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Research Article

Disease, Population Viability, and Recovery of Endangered Sierra Nevada Bighorn Sheep

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ABSTRACT Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) experienced a severe population decline after European settlement from which they have never recovered; this subspecies was listed as endangered under the United States Endangered Species Act (ESA) in 1999. Recovery of a listed species is accomplished via federally mandated recovery plans with specific population goals. Our main objective was to evaluate the potential impact of disease on the probability of meeting specific population size and persistence goals, as outlined in the Sierra Nevada bighorn sheep recovery plan. We also sought to heuristically evaluate the efficacy of management strategies aimed at reducing disease risk to or impact on modeled bighorn populations. To do this, we constructed a stochastic population projection model incorporating disease dynamics for 3 populations (Langley, Mono, Wheeler) based on data collected from 1980 to 2007. We modeled the dynamics of female bighorns in 4 age classes (lamb, yearling, adult, senescent) under 2 disease scenarios: 5% lower survival across the latter 3 age classes and persistent 65% lower lamb survival (i.e., mild) or 65% reduced survival across all age classes followed by persistent 65% lower lamb survival (i.e., severe). We simulated management strategies designed to mitigate disease risk: reducing the probability of a disease outbreak (to represent a strategy like domestic sheep grazing management) and reducing mortality rate (to represent a strategy that improved survival in the face of introduced disease). Results from our projection model indicated that management strategies need to be population specific. The population with the highest growth rate ($\hat{\lambda}$; Langley; $\hat{\lambda} = 1.13$) was more robust to the effects of disease. By contrast, the population with the lowest growth rate (Mono; $\hat{\lambda} = 1.00$) would require management intervention beyond disease management alone, and the population with a moderate growth rate (Wheeler; $\hat{\lambda} = 1.07$) would require management sufficient to prevent severe disease outbreaks. Because severe outbreaks increased adult mortality, disease can directly reduce the probability of meeting recovery plan goals. Although mild disease outbreaks had minimal direct effects on the populations, they reduced recruitment and the number of individuals available for translocation to other populations, which can indirectly reduce the probability of meeting overall, range-wide minimum population size goals. Based on simulation results, we recommend reducing the probability of outbreak by continuing efforts to manage high-risk (i.e., spatially close) allotments through restricted grazing regimes and stray management to ensure recovery for Wheeler and Mono. Managing bighorn and domestic sheep for geographic separation until Sierra Nevada bighorn sheep achieve recovery objectives would enhance the likelihood of population recovery. © 2011 The Wildlife Society.

KEY WORDS California, disease, domestic sheep, endangered species management, *Ovis canadensis sierrae*, recovery plan, Sierra Nevada bighorn sheep, Sierra Nevada mountains, stochastic population projection model.

Bighorn sheep (*Ovis canadensis*) populations in North America declined precipitously beginning with European settlement, and the geographic distribution of remaining populations has been greatly reduced (Krausman 2000). Various environmental and demographic factors have been implicated, including unregulated hunting, habitat loss, predation, and diseases introduced by livestock (e.g., Wehausen 1996, Singer et al. 2001). Bighorn sheep are closely related to domestic sheep (*Ovis aries*) and are highly susceptible to certain bacterial infections from them (Onderka and Wishart 1988; Foreyt, 1989, 1994; Lawrence et al. 2010). Today, respiratory disease is one of the greatest obstacles to the

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stability and persistence of bighorn populations in ranges throughout the United States and southern Canada. In particular, bacteria in the genera *Mannheimia*, *Bibersteinia*, and *Pasteurella* (collectively called *Pasteurellaceae*) can cause pneumonia epizootics with high infection rates in wild sheep populations, resulting in all-age die-offs followed by years of depressed reproductive success due to fatal pneumonia in lambs (Foreyt 1990, Coggins and Matthews 1992, Ward et al. 1992, Foreyt 1994). Domestic sheep commonly carry strains of *Pasteurellaceae* that are highly pathogenic in bighorn sheep (Onderka and Wishart 1988; Foreyt, 1989, 1990; Council for Agricultural Science and Technology 2008; Lawrence et al. 2010), and several studies have shown the presence and proximity of domestic sheep to be negatively correlated with bighorn sheep population persistence (Goodson 1982, Gross et al. 2000, Singer et al. 2001, Epps et al. 2004).

The impact of respiratory disease on bighorn sheep populations can vary. Some respiratory pathogens cause illness but not high mortality of adults (hereafter mild outbreaks; Singer et al. 2000, Cassirer and Sinclair 2006). Other respiratory pathogens (especially introduced, leukotoxigenic *Pasteurellaceae* strains) cause catastrophic all-age die-offs with high (>50%) mortality in affected bighorn populations (hereafter severe outbreaks; Foreyt and Jessup 1982, Onderka and Wishart 1984, Coggins and Matthews 1992, George et al. 2008). Whether mild or severe, most respiratory disease outbreaks in bighorn populations are followed by several years of pneumonia caused mortality of lambs resulting in low recruitment rates and juvenile survival (Festa-Bianchet 1988, Coggins and Matthews 1992, Ryder et al. 1994, Jorgenson et al. 1997, George et al. 2008). Continuing lamb infection apparently results from females that remain infective following an outbreak, although mortality or morbidity among the females may not be detectable (Foreyt 1990, Miller et al. 1997, Cassirer and Sinclair 2006). Such recurring lamb infections can substantially delay the recovery of depleted populations to pre-outbreak levels.

Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) historically occurred along and east of the central and southern Sierra Nevada crest in California (U.S. Fish and Wildlife Service [USFWS] 2007). Unregulated hunting and introduced disease are hypothesized as the cause of the precipitous population decline after European settlement, which left only 2 surviving herds by the 1970s (Wehausen 1980, USFWS 2007). Recovery of the population in one of those areas allowed reestablishment of 3 herds in 3 additional areas through reintroduction, but this was followed by a widespread decline to just over 100 total individuals in the mid 1990s, and the subspecies was listed as endangered in April 1999 (Wehausen 1999, USFWS 2007). Infectious disease is a threat to recovery and persistence of local bighorn sheep populations, although mountain lion (*Puma concolor*) predation may be impacting some Sierra Nevada bighorn populations (Wehausen 1996, USFWS 2007). Several grazing allotments for domestic sheep create risk of pathogen exposure to bighorn sheep populations and continued proximity of domestic sheep to bighorn sheep is considered a risk to recovery efforts (USFWS 2007, Clifford et al. 2009).

The United States Endangered Species Act stipulates that actions on federal lands must not jeopardize the persistence of endangered species (U.S. Endangered Species Act of 1973, 1973). Recovery of endangered species under the Endangered Species Act is accomplished via federally mandated recovery plans that include specific population goals. Our objective was to evaluate the potential influence of introduced respiratory disease on bighorn sheep demography relative to attaining specific population size and persistence criteria outlined in the Sierra Nevada bighorn recovery plan. We also sought to evaluate the effectiveness of hypothetical management strategies aimed at reducing disease risk or impact. To this end, we constructed a stochastic population projection model that incorporated disease dynamics for 3 Sierra Nevada bighorn populations and conducted simulations to evaluate management strategies and estimate probabilities of meeting recovery goals and other demographic outputs. This approach allowed us to heuristically assess the effects of disease on population dynamics, as well as the probability that potential management intervention can assist with meeting recovery plan objectives.

STUDY AREA

The 3 study populations were located on the eastern side of the Sierra Nevada mountain range. The Sierra Nevada extends approximately 650 km along the eastern side of California, ranging from 75 km to 125 km wide (Hill 1975). Climate in the Sierra Nevada is characterized by dry conditions in the warm season (May–Oct), with most of the annual precipitation received as snow in winter (Nov–Apr), which varied considerably by year (Major 1977). There is a strong rain shadow effect in precipitation east of the Sierra crest (Major 1977) resulting in more open, xeric vegetation communities along the lower eastern slope. Low elevations (1,500–2,500 m) were characterized by Great Basin sagebrush (*Artemesia tridentada*) and bitterbrush (*Purshia tridentada*) scrub; middle elevations (2,500–3,300 m) by pinyon (*Pinus monophylla*) woodland, subalpine meadows, and forests; and high elevations (>3,300 m) by sparse alpine vegetation including occasional meadows. Virtually all Sierra Nevada bighorn habitat was public land, managed primarily by Yosemite and Sequoia-Kings Canyon national parks, and Inyo, Humbolt-Toiyabe, and Sierra national forests.

Detailed demographic data were available for each study population, referred to here as the Langley, Wheeler, and Mono populations (Fig. 1) after the main geographic features of their range. The Mono population included the Mt. Warren and Mt. Gibbs herds as defined in the Recovery Plan (USFWS 2007). These discrete local populations were small (<40 females; Johnson et al. 2010*a*) and separated by >50 km of unoccupied habitat. The study populations were known to be geographically isolated; in addition bighorn marked in the 3 study areas with Global Positioning System (GPS; $n = 44$) and very high frequency (VHF) telemetry ($n = 57$) collars for >1 yr showed no movement

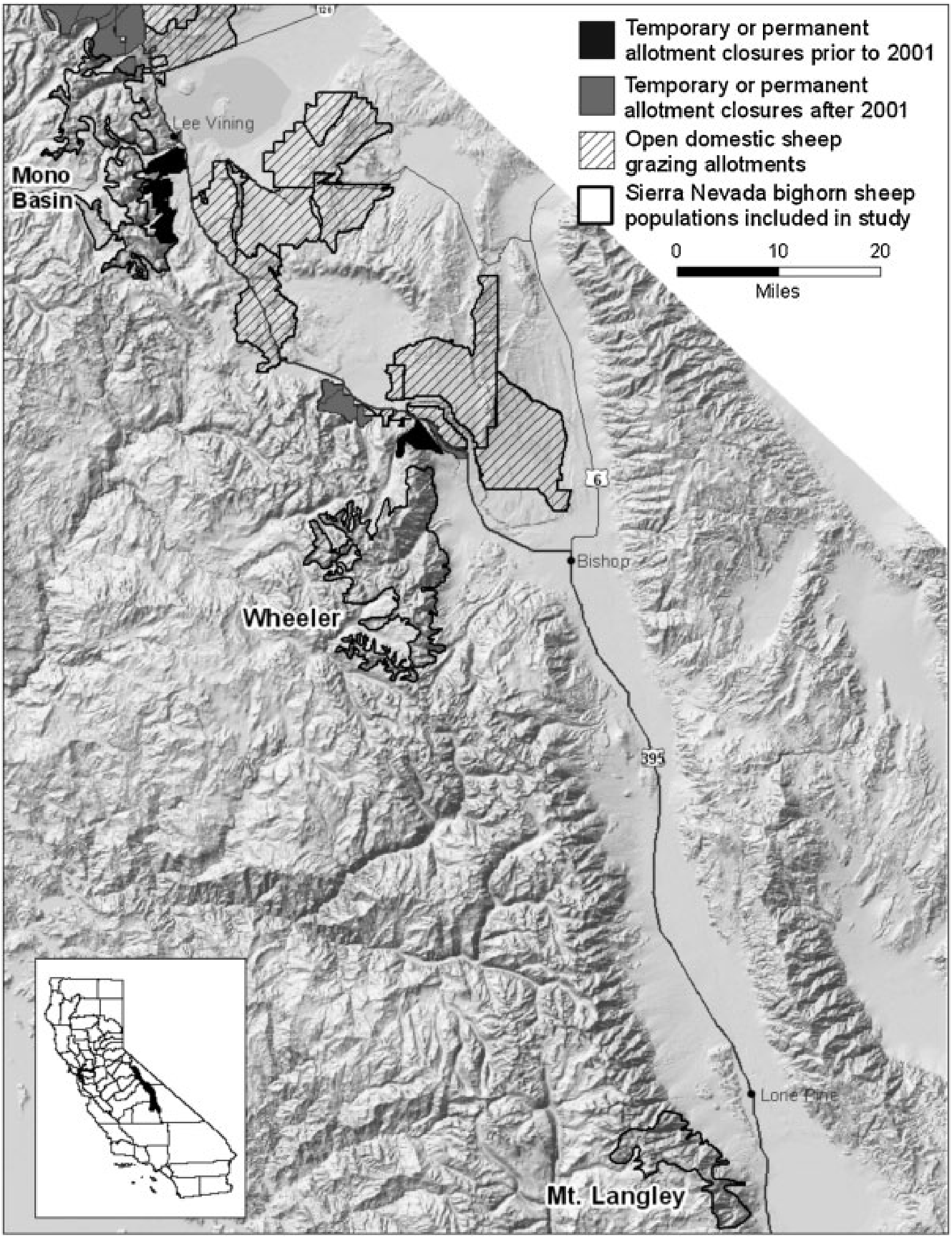

Figure 1. Locations of Langley, Wheeler, and Mono Sierra Nevada bighorn sheep populations and open, temporary, or permanently closed domestic sheep grazing allotments based on data collected 1980–2007 in the Sierra Nevada Mountains, California.

among the study populations. Because the populations were small and did not occupy the entire area considered to be potential habitat, we considered each a single population unit without substructure (i.e., if disease arrives, all individuals in the population would be exposed). No disease-related mortality was documented within the last 35 yr, when intensive research and management activities involving this subspecies were ongoing. Prior collection of field data on this animal was sparse (Wehausen 1980) thus unlikely to detect disease; nevertheless, a die-off of Sierra Nevada bighorn in the Kaweah Peaks in the 1870s was attributed to scabies thought to have been introduced from domestic sheep (Jones 1950). The Wheeler and Mono populations occurred within 8 km straight-line distance from seasonally grazed domestic sheep allotments, whereas the closest allotment to the Langley population was 40 km. We have documented incidences of domestic sheep straying into bighorn sheep habitat and of long-range movements (53 km) made by bighorn males in the Wheeler and Mono areas.

METHODS

Model Parameter Estimation

We based parameter estimates for population models on data collected 1980–2007 (Table 1). Because bighorn sheep are polygynous (Geist 1971), we restricted the model and its parameters to females (Morris and Doak 2002). Annual population surveys for each herd unit included systematic searches for bighorn sheep by experienced observers (see also Johnson et al. 2010*a*). Ground surveys within herd units

Table 1. Number of years of data used for each estimate and estimates used to parameterize population projection models for female Sierra Nevada bighorn sheep based on data collected 1980–2007 in Sierra Nevada Mountains, California.

Population	No. yr	*N*(0)[a]	Corrected mean[b]	Total variance[c]	Process variance
Langley					
Fecundity	11	9	0.331	0.035	0.007
Newborn survival	9	11	0.872	0.024	0.012
Adult survival	9	38	0.977	0.002	0.000
Wheeler					
Recruitment	13	6	0.313	0.022	0.006
Yearling survival	13	4	0.730	0.036	0.014
Adult survival	13	34	0.920	0.010	0.008
Mono					
Fecundity	9	4	0.360	0.007	0.000
Newborn survival	8	3	0.674	0.008	0.000
Adult survival	8	11	0.856	0.024	0.010

[a] *N*(0) is the starting population vector based on survey data from 2007. For Langley and Mono, *N*(0) associated with fecundity represents number of lambs, *N*(0) associated with newborns represents number of yearlings, and *N*(0) associated with adults represents number of adults, whereas for Wheeler, *N*(0) associated with recruitment represents number of yearlings, *N*(0) associated with yearlings represents number of 2-yr-olds, and *N*(0) associated with adults represents adults.

[b] We corrected parameter estimates with a maximum likelihood approach to remove sampling variance.

[c] Shown for reference; we used process variance in simulations.

occurred over areas ranging from 20 km^2 to 43 km^2. Multiple observers used binoculars and spotting scopes on established routes to completely survey defined habitat. Surveys occurred primarily in open alpine (Jul–Sep) and sagebrush steppe (Jan–Mar) habitats where animals were visible from long distances. Annual surveys provided minimum count data for lambs, yearlings, and adults. However, knowledge of habitat use patterns of each population, intensive monitoring including repeated field efforts when needed, and small (5–35 adult females) observable populations, allowed for annual counts to be near-complete censuses. We surveyed animals in accordance with University of Montana Institutional Animal Care and Use Committee protocol (024–07MHWB–071807).

The annual lambing period for Sierra Nevada bighorn occurs primarily from mid-April through mid-June, and females give birth to 1 offspring/year (Wehausen, 1996, 1980). We conducted surveys of Mono and Langley populations from July to September, just after new lambs were born (post-birth pulse). We conducted surveys of the Wheeler population in late March or early April just before new lambs were born (pre-birth pulse). We observed 3 stage classes during both surveys types; however, the timing of surveys resulted in distinct differences in the data collected that translate to different parameterizations of population projection matrices (Fig. 2; see Johnson et al. 2010*a* for a detailed explanation of age classes for post- and pre-birth pulse surveys).

We used count data of females from successive years to estimate fecundity or recruitment (*F* post-birth pulse or *R* pre-birth pulse) and survival (*S*) values for each life stage on an annual basis (Table 1). For Langley and Mono, populations surveyed post-birth pulse, we estimated fecundity of adult females (F_{A}), survival from newborn to yearling (S_{N}), and adult survival (S_{A}). We estimated fecundity as the number of female lambs/adult females or $N_{\mathrm{N}♀}(t)/N_{\mathrm{A}}(t)$. Given the influence of demographic stochasticity inherent with small sample sizes we used available data on the sex of yearlings in year $t + 1$ to correct for known numbers of female lambs in year t and assumed a 50:50 sex ratio for lambs of unknown gender. Based on other studies of reproduction of Rocky Mountain bighorns (Gross et al. 2000, Singer et al. 2000, Festa-Bianchet and King 2007) and our pregnancy data for 13 yearlings, we assumed that yearling fecundity was half that of adult females. We estimated newborn to yearling survival as $N_{\mathrm{Y}}(t)/N_{\mathrm{N}}(t-1)$, assuming equal survival between males and females, as we did not identify newborn lambs by sex. We calculated adult female survival as $N_{\mathrm{A}}(t)/[N_{\mathrm{A}}(t-1) + N_{\mathrm{Y}}(t-1)]$. Due to extremely small population sizes in Mono Basin, calculations of adult female survival exceeded 1.0 in 3 yr when we observed 1 (in 1996 and 2002) or 2 (in 2001) additional females in year t than those known to be alive in the previous year $t - 1$; we truncated survival in these cases at 1.0. Although field surveys were highly successful at being near-complete

Post-birth pulse (Langley and Mono)

$$\begin{bmatrix} 0 & 0 & F_A S_A \\ S_N & 0 & 0 \\ 0 & S_A & S_A \end{bmatrix}$$

Pre-birth pulse (Wheeler)

$$\begin{bmatrix} 0 & 0 & R_A \\ S_Y & 0 & 0 \\ 0 & S_A & S_A \end{bmatrix}$$

Figure 2. Pre- and post-birth pulse matrix models used to simulate female Sierra Nevada bighorn sheep population dynamics based on data collected 1980–2007 in the Sierra Nevada Mountains, California. Vital rates in the post-birth pulse model are fecundity (F_{A}), newborn to yearling female survival (S_{N}), and adult female survival (S_{A}). Vital Rates in the pre-birth pulse model are recruitment (R_{A}), 2-yr-old female survival (S_{Y}), and adult female survival (S_{A}). Recruitment (R_{A}) accounts for adult survival.

census counts, these calculations demonstrate error in the data that we account for later.

For the Wheeler population (sampled pre-birth pulse), we estimated recruitment (R_A), survival of yearling to 2-yr old (S_Y), and adult survival (S_A). We calculated recruitment for year t as the number of yearling females/adult females or $N_Y(t)/N_A(t-1)$. We calculated yearling to 2 yr old survival as $N_T(t)/N_Y(t-1)$, where N_T was number of 2-yr-olds, which were an identifiable class in the pre-birth pulse survey. Because this was a pre-birth pulse census, yearlings were still 1–3 months younger than 1-yr-olds and could not consistently be identified by sex in the field. Sex ratio among yearlings was 52% female and 48% male (T. Stephenson, California Department Fish and Game, unpublished data). Consequently, we assumed equal survival between males and females. We calculated adult female survival in year t as $N_A(t)/[N_A(t-1) + N_Y(t-1)]$.

Vital rate estimates included process variance, the true biological variation in a rate due to spatial and temporal factors (often called environmental stochasticity), demographic variance, and sampling variance, arising from inherent uncertainty in parameter estimation (Link and Nichols 1994, White 2000). Because we were only interested in the influence of process variance in vital rate estimates on Sierra Nevada bighorn population performance (White 2000, Mills and Lindberg 2002), we removed sampling (and confounded demographic) variance from our binary vital rate data and report the resulting estimators (Table 1; Burnham et al. 1987, Johnson 1989). We used the program Kendall.m in MATLAB (Morris and Doak 2002) to search >1,000 combinations of means and variances for each rate to estimate corrected population-specific vital rate parameters. We also estimated correlations (positive and negative) among rates for each population (Appendix) using annual vital rate estimates following Morris and Doak (2002). To evaluate if temporal autocorrelation could have induced correlations between vital rates, we estimated the temporal correlation in vital rates for each population using a lag of 1 yr. The results did not show any patterns of significant correlation.

Population Model

For the underlying population model, we constructed a stochastic, discrete time, stage-structured matrix model. Reproduction in our study populations occurred once per year in a short birthing season and adults were capable of reproduction in sequential years. Accordingly, we used a 1-yr (1 May–30 Apr) interval to model population growth. We based our model on 4 approximate life stages—approximate because animals could be 1–3 months older than stated age for post-birth models and 1–3 months younger for the pre-birth pulse model. For post-birth pulse populations, the stages were newborns (*N*; 0–1 yr old), yearlings (*Y*; 1–2 yr old), adults (*A*; 2–16 yr old), and senescent adults (*O*; >16 yr old). For pre-birth pulse populations, the stages were yearlings (*Y*; 1–2 yr old), 2-yr-olds (*T*; 2–3 yr old), adults (*A*; 3–16 yr old), and senescent adults (*O*; >16 yr old).

We included the senescent age class to eliminate accumulation of biologically improbably aged adults that can occur without a terminal stage (Mollet and Cailliet 2002). We estimated the probability that an animal survives the time step and transitions from the adult to senescent age class as (Crouse et al. 1987):

$$p_O = S_A^d \left(\frac{1-S_A}{1-S_A^d} \right)$$

where d is the duration spent in the adult age class for the oldest individuals. We calculated d based on a maximum life expectancy of free-ranging bighorn females of 16 yr (Geist 1971, Jorgenson et al. 1997, McCarty and Miller 1998). We assumed survival of animals in the senescent stage class was zero (Byers 1997). Although differences in survival and reproduction may occur among female adult age classes (McCarty and Miller 1998, Berube et al. 1999, Rubin et al. 2002, Festa-Bianchet and King 2007), available demographic data and current management practices do not allow for further resolution (USFWS 2007).

Because we did not document migration among occupied herd units during 10 yr of intensive study, we did not include immigration or emigration in the model. We tested for density dependence in local populations for the data used in the model (i.e., data collected 1980–2007), using regression analysis of vital rates versus population size (Morris and Doak 2002) and found no evidence of density-dependent effects on stage-specific survival and reproduction. At low numbers the effects of population density on bighorn sheep vital rates may be difficult to quantify (Rubin et al. 2002) and potentially complex relative to theoretical carrying capacity, which may change with habitat use patterns. Under an exponential growth model projected female bighorn population size in the Wheeler and Langley populations grew to untenable levels (e.g., >680 females for Langley by yr 20). Because more recent vital rate data (>2007) suggested density dependency, particularly in reproductive rates (Johnson et al. 2010*b*), we included density dependence in the population model and compared model outputs to a density-independent model.

We incorporated density dependence only in the survival of the youngest class (0–1 yr or 1–2 yr) because bighorn demographic studies have not found density dependence in vital rates of adults (Douglas and Leslie 1986, Wehausen et al. 1987, McCarty and Miller 1998, Festa-Bianchet and King 2007). In addition, long-term studies of large herbivores suggest that adult survival varies little compared to juveniles (Sinclair 1977, Gaillard et al. 1998). For all populations, we used 100 bighorn sheep for carrying capacity for these 3 areas. All 3 areas have had approximately 50 female bighorn (Johnson et al. 2010*a*). We used 100 bighorn sheep for carrying capacity for several reasons. First, from a modeling perspective, the higher the carrying capacity the less density dependent predictions vary from the density independent model for the time frames we used in this analysis. We wished to use the most extreme case, which is the lowest reasonable carrying capacity, to evaluate the case having the greatest divergence with the density independent results. Second, estimates of 100 for carrying capacity were derived in the Recovery Plan (USFWS 2007), based on density dependent patterns of population growth observed in several herds. Finally, because there were large areas of unoccupied habitat in the ranges used by these populations, it was our opinion that the populations could at least double before fill empty habitat.

We used 2 models for density dependence, a Ricker logistic model (Caswell 2001, Morris and Doak 2002) and a ceiling model (Gross et al. 2000, Morris and Doak 2002) in which we invoked the Ricker model of density dependence only after the population size increased to >100 bighorn sheep. For the Ricker model, we solved for the downward survival adjustment parameter so that the populations would grow to 100 by $t = 20$. For the ceiling model, we solved for the downward adjustment parameter such that survival of youngest class at $N = 100$ would yield lambda (λ) = 1 in a deterministic matrix model. We used both forms of the model to explore the potential impact of density dependence on meeting recovery plan goals.

To incorporate environmental variation, we multiplied the population vector for each year by a randomly drawn matrix of vital rate values. We used parametric bootstrapping to select a random value for each vital rate from beta distributions having means, process variances, and a correlation structure specific to each population (Morris and Doak 2002). We generated correlated beta variables by first creating a set of correlated normal random numbers from the vital rates (using Cholesky decomposition), recording their cumulative normal distribution values, and then identifying the numbers (vital rate) from their beta distributions with the same cumulative distribution value (Morris and Doak 2002). Because Sierra Nevada bighorn populations were small, we also incorporated demographic stochasticity in simulations, following Mills and Smouse (1994), for survival and reproduction. We used the randomly selected vital rates in the demographic stochasticity routine to project the population forward. For each model scenario we ran 1,000 iterations and calculated recovery outputs described below. We based the initial population vector on survey data from 2007 (Table 1).

Disease Structure

We incorporated disease by expanding the stage-structured projection matrix in a manner similar to a metapopulation model that includes movement transitions among populations (Morris and Doak 2002). To accomplish this, we expanded the discrete time population matrix to account for demography of individuals within disease states and the flow of individuals between disease states (Oli et al. 2006). Specifically, we embedded a susceptible-infected (SI) disease structure into the matrix by allocating elements to 4 submatrices of the larger matrix to represent populations of susceptible, infected, and transitioning (1 submatrix for susceptible to infected and 1 for infected to susceptible) individuals. The model proceeded in 2 steps: 1) transition in disease status (e.g., susceptible to infected) and 2) survival and, if required, transition to the next stage class.

In addition to vital rate estimates, the combined 4-stage population matrix model with disease (Fig. 3) included the following parameters (for a given yr): $1 - p_{\mathrm{O}}$ = probability of staying in adult class (not becoming senescent), p_{I} = probability that a susceptible becomes infected between t and $t + 1$, p_{S} = probability that an infected recovers and becomes susceptible between t and $t + 1$. Each 4 × 4 submatrix (Fig. 3) represents demography of bighorn in different disease states for each year as: 1) upper left submatrix, those that remained in the susceptible class; 2) upper right matrix, those that transition from infected to susceptible; 3)

$$\left[\begin{array}{cccc|cccc}
0 & (1-p_I)F_{YS}{}^{a}S_{AS} & (1-p_I)(1-p_O)F_{AS}S_{AS}{}^{b} & 0 & 0 & p_SF_{YS}S_{AS} & p_S(1-p_O)F_{AS}S_{AS} & 0 \\
(1-p_I)S_{NS} & 0 & 0 & 0 & p_SS_{NS} & 0 & 0 & 0 \\
0 & (1-p_I)S_{AS} & (1-p_I)(1-p_O)S_{AS} & 0 & 0 & p_SS_{AS} & p_S(1-p_O)S_{AS} & 0 \\
0 & 0 & 0^{c} & 0 & 0 & 0 & 0 & 0 \\
\hline
0 & p_IF_{YI}S_{AI} & p_I(1-p_O)F_{AI}S_{AI} & 0 & 0 & (1-p_S)F_{YI}S_{AI} & (1-p_S)(1-p_O)F_{AI}S_{AI} & 0 \\
p_IS_{NI} & 0 & 0 & 0 & (1-p_S)S_{NI} & 0 & 0 & 0 \\
0 & p_IS_{AI} & p_I(1-p_O)S_{AI} & 0 & 0 & (1-p_S)S_{AI} & (1-p_S)(1-p_O)S_{AI} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{array}\right]
\left[\begin{array}{c}
N_{NS} \\ N_{YS} \\ N_{AS} \\ N_{OS} \\ N_{NI} \\ N_{YI} \\ N_{AI} \\ N_{OI}
\end{array}\right]$$

Figure 3. Post-birth pulse disease matrix model for female Sierra Nevada bighorn sheep of the Langley and Mono populations, based on data collected 1980–2007 in the Sierra Nevada Mountains, California. $1 - p_{\mathrm{O}}$ = probability of staying in adult class (not becoming senescent) in a given year, p_{I} = probability of transitioning from susceptible to infected in a given year, p_{S} = probability of transitioning from infected to susceptible in a given year, N = newborn (subscript), Y = yearling (subscript), A = adult (subscript), S = susceptible (subscript), I = infected (subscript), and O = senescent (subscript). Subscripts for the vital rate parameters (i.e., F and S) indicate stage class and disease status. For example, F_{AS} represents fecundity of adult susceptibles, the subscript NS represents newborn susceptibles, NI represents newborn infecteds, etc. Yearling fecundity was half that of adult fecundity; $F_{\mathrm{Y}} = 0.5F_{\mathrm{A}}$. For Wheeler, which had a pre-birth pulse survey, we replaced F_{AS} S_{AS} with recruitment rate (R_{A}; see Fig. 2), which accounts for adult survival, and we replaced newborn survival (S_{N}) with 2-yr-old survival (S_{T}). We removed adults that transitioned to the senescent class from the population (essentially they died after transitioning).

lower left matrix, those that transition from susceptible to infected; and 4) the lower right matrix, those that remained in the infected class. We assumed that once an outbreak occurred, all animals transitioned from susceptible to infected (but not all died), that is $p_{\mathrm{I}} = 1$ and $p_{\mathrm{S}} = 0$. Similarly, when the disease course was over, all animals remaining transitioned back to susceptible ($p_{\mathrm{S}} = 1$ and $p_{\mathrm{I}} = 0$).

Although we modeled projections for each population using population-specific demographic parameters (derived from field data), we used a common set of disease and management parameters (derived from field data, data from other outbreaks, and expert opinion) for all populations. We fixed the annual probability of pathogen introduction giving rise to a new respiratory disease outbreak (p_{outbreak}) at 0.05 (1 outbreak in 20 yr) to represent a mid-range outbreak probability predicted for grazing practices in the vicinity of the Mono and Wheeler populations (Clifford et al. 2009). Thus, because there was no public grazing near the Langley population, results reflect what could happen if grazing was instituted near that population as well. We modeled all disease outbreaks such that during the first year of an outbreak all age classes were impacted by disease, and for ≥ 3 subsequent years lamb survival (for pre-birth pulse census this is survival 0–1 yr, whereas for post-birth census this is recruitment) remained reduced (details described below; Coggins and Matthews 1992, Jorgenson et al. 1997, Singer et al. 2000, Cassirer and Sinclair 2006, George et al. 2008). We allowed new outbreaks to overlap; if probability of a new outbreak (i.e., 0.05) was greater than a uniform random number for a given year and a disease outbreak was already in progress, then we reset the year of the outbreak to 1.

We also included reinfection of previously infected individual bighorn sheep in our model to represent the observed sustained effects of some pathogen introductions on bighorn recruitment (Singer et al. 2000, George et al. 2008). Because reinfection appears to primarily reduce recruitment, we only reduced newborn survival (post-birth pulse model) or recruitment (pre-birth pulse model). We modeled the probability of reinfection (p_{reinfect}) similarly to the probability of outbreak; that is, if p_{reinfect} was greater than a uniform random number for a given year (given an outbreak was in progress), we reset the year of disease outbreak to 1.

To evaluate the extremes of the potential range of introduced pathogen impacts, we simulated 2 disease scenarios. For the "mild" scenario, we reduced the survival of the 2 older age classes by 5% during the first year to represent a minor respiratory pathogen (Singer et al. 2000, Cassirer and Sinclair 2006). Because Sierra Nevada bighorn have not had exposure for a long period of time, especially compared to Rocky Mountain bighorn sheep, it is likely that disease, if introduced, would be severe and kill a high proportion of the population (Miller 2001, George et al. 2008). Thus, we simulated a severe scenario in which we reduced survival of all age classes by 65% to represent a catastrophic die-off, which is in the range observed in other populations (Onderka and Wishart 1984, Coggins and Matthews 1992, George et al. 2008). For both cases, we decreased newborn survival by 65% during the disease course (Jorgenson et al. 1997, Singer et al. 2000, Cassirer and Sinclair 2006, George et al. 2008). We did not mix mild and severe scenarios in the same model run (i.e., all outbreaks within one run of the model were either mild or severe). We did not model a catastrophic outcome. The results of an extreme outbreak that approached 100% mortality would lead to extinction and therefore we chose not to model it. Although our severe outbreak scenario represented 65% mortality across all age classes, recent outbreaks in wild populations have exceeded 80% (Western Association of Fish and Wildlife Agencies 2007). Indeed, catastrophic mortality following an outbreak would result in extinction of some bighorn herds and severely reduce the likelihood of achieving recovery.

The reported length of disease-related reduced lamb survival varies in free-ranging bighorn from 2 yr to 11 yr (Festa-Bianchet 1988, Coggins and Matthews 1992, Ryder et al. 1994, George et al. 2008) and tends to be longer after catastrophic ($\geq 50\%$) all-age die-offs (Coggins and Matthews 1992, George et al. 2008) than less dramatic ($<50\%$) outbreaks (Festa-Bianchet 1988, Ryder et al. 1994). We began with ≥ 2 yr of reduced lamb survival (beyond the first year, in which we reduced survival of all age groups), but to account for variability in the length of disease course and differences between milder and more catastrophic outbreaks, we used different probabilities of reinfection for the 2 scenarios. For the mild-outbreak scenario, we used $p_{\mathrm{reinfect}} = 0.10$, which yielded a 27% chance of reinfection during the 3-yr disease course such that 83% of the outbreaks lasted 2–4 yr, 12% for 5–6 yr, and 5% for 7–12 yr (max. = 12 yr). For the severe-outbreak scenario, we used $p_{\mathrm{reinfect}} = 0.25$, which yielded a 58% chance of reinfection during the 3-yr disease course such that that 65% of the outbreaks lasted 2–4 yr, 23% for 5–6 yr, and 12% for 7–14 yr (max. = 14 yr).

Management Strategies

We used simulation experiments to assess the potential efficacy of 2 disease management strategies on Sierra Nevada bighorn population dynamics and for meeting recovery plan goals. Management simulations represented current or potential strategies intended to reduce the risks and consequences of disease for Sierra Nevada bighorn sheep (SNBS). We applied each management strategy to the 2 disease models. We reduced the probability of an outbreak (p_{outbreak}) to represent a management action that decreases the potential for pathogen introduction (e.g., lowering the probability of contact between domestic and bighorn sheep). We reduced the initial probability of disease outbreak, p_{outbreak}, by 50% or 75%, changing it from the baseline simulation of 0.05 to 0.025 or 0.013. These probabilities represent reduced probabilities of outbreak (0.01–0.03) as estimated by Clifford et al. (2009) when domestic sheep grazing was reduced or spatially and temporally managed for separation in the vicinity of the Mono and Wheeler study areas. We compared outcomes to scenarios with no control (0% reduction in p_{outbreak}) and complete control (100% reduction).

We also reduced the mortality rate of diseased bighorn to represent a management action that improved bighorn survival in the face of introduced disease (e.g., vaccination). We decreased the mortality rate by 50% or 75% by decreasing disease mortality for all stage classes from 0.65 to 0.325 or 0.1625 for the severe case, respectively, to simulate 2 levels of management efficacy. For the mild case, we only decreased mortality for lambs (to 0.325 or 0.1625) to represent a strategy aimed at enhancing lamb survival and recruitment (Cassirer et al. 2001). For both severe and mild cases, we applied the lower lamb mortality rates in all years where disease depressed lamb survival.

Model Outputs

We performed all simulations with MATLAB 7.7 (The MathWorks, Inc., Natick, MA); we ran 1,000 iterations for each scenario. Although we allowed the models to project population dynamics over 20 yr, we present estimates of all outputs using 5- and 10-yr windows as well. Although 20 yr is useful for heuristic purposes, we considered 5 yr and 10 yr more appropriate time frames during which management plans are likely to be evaluated. To meet recovery, ≥12 populations in 4 recovery units must meet recovery goals. We focused on outputs that reflected major recovery plan downlisting or delisting criteria specific to populations (see below), as opposed to land management or regulatory mechanisms (USFWS 2007).

Downlisting (from endangered to threatened status) criterion requires achieving a minimum number of yearling and adult females (≥25 females ≥1 yr old) for each population. We calculated the probability that populations achieved downlisting objectives as a probability for each year as the number of simulations in which there were ≥25 yearling and adult females divided by the total number of simulations. Delisting (from threatened to recovered status) criterion requires maintaining a minimum number of yearling and adult females (≥25 females ≥1 yr old) for ≥7 consecutive years for each population. We calculated the probability that delisting targets were achieved as the number of simulations where there was ≥1 series of 7 consecutive years in which there were ≥25 yearling and adult females by the given output year, divided by the total number of total simulations. Complete delisting further requires that each population is viable with no significant risk of going extinct. We used a quasiextinction threshold of 5 yearling plus adult females for all local populations based on requirements for minimum population size for optimal foraging and antipredator strategies (Berger 1978, Berger and Cunningham 1988). We calculated the probability of quasiextinction for each year as the number of simulations in which the population size was ≤5 yearling and adult females divided by the total number of simulations.

We also calculated the time to achieve delisting criteria of having ≥25 females ≥1 yr old for ≥7 consecutive years for each population. We estimated the mean total female population size at each output year and the difference in number of total females between no control and the 2 management strategies (effect size) for the severe disease scenario.

RESULTS

Without disease, the Langley and Wheeler populations grew, whereas the Mono population remained stable (stochastic $\hat{\lambda}_{t=10}$ was 1.13, 1.07, and 1.00, respectively). Including density dependence changed the projected population sizes but did not materially impact recovery outputs at the time scale of importance to management (≤10 yr) for either the discrete logistic model or ceiling model (Table 2). For the ≤10-yr time frame, density dependent recovery probabilities were 0–4.5% lower than density independent probabilities, with the only exception being the probability of ≥25 sheep under the severe disease scenario (12% lower). Because we did not have compelling evidence for density dependence in our data and because there was little difference between the recovery outputs, we only present results for the simpler density-independent model.

The projected population curves were smooth, in part because all populations were close to their asymptotic stable stage distributions (Johnson et al. 2010*a*). In addition, the process variance on adult survival rates, which had the highest elasticity values for all populations (>0.85; Johnson et al. 2010*a*), was low (Table 1). In the absence of disease, the Langley and Wheeler populations would likely meet delisting criteria within 10 yr, as their estimated probability of quasiextinction was zero and the estimated probability of attaining and maintaining ≥25 females for ≥7 yr was ≥0.96 (Table 3). The Mono population would not likely meet delisting criteria within 10 yr, as the probability of attaining ≥25 females was 0.12, and the probability of attaining and maintaining ≥25 females for ≥7 yr was zero (Table 3).

On average, the Wheeler population performed well with respect to delisting criteria even under mild and severe disease scenarios (Fig. 4A). However, the 95% CI shows that there was a chance of population decline (Fig. 4B). For all populations, if an outbreak occurred, by chance, sooner rather than later, then the population may not grow, as shown by the example simulation trajectories in which an outbreak occurred in year 6 compared to if it happened in year 13 (Fig. 4C). This variation results in the uncertainty reflected in the trajectory CI (Fig. 4B). Under the severe disease scenario, the probability of having a population size ≥25 was ≥0.88 at the lowest (yr 5), and only in the first 10 yr was the probability <0.90 for attaining and maintaining ≥25 females for ≥7 yr (Table 3). The Wheeler population would withstand mild disease outbreaks and continue to grow and likely meet delisting criteria (Table 3). However, under the severe outbreak scenario, disease reduced Wheeler's population growth, which made achieving the minimum population size required to delist the species less likely. Although not likely to go extinct, by year 10 the probability of attaining ≥25 females was 0.69, and the probability of attaining and maintaining ≥25 females for ≥7 yr was 0.67 (Table 3). The Mono population would not be likely to recover without management intervention under any disease scenario; the probability of attaining ≥25 females was low (0.12 at yr 10 even with no disease), and maintaining that level for 7 yr was ≤0.11 for any time frame (Table 3).

Table 2. Projected recovery plan outputs for density independent and density-dependent (DD) models for female Sierra Nevada bighorn sheep of the Wheeler population. We show only Wheeler because it had the largest differences and represents the pattern for all 3 Sierra Nevada bighorn populations. We based population projections on data collected 1980–2007 in the Sierra Nevada Mountains, California.

Disease scenario and pop growth model	Yr	Pr($N < 5$)	Pr($N \geq 25$)[a]	Pr($N \geq 25$) for $\geq$7 consecutive yr[b]	N
No disease					
No DD	5	0.00	0.98		64
	10	0.00	0.99	0.96	91
	20	0.00	1.00	0.99	186
Full DD[a]	5	0.00	0.99		57
	10	0.00	0.98	0.97	70
	20	0.00	0.99	0.99	98
Ceiling DD[b]	5	0.00	0.99		56
	10	0.00	0.99	0.98	70
	20	0.00	0.99	0.99	93
Mild disease					
No DD	5	0.00	0.96		60
	10	0.00	0.95	0.93	78
	20	0.00	0.97	0.98	131
Full DD	5	0.00	1.00		53
	10	0.00	1.00	1.00	60
	20	0.00	1.00	1.00	75
Ceiling DD	5	0.00	0.98		53
	10	0.00	0.96	0.95	61
	20	0.00	0.96	0.97	74
Severe disease					
No DD	5	0.01	0.78		54
	10	0.05	0.69	0.71	63
	20	0.13	0.65	0.78	87
Full DD	5	0.01	0.75		47
	10	0.06	0.62	0.67	49
	20	0.16	0.54	0.71	47
Ceiling DD	5	0.01	0.78		47
	10	0.06	0.61	0.69	47
	20	0.16	0.53	0.72	46

[a] Full DD represents a discrete time Ricker logistic model with a carrying capacity of 100.

[b] Ceiling DD represents a model in which Ricker model density dependence was invoked only after $N > 100$.

Reducing the probability of outbreak or the mortality rate (which was the same as increasing survival rate) had little impact on reaching recovery plan goals when disease was mild (Fig. 5). Management had different impacts under severe disease scenarios; all results we provided here are for year 10. For Langley, the population with the highest growth rate, management yielded only minor improvements because probabilities of achieving recovery goals were already high (Fig. 5). For Wheeler, management to reduce the odds of disease appeared likely to increase the probability of achieving recovery goals. Decreasing p_{outbreak} or mortality rate by 50% increased the probability of attaining ≥25 adult females by 19% and 33%, respectively; gains in the probability of attaining and maintaining ≥25 adult females were similar (19% and 34%, respectively; Fig. 5). For Langley and Wheeler, management actions had little impact on probability of quasiextinction (Fig. 5). By contrast, for Mono decreasing p_{outbreak} or mortality rate by 50% decreased the probability of quasiextinction by 42% and 54%, respectively, while having little impact on the probabilities of the

Table 3. Projected recovery plan outputs for no disease and disease scenarios for female Sierra Nevada bighorn sheep. For the mild disease scenario, we reduced survival rates of >1-yr-olds by 5% and lamb survival by 65% for the year of disease outbreak. For severe the disease scenario, we reduced all survival rates by 65% for the year of disease outbreak. For both disease scenarios, we reduced lamb survival 65% for 2–14 yr following the first year of disease outbreak. We based population projections on data collected 1980–2007 in Sierra Nevada Mountains, California.

		Pr($N < 5$)[a]			Pr($N \geq 25$)[b]			Pr($N \geq 25$) for $\geq$7 consecutive yr[b]		
Population	**Yr**	**No**	**Mild**	**Severe**	**No**	**Mild**	**Severe**	**No**	**Mild**	**Severe**
Langley	5	0.00	0.00	0.00	1.00	1.00	0.88			
	10	0.00	0.00	0.02	1.00	1.00	0.90	1.00	1.00	0.84
	20	0.00	0.00	0.04	1.00	1.00	0.89	1.00	1.00	0.93
Wheeler	5	0.00	0.00	0.01	0.98	0.96	0.76			
	10	0.00	0.00	0.05	0.99	0.95	0.69	0.96	0.93	0.67
	20	0.00	0.00	0.13	1.00	0.97	0.65	0.99	0.98	0.78
Mono	5	0.01	0.02	0.16	0.03	0.02	0.02			
	10	0.04	0.09	0.33	0.12	0.08	0.06	0.00	0.00	0.00
	20	0.13	0.27	0.59	0.20	0.12	0.07	0.11	0.07	0.05

[a] Total female N.

[b] Adult (>1 yr-old) female N.

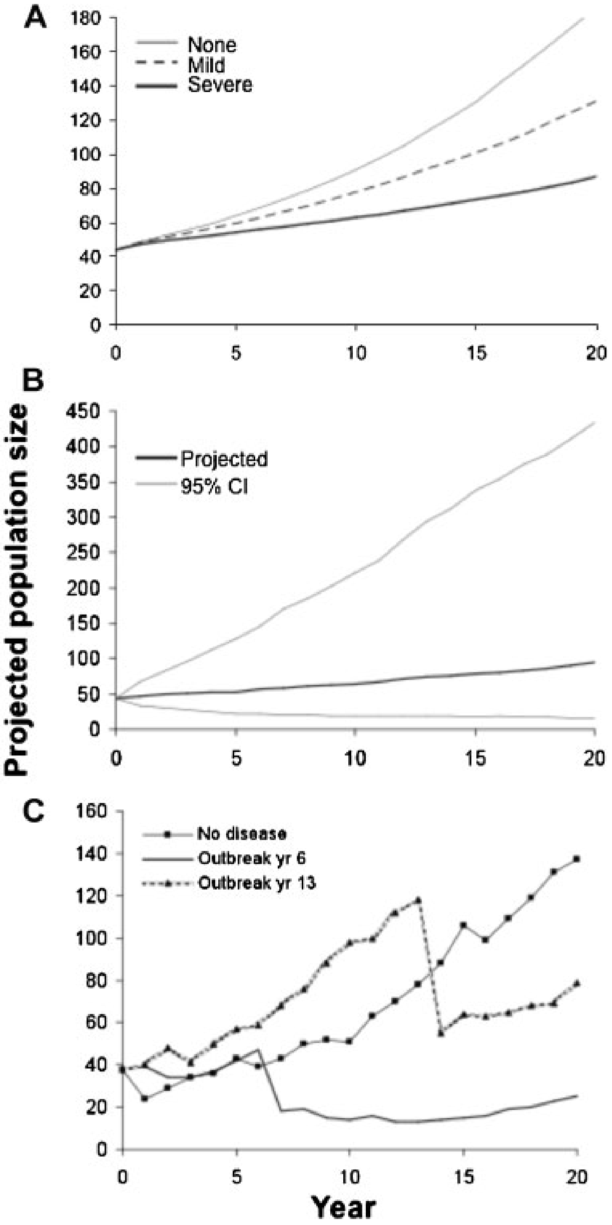

Figure 4. Projected population sizes of female Sierra Nevada bighorn sheep from the stochastic simulation model for Wheeler for (A) mean projected population size for no, mild, and severe disease scenarios, (B) mean projected population size and 95% confidence intervals for severe disease scenario, and (C) single population projections from 3 simulations; one with no disease and two with severe disease outbreaks at different random intervals. We based population projections on data collected 1980–2007 in the Sierra Nevada Mountains, California.

population attaining $\geq$25 females and of attaining and maintaining $\geq$25 females (Fig. 5). For all cases, reducing the disease mortality rate had a slightly greater benefit compared to reducing the probability of outbreak by the same percentages (Fig. 5).

The probability that time to recovery was $<$10 yr for Langley and Wheeler was high ($\geq$0.92) for no disease and mild disease scenarios (Table 4). For the severe disease scenario, probabilities that time to recovery was $<$10 yr dropped to 0.84 for Langley and 0.66 for Wheeler. More effective management actions (i.e., 75% reductions in probability of outbreak or mortality rate) increased the probability of recovering in $<$10 yr to $\geq$0.88 for both populations (Table 4). For Mono, the probability that time to recovery would be $\leq$10 yr was zero, and the probability of recovering in $\leq$20 yr was low ($\leq$0.10) for all disease cases and management scenarios (Table 4).

DISCUSSION

Results from our simulations are consistent with previous demonstrations of the negative influence of domestic sheep on bighorn sheep viability (Gross et al. 2000; Singer et al., 2000, 2001). Because population dynamics vary greatly among herds, effective management of Sierra Nevada bighorn requires strategies to be population-specific (Johnson et al. 2010*a*). Simulating respiratory disease in populations and evaluating disease management alternatives underscores this point. The 3 bighorn populations we studied exhibited different population growth rates (Langley $\hat{\lambda} = 1.13$, Wheeler $\hat{\lambda} = 1.07$, and Mono $\hat{\lambda} = 1.00$) and different responses to severe disease. Langley, with its high growth rate, appears robust to disease and may experience milder impacts, whereas Wheeler, with its moderate growth rate, would require disease management to prevent severe outbreaks and meet recovery plan goals. By contrast, Mono, with its flat growth rate, requires management intervention even in the absence of disease to achieve recovery goals. Accordingly, with respect to recovery plan objectives, inference from a nonrepresentative population could lead to incorrect intervention for some Sierra Nevada bighorn populations in the face of a disease outbreak and possibly extinction of some local populations.

Both severe and mild disease outbreaks can increase the time to meet recovery plan goals, although mild disease impacts are less direct. Simulations indicated severe disease can decrease population size and increase time to recovery for all populations, whereas mild disease appeared to have little impact on the recovery of a population. Other field studies have reported population declines only when disease caused increased mortality in all age classes (Coggins and Matthews 1992, Cassirer and Sinclair 2006, George et al. 2008). However, long-term low recruitment rates caused by disease may prevent populations from recovering (George et al. 2008) and, if recruitment is depressed for a long time, the herd may eventually go extinct. A population with a disease outbreak that affected only lamb survival (and hence recruitment), without an initial all-age die-off, will take longer to show a decline than the time span of our simulations, but will still reduce recovery prospects. Moreover, mild disease outbreaks that result in low lamb recruitment reduce the number of surplus animals available for translocation. Recovery of Sierra Nevada bighorn is dependent upon expanding their geographic distribution into historic range via translocations as well as keeping extant herds viable. Even if reduced recruitment does not lead to population declines, it may reduce or end translocation, which is an essential management action to meet recovery goals. Through a reduction in translocation, even a mild disease outbreak can increase the time to achieve the total minimum number of females required for delisting ($n = 305$; USFWS 2007), and hence,

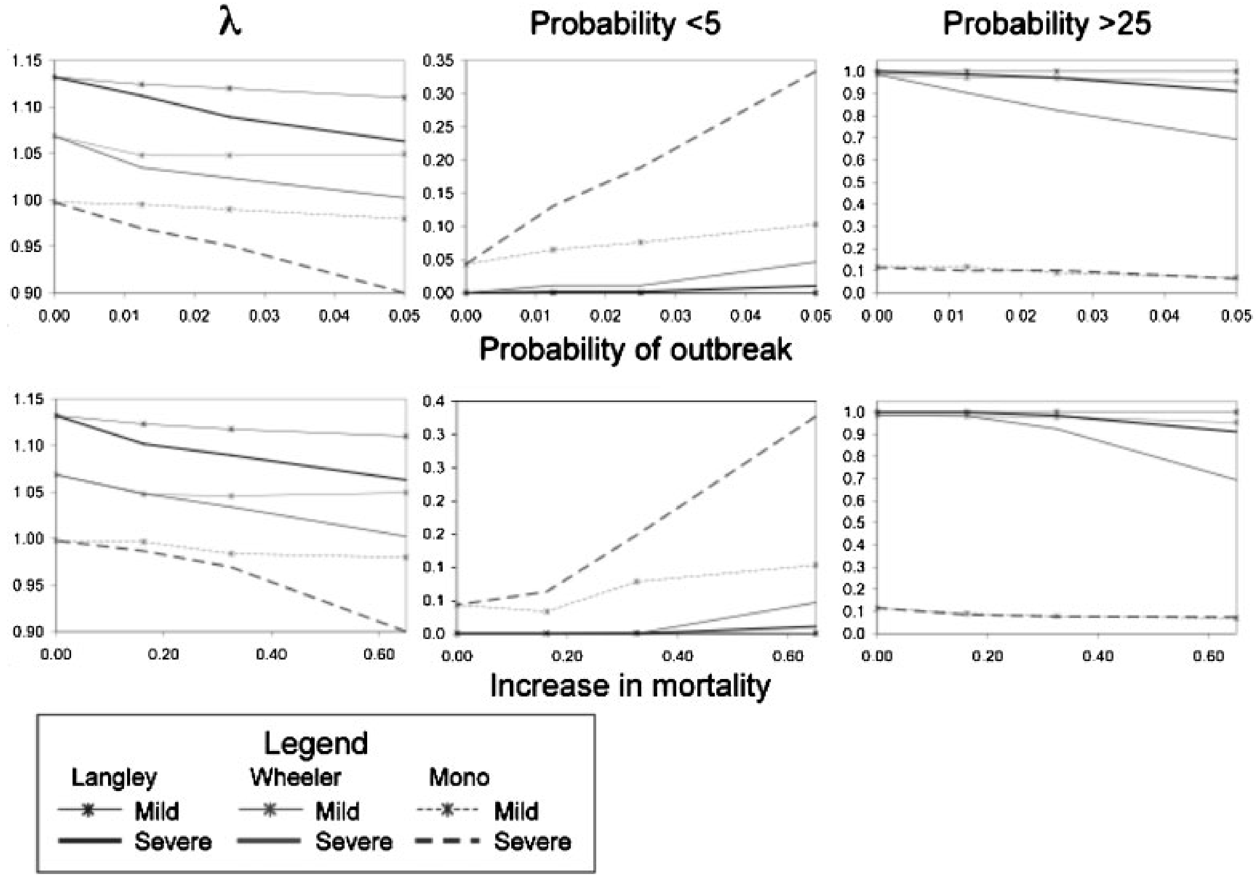

Figure 5. Projected impact of reducing probability of outbreak (p_{outbreak}) or mortality rate on recovery plan outputs for year 10 for mild and severe disease outbreaks for female Sierra Nevada bighorn sheep, represented here as the probability that the population falls below <5 females and ≤25 females. The mild disease scenario represents 5% reduced survival across yearling, adult, and senescent age classes and 65% lower lamb survival; severe disease represents 65% reduced survival across all age classes followed by persistent 65% lower lamb survival. We based population projections on data collected 1980–2007 in the Sierra Nevada Mountains, California.

indirectly reduce the overall probability of meeting Sierra Nevada bighorn recovery plan goals over the next 10–20 yr.

Our primary objective was to create a middle-of-the-road disease model to evaluate potential impacts of respiratory disease on Sierra Nevada bighorn population recovery. Because Sierra Nevada bighorn have not had a documented respiratory-disease-related event within 40 yr it is possible that this model underestimates the impact of a disease outbreak on local populations. A respiratory disease outbreak could result in a catastrophic all-age die-off with higher adult mortality than we estimated. For example, catastrophic population losses from respiratory disease of 75% were reported in Idaho (Cassirer et al. 1996) and 80% in Montana (Enk et al. 2001). Moreover, Sierra Nevada bighorn exist in small isolated populations and, therefore, are vulnerable to extinction due to environmental and demographic stochasticity

Table 4. Probabilities of time to recovery for female Sierra Nevada bighorn sheep for different disease scenarios and management strategies. Results shown are for management strategies applied to the severe disease scenario. We based population projections on data collected 1980–2007 in Sierra Nevada Mountains, California.

Population	Time to recovery (yr)[a]	No disease	Mild disease	Severe disease	Pr(outbreak) 50% Reduction	Pr(outbreak) 75% Reduction	Mortality rate 50% Reduction	Mortality rate 75% Reduction
Langley	<10	1.00	1.00	0.84	0.91	0.96	0.98	1.00
	10–20	0.00	0.00	0.08	0.07	0.03	0.01	0.00
	>20	0.00	0.00	0.08	0.02	0.01	0.01	0.00
Wheeler	<10	0.94	0.92	0.66	0.80	0.88	0.89	0.96
	10–20	0.05	0.06	0.10	0.07	0.06	0.07	0.03
	>20	0.01	0.02	0.24	0.13	0.08	0.04	0.01
Mono	<10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	10–20	0.04	0.03	0.02	0.08	0.09	0.06	0.07
	>20	0.96	0.97	0.98	0.92	0.91	0.94	0.93

[a] We define recovery as having ≥25 adult females for ≥7 consecutive years.

alone (Boyce 1992). Even with the severe scenario, an early outbreak could result in more severe consequences than portrayed by the mean population trajectory (Fig. 4). For any severe outbreak, even Langley, the population with the highest growth rate, could face extinction risk or, at a minimum, protracted recovery.

On the other hand, a counterargument can be made that our model overestimates the impact of disease because we did not include any population substructure. That is, if one sheep in the model becomes infected, all sheep in the model become infected and have the same increase in mortality probability. Behavioral or spatial population substructure can serve as a barrier to disease spread by decreasing the chance that one or more groups of sheep contact infected groups (Loehle 1995, Ball et al. 1997, Keeling 1999). Although substructure may exist in the populations we studied, the groups appear to be fission–fusion with mixing on winter range. In addition, male bighorn range far and unpredictably especially during the breeding season (Festa-Bianchet 1986). Fission–fusion substructure combined with male breeding movements are likely to attenuate any barrier effects that substructure can provide for disease spread (Cross et al. 2005, and e.g., George et al. 2008). We conclude that any substructure of Sierra Nevada bighorn is unlikely to influence our general conclusions and that, if anything, we may underestimate the impact a first contact with disease may have on SNBS.

A range of management actions can be employed to diminish disease risk by reducing the probability of outbreak. Disease management strategies include reducing or restricting domestic grazing in the vicinity of bighorn ranges, closely managing domestic sheep for strays, and in some cases, permanently closing allotments or choosing not to convert them to domestic sheep grazing (U.S. Forest Service 2006, Western Association of Fish and Wildlife Agencies 2007, Council for Agricultural Science and Technology 2008, Clifford et al. 2009). Our grazing management simulations reflect these types of actions. Simulation results indicated that reducing the probability of outbreak could increase the probability of meeting recovery goals by 19–34%. A 75% reduction in probability of outbreak would yield high probabilities (≥ 0.88) of meeting recovery plan goals for all 3 populations within 10 yr. And this size reduction may be attainable; the spatial risk model of Clifford et al. (2009) indicated that current grazing restrictions in the area may reduce the probability of outbreak by approximately 75%.

Although preventing or reducing risk by altering the configuration of grazing allotments is currently the most viable option for management, culling and vaccination are strategies that have been discussed or tested in other bighorn sheep populations (Miller et al. 1997; Cassirer et al. 2001; K. Hurley, Western Association of Fish and Wildlife Agencies, personal communication). We modeled the impact of vaccination, or a similar strategy, to compare this prospective management approach to what is presently used. In addition, we wanted our management simulations to serve a broader purpose as a heuristic tool, with application for other wildlife populations. Simulation results indicated that vaccination was slightly more effective than reducing the probability of outbreak with respect to meeting recovery goals for SNBS. However, the difference was not large enough to be of practical importance. We conclude that preventing disease outbreaks by altering the intensity, location, or duration of domestic sheep grazing remains the most viable and effective management option for mitigating disease risk.

Stochastic projection models are well recognized for their ability to synthesize data, identify data gaps, identify sensitive vital rates to target for management, and evaluate different population scenarios (e.g., varying predation rates, severe weather) and management actions (e.g., removals for translocations, habitat enhancements; e.g., Beissinger and Westphal 1998, Morris and Doak 2002). In the context of endangered species management, stochastic projection models are especially useful because they allow managers to develop a realistic assessment of the probability of meeting recovery plan goals and can be employed when a population's small size or status precludes experimentation. The addition of disease to such models is important. First, this approach explicitly addresses how disease can influence demographic properties and structure of populations (Cunningham and Daszak 1998). Second, it can help managers to evaluate the effect of multiple disease management strategies on population performance, as well as recovery and extinction probabilities.

Our approach to modeling disease outbreaks was an extension from similar models (Haydon et al. 2002, Oli et al. 2006), and provides a more realistic approach to modeling infection and reinfection of a certain class or classes. The model's inputs can be easily modified to represent other diseases with different probabilities of infection, lengths of infectivity, probabilities of reinfection, mortality rates, etc. In addition, model inputs include annual additions and subtractions of animals to allow managers to evaluate the impact of disease with different levels of predation and translocation (see Supporting Material available online at www.onlinelibrary.wiley.com). We hope this model provides an accessible flexible framework for incorporating disease in stochastic population projection modeling and will serve as a useful tool for other ungulate managers. The ability to generalize this model reflects our intent to provide a framework that will stimulate discussion and research leading to improvements on existing methodology and ungulate conservation.

MANAGEMENT IMPLICATIONS

Our simulation results indicate that management strategies for Sierra Nevada bighorn need to be population specific. Based on our findings, we recommend that multiple representative populations be monitored as part of any endangered species recovery and monitoring plan. Our stochastic population model supports Sierra Nevada bighorn recovery efforts because it allows managers to evaluate the probability of meeting recovery goals in light of disease risk. In general, we recommend that stochastic population models used for endangered species management include outputs cast as probabilities of meeting recovery plan goals. The risk of disease outbreaks for SNBS, whether mild or severe, must be mitigated to increase the probability of meeting recovery plan goals. That is, simulations indicate that severe outbreaks decrease population sizes and directly reduce the probability of meeting minimum population size goals, whereas mild outbreaks reduce recruitment and the number of individuals available for translocation to other populations and indirectly reduce the probability of meeting overall, range-wide minimum population size goals. Moreover, because it is possible that our model underestimates the impact disease will have on Sierra Nevada bighorn recovery, continued reduction of the risk of disease outbreak is paramount. At a minimum, to assist recovery for the Wheeler and Mono populations we recommend reducing the probability of outbreak by continuing efforts to manage high-risk (i.e., spatially close) allotments through restricted grazing regimes and stray management. We also recognize that closing grazing allotments until Sierra Nevada bighorn achieves recovery objectives would further population recovery. As managers consider reintroduction of wild sheep throughout the western United States, it is important that they determine the level of disease risk and consequences of outbreaks and evaluate potential management strategies.

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Appendix. Correlation matrices for Sierra Nevada bighorn sheep population vital rates based on data collected 1980–2007 in Sierra Nevada Mountains, California.

Population	Recruitment or fecundity	2-yr-old or yearling survival	Adult survival
Wheeler			
Recruitment	1.0		
2-yr-old survival	0.442	1.0	
Adult survival	0.262	0.696	1.0
Langley			
Fecundity	1.0		
Yearling survival	−0.127	1.0	
Adult survival	−0.172	−0.263	1.0
Mono			
Fecundity	1.0		
Yearling survival	−0.185	1.0	
Adult survival	−0.337	0.096	1.0

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