations of bighorn sheep.

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LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Proceedings of the 2nd International Symposium on Information Theory Akademiai Kiado, Budapest. (Reproduced in pages 610-624 *in* S. Kotzand and L. S. Johnson, editors. 1992. Breakthroughs in Statistics, Volume One, Foundations and Basic Theory. Springer-Verlag, New York, New York, USA).
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178.
- Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221-235.
- Beatley, J. C.1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856-863.
- Besser, T. E., E. F. Cassirer, K. A. Potter, J. VanderSchalie, A. Fischer, D. P. Knowles, D. R. Herndon, F. R. Rurangirwa, G. C. Weiser, and S. Srikumaran. 2008. Association of *Mycoplasma ovipneumoniae* infection with population limiting respiratory disease in free-ranging Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*). Journal of Clinical Microbiology 46:423-430.
- Besser, T. E., M. A. Highland, K. Baker, E. F. Cassirer, N. J. Anderson, J. M. Ramsey, K. Mansfield, D. L. Bruning, P. Wolff, J. B. Smith, and J. A. Jenks. 2012b. Causes of pneumonia epizootics among bighorn sheep, western United States, 2008-2010. Emerging Infectious Diseases 18:406-414.
- Besser, T. E., E. F. Cassirer, K. A. Potter, K. Lahmers, J. L. Oaks, S. Shanthalingam, S. Srikumaran, and W. J. Foreyt. 2014. Epizootic pneumonia of bighorn sheep following experimental exposure to *Mycoplasma ovipneumoniae*. PLOS ONE 9:1-9.
- Bleich, V. C. 1982. An illustrated guide to aging the lambs of mountain sheep (*Ovis canadensis ssp.*). Desert Bighorn Council Transactions 26:59-62.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:3-50.
- Bowden, D. C. and R. C. Kufeld. 1995. Generalized mark-resight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840-851.
- Bowyer, R. T., V. C. Bleich, K. M. Stewart, J. C. Whiting, and K. L. Monteith. 2014. Density dependence in ungulates: a review of causes and concepts with some clarification. California Fish and Game 100:550-572.
- Bunnell, F. L. 1982. The lambing period of mountain sheep: synthesis, hypotheses, and tests. Canadian Journal of Zoology 60:1-14.
- Burnham, K. P., and D. R. Anderson. 2010. Model selection and multimodel inference: a practical-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Cain III, J. W., R. C. Karsch, E. J. Goldstein, E. M. Rominger, and W. R. Gould. 2019. Survival and cause-specific mortality of desert bighorn sheep lambs. Journal of Wildlife Management 83:251-259.

- Cassirer, E. F., and A. R. E. Sinclair. 2007. Dynamics of pneumonia in a bighorn sheep metapopulation. Journal of Wildlife Management 71:1080-1088.
- Cassirer, E. F., R. K. Plowright, K. R. Manlove, P. C. Cross, A. P. Dobson, K. A. Potter, and P. J. Hudson. 2013. Spatio-temporal dynamics of pneumonia in bighorn sheep. Journal of Animal Ecology 82:518-528.
- Cassirer, E. F., K. R. Manlove, E. S. Almberg, P. Kamath, M. Cox, P. Wolff, A. Roug, J. Shannon, R. Robinson, R. B. Harris, B. J. Gonzales, R. K. Plowright, P. J. Hudson, P. C. Cross, A. Dobson, and T. E. Besser. 2018. Pneumonia in bighorn sheep: risk and resilience. Journal of Wildlife Management 82:32-45.
- Climate Engine. 2017. Desert Research Institute and University of Idaho. https://app.climateengine.org. Accessed 26 Aug 2017.
- Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. The American Naturalist 149:195-219.
- Coltman, D. W., K. Wilson, J. G. Pilkington, M. J. Stear, and J. M. Pemberton. 2000. A microsatellite polymorphism in the gamma interferon gene is associated with resistance to gastrointestinal nematodes in a naturally-parasitized population of Soay sheep. Parasitology 122:571-582.
- Creech, T. G., C. W. Epps, R. J. Monello, and J. D. Wehausen. 2016. Predicting diet quality and genetic diversity of a desert adapted ungulate with NDVI. Journal of Arid Environments 127:160-170.
- Cribari-Neto, F and A. Zeileis. 2010. Beta Regression in R. Journal of Statistical Software 34:1-24.
- Davies, G., M. J. Stear, M. Benothman, O. Abuagob, A. Kerr, S. Mitchell, and S. C. Bishop. 2006. Quantitative trait loci associated with parasitic infection in Scottish blackface sheep. Heredity 96:252-258.
- DeForge, J. R. and J. E. Scott. 1982. Ecological investigations into high lamb mortality. Desert Bighorn Council Transactions 26:65-76.
- Dekelaita, D. J., C. W. Epps, K. M. Stewart, J. S. Sedinger, J. G. Powers, B. J. Gonzales, R. K. Abella-Vu, N. W. Darby, and D. L. Hughson. *In review*. Survival of adult female bighorn sheep following a pneumonia epizootic. Journal of Wildlife Management.
- Digonnet, M. 2013. Hiking the Mojave Desert: natural and cultural heritage of Mojave National Preserve. Wilderness Press, Palo Alto, California, USA.
- Douglas, C. L. 2001. Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. Wildlife Society Bulletin 29:297-305.
- Douglas, C. L. and D. M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. Journal of Wildlife Management 50:153-156.
- Downs, C. J., B. V. Boan, T. D. Lohuis, and K. M. Stewart. 2018. Investigating relationships between reproduction, immune defenses, and cortisol in Dall sheep. Frontiers in Immunology 9:105. doi: 10.3389/fimmu.2018.00105.
- Epps, C. W., D. Dekelaita, and B. Dugovich. 2016. Updates on respiratory disease affecting bighorn sheep in and near Mojave National Preserve. Mojave National Preserve, Sweeney Granite Mountains Desert Research Center

Science Newsletter. <https://www.nps.gov/moja/learn/sciencenewsletter.htm>. Accessed 20 November 2018.

- Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714-724.
- ESRI. 2016. ArcGIS Desktop: Release 10.5. Environmental Systems Research Institute, Inc. Redlands, California.
- Ferrari, S. L. P. 2011. Diagnostic tools in beta regression with varying dispersion. Statistica Neerlandica 65:337–351.
- Ferrari, S. and F. Cribari-Neto. 2004. Beta regression for modelling rates and proportions. Journal of Applied Statistics 31:799-815.
- Festa-Bianchet, M., J. T. Jorgenson, and W. D. Wishart. 1994. Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not females. Behavioral Ecology 5:21-27.
- Funk, C., P. Peterson, M. Landsfeld, D. Pedreros, J. Verdin, S. Shukla, G. Husak, J. Rowland, L. Harrison, A. Hoell, and J. Michaelsen. 2015. The climate hazards infrared precipitation with stations – a new environmental record for monitoring extremes. Scientific Data 2:150066. doi 10.1038/sdata.2015.66.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.
- Hanski, I. 1998. Metapopulation dynamics. Nature 396:41-49. Hansson, B. and L. Westerberg. 2002. On the correlation between heterozygosity and fitness in natural populations. Molecular Ecology 11:2467-2474.
- Hass, C. C. 1989. Bighorn lamb mortality: predation, inbreeding, and population effects. Canadian Journal of Zoology 67:699-705.
- Hass, C. C. 1997. Seasonality of births in bighorn sheep. Journal of Mammalogy 78:1251-1260.
- Hefnawy, A. E. G. and J. L. Tórtora-Pérez. 2010. The importance of selenium and the effects of its deficiency in animal health. Small Ruminant Research 89:185-192.
- Hereford, R., R. H. Webb, and C. I. Longpre. 2004. Precipitation history of the Mojave Desert Region, 1893-2001. USGS Fact Sheet 117-03. https://doi.org/10.3133/fs11703>. Accessed 20 November 2018.
- Hess, G. 1996. Disease in metapopulation models: implication for conservation. Ecology 77:1617-1632.
- Hnilicka, P. A., J. Mionczynski, B. J. Mincher, J. States, M. Hinschberger, S. Oberlie, C. Thompson, B. Yates, and D. D. Siemer. 2002. Bighorn sheep lamb survival, trace minerals, rainfall, and pollution: are there any connections? Biennial Symposium of the Northern Wild Sheep and Goat Council 13:69-94.
- Huntington, J. L., K. C. Hegewisch, B. Daudert, C. G. Morton, J. T. Abatzoglou, D. J. McEvoy, and T. Erickson. 2017. Climate Engine: Cloud computing of climate and remote sensing data for advanced natural resource monitoring and process understanding. Bulletin of the American Meteorological Society 98:2397-2410.

- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Keeling, M. J., and K. T. D. Eames. 2005. Networks and epidemic models. Journal of the Royal Society Interface 2:295-307.
- Lande, R. 1998. Anthropogenic, ecological, and genetic factors in extinction and conservation. Population Ecology 40:259-269.
- Manlove, K., E. F. Cassirer, P. C. Cross, R. K. Plowright, and P. J. Hudson. 2014. Costs and benefits of group living with disease: a case study of pneumonia in bighorn lambs (*Ovis canadensis*). Proceedings of the Royal Society 281:20142331. doi 10.1098/ rspb.2014. 2331.
- Manlove, K., E. F. Cassirer, P. C. Cross, R. K. Plowright, and P. J. Hudson. 2016. Disease introduction is associated with a phase transition in bighorn sheep demographics. Ecology 97:2593-2602.
- Mazerolle, M. J. 2019. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-2.
- McCoy, J. C., S. S. Ditchkoff, J. B. Raglin, B. A. Collier, and C. Ruth. 2013. Factors influencing survival of white-tailed deer fawns in coastal South Carolina. Journal of Fish and Wildlife Management 14:280-289.
- McCullough, D. R. 1979. The George Reserve Deer Herd: Population Ecology of a K-Selected Species. University of Michigan Press, Ann Arbor, USA.
- Monello, R. J., D. L. Murray, and E. F. Cassirer. 2001. Ecological correlates of pneumonia epizootics in bighorn sheep herds. Canadian Journal of Zoology 79:1423-1432.
- National Geographic Society. 2008. Mojave National Preserve [map]. National Geographic Maps, Evergreen, Colorado, USA.
- National Park Service [NPS]. 2016. Mojave weather. https://www.nps.gov/moja/planyourvisit/weather.htm>. Accessed 9 Apr 2018.
- Onozuka, D., M. Hashizume, and A. Hagihara. 2009. Impact of weather factors on *Mycoplasma pneumoniae* pneumonia. Thorax 64:507-511.
- Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology 21:869-879.
- Plowright, R. K., K. R. Manlove, T. E. Besser, D. J. Paez, K. R. Andrews, P. E. Matthews, L. P. Waits, P. J. Hudson, and E. F. Cassirer. 2017. Age-specific infectious period shapes dynamics of pneumonia in bighorn sheep. Ecology Letters 20:1325-1336.
- Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology 245:271-278.
- Preisler, H. K., N. E. Grulke, Z. Heath, and S. L. Smith. 2017. Analysis and out-year forecast of beetle, borer, and drought-induced tree mortality in California. Forest Ecology and Management 399:166-178.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- Shuman, R. M., M. J. Cherry, T. N. Simoneaux, E. A. Dutoit, J. C. Kilgo, M. J. Chamberlain, and K. V. Miller. 2017. Survival of white-tailed deer neonates in Louisiana. Journal of Wildlife Management 81:834-845.
- Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235-253.
- Silverman, B. W. 1986. Density estimation for statistics and data analysis. Monographs on Statistics and Applied Probability. Chapman and Hall, London, England.
- Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. Conservation Biology 1:63-71.
- Smith, J. B., J. A. Jenks, T. W. Grovenburg, and R. W. Klaver. 2014. Disease and predation: sorting out causes of a bighorn sheep (*Ovis canadensis*) decline. PLOS ONE 9: e88271.
- Swift, P. K., J. D. Wehausen, H. B. Ernest, R. S. Singer, A. M. Pauli, H. Kinde, T. E. Rocke, and V. C. Bleich. 2000. Desert bighorn sheep mortality due to presumptive type c botulism in California. Journal of Wildlife Diseases 36:184-189.
- Thompson, R. W. and J. C. Turner. 1982. Temporal geographic variation in the lambing season of bighorn sheep. Canadian Journal of Zoology 60:1781-1793.
- Tomassini, L., B. Gonzales, G. C. Weiser, and W. Sischo. 2009. An ecological study comparing *Pasteurella trehalosi* and *Mannheimia haemolytica* between Sierra Nevada bighorn sheep, White Mountain bighorn sheep, and domestic sheep. Journal of Wildlife Diseases 45:930-940.
- Wehausen, J. D. 2005. Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. Pages 37-50 in J. Goerrissen and J. M. Andre, editors. Sweeney Granite Mountains Desert Research Center 1978-2003: A Quarter Century of Research and Teaching. University of California Natural Reserve Program, Riverside, USA.
- Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California sheep population. Journal of Wildlife Management 51:86-98.
- Wickham, H., W. Chang, L. Henry, T. L. Pedersen, K. Takahashi, C. Wilke, K. Woo, H. Yutani, and D. Dunnington. 2020. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. R package version 3.3.0.
- Wood, A. K., R. E. Short, A.-E. Darling, G. L. Dusek, R. G. Sasser, and C. A. Ruder. 1986. Serum assays for detecting pregnancy in mule and white-tailed deer. Journal of Wildlife Management 50:684-687.
- Wood, M. E., K. A. Fox, J. Jennings-Gaines, H. J. Killion, S. Amundson, M. W. Miller, and W. H. Edwards. 2017. How respiratory pathogens contribute to lamb mortality in a poorly performing bighorn sheep (*Ovis canadensis*) herd. Journal of Wildlife Diseases 53:126-130.
- Zeileis, A., F. Cribari-Neto, B. Gruen, and I. Kosmidis. 2019. betareg: Beta Regression. R package version 3.1-2.

TABLES AND FIGURES

Table 2.1. Proportions of lambs surviving up to 5 months of age with radio-collared females, and mean late-season (15 August to 30 September) lamb-ewe ratios in 2014-2016 from 7 populations in the Mojave Desert, California, USA following a pneumonia outbreak in 2013. Proportions of lambs surviving were based on samples of collared females (n). We used data collected from remote cameras at water sites to produce late-season ratios. Mean ratios were derived from cumulative numbers of females (f) and lambs observed across multiple sampling occasions in each mountain range. Dash indicates missing data.

Population (Year)	n	Proportion Surviving f Late-S		Late-Season Ratio
Old Dad Peak/Kelso (2014)	10	0.10	44	0.11
Old Dad Peak/Kelso (2015)	11	0.18	102	0.13
Old Dad Peak/Kelso (2016)	12	0.08	168	0.11
Marble (2014)	11	0.09	87	0.03
Marble (2015)	14	0.36	253	0.20
Marble (2016)	12	0.50	148	0.45
South Bristol (2014)	5	0.00	40	0.00
South Bristol (2015)	5	0.00	110	0.11
South Bristol (2016)	13	0.92	77	0.57
Cady (2015)	8	0.00	130	0.11
Cady (2016)	6	0.17	226	0.33
Clipper (2015)	0	-	10	0.10
Clipper (2016)*	6	0.17	30	0.60
North Bristol (2015)*	2	1	62	0.21
North Bristol (2016)	10	0.20	52	0.06
South Soda (2015)	3	0.33	66	0.24
South Soda (2016)	5	0.80	64	0.69

* Difference in the proportion of lambs surviving and late-season lamb-ewe ratio >0.40 (likely from sampling error associated with small samples used to generate proportions).

Table 2.2. Estimated population abundance for adult female bighorn and total precipitation in October-April 2013-14 to 2015-16 and May-August 2014-2016 in 7 mountain ranges in the Mojave Desert, California, USA. Abundance estimates were derived from remote camera data collected at point-source water features in 2016, BL4 richness was estimated from fecal samples collected in 2013-2015, and precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS). Data were used in combination with late-season (15 August to 30 September) lamb-ewe ratios to model lamb survival across populations and years following a pneumonia outbreak in 2013. Lamb-ewe ratios were based on observations from remote camera data collected at water sites. Dashes indicate values that are missing for populations and years not included in the study.

		2013-14	2014	2014-15	2015	2015-16	2016
Range (Population)	Adult F Abundance (95% CI)	Total Precipitation Oct-Apr (mm)	Total Precipitation May-Aug (mm)	Total Precipitation Oct-Apr (mm)	Total Precipitation May-Aug (mm)	Total Precipitation Oct-Apr (mm)	Total Precipitation May-Aug (mm)
Clipper	65 (28-102)	-	-	51.13	29.64	72.62	14.78
Marble	135 (67-202)	32.78	23.62	36.46	22.51	56.82	10.47
S. Bristol	46 (25-68)	31.62	21.57	31.14	24.83	48.46	10.79
S. Soda	28 (5-52)	-	-	52.59	22.95	68.58	10.17
Old Dad Peak	41 (18-63)	50.89	29.57	55.68	37.49	81.42	19.62
N. Bristol	101 (26-175)	-	-	59.03	27.27	77.20	11.24
Cady	71 (0-144)	-	-	57.17	20.20	74.51	9.99

Table 2.3. Results from initial beta regression modeling (without yearly effects) of lamb survival using late-season (15 August to 30 September) lamb-ewe ratios from 7 populations in 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak. We tested covariates for the mean parameter (μ) and assumed constant dispersion for the precision parameter (ϕ). We evaluated effects of precipitation in October-April and May-August on lamb survival, and included quadratic and pseudothreshold (i.e., natural log [LN]) functional forms respectively. Lamb-ewe ratios and abundance estimates were derived from remote camera data collected at point-source water features and precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS).

Model	Model Structure (μ)	K^{a}	ΔAICc	wi ^b	LL ^c
No.					
1	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip)	5	0	0.38	23.04
2	Oct-Apr Precip ² + Oct-Apr Precip + May-Aug Precip	5	0.38	0.31	22.85
3	Oct-Apr Precip ² + Oct-Apr Precip	4	1.86	0.15	20.05
4	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip) + Abundance	6	4.49	0.04	23.27
5	Oct-Apr Precip ² + Oct-Apr Precip + May-Aug Precip + Abundance	6	4.91	0.03	23.06
6	Oct-Apr Precip	3	5.18	0.03	16.65
7	Oct-Apr Precip ² + Oct-Apr Precip + Abundance	5	5.83	0.02	20.13
8	Oct-Apr Precip + LN(May-Aug Precip)	4	7.71	0.01	17.13
9	Oct-Apr Precip + May-Aug Precip	4	8.26	0.01	16.85
10	Oct-Apr Precip + Abundance	4	8.30	0.01	16.83
11	LN(May-Aug Precip)	3	8.92	0	14.78
12	Null	2	10.17	0	12.66
13	May-Aug Precip	3	10.65	0	13.91
14	Oct-Apr Precip + LN(May-Aug Precip) + Abundance	5	11.69	0	17.19
15	Oct-Apr Precip + May-Aug Precip + Abundance	5	12.17	0	16.96
16	LN(May-Aug Precip) + Abundance	4	12.32	0	14.82
17	Abundance	3	12.70	0	12.89
18	May-Aug Precip + Abundance	4	13.98	0	13.99
	^a Number of model parameters.				

^bAkaike model weight.

^cLog-likelihood.

Table 2.4. Parameter estimates from our initial top beta regression model (without yearly effects) evaluating lamb survival using late-season (15 August to 30 September) lamb-ewe ratios from 7 populations in 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak. We tested covariates for the mean parameter (μ) and assumed constant dispersion for the precision parameter (ϕ). We evaluated effects of precipitation in October-April and May-August on lamb survival with quadratic and pseudothreshold (i.e., natural log [LN]) functional forms respectively. Lamb-ewe ratios and abundance estimates were derived from remote camera data collected at point-source water features and precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS).

Parameters	β	SE	[90% CI]
(μ submodel)			
Intercept	-8.52	3.16	[-13.71, -3.32]
Precip OctApr ²	-0.0034	0.0009	[-0.0049, -0.0019]
Precip OctApr	0.41	0.10	[0.24, 0.58]
LN (Precip MayAug)	-1.44	0.51	[-2.28, -0.61]
(ϕ submodel)			
Intercept	2.01	0.36	[1.43, 2.60]

Table 2.5. Results from subsequent beta regression modeling (with yearly effects) of lamb survival using late-season (15 August to 30 September) lamb-ewe ratios from 7 populations in 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak. We tested covariates for the mean parameter (μ) and assumed constant dispersion for the precision parameter (ϕ). We evaluated effects of precipitation in October-April and May-August on lamb survival, and included quadratic and pseudothreshold (i.e., natural log [LN]) functional forms respectively. We also evaluated yearly effects in 4 models, whereby 2014-2015 are indicator variables and 2016 is the reference category. Lamb-ewe ratios and abundance estimates were derived from remote camera data collected at point-source water features and precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS).

Model No.	Model Structure (μ)	K ^a	ΔAICc	wi ^b	LL ^c
1	Oct-Apr Precip ² + Oct-Apr Precip + $Yr^{2014} + Yr^{2015}$	6	0	0.37	26.80
2	$Yr^{2014} + Yr^{2015}$	4	0.47	0.29	22.03
3	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip)	5	2.58	0.1	23.04
4	Oct-Apr Precip ² + Oct-Apr Precip + MayAug Precip	5	2.96	0.08	22.85
5	$LN(May-Aug Precip) + Yr^{2014} + Yr^{2015}$	5	4.01	0.05	22.32
6	Oct-Apr Precip ² + Oct-Apr Precip	4	4.44	0.04	20.05
7	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip) + $Yr^{2014} + Yr^{2015}$	7	5.90	0.02	26.88
8	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip) + Abundance	6	7.07	0.01	23.27
9	Oct-Apr Precip ² + Oct-Apr Precip + May-Aug Precip + Abundance	6	7.49	0.01	23.06
10	Oct-Apr Precip	3	7.76	0.01	16.65
11	Oct-Apr Precip ² + Oct-Apr Precip + Abundance	5	8.41	0.01	20.13
12	Oct-Apr Precip + LN(May-Aug Precip)	4	10.28	0	17.13
13	Oct-Apr Precip + May-Aug Precip	4	10.84	0	16.85
14	Oct-Apr Precip + Abundance	4	10.88	0	16.83
15	LN(May-Aug Precip)	3	11.50	0	14.78
16	Null	2	12.75	0	12.66
17	May-Aug Precip	3	13.23	0	13.91
18	Oct-Apr Precip + LN(May-Aug Precip) + Abundance	5	14.27	0	17.19
19	Oct-Apr Precip + May-Aug Precip + Abundance	5	14.75	0	16.96
20	LN(May-Aug Precip) + Abundance	4	14.90	0	14.82
21	Abundance	3	15.28	0	12.89
22	May-Aug Precip + Abundance	4	16.56	0	13.99
	^a Number of model parameters.				

^bAkaike model weight. ^cLog-likelihood. Table 2.6. Parameter estimates from our top beta regression model evaluating lamb survival with yearly effects using late-season (15 August to 30 September) lamb-ewe ratios from 7 populations in 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak. We modeled years 2014-2015 as indicator variables and 2016 as the reference category. The model also includes quadratic and linear terms estimating effects of October-April precipitation. We tested covariates for the mean parameter (μ) and assumed constant dispersion for the precision parameter (ϕ). Lamb-ewe ratios and abundance estimates were derived from remote camera data collected at point-source water features and precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS).

Parameters	β	SE	[90% CI]
(μ submodel)			
Intercept	-6.70	2.69	[-11.13, -2.27]
Precip OctApr ²	-0.0026	0.0008	[-0.0040, -0.0013]
Precip OctApr	0.27	0.09	[0.12, 0.43]
Year ²⁰¹⁴	-3.43	0.81	[-4.77, -2.10]
Year ²⁰¹⁵	-1.81	0.47	[-2.59, -1.03]
(ϕ submodel)			
Intercept	2.38	0.35	[1.80, 2.97]



Figure 2.1. Delineations of 7 bighorn sheep populations in the Mojave Desert, California, USA where we monitored lamb survival in 2014-2016 following a pneumonia outbreak.



Figure 2.2. Predictions from our initial top beta regression model (before testing yearly effects) evaluating lamb survival using late-season (15 August to 30 September) lamb-ewe ratios from 7 populations in 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak. We tested covariates for the mean parameter (μ) and assumed constant dispersion for the precision parameter (ϕ). We evaluated effects of precipitation in October-April and May-August on lamb survival with quadratic and pseudothreshold (i.e., natural log [LN]) functional forms respectively. Lamb-ewe ratios and abundance estimates were derived from remote camera data collected at point-source water features and precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS). We plotted predicted lamb survival given the following scenarios: (A) increasing October-April precipitation and no May-August precipitation, (B) a constant optimum of 60 mm precipitation in October-April and increasing May-August precipitation, (C) a constant of 40 mm precipitation in October-April and increasing May-August precipitation, and (D) a constant of 80 mm precipitation in October-April and increasing May-August precipitation. Dotted lines represent 90% confidence intervals.



Figure 2.3. Pairwise scatterplots with fitted regression curves from models evaluating effects of (A) October-April precipitation with quadrature and (B) natural log of May-August precipitation (LN Precip May-Aug) on lamb survival (as estimated by lamb-ewe ratios). We used beta regression to model these relationships across bighorn populations in 7 ranges from 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak.

CHAPTER 3: INTERMOUNTAIN MOVEMENTS AND POTENTIAL TRANSMISSION RISK ASSOCIATED WITH A RESPIRATORY PATHOGEN IN A METAPOPULATION OF BIGHORN SHEEP

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ABSTRACT

We used Global Positioning Systems (GPS) data from 135 radio-collared desert bighorn sheep (27 males and 108 females) from 14 populations to evaluate movement trends following a pneumonia outbreak linked to the pathogen Mycoplasma ovipneumoniae (M. ovi) in the Mojave Desert, California, USA. We captured animals in November 2013-2015 and March 2017, and collected location data from November 2013 to December 2018. Our objective was to model intermountain movement as a binary response and evaluate effects of sex, age, and *M. ovi* infection status at capture (determined from polymerase chain reaction [PCR] testing of nasal swabs collected from animals at capture), in order to assess the potential transmission risk individuals posed between populations by inferring potential for contact from movement behavior. We also examined seasonal trends by calculating proportions of intermountain movements by season for males and females. In a secondary analysis, we tested effects on mean seasonal daily movement rates using linear regression. We found that males were more likely to undertake intermountain movements than females, older animals (> 5 years) were more likely than younger animals (< 5 years), and individuals that were PCR-positive for *M. ovi* at capture were less likely than those that were PCR-negative. Additionally, intermountain movements were more

frequent during the breeding season (July-November) for males and during the period of mid-gestation to lambing (October-April) for females. The breeding season was also associated with higher mean daily movement rates for males, while effects of age and PCR status at capture were not supported. For females, positive PCR status and the period of mid-gestation to lambing were both negatively associated with mean daily movement rates and the effect of age was not supported. As such, we infer that the potential transmission risk posed within and across populations by an individual likely varies depending on time of year and sex, while *M. ovi* infection may also inhibit animal movement and consequently potential transmission risk.

INTRODUCTION

The Mojave Desert ecosystem features an assemblage of mountain ranges separated by low-lying areas that are fragmented by roads, freeways, and other anthropogenic structures (Epps et al. 2007). Populations of desert bighorn sheep (Ovis canadensis *nelsoni*) occupy many of these ranges, and despite distance and fragmentation, a network maintained by occasional animal movements exists among these populations, allowing for gene flow and the persistence of metapopulation dynamics (Epps et al. 2018). Such networks are important to conservation of wildlife populations as connectivity buffers against extinction from demographic stochasticity while maintaining genetic diversity, and consequently promotes long-term population persistence and viability (Simberloff and Cox 1987, Hanski 1998, Lande 1998). Networks among populations, however, can similarly maintain host-pathogen dynamics within a system and cause outbreaks or facilitate disease persistence (Hess 1996, Keeling and Eames 2005), which can ultimately undermine conservation of wildlife populations in theory. We evaluated intermountain/interpopulation movements of bighorn sheep following a pneumonia outbreak in the Mojave Desert to identify factors influencing these movements and gain a better understanding of potential transmission risk across populations.

Pneumonia is a major disease affecting bighorn sheep (*O. canadensis*) in North America and is associated with multiple respiratory pathogens, including *Mycoplasma ovipneumoniae* (*M. ovi*), leukotoxigenic *Mannheimia haemolytica* (*M. haemolytica*), *Bibersteinia trehalosi* (*B. trehalosi*), and *Pasteurella multocida* (*P.* *multocida*; Monello et al. 2001, Besser et al. 2008, 2012, Tomassini et al. 2009, Wood et al. 2017, Cassirer et al. 2018). Pneumonia outbreaks typically result from direct contact between infected domestic livestock and wild sheep, although once the disease is introduced, infected bighorn can easily spread pathogens within and across populations (Cassirer et al. 2013, 2018). All-age die offs usually ensue in naïve populations following initial exposure to respiratory pathogens (Cassirer et al. 2013), and while some individuals survive infection and likely develop strain-specific immunity, pneumonic pathogens can be maintained in bighorn populations for decades after the initial outbreak, and new disease events can occur even after an apparent fade-out (Plowright et al. 2017, Cassirer et al. 2013, 2017, 2018). Populations seem to be most at risk of disease spread and new outbreaks during periods when contact rates are high, for example during the breeding season when animals disperse, aggregate, and commingle in high concentrations (Onderka and Wishart 1988, Cassirer et al. 2013), and as such, transmission risk across populations may be influenced by seasonality as well.

A pneumonia outbreak linked to M. ovi occurred at Old Dad Peak (Kelso Mountains) in the Mojave Desert, California, USA, and led to an all-age bighorn sheep die-off in May and June 2013 (Epps et al. 2016, Dekelaita et al. In review). To date, this event is the only confirmed bighorn die-off associated with pneumonia in the Mojave Desert of California, although clinical signs of disease were observed in neighboring bighorn populations subsequent to the outbreak. Prior to the outbreak, these populations were thought to be insulated from the threat of pneumonia due to reduced connectivity with bighorn populations and domestic herds outside the system, but retrospective screening of banked serum collected in 2002-2005, and tested in 2014, revealed that some animals were in fact seropositive for *M. ovi* antibodies as early as 2002, although bighorn at Old Dad Peak were seronegative in 2005 (CDFW, unpublished data). In November 2013, 2014, 2015, adult bighorn from Old Dad Peak and 13 nearby ranges (i.e., South Soda, Cady, North Bristol, South Bristol, Granite, Marble, Clipper, Hackberry, Woods, Newberry, Ord, Old Woman and Black Mountains) were captured and tested for *M. ovi* infection via polymerase chain reaction (PCR) of nasal swab samples. Animals were also fitted with Global

Positioning Systems (GPS) radio-collars that collected location data and tracked movements.

Disease transmission is defined by infected hosts contacting and infecting susceptible individuals (Begon et al. 2002). Our objective was to assess contact potential and thereby potential transmission risk (i.e., the potential risk of transmission posed by an infected individual) between bighorn populations by evaluating intermountain movements (i.e., movements from one mountain range to another) with respect to age, sex, and *M. ovi* infection status at the individual level. We assumed that individuals who were more likely to make intermountain movements were also more likely to be vectors of disease across populations, although infected animals could be less likely to make such movements because of decreased health. We had 2 hypotheses: H1) Males are more likely to make intermountain movements, which are further dictated by age and seasonality. Dispersal and long-range movements have been observed more frequently in males than females (Geist 1971, Bleich et al. 1990, 1997, Borg et al. 2017), and given seasonal differences in behavior and physiological requirements associated with reproductive phases within and between sexes (Bleich et al. 1997, Rubin et al. 2000, Barboza and Bowyer 2001, Pelletier et al. 2009), we predicted that time of year would further influence such movements and potential for disease spread. We also speculated that individuals > 5 years old would be more likely to make intermountain movements given that males typically leave female groups when they are 2-4 years old (Geist 1971, Festa-Bianchet 1991), and females have been observed to behave more independently at 4-5 years old (Hass 1991). H2) Bighorn that tested positive for *M. ovi infection are less likely to make intermountain movements.* We assumed that animals who tested positive for *M. ovi* at time of capture may have had lingering effects associated with infection (Dekelaita et al. In review) that might inhibit longrange movements. Since movement rates increase with longer movements over discrete time steps (i.e., longer travel distances over metered time steps within a series

yield higher rates of movement), as a secondary approach to our analysis, we also examined effects of seasonality, age, and infection status on seasonal daily movement rates for males and females, calculated from distances between daily locations.

STUDY AREA

The Mojave is considered high elevation desert, characterized by dry, hot summers and cold, wet winters, but also experiences late summer monsoons that account for at least 25% of the total annual rainfall (Hereford et al. 2004, National Geographic Society 2008). Temperatures and precipitation vary with elevation; temperatures typically range from average lows of -1°C in the winter to average highs of 34°C in the summer, and can exceed 40°C in the lower lying areas (NPS 2016). Mean annual precipitation is approximately 21 cm, with lower elevations receiving as little as 9 cm and higher elevations receiving as much as 25 cm annually (NPS 2016). Temperatures and precipitation vary with elevation; temperatures typically range from average lows of -1°C in the winter to average highs of 34°C in the summer, and can exceed 40°C in the lower lying areas (NPS 2016). Mean annual precipitation is approximately 21 cm, with lower average highs of 34°C in the summer, and can exceed 40°C in the lower lying areas (NPS 2016). Mean annual precipitation is approximately 21 cm, with lower elevations receiving as little as 9 cm and higher elevations receiving as much as 25 cm annually (NPS 2016).

Our study area encompassed bighorn sheep populations across multiple mountain ranges in the eastern and southern Mojave Desert, including Kelso, South Soda, Cady, North Bristol, South Bristol, Granite, Providence, Marble, Clipper, Hackberry, Woods, Piute, Newberry, Rodman, Ord, Old Woman, and Bullion Mountains, and additionally in the Black and Owlshead Mountains in the northern Mojave Desert (Fig. 3.1). Ranges in the eastern and southern Mojave were located east of Barstow, CA, south of Interstates 15 and 40, on lands managed by the Bureau of Land Management (BLM) and National Park Service, Mojave National Preserve (MNP); the Black and Owlshead Mountains were located north of Baker, CA in Death Valley National Park (DVNP). The study area occurred between 36°00'00" N and 34°15'00" N and between 116°56'00" W and 114°53'25" W. Elevations ranged from approximately 300 m to 2,000 m. Mountain ranges featured common desert scrub vegetation including catclaw acacia (Senegalia greggii), creosote bush (Larrea tridentata), rabbitbrush (Ericameria sp.), brittlebush (Encelia farinosa), white bursage (Ambrosia dumosa), blackbrush (Coleogyne ramosissima), Mormon tea (Ephedra spp.), silver and buckhorn cholla (Cylindropuntia echinocarpa and Cylindropuntia acanthocarpa), Mojave yucca (Yucca schidigera), California barrel

cactus (*Ferocactus cylindraceus*), and annual grasses and forbs that appeared seasonally in response to rainfall (Digonnet 2013, Creech et al. 2016). Common native mammal species included antelope ground squirrel (*Ammospermophilus leucurus*), black-tailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), kit fox (*Vulpes macrotis*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and desert bighorn sheep. Mountain lion (*Puma concolor*), mule deer (*Odocoileus hemionus*), and free-ranging burro (*Equus asinus*) also occurred in some ranges, although burros are not native to the Mojave Desert.

METHODS

Collaring, Disease Testing and Aging

Adult bighorn sheep were captured and fitted with GPS radio-collars in November 2013, 2014, 2015 and March 2017 in the following ranges: Old Dad Peak/Kelso (n = 18), South Soda (n = 8), Cady (n = 10), North Bristol (n = 18), South Bristol (n = 19), Granite (n = 4), Marble (n = 26), Clipper (n = 13), Hackberry (n = 6), Woods (n = 6), Newberry (n = 2), Ord (n = 2), Old Woman Mountains (n = 1), and Black Mountains (n = 2). Animals were located aerially and captured using a net-gun fired from helicopter (Krausman et al. 1985), and were processed in the field following guidelines approved by CDFW and the National Park Service Institutional Animal Care and Use Committee (ACUP)

#PWR_MOJA_Epps.Powers_DesertBighorn_2013.A3, 2013-2015), and as established by the American Society of Mammalogists for use of wild animals in research (Sikes et al. 2016). Nasal swabs were collected to determine infection status of individuals at time of capture; swabs were tested via PCR to detect *M. ovi* specific DNA sequences by Washington Animal Disease Diagnostic Laboratory (WADDL; Pullman, WA). Strain typing consisted of multi-locus sequence typing based on partial DNA sequences of the 16S-23S intergenic spacer region, the 16S ribosomal subunit, and RNA polymerase B and gyrase B genes, as described in Cassirer et al. (2017). Additionally, we aged animals based on horn growth (i.e., number of horn annuli) and tooth eruption patterns (Deming 1952, Geist 1966, Heffelfinger 1997).

Location Data and Movement Metrics

Location data were obtained from animals fitted with store-on-board or GPS satellite collars: ATS G2110 (Advanced Telemetry Systems, Isanti, MN, USA), Lotek 4400 and Lifecycle (Lotek Wireless Inc., Newmarket, Ontario, Canada), Vectronic Survey (Vectronic Aerospace GmbH, Berlin, Germany), Tellus Iridum 1D (Tellus GPS System/Followit AB, Lindesberg, Sweden). Collars were programmed to record locations between 1 and 10 times a day, varying by model type, and signaled mortality if they were motionless for more than 8 hours. Data were either received through the Iridium satellite system (Iridium Communications, McLean, Virginia), Globalstar (Globalstar, Inc., Covington, Louisiana), or were downloaded when collars were recovered from animals.

We used adehabitatLT in Program R (Calenge 2019; R Development Core Team 2019) to produce movement metrics such as step-lengths, turning angles, and time intervals (Turchin 1998, Morales et al. 2004, Fryxell et al. 2008) based on sequential location data for all animals. We identified and removed errant data points if the distance traveled was > 3 standard deviations of the mean travel rate and the ratio of the distance traveled from three sequential points (1,2, and 3) for 1 to 2/2 to 3 was < 0.9 and the turning angle 123 was > 3 radians, following Villepique et al. (2008). For best location accuracy with minimal data reduction, we also discarded GPS locations if < 3 satellites were used to obtain a fix (Ironside et al. 2017).

Movement Modeling

We identified intermountain movements based on location data indicating that an animal had moved to a new mountain range, even if temporarily, and classified those individuals as movers. We modeled intermountain movement as an individual response (i.e., whether or not an animal had made at least 1 intermountain movement) using logistic regression with a binomial distribution and logit link; models were fit with the glm function in Program R (R Development Core Team 2019). We assigned a value of 1 to movers (i.e., animals that made at least 1 intermountain movement) and 0 to nonmovers (i.e., animals that did not make any intermountain movements), and evaluated models with variables for PCR status at capture, sex, and age. We modeled PCR status as a continuous indicator variable whereby individuals received

covariate values of 1 if they were PCR-positive for *M. ovi* (i.e., positive for *M. ovi* infection) at time of capture, values of 0 if they were negative, and a mean value of 0.5 if a test result was indeterminate based on results from WADDL, or if infection status was otherwise unknown due to missing data. Sex and age were also modeled as indicator variables, whereby females received a covariate value of 0 and males received a covariate value of 1, while individuals < 5 years old received a covariate value of 0 and individuals > 5 years old received a value of 1. Animals that became older than 5 years during the study were moved from the former cohort to the latter upon aging out (capture dates were used to mark yearly intervals for aging).

To examine seasonal effects, we calculated proportions of intermountain movements by season for males and females; seasons were defined based on a climograph for Mojave National Preserve (McKee et al. 2015), whereby October and November represented autumn, December through March represented winter, April through June represented spring, and July through September represented summer. The proportions of intermountain movements were higher for males in summer and autumn, and higher for females in autumn and winter which coincided with the breeding season for males and the period of mid-gestation to lambing (i.e., peak of lactation; Bleich et al. 1997) for females. As such, we inferred a biological basis for higher movement activity during these periods. For males, we identified biologically relevant seasons based on breeding from July to November and nonbreeding from December to June, and for females based on mid-gestation to lambing from October to April and post-lambing to early-gestation from May to September, as observed in desert bighorn sheep (Lenarz 1979, Bleich et al. 1997, Hass 1997). We tested the statistical significance of apparent seasonal differences in the number of movements associated with biological seasons for males (i.e., breeding vs. nonbreeding) and females (i.e., mid-gestation to lambing vs. post-lambing to early-gestation) using Welch's *t*-test.

Additionally, we used standard linear regression to test effects of biological season, age, and PCR status at capture on daily movement rates in separate analyses for males and females, in order to further investigate movement behavior regardless of intermountain activity. To generate daily movement rates, radio-collar data were

resampled to 1 location per day for all individuals by removing extraneous locations such that consecutive locations for each animal were between 20 and 28 hours apart. In cases where locations were missing and time lags exceeded 28 hours, we retained the next location to allow for the next daily time step. We calculated daily movement rates from step-lengths (i.e., Euclidean distance between 2 consecutive locations measured in meters) divided by time lags between resampled locations, and multiplied rates by 24 hours to yield meters per day (m/day). Daily movement rates were then partitioned by biological season and averaged to produce seasonal mean daily movement rates for each individual. We modeled seasonal effects categorically, whereby each animal had 2 responses (i.e., one for each season) and received seasonal covariate input values of 1 for mean movement rates associated with breeding (for males) and mid-gestation to lambing (for females) and values of 0 for alternate periods. Age and PCR status were modeled as described in the intermountain movement analysis. We added a random effect to our most strongly supported models in order to evaluate individual variation in the intercept *post hoc* and potentially improve model fit (Harrison et al. 2001). We fit fixed effects models with the lm function in Program R (R Development Core Team 2019) and mixed effects models were fit with the lme4 package (Bates et al. 2019).

For both the intermountain movement and seasonal movement rate analyses we ranked models using Akaike's Information Criterion adjusted for small sample sizes (AICc; Akaike 1973, Hurvich and Tsai 1989) with the AICcmodavg package in Program R (Mazerolle 2019; R Development Core Team 2019). We considered the effects of all variables in our top models (Δ AICc scores < 2) and interpreted covariate effects based on 90% confidence intervals (CIs) for a conservative evaluation of parameter importance (Burnham and Anderson 2010, Arnold 2010). For the intermountain movement analysis, we applied area under the receiver operating characteristic (ROC) curve (AUC) to evaluate goodness-of-fit of our top model (Hanley and McNeil 1982) using LogisticDx in Program R (Dardis 2015; R Development Core Team 2019). For the seasonal movement rate analyses, we interpreted goodness-of-fit of our top models based on the coefficient of determination (R^2) and assessed normality and equal variance of residuals via quantile
and residual plots using the olsrr package in Program R (Hebbali 2020; R Development Core Team 2019). We used analysis of variance (ANOVA) to test the significance of the added random effects and calculated R^2 for the mixed effects model using the MuMIn package in Program R (Barton 2019; R Development Core Team 2019). We also assessed normality of the random effect for females using a normal quantile plot for the mixed effects model, which we generated with the qqnorm function in Program R (R Development Core Team 2019).

RESULTS

We used data from 135 radio-collared bighorn (27 males and 108 females) from 14 populations in the Mojave Desert (Fig. 3.1) to evaluate movement trends with respect to sex, age, season, and PCR status at capture between November 2013 and December 2018. We collected > 1 year of data from 128 individuals in our sample, and > 6 months to 1 year of data from the remaining 7 individuals (collars had an average lifespan of 2 years). Across our study, 27 individuals (10 males and 17 females) made 155 intermountain movements (males: 45, females: 110; Fig. 3.2), and 108 individuals (17 males and 91 females) did not make intermountain movements. Based on proportions of intermountain movements occurring by season, there appeared to be a seasonal bias whereby most intermountain movements occurred during autumn (30%) and winter (35%) for females, and during autumn (47%) and summer (33%) for males, with lowest proportions occurring in spring (19%) and summer (15%) for females, and in spring (4%) and winter (16%) for males (Fig. 3.3). Differences across biologically relevant seasons for females and males were statistically significant based on Welch's t-test. Among movers, the mean number of intermountain movements per female during mid-gestation to lambing over the study period was 4.3 and during post-lambing to early-gestation was 1.8 ($t_{125.61} = 2.2, p =$ (0.0349). The mean number of intermountain movements per male during breeding over the study period was 3.6 and during nonbreeding was 0.9 ($t_{11,91} = 2.5$, p =0.0283).

Additionally, we did not detect any definitive dispersal movements (i.e., oneway movements away from source populations; Fryxell et al. 2014), in that all intermountain movements were typically followed by return trips back to the mountain range of origin (Fig. 3.4), with some individuals making multiple round-trip movements over the study period. In 3 instances animals died before returning to the mountain range of origin, but only after making multiple round-trip movements. In 1 other instance, an animal moved from the mountain range of origin to a neighboring mountain range on the same day it was captured, and made no other intermountain movements during the study; we suspected that this animal may have originally been from the neighboring range and likely returned immediately after being collared. All animals that made intermountain movements displayed long-range movement spurts whereby movements between mountain ranges were completed in 1-3 days and occurred at speeds as high as 16.4 km/day.

In the intermountain movement analysis, our top model indicated that age, sex, and PCR status at capture were all important variables influencing intermountain movements (Table 3.1, Table 3.2). Age was positively correlated with intermountain movements ($\beta = 1.06$, 90% CI [0.24, 1.88]), whereby the odds of an individual > 5 years old making an intermountain movement were 2.89 times higher than an individual < 5 years old. The effect associated with being male was also positive ($\beta = 1.17$, 90% CI [0.35, 1.99]), whereby the odds of a male making an intermountain movement were 3.22 times higher than a female. Lastly, the apparent effect of positive infection status was negatively correlated with intermountain movements ($\beta = -1.33$, 90% CI [-2.38, -0.28]) such that the odds of an individual undertaking an intermountain movement were 74% less if the individual was PCR-positive for *M. ovi* at capture. The goodness-of-fit test for this model indicated acceptable predictability (AUC = 71.8%, 95% CI [62.9%, 80.7%]; Appendix E).

Based on parameter estimates, the probability of a male > 5 years old and PCR-negative at capture making an intermountain movement was 52% (\pm 12% SE), while the probability for a male > 5 years old and PCR-positive at capture was 22% (\pm 12% SE; Fig. 3.5). Alternately, for a male < 5 years old and PCR-negative at capture the probability of an intermountain movement was 27% (\pm 10% SE), and the probability for a male < 5 years old and PCR-positive at capture was 9% (\pm 6% SE). In contrast, the probability of an intermountain movement for a female > 5 years old and PCR-negative at capture was 25% (\pm 6% SE), while the probability for a female > 5 years old and PCR-positive at capture was 8% (\pm 4% SE). Alternately, for a female < 5 years old and PCR-negative at capture the probability of an intermountain movement was 10% (\pm 4% SE), and the probability for a female < 5 years old and PCR-positive at capture was 3% (\pm 2% SE).

In the movement rate analysis, our highest ranking fixed effects model for females indicated that season and PCR status were important variables influencing mean daily movement rates ($R^2 = 0.08$; Table 3.3). The random intercept accounting for individual variation in the corresponding mixed effects model was statistically significant ($\chi^2 = 15.2, p < 0.0001$) and improved model fit ($R^2 = 0.40$). The season of mid-gestation to lambing was negatively associated with mean daily movement rates (mixed: $\beta = -108.83$ [m/day], SE = 26.81). Positive PCR status at capture was also negatively associated with mean daily movement rates (mixed: $\beta = -118.67$ [m/day], SE = 41.61). The fixed intercept (β_0) in the mixed effects model and variance components for the random intercept (σ_{u}^{2}) and residual variance (σ_{e}^{2}) were as follows: $\beta_0 = 1027.07$ (m/day), SE = 27.44; $\sigma_u^2 = 23187$, $\sigma_e^2 = 44424$. Quantile and residual plots for our top model indicated that the assumptions of normality and equal variance had been met for linear regression and the random effect was normally distributed (Appendix F). We note that the age parameter was included in the second highest ranking fixed effects model, but the estimated effect was not statistically supported (i.e., 90% CI overlapped 0). For males, our highest ranking fixed effects model indicated that season was the only important variable influencing mean daily movement rates ($R^2 = 0.45$; Table 3.4). The random intercept accounting for individual variation in the corresponding mixed effects model was not statistically significant ($\chi^2 = 0.3$, p = 0.61). The breeding season was positively associated with mean daily movement rates ($\beta = 480.74 \text{ [m/day]}$, SE = 70.34; $\beta_0 = 910.16 \text{ [m/day]}$, SE = 49.74) and parameter estimates for age and PCR status in top models were not supported (i.e., 90% CIs overlapped 0). Quantile and residual plots for the highest ranking model indicated that the assumptions of normality and equal variance had been met for linear regression (Appendix F). Based on mean parameter estimates, females that were PCR-negative at capture moved 109 m/day less on average during the season of mid-gestation to lambing (October-April) than during post-lambing

(May-September), and females that were PCR-positive moved an additional 119 m/day less on average, while males moved 481 m/day more during the breeding season (July-November) than the nonbreeding season (December-June) on average, regardless of PCR status and age.

DISCUSSION

We found that intermountain movements by bighorn were influenced by sex, age, and *M. ovi* status at capture. Apparent effects associated with sex and age indicated that males were more likely to undertake intermountain movements than females and older animals were more likely than younger animals. These results are consistent with our hypotheses and are largely indicated by other studies as well (Geist 1971, Hass 1991, Bleich et al. 1997, Krausman et al. 1999, Borg et al. 2017). Some studies suggest, however, that males < 5 years old are as likely to disperse and move long distances as older males (Geist 1971, Festa-Bianchet 1991), and that such movements occur rarely to never in females (Rubin et al. 1998, DeCesare and Pletscher 2006). In our study the proportion of females that made intermountain movements was smaller than the proportion of males (16% vs. 37%), but females made more intermountain movements on average during the study. Moreover, intermountain movements among both males and females could not be classified as dispersal movements, because all but 1 individual made round-trip movements. Bleich et al. (1996) reported a similar pattern for female bighorn in the Mojave Desert, and concluded these movements were either migratory or exploratory.

We also found that animals who were PCR-negative for *M. ovi* at capture were more likely to make intermountain movements than animals who were PCR-positive. Recent studies have reported that bighorn sheep can become chronically infected with *M. ovi* (Plowright et al. 2017, Wood et al. 2017, Cassirer et al. 2018), and may remain infected for 3 years or longer without displaying clinical signs of disease (Plowright et al. 2017). Our results indicate that positive infection status at capture was negatively associated with intermountain movements, suggesting that animals who were PCR-positive for *M. ovi* at capture may have suffered lingering effects from infection that hindered movement behavior. The possibility of lingering effects from *M. ovi* infection is corroborated by Dekelaita et al. (*In review*) who found

that positive infection status at capture was associated with lower survival among adult female bighorn for several years following the 2013 pneumonia outbreak in the Mojave Desert.

Seasonality also appeared to influence movement activity. Males were more likely to make intermountain movements during the breeding season, while females were more likely to make intermountain movements during the period of midgestation to lambing. Our movement rate analysis provided additional support for the apparent seasonal effect on intermountain movements by males, whereby males had higher movement rates during the breeding season, a finding supported in the literature (Geist 1971, Festa-Bianchet 1991, Bleich et al. 1997, Krausman et al. 1999, Borg et al. 2017). As such, we conclude that higher proportions of intermountain movements and higher mean daily movement rates during breeding were likely a function of rutting behavior in males.

For females, results from the movement rate analysis were contrary to what we expected based on the seasonal bias of intermountain movements. Females had lower mean daily movement rates associated with the period of mid-gestation to lambing, when intermountain movements were highest. We speculate that daily movement rates were likely higher during the post-lambing period (May-September) due to forage availability becoming more limited and scattered during the dry season, when animals were also constrained by limited water availability. Several studies have similarly concluded that larger home ranges used by desert bighorn sheep in the summer are the result of widely scattered resources (Krausman et al. 1999). Alternately, the period of mid-gestation to lambing (October to April) coincides with the growing season in the Mojave Desert (Wehausen 2005); females may have had lower daily movement rates during this period because availability of resources was greater and animals likely did not have to move as far to acquire them. By similar reasoning, intermountain movements may have been higher for females when resource constraints were lifted. As such, we conclude that movement patterns in females may have been dictated by environmental variables, and we speculate that additional biological factors related to parturition may have also influenced movement behavior. For example, females may have been more likely to make

intermountain movements if they did not become pregnant or have offspring at heel, but may have also made such movements for the purpose of lambing; Bleich et al. (1996) observed 44 seasonal intermountain movement events by females in the Mojave between 1984 and 1996, in which births occurred in at least 5 out of 6 destination ranges (round-trip movements occurred in all but 1 of these events). Positive infection status at capture also appeared to have a negative effect on daily movement rates in females, as with intermountain movements, regardless of season. We note that the effect of infection on movement rate was not supported for males (i.e., 90% CI overlapped 0), which might have resulted from reduced statistical power in separate analyses for males and females, given a substantially smaller sample size of males.

In terms of potential transmission risk, if home ranges are larger when resources are more abundant, home ranges may be more likely to overlap resulting in increased potential for contact among individuals and across groups. Bighorn sheep are gregarious animals that typically live in sexually segregated social groups yearround, but these groups vary in size and stability depending on time of year (Geist 1971, Bleich et al. 1997, Manlove et al. 2014), and aggregations of males and females occur in August through November in the Mojave Desert (Bleich et al. 1997). It is reasonable to conclude that female groups would be more stable and less mixing between groups would occur during the period of mid-gestation to lambing, when movement rates were lower and contact potential between groups likely decreased, while during post-lambing, when movement rates were higher and contact potential likely increased, groups would be less stable and more mixing would occur. For this reason, we suspect that potential transmission risk across female groups within a given mountain range may be higher during the post-lambing period when groups are likely less stable in the Mojave Desert. Conversely, we expect females to pose the highest potential transmission risk across mountain ranges in the Mojave Desert during the period of mid-gestation to lambing, when the frequency of intermountain movements among females was highest. For males, movement rates and frequency of intermountain movements were highest during the breeding season (July to November), and as such, we would expect the potential transmission risk posed by an

infected male both within and across mountain ranges to be highest during this period, which is also when aggregations of males and females occur.

We note that the intermountain movement analysis largely assumes that individuals were solitary, especially with respect to the apparent age effect. By extension, the movement rate analysis, which did not support age as a factor influencing movement activity in either sex, may indicate that within ranges movement rates reflected group activity. We recognize, however, that there was a high level of unexplained variance (> 50%) associated with top models in the movement rate analysis. We suspect that given the stochastic nature of resource availability in the desert (Douglas and Leslie 1986), much of the unexplained variance may have resulted from fluctuations in environmental conditions across seasons and years, which could not be addressed with our dataset. Moreover, we suspect that the variance among individual females may have been due to additional biological factors (e.g., pregnancy/lambing status and nutritional condition) we were unable to observe and account for throughout the study, which may have also overwhelmed effects of age. We suspect that males were more similar to each other because they were not subject to the demands of parturition that can variably alter nutritional condition and movement capability in females.

Population substructuring (i.e., group living within populations), spatial distribution, and social dynamics of bighorn sheep are all factors that can ultimately influence contact rates between individuals and may therefore largely influence how respiratory disease is communicated and spread within a population sharing the same range (Manlove et al. 2014, Borg et al. 2017, Cassirer et al. 2018). Those factors also have indirect implications for spreading disease across populations as well, but host response to infection is arguably another important factor ultimately influencing transmission (Ewald 2004). Our study revealed that potential transmission risk within and across populations may vary depending on time of year and sex of an individual, but positive infection status may also inhibit animal movement and consequently potential transmission risk. Animals that were PCR-positive for *M. ovi* at time of capture appeared less likely to make intermountain movements, which implies that stronger, healthier animals were more likely to make these movements. Whether

animals that tested positive for *M. ovi* at capture remained chronically infected throughout the study is unknown, but our results suggest that these animals suffered lingering effects from infection that may have limited their movement capabilities. Intermountain movements often require animals to move long distances and travel across undesirable habitat, overcoming movement barriers of varying degrees (Schwartz et al. 1986, Epps et al. 2007, Creech et al. 2014). In our study, at least 16 animals made multiple intermountain movements across secondary roads (i.e., paved and unpaved 2-lane byways), lava beds, or low-lying flatlands, and only 3 animals crossed interstate highways (Fig. 3.4), which have been identified as major movement barriers reducing connectivity among bighorn populations in the Mojave (Epps et al. 2005, 2018). If chronic infection reduced movement activity in animals that tested positive for M. ovi, reduced connectivity between mountain ranges may have further decreased the likelihood of those individuals making intermountain movements and posing a transmission risk across populations. We did not consider effects of barriers on intermountain movements in this study because movement paths between mountain ranges were loosely approximated from location data and barriers are difficult to assess (Epps et al. 2018), but we speculate that given the presence of M. ovi in some populations 10 years earlier, reduced connectivity within the system may be one reason why the pneumonia outbreak in 2013 was the first one documented in our study area. While connectivity is essential to maintaining metapopulation dynamics and gene flow (Bleich et al. 1990, 1996, Lande 1998, Epps et al. 2007), we recommend additional study to examine how different levels of connectivity may further increase or decrease potential transmission risk across populations, and to assess potential tradeoffs for conservation and restoration of bighorn populations affected by respiratory disease.

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LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Proceedings of the 2nd International Symposium on Information Theory Akademiai Kiado, Budapest. (Reproduced in pages 610-624 *in* S. Kotzand and L. S. Johnson, editors. 1992. Breakthroughs in Statistics, Volume One, Foundations and Basic Theory. Springer-Verlag, New York, New York, USA).
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178.
- Barboza, P. S., and R. T. Bowyer. 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces* 37:275-292.
- Barton, K. 2019. MuMIn: multi-model inference. R package version 1.43.15.
- Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, and J. Fox. 2019. LME4: linear mixed-effects models using eigen and S4. R package version 1.1-21.
- Begon, M., M. Bennett, R. G. Bowers, N. P. French, S. M. Hazel, and J. Turner. 2002. A clarification of transmission terms in host-microparasite models: numbers, densities, and areas. Epidemiology and Infection 129:147-153.
- Besser, T. E., E. F. Cassirer, K. A. Potter, J. VanderSchalie, A. Fischer, D. P. Knowles, D. R. Herndon, F. R. Rurangirwa, G. C. Weiser, and S. Srikumaran. 2008. Association of *Mycoplasma ovipneumoniae* infection with population limiting respiratory disease in free-ranging Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*). Journal of Clinical Microbiology 46:423-430.
- Besser, T. E., M. A. Highland, K. Baker, E. F. Cassirer, N. J. Anderson, J. M. Ramsey, K. Mansfield, D. L. Bruning, P. Wolff, J. B. Smith, and J. A. Jenks. 2012. Causes of pneumonia epizootics among bighorn sheep, western United States, 2008-2010. Emerging Infectious Diseases 18:406-414.
- Bleich, V. C., J. D. Wehausen, R. R. Ramey II, and J. L. Rechel. 1996.
 Metapopulation theory and mountain sheep: implications for conservation.
 Pages 353-373 *in* D. R. McCullough, editor. Metapopulations and Wildlife Conservation. Island Press, Covelo, California, USA.
- Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Conservation Biology 4:383-390.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:3-50.

- Borg, N. J., M. S. Mitchell, P. M. Lukacs, C. M. Mack, L. P. Waits, and P. R. Krausman. 2017. Behavioral connectivity among bighorn sheep suggests potential for disease spread. Journal of Wildlife Management 81:38-45.
- Burnham, K. P., and D. R. Anderson. 2010. Model selection and multimodel inference: a practical-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Calenge, C. 2019. Analysis of animal movements in R: the adehabitatLT package. R package version 0.3.24.
- Cassirer, E. F., K. R. Manlove, E. S. Almberg, P. Kamath, M. Cox, P. Wolff, A.
 Roug, J. Shannon, R. Robinson, R. B. Harris, B. J. Gonzales, R. K. Plowright,
 P. J. Hudson, P. C. Cross, A. Dobson, and T. E. Besser. 2018. Pneumonia in
 bighorn sheep: risk and resilience. Journal of Wildlife Management 82:32-45.
- Cassirer, E. F., K. R. Manlove, R. K. Plowright, and T. E. Besser. 2017. Evidence for strain-specific immunity to pneumonia in bighorn sheep. Journal of Wildlife Management 81:133-143.
- Cassirer, E. F., R. K. Plowright, K. R. Manlove, P. C. Cross, A. P. Dobson, K. A. Potter, and P. J. Hudson. 2013. Spatio-temporal dynamics of pneumonia in bighorn sheep. Journal of Animal Ecology 82:518-528.
- Creech, T. G., C. W. Epps, R. J. Monello, and J. D. Wehausen. 2014. Using network theory to prioritize management in a desert bighorn sheep metapopulation. Landscape Ecology. doi 10.1007/s10980-014-0016-0.
- Dardis, C. 2015. LogisticDx: diagnostic tests for models with a binomial response. R package version 0.2.
- DeCesare, N. J., and D. H. Pletscher. 2006. Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. Journal of Mammalogy 87:531-538.
- Dekelaita, D. J., C. W. Epps, K. M. Stewart, J. S. Sedinger, J. G. Powers, B. J. Gonzales, R. K. Abella-Vu, N. W. Darby, and D. L. Hughson. *In review*. Survival of adult female bighorn sheep following a pneumonia epizootic. Journal of Wildlife Management.
- Deming, O. V. 1952. Tooth development of the Nelson bighorn sheep. California Fish and Game 38:523-529.
- Douglas, C. L., and D. M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. Journal of Wildlife Management 50:153-156.
- Epps, C. W., D. Dekelaita, and B. Dugovich. 2016. Updates on respiratory disease affecting bighorn sheep in and near Mojave National Preserve. Mojave National Preserve, Sweeney Granite Mountains Desert Research Center Science Newsletter. https://www.nps.gov/moja/learn/science-newsletter.https://www.nps.gov/moja/learn/science-newsletter.htm>. Accessed 20 November 2018.
- Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714-724.
- Epps, C. W., P. J. Palsboll, J. D. Wehausen, G. K. Roderick, R. R. Ramey II, and D. R. McCullough. 2005. Highways block gene flow and cause rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8:1029-1038.

- Epps, C. W., R. S. Crowhurst, B. S. Nickerson. 2018. Assessing change in functional connectivity in desert bighorn sheep metapopulation after two generations. Molecular Ecology 27:2334-2346.
- Ewald, P. W. 2004. Evolution of virulence. Infectious disease clinics of North America 18:1-15.
- Festa-Bianchet, M. 1991. The social system of bighorn sheep: grouping patterns, kinship, and female dominance rank. Animal Behavior 42:71-82.
- Fryxell, J. M., M. Hazella, L. Börger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. PNAS doi: 10.1073_pnas.0801737105.
- Geist. V. 1966. Validity of horn segment counts in aging bighorn sheep. Journal of Wildlife Management 30:634-635.
- Geist, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, Illinois, USA.
- Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29-36.
- Hanski, I. 1998. Metapopulation dynamics. Nature 396:41-49.
- Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2001. A brief introduction to mixed effects modelling a multi-model inference in ecology. PeerJ 6:e4794.
- Hass, C. C. 1991. Social status in female bighorn sheep (*Ovis canadensis*): expression, development and reproductive correlates. Journal of Zoology (London) 225:509-523.
- Hass, C. C. 1997. Seasonality of births in bighorn sheep. Journal of Mammalogy 78:1251-1260.
- Hebbali, A. 2020. olsrr: Tools for Fitting OLS Regression Models. R package version 0.5.3.
- Heffelfinger, J. 1997. Age criteria for Arizona game species. Arizona Game and Fish Department, Special Report No. 19. Arizona Game and Fish Department, Phoenix, Arizona, USA.
- Hereford, R., R. H. Webb, and C. I. Longpre. 2004. Precipitation history of the Mojave Desert Region, 1893-2001. USGS Fact Sheet 117-03. https://doi.org/10.3133/fs11703>. Accessed 20 November 2018.
- Hess, G. 1996. Disease in metapopulation models: implication for conservation. Ecology 77:1617-1632.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Ironside, K. E., D. J. Mattson, T. R. Arundel, and J. R. Hansen. 2017. Is GPS telemetry location screening beneficial? Wildlife Biology 2017. doi 10.2981/wlb.00229.
- Keeling, M. J., and K. T. D. Eames. 2005. Networks and epidemic models. Journal of the Royal Society Interface 2:295-307.
- Krausman, P. R., A. V. Sandoval, and R. C. Etchberger. 1999. Natural history of desert bighorn sheep. Pages 139-191 *in* R. Valdez and P. R. Krausman,

editors. Mountain Sheep of North America. University of Arizona Press, Tucson, Arizona, USA.

- Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71-73.
- Lande, R. 1998. Anthropogenic, ecological, and genetic factors in extinction and conservation. Population Ecology 40:259-269.
- Lenarz, M. S. 1979. Social structure and reproductive strategy in desert bighorn sheep (*Ovis canadensis mexicana*). Journal of Mammalogy 60:671-678.
- Manlove, K., E. F. Cassirer, P. C. Cross, R. K. Plowright, and P. J. Hudson. 2014. Costs and benefits of group living with disease: a case study of pneumonia in bighorn lambs (*Ovis canadensis*). Proceedings of the Royal Society 281:20142331. doi 10.1098/rspb.2014.2331.
- Mazerolle, M. J. 2019. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-2.
- McKee, C. J., K. M. Stewart, J. S. Sedinger, A. P. Bush, N. W. Darby, D. L. Hughson, and V. C. Bleich. 2015. Spatial distributions and resource selection by mule deer in an arid environment: responses to provision of water. Journal of Arid Environments 2015:76-84.
- Monello, R. J., D. L. Murray, and E. F. Cassirer. 2001. Ecological correlates of pneumonia epizootics in bighorn sheep herds. Canadian Journal of Zoology 79:1423-1432.
- Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movements models as mixtures of random walks. Ecology 85: 2436-2445.
- National Geographic Society. 2008. Mojave National Preserve [map]. National Geographic Maps, Evergreen, Colorado, USA.
- National Park Service [NPS]. 2016. Mojave weather. https://www.nps.gov/moja/planyourvisit/ weather.htm>. Accessed 9 Apr 2018.
- Onderka, D. K., and W. D. Wisehart. 1988. Experimental contact transmission of *Pasteurella haemolytica* from clinically normal domestic sheep causing pneumonia in Rocky Mountain bighorn sheep. Journal of Wildlife Diseases 24:663-667.
- Pelletier, F., J. Mainguy, and S. D. Cote. 2009. Rut-induced hypophagia in male bighorn sheep and mountain goats: foraging under time budget constraints. Ethology 115:141-151.
- Plowright, R. K., K. R. Manlove, T. E. Besser, D. J. Paez, K. R. Andrews, P. E. Matthews, L. P. Waits, P. J. Hudson, and E. F. Cassirer. 2017. Age-specific infectious period shapes dynamics of pneumonia in bighorn sheep. Ecology Letters 20:1325-1336.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rubin, E. S., W. M. Boyce, M. J. Jorgenson, S. G. Torres, C. L. Hayes, C. S. O'Brien, and D. A. Jessup. 1998. Distribution and abundance of bighorn sheep in the Peninsular Ranges, California. Wildlife Society Bulletin 26:539-551.

- Rubin, E. S., W. M. Boyce, and V. C. Bleich. 2000. Reproductive strategies of desert bighorn sheep. Journal of Mammalogy 81:769-786.
- Schwartz, A. O., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelson*. Biological Conservation 37:179-190.
- Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235-253.
- Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. Conservation Biology 1:63-71.
- Tomassini, L., B. Gonzales, G. C. Weiser, and W. Sischo. 2009. An ecological study comparing *Pasteurella trehalosi* and *Mannheimia haemolytica* between Sierra Nevada bighorn sheep, White Mountain bighorn sheep, and domestic sheep. Journal of Wildlife Diseases 45:930-940.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, USA.
- Villepique, J. T., V. C. Bleich, B. M. Pierce, T. R. Stephenson, R. A. Botta, and R. T. Bowyer. 2008. Evaluating GPS collar error: a critical evaluation of Televilt POSREC-ScienceTM collars and a method for screening location data. California Fish and Game 94:155-168.
- Wehausen, J. D. 2005. Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. Pages 37-50 in J. Goerrissen and J. M. Andre, editors. Sweeney Granite Mountains Desert Research Center 1978-2003: A Quarter Century of Research and Teaching. University of California Natural Reserve Program, Riverside, USA.
- Wood, M. E., K. A. Fox, J. Jennings-Gaines, H. J. Killion, S. Amundson, M. W. Miller, and W. H. Edwards. 2017. How respiratory pathogens contribute to lamb mortality in a poorly performing bighorn sheep (*Ovis canadensis*) herd. Journal of Wildlife Diseases 53:126-130.

TABLES AND FIGURES

Table 3.1. Modeling results from an analysis evaluating intermountain movements of adult bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Intermountain movements were detected using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. We tested effects of sex, age (i.e., < or > 5 years old), and *Mycoplasma ovipneumoniae* (*M. ovi*) infection (determined from polymerase chain reaction [PCR] testing of nasal swabs collected from animals at time of capture) on intermountain movements as a binary response. Models were evaluated using Akaike's Information Criterion adjusted for small sample sizes (AICc).

Model No.	Model Structure	K ^a	ΔAICc	w _i ^b	LL ^c
1	Age + PCR status + Sex	4	0.00	0.58	-64.53
2	PCR status + Sex	3	2.97	0.13	-67.07
3	Age + PCR status	3	3.24	0.11	-67.21
4	Age + Sex	3	3.33	0.11	-67.25
5	PCR status	2	5.45	0.04	-69.35
6	Sex	2	6.60	0.02	-69.92
7	Age	2	8.11	0.01	-70.68
8	Null	1	10.73	0.00	-73.02

^aNumber of model parameters.

^bAkaike model weight.

^cLog-likelihood.

Table 3.2. Parameter estimates from our top model evaluating intermountain movements of adult bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Intermountain movements were detected using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. We tested effects of sex, age (i.e., < or > 5) years old), and Mycoplasma ovipneumoniae (M. ovi) infection (determined from polymerase chain reaction [PCR] testing of nasal swabs collected from animals at time of capture) on intermountain movements as a binary response whereby animals that moved received values of 1 and nonmovers received values of 0. We modeled PCR status as a continuous indicator variable whereby individuals received covariate values of 1 if they were PCR-positive for M. ovi (i.e., positive for M. ovi infection) at time of capture, values of 0 if they were negative, and a mean value of 0.5 if a test result was indeterminate or if infection status was otherwise unknown. Sex and age were also modeled as indicator variables, whereby females received a covariate value of 0 and males received a covariate value of 1, while individuals < 5 years old received a covariate value of 0 and individuals > 5 years old received a value of 1.

Parameters	β	SE	[90% CI]
Intercept	-2.17	0.47	[-2.95, -1.39]
Age (>5 yr)	1.06	0.50	[0.24, 1.88]
PCR-positive	-1.33	0.63	[-2.38, -0.28]
Male	1.17	0.50	[0.35, 1.99]

Table 3.3. Modeling results from an analysis evaluating mean seasonal daily movement rates of adult female bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Mean daily movement rates were calculated using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. We tested effects of age (i.e., < or > 5 years old), *Mycoplasma ovipneumoniae* (*M. ovi*) infection (determined from PCR testing of nasal swabs collected from animals at time of capture), and season on mean seasonal daily movement rates using standard linear regression. Seasons were defined by the period of mid-gestation to lambing (October-April) and post-lambing to early-gestation (May-September). Models were evaluated using Akaike's Information Criterion adjusted for small sample sizes (AICc).

Model No.	Model Structure	K ^a	ΔAICc	$W_i^{\ b}$	LL ^c
1	Season + PCR status	4	0.00	0.61	-1729.38
2	Season + Age + PCR status	5	1.02	0.37	-1728.85
3	PCR status	3	8.67	0.01	-1734.75
4	Season	3	8.72	0.01	-1734.78
5	Age + PCR status	4	9.68	0.00	-1734.22
6	Season + Age	4	10.10	0.00	-1734.43
7	Null	2	16.85	0.00	-1739.86
8	Age	3	18.20	0.00	-1739.52

^aNumber of model parameters.

^bAkaike model weight.

^cLog-likelihood.

Table 3.4. Modeling results from an analysis evaluating mean seasonal daily movement rates of adult male bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Mean daily movement rates were calculated using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. We tested effects of age (i.e., < or > 5 years old), *Mycoplasma ovipneumoniae* (*M. ovi*) infection (determined from PCR testing of nasal swabs collected from animals at time of capture), and season on mean seasonal daily movement rates using standard linear regression. Seasons were defined by the breeding period (July-November) and nonbreeding period (December-June). Models were evaluated using Akaike's Information Criterion adjusted for small sample sizes (AICc).

Model	Model Structure	K ^a	ΔAICc	W_i^b	LL ^c
No.					
1	Season	3	0.00	0.31	-405.52
2	Season + Age	4	0.44	0.25	-404.59
3	Season + PCR status	4	0.49	0.24	-404.61
4	Season + Age + PCR status	5	0.77	0.21	-403.55
5	Null	2	32.96	0.00	-423.11
6	Age	3	34.17	0.00	-422.61
7	PCR status	3	34.20	0.00	-422.62
8	Age + PCR status	4	35.38	0.00	-422.06

^aNumber of model parameters.

^bAkaike model weight.

^cLog-likelihood.



Figure 3.1. Delineations of 14 bighorn sheep populations in the Mojave Desert, California, USA where we collared animals to track movements from 2013-2018 following a pneumonia outbreak.



Figure 3.2. Number of intermountain movements by individual bighorn sheep in the Mojave Desert, California, USA from 2013-2018 following a pneumonia outbreak. Light gray bars represent female movements and dark gray bars represent male movements.



Figure 3.3. Proportions of bighorn intermountain movements occurring by season for males and females in the Mojave Desert, California, USA from 2013-2018 following a pneumonia outbreak.



Figure 3.4. Intermountain movements (indicated by arrows) between bighorn sheep populations in the Mojave Desert, California, USA. Movements were detected using location data from animals with GPS radio-collars that were monitored from 2013-2018. Bidirectional arrows indicate two-way movements and unidirectional arrows indicate one-way movements; *n* denotes the number of animals that moved.



Figure 3.5. Estimated probabilities of a bighorn sheep making an intermountain movement given sex, age (< or > 5 years old), and *Mycoplasma ovipneumonia* infection status of an individual, based on logistic regression modeling of intermountain movements by adult bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Intermountain movement was modeled as a binary response whereby animals that moved received values of 1 and nonmovers received values of 0. Intermountain movements were detected using location data from animals that were captured and received GPS radio-collars in

November 2013-2015 and March 2017. Infection status was determined by polymerase chain reaction (PCR) testing of nasal swabs collected from animals at time of capture. We modeled PCR status as a continuous indicator variable whereby individuals received covariate values of 1 if they were PCR-positive for *M. ovi* (i.e., positive for *M. ovi* infection) at time of capture, values of 0 if they were negative, and a mean value of 0.5 if a test result was indeterminate or if infection status was otherwise unknown. Sex and age were also modeled as indicator variables, whereby females received a covariate value of 0 and males received a covariate value of 1, while individuals < 5 years old received a covariate value of 0 and individuals > 5 years old received a value of 1. PCR-pos is the condition of being positive for *M. ovi* infection of being negative, and PCR-unk is the condition of having unknown infection status. Dashed lines represent standard errors.

GENERAL CONCLUSION

Pneumonia has posed a major challenge to management of bighorn sheep since the early 1900s and remains an ongoing problem in many populations (Buechner 1960, Cassirer et al. 2018). Much still remains unknown about the dynamics of the disease, but one reason it continues to re-emerge and plague bighorn (*Ovis canadensis*) may be that it is a poly-factorial, poly-microbial condition (Besser et al. 2013) for which there is no single management solution. Through my research, I sought to explore factors that might be influencing differences in apparent disease effects in populations across space and time, and understand the potential transmission risk posed by individuals following an outbreak. My ultimate objective was to identify specific factors that could potentially shed light on ways to mitigate effects of disease.

In my first chapter, I found that Mycoplasma ovipneumoniae (M. ovi) infection, as determined at time of capture, was associated with a substantial reduction in survival of adult female bighorn following a pneumonia outbreak in 2013 in the Mojave Desert, which is consistent with many studies that have linked M. ovi to pneumonia epizootics and acute mortality in bighorn sheep populations (Besser et al. 2012b, Cassirer et al. 2018), although my study suggests a lingering post-outbreak effect. Environmental variables also appeared to influence adult female survival, and in particular, higher forage quality in summer and autumn (as approximated by the normalized difference vegetation index) was positively associated with survival of infected and uninfected individuals, suggesting that better nutrition might partially offset negative effects associated with the pathogen. Population abundance was negatively associated with survival, suggesting that density dependence further added to effects associated with infection. The results from my second chapter reveal that precipitation likely influenced lamb survival in populations exposed to M. ovi and genetics may have played a role as well. In my third chapter, I found that intermountain movements appeared to be influenced by *M. ovi* infection, sex, age, and season. Moreover, daily movement rates also appeared to be influenced by sex and season, and *M. ovi* status was negatively associated with movement rates in females.

We found evidence that *M. ovi* infection may have lingering effects on survival and movement, which has clear implications for disease transmission. Results from this study also corroborate findings from other studies regarding factors influencing bighorn sheep survival (i.e., forage quality, population abundance, precipitation) and movement (i.e., sex, age, seasonality). Further investigation may be needed to improve our understanding of the extent to which these factors control disease dynamics, and to help guide future management efforts aimed at mitigating effects of respiratory disease in bighorn sheep populations. My hope is that the research I conducted will serve to direct future studies and planning efforts to conserve existing populations and restore those affected by respiratory disease.

LITERATURE CITED

- Besser, T. E., M. A. Highland, K. Baker, E. F. Cassirer, N. J. Anderson, J. M. Ramsey, K. Mansfield, D. L. Bruning, P. Wolff, J. B. Smith, and J. A. Jenks. 2012b. Causes of pneumonia epizootics among bighorn sheep, western United States, 2008-2010. Emerging Infectious Diseases 18:406-414.
- Besser, T. E., E. F. Cassirer, M. A. Highland, P. Wolff, A. Justice-Allen, K. Mansfield, M. A. Davis, and W. Foreyt. 2013. Bighorn sheep pneumonia: sorting out the cause of polymicrobial disease. Preventive Veterinary Medicine 108:85-93.
- Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildlife Monographs 4:3-174.
- Cassirer, E. F., K. R. Manlove, E. S. Almberg, P. Kamath, M. Cox, P. Wolff, A. Roug, J. Shannon, R. Robinson, R. B. Harris, B. J. Gonzales, R. K. Plowright, P. J. Hudson, P. C. Cross, A. Dobson, and T. E. Besser. 2018. Pneumonia in bighorn sheep: risk and resilience. Journal of Wildlife Management 82:32-45.

BIBLIOGRAPHY

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Proceedings of the 2nd International Symposium on Information Theory Akademiai Kiado, Budapest. (Reproduced in pages 610-624 *in* S. Kotzand and L. S. Johnson, editors. 1992. Breakthroughs in Statistics, Volume One, Foundations and Basic Theory. Springer-Verlag, New York, New York, USA).
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178.
- Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221-235.
- Barboza, P. S., and R. T. Bowyer. 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces* 37:275-292.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction arrived? Nature 471:51-57.
- Barton, K. 2019. MuMIn: multi-model inference. R package version 1.43.15.
- Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, and J. Fox. 2019. LME4: linear mixed-effects models using eigen and S4. R package version 1.1-21.
- Beatley, J. C.1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856-863.
- Begon, M., M. Bennett, R. G. Bowers, N. P. French, S. M. Hazel, and J. Turner. 2002. A clarification of transmission terms in host-microparasite models: numbers, densities, and areas. Epidemiology and Infection 129:147-153.
- Belden, E. L., E. S. Williams, E. T. Thorne, H. J. Harlow, K. White, and S. L. Anderson. 1990. Effect of chronic stress on immune system function of Rocky Mountain Bighorn Sheep. Biennial Symposium of the Northern Wild Sheep and Goat Council 7:76-91.
- Bender, L. C., and M. E. Weisenberger. 2005. Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. Wildlife Society Bulletin 33:956-964.
- Beringer, J., L. P. Hansen, W. Wilding, J. Fischer, and S. L. Sheriff. 1996. Factors affecting capture myopathy in white-tailed deer. Journal of Wildlife Management 60: 373-380.
- Besser, T. E., E. F. Cassirer, K. A. Potter, J. VanderSchalie, A. Fischer, D. P. Knowles, D. R. Herndon, F. R. Rurangirwa, G. C. Weiser, and S. Srikumaran. 2008. Association of *Mycoplasma ovipneumoniae* infection with population limiting respiratory disease in free-ranging Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*). Journal of Clinical Microbiology 46:423-430.
- Besser, T. E., E. F. Cassirer, C. Yamada, K. A. Potter, C. Herndon, W. J. Foreyt, D. P. Knowles, and S. Srikumaran. 2012*a*. Survival of bighorn sheep (*Ovis*

canadensis) commingled with domestic sheep (*Ovis aries*) in the absence of *Mycoplasma ovipneumoniae*. Journal of Wildlife Diseases 48:168-172.

- Besser, T. E., M. A. Highland, K. Baker, E. F. Cassirer, N. J. Anderson, J. M. Ramsey, K. Mansfield, D. L. Bruning, P. Wolff, J. B. Smith, and J. A. Jenks. 2012b. Causes of pneumonia epizootics among bighorn sheep, western United States, 2008-2010. Emerging Infectious Diseases 18:406-414.
- Besser, T. E., E. F. Cassirer, M. A. Highland, P. Wolff, A. Justice-Allen, K. Mansfield, M. A. Davis, and W. Foreyt. 2013. Bighorn sheep pneumonia: sorting out the cause of polymicrobial disease. Preventive Veterinary Medicine 108:85-93.
- Besser, T. E., E. F. Cassirer, K. A. Potter, K. Lahmers, J. L. Oaks, S. Shanthalingam, S. Srikumaran, and W. J. Foreyt. 2014. Epizootic pneumonia of bighorn sheep following experimental exposure to *Mycoplasma ovipneumoniae*. PLOS ONE 9:1-9.
- Bleich, V. C. 1982. An illustrated guide to aging the lambs of mountain sheep (*Ovis canadensis ssp.*). Desert Bighorn Council Transactions 26:59-62.
- Bleich, V. C., J. D. Wehausen, R. R. Ramey II, and J. L. Rechel. 1996.
 Metapopulation theory and mountain sheep: implications for conservation.
 Pages 353-373 *in* D. R. McCullough, editor. Metapopulations and Wildlife Conservation. Island Press, Covelo, California, USA.
- Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Conservation Biology 4:383-390.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:3-50.
- Borg, N. J., M. S. Mitchell, P. M. Lukacs, C. M. Mack, L. P. Waits, and P. R. Krausman. 2017. Behavioral connectivity among bighorn sheep suggests potential for disease spread. Journal of Wildlife Management 81:38-45.
- Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz, and T. Coulson. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. The American Naturalist 168:471-485.
- Bowden, D. C. and R. C. Kufeld. 1995. Generalized mark-resight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840-851.
- Bowyer, R. T., V. C. Bleich, K. M. Stewart, J. C. Whiting, and K. L. Monteith. 2014. Density dependence in ungulates: a review of causes and concepts with some clarification. California Fish and Game 100:550-572.
- Brunner, F. S., P. Schmid-Hempel, and S. M. Barribeau. 2014. Protein-poor diet reduces host-specific immune gene expression in *Bombus terrestris*.
 Proceedings of the Royal Society 281:20140128. doi 10.1098/rspb.2014.0128.
- Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildlife Monographs 4:3-174.
- Bunnell, F. L. 1982. The lambing period of mountain sheep: synthesis, hypotheses, and tests. Canadian Journal of Zoology 60:1-14.

- Burnham, K. P., and D. R. Anderson. 2010. Model selection and multimodel inference: a practical-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Butler, C. J., W. H. Edwards, J. E. Jennings-Gaines, H. J. Killion, M. E. Wood, D. E. McWhirter, J. T. Paterson, K. M. Proffitt, E. S. Almberg, P. J. White, J. J. Rotella, and R. A. Garrott. 2017. Assessing respiratory pathogen communities in bighorn sheep populations: sampling realities, challenges, and improvements. PLOS ONE 12:e0180689.
- Cain III, J. W., R. C. Karsch, E. J. Goldstein, E. M. Rominger, and W. R. Gould. 2019. Survival and cause-specific mortality of desert bighorn sheep lambs. Journal of Wildlife Management 83:251-259.
- Calenge, C. 2019. Analysis of animal movements in R: the adehabitatLT package. R package version 0.3.24.
- Cassirer, E. F., and A. R. E. Sinclair. 2007. Dynamics of pneumonia in a bighorn sheep metapopulation. Journal of Wildlife Management 71:1080-1088.
- Cassirer, E. F., K. R. Manlove, E. S. Almberg, P. Kamath, M. Cox, P. Wolff, A. Roug, J. Shannon, R. Robinson, R. B. Harris, B. J. Gonzales, R. K. Plowright, P. J. Hudson, P. C. Cross, A. Dobson, and T. E. Besser. 2018. Pneumonia in bighorn sheep: risk and resilience. Journal of Wildlife Management 82:32-45.
- Cassirer, E. F., K. R. Manlove, R. K. Plowright, and T. E. Besser. 2017. Evidence for strain-specific immunity to pneumonia in bighorn sheep. Journal of Wildlife Management 81:133-143.
- Cassirer, E. F., R. K. Plowright, K. R. Manlove, P. C. Cross, A. P. Dobson, K. A. Potter, and P. J. Hudson. 2013. Spatio-temporal dynamics of pneumonia in bighorn sheep. Journal of Animal Ecology 82:518-528.
- Climate Engine. 2017. Desert Research Institute and University of Idaho. https://app.climateengine.org. Accessed 26 Aug 2017.
- Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. The American Naturalist 149:195-219.
- Coltman, D. W., J. G. Pilkington, J. A. Smith, and J. M. Pemberton. 1999. Parasitemediated selection against inbred Soay sheep in a free-living island population. Evolution 53:1259-1267.
- Coltman, D. W., K. Wilson, J. G. Pilkington, M. J. Stear, and J. M. Pemberton. 2000. A microsatellite polymorphism in the gamma interferon gene is associated with resistance to gastrointestinal nematodes in a naturally-parasitized population of Soay sheep. Parasitology 122:571-582.
- Cooch, E. G., and G. C. White, editors. 2017. Program MARK: a gentle introduction. Seventeenth edition. Colorado State University, Fort Collins, Colorado, USA.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1-61.
- Cotter, S. C., S. J. Simpson, D. Raubenheimer, and K. Wilson. 2011. Macronutrient balance mediates trade-offs between immune function and life history traits. Functional Ecology 25:186-198.

- Creech, T. G., C. W. Epps, R. J. Monello, and J. D. Wehausen. 2014. Using network theory to prioritize management in a desert bighorn sheep metapopulation. Landscape Ecology. doi 10.1007/s10980-014-0016-0.
- Creech, T. G., C. W. Epps, R. J. Monello, and J. D. Wehausen. 2016. Predicting diet quality and genetic diversity of a desert adapted ungulate with NDVI. Journal of Arid Environments 127:160-170.
- Cribari-Neto, F and A. Zeileis. 2010. Beta Regression in R. Journal of Statistical Software 34:1-24.
- Cunningham, A. A., P. Daszak, and J. L. N. Wood. 2017. One Health, emerging infectious diseases and wildlife: two decades of progress? Philosophical Transactions B 372: 20160167.
- Dardis, C. 2015. LogisticDx: diagnostic tests for models with a binomial response. R package version 0.2.
- Davies, G., M. J. Stear, M. Benothman, O. Abuagob, A. Kerr, S. Mitchell, and S. C. Bishop. 2006. Quantitative trait loci associated with parasitic infection in Scottish blackface sheep. Heredity 96:252-258.
- DeCesare, N. J., and D. H. Pletscher. 2006. Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. Journal of Mammalogy 87:531-538.
- DeForge, J. R. and J. E. Scott. 1982. Ecological investigations into high lamb mortality. Desert Bighorn Council Transactions 26:65-76.
- Dekelaita, D. J., C. W. Epps, K. M. Stewart, J. S. Sedinger, J. G. Powers, B. J. Gonzales, R. K. Abella-Vu, N. W. Darby, and D. L. Hughson. *In review*. Survival of adult female bighorn sheep following a pneumonia epizootic. Journal of Wildlife Management.
- Deming, O. V. 1952. Tooth development of the Nelson bighorn sheep. California Fish and Game 38:523-529.
- Dhabhar, F. S. and B. S. McEwen. 1997. Acute stress enhances while chronic stress suppresses cell-mediated immunity *in vivo*: a potential role for leukocyte trafficking. Brain, Behavior, and Immunity 11:286-306.
- Diefenbach, D. R. 2009. Estimating avian population size using Bowden's estimator. The Auk 126:211-217.
- Digonnet, M. 2013. Hiking the Mojave Desert: natural and cultural heritage of Mojave National Preserve. Wilderness Press, Palo Alto, California, USA.
- Douglas, C. L. 2001. Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. Wildlife Society Bulletin 29:297-305.
- Douglas, C. L. and D. M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. Journal of Wildlife Management 50:153-156.
- Downs, C. J., B. V. Boan, T. D. Lohuis, and K. M. Stewart. 2018. Investigating relationships between reproduction, immune defenses, and cortisol in Dall sheep. Frontiers in Immunology 9:105. doi: 10.3389/fimmu.2018.00105.
- Dunbar, M. R. 1992. Theoretical concepts of disease versus nutrition as primary factors in population regulation of wild sheep. Biennial Symposium of the Northern Wild Sheep and Goat Council 8:174-192.

- Epps, C. W., D. Dekelaita, and B. Dugovich. 2016. Updates on respiratory disease affecting bighorn sheep in and near Mojave National Preserve. Mojave National Preserve, Sweeney Granite Mountains Desert Research Center Science Newsletter. https://www.nps.gov/moja/learn/science-newsletter.htm. Accessed 20 November 2018.
- Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714-724.
- Epps, C. W., P. J. Palsboll, J. D. Wehausen, G. K. Roderick, and D. R. McCullough. 2006. Elevation and connectivity define genetic refugia for mountain sheep as climate warms. Molecular Ecology 15:4295-4302.
- Epps, C. W., P. J. Palsboll, J. D. Wehausen, G. K. Roderick, R. R. Ramey II, and D. R. McCullough. 2005. Highways block gene flow and cause rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8:1029-1038.
- Epps, C. W., R. S. Crowhurst, B. S. Nickerson. 2018. Assessing change in functional connectivity in desert bighorn sheep metapopulation after two generations. Molecular Ecology 27:2334-2346.
- ESRI. 2016. ArcGIS Desktop: Release 10.5. Environmental Systems Research Institute, Inc. Redlands, California.
- Ewald, P. W. 2004. Evolution of virulence. Infectious disease clinics of North America 18:1-15.
- Ferrari, S. L. P. 2011. Diagnostic tools in beta regression with varying dispersion. Statistica Neerlandica 65:337–351.
- Ferrari, S. and F. Cribari-Neto. 2004. Beta regression for modelling rates and proportions. Journal of Applied Statistics 31:799-815.
- Festa-Bianchet, M. 1991. The social system of bighorn sheep: grouping patterns, kinship, and female dominance rank. Animal Behavior 42:71-82.
- Festa-Bianchet, M., J. T. Jorgenson, and W. D. Wishart. 1994. Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not females. Behavioral Ecology 5:21-27.
- Formica, V. A., M. E. Augat, M. E. Barnard, R. E. Butterfield, C. W. Wood, and E. D. Brodie III. 2010. Using home range estimates to construct social networks for species with indirect behavioral interactions. Behavioral Ecology and Sociobiology 64:1199-1208.
- Fox, K. A., N. M. Rouse, K. P. Huyvaert, K. A. Griffin, H. J. Killion, J. Jennings-Gaines, W. H. Edwards, S. L. Quackenbush, and M. W. Miller. 2015. Bighorn sheep (*Ovis canadensis*) sinus tumors are associated with coinfections by potentially pathogenic bacteria in the upper respiratory tract. Journal of Wildlife Diseases 51:19-27.
- Fryxell, J. M., M. Hazella, L. Börger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. PNAS doi: 10.1073_pnas.0801737105.
- Funk, C., P. Peterson, M. Landsfeld, D. Pedreros, J. Verdin, S. Shukla, G. Husak, J. Rowland, L. Harrison, A. Hoell, and J. Michaelsen. 2015. The climate hazards

infrared precipitation with stations – a new environmental record for monitoring extremes. Scientific Data 2:150066. doi 10.1038/sdata.2015.66.

- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.
- Galloway, A, W. H. Birkby, A. M. Jones, T. E. Henry, and B. O. Parks. 1989. Decay rates of human remains in an arid environment. Journal of Forensic Sciences 34:607-616.
- Geist. V. 1966. Validity of horn segment counts in aging bighorn sheep. Journal of Wildlife Management 30:634-635.
- Geist, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, Illinois, USA.
- Goudet, J. 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. Journal of Heredity 86:485-486.
- Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29-36.
- Hanski, I. 1998. Metapopulation dynamics. Nature 396:41-49. Hansson, B. and L. Westerberg. 2002. On the correlation between heterozygosity and fitness in natural populations. Molecular Ecology 11:2467-2474.
- Hansson, B. and L. Westerberg. 2002. On the correlation between heterozygosity and fitness in natural populations. Molecular Ecology 11:2467-2474.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carryover effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4-18.
- Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2001. A brief introduction to mixed effects modelling a multi-model inference in ecology. PeerJ 6:e4794.
- Hass, C. C. 1989. Bighorn lamb mortality: predation, inbreeding, and population effects. Canadian Journal of Zoology 67:699-705.
- Hass, C. C. 1991. Social status in female bighorn sheep (*Ovis canadensis*): expression, development and reproductive correlates. Journal of Zoology (London) 225:509-523.
- Hass, C. C. 1997. Seasonality of births in bighorn sheep. Journal of Mammalogy 78:1251-1260.
- Hebbali, A. 2020. olsrr: Tools for Fitting OLS Regression Models. R package version 0.5.3.
- Heffelfinger, J. 1997. Age criteria for Arizona game species. Arizona Game and Fish Department, Special Report No. 19. Arizona Game and Fish Department, Phoenix, Arizona, USA.
- Heffelfinger, L. J., K. M. Stewart, A. P. Bush, J. S. Sedinger, N. W. Darby, and V. C. Bleich. 2017. Timing of precipitation in an arid environment: effects on population performance of a large herbivore. Ecology and Evolution 2017:1-13. doi 10.1002/ece3.3718.

- Hefnawy, A. E. G. and J. L. Tórtora-Pérez. 2010. The importance of selenium and the effects of its deficiency in animal health. Small Ruminant Research 89:185-192.
- Hereford, R., R. H. Webb, and C. I. Longpre. 2004. Precipitation history of the Mojave Desert Region, 1893-2001. USGS Fact Sheet 117-03. https://doi.org/10.3133/fs11703>. Accessed 20 November 2018.
- Hess, G. 1996. Disease in metapopulation models: implication for conservation. Ecology 77:1617-1632.
- Hnilicka, P. A., J. Mionczynski, B. J. Mincher, J. States, M. Hinschberger, S. Oberlie, C. Thompson, B. Yates, and D. D. Siemer. 2002. Bighorn sheep lamb survival, trace minerals, rainfall, and pollution: are there any connections? Biennial Symposium of the Northern Wild Sheep and Goat Council 13:69-94.
- Holmes, B. 2006. Earth without humans. New Scientist 192:37-41.
- Huntington, J. L., K. C. Hegewisch, B. Daudert, C. G. Morton, J. T. Abatzoglou, D. J. McEvoy, and T. Erickson. 2017. Climate Engine: Cloud computing of climate and remote sensing data for advanced natural resource monitoring and process understanding. Bulletin of the American Meteorological Society 98:2397-2410.
- Hurley, M. A., M. Hebblewhite, J.-M. Gaillard, S. Dray, K. A. Taylor, W. K. Smith, P. Zager, and C. Bonenfant. 2014. Functional analysis of Normalized Difference Vegetation Index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. Philosophical Transactions of the Royal Society 369:20130196. doi 10.1098/rstb.2013.0196.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Ironside, K. E., D. J. Mattson, T. R. Arundel, and J. R. Hansen. 2017. Is GPS telemetry location screening beneficial? Wildlife Biology 2017. doi 10.2981/wlb.00229.
- Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. Ecology 78:1019-1032.
- Kassambara, A. 2020. 'ggplot2' Based Publication Ready Plots. R package version 0.2.5.
- Keeling, M. J., and K. T. D. Eames. 2005. Networks and epidemic models. Journal of the Royal Society Interface 2:295-307.
- Kock, M. D., R. K. Clark, C. E. Franti, D. A. Jessup, and J. D. Wehausen. 1987. Effects of capture on biological parameters in free-ranging bighorn sheep (*Ovis canadensis*): evaluation of normal, stressed and mortality outcomes and documentation of postcapture survival. Journal of Wildlife Diseases 23:652-662.
- Krausman, P. R., A. V. Sandoval, and R. C. Etchberger. 1999. Natural history of desert bighorn sheep. Pages 139-191 in R. Valdez and P. R. Krausman, editors. Mountain Sheep of North America. University of Arizona Press, Tucson, Arizona, USA.
- Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71-73.

- Krebs, C. J. 1999. Ecological Methodology. Second edition. Addison-Wesley Education Publishers, Inc., Menlo Park, California, USA.
- Lande, R. 1998. Anthropogenic, ecological, and genetic factors in extinction and conservation. Population Ecology 40:259-269.
- Lenarz, M. S. 1979. Social structure and reproductive strategy in desert bighorn sheep (*Ovis canadensis mexicana*). Journal of Mammalogy 60:671-678.
- Lloyd-Smith, J. O., P. C. Cross, C. J. Briggs, M. Daugherty, W. M. Getz, J. Latto, M. S. Sanchez, A. B. Smith, and A. Swei. 2005. Should we expect population thresholds for wildlife disease. Trends in Ecology and Evolution 20:511-519.
- Lochmiller, R. L. and C. Deerenberg. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? Oikos 88:87-98.
- Luikart, G., K. Pilgrim, J. Visty, V. O. Ezenwa, and M. K. Schwartz. 2008. Candidate gene microsatellite variation is associated with parasitism in wild bighorn sheep. Biology Letters 4:228-231.
- Mangiafico, S. 2020. rcompanion: Functions to Extension Education Program Evaluation. R package version 2.3.25.
- Manlove, K., E. F. Cassirer, P. C. Cross, R. K. Plowright, and P. J. Hudson. 2014. Costs and benefits of group living with disease: a case study of pneumonia in bighorn lambs (*Ovis canadensis*). Proceedings of the Royal Society 281:20142331. doi 10.1098/rspb.2014.2331.
- Manlove, K., E. F. Cassirer, P. C. Cross, R. K. Plowright, and P. J. Hudson. 2016. Disease introduction is associated with a phase transition in bighorn sheep demographics. Ecology 97:2593-2602.
- Martin, L. B. 2009. Stress and immunity in wild vertebrates: timing is everything. General and Comparative Endocrinology 163:70-76.
- Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88-90.
- Mazerolle, M. J. 2019. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-2.
- McClintock, B. T. and G. C. White. 2007. Bighorn sheep abundance following a suspected pneumonia epidemic in Rocky Mountain National Park. Journal of Wildlife Management 71:183-189.
- McClintock, B. T., G. C. White, and K. P. Burnham. 2006. A robust design markresight abundance estimator. Journal of Agricultural, Biological, and Environmental Statistics 11:231-248.
- McCoy, J. C., S. S. Ditchkoff, J. B. Raglin, B. A. Collier, and C. Ruth. 2013. Factors influencing survival of white-tailed deer fawns in coastal South Carolina. Journal of Fish and Wildlife Management 14:280-289.
- McCullough, D. R. 1979. The George Reserve Deer Herd: Population Ecology of a K-Selected Species. University of Michigan Press, Ann Arbor, USA.
- McIlroy, S. G., E. A. Goodall, R. M. McCracken, and D. A. Stewart. 1989. Rain and windchill as factors in the occurrence of pneumonia in sheep. The Veterinary Record 125:79-82.
- McKee, C. J., K. M. Stewart, J. S. Sedinger, A. P. Bush, N. W. Darby, D. L. Hughson, and V. C. Bleich. 2015. Spatial distributions and resource selection

by mule deer in an arid environment: responses to provision of water. Journal of Arid Environments 2015:76-84.

- Miller, D. S., E. Hoberg, G. Weiser, K. Aune, M. Atkinson, and C. Kimberling. 2012. A review of hypothesized determinants associated with bighorn sheep (*Ovis canadensis*) die-offs. Veterinary Medicine International 2012:1-19.
- Miller, D. S., G. C. Weiser, A. C. S. Ward, M. L. Drew, P. L. Chapman. 2011. Domestic sheep (*Ovis aries*) *Pasteurellaceae* isolates from diagnostic submissions to the Caine Veterinary Teaching Center (1990–2004). Veterinary Microbiology 150:284-288.
- Monello, R. J., D. L. Murray, and E. F. Cassirer. 2001. Ecological correlates of pneumonia epizootics in bighorn sheep herds. Canadian Journal of Zoology 79:1423-1432.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Connor, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1-56.
- Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movements models as mixtures of random walks. Ecology 85: 2436-2445.
- National Geographic Society. 2008. Mojave National Preserve [map]. National Geographic Maps, Evergreen, Colorado, USA.
- National Park Service [NPS]. 2016. Mojave weather. https://www.nps.gov/moja/planyourvisit/weather.htm. Accessed 9 Apr 2018.
- Onderka, D. K., and W. D. Wisehart. 1988. Experimental contact transmission of *Pasteurella haemolytica* from clinically normal domestic sheep causing pneumonia in Rocky Mountain bighorn sheep. Journal of Wildlife Diseases 24:663-667.
- Onozuka, D., M. Hashizume, and A. Hagihara. 2009. Impact of weather factors on *Mycoplasma pneumoniae* pneumonia. Thorax 64:507-511.
- Pelletier, F., J. Mainguy, and S. D. Cote. 2009. Rut-induced hypophagia in male bighorn sheep and mountain goats: foraging under time budget constraints. Ethology 115:141-151.
- Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15-27.
- Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology 21:869-879.
- Plowright, R. K., K. R. Manlove, T. E. Besser, D. J. Paez, K. R. Andrews, P. E. Matthews, L. P. Waits, P. J. Hudson, and E. F. Cassirer. 2017. Age-specific infectious period shapes dynamics of pneumonia in bighorn sheep. Ecology Letters 20:1325-1336.
- Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology 245:271-278.

- Preisler, H. K., N. E. Grulke, Z. Heath, and S. L. Smith. 2017. Analysis and out-year forecast of beetle, borer, and drought-induced tree mortality in California. Forest Ecology and Management 399:166-178.
- Pruett, S. B. 2003. Stress and the immune system. Pathophysiology 9:133-153.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Romero, L. M. 2004. Physiological stress in ecology: lessons from biomedical research. Trends in Ecology and Evolution 19:249-255.
- Rubin, E. S., W. M. Boyce, M. J. Jorgenson, S. G. Torres, C. L. Hayes, C. S. O'Brien, and D. A. Jessup. 1998. Distribution and abundance of bighorn sheep in the Peninsular Ranges, California. Wildlife Society Bulletin 26:539-551.
- Rubin, E. S., W. M. Boyce, and V. C. Bleich. 2000. Reproductive strategies of desert bighorn sheep. Journal of Mammalogy 81:769-786.
- Rudnick, D. A., S. J. Ryan, P. Beier, S. A. Cushman, F. Dieffenbach, C. W. Epps, L.
 R. Gerber, J. Hartter, J. S. Jenness, J. Kintsch, A. M. Merenlender, R. M.
 Perkl, D. V. Preziosi, and S. C. Trombulak. 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology, Ecological Society of America. Report 16.
- Ryan, S. J., P. C. Cross, J. Winnie, C. Hay, J. Bowers, and W. M. Getz. 2012. The utility of normalized difference vegetation index for predicting African buffalo forage quality. Journal of Wildlife Management 76:1499-1508.
- Ryder, T. J., E. S. Williams, K. W. Mills, K. H. Bowles, and E. T. Thorne. 1992. Effect of pneumonia on population size and lamb recruitment in Whiskey Mountain bighorn sheep. Biennial Symposium of the Northern Wild Sheep and Goat Council 8:136-146.
- Schwartz, A. O., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelson*. Biological Conservation 37:179-190.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.
- Shuman, R. M., M. J. Cherry, T. N. Simoneaux, E. A. Dutoit, J. C. Kilgo, M. J. Chamberlain, and K. V. Miller. 2017. Survival of white-tailed deer neonates in Louisiana. Journal of Wildlife Management 81:834-845.
- Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235-253.
- Silverman, B. W. 1986. Density estimation for statistics and data analysis. Monographs on Statistics and Applied Probability. Chapman and Hall, London, England.
- Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. Conservation Biology 1:63-71.
- Singer, F. J., L. C. Zeigenfuss, and L. Spicer. 2001. Role of patch size, disease, and movement in rapid extinction of bighorn sheep. Conservation Biology 15:1347-1354.

- Smith, J. B., J. A. Jenks, T. W. Grovenburg, and R. W. Klaver. 2014. Disease and predation: sorting out causes of a bighorn sheep (*Ovis canadensis*) decline. PLOS ONE 9: e88271.
- Spears, J. W. 1994. Minerals in forages. Pages 281-317 in G. C. Fahey, Jr., editor. Forage Quality, Evaluation, and Utilization. American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, Madison, Wisconsin, USA.
- Swift, P. K., J. D. Wehausen, H. B. Ernest, R. S. Singer, A. M. Pauli, H. Kinde, T. E. Rocke, and V. C. Bleich. 2000. Desert bighorn sheep mortality due to presumptive type c botulism in California. Journal of Wildlife Diseases 36:184-189.
- Symonds, M. R. E. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13-21.
- Thompson, R. W. and J. C. Turner. 1982. Temporal geographic variation in the lambing season of bighorn sheep. Canadian Journal of Zoology 60:1781-1793.
- Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keisler, and N. Dasgupta. 2008. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. Journal of Wildlife Management 74:974-986.
- Tomassini, L., B. Gonzales, G. C. Weiser, and W. Sischo. 2009. An ecological study comparing *Pasteurella trehalosi* and *Mannheimia haemolytica* between Sierra Nevada bighorn sheep, White Mountain bighorn sheep, and domestic sheep. Journal of Wildlife Diseases 45:930-940.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, USA.
- Ullrey, D. E. 1993. Nutrition and predisposition to infectious disease. Journal of Zoo and Wildlife Medicine 24:304-314.
- United States Geological Survey [USGS]. 2018. Mineral resources online spatial data. https://mrdata.usgs.gov/. Accessed 9 Apr 2018.
- Valdez, R. and P. R. Krausman. 1999. Description, distribution and abundance of mountain sheep. Pages 1-22 in R. Valdez and P. R. Krausman, editors. Mountain Sheep of North America. University of Arizona Press, Tucson, USA.
- Villepique, J. T., V. C. Bleich, B. M. Pierce, T. R. Stephenson, R. A. Botta, and R. T. Bowyer. 2008. Evaluating GPS collar error: a critical evaluation of Televilt POSREC-ScienceTM collars and a method for screening location data. California Fish and Game 94:155-168.
- Waites, K. B., and D. F. Talkington. 2004. *Mycoplasma pneumoniae* and its role as a human pathogen. Clinical Microbiology Reviews 17:697-728.
- Washington Animal Disease Diagnostic Laboratory [WADDL]. 2017. Washington State University. https://waddl.vetmed.wsu.edu/animal-disease-faq/mycoplasma-ovipneumoniae-diagnostics-in-domestic-and-wild-sheep-and-goats. Accessed 17 Oct 2018.

- Washington Animal Disease Diagnostic Laboratory [WADDL]. 2020. Washington State University. https://waddl.vetmed.wsu.edu/search-tests/Panels/Test-Details?id=455>. Accessed 22 May 2020.
- Wehausen, J. D. 2005. Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. Pages 37-50 in J. Goerrissen and J. M. Andre, editors. Sweeney Granite Mountains Desert Research Center 1978-2003: A Quarter Century of Research and Teaching. University of California Natural Reserve Program, Riverside, USA.
- Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California sheep population. Journal of Wildlife Management 51:86-98.
- Wehausen. J. D., S. T. Kelley, and R. R. Ramey II. 2011. Domestic sheep, bighorn sheep, and respiratory disease: a review of the experimental evidence. California Fish and Game 97:7-24.
- Western Association of Fish and Wildlife Agencies (WAFWA). 2010. Summary on 9 bighorn sheep die-offs in 5 western states in Winter 2009-2010. www.wafwa.org>. Accessed 26 March 2016.
- White, G. C. 1996. Program NOREMARK Software Reference Manual. https://sites.warnercnr.colostate.edu/gwhite/wp-content/uploads/sites/73/2017/05/noremark.pdf>. Accessed 21 November 2018.
- White, G. C. and E. G. Cooch. 2017. Population abundance estimation with heterogeneous encounter probabilities using numerical integration. Journal of Wildlife Management 81:322-336.
- White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-139.
- Wickham, H., W. Chang, L. Henry, T. L. Pedersen, K. Takahashi, C. Wilke, K. Woo, H. Yutani, and D. Dunnington. 2020. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. R package version 3.3.0.
- Wolfe, L. L., B. Diamond, T. R. Spraker, M. A. Sirochman, D. P. Walsh, C. M. Machin, D. J. Bade, and M. W. Miller. 2010. A bighorn sheep die-off in southern Colorado involving a *Pasteurellaceae* strain that may have originated from synoptic cattle. Journal of Wildlife Diseases 46:1262-1268.
- Wood, A. K., R. E. Short, A.-E. Darling, G. L. Dusek, R. G. Sasser, and C. A. Ruder. 1986. Serum assays for detecting pregnancy in mule and white-tailed deer. Journal of Wildlife Management 50:684-687.
- Wood, M. E., K. A. Fox, J. Jennings-Gaines, H. J. Killion, S. Amundson, M. W. Miller, and W. H. Edwards. 2017. How respiratory pathogens contribute to lamb mortality in a poorly performing bighorn sheep (*Ovis canadensis*) herd. Journal of Wildlife Diseases 53:126-130.
- Zeileis, A., F. Cribari-Neto, B. Gruen, and I. Kosmidis. 2019. betareg: Beta Regression. R package version 3.1-2.
APPENDICES

APPENDIX A: A POSTERIORI MODELING

We conducted 2 separate *a posteriori* analyses to evaluate effects of age (Table A.1) and exposure to *M. ovi* (i.e., cELISA status; Table A.2) on survival. We decided to test these covariates because we found a strong negative effect associated with PCR-positive status on survival that we wanted to explore further, and older age has been linked to higher rates of *M. ovi* infection among adult bighorn (Plowright et al. 2017). Age and exposure status were included as individual covariates and coded as dummy variables (Cooch and White 2017). Females estimated to be 2-9 years old received a covariate value of 0, and females > 9 years old received a value of 1. Females that became older than 9 years during the study, based on minimum age estimates, were moved from the former cohort to the latter upon aging out. Individuals received covariate values of 1 if they were cELISA-positive at time of capture (i.e., *M. ovi* antibodies were detected), values of 0 if they were negative (i.e., antibodies were not detected), and a mean value of 0.5 if a test result was indeterminate or otherwise unknown. Models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc; Akaike 1973, Hurvich and Tsai 1989).

Table A.1. *A posteriori* results from known-fate modeling in Program MARK of monthly adult female bighorn survival from 2013-2017 across populations occupying 9 different mountain ranges, following a pneumonia outbreak in the Mojave Desert, California, USA. Age was modeled as a binary variable whereby we tested effect differences for females estimated to be 2-9 years old and > 9 years old. PCR status was based on results from PCR (polymerase chain reaction) testing for *Mycoplasma ovipneumoniae* infection using nasal swabs collected from females at time of capture. Adult female population abundance was derived from remote camera data we collected at point-source water features in 2016 in each mountain range. We tested effects of winter precipitation totals, and mean summer and autumn NDVI (Normalized Difference Vegetation Index) in each mountain range on survival in winter months only. We evaluated models using Akaike's Information Criterion adjusted for small sample sizes (AICc).

Model No.	Model Structure	K^{a}	ΔAICc	wi ^b	Deviance
1	Summer NDVI lag + Winter precipitation + PCR status + Abundance	5	0.00	0.18	322.88
2	Summer NDVI lag + Winter precipitation + PCR status + Abundance + Age	6	0.37	0.15	321.24
3	Autumn NDVI lag + Winter precipitation + PCR status + Abundance	5	1.38	0.09	324.25
4	Autumn NDVI lag + PCR status + Abundance	4	1.46	0.09	326.35
5	Autumn NDVI lag + Winter precipitation + PCR status + Abundance + Age	6	1.73	0.08	322.59
6	Summer NDVI lag + PCR status + Abundance	4	1.84	0.07	326.72
7	Autumn NDVI lag + PCR status + Abundance + Age	5	1.90	0.07	324.77
8	Summer NDVI lag + PCR status + Abundance + Age	5	2.48	0.05	325.35
9	Summer NDVI lag + Winter precipitation + PCR status + Age	5	3.15	0.04	326.02
10	Summer NDVI lag + Winter precipitation + PCR status	4	3.38	0.03	328.27
11	Summer NDVI lag + PCR status	3	4.87	0.02	331.75
12	Autumn NDVI lag + Winter precipitation + PCR status + Age	5	4.89	0.02	327.77
13	Summer NDVI lag + PCR status + Age	4	4.91	0.02	329.80
14	Autumn NDVI lag + PCR status + Age	4	5.14	0.01	330.03
15	Autumn NDVI lag + Winter precipitation + PCR status	4	5.18	0.01	330.06
16	Autumn NDVI lag + PCR status	3	5.33	0.01	332.21
17	Winter precipitation + PCR status + Abundance	4	6.07	0.01	330.95
18	Winter precipitation + PCR status + Abundance + Age	5	6.78	0.01	329.65
19	Summer NDVI lag + Winter precipitation + Abundance	4	7.68	0.00	332.56
20	Summer NDVI lag + Abundance	3	7.77	0.00	334.66
21	Summer NDVI lag + Winter precipitation + Abundance + Age	5	7.91	0.00	330.79
22	Autumn NDVI lag + Abundance	3	8.13	0.00	335.02
23	Summer NDVI lag + Abundance + Age	4	8.25	0.00	333.13
24	Autumn NDVI lag + Abundance + Age	4	8.41	0.00	333.29
25	Autumn NDVI lag + Winter precipitation + Abundance	4	9.05	0.00	333.93
26	Autumn NDVI lag + Winter precipitation + Abundance + Age	5	9.24	0.00	332.11
27	Summer NDVI lag + Winter precipitation + Age	4	9.58	0.00	334.46
28	Summer NDVI lag + Age	3	9.69	0.00	336.58
29	Summer NDVI lag	2	9.76	0.00	338.65

30	Summer NDVI lag + Winter precipitation	3	9.90	0.00	336.78
31	Autumn NDVI lag + Age	3	10.40	0.00	337.29
32	Autumn NDVI lag	2	10.70	0.00	339.59
33	PCR status + Abundance	3	11.19	0.00	338.08
34	Autumn NDVI lag + Winter precipitation + Age	4	11.21	0.00	336.09
35	Autumn NDVI lag + Winter precipitation	3	11.61	0.00	338.49
36	PCR status + Abundance + Age	4	12.10	0.00	336.98
37	Winter precipitation + PCR status + Age	4	12.47	0.00	337.35
38	Winter precipitation + Abundance	3	12.67	0.00	339.55
39	Winter precipitation + PCR status	3	12.69	0.00	339.58
40	Winter precipitation + Abundance + Age	4	13.19	0.00	338.07
41	Range	9	14.90	0.00	329.73
42	PCR status	2	15.24	0.00	344.13
43	PCR status + Age	3	15.33	0.00	342.22
44	Abundance	2	15.80	0.00	344.69
45	Abundance + Age	3	16.53	0.00	343.42
46	Winter precipitation + Age	3	17.47	0.00	344.36
47	Winter precipitation	2	17.80	0.00	346.69
48	Age	2	19.01	0.00	347.90
49	Null	1	19.07	0.00	349.96

^aNumber of model parameters. ^bAkaike model weight.

Table A.2. *A posteriori* results from known-fate modeling in Program MARK of monthly adult female bighorn survival from 2013-2017 across populations occupying 9 different mountain ranges, following a pneumonia outbreak in the Mojave Desert, California, USA. PCR status was based on results from PCR (polymerase chain reaction) testing for *Mycoplasma ovipneumoniae* infection using nasal swabs collected from females at time of capture; ELISA status was based on results from cELISA (competitive enzyme-linked immunosorbent assay) testing for *Mycoplasma ovipneumoniae* antibodies in blood serum samples. Adult female population abundance was derived from remote camera data we collected at point-source water features in 2016 in each mountain range. We tested effects of winter precipitation totals, and mean summer and autumn NDVI (Normalized Difference Vegetation Index) in each mountain range on survival in winter months only. We evaluated models using Akaike's Information Criterion adjusted for small sample sizes (AICc).

Model No.	Model Structure	Ka	ΔAICc	w_i^b	Deviance
1	Summer NDVI lag + Winter precipitation + PCR status + Abundance	5	0.00	0.33	322.88
2	Autumn NDVI lag + Winter precipitation + PCR status + Abundance	5	1.38	0.17	324.25
3	Autumn NDVI lag + PCR status + Abundance	4	1.46	0.16	326.35
4	Summer NDVI lag + PCR status + Abundance	4	1.84	0.13	326.72
5	Summer NDVI lag + Winter precipitation + PCR status	4	3.38	0.06	328.27
6	Summer NDVI lag + PCR status	3	4.87	0.03	331.75
7	Autumn NDVI lag + Winter precipitation + PCR status	4	5.18	0.02	330.06
8	Autumn NDVI lag + PCR status	3	5.33	0.02	332.21
9	Winter precipitation + PCR status + Abundance	4	6.07	0.02	330.95
10	Summer NDVI lag + Winter precipitation + Abundance	4	7.68	0.01	332.56
11	Summer NDVI lag + Abundance	3	7.77	0.01	334.66
12	Summer NDVI lag + Winter precipitation + ELISA status + Abundance	5	8.00	0.01	330.88
13	Autumn NDVI lag + Abundance	3	8.13	0.01	335.02
14	Summer NDVI lag + ELISA status + Abundance	4	8.76	0.00	333.64
15	Autumn NDVI lag + ELISA status + Abundance	4	8.84	0.00	333.72
16	Range	6	8.87	0.00	329.73
17	Autumn NDVI lag + Winter precipitation + Abundance	4	9.05	0.00	333.93
18	Autumn NDVI lag + Winter precipitation + ELISA status + Abundance	5	9.33	0.00	332.21
19	Summer NDVI lag	2	9.76	0.00	338.65
20	Summer NDVI lag + Winter precipitation + ELISA status	4	9.80	0.00	334.68
21	Summer NDVI lag + Winter precipitation	3	9.90	0.00	336.78
22	Summer NDVI lag + ELISA status	3	10.36	0.00	337.25
23	Autumn NDVI lag	2	10.70	0.00	339.59
24	Autumn NDVI lag + ELISA status	3	11.07	0.00	337.96
25	PCR status + Abundance	3	11.19	0.00	338.08
26	Autumn NDVI lag + Winter precipitation + ELISA status	4	11.48	0.00	336.36
27	Autumn NDVI lag + Winter precipitation	3	11.61	0.00	338.49
28	Winter precipitation + Abundance	3	12.67	0.00	339.55
29	Winter precipitation + PCR status	3	12.69	0.00	339.58

30	Winter precipitation + ELISA status + Abundance	4	13.12	0.00	338.00
31	PCR status	2	15.24	0.00	344.13
32	Abundance	2	15.80	0.00	344.69
33	ELISA status + Abundance	3	17.11	0.00	343.99
34	Winter precipitation + ELISA status	3	17.41	0.00	344.30
35	Winter precipitation	2	17.80	0.00	346.69
36	Null	1	19.07	0.00	349.96
37	ELISA status	2	19.69	0.00	348.58
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^aNumber of model parameters.

^bAkaike model weight.

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Proceedings of the 2nd International Symposium on Information Theory Akademiai Kiado, Budapest. (Reproduced in pages 610-624 *in* S. Kotzand and L. S. Johnson, editors. 1992. Breakthroughs in Statistics, Volume One, Foundations and Basic Theory. Springer-Verlag, New York, New York, USA).
- Cooch, E. G., and G. C. White, editors. 2017. Program MARK: a gentle introduction. Seventeenth edition. Colorado State University, Fort Collins, Colorado, USA.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Plowright, R. K., K. R. Manlove, T. E. Besser, D. J. Paez, K. R. Andrews, P. E. Matthews, L. P. Waits, P. J. Hudson, and E. F. Cassirer. 2017. Age-specific infectious period shapes dynamics of pneumonia in bighorn sheep. Ecology Letters 20:1325-1336.

APPENDIX B: PEARSON CORRELATION TEST FOR LAMB SURVIVAL INDICES

Lamb-ewe ratios have been commonly used to gauge lamb survival at the population level (Picton 1984, Douglas and Leslie 1986, Wehausen et al. 1987, Douglas 2001). As such, we used mean late-season (15 August to 30 September) lamb-ewe ratios as an index for lamb survival through weaning. Lambs usually begin weaning at 4-5 months of age (Festa-Bianchet et al. 1994) and are typically in the weaning phase by late August/early September in the Mojave Desert. To validate camera-derived late-season ratios as a proxy for survival to weaning, we tracked survival of lambs with collared adult females up to 5 months (i.e., approximately 18-20 weeks) using camera and field observations to develop a secondary metric for comparison. We calculated proportions of lambs surviving with collared females and used the Pearson correlation test to evaluate how well mean late-season lamb-ewe ratios corresponded with these proportions across all populations and years for which we had both types of data (Table 2.1). There was a strong correlation between the metrics across populations and years (r = 0.92, $p = 4.4 \times 10^{-6}$). We regressed proportions on ratios using the ggpubr package in Program R (Kassambara 2020; R Development Core Team 2019).



Figure B.1. Scatterplot and regression line showing the relationship between the proportion of lambs surviving to 5 months (Proportion) and corresponding mean lateseason (15 August to 30 September) lamb-ewe ratios (Ratio) from 7 populations in the Mojave Desert, California, USA, monitored between 2014-2016 following a pneumonia outbreak. The gray area represents the 95% confidence interval and *R* is the Pearson correlation coefficient.

- Douglas, C. L. 2001. Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. Wildlife Society Bulletin 29:297-305.
- Douglas, C. L. and D. M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. Journal of Wildlife Management 50:153-156.
- Festa-Bianchet, M., J. T. Jorgenson, and W. D. Wishart. 1994. Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not females. Behavioral Ecology 5:21-27.
- Kassambara, A. 2020. 'ggplot2' Based Publication Ready Plots. R package version 0.2.5.
- Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology 21:869-879.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California sheep population. Journal of Wildlife Management 51:86-98.

APPENDIX C: PEARSON CORRELATION TESTS FOR A PRIORI COVARIATES

We used the Pearson correlation coefficient to assess pairwise relatedness of covariates in models estimating lamb survival in 7 populations from 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak. Models included the following covariates: October-April precipitation, May-August precipitation, and population abundance. We used the ggpubr package in Program R (Kassambara 2020; R Development Core Team 2019) to produce regression plots and correlation estimates presented below.



Figure C.1. Scatterplot and regression line showing the relationship between October-April precipitation (Precip_OctApr) and May-August precipitation (Precip_MayAug) in 7 mountain ranges from 2014-2016 in the Mojave Desert, California, USA. The gray area represents the 95% confidence interval and *R* is the Pearson correlation coefficient.



Figure C.2. Scatterplot and regression line showing the relationship between October-April precipitation (Precip_OctApr) and population abundance (Population) in 7 mountain ranges from 2014-2016 in the Mojave Desert, California, USA. The gray area represents the 95% confidence interval and *R* is the Pearson correlation coefficient.



Figure C.3. Scatterplot and regression line showing the relationship between May-August precipitation (Precip_MayAug) and population abundance (Population) in 7 mountain ranges from 2014-2016 in the Mojave Desert, California, USA. The gray area represents the 95% confidence interval and *R* is the Pearson correlation coefficient.

- Kassambara, A. 2020. 'ggplot2' Based Publication Ready Plots. R package version 0.2.5.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

APPENDIX D: EVALUATING THE EFFECT OF BL4 ALLELIC RICHNESS

In a *post hoc* analysis, we evaluated the effect of a genetic covariate, allelic richness at locus BL4, that could potentially influence immune function. Locus BL4 is close to the interferon gamma gene associated with ovine resistance to strongyle infection (Coltman et al. 2000) and was linked to immunoglobulin A activity among Scottish Blackface lambs in a study by Davies et al. (2006). We hypothesized that higher BL4 allelic richness within populations promotes lamb survival, given the association with this locus and immune activity in domestic lambs, and since heterozygosity is generally associated with higher fitness in wildlife populations (Hansson and Westerberg 2002). Allelic richness at locus BL4 was estimated using 11-50 samples per population collected during 2013-2015 as described in Epps et al. (2018). We used FSTAT (Goudet 1995) to estimate allelic richness and corrected for differences in sample sizes using the minimum sample size at that locus (n = 11).

We tested effects of BL4 richness, population abundance, and linear, quadratic, and pseudothreshold (i.e., natural log [LN]) forms of October-April and May-August precipitation on lamb survival using beta regression for proportions (Ferrari and Cribari-Neto 2004, Ferrari 2011) with a logit link function for the mean (μ) submodel and log link function for the precision (ϕ) submodel. We used the betareg package in Program R (Cribari-Neto and Zeileis 2010, Zeileis et al. 2019; R Development Core Team 2019) to fit our models and assumed constant dispersion for ϕ (i.e., we did not include regressors to model ϕ). Models were evaluated using Akaike's Information Criterion adjusted for small sample sizes (AICc; Akaike 1973, Hurvich and Tsai 1989) and the AICcmodavg package in Program R (Mazerolle 2019; R Development Core Team 2019). We used the Pearson correlation coefficient to assess pairwise relatedness between BL4 richness and alternate covariates prior to model fitting (Fig. D.1-D.3). We present the model set including linear and alternate functional forms of precipitation most strongly supported (Table D.1).

Our top model indicated that the quadratic form of October-April precipitation and the pseudothreshold form of May-August precipitation were the most important variables influencing lamb survival (Table D.1). The effect of BL4 richness was supported in the second highest ranking model. Parameter estimates for the second highest ranking model are presented in Table D.2. We found a negative effect associated with BL4 richness and lamb survival but we did not consider the apparent effect to be directly associated with connectivity since our study occurred over a short-term period and genes at this locus are likely under selective pressure as well.



Figure D.1. Scatterplot and regression line showing the relationship between October-April precipitation (Precip_OctApr) and BL4 allelic richness (BL4) in bighorn populations across 7 mountain ranges from 2014-2016 in the Mojave Desert, California, USA. The gray area represents the 95% confidence interval and *R* is the Pearson correlation coefficient.



Figure D.2. Scatterplot and regression line showing the relationship between May-August precipitation (Precip_MayAug) and BL4 allelic richness (BL4) in bighorn populations across 7 mountain ranges from 2014-2016 in the Mojave Desert, California, USA. The gray area represents the 95% confidence interval and *R* is the Pearson correlation coefficient.



Figure D.3. Scatterplot and regression line showing the relationship between population abundance (Population) and BL4 allelic richness (BL4) in bighorn populations across 7 mountain ranges from 2014-2016 in the Mojave Desert, California, USA. The gray area represents the 95% confidence interval and *R* is the Pearson correlation coefficient.

Table D.1. Results from beta regression modeling of lamb survival using late-season (15 August to 30 September) lamb-ewe ratios from 7 populations in 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak. We tested covariates for the mean parameter (μ) and assumed constant dispersion for the precision parameter (ϕ). We evaluated effects of precipitation in October-April and May-August on lamb survival with quadratic and pseudothreshold (i.e., natural log [LN]) functional forms respectively. We also tested effects of population-level allelic richness at genetic locus BL4 (linked to immune activity in domestic sheep) and population abundance of adult female bighorn. Lamb-ewe ratios and abundance estimates were derived from remote camera data collected at point-source water features, BL4 richness was estimated from fecal samples collected in 2013-2015, and precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS).

Model No.	Model Structure for μ	K ^a	ΔAICc	wi ^b	LL ^c
1	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip)	5	0.00	0.20	23.04
2	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip) + BL4 Richness	6	0.03	0.19	25.50
3	Oct-Apr Precip ² + Oct-Apr Precip + May-Aug Precip + BL4 Richness	6	0.37	0.16	25.33
4	Oct-Apr Precip ² + Oct-Apr Precip + May-Aug Precip	5	0.38	0.16	22.85
5	Oct-Apr Precip ² + Oct-Apr Precip	4	1.86	0.08	20.05
6	Oct-Apr Precip ² + Oct-Apr Precip + BL4 Richness	5	1.91	0.08	22.09
7	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip) + Abundance	6	4.49	0.02	23.27
8	Oct-Apr Precip ² + Oct-Apr Precip + May-Aug Precip + Abundance	6	4.91	0.02	23.06
9	Oct-Apr Precip	3	5.18	0.01	16.65
10	Oct-Apr Precip ² + Oct-Apr Precip + LN(May-Aug Precip) + Abundance + BL4 Richness	7	5.31	0.01	25.88
11	Oct-Apr Precip ² + Oct-Apr Precip + May-Aug Precip + Abundance + BL4 Richness	7	5.74	0.01	25.67
12	Oct-Apr Precip ² + Oct-Apr Precip + Abundance	5	5.83	0.01	20.13
13	Oct-Apr Precip + BL4 Richness	4	6.32	0.01	17.82
14	Oct-Apr Precip ² + Oct-Apr Precip + Abundance + BL4 Richness	6	6.73	0.01	22.15
15	Oct-Apr Precip + LN(May-Aug Precip)	4	7.71	0.00	17.13
16	Oct-Apr Precip + May-Aug Precip	4	8.26	0.00	16.85
17	Oct-Apr Precip + Abundance	4	8.30	0.00	16.83
18	LN(May-Aug Precip)	3	8.92	0.00	14.78
19	Oct-Apr Precip + LN(May-Aug Precip) + BL4 Richness	5	9.23	0.00	18.43
20	Oct-Apr Precip + May-Aug Precip + BL4 Richness	5	9.99	0.00	18.05
21	Oct-Apr Precip + Abundance + BL4 Richness	5	10.07	0.00	18.00
22	Null	2	10.17	0.00	12.66
23	May-Aug Precip	3	10.65	0.00	13.91
24	Oct-Apr Precip + LN(May-Aug Precip) + Abundance	5	11.69	0.00	17.19
25	Oct-Apr Precip + May-Aug Precip + Abundance	5	12.17	0.00	16.96

26	LN(May-Aug Precip) + Abundance	4	12.32	0.00	14.82
27	LN(May-Aug Precip) + BL4 Richness	4	12.37	0.00	14.80
28	Abundance	3	12.70	0.00	12.89
29	BL4 Richness	3	13.03	0.00	12.72
30	May-Aug Precip + Abundance	4	13.98	0.00	13.99
31	Oct-Apr Precip + LN(May-Aug Precip) + Abundance + BL4 Richness	6	14.08	0.00	18.47
32	May-Aug Precip + BL4 Richness	4	14.14	0.00	13.91
33	Oct-Apr Precip + May-Aug Precip + Abundance + BL4 Richness	6	14.73	0.00	18.15
34	Abundance + BL4 Richness	4	16.04	0.00	12.96
35	LN(May-Aug Precip) + Abundance + BL4 Richness	5	16.41	0.00	14.84
36	May-Aug Precip + Abundance + BL4 Richness	5	18.10	0.00	13.99
	^a Number of model permeters				

^aNumber of model parameters. ^bAkaike model weight. ^cLog-likelihood.

Table D.2. Parameter estimates from the second highest ranking beta regression model evaluating lamb survival using late-season (15 August to 30 September) lambewe ratios from 7 populations in 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak. We tested covariates for the mean parameter (μ) and assumed constant dispersion for the precision parameter (ϕ). We evaluated effects of precipitation in October-April and May-August on lamb survival, and included quadratic and pseudothreshold (i.e., natural log [LN]) functional forms respectively. We also tested effects of population-level allelic richness at genetic locus BL4 (linked to immune activity in domestic sheep) and population abundance of adult female bighorn. Lamb-ewe ratios and abundance estimates were derived from remote camera data collected at point-source water features and precipitation totals were obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS).

Parameters	β	SE	[90% CI]
(μ submodel)			
Intercept	-6.63	3.15	[-11.82, -1.45]
Precip OctApr ²	-0.0035	0.0008	[-0.0049, -0.0022]
Precip OctApr	0.44	0.10	[0.27, 0.60]
LN (Precip MayAug)	-1.40	0.46	[-2.15, -0.65]
BL4 Richness	-1.06	0.46	[-1.81, -0.31]
(ϕ submodel)			
Intercept	2.35	0.36	[1.76, 2.94]

Lastly, we examined relationships between lamb survival and predictor variables by comparing pairwise scatterplots to bivariate regression curves (Fig. D.4). We used beta regression modeling (Ferrari and Cribari-Neto 2004, Ferrari 2011) to produce regression curves visualizing the relationship between lamb survival and individual predictors. Beta regression models were fit with the betareg package in Program R (Cribari-Neto and Zeileis 2010, Zeileis et al. 2019; R Development Core Team 2019). Bivariate regression plots were generated using the rcompanion package in Program R (Mangiafico 2020; R Development Core Team 2019).



Figure D.4. Pairwise scatterplots with fitted regression curves from models evaluating effects of (A) October-April precipitation with quadrature, (B) natural log of May-August precipitation (LN Precip May-Aug), and (C) population-level allelic richness at genetic locus BL4 on lamb survival (as estimated by lamb-ewe ratios). We used beta regression to model these relationships across 7 bighorn populations from 2014-2016 in the Mojave Desert, California, USA, following a pneumonia outbreak.

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Proceedings of the 2nd International Symposium on Information Theory Akademiai Kiado, Budapest. (Reproduced in pages 610-624 *in* S. Kotzand and L. S. Johnson, editors. 1992. Breakthroughs in Statistics, Volume One, Foundations and Basic Theory. Springer-Verlag, New York, New York, USA).
- Climate Engine. 2017. Desert Research Institute and University of Idaho. https://app.climateengine.org. Accessed 26 Aug 2017.
- Coltman, D. W., K. Wilson, J. G. Pilkington, M. J. Stear, and J. M. Pemberton. 2000. A microsatellite polymorphism in the gamma interferon gene is associated with resistance to gastrointestinal nematodes in a naturally-parasitized population of Soay sheep. Parasitology 122:571-582.
- Cribari-Neto, F and A. Zeileis. 2010. Beta Regression in R. Journal of Statistical Software 34:1-24.
- Davies, G., M. J. Stear, M. Benothman, O. Abuagob, A. Kerr, S. Mitchell, and S. C. Bishop. 2006. Quantitative trait loci associated with parasitic infection in Scottish blackface sheep. Heredity 96:252-258.
- Epps, C. W., R. S. Crowhurst, B. S. Nickerson. 2018. Assessing change in functional connectivity in desert bighorn sheep metapopulation after two generations. Molecular Ecology 27:2334-2346.
- Ferrari, S. L. P. 2011. Diagnostic tools in beta regression with varying dispersion. Statistica Neerlandica 65:337–351.
- Ferrari, S. and F. Cribari-Neto. 2004. Beta regression for modelling rates and proportions. Journal of Applied Statistics 31:799-815.
- Festa-Bianchet, M., J. T. Jorgenson, and W. D. Wishart. 1994. Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not females. Behavioral Ecology 5:21-27.
- Funk, C., P. Peterson, M. Landsfeld, D. Pedreros, J. Verdin, S. Shukla, G. Husak, J. Rowland, L. Harrison, A. Hoell, and J. Michaelsen. 2015. The climate hazards infrared precipitation with stations – a new environmental record for monitoring extremes. Scientific Data 2:150066. doi 10.1038/sdata.2015.66.
- Goudet, J. 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. Journal of Heredity 86:485-486.
- Hansson, B. and L. Westerberg. 2002. On the correlation between heterozygosity and fitness in natural populations. Molecular Ecology 11:2467-2474.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Kassambara, A. 2020. 'ggplot2' Based Publication Ready Plots. R package version 0.2.5.
- Mangiafico, S. 2020. rcompanion: Functions to Extension Education Program Evaluation. R package version 2.3.25.
- Mazerolle, M. J. 2019. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-2.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Zeileis, A., F. Cribari-Neto, B. Gruen, and I. Kosmidis. 2019. betareg: Beta Regression. R package version 3.1-2.

APPENDIX E: AREA UNDER THE RECEIVER OPERATING CURVE

For the intermountain movement analysis in Chapter 3, we applied area under the receiver operating characteristic (ROC) curve (AUC) to evaluate goodness-of-fit of our top model (Hanley and McNeil 1982) using LogisticDx in Program R (Dardis 2015; R Development Core Team 2019). Our top model indicated that age (<or > 5 years old), sex, and *Mycoplasma ovipneumonia* infection status at capture were all important variables influencing intermountain movements.



Receiver Operating Curve

Figure E.1. Area under the receiver operating curve for the top intermountain movement model which estimated effects of age (< or > 5 years old), sex, and *Mycoplasma ovipneumonia* infection status (as determined from polymerase chain reaction [PCR] testing of nasal swabs collected from animals at time of capture), using logistic regression applied to intermountain movement as a binary response. Movements were detected using location data from animals with GPS radio-collars that were monitored from 2013-2018 in the Mojave Desert, California, USA following a pneumonia outbreak.

- Dardis, C. 2015. LogisticDx: diagnostic tests for models with a binomial response. R package version 0.2.
- Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29-36.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

APPENDIX F: QUANTILE AND RESIDUAL PLOTS

We used standard linear regression to test effects of biological season, age, and PCR status at capture on daily movement rates in separate analyses for males and females, in order to further investigate movement behavior regardless of intermountain activity. To generate daily movement rates, radio-collar data were resampled to 1 location per day for all individuals by removing extraneous locations such that consecutive locations for each animal were between 20 and 28 hours apart. In cases where locations were missing and time lags exceeded 28 hours, we retained the next location to allow for the next daily time step. We calculated daily movement rates from step-lengths (i.e., Euclidean distance between 2 consecutive locations measured in meters) divided by time lags between resampled locations, and multiplied rates by 24 hours to yield meters per day (m/day). Daily movement rates were then partitioned by biological season and averaged to produce seasonal mean daily movement rates for each individual. We modeled seasonal effects categorically, whereby each animal had 2 responses (i.e., one for each season) and received seasonal covariate input values of 1 for mean movement rates associated with breeding (for males) and midgestation to lambing (for females) and values of 0 for alternate periods. Age and PCR status were modeled as described in the intermountain movement analysis. We added a random effect to our most strongly supported models in order to evaluate individual variation in the intercept *post hoc* and potentially improve model fit (Harrison et al. 2001). We fit fixed effects models with the lm function in Program R (R Development Core Team 2019) and mixed effects models were fit with the lme4 package (Bates et al. 2019).

Our highest ranking fixed effects model for females indicated that season and PCR status were important variables influencing mean daily movement rates ($R^2 = 0.08$; Table 3.3). The random intercept accounting for individual variation in the corresponding mixed effects model was statistically significant ($\chi^2 = 15.2$, p < 0.0001) and improved model fit ($R^2 = 0.40$). For males, our highest ranking fixed effects model indicated that season was the only important variable influencing mean daily movement rates ($R^2 = 0.45$; Table 3.4). The random intercept accounting for individual variation in the corresponding mixed effects model was not statistically

significant ($\chi^2 = 0.3$, p = 0.61). We assessed normality and equal variance of residuals via quantile and residual plots for top fixed effects models using the olsrr package in Program R (Hebbali 2020; R Development Core Team 2019). We also assessed normality of the random effect for females using a normal quantile plot for the mixed effects model, which we generated with the qqnorm function in Program R (R Development Core Team 2019). Plots are presented below.



Normal Q-Q Plot

Figure F.1. Normal quantile plot for the top fixed effects model analyzing mean seasonal daily movement rates of adult female bighorn sheep in the Mojave Desert,

California, USA from 2013-2018, following a pneumonia outbreak. Mean daily movement rates were calculated using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. The model evaluated effects of *Mycoplasma ovipneumoniae* (*M. ovi*) infection (determined from PCR testing of nasal swabs collected from animals at time of capture) and season on mean seasonal daily movement rates using standard linear regression. Seasons were defined by the period of mid-gestation to lambing (October-April) and post-lambing to early-gestation (May-September).



Figure F.2. Residual plot for the top fixed effects model analyzing mean seasonal daily movement rates of adult female bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Mean daily movement rates were calculated using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. The model evaluated effects of *Mycoplasma ovipneumoniae* (*M. ovi*) infection (determined from PCR testing of nasal swabs collected from animals at time of capture) and season on mean seasonal daily movement rates using standard linear regression. Seasons were defined by the period of mid-gestation to lambing (October-April) and post-lambing to early-gestation (May-September).





Theoretical Quantiles

Figure F.3. Normal quantile plot for the top mixed effects model that includes a random intercept to account for individual variation and analyzes mean seasonal daily movement rates of adult female bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Mean daily movement rates were calculated using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. The model evaluated effects of *Mycoplasma ovipneumoniae* (*M. ovi*) infection (determined from PCR testing of nasal swabs collected from animals at time of capture) and season on mean seasonal daily movement rates using standard linear regression. Seasons were defined by the period of mid-gestation to lambing (October-April) and post-lambing to early-gestation (May-September).



Figure F.4. Normal quantile plot for the top fixed effects model analyzing mean seasonal daily movement rates of adult male bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Mean daily movement rates were calculated using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. The model evaluated effects of *Mycoplasma ovipneumoniae* (*M. ovi*) infection (determined from PCR testing of nasal swabs collected from animals at time of capture) and season on mean seasonal daily movement rates using standard linear regression. Seasons were defined by the breeding period (July-November) and nonbreeding period (December-June).



Figure F.5. Residual plot for the top fixed effects model analyzing mean seasonal daily movement rates of adult male bighorn sheep in the Mojave Desert, California, USA from 2013-2018, following a pneumonia outbreak. Mean daily movement rates were calculated using location data from animals that were captured and received GPS radio-collars in November 2013-2015 and March 2017. The model evaluated effects of *Mycoplasma ovipneumoniae* (*M. ovi*) infection (determined from PCR testing of nasal swabs collected from animals at time of capture) and season on mean seasonal daily movement rates using standard linear regression. Seasons were defined by the breeding period (July-November) and nonbreeding period (December-June).

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- Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, and J. Fox. 2019. LME4: linear mixed-effects models using eigen and S4. R package version 1.1-21.
- Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2001. A brief introduction to mixed effects modelling a multi-model inference in ecology. PeerJ 6:e4794.
- Hebbali, A. 2020. olsrr: Tools for Fitting OLS Regression Models. R package version 0.5.3.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.