



Assessing disease risk at the wildlife–livestock interface: A study of Sierra Nevada bighorn sheep

Deana L. Clifford^{a,*}, Brant A. Schumaker^a, Thomas R. Stephenson^b, Vernon C. Bleich^{b,1}, Maya L. Cahn^c, Ben J. Gonzales^d, Walter M. Boyce^a, Jonna A.K. Mazet^a

^aWildlife Health Center, School of Veterinary Medicine, One Shields Ave., University of California, Davis, CA 95616-5270, USA

^bSierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, 407 West Line Street, Bishop, CA 93514-3321, USA

^cYale University School of Forestry and Environmental Studies, Greeley Memorial Laboratory, 370 Prospect Street, New Haven, CT 06511-2104, USA

^dWildlife Investigations Laboratory, California Department of Fish and Game, 1701 Nimbus Road, Rancho Cordova, CA 95670-4503, USA

ARTICLE INFO

Article history:

Received 17 June 2008

Received in revised form 6 February 2009

Accepted 1 June 2009

Available online 3 July 2009

Keywords:

Risk assessment

Modeling

Domestic sheep

Pasteurella

Ovis aries

Ovis canadensis sierrae

ABSTRACT

Despite evidence that domestic sheep diseases threaten the persistence of bighorn sheep populations, the economic consequences of restricting domestic sheep grazing has polarized the debate, with some arguing that disease risk posed by domestic sheep has been exaggerated and grazing restrictions should be eased. We constructed a model to assess how different management strategies (grazing allotment closures, grazing time reductions, and reduced probability of stray domestic sheep) affect the risk of respiratory disease transmission from domestic sheep to endangered Sierra Nevada bighorn sheep, and to predict population-level impacts of an outbreak. Even when management strategies reduced risk of interspecies contact to less than 2% per year, our model predicted a 50% probability of a catastrophic respiratory disease outbreak during the next 10 bighorn sheep generations. If an outbreak occurs in the near future, the model predicts that the smallest Sierra Nevada bighorn sheep population would have a 33% probability of quasi-extinction. To eliminate all risk of contact and potential disease transmission, domestic sheep cannot be grazed on allotments that overlap with areas utilized by Sierra Nevada bighorn sheep. Where wildlife and domestic animal populations share limited habitat, and there is documented evidence of a substantial disease threat and extinction risk, stakeholders must recognize that the only way to eliminate contact and risk of disease transmission is to give priority to one species or the other. If conservation is the priority, difficult decisions will need to be made to balance trade-offs between economic livelihoods and species conservation.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

The challenge of balancing species conservation and livestock-based livelihoods is exemplified by the respiratory disease complex affecting North American bighorn sheep (*Ovis canadensis*). Formerly abundant throughout western North America, many bighorn sheep populations declined or were eliminated by the early 1900s due to over-hunting, disease, competition with domestic livestock for forage, and competition with humans for space (Beuchner, 1960). Active recovery efforts (transplantation into unoccupied habitat, augmentation of existing herds, and habitat manipulation)

have had varying success but have been consistently unsuccessful in areas where contact with domestic sheep has occurred (Schommer and Woolever, 2001).

Although closely related to domestic sheep (*Ovis aries*), bighorn sheep did not evolve with them or their pathogens and thus are vulnerable to many infectious diseases commonly carried by domestic sheep, including respiratory diseases of viral and bacterial origin, contagious ecthyma, and psoroptic scabies (Jessup and Boyce, 1993). There is substantial, albeit circumstantial, evidence that contact with domestic sheep is associated with respiratory disease outbreaks causing significant morbidity and mortality in free-ranging bighorn sheep populations (Martin et al., 1996).

These large-scale respiratory disease die-offs in free-ranging bighorn are most often attributed to pneumonia caused by *Pasteurella* genus bacteria, specifically *Manheimia haemolytica*, *Pasteurella multocida*, and *Pasteurella trehalosi* (Garde et al., 2005; Schommer and Woolever, 2008). Outbreaks manifest acutely as an all-age mortality event often followed by 3–5 years of low survival of lambs born to possibly chronically infected ewes (Coggins, 1988;

* Corresponding author. Tel.: +1 530 752 4167; fax: +1 530 752 3318.

E-mail addresses: dlclifford@ucdavis.edu (D.L. Clifford), theschu@ucdavis.edu (B.A. Schumaker), TStephenson@dfg.ca.gov (T.R. Stephenson), vbleich@ndsupernet.com (V.C. Bleich), maya.cahn@yale.edu (M.L. Cahn), BGonzalez@dfg.ca.gov (B.J. Gonzales), wmboyce@ucdavis.edu (W.M. Boyce), jkmazet@ucdavis.edu (J.A.K. Mazet).

¹ Present address: Department of Biological Sciences, Idaho State University, 921 South 8th Ave., Pocatello, ID 83209-0001, USA.

Coggins and Matthews, 1990; Foreyt, 1990; George et al., 2008). Although bighorn sheep that have had no known contact with domestic sheep may also carry *Pasteurella* spp. and *M. haemolytica* strains, and respiratory disease outbreaks in free-ranging bighorn sheep have occurred in the absence of any known association with domestic sheep (Goodson, 1982), the majority of documented bighorn sheep die-offs follow contact with domestic sheep (Foreyt, 1994; Martin et al., 1996). Treatment or vaccination of free-ranging bighorn are not considered viable management options due to limited drug effectiveness and inherent logistical difficulties associated with delivering multiple doses of medication or vaccine in remote, inaccessible terrain (Cassirer et al., 2001; Foreyt, 1992; Foreyt and Silflow, 1996; Kraabel et al., 1998; Miller et al., 1997; Ward et al., 1999).

Pasteurella and *Manheimia* spp. bacteria are associated with multifactorial pneumonia, but are rarely thought to be a primary pathogen in domestic sheep (Kimberling, 1988). Transmission between animals occurs via nose to nose contact or through contact with aerosolized droplets containing the bacteria. Direct contact may not be necessary for transmission, as *P. multocida* remains viable when aerosolized for up to 18 m (Dixon et al., 2002). Furthermore, *M. haemolytica* has been isolated from grass in a field grazed by domestic sheep and is known to remain viable in straw for up to 48 h (24 h at 25 °C, and 48 h at 4 °C), and in water stored at 4 °C for up to 7 days (Burriel, 1997).

Both planned pen experiments (Callan et al., 1991; Foreyt, 1989, 1990, 1994; Onderka and Wishart, 1988) and observations of accidental interspecies contacts of semi-free ranging bighorn sheep (Foreyt and Jessup, 1982) held in large enclosures (2.5–445 ha) further support the hypotheses that bighorn sheep contract fatal respiratory disease from apparently healthy domestic sheep. In these 12 trials, all but one (79/80) of the exposed bighorn died from pneumonia while all domestic and domestic-exotic hybrid sheep remained healthy (Schommer and Woolever, 2008).

Despite a large body of evidence that domestic sheep diseases threaten the persistence of bighorn sheep populations, the economic consequences of restricting domestic sheep grazing has polarized the debate, with some arguing that disease risk posed by domestic sheep has been exaggerated and grazing restrictions should be eased. In response, the Western Association of Fish and Wildlife Agencies recently recommended the use of risk assessments to encourage objective decision making by land managers (Western Association of Fish and Wildlife Agencies, 2007). To date, attempts to characterize risk and investigate management solutions have been solely qualitative in nature (Garde et al., 2005; US Department of Agriculture Forest Service, 2006) because of data uncertainties and the complexities involved with making a model that is relevant for land-use decision makers (US Department of Agriculture Forest Service, 2006). Bias can be exhibited when qualitatively evaluating risk (Hunter and Fewtrell, 2001), and risk trade-offs often may favor the traditional economics of a situation (Graham and Wiener 1995). Consequently people may resist responding proactively to a threat of an event that has a low probability of occurring even though there are major consequences if the event does occur. For example, the likelihood of a disease outbreak in bighorn sheep may be low, but the consequences of such an outbreak could lead to extinction of local populations. The net effect of this uncertainty is that despite evidence of a threat, land managers across the west have not substantially modified activities regarding the permitting of domestic sheep grazing on federal lands in proximity to bighorn sheep ranges.

There is a clear need for an objective method to help land managers identify and mitigate risk, but a repeatable approach for quantitatively modeling disease risk posed by domestic sheep in specific situations has not been available. Accordingly, we developed a spatially explicit disease transmission model to quantita-

tively assess the risk of respiratory disease transmission from domestic to bighorn sheep and to predict impacts of a respiratory disease outbreak in terms of mortality and risk of disease spread within and among populations. We parameterized our model with the best available spatial, demographic, and disease data from an intensively monitored endangered bighorn sheep population and tailored our predictions to investigate domestic sheep management options to reduce risk. We evaluated whether or not reducing the available grazing area, restricting grazing time on allotments perceived as high risk, or improving stray sheep management would reduce the risk of interspecies disease transmission. Our broader goals were to provide scientifically-based recommendations to those responsible for managing bighorn sheep and the lands they inhabit, and to develop a tool that could be applied to other diseases transmitted between species at the wildlife–live-stock interface.

2. Methods

2.1. Study area and populations

The Sierra Nevada (37°24'N, 118°41'W) extends 650 km along the eastern edge of California, ranging from 75 to 125 km in width (Hill, 2006). Approximately 400 endangered Sierra Nevada bighorn sheep occur in eight small but increasing subpopulations comprising three distinct populations (US Fish and Wildlife Service, 2000). Domestic sheep are grazed on public and private lands within or adjacent to habitat currently occupied by Sierra Nevada bighorn sheep. Although direct contact between Sierra Nevada bighorn sheep (hereafter termed bighorn sheep) and domestic sheep has not been documented in the past 30 years (possibly as a result of the limited distribution and low numbers of bighorn sheep and limited human presence in remote areas), in recent years bighorn sheep have traveled into domestic sheep grazing allotments. Efforts by management agencies to mitigate disease risk from interspecies contact have included closing high elevation domestic sheep grazing areas in bighorn sheep habitat, restricting domestic sheep grazing time on allotments perceived as high risk, and encouraging good domestic sheep husbandry practices to reduce the likelihood of animals straying from the herd.

2.2. Disease risk assessment

We assessed the risk of respiratory disease for three bighorn sheep populations (North, Central, and South) differing in their spatial and temporal overlap with domestic sheep. We first evaluated the risk of disease transmission by deriving probabilities of interspecies contact from bighorn sheep population monitoring data and domestic sheep grazing data. Next, we predicted the short-term population-level impacts of a respiratory disease outbreak in bighorn sheep using an epidemiologic simulation model. We then focused our analysis on the bighorn sheep population with the highest risk of disease transmission and evaluated the other two populations in the context of spread of an introduced disease from the source population. Data were gathered from demographic monitoring efforts, pertinent literature, and county and government records. We relied on expert opinion rarely when other sources were not available.

2.2.1. Determination of interspecies contact and disease transmission

Satellite telemetry (GPS) collar data collected from 2002 to 2006 for 34 (15 male: 19 female) adult bighorn sheep were used to determine the probability distribution in each population for spring–summer (March–September) and rut (October–November). Probability distributions were calculated using 50%, 60%, 70%, 80%, 90%, and 100% fixed kernel estimators, (Rodgers and Carr, 1998)

with a bandwidth of 0.80 to attenuate measurement/sampling error and to adequately reflect peripheral movement (Powell, 2000). We used the 100% volume contour to estimate the maximum area used by the entire population. A sample of available locations ($n = 10,215$) with a minimum separation of 12 h between fixes was utilized for kernel estimation to avoid spatial autocorrelation (Swihart and Slade, 1985).

The area (km^2) of all federal grazing allotments and non-federal (not owned or managed by the federal government) lands located within or adjacent to bighorn sheep habitat was derived from spatial files provided by the Humboldt-Toiyabe and Inyo National Forests, the Bureau of Land Management, and the public domain, or calculated using ArcGIS v9.0 (Environmental Systems Research Institute, Redlands, CA, USA) and Hawth's Tools v3.26 (Beyer, 2004). Based on radio-telemetry and observational data from a sample of domestic sheep, we created a 1-km buffer around individual grazing allotment boundaries to account for potential movements of stray individuals or herds outside an allotment (California Department of Fish and Game, 2006). The area of overlap for individual grazing allotments (with and without the 1-km buffer) within each fixed kernel contour for bighorn sheep populations was calculated for spring–summer and rut.

The probability of interspecies co-habitation on each allotment, $p(\text{IC})$, was the product of the probability that a bighorn sheep was on the grazing allotment and the probability that a domestic sheep was within one or more of the bighorn sheep kernel contours during that season. We assumed an equal likelihood of a domestic sheep being present on any portion of the grazing allotment at any time during the approved grazing period because detailed radiotelemetry data describing the movements of domestic sheep bands did not exist for most allotments. We then adjusted for temporal overlap between the species by reducing the $p(\text{IC})$ for each allotment according to the fraction of the season domestic sheep were permitted to graze each allotment. Domestic sheep grazing schedules were available for only two non-federal land parcels, thus $p(\text{IC})$ s for the other non-federal parcels were not calculated. Individual allotment probabilities were summed to yield a $p(\text{IC})$ for spring–summer and for rut; these two seasonal probabilities were then combined to determine the total $P(\text{IC})$ for each population during the entire grazing season.

We assumed that co-habitation was equivalent to contact between the two species for the following reasons: (1) bighorn sheep are attracted to domestic sheep when they are in proximity, especially bighorn males that often show interest in and have mated with domestic ewes (Young and Manville, 1960); (2) stray domestic sheep have been found co-grazing with bighorn herds prior to outbreaks (George et al., 2008; Martin et al., 1996) and (3) survival of *Pasteurella* in droplets, on grass and in water indicates direct nose-to-nose contact may not always be necessary for transmission (Burriel, 1997; Dixon et al., 2002).

Accordingly, the probability of at least one bighorn sheep respiratory disease case resulting from contact with a domestic sheep, P_{case} , was modeled as a product of the total $P(\text{IC})$ and the probability of disease transmission, P_d , from a domestic sheep to a bighorn sheep. Data available suggest the P_d is relatively high. Multiple studies have shown that 90–100% of clinically healthy domestic sheep and lambs had one or more isolatable *Pasteurella* and *Manheimia* spp. in oronasal swabs (Casamitjana, 1994; Shreeve and Thompson, 1970; Clifford, unpublished). Although detailed disease transmission data are lacking under field conditions, pen transmission studies (Callan et al., 1991; Foreyt, 1989, 1990; Onderka and Wishart, 1988) showed that 100% of bighorn sheep contracted respiratory disease after being co-housed with apparently healthy domestic sheep. Even though data support the premise that a very high proportion of domestic sheep carry *Pasteurella* and *Manheimia* spp. at any given time, shedding may be intermittent and not all

strains are infective to bighorn. To account for this uncertainty we determined the P_{case} for the expected P_d of 100% and for a conservative P_d of 50%.

2.2.2. Assessment of management changes on the risk of disease transmission

We examined the effect of the following management changes implemented in 2006 on the P_{case} for the North: (1) reduction of available domestic sheep grazing area secondary to closure of select high elevation grazing areas in bighorn sheep habitat, (2) restriction of domestic sheep grazing time on allotments perceived as high risk, and (3) improved domestic sheep stray management. Grazing time was defined as maximum (domestic sheep allotments within bighorn habitat open and grazed the entire season), moderate (current grazing management practice), and restricted (reduced grazing time for perceived high risk allotments). For the Central population, only the effect of improved stray management and grazing time were evaluated, because domestic sheep grazing areas perceived to be high risk had not been delineated for closure.

2.2.3. Predicting population-level impacts of a respiratory disease outbreak

We used a simple stochastic logistic population growth model to predict the bighorn sheep population size at the time of a respiratory disease outbreak (May, 1974). Only females were included, as population growth is related to female survival and recruitment (Cassirer and Sinclair, 2007) and because population recovery goals are specified in terms of the number of ewes (US Fish and Wildlife Service, 2007). Parameters were derived from demographic monitoring and expert opinion, and the model was initiated with female population estimates from 2005 (Table 1). Beta General distributions were used to account for environmental stochasticity, and model parameters were validated by comparing predictions to past population growth rates (Wehausen and Stephenson, 2005).

We then developed a state transition (SI-type) disease model (Abbey, 1952) to predict the cumulative bighorn sheep mortality associated with an outbreak using Excel (Microsoft Inc., Redlands, WA, USA) and @Risk v4.5 (Palisade Corp, Newfield, NY, USA). An epidemic curve estimated from the Lostine bighorn sheep pneumonia outbreak (Coggins, 1988; Coggins and Matthews, 1990) was used to fit the model mortality and contact parameters (Table 1). The model incorporated three populations to mimic Sierra Nevada bighorn sheep population structure (US Fish and Wildlife Service, 2007).

A spreadsheet matrix consisting of four disease states: infectious (C), persistently infected (P), susceptible (S), and mortality (M) was created. Binomial distributions were used to determine the transition between states, making the initial deterministic model stochastic. Infected bighorn sheep (C) could either die (M) or become persistently infected (P). In the simulation, infection of bighorn sheep after the incident (initial) bighorn case could arise from one of three sources: (1) contact with acutely infected bighorn sheep (k_a), (2) contact with persistently infected bighorn sheep (k_b), and (3) contact with active or persistently infected bighorn sheep from a neighboring population (k_c). The number of adequate contacts was reduced 100-fold between k_a and k_b and again between k_b and k_c to reflect the decreasing likelihood of disease transmission from the persistently infected state and from a neighboring herd unit. The persistent state was included to describe chronically infected bighorn sheep that have a lower probability of transmitting disease and a greater probability of survival than acutely infected sheep (Coggins, 1988; Coggins and Matthews, 1990; Foreyt, 1988; Foreyt, 1989). Finally, persistently infected bighorn sheep had the potential to become susceptible again after an extended period of time (r). The number of newly infectious cases in the subsequent time period was modeled as:

Table 1
Input parameters for an infectious disease and population demographic spreadsheet model used to assess the impact of a respiratory disease outbreak in Sierra Nevada bighorn sheep.

Description of variables	Notation	Value/distribution	Source
<i>Infectious disease model</i>			
Mean # of contacts adequate to transmit disease made by an infected bighorn in a single time period	k_a	2	Coggins (1988)
Probability of adequate contact between a susceptible bighorn and a persistently infected bighorn	k_b	0.02 (1 contact/year)	T.R.S. (unpublished)
Probability of adequate contact with an infected bighorn in a neighboring population	k_c	0.0002 (1 contact/10 years)	Sierra Nevada bighorn location data
Probability of dying while infected	m_c	0.6	Coggins (1988), Foreyt et al. (1994)
Probability of dying while persistently infected	m_p	0.100001 (1 death/2 years)	Coggins (1988), Foreyt et al. (1990)
Probability of recovering from infection	r	0.05 (20 weeks)	Foreyt (1990)
Incubation period (time period) for initial infection	t	1 week	Foreyt and Jessup (1982), Foreyt (1989)
<i>Population growth model</i>			
# ewes in the Northern population	N_n	16	Wehausen (2005)
# ewes in the Central population	N_c	40	Wehausen (2005)
# ewes in the Southern population	N_s	92	Wehausen (2005)
Probability of a case in at least one bighorn	P_{case}	Variable	Spatio-temporal data
Carrying capacity of Northern population	K_n	BetaGeneral (2,2,40,100) Mean = 70, SD = 13.42	J. Wehausen, pers. comm. T.R.S. (unpublished data)
Carrying capacity of Central population	K_c	BetaGeneral (2,2,50,125) Mean = 88, SD = 16.77	T.R.S. (unpublished data)
Carrying capacity of Southern population	K_s	BetaGeneral (2,2,155,410) Mean = 283, SD = 57.02	T.R.S. (unpublished data)
Average ewe lifespan	L	12 years	V.B. (unpublished)
Ewe recruitment rate Northern population	B_n	BetaGeneral (12,67,0,1) Mean = 0.15, SD = 0.04	Sierra Nevada bighorn monitoring data
Ewe recruitment rate Central population	B_c	BetaGeneral (45,140,0,1) Mean = 0.24, SD = 0.03	Sierra Nevada bighorn monitoring data
Ewe recruitment rate Southern population	B_s	BetaGeneral (70,177,0,1) Mean = 0.28, SD = 0.03	Sierra Nevada bighorn monitoring data
Ewe mortality rate (all populations)	M	BetaGeneral (2,22,0,1) Mean = 0.08, SD = 0.05	Sierra Nevada bighorn monitoring data

$C_{t+1} = S_t * (1 - (q_a^{C_t} * q_b^{P_t} * q_c^{C_t+P_t}))$, where t was the time period; C_{t+1} was the number of infectious individuals in the following time period; S_t was the number of susceptible individuals in time period t ; P_t was the number of persistently infected individuals in time period t ; q_a , q_b , and q_c were the probabilities of an individual bighorn sheep avoiding adequate contact with an acutely infected bighorn sheep in the same population (q_a), a persistently infected bighorn sheep in the same population (q_b), and an active or persistently infected bighorn sheep from a neighboring population (q_c) in the specified time interval; and $P_t^* + C_t^*$ was the sum of the diseased animals in a neighboring population (Abbey, 1952; Wahlstrom et al., 1998). The probability of avoiding adequate contact (q) was equal to $1 - p$, where p was the probability of an individual bighorn sheep having adequate contact with another sheep during the weekly time step (t). In addition, p is calculated as $p = k/(N-1)$, where k equals the mean number of adequate contacts made by an individual in the weekly time step; and N was the total number of individuals in the bighorn sheep population (Wahlström et al., 1998).

To estimate variability in mortality due to the potential for persistently infected individuals, we used: $M_{t+1} = M_t + C_t * m_c + P_t * m_p$, where M_{t+1} was the number of cumulative mortality events in time period $t+1$, m_c was the probability of mortality from the infectious state, and m_p was the probability of mortality from the persistently infected state. In addition, $S_{t+1} = S_t * (q_a^{C_t} * q_b^{P_t} * q_c^{C_t+P_t}) + P_t * r$, where r was the probability of recovery from the persistently infected state. Finally, $P_{t+1} = C_t * (1 - m_c) + P_t * (1 - m_p - r)$. The most appropriate val-

ues for m_c , m_p , k_a , and k_b , and r , were determined based on the Los-tine outbreak data, and a chi-square function was used to compare the estimated cases to the cases received from the model.

Model assumptions also included: (1) a time step equal to an incubation time period (t) of 1 week for an initial infection (Foreyt, 1989; Foreyt and Jessup, 1982); (2) bighorn sheep becoming infectious to others in the time period following infection ($t + 1$); (3) bighorn sheep surviving the first infectious time period ($t + 1$) becoming persistently infected; (4) no fully immune state but potential for transition back to the susceptible state; (5) random mixing of bighorn sheep within a population; and (6) ability of bighorn sheep to travel from one population to an adjacent population within a single time interval.

The P_{case} was modeled as a risk discrete distribution in the population growth model and linked to the disease model to provide the predicted population sizes at the start of an outbreak. Each management alternative was run with 10,000 Monte Carlo iterations, and summary statistics were reported for cumulative mortality and time to outbreak. Simulations were run for 70 years to generate predictions for a period of 10 bighorn sheep generations (Ramey, 1995; US Fish and Wildlife Service, 2007).

We examined the cumulative probabilities of a respiratory disease case causing mortality over the next 70 years, using 40% mortality as a benchmark level that management agencies would consider highly significant or even catastrophic, and lead to a management trigger for an intensive response. Additionally, we believed a respiratory disease case resulting in $\geq 4\%$ mortality (roughly 1 in 20 sheep) could be detected by field crews and

reported as an unusual event warranting further investigation. Thus, we used $\geq 4\%$ as our threshold for an outbreak classified as detectable mortality.

We examined the likelihood of an outbreak causing quasi-extinction by determining the cumulative probability of cases resulting in outbreaks that drop the population to < 5 ewes. Groups this small are considered highly vulnerable to extinction from a single stochastic event (US Fish and Wildlife Service, 2007), and are known to forage less efficiently, possibly due to increased predator vulnerability (Berger, 1978). Lastly we seeded the epidemic

model with the 2005 reported ewe population estimate for the North (the smallest population; Table 1) without incorporating population growth to examine the likelihood of quasi-extinction and population mortality if an outbreak were to occur in the very near future.

2.2.4. Model parameter sensitivity analysis

Disease model parameters k_a , k_b , k_c , m_c , m_p , and r were varied using the @Risk Advanced Sensitivity Analysis tool and the resultant mortality proportions for each population were evaluated.

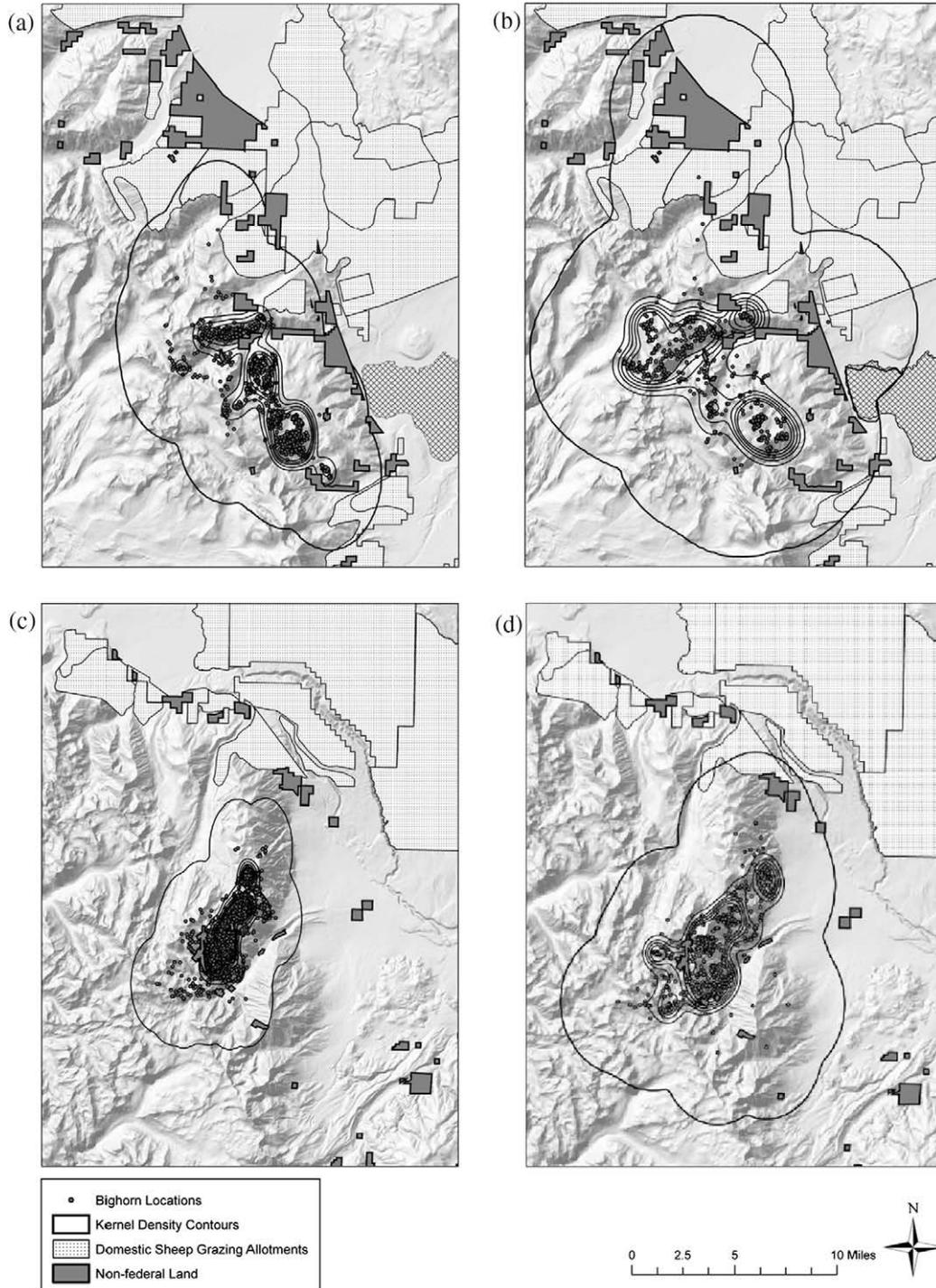


Fig. 1. Spatial overlap between federal domestic sheep allotments, non-federal lands, and the 50% (core), 60%, 70%, 80%, 90%, and 100% (outer contour) fixed kernel distributions for GPS-collared Sierra Nevada bighorn sheep in the North (a and b) and Central (c and d) populations during the spring–summer (March–September; a and c) and rut (October–November; b and d).

The number of contacts with acutely infected bighorn sheep (k_a) was varied from zero to four with five steps, while the other parameters were varied between zero and one with five steps. One hundred iterations of each simulation were run, for a total of 3000 iterations for each of the three outputs. In addition to the mortality proportion, the probability of a respiratory disease case resulting in significant mortality and quasi-extinction were examined when k_a was three and four in order to evaluate the possibility that larger populations might have increased contact among members.

3. Results

3.1. Effect of management on the probability of respiratory disease in bighorn sheep

Bighorn sheep in the North and Central populations utilized over twice as much area during rut (738 and 433 km², respectively) compared to spring–summer (360 and 182 km²), resulting in increased spatial overlap with domestic sheep grazing areas during rut (Fig. 1). The proportion of the bighorn sheep home range overlapping with domestic sheep grazing allotments increased from 5% (18/360 km²) to 7.9% (58/738 km²) during rut in the North and from 2.2% (4/182 km²) to 3.5% (15/433 km²) during rut in the Central population. The highest probabilities of a bighorn sheep respiratory disease case resulting from disease transmission from domestic sheep occurred in the North (Table 2). If domestic sheep were allowed to graze all allotments within the bighorn kernels (maximal grazing) and stray management was not improved, the annual P_{case} ranged from 3.7% to 7.3% for P_d between 50% and 100%. When grazing time was restricted for perceived high risk allotments and grazing area reduced from 337.9 to 322.2 km², the annual P_{case} for the North decreased to 0.6–1.2%, with 81% of the reduction in disease risk due to the restricted grazing time (Table 2).

Grazing time restrictions had the most impact on reducing risk of disease, resulting in a 76–82% reduction in the annual P_{case} for the North. Improved stray management alone resulted in a 47–60% reduction in the annual P_{case} for the North. Eliminating grazing in higher elevation areas perceived to be high risk had less but still substantial effect; with a 13–38% reduction in annual P_{case} for the North (Table 2).

The probability of a bighorn sheep respiratory disease case resulting from domestic sheep contact was about 30 times more likely in the North than in the Central population. Although there is spatial overlap with two grazing allotments in the Central bighorn sheep population kernel during rut (Fig. 1), the 2006 manage-

ment policy of not grazing sheep in these allotments during rut eliminated any temporal overlap between the species and resulted

Table 2

Effect of altering the domestic sheep grazing schedule (maximum = all allotments open the entire season, moderate = current grazing management practice, restricted = reduced grazing time for perceived high risk allotments), reducing the area available for domestic sheep grazing, and improved domestic sheep stray management on the annual probability of a respiratory disease case (P_{case}) in the North population of Sierra Nevada bighorn sheep resulting from contact with domestic sheep. Annual P_{case} probabilities show the range for low (50%) and high (100%) disease transmission risk scenarios.

Domestic sheep grazing schedule	Area (km ²) available for domestic sheep grazing	Improved stray management	Annual P_{case}
Maximum	337.9	No	0.039–0.077
Maximum	322.2	No	0.034–0.067
Maximum	337.9	Yes	0.017–0.033
Maximum	322.2	Yes	0.014–0.027
Moderate	337.9	No	0.008–0.015
Restricted	322.2	No	0.006–0.012
Moderate	337.9	Yes	0.004–0.008
Restricted	322.2	Yes	0.003–0.005

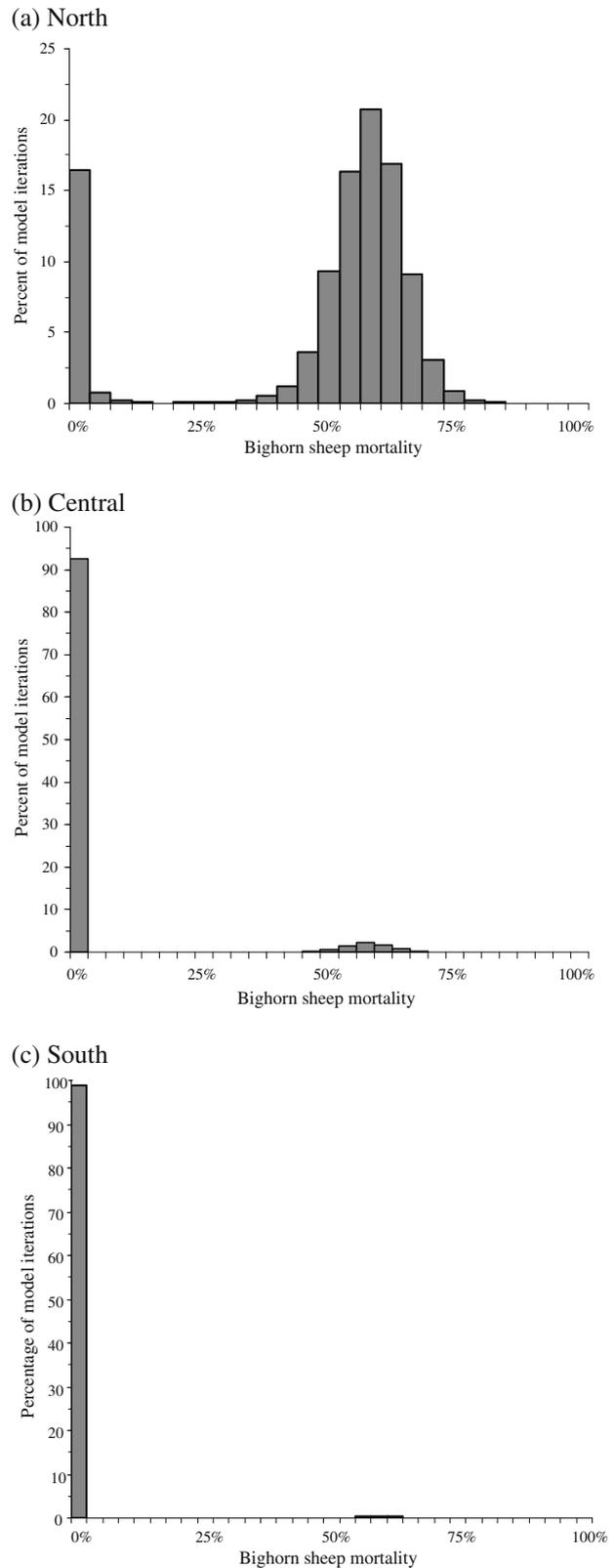


Fig. 2. Frequency distribution (based on percent of 10,000 model iterations) of Sierra Nevada bighorn sheep mortality for: (a) the North population resulting from a bighorn sheep respiratory disease case starting within the population, (b) the Central population resulting from a bighorn sheep respiratory disease case that originated in the North, and (c) the South population resulting from a bighorn sheep respiratory disease case that originated in the North.

in an incalculable P_{case} . If domestic sheep were permitted to graze in these two allotments the entire season, P_{case} for the Central population ranged from 0.15% to 0.3% without and 0.05–0.1% (a 67% reduction in risk) with improved stray management. There were no public domestic sheep grazing allotments within or adjacent to the South population; thus the P_{case} was zero. Based on these calculations, P_{case} values ranging from 0.005 to 0.077 representing the relevant management scenarios were used to seed the SI model (Table 2).

3.2. Population-level impacts of a respiratory disease outbreak

Model iterations to simulate the spread of a bighorn sheep respiratory disease case resulted in a bimodal distribution of population mortality (Fig. 2). In the North 84% of the respiratory disease cases resulted in 15–90% mortality, while the remaining 16% of cases resulted in 0–1% mortality. Population mortality between 35% and 74% was predicted most frequently (82%; Fig. 2a). The distribution of predicted mortality from a bighorn respiratory case was similar for the Central population (mean = 51%, SD = 23.4% compared to mean = 50%, SD = 16.2% in the North). Eighty-three percent of respiratory disease cases were predicted to cause 40–81% mortality, while the remaining 17% of cases resulted in 0–1% mortality. Mortality ranging from 45% to 77% was predicted for 69% of cases.

Only 7% of cases originating in the North were predicted to spread and result in high mortality (44–75%) in the Central population, while the remaining 93% of respiratory disease cases originating in the North did not result in detectable mortality (>4%) in the Central population (Fig. 2b). Similarly, 1% of cases originating in North were predicted to spread and result in high (50–66%) mortality in the South, while the remaining 99% of respiratory disease cases originating in the North did not cause detectable mortality in the South (Fig. 2c). Approximately 12% of outbreaks starting in the Central population spread to either the North or the South, and were predicted to cause 36–80% mortality in the North and 40–71% mortality in the South.

The cumulative probabilities of a respiratory disease outbreak causing significant (>40%) population mortality within the next 10 bighorn sheep generations (70 years) were also highest in the North (Fig. 3). Despite restricted grazing time and reduced grazing area, the chance of a respiratory disease outbreak causing significant mortality in the North in the next five years was 5%, increasing to 50% by 70 years. If domestic sheep were allowed to graze the entire season (maximal grazing) and stray management was not improved, the probability of a significant outbreak within the next five and 70 years increased to 26% and 98%, respectively (Fig. 3a). In the Central population, the probability of an outbreak causing significant mortality in the next 70 years ranged from 5% to 14% if domestic sheep were allowed to graze on currently closed allotments (Fig. 3b).

The probability of a respiratory disease outbreak causing quasi-extinction in the next 70 years was 6% when maximal grazing and grazing area were allowed and stray management was not improved. Under the current management for the North (restricted grazing, reduced grazing area, but no improvement in stray management) quasi-extinction risk in the next 70 years was reduced to 1%. Under the most restrictive scenario (restricted grazing time, reduced grazing area, and improved stray management) the probability of quasi-extinction decreased to near zero (0.4%).

When an outbreak was seeded to occur this year for a North population numbering 16 ewes (2005 estimate; Table 1), 81% of the respiratory disease cases resulted in 31–100% mortality, while the remaining 19% of cases resulted in 0–25% mortality. Population mortality between 31% and 81% was predicted most frequently (77%), and the risk of quasi-extinction was predicted to be 33%.

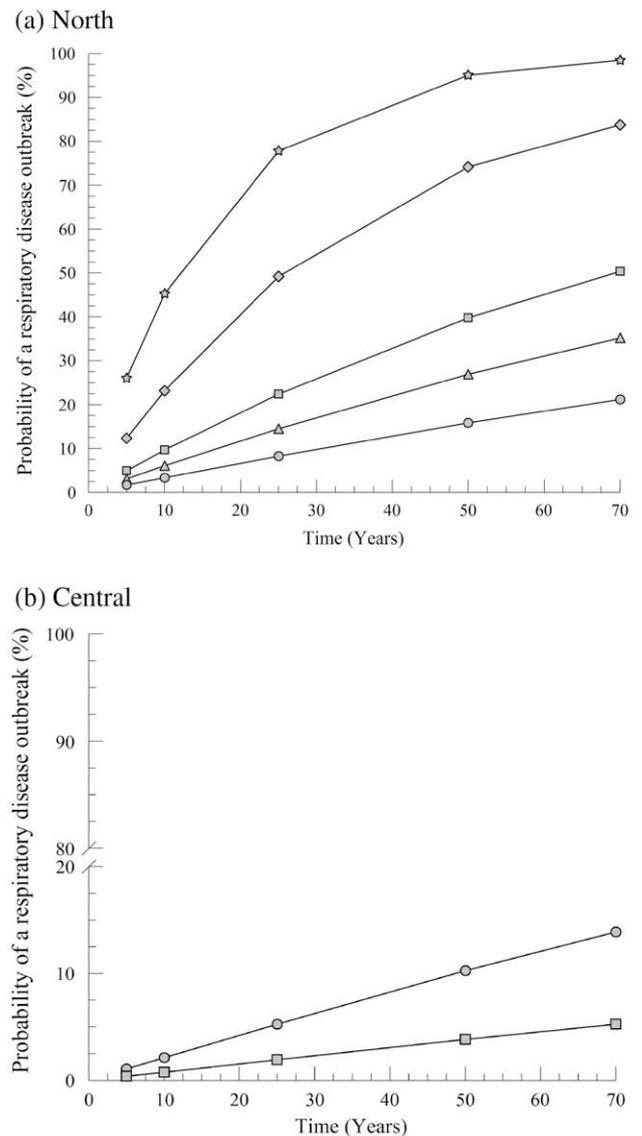


Fig. 3. (a) Predicted cumulative probability of at least one respiratory disease outbreak in Sierra Nevada bighorn sheep from the North population causing significant ($\geq 40\%$) mortality over the next 70 years if: (1) domestic sheep were allowed to graze all allotments within the bighorn kernels and stray management was not improved (☆); (2) domestic sheep were allowed to graze all allotments within the bighorn kernels and stray management was improved (◇); (3) grazing time restricted, grazing area reduced, and stray management not improved (□); (4) moderate grazing employed and stray management improved (△); and (5) grazing time further restricted, grazing area reduced, and stray management improved (○). (b) Predicted cumulative probability of at least one respiratory disease outbreak in Sierra Nevada bighorn sheep from the Central population causing significant ($\geq 40\%$) mortality over the next 70 years if domestic sheep were allowed to graze all allotments within the bighorn kernels and stray management was not improved (○) or stray management was improved (□).

3.3. Sensitivity analysis

Mortality proportion was most sensitive to the number of susceptible bighorn contacts with infected individuals (k_a); resulting in greater mortality as the number of contacts increased (Fig. 4a). For example, increasing the number of adequate contacts from 2 to 4 in the North shifted the distribution of population mortality higher with 90% of the cases predicted to cause 64–86% mortality. Similarly, the probability of quasi-extinction in the next 70 years increased seven-fold when the number of adequate contacts per time period was doubled from 2 to 4.

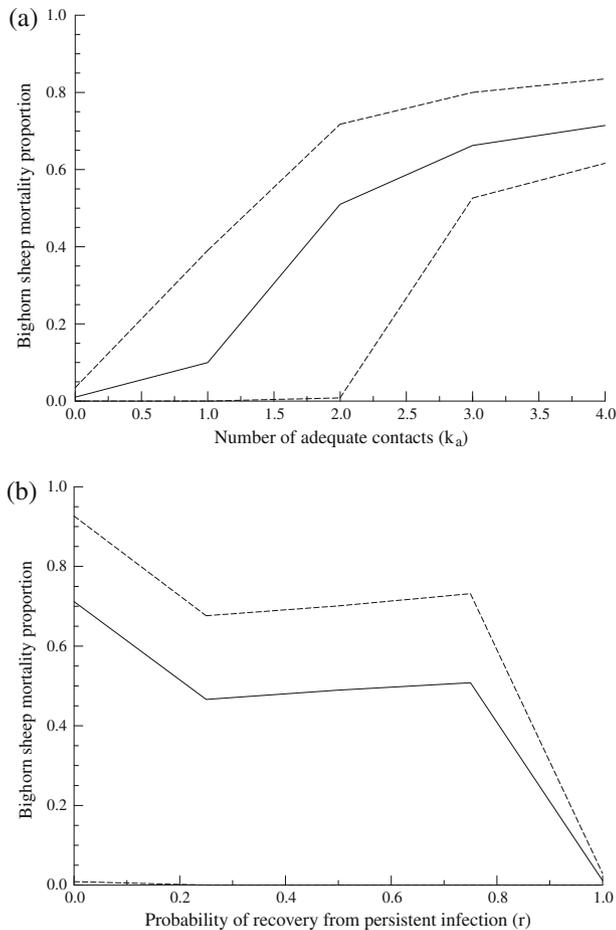


Fig. 4. Sensitivity of bighorn sheep mortality proportion to changes in: (a) the number of adequate contacts with infected bighorn sheep within the same population (k_a), and (b) the probability that a bighorn sheep will recover from the persistently infected state (r). The mean mortality proportion (—), lower 5% confidence limit (---) and upper 95% confidence limit (-.-) are shown.

Mortality proportion had an inverse relationship with the probability of recovery from the persistently infected state; being resistant to changes in r values between 0.25 and 0.75, but increasing as r approached zero (Fig. 4). Mortality proportion decreased from 74.5% to 44.1% when the number of adequate contacts with persistently infected individuals (k_b) was less than 0.25. For outbreaks originating in the North, increasing the number of adequate contacts with active cases and persistently infected individuals in a neighboring population (k_c), increased the mean mortality proportion to a maximum of 86.4% in the Central and 57.6% in the Southern population when $k_c = 0.25$.

4. Discussion

Even though our risk assessment predicted that respiratory disease outbreaks will occur infrequently in bighorn sheep populations as a result of contact with domestic sheep, the population-level impacts of even a single outbreak are predicted to be significant. For instance, if a respiratory disease case occurred this year in the North, our model most often predicts 31–81% mortality, meaning that only 3–11 ewes would survive. Furthermore, the model predicts a 33% chance of quasi-extinction with 5 or fewer ewes surviving. Previous work demonstrated that only 5% of bighorn herds of comparable size were able to persist after a disease outbreak (Singer et al., 2001).

Our analysis indicates that current management efforts directed at lowering the risk of disease transmission between domestic and

Sierra Nevada bighorn sheep are not adequate for long-term conservation. Even with grazing restrictions and reduced grazing in areas perceived as high risk, there still remains a 50% chance that a respiratory disease outbreak causing significant population-level mortality will occur in the next 70 years. If current grazing restrictions are eliminated, the risk that a respiratory disease outbreak will cause significant population-level mortality in the next 70 years increases to almost certainty (98%). Many have advocated maintaining a spatial zone of no contact (≥ 23 km) to reduce the risk of disease transmission at the interface between domestic and bighorn sheep (Gross et al., 2000; Martin et al., 1996; Schommer and Woolever, 2001; Singer et al., 2000). Implicit in those recommendations is the concern that the two species will come into contact, either through straying of domestic sheep or through long-distance movements by bighorn sheep (Sierra Nevada Bighorn Sheep Recovery Program, 2004). In reality, it will be difficult, if not impossible, to maintain such large zones of no contact in a landscape with multiple land uses.

As the population grows over time, the risk of quasi-extinction from a single outbreak will decrease, but the cumulative probability of an outbreak occurring is predicted to increase. Additionally, there will be increased movement of individuals between populations and out of the current range distribution. This increased movement will help to enhance genetic exchange (Bleich et al., 1996); unfortunately, the benefit of increased genetic exchange between populations may come at the expense of increased potential for disease spread unless risk is mitigated (Hess, 1996).

Therefore, at a minimum, domestic sheep grazing should not occur within the known population probability distribution of Sierra Nevada bighorn sheep. Given that seasonal changes in this distribution do occur, it may be possible to graze some allotments during the spring–summer, but only if vigilant herd management is practiced to reduce domestic strays and domestic sheep are removed well before the onset of rut.

Male and female bighorn sheep use habitat differently for the majority of the year (Bleich et al., 1997), and differential habitat use by the sexes has important implications for disease transmission and, ultimately, for conservation (Rubin and Bleich, 2005). Larger group sizes typically associated with larger populations (Singer et al., 2001) may increase the number of adequate contacts among bighorn sheep, the parameter our model is most sensitive to, thereby increasing the severity of an outbreak. We used a conservative estimate of the number of adequate contacts that did not vary for larger predicted population sizes. Behavioral research to estimate bighorn–bighorn contact rates in relation to group size and population density is needed to account for potential density-dependent effects.

Together with continued monitoring of bighorn sheep, higher resolution data showing where domestic sheep graze on existing allotments could help improve estimates of the probability of interspecies contact. Domestic sheep herders could use handheld GPS units so that herd movements are recorded and updated in real-time. Focus should also be directed to domestic sheep held on private lands, as these areas are located inside the current population distribution of bighorn sheep and represent potential for year-round disease risk. Education programs and even incentives for people not to maintain domestic sheep in areas close to bighorn sheep habitat could reduce this risk.

4.1. Limitations of our analysis

Although our model relies on disease transmission data from trials conducted in enclosures or experimental situations, the estimates of interspecies contact presented here are likely conservative. Additional aerial survey, VHF-collar, and opportunistic observational data not included in our study confirm that Sierra

bighorn sheep move outside our GPS-based population kernels. Therefore, current bighorn sheep home ranges are likely larger, resulting in a greater percentage of overlap with domestic sheep allotments. We chose to base our results only on the GPS data to ensure consistency of the data and rigor of our conclusions. We also did not model future movements that may occur as a result of population growth or exploration by bighorn rams seeking mates.

We could not quantify and thus did not model domestic sheep husbandry practices that may increase risk of interspecies contact, such as grazing estrous females during the bighorn sheep rut, trailing domestic sheep between allotments instead of transporting via truck, and variations in the ability of herders to prevent contact when in proximity to bighorn sheep. Despite these potential shortcomings, our results are consistent with a management goal that strives to minimize the probability of contact between these species.

The absence of model runs predicting total extinction is due to the disease model design that requires contacts between infected and susceptible individuals. Therefore at very small population numbers, the disease outbreak dies out prior to total extinction, as there are not enough bighorn sheep left to have enough adequate contacts during a single time period. Our model is sensitive to the number of adequate contacts; therefore if we have underestimated the degree of contacts within a herd, mortality may be higher. Furthermore, our model predictions did not incorporate other unpredictable catastrophic mortality events (avalanche, fire, severe weather) that could contribute to the extinction of a population reduced to low numbers by disease. Even with these considerations, our most frequently predicted levels of population mortality due to disease (33–76% in the North; 45–77% in Central) are consistent with mortality estimates ranging from 25% to 80% reported in respiratory disease outbreaks of free-ranging bighorn sheep populations (Cassirer et al., 1996; Enk et al., 2001; Festa-Bianchet, 1988; George et al., 2008; Ryder et al., 1992).

4.2. Conservation implications

Conservationists and animal agriculturalists need a science-based framework to reduce disease transmission at the wildlife–livestock interface (Bengis et al., 2002). In the Sierra Nevada, efforts to reduce disease transmission must focus on reducing opportunities for domestic and wild sheep to directly interact. This same approach applies to many other domestic–wildlife conflicts because many of the pathogens that pose a significant threat are transmitted by close contact rather than vector-borne routes (Pedersen et al., 2007). In theory, a solution could be achieved by spatial or temporal separation of the domestic and wild populations, husbandry alterations for domestic animals, or in some cases vaccination (Plumb et al., 2007). However, in situations where there is no other place for the wildlife species to go, and there is documented evidence of a substantial disease threat and extinction risk, stakeholders must recognize that the only way to eliminate contact and risk of disease transmission is to give priority to one species or the other. In the case of Sierra Nevada bighorn sheep, the only way to totally eliminate the risk posed by domestic sheep on public grazing allotments is to make sure that no allotments overlap with areas used by bighorn sheep.

Without an objective scientific framework from which to evaluate the magnitude of risk and the mitigation potential of different alternatives, implementing management solutions to the incompatibility of domestic and wild populations will be difficult. By employing an integrated demographic and disease modeling approach based on the best available scientific available data, we have provided a quantitative and defensible tool useful for assessing the risk of interspecies disease transmission and for evaluating

the relative risks associated with land management alternatives. This approach can be adapted for other species and diseases and updated as new data from either wildlife or domestic animals is incorporated.

Acknowledgments

We thank T. Carpenter, B. Dickey, J. Wehausen, and E. Garde for advice early in this project; C. Epps and H. Johnson for assistance with spatial analysis; D. German, D. Jensen, and C. Schroeder for field assistance; P. Partridge and G. Schales for conducting telemetry flights; and two anonymous reviewers for comments that greatly improved the manuscript. This project was supported by the California Department of Fish and Game Resource Assessment Program and the University of California, Davis' Wildlife Health Center in the School of Veterinary Medicine.

References

- Abbey, H., 1952. An examination of the Reed–Frost theory of epidemics. *Human Biology* 24, 201–233.
- Bengis, R.G., Kock, R.A., Fischer, J., 2002. Infectious animal diseases: the wildlife/livestock interface. *Revue Scientifique et Technique-Office International des Epizooties* 21, 53–65.
- Berger, J., 1978. Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. *Behavioral Ecology and Sociobiology* 4, 91–99.
- Beuchner, H.K., 1960. The bighorn sheep in the United States, its past, present and future. *Wildlife Monographs* 4, 1–174.
- Beyer HL, 2004. Hawth's analysis tools for ArcGIS. <<http://www.spatial ecology.com/htools>> (accessed March 2006).
- Bleich, V.C., Bowyer, R.T., Wehausen, J.D., 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134, 1–50.
- Bleich, V.C., Wehausen, J.D., Ramey II, R.R., Rechel, J.L., 1996. Metapopulation theory and mountain sheep: implications for conservation. In: McCullough, D.R. (Ed.), *Metapopulations and Wildlife Conservation*. Island Press, Covelo, California, USA, pp. 353–373.
- Burriel, A.R., 1997. Isolation of *Pasteurella haemolytica* from grass, drinking water, and straw bedding used by sheep. *Current Microbiology* 35, 316–318.
- California Department of Fish and Game, 2006. The efficacy of measures to minimize contact between domestic sheep and Sierra Nevada bighorn sheep on the Humboldt-Toiyabe National Forest, Mono County, California. In: A Report by the California Department of Fish and Game on the Results of Challenge Cost Share Agreement (FS #05-CS-11041730-070, FWS #1448-84320-5-3223) with the Humboldt-Toiyabe National Forest and the US Fish and Wildlife Service.
- Callan, R.J., Bunch, T.D., Workman, G.W., Mock, R.E., 1991. Development of pneumonia in desert bighorn sheep after exposure to a flock of exotic wild and domestic sheep. *Journal of the American Veterinary Medical Association* 188, 1052–1056.
- Casamitjana, P., 1994. Respiratory disease in sheep. *Bulletin des GTV* 3.
- Cassirer E.F., Oldenburg L.E., Coggins V.L., Fowler P., Rudolph K.M., Hunter D.L., Foreyt W.J., 1996. Overview and preliminary analysis of a bighorn sheep dieoff, Hells Canyon 1995–96. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council*, vol. 10.
- Cassirer, E.F., Rudolph, K.M., Fowler, P., Coggins, V.L., Hunter, D.L., Miller, M.W., 2001. Evaluation of ewe vaccinations as a tool for increasing bighorn lamb survival following pasteurellosis epizootics. *Journal of Wildlife Diseases* 37, 49–57.
- Cassirer, E.F., Sinclair, A.R.E., 2007. Dynamics of pneumonia in a bighorn sheep metapopulation. *Journal of Wildlife Management* 71, 1080–1088.
- Coggins, V.L., 1988. The Lostine Rocky Mountain bighorn sheep die-off and domestic sheep. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council*, vol. 6, pp. 57–64.
- Coggins, V.L., Matthews, P.E., 1990. Lamb survival and herd status of the Lostine Bighorn herd following a *Pasteurella* die-off. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council*, vol. 8, pp. 147–154.
- Dixon, D.M., Rudolph, K.M., Kinsel, M.L., Cowan, L.M., Hunter, D.L., Ward, A.C.S., 2002. Viability of airborne *Pasteurella* spp. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council*, vol. 13, pp. 6–13.
- Enk, T.A., Picton, H.D., Williams, J.S., 2001. Factors limiting a bighorn sheep population in Montana following a die-off. *Northwest Science* 75, 280–291.
- Festa-Bianchet, M., 1988. A pneumonia epizootic in bighorn sheep, with comments on preventive management. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council*, vol. 6, pp. 66–76.
- Foreyt, W.J. 1988. Pneumonia in bighorn sheep: effects of *Pasteurella haemolytica* from domestic sheep and effects on survival and long term reproduction. In: *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council*, vol. 6, pp. 92–101.
- Foreyt, W.J., 1989. Fatal *Pasteurella haemolytica* pneumonia in bighorn sheep after direct contact with clinically normal domestic sheep. *American Journal of Veterinary Research* 50, 341–344.

- Foreyt, W.J., 1990. Pneumonia in bighorn sheep: effects of *Pasteurella haemolytica* from domestic sheep and effects on survival and long term reproduction. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, vol. 7, pp. 92–101.
- Foreyt, W.J., 1992. Failure of an experimental *Pasteurella haemolytica* vaccine to prevent respiratory disease and death in bighorn sheep after exposure to domestic sheep. proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, vol. 8, pp. 155–163.
- Foreyt, W.J., 1994. Fatal pneumonia following inoculation of healthy bighorn sheep with *Pasteurella haemolytica* from healthy domestic sheep. Journal of Wildlife Diseases 30, 137–145.
- Foreyt, W.J., Jessup, D.A., 1982. Fatal pneumonia in bighorn sheep following association with domestic sheep. Journal of Wildlife Diseases 18, 163–168.
- Foreyt, W.J., Silflow, R.M., 1996. Attempted protection of bighorn sheep (*Ovis canadensis*) from pneumonia using a nonlethal cytotoxic strain of *Pasteurella haemolytica* Biotype A, Serotype 11. Journal of Wildlife Diseases 32, 586–593.
- Garde, E., Kutz, S., Schwantje, H., Veitch, A., Jenkins, E., Elkin, B., 2005. Examining the Risk of Disease Transmission between Wild Dall's Sheep and Mountain Goats and Introduced Domestic Sheep, Goats, and Llamas in the Northwest Territories. Canadian Cooperative Wildlife Health Centre. (14.06.08) <http://www.cwhc.ca/Publications/NWT_Dall_Mtn_goats_Domestic_sheep_goats_RiskAssessment.pdf>.
- George, J.L., Martin, D.J., Lukacs, P.M., Miller, M.W., 2008. Epidemic Pasteurellosis in a bighorn sheep populations coinciding with the appearance of a domestic sheep. Journal of Wildlife Diseases 44, 388–403.
- Goodson, N.J., 1982. Effects of domestic sheep grazing on bighorn sheep populations: a review. Biennial Symposium of the Northern Wild Sheep and Goat Council, vol. 3, pp. 287–313.
- Graham, J.D., Weiner, J.B., 1995. Risk vs. Risk: Tradeoffs in Protecting Health and the Environment. Harvard University Press, Cambridge, Massachusetts, USA.
- Gross, J.E., Singer, F.J., Moses, M.E., 2000. Effects of disease, dispersal, and area on bighorn sheep restoration. Restoration Ecology 8, 25–37.
- Hess, G., 1996. Disease in metapopulations models: implications for conservation. Ecology 77, 1617–1632.
- Hill, M., 2006. Geology of the Sierra Nevada, 2nd ed. The University of California Press, Berkeley, California, USA.
- Hunter, P.R., Fewtrell, L., 2001. Acceptable risk. In: Fewtrell, L., Bartram, J. (Eds.), Water Quality: Guidelines, Standards, and Health. IWA Publishing, London, UK.
- Jessup, D.A., Boyce, W.M., 1993. Diseases of wild sheep. In: Fowler, M.E. (Ed.), Current Veterinary Therapy 3: Zoo and Wild Animal Medicine. W.B. Saunders Co., Philadelphia, PA, USA, pp. 554–560.
- Kimberling, C.V., 1988. Jensen and Swift's Diseases of Sheep. Lea & Febiger, Philadelphia, PA, p. 394.
- Kraabel, B.J., Miller, M.W., Conlon, J.A., McNeil, H.J., 1998. Evaluation of a multivalent *Pasteurella haemolytica* vaccine in bighorn sheep: protection from experimental challenge. Journal of Wildlife Diseases 34, 325–333.
- Martin, K.D., Schommer, T., Coggins, V.L., 1996. Literature review regarding the compatibility between bighorn and domestic sheep. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, vol. 10, pp. 72–77.
- May, R.M., 1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science 186, 645–647.
- Miller, M.W., Conlon, J.A., McNeil, H.J., Bulgin, J.M., Ward, A.C.S., 1997. Evaluation of multivalent *Pasteurella haemolytica* vaccine in bighorn sheep: safety and serologic responses. Journal of Wildlife Diseases 33, 738–748.
- Onderka, D.K., Wishart, W.D., 1988. Experimental contact transmission of *Pasteurella haemolytica* from clinically normal domestic sheep causing pneumonia in Rocky Mountain bighorn sheep. Journal of Wildlife Diseases 24, 663–667.
- Pedersen, A.B., Jones, K.E., Nunn, C.L., Altizer, S., 2007. Infectious diseases and extinction risk in wild mammals. Conservation Biology 21, 1269–1279.
- Plumb, G., Babiuk, L., Mazet, J., Olsen, S., Pastoret, P., Rupprecht, C., Slate, D., 2007. Vaccination in conservation medicine. Revue Scientifique et Technique-Office International des Epizooties 26, 229–241.
- Powell, R.A., 2000. Animal home ranges and territories and home range estimators. In: Research Techniques in Animal Ecology. Columbia University Press, New York, USA.
- Ramey, R.R., 1995. Mitochondrial DNA variation, population structure, and evolution of mountain sheep in the south-western United States and Mexico. Molecular Ecology 4, 429–439.
- Rodgers, A.R., Carr, A.P., 1998. HRE: The Home Range Extension for ArcView. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
- Rubin, E.S., Bleich, V.C., 2005. Sexual segregation: a necessary consideration in wildlife conservation. In: Ruckstuhl, K.E., Neuhaus, P. (Eds.), Sexual Segregation in Vertebrates: Ecology of the Two Sexes. Cambridge University Press, Cambridge, United Kingdom, pp. 379–391.
- Ryder, T.J., Williams, E.S., Mills, K.W., Bowles, K.H., Thorne, E.T., 1992. Effect of pneumonia on population size and lamb recruitment in Whiskey Mountain bighorn sheep. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, vol. 8, pp. 136–146.
- Schommer, T., Woolever, M., 2001. A Process for Finding Management Solutions to the Incompatibility between Domestic and Bighorn Sheep. USDA Forest Service, Wallowa-Whitman National Forest, Baker City, OR, USA, p. 20.
- Schommer, T., Woolever, M., 2008. A Review of Disease Related to Conflicts between Domestic Sheep and Goats and Bighorn Sheep. Gen. Tech. Rep. RMRS-GTR-209. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, 17 p.
- Shreeve, B.J., Thompson, D.A., 1970. Studies on the carriage of *Pasteurella haemolytica* in lambs. Journal of Comparative Pathology 80, 107–112.
- Sierra Nevada Bighorn Sheep Recovery Program, 2004. Sierra Nevada Bighorn Sheep Progress Report 2003, Outdoor California, vol. 65, pp. 4–17.
- Singer, F.J., Papouchis, C.M., Symonds, K.K., 2000. Translocations as a tool for restoring populations of bighorn sheep. Restoration Ecology 8, 6–13.
- Singer, F.J., Zeigenfuss, L.C., Spicer, L., 2001. Role of patch size, disease, and movement in rapid extinction of bighorn sheep. Conservation Biology 15, 1347–1354.
- Swihart, R.K., Slade, N.A., 1985. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49, 1019–1025.
- US Department of Agriculture Forest Service, 2006. Risk Analysis of Disease Transmission between Domestic Sheep and Bighorn Sheep on the Payette National Forest. USDA Forest Service, Intermountain Region, Payette National Forest, McCall, Idaho, USA.
- US Fish and Wildlife Service, 2000. Final rule to list the Sierra Nevada distinct population segment of California bighorn sheep as endangered. Federal Register 65(January 3), 20–30.
- US Fish and Wildlife Service, 2007. Recovery Plan for the Sierra Nevada Bighorn Sheep, Sacramento, California, xiv + 199 p.
- Wahlstrom, H., Englund, L., Carpenter, T.E., 1998. A Reed–Frost model of the spread of tuberculosis within seven Swedish extensive farmed fallow deer herds. Preventive Veterinary Medicine 35, 181–193.
- Ward, A.C.S., Hunter, D.L., Rudolph, K.M., DeLong, W.J., Bulgin, J.M., Cowan, L.M., McNeil, H.J., Miller, M.W., 1999. Immunologic responses of domestic and bighorn sheep to multivalent *Pasteurella haemolytica* vaccine. Journal of Wildlife Diseases 35, 285–296.
- Wehausen, J.D., Stephenson, T.R., 2005. Sierra Nevada Bighorn Sheep: 2004–2005 Status. Unpublished Administrative Report, California Department of Fish and Game, Bishop, CA.
- Western Association of Fish and Wildlife Agencies, 2007. Recommendations for Domestic Sheep and Goat Management in Wild Sheep Habitat. WAFWA Wild Sheep Working Group. (16.06.08) <<http://www.mwvrcr.org/bighorn/wafwawildsheepreport.pdf>>.
- Young, S.P., Manville, R.H., 1960. Records of bighorn hybrids. Journal of Mammalogy 41, 523–525.