



Research Article

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 2013, a pneumonia outbreak linked to the pathogen *Mycoplasma ovipneumoniae* led to an all-age die-off of desert bighorn sheep (*O. c. nelsoni*) at Old Dad Peak in the Kelso Mountains of the Mojave Desert in California, USA. Subsequently, we observed clinical signs of respiratory disease among bighorn sheep 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. ovipneumoniae* infection and survival, while testing effects of range factors that could potentially influence differences in adult female survival (i.e., forage quality, winter precipitation, 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 for summer and autumn, was positively correlated with overwinter survival, whereas winter precipitation (a proxy for winter severity) was negatively correlated with overwinter survival. Population abundance was negatively correlated with annual survival, suggesting a potential density-dependent effect. Model-averaged annual survival estimates ranged from 0.700 ± 0.07 (SE) to 0.945 ± 0.026 for infected individuals and 0.896 ± 0.03 to 0.983 ± 0.011 for uninfected individuals. We conclude that summer and autumn forage quality, indexed by NDVI, may partially offset the negative effect associated with *M. ovipneumoniae* 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. ovipneumoniae*) at time of capture. We propose 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. © 2020 The Wildlife Society.

KEY WORDS bighorn sheep, density dependence, Mojave Desert, *Mycoplasma ovipneumoniae*, PCR, pneumonia, radio-collars, survival.

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 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* has been identified as a primary causal agent associated with pneumonia outbreaks (Besser et al. 2008, 2013; Plowright et al. 2017; Cassirer et al. 2018);

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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*; Besser et al. 2008, Tomassini et al. 2009, 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. 2012*b*), which was true in 6 out of 9 events documented in the western United States in 2009 and 2010 (Western Association of Fish and Wildlife Agencies [WAFWA] 2010).

In May and June 2013, a pneumonia outbreak linked to *M. ovipneumoniae* led to an all-age die-off of desert bighorn sheep (*O. c. nelsoni*) at Old Dad Peak in the Kelso Mountains of the Mojave Desert in California, USA (Epps et al. 2016). Previously, bighorn sheep in this region of the Mojave Desert 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, we captured adult bighorn from Old Dad Peak and 8 neighboring ranges (i.e., South Soda, Cady, North Bristol, South Bristol, Marble, Clipper, Hackberry, Woods mountains) and tested animals for *M. ovipneumoniae* infection via polymerase chain reaction (PCR) analysis of nasal swab samples. We detected the same strain of *M. ovipneumoniae* in adult bighorn from all ranges except the South Soda Mountains, where animals were *M. ovipneumoniae*-negative but seropositive for *M. ovipneumoniae* antibodies. Attempts to screen for additional respiratory pathogens, including leukotoxigenic *M. haemolytica* and *B. trehalosi*, were also undertaken but were unsuccessful because of 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 neighboring populations were seropositive for *M. ovipneumoniae* antibodies as early as 1986, and bighorn at Old Dad Peak were seropositive in 1989 (CDFW, unpublished data). The strain of *M. ovipneumoniae* 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, USA; 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).

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

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; 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 (e.g., weather, range condition) may also influence expression of the disease (Dunbar 1992, Ryder et al. 1992, Monello et al. 2001, Wolfe et al. 2010). For example, precipitation is 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 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 (>2yr) across 9 populations from November 2013 to March 2017 in the Mojave Desert in California. We had 2 hypotheses. First, *M. ovipneumoniae* infection lowers post-outbreak survival of adult females. We assumed that females who were carrying the *M. ovipneumoniae* 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 induce chronic and latent disease states in animals and humans (Waites and Talkington 2004), and bighorn sheep exposed to *M. ovipneumoniae* can become chronic, non-clinical carriers of the pathogen (Plowright et al. 2017). Second, 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 meta-population 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 Desert is high desert, characterized by dry, hot summers (Jul–Sep) and cold, wet winters (Dec–Mar) but also experiences late summer monsoons that account for $\geq 25\%$ of the 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 (National Park Service [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). We defined annual seasons based on a climograph for Mojave National Preserve (McKee et al. 2015), whereby autumn corresponded with

October and November, winter corresponded with December through March, spring corresponded with April through June, and summer corresponded with July through September.

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). The entire study area spanned approximately $6,000\text{ km}^2$ and occurred on lands managed by the Bureau of Land Management (BLM) and NPS, 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

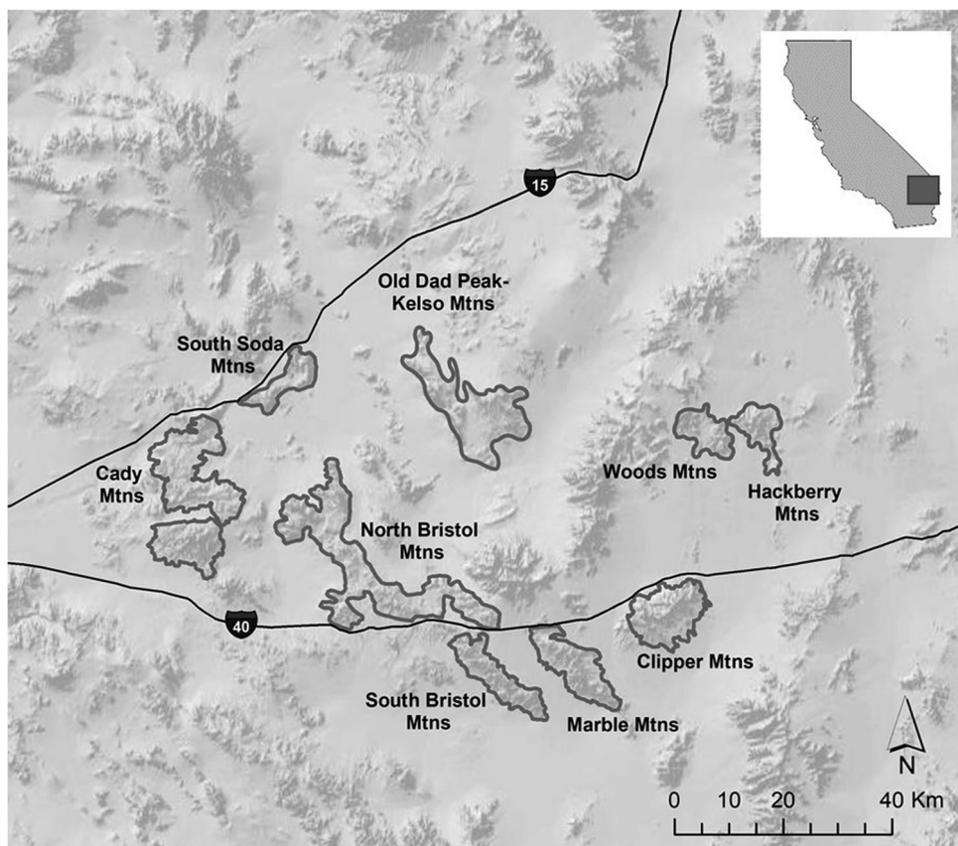


Figure 1. Nine bighorn sheep populations in mountains (mnts) of the Mojave Desert, California, USA, that we monitored from 2013–2017 following a pneumonia outbreak.

2016, with higher rainfall averages occurring in December 2016 to March 2017. Average winter rainfall, across the 9 ranges, ranged from 22 mm to 42 mm in 2013–2016 and was 82 mm in 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 (U.S. Geologic Survey 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* spp.), silver and buckhorn cholla (*Cylindropuntia echinocarpa* and *C. acanthocarpa*, respectively), 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 (Halloran and Deming 1958, Swift et 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 ≥ 1 water source, and some ranges contained multiple water features of varying types.

METHODS

Collaring, Disease Testing, and Mortality Recovery

We captured and radio-collared adult female bighorn sheep in November 2013, 2014, and 2015. We located animals aerially, captured them using a net-gun fired from helicopter (Krausman et al. 1985), and processed them in the field following guidelines approved by CDFW and the NPS 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. 2011). We fit all adult females with both global positioning system (GPS) and very high frequency (VHF) collars and ear tags with unique color and number combinations.

We collected blood and nasal swabs from individuals at time of capture. Prior to testing, we stored blood serum in cryogenic vials at -20°C , and stored swabs dry at -20°C . Washington Animal Disease Diagnostic Laboratory (WADDL; Pullman, WA, USA) performed serology for *M. ovipneumoniae*-specific antibodies in serum samples using competitive enzyme-linked immunosorbent assays (cELISA). Technicians used nasal swabs to detect *M. ovipneumoniae*-specific DNA sequences via PCR testing; 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).

We monitored and tracked adult females via satellite- and radio-telemetry. We received the global positioning system (GPS) data through the Iridium and Globalstar satellite systems (Iridium Communications, McLean, VA, USA; Globalstar, Covington, LA, USA); systems recorded collar locations between 2 times a day and once every 3 days, and collars signaled a mortality if they were motionless for ≥ 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 yr and VHF collars had an average lifespan of 9 yr). We typically recovered mortalities 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, we collected inner ear, nasal, and lung swab samples for *M. ovipneumoniae* PCR. We also collected lung tissue samples from dead animals < 12 hours post-mortem (as determined based on time of death from GPS-collars) for histological examination. We kept swab and tissue samples on ice in the field; we stored swabs dry or in a tryptic soy broth media at -20°C and lung samples in 10% neutral buffered formalin at 4°C prior to laboratory submission. The California Health and Food Safety Laboratory (San Bernardino, CA) and Colorado State University Veterinary Diagnostic Lab (Fort Collins, CO, USA) 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 (e.g., lacerations, bite marks, broken bones, body position, bullet wounds, color of bone marrow), and inspection of surrounding areas for other evidence (e.g.,

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. Mortality investigations allowed us to rule out potential causes of death, but 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.

We assumed death dates from GPS-collars to be the actual time of death for individuals with active GPS-collars (i.e., the day movement stopped); if we detected a mortality 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. We classified assessments of carcass condition based on mortalities we recovered that had known death dates, and they 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 at least 1 week 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 ≥ 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. We estimated seasonal home ranges in each mountain range by grouping collar location data for all individuals by season. We used the kernel density tool in ArcGIS 10.5 (Esri 2016) to produce home range estimates with fixed kernels and reference bandwidth (Silverman 1986). We used a 95% contour 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, Creech et al. 2016, Heffelfinger et al. 2017), and extracted NDVI and precipitation data from Climate Engine (2017; Huntington et al. 2017). For NDVI, we used a composite of Landsat 4, 5, 7, and 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; fecal nitrogen (an index of diet quality) and mean seasonal NDVI within home ranges were strongly correlated for

populations of desert bighorn (Creech et al. 2016). 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 Desert, especially during the hot summer months (Halloran and Deming 1958, 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). We then used survey data from cameras to generate counts of marked and unmarked individuals for abundance estimation. We used Bushnell Trophy cameras (standard and hybrid 8MP; Bushnell, Overland Park, KS, USA) set to a 1-second delay to collect photos and video from June through September 2016. We serviced camera stations every 2 weeks to replace batteries and camera cards, adjust mis-angled cameras, and replace faulty equipment if necessary.

We applied the generalized form of Bowden's estimator (\bar{N} ; Bowden and Kufeld 1995) to the 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, we first sorted photos and videos into activity periods by day and then counted individuals present (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. We generally censored days if there were any activity periods that elapsed for >1.5 hours with >5 adult females present because longer time periods with more individuals could render uncertainty in count totals. We counted all marked and unmarked adult females (i.e., >2 yr 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 defined occasion in this context as a single sampling day. We identified unmarked individuals by unique horn and pelage characteristics (e.g., color, annuli or molt patterns, breakages, scars), and identified marked individuals 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 or bad angles preventing close inspection of features), we censored the entire occasion.

We attempted to use ≥ 16 occasions for each population to achieve an average of marked animal sightings/individual >1 (i.e., >1 sighting of each marked animal on average), with a higher proportion of the marked sample

detected (>0.7 in most cases) 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 because of cameras that were knocked down and other temporary technical failings remedied when we serviced cameras. 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 we collected camera data 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 number of times we observed a marked individual 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 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 abundance of adult females within each mountain range over the study period.

Survival Modeling

We evaluated the relationship between *M. ovipneumoniae* and seasonal survival, and tested effects of range factors that could potentially lead to differences in adult female survival. 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 dead or alive at the beginning and end of each sampling occasion. We included infection status (i.e., whether an individual was PCR-positive [infected] or negative [not infected] for *M. ovipneumoniae* at capture) as an individual covariate in our models, and included population abundance, NDVI, and winter precipitation as group covariates (Cooch and

White 2017). Winter precipitation and NDVI were time-varying covariates, and 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 S1, available online in Supporting Information). 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% CI did not overlap zero). 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 Desert, we also evaluated a lag effect of summer forage quality (i.e., \bar{x} 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*. We modeled infection status as a continuous indicator variable whereby individuals received a covariate value of 1 if they were PCR-positive at time of capture (i.e., infected with *M. ovipneumoniae*), a value of zero 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 if status was otherwise unknown because of missing data (we assumed information was missing at random and imputed missing values assuming a probability of 0.5 for either outcome, which we think is conservative insofar as accounting for uncertainty in the status of these individuals). We z -standardized all of our continuous variable inputs (NDVI, winter precipitation, and population abundance); 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. ovipneumoniae* (i.e., cELISA status) on survival (Tables S2 and S3, available online in Supporting Information). We tested these covariates because we found a strong negative effect associated with PCR-positive status on survival, and older age has been linked to higher rates of *M. ovipneumoniae* infection among adult bighorn (Plowright et al. 2017). We included age and exposure status as individual covariates and coded them as indicator variables. Females estimated to be 2–9 years old received a covariate value of zero, and females >9 years old received a value of 1. We moved females that became older than 9 years during the study, based on minimum age estimates, 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. ovipneumoniae* antibodies were detected), values of zero

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.

We ranked models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c ; Akaike 1973, Hurvich and Tsai 1989). In the candidate model set, we considered the effects of all variables in models with ΔAIC_c scores <2 and interpreted covariate effects based on model-averaged estimates with 90% confidence intervals (Arnold 2010, Burnham and Anderson 2010, Symonds and Moussalli 2011, Monteith et al. 2014), which we compared to results from our top 2 highest ranking 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).

We produced annual and winter survival estimates for infected and uninfected individuals for every population by multiplying model-averaged monthly survival probabilities; we calculated model-averaged standard error estimates using the delta method (Cooch and White 2017). We estimated annual survival from January through December for a given year and estimated winter survival from December through March across successive years.

RESULTS

We radio-collared 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 5

individuals (Hackberry Mountains) to 24 individuals (Marble Mountains; Table 1). Seventeen females were >9 years old during the study.

M. ovipneumoniae Status

Of the 115 animals in our sample, 36 tested positive for *M. ovipneumoniae* infection at time of capture, 15 had indeterminate PCR results or otherwise unknown infection status, 70 were seropositive, and 22 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. ovipneumoniae* at capture, 5 were PCR-negative, and 9 were of unknown infection status. The proportion of PCR-positive individuals among our samples within each range varied from zero (South Soda Mountains) to 75% (South Bristol Mountains), and the proportion of mortalities varied from zero (Hackberry, Woods, and Clipper mountains) to 54% (Marble Mountains; Table 1) over the study period. The lowest proportions of PCR-positive individuals ($<20\%$) occurred in the South Soda (0%), North Bristol, and Woods mountains (Table 1). Intermediate proportions occurred in the Cady (22%) and Old Dad Peak-Kelso (31%) mountains (Table 1). Highest proportions of infected individuals ($>40\%$) occurred in the Marble, Clipper, Hackberry, and South Bristol mountains (Table 1).

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), but we acknowledge that *M. ovipneumoniae* pathogen and antibody detection can fail, and although false positives are highly unlikely, false negatives may occur because of low pathogen load or antibody levels that become less over time (Plowright et al. 2017), or from mishandling of samples.

Table 1. Sample sizes and results of polymerase chain reaction (PCR) testing for *Mycoplasma ovipneumoniae* from adult female bighorn radio-collared between 2013 and 2015 for survival monitoring from 2013–2017 in the Mojave Desert, California, USA. *D* = *M. ovipneumoniae* detected (PCR-positive at capture), *ND* = *M. ovipneumoniae* 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 percentage of samples that were PCR-positive (i.e., infected with *M. ovipneumoniae*) and seropositive for *M. ovipneumoniae* antibodies (i.e., previously exposed).

Range (population)	Adult female sample			All years	Mortalities	Infected (%) ^a	Mortalities (%) ^b	Exposed (%) ^c
	2013–2014	2014–2015	2015–2017					
Marble	19	18	21	7 ^D , 9 ND , 8 ^{Unk} (24)	6 ^D , 2 ND , 5 ^{Unk} (13)	44	54	100
S. Bristol	16	15	15	12 ^D , 4 ND , 5 ^{Unk} (21)	4 ^D , 3 ^{Unk} (7)	75	33	94
Old Dad Peak-Kelso	13	13	14	5 ^D , 11 ND , 1 ^{Unk} (17)	3 ^D , 1 ND , 1 ^{Unk} (5)	31	29	73
N. Bristol	5	5	14	2 ^D , 12 ND (14)	1 ND (1)	14	7	30
Hackberry	4	5	5	2 ^D , 2 ND , 1 ^{Unk} (5)	0	50	0	67
Woods	0	0	7	1 ^D , 6 ND (7)	0	14	0	14
Clipper	3	3	11	5 ^D , 6 ND (11)	0	46	0	100
Cady	0	9	7	2 ^D , 7 ND (9)	1 ^D , 3 ND (4)	22	44	75
S. Soda	4	4	7	7 ND (7)	1 ND (1)	0	14	60
Total	64	72	101	36 ^D , 64 ND , 15 ^{Unk} (115)	14 ^D , 8 ND , 9 ^{Unk} (31)	36	27	75

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

^b Percentage of individuals that suffered mortality between 2013 and 2017.

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

Abundance Estimates

Marked animals detected on camera were typically within 9 km of point-source water features during the sampling period (Jun–Sep). 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 2). We recorded 214 marked animal sightings (detecting 78% of our total sample) and 858 unmarked animal sightings across all mountain ranges (Table S2), 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 3.3–5.1% (Table S2). 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 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 2). Yearly winter precipitation varied from 14 mm to 118 mm across ranges (Table 2). 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 2). 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 2016–2017 in all ranges, with totals doubling those from the previous year (Table 2).

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

Table 2. Estimated population abundance for adult female bighorn in 2016, mean summer and autumn normalized difference vegetation index (NDVI) values for 2013–2016, and precipitation (precip) in winter 2013–2014 to winter 2016–2017 in 9 mountain ranges in the Mojave Desert, California, USA. We derived abundance estimates from remote camera data we collected at point-source water features in each mountain range in summer 2016. We obtained mean summer and autumn NDVI from Landsat 4, 5, 7, and 8, and winter precipitation totals from Climate Hazards Group InfraRed Precipitation with Station data.

Mountain range	Adult female abundance ^a (95% CI)	2013		2013–2014		2014		2014–2015		2015		2015–2016		2016		2016–2017		
		Summer	Autumn	Summer	Autumn	precip (mm)												
Hackberry	14 (0–28)	0.16	0.18	27.56	0.18	0.17	0.18	63.46	0.13	0.13	49.72	0.15	0.16	0.15	118.22	0.15	0.15	118.22
Woods	18 (6–29)	0.16	0.18	27.56	0.18	0.17	0.18	63.46	0.13	0.13	49.72	0.15	0.16	0.15	118.22	0.15	0.15	118.22
Clipper	65 (28–102)	0.13	0.14	20.54	0.17	0.13	0.17	38.29	0.11	0.13	34.67	0.13	0.11	0.11	82.75	0.11	0.11	82.75
Old Dad Peak	41 (18–63)	0.10	0.11	23.18	0.14	0.10	0.14	40.81	0.10	0.13	36.23	0.13	0.10	0.11	77.73	0.11	0.11	77.73
Marble	135 (67–202)	0.11	0.12	14.27	0.13	0.10	0.13	26.33	0.09	0.11	24.86	0.11	0.09	0.10	58.10	0.10	0.10	58.10
S. Soda	28 (5–52)	0.09	0.10	21.66	0.10	0.09	0.10	39.09	0.09	0.10	32.56	0.10	0.09	0.10	68.76	0.10	0.10	68.76
S. Bristol	46 (25–68)	0.10	0.12	14.05	0.12	0.10	0.12	22.22	0.09	0.10	19.43	0.10	0.09	0.09	52.15	0.09	0.09	52.15
Cady	71 (0–144)	0.09	0.10	26.35	0.12	0.11	0.12	42.27	0.10	0.10	35.64	0.10	0.10	0.10	70.32	0.10	0.10	70.32
N. Bristol	101 (26–175)	0.09	0.10	28.23	0.11	0.09	0.11	44.21	0.09	0.10	39.36	0.10	0.09	0.09	87.73	0.09	0.09	87.73

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

statistical support for relationships (i.e., $P > 0.05$). There was a small negative correlation between population abundance and summer NDVI ($r = -0.40$) that was significant, whereas the correlation between population abundance and autumn NDVI ($r = -0.33$) lacked statistical support. 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 3).

Our global models alternately containing summer and autumn NDVI were the most strongly supported (Table 3). 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 4). Model-averaged parameter estimates substantiated these results (Table 4). Summer and autumn NDVI were competing predictor variables, although the relative variable importance (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. ovispneumoniae* 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

Table 3. 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. Polymerase chain reaction (PCR) status was based on results from PCR testing for *Mycoplasma ovispneumoniae* 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 normalized difference vegetation index (NDVI) in each mountain range on survival in winter months only. We evaluated models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c).

Model number	Model structure	K^a	ΔAIC_c	w_i^b	Deviance
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

^a Number of model parameters.

^b Akaike model weight.

Table 4. 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. Polymerase chain reaction (PCR) status was based on results from PCR testing for *Mycoplasma ovipneumoniae* infection using nasal swabs collected from females at time of capture, and was modeled as an indicator 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 normalized difference vegetation index (NDVI) in each mountain range on survival in winter months only.

	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

^a Summer and autumn NDVI are correlated and model averages are not jointly additive.

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 (we scaled back CIs 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 5). Estimated annual survival was highest in the Hackberry, Woods, and Clipper mountains, ranging from 0.958 ± 0.016 (SE) to 0.983 ± 0.011 for uninfected females and from 0.869 ± 0.034 to 0.945 ± 0.026 for infected females, intermediate in Old Dad Peak-Kelso, South Bristol, and South Soda mountains (uninfected: 0.943 ± 0.026 to 0.966 ± 0.017 ; infected: 0.828 ± 0.057 to 0.893 ± 0.038), and lowest in the Cady, Marble, and North Bristol mountains (uninfected: 0.896 ± 0.030 to 0.953 ± 0.017 ; infected: 0.700 ± 0.070 to 0.856 ± 0.036 ; Table 5).

Sixty-five percent ($n = 20$) of all 31 mortalities among collared females occurred during winter. In winter 2016–2017, which was the most severe winter in terms of precipitation, observed mortality among collared females was highest with 10 deaths, and estimated overwinter survival was lowest in some populations (Table S3). 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 (Table S3).

A Posteriori Covariate Testing

We evaluated estimated age and *M. ovipneumoniae* exposure (i.e., cELISA status) *a posteriori*. The potential effect of older age (i.e., >9 yr) on survival was not supported (i.e., 90% CIs overlapped zero), although age was included in 3 of 7 top models (ΔAIC_c scores <2; Table S4, available online in Supporting Information). 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. ovipneumoniae* exposure on survival, based on cELISA testing, was not supported in our evaluation. The cELISA covariate occurred in models with ΔAIC_c scores ≥ 8 (Table S5, available online in Supporting Information) and all estimates for the effect had 90% confidence intervals overlapping zero. 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 (≥ 2 weeks) for sampling in 18 cases, and in 3 cases field sampling failed. We detected 13 of the 31 mortalities 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 we tested post-mortem, 2 animals were PCR-positive for *M. ovipneumoniae* at death and at time of capture (1 yr and 2 yr 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. ovipneumoniae* at death or time of capture. In the 7 other mortality cases,

Table 5. 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; we generated estimates using the known-fate model in Program MARK. Table shows estimates for individuals that were positive for *Mycoplasma ovipneumoniae* infection at capture (i.e., infected) and negative at capture (i.e., not infected) based on results from polymerase chain reaction (PCR) testing of nasal swabs collected from females at time of capture, and indicates different levels of mean normalized difference vegetation index (NDVI) and estimated adult female population abundance for mountain ranges (*=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], as estimated from remote camera data). We estimated annual survival from January through December for a given year; estimates are model-averaged.

Mountain range	PCR-positive						PCR-negative					
	2014		2015		2016		2014		2015		2016	
	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

M. ovipneumoniae infection was not confirmed post-mortem, but 5 animals tested positive for *M. ovipneumoniae* infection <1 year ($n=1$) and 1–4 years ($n=4$) prior. We could not confirm the infection status of the 2 remaining cases 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. Negative results from samples collected post-mortem are not reliable because of the likelihood of pathogen degeneration following host mortality.

The WADDL also screened 8 individuals for leukotoxigenic *Pasteurellaceae* post-mortem via PCR testing of lung swabs (Besser et al. 2012b) and Colorado Parks and Wildlife screened sinus tissue (Fox et al. 2015). Of these animals, only 1 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

In our study, *M. ovipneumoniae* 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. ovipneumoniae* infection on adult female bighorn sheep survival is consistent with other studies that have linked *M. ovipneumoniae* to pneumonia epizootics and acute mortality in bighorn sheep populations (Besser et al. 2012a, b, 2014; Cassirer et al. 2017), although our study suggests a lingering post-outbreak 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, 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. Also, 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 Desert 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) reported 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 2016–2017, which was

the most severe in terms of precipitation, mortality among collared females 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. ovipneumoniae* (as per cELISA testing and demonstration of *M. ovipneumoniae*-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 and 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. ovipneumoniae* (Cassirer et al. 2017, Plowright et al. 2017, Wood et al. 2017), and infectious periods can last >3 years (Plowright et al. 2017). Eighty-four percent of mortalities in the study occurred >1 year after capture, and we confirmed *M. ovipneumoniae* 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. ovipneumoniae* 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. ovipneumoniae* 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. ovipneumoniae* within infected populations. We note that female bighorn who were PCR-positive for *M. ovipneumoniae* at time of capture had lower survival odds, which implies natural culling from populations over time as well.

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) reported that *M. ovipneumoniae* prevalence in adults decreased between ages 2 and 9, and increased after 9 years of age, with highest prevalence occurring among individuals >15 years old. This result 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. ovipneumoniae* at capture. We therefore conclude that the negative effect associated with *M. ovipneumoniae* infection in our study largely reflects the effect 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. 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 by 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 results. Moreover, we also model-averaged estimated annual and winter survival to account for model selection uncertainty (Cooch and White 2017).

Although 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 (1 infected with pneumonia) in Alberta, Canada. We speculate that our study of adult female bighorn survival in populations recently exposed to *M. ovipneumoniae* 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. ovipneumoniae* infection, and although *M. ovipneumoniae* 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, 2013; 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. 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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